

**HYDROLOGY AND LARVAL FISH DYNAMICS IN TEXAS RIVERS:
SCIENCE TO EVALUATE ENVIRONMENTAL FLOW STANDARDS**

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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August 2015

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Given increasing human demands for freshwater, it is imperative to identify environmental flows that maintain native species, their habitats, and key ecosystem dynamics. A major challenge is determining requirements for seasonal flow pulses that promote fish spawning, early life stage survival, dispersal, and other processes that maintain native stocks. Our study investigated hydrology, fish reproduction, larval abundance, survivorship, and community assemblage of larval fish in both the lower Brazos and middle Trinity rivers in Texas and the littoral fish assemblage in the lower Brazos River. From March 2013 to March 2014, abiotic environmental data were collected along with data on fish abundance, reproduction, and recruitment. Larval fish were collected bimonthly at night using three arrays of stationary driftnets arranged along transects perpendicular to the shoreline. Seine nets were used to sample fish assemblages in shallow littoral habitats. Asteriscus otoliths, from metalarvae and juvenile *Macrhybopsis hyostoma*, were removed and patterns between hatch date estimates and discharge were analyzed to determine if recruitment was related to streamflow.

Multivariate statistical analyses based on seine samples revealed that discharge significantly explained variation in the littoral fish assemblage in the Brazos River. In both the Brazos and Trinity Rivers, multivariate analyses of driftnet data indicated that water temperature had the strongest association with patterns of larval fish abundance, based on evaluations at the family level. Cyprinid protolarvae, in aggregate, did not

seem to be constrained by hydrology, as evidenced by their high abundance throughout the reproductive season (April–September). Hatch dates from surviving *Macrhybopsis hyostoma* indicated that recruitment was greater on flow pulses and on days with increasing discharge. Ongoing work to identify larval fish to species level is needed to elucidate how flow regime components influence reproduction and recruitment of fluvial specialists. This information will significantly augment our currently limited knowledge of the life histories of minnows inhabiting Gulf coastal rivers, which in turn will assist in evaluating environmental flow regimes.

DEDICATION

I would like to dedicate this thesis to my late grandfather, William Rodger. My love for the outdoors, especially my love for aquatic environments and all the mysteries that lie beneath them, was greatly enhanced by the countless days spent fishing with my grandpa throughout my childhood. These early encounters with aquatic ecosystems fostered a passion to pursue a career in fisheries sciences, so I would not be where I am today had it not been for him. More than a skilled fisherman, my Grandpa Bill lived his life as a perfect example of what it means to put others first. I could never repay his time, effort, or patience during all those early fishing lessons when he spent more time removing snarls from my reel than fishing himself. He instilled in me a desire to conserve aquatic resources so that I can share my love for fishing, as well as my appreciation for the wonderful biodiversity that aquatic ecosystems contain, with all those who I come in contact with. My Grandpa Bill was truly a blessing from God, and I am thankful for all the time I shared with him and the memories that I will forever hold dear to my heart.

ACKNOWLEDGEMENTS

First I need to thank my committee chair and academic advisor, Dr. Winemiller, for the incredible opportunity to study in his lab. Dr. Winemiller was instrumental in sharpening my mind as an aquatic ecologist and his expert revisions greatly enhanced the context of this thesis. More importantly I came to really enjoy our friendship and mutual love for fishing and college football. My experience at Texas A&M far exceeded my highest expectations, and Dr. Winemiller was responsible for a large part of that.

I also want to thank my committee members, Dr. Conway and Dr. Olszewski, for their much appreciated guidance throughout the course of this research. Dr. Conway was instrumental in providing assistance with larval fish identification, and he permitted me to use a lot of his equipment to carry out my lab work. Dr. Olszewski provided a lot of guidance towards developing the statistical methodologies for this thesis. I also want to thank Dr. Gelwick for sitting in during my thesis defense as a proxy for Dr. Conway and for providing constructive feedback on my thesis. Kevin Mayes and Clint Robertson, both staff members with the Texas Parks and Wildlife Department, helped get this project started and provided useful feedback throughout this process. Thanks also go to my fellow Dr. Winemiller lab mates. Whether it was volunteering to help me sample or bouncing ideas around for analyses, my lab mates were always there for me. I hope you learned as much from me as I have learned from you. I wish you all the best in your future endeavors. I also want to acknowledge all the undergraduate students that assisted with field and/or laboratory work. Due to the enormous amount of man power and hours

needed to conduct field surveys and finish the laboratory work, I would not have been able to finish this project without their help.

My main funding source for this project was the Texas Parks and Wildlife Department, and I am grateful to them for giving me this opportunity to conduct research at Texas A&M. I also need to thank the Texas Water Resources Institute for awarding me the Mill's Scholarship, which provided additional financial assistance to cover the cost of tuition and Texas A&M University for awarding me the Graduate Merit Fellowship.

Lastly, and most importantly I want to thank my family for their never ending love and support. My parents, Doug and Juanita, always put their children first and gave me every advantage in life they could afford. I was fortunate to grow up under their guidance, and I aspire to live up to the example they set for me. I also want to acknowledge my sisters Mandi and Crystal. Growing up I tormented my sisters like all brothers do, but as the years pass I grow more and more thankful for their presence in my life. Through their faith in God, their love for people and desire to serve others has become an inspiration for me, and they are a continuing reminder of the importance of keeping life's priorities in order.

NOMENCLATURE

| | |
|--------|---|
| ANOSIM | One-way analysis of similarities |
| CCA | Canonical correspondence analysis |
| CCA1 | Canonical correspondence analysis axis 1 |
| CCA2 | Canonical correspondence analysis axis 2 |
| CFS | Cubic feet per second |
| CPUE | Catch per unit effort |
| pCCA | Partial canonical correspondence analysis |
| SL | Standard length |
| TL | Total length |
| TPWD | Texas Parks and Wildlife Department |
| USGS | United States Geological Service |

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CHAPTER I

INTRODUCTION

Freshwater constitutes less than 1% of the water on our planet, yet it not only contains a remarkable variety of biotic diversity, but fresh water, delivered by rivers and streams, provides critical goods and services to human societies (Dudgeon et al. 2006, Arthington et al. 2010). Flow is considered a “master variable” in lotic systems because of its influence over a suite of physicochemical characteristics and ecological processes (Power et al. 1995, Poff et al. 1997). The natural flow regime of a river is determined by its historical pattern in magnitude, rate of change, timing, frequency, and predictability of flows (Poff et al. 1997). Dynamic, variable flows are important for preserving native biodiversity, excluding invasive species, and maintaining key ecological processes, such as sustaining important interactions between channel and flood-plain habitats, creating habitat heterogeneity, and regulating channel geomorphology in lotic ecosystems (Meffe 1984, Poff et al. 1997, Lytle and Poff 2004).

Despite the critical role of natural flow regimes, anthropogenic modifications to lotic systems are pervasive. Major anthropogenic disturbances to fresh waters can be divided into the following categories: fragmentation, overexploitation, water pollution, degradation of habitat, and invasion by exotic species (Malmqvist and Rundle 2002, Dudgeon et al. 2006). Dams are the most obvious modifiers of flow. On a global scale, flow modification by dams is nearly ubiquitous. An estimated 15% of the total annual run-off from the worlds’ rivers is held back by dams (Nilsson et al. 2005). During the 20th century, construction of dams in the U.S. increased dramatically, and now most’

rivers and streams have been modified (Benke 1990). In the Great Plains region there are over 19,000 barriers that fragment stream networks and alter flow regimes (Cooper 2013). These anthropogenic modifications have resulted in Great Plains streams being considered among the most regulated in the world (Lehner et al. 2011, Costigan and Daniels 2012). Changes to natural flow regimes have had many adverse effects. Many native species appear to be poorly adapted for altered flow regimes; consequently, fish species listed for conservation status in the southern United States have risen 75% (Warren et al. 2000). Fragmentation as well as desiccation from water withdrawals have resulted in the extirpation of small-bodied pelagophilic and lithopelagophilic fishes from parts of their ranges in the Great Plains. The loss of these species has not only resulted in reduction of taxonomic diversity, but their absence has shifted once functionally diverse fish assemblages towards homogenized assemblages dominated by benthic reproductive guilds (Perkin et al. 2015).

Balancing scientifically-sound management of freshwater ecosystems with human needs for freshwater is a major challenge in the face of global climate change and rising human populations. In Texas, human population is expected to increase 82% between 2010 and 2060, from 25.4 million to 46.3 million people. Water use is expected to increase 22% with the rise in population (TWDB (Texas Water Development Board) 2012). Population growth leads to greater urban water demands. Consequently, population growth coupled with Texas' variable climate and river flow conditions, and predicted climate change (rising temperatures, higher frequency of heat-stress events, and severity of droughts in this region (NAST 2001)), will likely lead to more water

shortages (NRC 2005). Conflicts among stakeholders will continue to rise as goals for conservation of fish and wildlife clash with human needs.

Establishing environmental flow regimes (i.e. the flows selected to sustain key ecological services) represent a management strategy for sustaining freshwater ecosystems and human livelihoods (Arthington et al. 2010). Achievement of environmental flow standards remains a difficult task due to natural flow variability and poor understanding of how much alteration a lotic system can endure before undesirable ecological changes occur (Gladwell 2000, Merritt et al. 2010, Arthington et al. 2010). To begin to address this challenge, the state of Texas developed the Texas Instream Flow Program (TIFP) as part of legislation in Senate Bill 2 (2001). The TIFP charged three state resource agencies— Texas Parks and Wildlife Department (TPWD), Texas Water Development Board, and Texas Commission on Environmental Quality— to conduct research to estimate flow conditions that maintain a sound ecological environment in the state’s streams, rivers, and estuaries (TIFP 2008). In addition, the *Texas Conservation Action Plan* (TPWD 2012) outlines major conservation goals that include maintaining adequate water quantity and increasing knowledge and understanding of aquatic ecosystems.

The overall goal of the research conducted for this thesis was to elucidate relationships between fish species identified as fluvial specialists and streamflow that will be useful for evaluating environmental flow regimes in the lower Brazos River and the middle Trinity River. In Chapter II, I focus on how environmental factors, especially those related to discharge, structure larval fish assemblages in the lower Brazos and

middle Trinity Rivers. Prior research in the Brazos River has determined spatial and temporal drift patterns of larval fish (Williams 2011), but to date, the role of intra-annual variation in discharge has not been studied in relation to larval fish abundance. My goal was to elucidate taxon-specific relationships between larval fish abundance and the hydrological regime.

In Chapter III, I investigate relationships between hatch dates and streamflow for Shoal Chub *Macrhybopsis hyostoma*. The Shoal Chub is a fluvial specialist, member of a reproductive guild of cyprinids that broadcast-spawns semi-buoyant ova into the pelagic zone of lotic systems. Flow pulses have been shown to cue population-wide synchronized spawning in other members of this reproductive guild (Durham and Wilde 2008b). My goal was to determine if flow pulses result in increased recruitment success by analyzing the number of surviving Shoal Chubs in the metalarvae and juvenile stage and then back-calculating hatch dates to examine abundance patterns in relation to streamflow.

In Chapter IV, I examine the assemblage of adult and juvenile fishes in littoral habitats in relation to streamflow. Most prior research investigating the influence of hydrology on fish communities has focused on inter-annual variation among years of varying hydrological conditions and differences between systems with contrasting natural flow regimes (Seegrist and Gard 1972, Schlosser 1985, Poff and Allan 1995, Scheidegger and Bain 1995, Bonner and Wilde 2000, Olden and Kennard 2010, Stanley et al. 2012, Erős et al. 2012). My goal was to determine if intra-annual flow variability influences littoral fish assemblage structure in the lower Brazos River. Because the

lower Brazos River main channel has a fish assemblage that is relatively distinct from those in oxbow lakes located in its floodplain (Zeug et al. 2005), there could be an influence of flow pulse history and lateral connectivity on fish assemblages in both habitats. Lateral connections facilitate meta-population dynamics for several species that are apparently rare in the main channel, but common in oxbows (Winemiller et al. 2000, Zeug et al. 2005). I analyzed fish assemblage structure at one site in the lower Brazos River channel during a year with varying hydrological conditions to determine if fish assemblages were different under varying levels of flow. My hypothesis was that species more commonly found in oxbows would have positive relationships with high flow pulses.

CHAPTER II

SEASONAL VARIATION IN LARVAL FISH ASSEMBLAGES IN TWO TEXAS

GULF COAST RIVERS

Introduction

The most influential environmental factor affecting fish community structure in lotic ecosystems is flow (Poff et al. 1997, Grossman et al. 1998, 2010). Research on the functional traits of fishes in lotic ecosystems has demonstrated relationships between varying hydrological regimes and life history strategies (Winemiller and Rose 1992, Mims and Olden 2012). For example, species with a periodic life history strategy (large bodied, delayed maturation, high fecundity, episodic recruitment) dominate in highly predictable seasonal environments, such as tropical rivers (Winemiller and Rose 1993, Olden and Kennard 2010, Winemiller 2010). In lotic ecosystems in which the hydrologic regime exhibits unpredictable variations in discharge, such as the Great Plains of the United States, opportunistic species (small bodied, early maturation, continuous reproduction, low survivorship) are predicted to dominate (Olden and Kennard 2010, Winemiller 2010, Mims and Olden 2012). Olden and Kennard (2010) found high levels of convergence across continents in regards to life history strategies along a gradient of hydrologic variability, suggesting hydrological mechanisms that structure lotic fish communities can be applied globally.

Whereas functional traits and hydrological variation determine the dominant life history strategies of local fish assemblages (Mims and Olden 2012), multiple mechanisms can constrain larval fish communities at the local scale. The low-flow

hypothesis (Humphries et al. 1999) maintains that certain fish species invest greater reproductive effort during reduced flow periods with increased water temperatures. This hypothesis also maintains that larval fish produced under low flow conditions are largely restricted to pool or other slack water habitats (Humphries et al. 1999). One benefit of this strategy is development of eggs, embryos, and larvae are positively correlated with temperature (Moore 1944, Platania and Altenbach 1998, Humphries et al. 1999).

Accelerated development is imperative to larval fish survival, because larger size is associated with better swimming ability, which is critical for avoiding predation and capturing prey (Fuiman 1989, Bone et al. 1995, Mann and Bass 1997). During this susceptible time period, mortality from starvation is believed to be high because larval stages of fishes lack the ability to capture appropriately sized prey items efficiently (Humphries et al. 1999). During low flow conditions, larval fish may have an advantage in capturing prey because resource densities are higher (Humphries et al. 1999).

However, low flow conditions are not without their disadvantages. Due to reductions in the amount of habitat during these conditions, larval fish are potentially subjected to increased competition, risks of predation, low dissolved oxygen levels, habitat desiccation, and water temperatures that can reach the upper limits of their physiological tolerances (Harvey 1991, Copp 1992, Humphries et al. 1999).

Conversely, the flood-pulse concept maintains that fish reproduction is greater during periods of increased discharge. Flood pulses serve as spawning cues, and an expanded aquatic habitat, due to increased channel water depth and inundation of floodplains, provides spawning and nursery habitat for a variety of fish species (Junk et

al. 1989, Welcomme and Petr 2003). As flood pulses recede, they leave behind shallow habitat patches with slow current velocities that are ‘hot spots’ for primary production, (Bowen et al. 2003, Hoagstrom and Turner 2013). Two other likely benefits of spawning on a flood pulse are reduced predator densities during high volume periods and increased dispersion of larval fish that aids in reducing competition (Hoagstrom and Turner 2013). The benefit of a flow pulse for successful reproduction depends on both its duration and timing (Finger and Stewart 1987). In the Great Plains of the United States, relationships between flow pulses and population-wide synchronized spawning events have been documented for several fluvial specialist species within the family Cyprinidae (Durham and Wilde 2008b, 2014).

Prior research on the lower Brazos River in Texas determined that larval fish spatial and temporal drift patterns were not random (Williams 2011). Densities of larval fish in the water column were highest at night. Habitats most commonly used by drifting larval fish were near shore, channel margin habitats with relatively low water velocities. Additionally, larval fish densities in the water column differed between the two years of sampling. Compared to one year of the study where flow was at the 41st percentile, larval fish densities were higher during a wet year when daily mean flows were at the 94th percentile of historical daily mean average (Williams 2011). William’s (2011) study suggests that fish reproduction in the lower Brazos River adheres to the flood-pulse hypothesis. Despite an understanding of spatial and daily temporal drift patterns and evidence for inter-annual variation in drift densities, little is known about the role that

intra-annual variations in discharge and environmental variables play in structuring larval fish assemblages in rivers.

Improved understanding of how flow pulses influence reproduction and recruitment of fluvial specialist species is needed for conservation of native biodiversity because fish reproduction is governed by the natural hydrologic regime, and flow alterations can modify species assemblage structure (Humphries et al. 2002). The objectives for this study were to examine patterns of larval fish abundance in relation to environmental variables, particularly discharge, to determine mechanisms that structure larval fish communities in the Brazos and Trinity Rivers of the Texas Gulf Coast. Information about relationships among fish reproduction, recruitment, and streamflow will be useful for evaluating environmental flow regimes for native fish communities in the lower Brazos River and the middle Trinity River. An environmental flow regime attempts to balance human needs for water resources while maintaining flows that fulfill the ecological functions of the historical natural flow regime. Of greatest interest for evaluating environmental flow regimes in the Brazos and Trinity Rivers are cyprinid fluvial specialists that belong to a reproductive guild that broadcast spawn non-adhesive, semi-buoyant eggs in the pelagic zone of lotic systems. Many species in this reproductive guild have experienced population reductions and/or suffered documented range declines in rivers of the Great Plains and arid Southwest due to habitat fragmentation, alterations to the natural flow regime, and water withdrawals (Luttrell et al. 1999, Bonner and Wilde 2000, Hoagstrom et al. 2011, Perkin and Gido 2011). Given that life history information has and will continue to be used to develop instream flow

recommendations, a research strategy that targets species known to be sensitive to flow and that occur in multiple basins provides the most efficient approach for producing insights that extend beyond the basins, populations, and species studied herein. Given increasing human demands for freshwater, it is imperative to identify environmental flows that maintain native species, their habitats, and natural ecosystem dynamics.

Methods

Study Locations

Field collections were made at one site on the lower Brazos River near State Highway 105 bridge near Navasota, Brazos County, Texas (30° 21' 45.1" N, 96° 09' 16.8" W) and one site on the middle Trinity River near the crossing with State Highway 7, approximately 13 miles west of Crockett, Leon County, Texas (31° 19' 08.6" N, 95° 40' 07.8" W) (Figure 1). My study sites were chosen based on presence of point sandbars that facilitated setting drift nets. Prior sampling by Texas Parks and Wildlife Department (TPWD) revealed occurrence of fluvial specialist fishes including: Shoal Chub *Macrhybopsis hyostoma*, Ghost Shiner *Notropis buchanani*, Silverband Shiner *Notropis shumardi*, and Mississippi Silvery Minnow *Hybognathus nuchalis* in either one or both rivers.

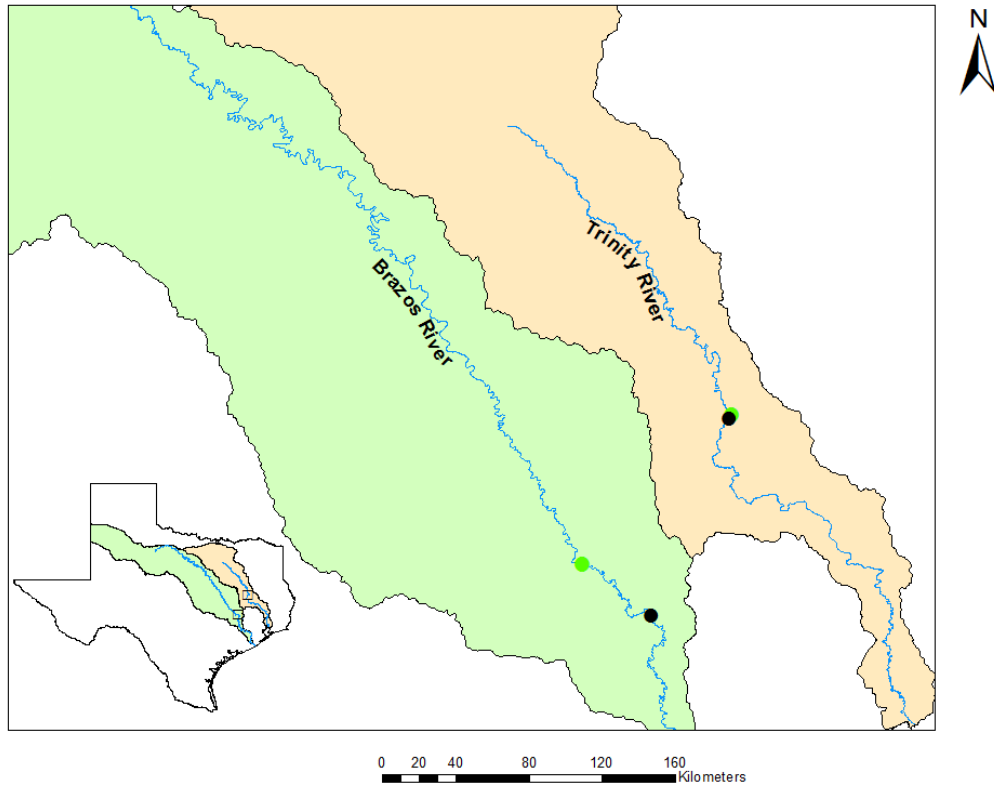


Figure 1 Site map of Brazos and Trinity River survey sites. Black dots represent field sites and green dots represent the nearest upstream USGS streamflow gauge.

The Brazos River is the third longest river in Texas. Originating in northwest Texas, the Brazos River flows approximately 1,700 miles southeast and discharges into the Gulf of Mexico at Freeport, Texas (Brazos Bay and Basin Expert Science Team [Brazos BBEST 2012]). Annual precipitation is 38-64 centimeters per year in the northern extent of the basin and 114-127 inches per year in the southern range of the basin (Brazos BBEST 2012). The Brazos River main stem and tributaries have been altered by the construction of 16 reservoirs for flood control and water supply (Brazos

BBEST 2012). However, the lower Brazos River maintains an unregulated 330-km stretch of river that extends from Waco, Texas, to the Gulf of Mexico. Historic flow conditions indicate winter and spring are typically associated with the highest monthly flows (Zeug and Winemiller 2008). Summer rainstorm events create unpredictable flows. High nutrient concentrations, moderate pH, and high transport of fine sediments resulting in high levels of turbidity are common physicochemical characteristics of the lower Brazos River (Roach and Winemiller 2011). The lower Brazos River fish community has maintained moderate fish assemblage integrity, notwithstanding several noticeable disappearances and population declines of fluvial specialists including Sharpnose Shiner *Notropis oxyrinchus*, Smalleye Shiner *Notropis buccula*, Plains Minnow *Hybognathus placitus*, and Chub Shiner *Notropis potteri* (Bonner and Runyan 2007).

The Trinity River is another large river in Texas characterized by high turbidity (NRC 2005). Its basin encompasses approximately 18,000 square miles and reaches 350 miles inland from the Gulf of Mexico (Trinity Bay and Basin Expert Science Team [Trinity BBEST 2009]). Trinity headwaters are located near a metropolitan area, west of the city of Fort Worth, in north Texas. The Trinity discharges into Trinity Bay before reaching the Gulf of Mexico (Phillips et al. 2004). The northern portion of the basin receives approximately 64 centimeters of rain per year, whereas along the coast, precipitation averages 140 centimeters per year (Trinity BBEST (Basin and Bay Expert Science Team) 2009). Anthropogenic impacts on the Trinity River include construction of 31 reservoirs, as well as withdrawals of water for human use. These anthropogenic

disturbances have produced an altered flow regime (Trinity BBEST (Basin and Bay Expert Science Team) 2009). The Trinity River Basin is one of the most fragmented basins in Texas (Trinity BBEST (Basin and Bay Expert Science Team) 2009). However, much like the Brazos River, the Trinity River has an unpredictable hydrologic regime driven by precipitation events.

Field Collections

Sampling took place over a one-year interval from March 2013 to March 2014. During the peak fish reproductive season (May-September) drift net collections were conducted every other week at each survey site, alternating weeks between the Brazos and Trinity rivers (two surveys per month for each river). Outside of the known reproductive season for most species of fishes (October-April), each sampling site was sampled once per month to survey for evidence of fish reproductive activity. To collect drifting larval fishes, drift nets 1 m in length, 0.45 m wide, and 0.30 m tall with a mesh size of 500 μm were set at wadeable depths on sandbars. Drift nets were set in three linear arrays perpendicular to the shoreline. Each array consisted of three drift nets. Individual drift nets within an array were positioned in a straight line extending out from shore towards the middle of the channel. The distance from shore (m) was measured using a 30-m measuring tape after nets were set, and the depth (cm) and current velocity (m/s) were measured in the center of each drift net at the beginning and end of each collecting period using a meter stick and Marsh-McBirney current meter (Flo-Mate Model 2000, Frederick, MD, U.S.A). Drift net samples were standardized by total water filtered in order to calculate drift net catch per unit effort (CPUE). Total water filtered

through each net was calculated as the product of mean current velocity in each net (m/s), net area (m²; width X submerged portion of net), and duration of sampling (s). Drift net samples were collected every two hours, with the first sample collected at 1800 h and the last sample collected at 0200 h (yielding a total of 36 individual driftnet samples on each date). Outside of the peak spawning period, sampling effort was reduced, with the last collections at 2200 h (yielding a total of 18 individual driftnet samples). After each 2-h interval, contents of each drift net were washed into individual Whirl-Pac® bags and stored in 95% ethanol. Samples were then transported to the lab at Texas A&M for processing. Additional environmental parameters measured on each date at each survey site using a YSI 85 meter included water temperature (°C), dissolved oxygen (mg/L), conductivity (µmhos/cm), and salinity (ppt). Water transparency (cm) was measured using a Secchi disk, and pH was measured using a Multi-parameter PCSTestr 35.

Streamflow Data Collection

Discharge data were obtained from United States Geological Survey (USGS) surface water monitoring stations located upstream from each survey site. Streamflow data for the Brazos River was obtained from USGS 8108700 near Bryan, TX, and USGS 08065350 near Crockett, TX was used for the Trinity River. USGS 8108700 is located approximately 57 river miles upstream of our Brazos River site. USGS 08065350 is located approximately 2.5 river miles upstream of our Trinity River site.

Laboratory Methods

Larval fishes were separated from other contents of the Whirl-Pacs®, counted, and stored in labeled vials in 70% ethanol. Developmental stages of larval fishes were determined following characteristics given by Snyder (1998): *protolarvae*, complete absence of spines and rays; *mesolarvae*, at least one dorsal, anal, or caudal-fin spine or ray, but still lacking the full set of adult soft rays in at least one median fin, or lacking pelvic-fin buds; *metalarvae*, full set of principal soft rays in all median fins and pelvic-fin buds or pelvic fins, with the fin fold still present; *juveniles*, full set of adult median and paired-fin rays and spines with the fin fold completely absorbed. After specimens were sorted by their developmental stage, identification began with the oldest stage, juveniles, and proceeded downward to protolarvae. To date there are no published keys that provide a way to identify protolarvae of Cyprinidae to species for the southern region of the United States. Therefore, larval identification was carried out to family level for each specimen based primarily on Snyder and Seal (2008), Auer (1982), and Fuiman et al. (1983). For a small portion of drift net samples from the Trinity River that were very large, counts were made from sub-samples. After 500 individuals were identified at the family level for 9 vials of mesolarvae and 1 vial of protolarvae from the Trinity River, these counts were extrapolated to estimate total abundances. All other larval fish samples were identified and counted as individual specimens.

Statistical Analysis

Canonical correspondence analysis (CCA) was used to ordinate protolarvae assemblage structure and environmental variables in the Brazos and Trinity rivers, and to determine associations between assemblage gradients and environmental gradients. CCA

is a common statistical method employed by aquatic ecologists to elucidate patterns that associate species occurrence to environmental variables responsible for determining community composition (ter Braak and Verdonschot 1995). Environmental variables included in this analysis were total discharge (cfs), fluctuation of discharge (%), maximum increase of discharge (%), maximum decrease of discharge (%), water temperature (°C), and water transparency (cm). Total discharge, fluctuation of discharge, maximum increase of discharge, and maximum decrease of discharge were calculated over a 6-day period preceding the sampling date. A lag period of 6 days was chosen as the time period most likely to produce protolarvae, given that Moore (1944) and Bottrell (1964) estimated that minnow eggs hatch in 1-2 days and development of the gas bladder occurs in about four days (Dudley and Platania 2007). The formation of the gas bladder is associated with a larva's ability to initiate horizontal movement and actively seek out favorable nursery habitat (Platania and Altenbach 1998). Total discharge was the total water volume passing the upstream gage station during the 6-day period. Daily mean discharges (cfs) during the 6-day interval were multiplied by 86,400 (number of seconds in a day) and these values were then summed across the entire 6-day period to yield total discharge for the period. Discharge fluctuation was calculated as the average absolute value of percent change in mean daily discharge from the previous day's discharge. This variable gives an indication of the magnitude of variation in discharge levels, but does not indicate whether the overall trend was increasing or decreasing. Maximum increase of discharge was the largest positive percent change in mean daily discharge relative to the previous day's discharge during the 6-day period. Similarly, the

maximum decrease of discharge was the largest negative percent change in mean daily discharge relative to the previous day's discharge during the 6-day period. Water temperature and transparency were both measured on each sampling date and were not averaged over a 6-day window. A Monte Carlo permutation test (999 permutations) was used to identify environmental variables and constrained ordination axes that were statistically significant ($p \leq 0.05$). For both rivers, sampling dates from March 2013 to September 2013 and an additional sampling date in March 2014 were included in the CCA. Only the first two canonical axes from the CCA (dominant axes) were interpreted. Total counts of protolarvae were first calculated to represent a standardized catch-per-unit-effort (# protolarvae per 100 m³). Protolarvae CPUE's were $\log(x+1)$ transformed prior to analysis, and rare families (present in < 10% of survey dates) were removed from the CCA analysis to reduce the effect of rare species (Legendre and Legendre 1998). All multivariate ordinations and Monte Carlo permutation tests were performed using the Vegan package in R (Oksanen et al. 2015).

Results

Brazos River Larval Fish Assemblage

Within Brazos River drift net samples, 14,625 individual larvae were identified from eleven different families of fishes. Protolarva was the most abundant stage collected (9,767), followed by mesolarva (2,883), juveniles (1,382), metalarva (519), and adults (74). Cyprinid larvae made up approximately 69% of the identifiable catch across all stages. The next most abundant family was Centrarchidae (3,339, ~23%) followed by Clupeidae (894, ~6%), Poeciliidae (139, ~1%), and Catostomidae (123, ~1%).

Aphredoderidae, Atherinopsidae, Ictaluridae, Lepisosteidae, Moronidae, and Percidae were the other families represented in Brazos River drift net samples.

Percid, catostomid, clupeid, and moronid protolarvae were captured in drift net samples during early spring (beginning March 8, 2013). Larvae from these families, as well as one centrarchid larva, were also present in the March 25, 2014 sample. Spawning activity by members of the Catostomidae, Clupeidae, Percidae, and Moronidae families were largely restricted to the early spring period (March-April); protolarvae CPUE soon declined and protolarvae from these families were absent or uncommon after May.

Based on difference in spawning times, the 15 individual catostomid protolarvae collected during two sampling dates during the summer (July 24 and August 8) could have represented different species than the catostomid protolarvae collected during early spring. Four atherinopsid protolarvae were present in the April 20, 2013 sample.

Centrarchid protolarvae were present in 2013 beginning in late April, but the majority of centrarchid protolarvae were captured from July to September. Total catches of centrarchid protolarvae were much higher in the Brazos River than the Trinity River, likely due to the chronic low-flow conditions of the Brazos River during the drought that were conducive to centrarchid nesting and brood care. Cyprinid protolarvae first appeared in our March 29, 2013 Brazos River drift net sample, although they were absent from our March 25, 2014 sample. Cyprinid protolarvae exhibited a bimodal distribution with one spring peak occurring during late April and early May, and one summer peak occurring during late July and early August. On all but two survey dates

(March 8, 2013 and March 25, 2014), cyprinid protolarvae were the most abundant taxon (Table 1).

Table 1 Brazos River drift net protolarvae CPUE (individuals/100m³).

| Date | Atherinopsidae | Catostomidae | Centrarchidae | Clupeidae | Cyprinidae | Moronidae | Percidae |
|----------|----------------|--------------|---------------|-----------|------------|-----------|----------|
| 03/08/13 | 0.00 | 0.16 | 0.00 | 0.03 | 0.00 | 0.00 | 0.39 |
| 03/29/13 | 0.00 | 0.15 | 0.00 | 0.81 | 0.29 | 0.00 | 0.03 |
| 04/20/13 | 0.05 | 0.37 | 0.11 | 7.21 | 20.07 | 0.01 | 0.05 |
| 05/04/13 | 0.00 | 0.08 | 0.28 | 0.83 | 30.21 | 0.00 | 0.03 |
| 05/16/13 | 0.00 | 0.16 | 0.01 | 0.04 | 1.35 | 0.00 | 0.00 |
| 06/10/13 | 0.00 | 0.05 | 0.08 | 0.12 | 1.95 | 0.00 | 0.00 |
| 06/20/13 | 0.00 | 0.00 | 0.02 | 0.02 | 0.12 | 0.00 | 0.00 |
| 07/02/13 | 0.00 | 0.00 | 0.89 | 0.00 | 6.42 | 0.00 | 0.00 |
| 07/24/13 | 0.00 | 0.28 | 0.62 | 0.00 | 23.97 | 0.00 | 0.00 |
| 08/08/13 | 0.00 | 0.03 | 1.29 | 0.00 | 13.72 | 0.00 | 0.00 |
| 08/21/13 | 0.00 | 0.00 | 8.08 | 0.00 | 10.27 | 0.00 | 0.00 |
| 09/04/13 | 0.00 | 0.00 | 2.60 | 0.00 | 3.64 | 0.00 | 0.00 |
| 09/18/13 | 0.00 | 0.00 | 1.17 | 0.00 | 1.18 | 0.00 | 0.00 |
| 10/05/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 |
| 10/25/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 11/20/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 12/11/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 01/11/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 02/20/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/25/14 | 0.00 | 0.76 | 0.04 | 1.76 | 0.00 | 0.04 | 0.17 |

Centrarchidae represented approximately 78% of the mesolarvae catch. The largest number of centrarchid mesolarvae appeared from July to September. Cyprinidae was the next most abundant taxon in sample of mesolarvae. Cyprinid mesolarvae were present in every sample from April 20, 2013 to October 25, 2013. Cyprinid mesolarvae also displayed a bimodal distribution with one peak on May 16, 2013 and another peak on August 8, 2013. All clupeid mesolarvae were captured from March 29, 2013 to May

16, 2013. The only lepisosteid larvae in driftnet samples were two mesolarvae captured on May 16, 2013 (Table 2).

Table 2 Brazos River drift net mesolarvae CPUE (individuals/100m³).

| Date | Catostomidae | Centrarchidae | Clupeidae | Cyprinidae | Lepisosteidae | Moronidae | Percidae |
|----------|--------------|---------------|-----------|------------|---------------|-----------|----------|
| 03/08/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/29/13 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| 04/20/13 | 0.00 | 0.00 | 0.53 | 0.06 | 0.00 | 0.00 | 0.00 |
| 05/04/13 | 0.01 | 0.25 | 0.47 | 0.36 | 0.00 | 0.00 | 0.00 |
| 05/16/13 | 0.04 | 0.01 | 0.02 | 1.19 | 0.02 | 0.01 | 0.00 |
| 06/10/13 | 0.00 | 0.00 | 0.00 | 0.18 | 0.00 | 0.00 | 0.00 |
| 06/20/13 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| 07/02/13 | 0.00 | 0.41 | 0.00 | 1.03 | 0.00 | 0.00 | 0.00 |
| 07/24/13 | 0.00 | 2.39 | 0.00 | 2.00 | 0.00 | 0.00 | 0.00 |
| 08/08/13 | 0.00 | 1.38 | 0.00 | 2.05 | 0.00 | 0.00 | 0.00 |
| 08/21/13 | 0.00 | 16.52 | 0.00 | 0.64 | 0.00 | 0.00 | 0.00 |
| 09/04/13 | 0.00 | 7.57 | 0.00 | 0.30 | 0.00 | 0.00 | 0.00 |
| 09/18/13 | 0.01 | 5.43 | 0.00 | 0.21 | 0.00 | 0.00 | 0.00 |
| 10/05/13 | 0.00 | 0.00 | 0.00 | 0.27 | 0.00 | 0.00 | 0.00 |
| 10/25/13 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 |
| 11/20/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 12/11/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 01/11/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 02/20/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/25/14 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 |

Abundance of metalarvae was low for every taxon except Cyprinidae. Cyprinid metalarvae constituted 96% of the metalarvae total. Only four centrarchid metalarvae were collected, with two being caught on May 16, 2013, and one each on July 24 and September 18, 2013. The only representative of the Aphredoderidae family was one Pirate Perch *Aphredoderus sayanus* metalarvae collected on March 25, 2014 (Table 3).

Pirate Perch are reported to spawn as early as January in Florida and February in Louisiana (McLane 1955, Fontenot and Rutherford 1999).

Table 3 Brazos River drift net metalarvae CPUE (individuals/100m³).

| Date | Aphredoderidae | Catostomidae | Centrarchidae | Clupeidae | Cyprinidae |
|----------|----------------|--------------|---------------|-----------|------------|
| 03/08/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/29/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 04/20/13 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 |
| 05/04/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.09 |
| 05/16/13 | 0.00 | 0.05 | 0.02 | 0.13 | 0.27 |
| 06/10/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 06/20/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 07/02/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 |
| 07/24/13 | 0.00 | 0.00 | 0.02 | 0.00 | 6.39 |
| 08/08/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 |
| 08/21/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.37 |
| 09/04/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.16 |
| 09/18/13 | 0.00 | 0.00 | 0.01 | 0.00 | 0.33 |
| 10/05/13 | 0.00 | 0.00 | 0.00 | 0.00 | 1.32 |
| 10/25/13 | 0.00 | 0.00 | 0.00 | 0.00 | 1.13 |
| 11/20/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 12/11/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 01/11/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 02/20/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/25/14 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 |

Cyprinids comprised 81% of the juvenile catch. Cyprinid juveniles were captured beginning March 8, 2013 and were periodically captured throughout the reproductive season. Juvenile cyprinids were most common in the month of October, which is near the end of the 2013 reproductive season. Eighty-three centrarchid juveniles were collected, which is notable given that only four centrarchid metalarvae were obtained in our samples. Poeciliids are livebearers, and juveniles were the earliest developmental stage collected in our drift net samples. There were two peaks in juvenile poeciliid

abundance, one in May and another in October. The other families represented in the juvenile drift net samples were Aphredoderidae, Catostomidae, and Clupeidae (Table 4).

Table 4 Brazos River drift net juvenile CPUE (individuals/100m³)

| Date | Catostomidae | Centrarchidae | Cyprinidae | Ictaluridae | Percidae | Poeciliidae |
|----------|--------------|---------------|------------|-------------|----------|-------------|
| 03/08/13 | 0.00 | 0.00 | 0.32 | 0.00 | 0.00 | 0.00 |
| 03/29/13 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 |
| 04/20/13 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 |
| 05/04/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 05/16/13 | 0.04 | 0.02 | 0.02 | 0.06 | 0.01 | 0.49 |
| 06/10/13 | 0.00 | 0.00 | 0.02 | 0.03 | 0.00 | 0.00 |
| 06/20/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 07/02/13 | 0.00 | 0.02 | 0.02 | 0.02 | 0.00 | 0.00 |
| 07/24/13 | 0.00 | 0.02 | 3.31 | 0.04 | 0.00 | 0.24 |
| 08/08/13 | 0.00 | 0.00 | 0.04 | 0.01 | 0.00 | 0.00 |
| 08/21/13 | 0.00 | 0.00 | 0.11 | 0.03 | 0.00 | 0.00 |
| 09/04/13 | 0.00 | 0.01 | 0.07 | 0.03 | 0.00 | 0.00 |
| 09/18/13 | 0.00 | 0.01 | 0.36 | 0.06 | 0.00 | 0.00 |
| 10/05/13 | 0.00 | 0.32 | 6.39 | 0.23 | 0.00 | 0.96 |
| 10/25/13 | 0.00 | 0.99 | 10.87 | 0.27 | 0.00 | 0.73 |
| 11/20/13 | 0.00 | 0.16 | 0.38 | 0.00 | 0.00 | 0.27 |
| 12/11/13 | 0.00 | 0.08 | 1.89 | 0.04 | 0.00 | 0.13 |
| 01/11/14 | 0.00 | 0.00 | 0.14 | 0.00 | 0.00 | 0.00 |
| 02/20/14 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 |
| 03/25/14 | 0.00 | 0.00 | 0.13 | 0.00 | 0.00 | 0.00 |

Cyprinid protolarvae CPUE (individuals/100m³) was examined for patterns in relation to streamflow on the Brazos River (Figure 2). The first peak of protolarvae occurred during a period of relatively stable flows early in the reproductive season (April 20, 2013 and May 4, 2013). A peak of protolarvae abundance occurred on July 24, 2013, shortly after a pronounced flow pulse. Two subsequent surveys after July 24, 2013 yielded high protolarvae CPUE. This period had stable base flows without high flow pulses. However, patterns of cyprinid protolarvae abundance in relation to streamflow

are masked when identification is made at the family level due to interspecific variation in reproductive ecology.

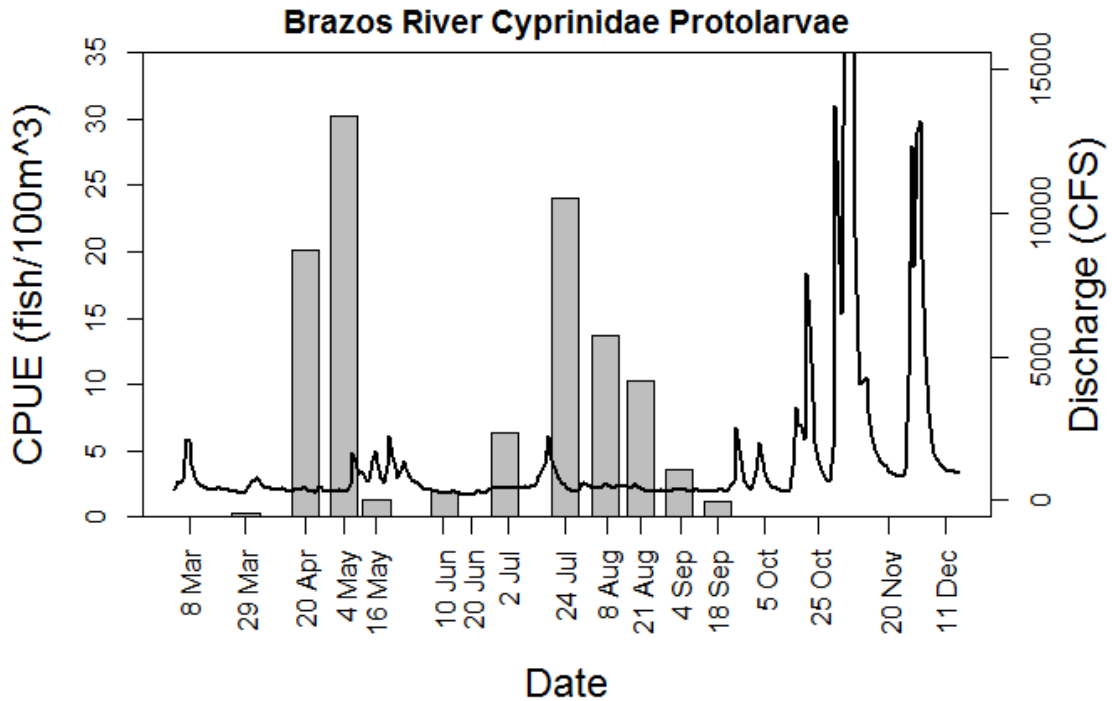


Figure 2 Cyprinid protolarvae CPUE and Brazos River discharge. The black line represents discharge as measured at USGS 8108700 and bars represent CPUE (individuals/100m³) of Cyprinidae protolarvae.

Protolarvae and mesolarvae were grouped together and metalarvae and juveniles were grouped together to facilitate examination of patterns of survival in the Brazos River (Figure 3). There were two peaks in abundance of early larvae (protolarvae and mesolarvae) that appeared to result in subsequent peaks in abundance of late larval stages (metalarvae and juvenile). Another peak in CPUE of late larval stages followed a

second peak of early larval abundance. Assuming there was no bias in catchability throughout the reproductive season, cyprinids spawned later in the year in 2013 probably had higher survival rates

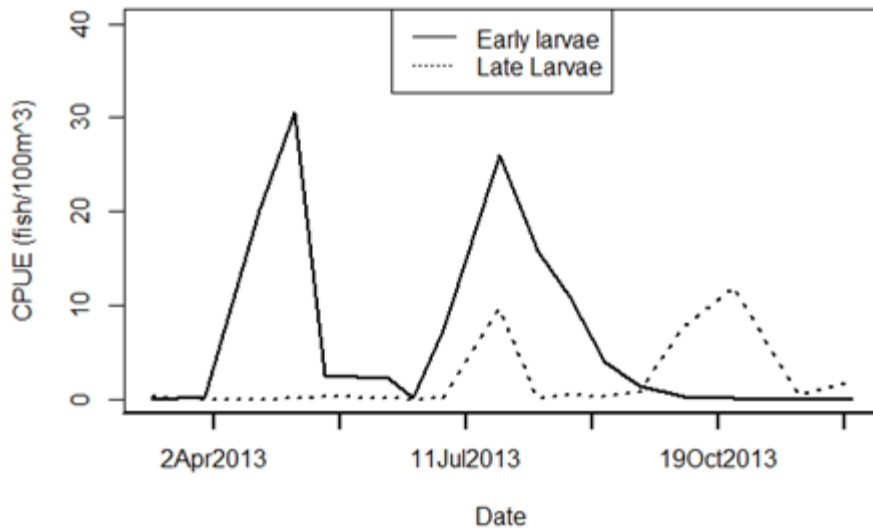


Figure 3 Brazos River early and late Cyprinidae CPUUE (individuals/100m³). Early larvae are graphed as a combination of protolarvae and mesolarvae. Late larvae are graphed as a combination of metalarvae and juveniles.

Trinity River Larval Fish Assemblage

Within Trinity River drift net samples, 41,777 individual specimens were identified, which corresponded to nine families. Mesolarva was the most abundant stage collected (25,494 specimens), followed by protolarva (10,121 specimens), metalarva (4,696 specimens), juvenile (1,450 specimens), and adult (16 specimens) stages. Cyprinid larvae made up approximately 98% of the identifiable catch across all stages.

The remaining 2% was made up of Centrarchidae (432 specimens), Percidae (217 specimens), Poeciliidae (208 specimens), Catostomidae (72 specimens), Clupeidae (19 specimens), Ictaluridae (16 specimens), Moronidae (2 specimens), and Aphredoderidae (1 specimen).

Percid and catostomid protolarvae were the only taxa sampled on the first sampling trip, which took place on March 11, 2013. Percid, catostomid, and clupeid protolarvae were more prevalent during early spring surveys in the Trinity River. Two moronid protolarvae were captured during early June. Two ictalurid protolarvae were collected during May. Cyprinid protolarvae were not collected until May 1, 2013; however, the only April sampling date was April 6, 2013. One cyprinid protolarva and 90 percid protolarvae were captured on March 20, 2014. Cyprinid protolarvae CPUE in the Trinity River exhibited a major peak occurring on August 18, 2013. Except for sampling dates in March and April, Cyprinidae was the most abundant taxon (97% of the collective protolarvae sample). Centrarchid protolarvae did not appear until July and had a minor peak (19 specimens) on August 18, 2013 (Table 5).

Table 5 Trinity River drift net protolarvae CPUE (individuals/100m³).

| Date | Catostomidae | Centrarchidae | Clupeidae | Cyprinidae | Ictaluridae | Moronidae | Percidae |
|----------|--------------|---------------|-----------|------------|-------------|-----------|----------|
| 03/11/13 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.29 |
| 04/06/13 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.60 |
| 05/01/13 | 0.00 | 0.00 | 0.01 | 0.99 | 0.00 | 0.00 | 0.04 |
| 05/08/13 | 0.00 | 0.00 | 0.01 | 22.58 | 0.04 | 0.00 | 0.08 |
| 05/27/13 | 0.02 | 0.00 | 0.24 | 6.86 | 0.02 | 0.00 | 0.02 |
| 06/14/13 | 0.11 | 0.00 | 0.00 | 21.03 | 0.00 | 0.08 | 0.00 |
| 06/27/13 | 0.00 | 0.00 | 0.00 | 2.60 | 0.00 | 0.00 | 0.00 |
| 07/18/13 | 0.00 | 0.02 | 0.00 | 1.69 | 0.00 | 0.00 | 0.00 |
| 07/31/13 | 0.00 | 0.08 | 0.00 | 19.77 | 0.00 | 0.00 | 0.00 |

Table 5 Continued.

| Date | Catostomidae | Centrarchidae | Clupeidae | Cyprinidae | Ictaluridae | Moronidae | Percidae |
|----------|--------------|---------------|-----------|------------|-------------|-----------|----------|
| 08/18/13 | 0.00 | 0.31 | 0.00 | 82.51 | 0.00 | 0.00 | 0.00 |
| 08/28/13 | 0.00 | 0.08 | 0.00 | 9.52 | 0.00 | 0.00 | 0.00 |
| 09/11/13 | 0.00 | 0.06 | 0.00 | 1.73 | 0.00 | 0.00 | 0.00 |
| 09/27/13 | 0.00 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 | 0.00 |
| 10/09/13 | 0.00 | 0.00 | 0.00 | 0.20 | 0.00 | 0.00 | 0.00 |
| 11/11/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 12/10/13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 01/07/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 02/08/14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/20/14 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 4.27 |

Of the total 25,494 mesolarvae captured from the Trinity River, 23,695 specimens were cyprinids captured on August 18, 2013. There were 9,070 more cyprinid mesolarvae captured from the Trinity during that single survey date than were captured during all of our drift net surveys of the Brazos River combined. There was another peak, albeit much smaller in comparison, of cyprinid mesolarvae on June 14, 2013 (674 specimens). Centrarchid mesolarvae were most prevalent on August 18, 2013. Collection of catostomid mesolarvae was confined to the first three survey dates (March 11-May 1, 2013). There were two percid mesolarvae sampled on March 20, 2014 (Table 6).

Table 6 Trinity River drift net mesolarvae CPUE (individuals/100m³).

| Date | Catostomidae | Centrarchidae | Cyprinidae | Percidae |
|----------|--------------|---------------|------------|----------|
| 03/11/13 | 0.14 | 0.00 | 0.00 | 0.00 |
| 04/06/13 | 0.88 | 0.00 | 0.00 | 0.00 |
| 05/01/13 | 0.04 | 0.00 | 0.47 | 0.00 |
| 05/08/13 | 0.00 | 0.00 | 0.27 | 0.00 |
| 05/27/13 | 0.00 | 0.00 | 0.63 | 0.00 |
| 06/14/13 | 0.00 | 0.00 | 25.50 | 0.00 |
| 06/27/13 | 0.00 | 0.00 | 0.03 | 0.00 |
| 07/18/13 | 0.00 | 0.12 | 0.79 | 0.00 |

Table 6 Continued.

| Date | Catostomidae | Centrarchidae | Cyprinidae | Percidae |
|----------|--------------|---------------|------------|----------|
| 07/31/13 | 0.00 | 0.13 | 0.84 | 0.00 |
| 08/18/13 | 0.00 | 1.47 | 387.23 | 0.00 |
| 08/28/13 | 0.00 | 0.97 | 5.58 | 0.00 |
| 09/11/13 | 0.00 | 0.55 | 4.27 | 0.00 |
| 09/27/13 | 0.00 | 0.01 | 1.50 | 0.00 |
| 10/09/13 | 0.00 | 0.00 | 0.06 | 0.00 |
| 11/11/13 | 0.00 | 0.00 | 0.00 | 0.00 |
| 12/10/13 | 0.00 | 0.00 | 0.00 | 0.00 |
| 01/07/14 | 0.00 | 0.00 | 0.00 | 0.00 |
| 02/08/14 | 0.00 | 0.00 | 0.00 | 0.00 |
| 03/20/14 | 0.00 | 0.00 | 0.00 | 0.09 |

Cyprinid metalarvae comprised approximately 99% of the total metalarvae sample. The two largest catches of cyprinid metalarvae occurred on August 18, 2013, and September 27, 2013. The only other metalarvae taxon collected was Centrarchidae (44 specimens) on August 18, 2013 (Table 7).

Table 7 Trinity River drift net metalarvae CPUE (individuals/100m³).

| Date | Centrarchidae | Cyprinidae |
|----------|---------------|------------|
| 03/11/13 | 0.00 | 0.00 |
| 04/06/13 | 0.00 | 0.00 |
| 05/01/13 | 0.00 | 0.00 |
| 05/08/13 | 0.00 | 0.00 |
| 05/27/13 | 0.00 | 0.33 |
| 06/14/13 | 0.00 | 0.04 |
| 06/27/13 | 0.00 | 0.00 |
| 07/18/13 | 0.00 | 0.05 |
| 07/31/13 | 0.00 | 0.77 |
| 08/18/13 | 0.72 | 66.46 |
| 08/28/13 | 0.00 | 0.63 |
| 09/11/13 | 0.00 | 0.20 |
| 09/27/13 | 0.00 | 5.69 |
| 10/09/13 | 0.00 | 0.76 |
| 11/11/13 | 0.00 | 0.00 |

Table 7 Continued.

| Date | Centrarchidae | Cyprinidae |
|----------|---------------|------------|
| 12/10/13 | 0.00 | 0.00 |
| 01/07/14 | 0.00 | 0.00 |
| 02/08/14 | 0.00 | 0.00 |
| 03/20/14 | 0.00 | 0.00 |

Cyprinid juveniles constituted 73% of the total juvenile sample from the Trinity River site. September 27, 2013, had the highest CPUE of cyprinid juveniles (604 specimens), followed by November 11, 2013 (156 specimens). The largest peak of centrarchid juveniles occurred on August 18, 2013. A smaller peak occurred on September 27, 2013. Poeciliid juveniles first appeared in May (1 specimen), but were most prevalent on September 27, 2013 and August 18, 2013. Ictalurid juveniles were captured in low numbers throughout the reproductive season, with the first individual captured during April and the last individual captured during September (Table 8).

Table 8 Trinity River drift net juvenile CPUE (individuals/100m³).

| Date | Aphredoderidae | Centrarchidae | Clupeidae | Cyprinidae | Ictaluridae | Poeciliidae |
|-----------|----------------|---------------|-----------|------------|-------------|-------------|
| 3/11/2013 | 0.00 | 0.00 | 0.00 | 0.09 | 0.00 | 0.00 |
| 4/6/2013 | 0.02 | 0.02 | 0.00 | 0.04 | 0.02 | 0.00 |
| 5/1/2013 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 5/8/2013 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 |
| 5/27/2013 | 0.00 | 0.02 | 0.04 | 0.06 | 0.02 | 0.02 |
| 6/14/2013 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 6/27/2013 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7/18/2013 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 |
| 7/31/2013 | 0.00 | 0.02 | 0.00 | 0.12 | 0.07 | 0.10 |
| 8/18/2013 | 0.00 | 1.78 | 0.00 | 2.75 | 0.03 | 0.75 |
| 8/28/2013 | 0.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.02 |
| 9/11/2013 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 |
| 9/27/2013 | 0.00 | 0.54 | 0.03 | 8.23 | 0.01 | 2.00 |
| 10/9/2013 | 0.00 | 0.12 | 0.00 | 1.15 | 0.00 | 0.09 |

Table 8 Continued.

| Date | Aphredoderidae | Centrarchidae | Clupeidae | Cyprinidae | Ictaluridae | Poeciliidae |
|------------|----------------|---------------|-----------|------------|-------------|-------------|
| 11/11/2013 | 0.00 | 0.04 | 0.00 | 6.15 | 0.00 | 0.04 |
| 12/10/2013 | 0.00 | 0.05 | 0.00 | 0.30 | 0.00 | 0.00 |
| 1/7/2014 | 0.00 | 0.00 | 0.00 | 0.67 | 0.00 | 0.00 |
| 2/8/2014 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3/20/2014 | 0.00 | 0.00 | 0.00 | 0.24 | 0.00 | 0.00 |

Cyprinid protolarvae CPUEs (individuals/100m³) were examined for patterns in relation to streamflow on the Trinity River (Figure 4). The dominant peak of protolarvae CPUE occurred on August 18, 2013. From July 21, 2013 to August 16, 2013 the Trinity River was in either subsistence or base flow conditions. August 17, 2013 marked the first day of a flow pulse. The peak in cyprinid protolarvae might be due to the onset of a flow pulse, but might also represent an artifact of prolonged subsistence and base flow conditions allowing Red Shiner and Bullhead Minnow to maximize recruitment. Shorter sampling windows would be the only way to determine which hypothesis is correct. No discernible pattern was identifiable among the remaining sampling dates, with some dates corresponding to higher CPUE's after flow pulses, and others not corresponding to periods following high flow pulses.

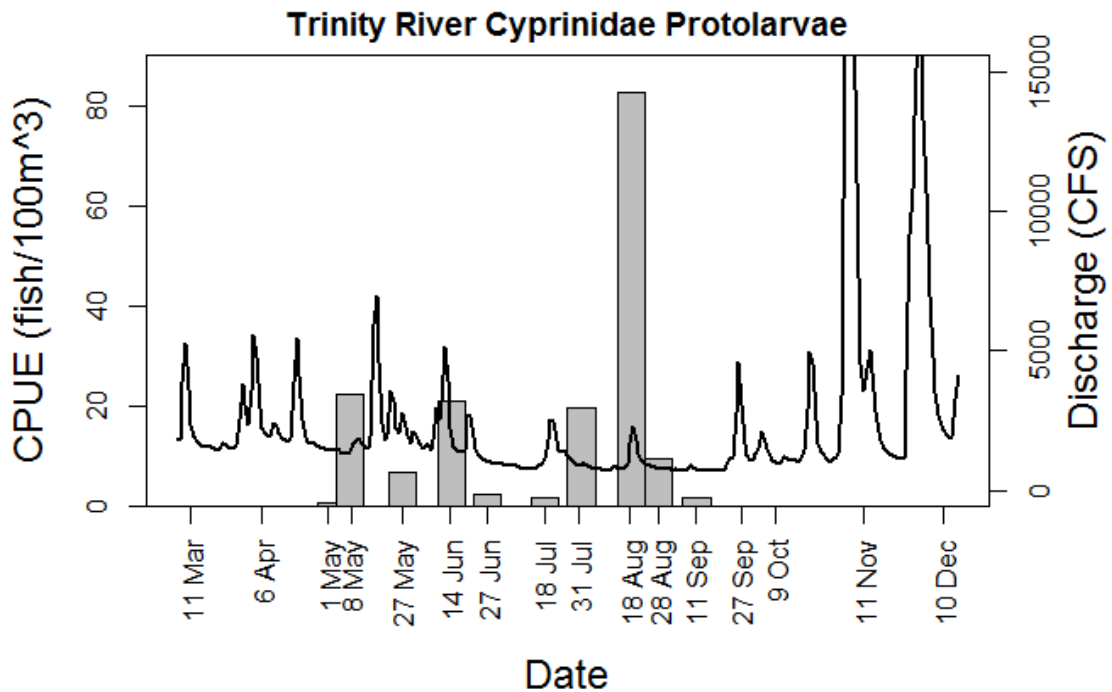


Figure 4 Cyprinid protolarvae CPUE and Trinity River discharge. The black line represents discharge as measured at USGS 08065350 and the bars represent CPUE (individuals/100m³) of Cyprinidae protolarvae.

Protolarvae and mesolarvae were grouped together and metalarvae and juveniles were grouped together to examine survival patterns in the Trinity River (Figure 5). There was a small peak of early larval abundance (protolarvae and mesolarvae) between May and June. This peak was minor compared to the peak that occurred on August 18, 2013. Late larvae also had their greatest peak on August 18, 2013.

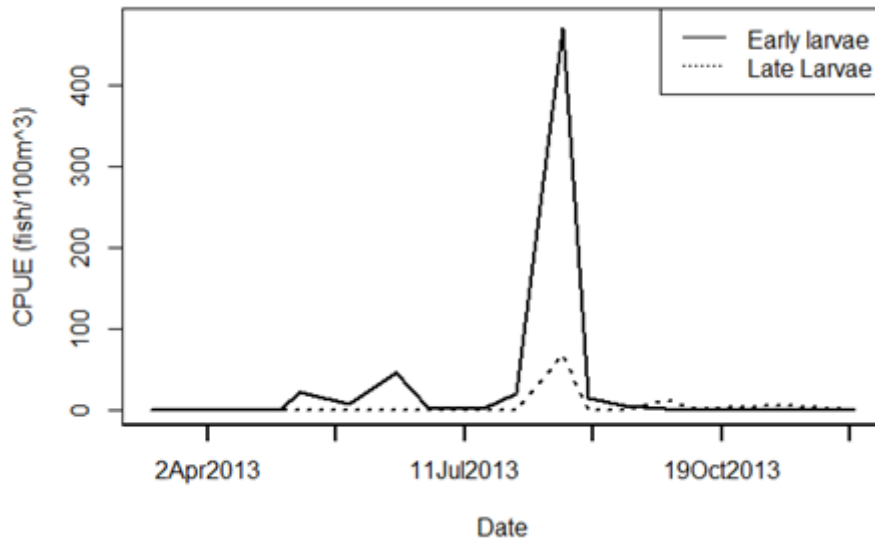


Figure 5 Trinity River early and late Cyprinidae CPUE (individuals/100m³). Early larvae are graphed as a combination of protolarvae and mesolarvae. Late larvae are graphed as a combination of metalarvae and juveniles.

Multivariate Ordination of Brazos River Protolarvae CPUE and Environmental Data

CCA axis 1 (CCA1) generally described a water temperature gradient, with lower temperatures represented by negative values and higher temperatures represented by more positive values. CCA1 alone explained 75.1% of the variation in this plot. Positive values on CCA axis 2 (CCA2) were generally associated with higher water transparency. CCA2 explained an additional 18.3% of the total variation, resulting in 93.3% of the total variation explained by the first two axes (Table 9). Both CCA1 and CCA2 were statistically significant axes (Monte Carlo permutation test, n=999, p= 0.002 and p= 0.026, respectively). Temperature was the only environmental variable that explained a statistically significant relationship (Monte Carlo permutation test, n=999,

p= 0.007) with larval fish assemblage structure at the family level. The March 8, 2013 sample had a large negative loading on CCA1 (-3.83) and a high positive loading on CCA2 (8.08). This outlier was not included in the ordination graph to allow better visualization of remaining survey dates (this was done by editing the plotting of graph axes in R). The most probable reason for the March 8, 2013 sample differing significantly from the other samples is there were no cyprinid protolarvae captured on that date while on all other dates, except one, cyprinids were the most abundant taxa. Ordination of larval fish surveys from the Brazos River revealed three distinct groupings based largely on seasons: early spring (March and April), early to mid-summer (May 4th through August 8th), and late summer (August 21st through September 18th) (Figure 6).

Table 9 Summary statistics for axes 1 and 2 of the Brazos River CCA.

| Brazos River Protolarvae CCA | | |
|------------------------------|---------|----------|
| | CCA1 | CCA2 |
| Eigenvalue | 0.4522 | 0.1101 |
| Proportion explained | 0.7505 | 0.1828 |
| Cumulative proportion | 0.7505 | 0.9333 |
| Species scores | | |
| | CCA1 | CCA2 |
| Catostomidae | -1.1968 | 0.24334 |
| Centrarchidae | 0.6795 | 0.52846 |
| Clupeidae | -1.2317 | -0.08316 |
| Cyprinidae | 0.2000 | -0.20374 |
| Moronidae | -1.7241 | 0.17778 |
| Percidae | -2.0341 | 1.28297 |

Table 9 Continued.

| Constraining variables | CCA1 | CCA2 |
|------------------------|----------|----------|
| Discharge | -0.06022 | -0.19583 |
| Rate of change | -0.37337 | -0.29930 |
| Temperature | 0.92744 | 0.08312 |
| Transparency | 0.55669 | 0.70072 |
| Max Increase | -0.38384 | -0.01277 |
| Max Decrease | -0.26562 | -0.41945 |

Brazos Site Scores

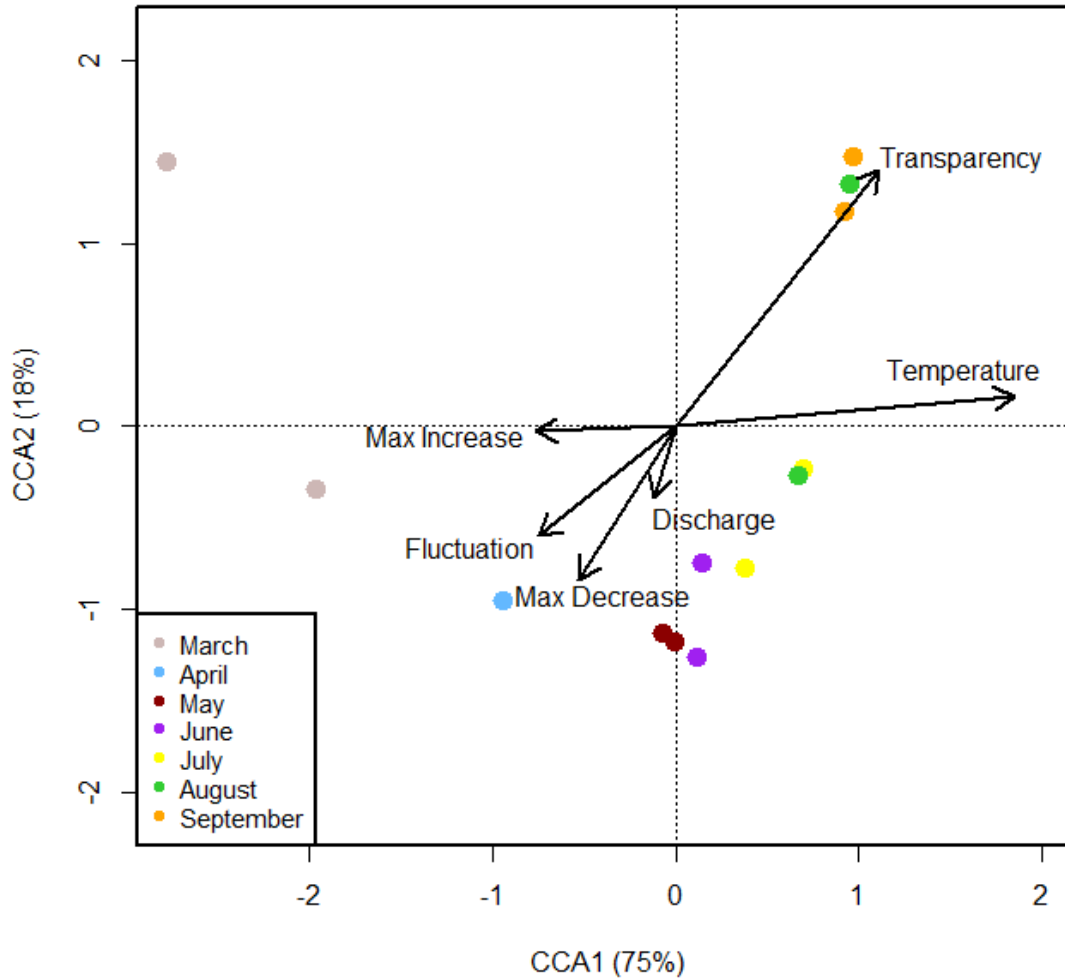


Figure 6 Brazos River sample date score CCA ordination. Larval fish sample (based on protolarvae CPUE at family level) ordination on canonical correspondence analysis (CCA) axes 1 and 2 from CCA, with vectors representing environmental variables for the Brazos River with all survey dates included. Points represent scores for each sampling date. March 8, 2013 was included in the analysis, but was not plotted on the graph as explained in the text.

Catostomidae, Clupeidae, Moronidae, and Percidae all had large negative loadings on CCA1, indicating that protolarvae of these species were most abundant early in the spring. Centrarchidae had a high positive loading on CCA1 and CCA2, indicating the majority of centrarchid protolarvae were produced later in the summer. Percidae and Centrarchidae had large positive loadings on CCA2, indicating the protolarvae were collected on survey dates when discharge tended to be lower, fluctuation in discharge was lower, and water transparency was higher. Cyprinid protolarvae were not strongly correlated with either CCA1 or CCA2 (Figure 7), probably because larvae of Cyprinidae were abundant throughout the entire reproductive season and species-specific differences in reproductive strategies could not be accounted for due to low taxonomic resolution (i.e., family level).

Brazos Family Scores

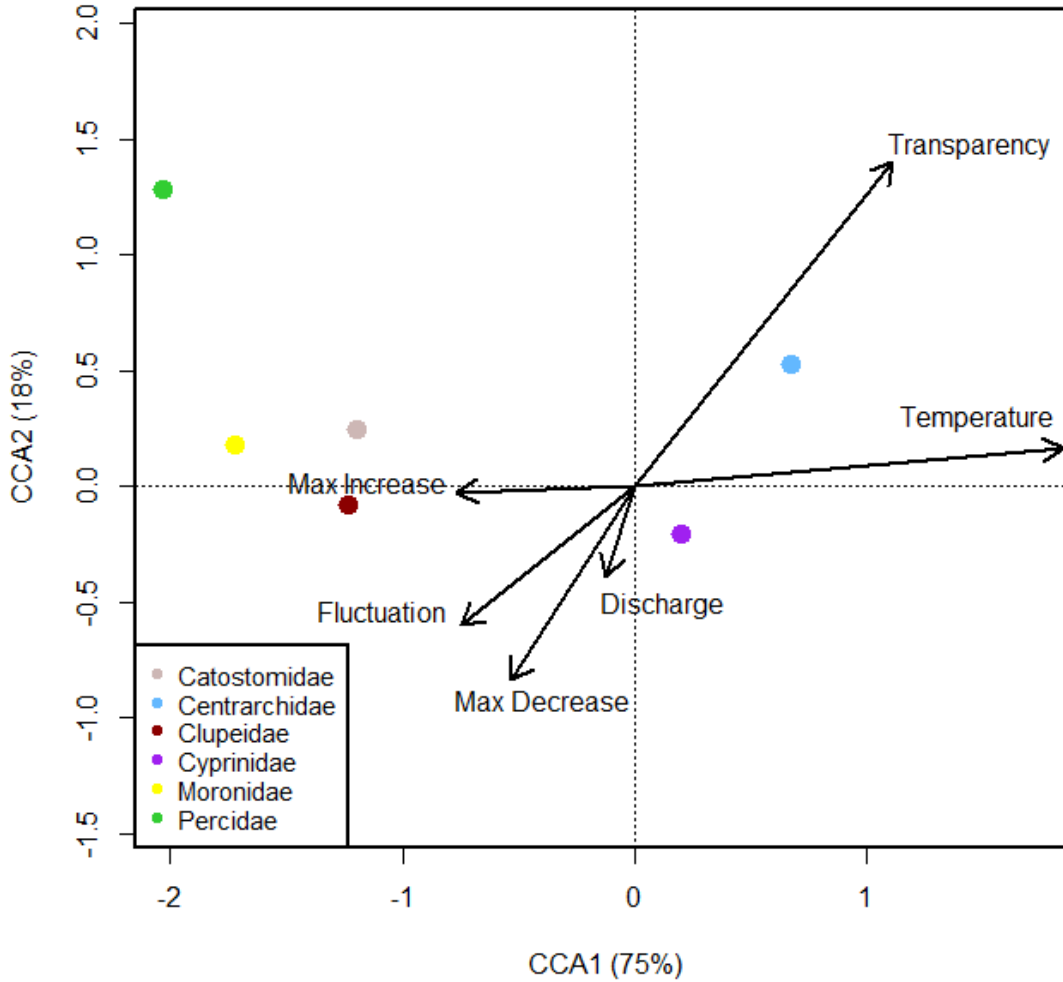


Figure 7 Brazos River family score CCA ordination. Fish sample (based on protolarvae CPUE at family level) ordination on canonical correspondence analysis (CCA) axes 1 and 2 from CCA, with vectors representing environmental variables for the Brazos River with all survey dates included. Points represent scores for each family of protolarvae captured in drift nets.

Multivariate Ordination of Trinity River Protolarvae CPUE and Environmental Data

The patterns shown by the first two canonical axes for Trinity River were similar to those for the Brazos River. CCA1 for the Trinity River site shows a predominant water temperature gradient, with lower water temperatures represented by negative scores and higher water temperatures represented by more positive scores, and CCA1 explained 87.9% of the total variation. Positive loadings on CCA2 were associated with greater transparency and higher temperature. Negative loadings on CCA2 were associated with larger percent decreases in mean discharge (max decrease) and higher volumes of discharge. CCA2 only explained an additional 7.8% of variation resulting in a total of 95.7% of the total variation explained by the first two axes (Table 10). Both CCA1 and CCA2 were statistically significant axes (Monte Carlo permutation test, $n=999$, $p= 0.001$ and $p= 0.019$, respectively). Temperature and discharge had statistically significant relationships (Monte Carlo permutation test, $n=999$, $p= 0.001$ and $p=0.045$ respectively) between larval fish family assemblage structure and environmental variables.

Table 10 Summary statistics for axes 1 and 2 of the Trinity River CCA.

| Trinity River Protolarvae CCA | | |
|-------------------------------|--------|---------|
| | CCA1 | CCA2 |
| Eigenvalue | 0.8005 | 0.07147 |
| Proportion explained | 0.8792 | 0.07849 |
| Cumulative proportion | 0.8792 | 0.95769 |

Table 10 Continued.

| Species scores | CCA1 | CCA2 |
|----------------|---------|----------|
| Catostomidae | -0.3187 | -0.39340 |
| Centrarchidae | 0.4162 | 0.70040 |
| Clupeidae | 0.3115 | -2.45395 |
| Cyprinidae | 0.3237 | 0.01670 |
| Ictaluridae | 0.0637 | -1.03195 |
| Percidae | -2.4937 | 0.01251 |

| Constraining variables | CCA1 | CCA2 |
|------------------------|---------|---------|
| Discharge | -0.2600 | -0.6914 |
| Rate of change | -0.2188 | -0.4246 |
| Temperature | 0.8891 | 0.2293 |
| Transparency | 0.3553 | 0.2725 |
| Max increase | -0.3852 | -0.1647 |
| Max decrease | 0.0256 | -0.8320 |

The same overall pattern of seasonality in species assemblages that was observed in the Brazos was present in the Trinity (Figure 8). The species-scores ordination diagram shows that Percidae and Catostomidae had negative loadings on CCA1 indicating that members of these families spawn in the spring when the water temperature is low. Similar results were obtained for the Brazos River dataset, with the exception that Clupeidae was less constrained by lower water temperatures. Spring protolarvae CPUE data show spawning by members of Clupeidae to be confined to the early spring, but low sample sizes apparently weakened negative associations with temperature, such as was observed for these families in the Brazos River. Centrarchidae had the highest positive loadings on CCA1 and CCA2, indicating that, much like in the Brazos River, the peak centrarchid spawning season was during the middle and latter parts of summer when transparency was high. Cyprinid larvae in the Trinity River were not strongly associated with either CCA axis because, similar to the Brazos River findings, cyprinid protolarvae generally were abundant throughout the year (Figure 9). Clupeidae and Ictaluridae negative loadings on CCA2 indicate protolarvae of these families were most abundant when discharge was higher and there was a large decrease in the discharge rate (i.e. the descending limb of flow pulse); and, more importantly, larvae of these two families were not captured after May during the 2013 reproductive season.

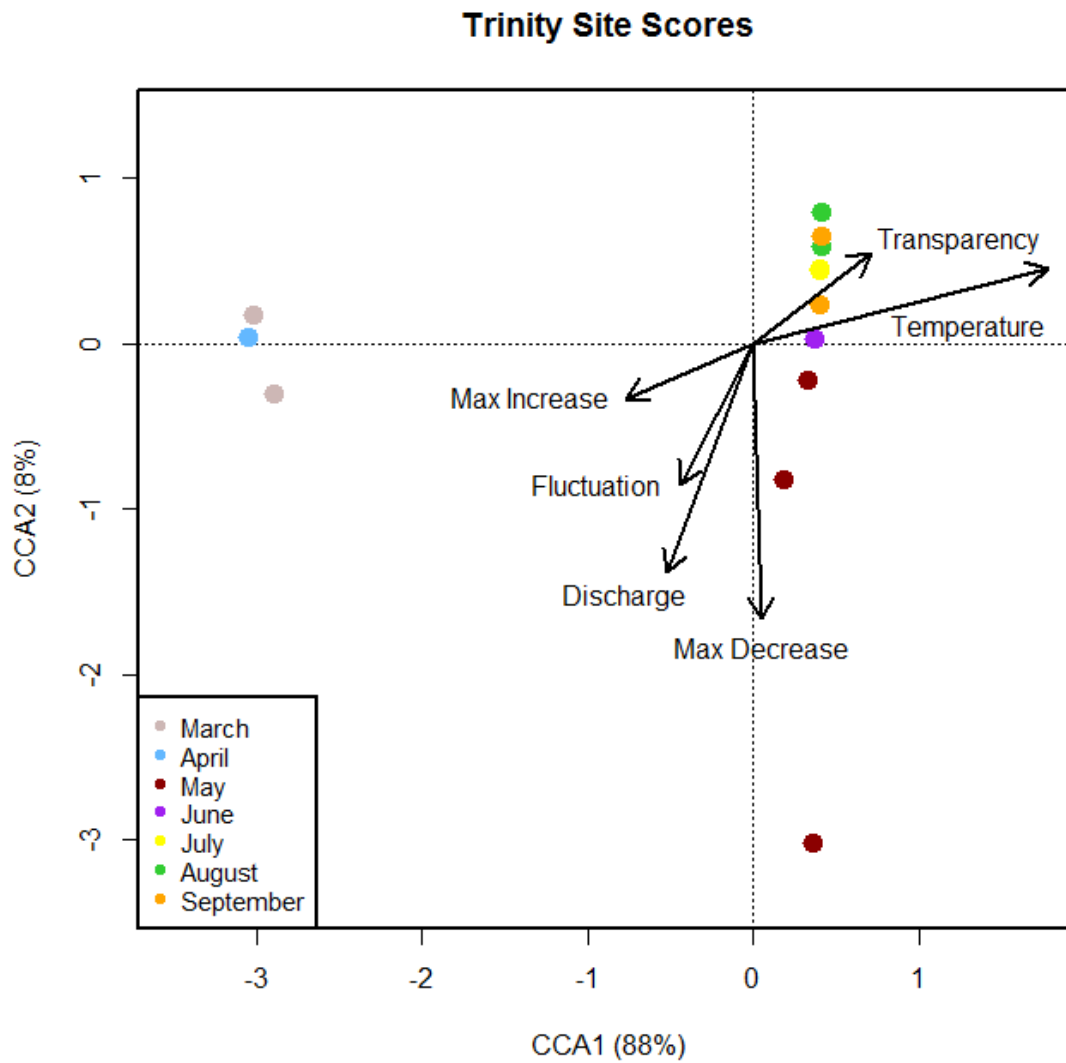


Figure 8 Trinity River sample date score CCA ordination. Larval fish sample (based on protolarvae CPUE at family level) ordination on canonical correspondence analysis (CCA) axes 1 and 2 from CCA, with vectors representing environmental variables for the Trinity River with all survey dates included. Points represent scores for each sampling date.

Trinity Family Scores

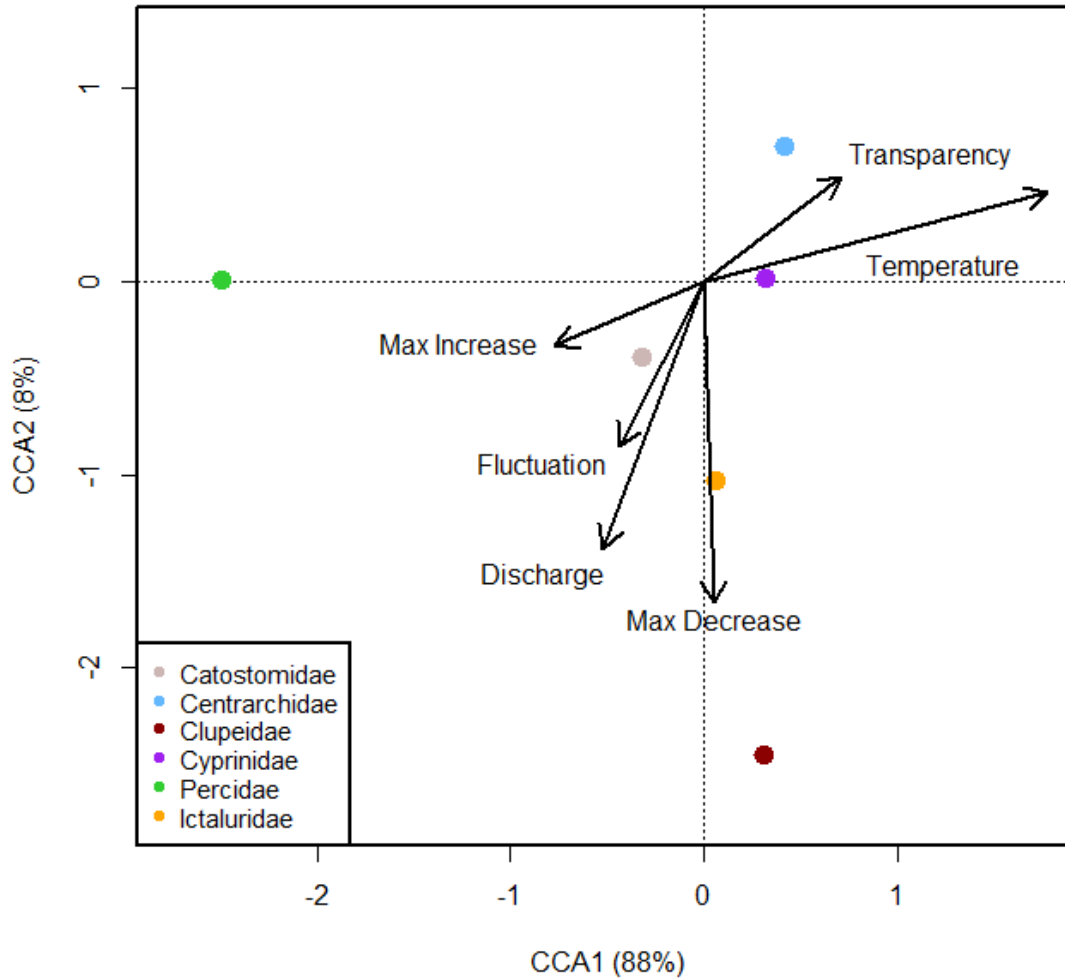


Figure 9 Trinity River family score CCA ordination. Larval fish sample (based on protolarvae CPUE at family level) ordination on canonical correspondence analysis (CCA) axes 1 and 2 from CCA, with vectors representing environmental variables for the Trinity River with all survey dates included. Points represent scores for each family of protolarvae captured in drift nets.

Discussion

Across all developmental stages, eleven fish families were captured in the Brazos River. In the Trinity River only 9 fish families were sampled. The two families not represented in Trinity River drift net samples that were captured in drift nets in the Brazos River were Atherinopsidae and Lepisosteidae, although adults representing both families were present in Trinity River seine samples (seine net sampling was conducted simultaneously with drift net collections in 2013 and 2014 as part of a concurrent study). Larval fish assemblage composition in the Brazos and Trinity Rivers are consistent with predictions from the triangular continuum model of life history variation (Winemiller and Rose 1992). In lotic systems with hydrological regimes characterized by large and relatively unpredictable variation, small bodied opportunistic-type strategists with rapid maturation, continuous reproductive effort, and low juvenile and adult survivorship are predicted to dominate (Winemiller 1989, Winemiller and Rose 1992, Mims and Olden 2012). These characteristics describe the life history strategy of small cyprinids in the Brazos and Trinity Rivers. Cyprinids made up 80% and 97% of the protolarvae captured from the Brazos and Trinity River, respectively. Concurrent seine sampling of adult fishes from littoral habitats within these systems revealed that small-bodied cyprinids constituted over 94% of total fish specimens in samples from both rivers. Apart from a dominance of cyprinids in both rivers, larval fish samples from the Brazos and Trinity Rivers had different patterns of taxon relative abundance. Trinity River samples tended to have more percid larvae and fewer clupeid and centrarchid larvae relative to the Brazos River.

It is uncertain how ontogeny and hydrological conditions interact to affect larval fish catchability in drift nets. The swimming ability of larval fish increases with maturity, but abiotic or biotic conditions could influence the susceptibility of larval fish to drift nets. In the Brazos River, centrarchid mesolarvae were abundant, but only four metalarvae were captured. This could indicate low survival of centrarchid larvae or this could be a reflection of centrarchids having a greater ability to avoid drift nets at the metalarvae stage. However, given that 83 centrarchid juveniles were captured in drift net samples it may be that hydrological conditions such as, elevated discharge, which also increases turbidity, might disorient larval fish and reduce detection of drift nets. Alternatively, juvenile fish might use drift nets as cover or areas for feeding because drift nets can collect and concentrate their potential food resources (smaller larval fish and drifting macroinvertebrates). Centrarchids, as well as juvenile ictalurids, might have sought out drift nets for this very reason. On several instances juvenile flathead catfish were captured in drift nets and dissections revealed large concentrations of larval fish in their stomachs.

Analysis of larval fish CPUE at the family level greatly compromised my ability to analyze the spawning and recruitment dynamics of fluvial specialist species, because families may contain multiple species with divergent reproductive tactics (e.g. Cyprinidae). My inability to identify protolarvae to species made it impossible to discern whether or not hydrological variation synchronized spawning activity by fluvial specialist minnows. Synchronized spawning during periods of elevated flow has been documented in cyprinid fluvial specialists in the upper Brazos River by studying the

reproductive ecology of adult specimens (Durham and Wilde 2008, Durham and Wilde 2014). I hypothesize that had I been able to analyze my data at the species level, I would have seen high interspecific variation of protolarvae abundance in relation to discharge.

Prior research on the lower Brazos River (Williams 2011) documented greater larval fish drift densities during a year of elevated discharge, thus lending support that Texas Gulf Coast rivers may conform to the flow-pulse hypothesis where increased discharge results in greater larval fish production (Junk et al. 1989). However, greater larval fish drift densities during the wet year were attributed to higher metalarvae and juvenile drift rates, while drift rates of protolarvae and mesolarvae fish were fairly similar between years. William's (2011) finding suggests that higher discharge contributed to higher larval survival rates, but did not have a large influence on spawning activity. Perhaps neither the low-flow or flood-pulse hypothesis can fully explain the relationship between intra-annual variation in discharge and protolarvae abundance in the Brazos and Trinity River because each represents a diverse fish assemblage comprising species with divergent life history strategies.

Life history variation within Cyprinidae appears to be associated with differential responses to environmental conditions and success of spawning and recruitment. For example, Red Shiner probably conform to the low-flow hypothesis whereas Shoal Chub conform to the flow-pulse hypothesis (Platania and Altenbach 1998, Durham and Wilde 2006, Wilde and Durham 2008b). At the family level, cyprinid protolarvae were almost certainly dominated by two extremely common minnows that are not fluvial specialists—Red Shiner and Bullhead Minnow. Red Shiner and Bullhead

Minnow together accounted for 88% and 78% of the fishes captured from littoral habitats in the Brazos and Trinity River seine samples, respectively. Both Red Shiner and Bullhead Minnow possess demersal, adhesive eggs (Holland-Bartels et al. 1990, Durham and Wilde 2006). This egg deposition strategy is well suited for early life stage survival under low-flow or stable-flow conditions; therefore, a positive relationship between increased or fluctuating discharge and reproductive effort would not be expected for these species (Platania and Altenbach 1998, Durham and Wilde 2006). In the Trinity River, metalarvae and juvenile cyprinids had very high CPUE on August 18, 2013. The high CPUE on August 18, 2013 confirms there was high survival of cyprinid protolarvae prior to this date because larvae would have needed sufficient time to develop into metalarvae and juveniles. The hydrograph preceding this survey date was characterized by prolonged subsistence and base flow conditions. Thus, Red Shiner and Bullhead Minnow likely enjoyed great reproductive success during these low-flow conditions.

Members within the Centrarchidae family also appear to conform very well with the low flow hypothesis (Schlosser 1985). Abundance of centrarchid protolarvae was positively correlated with high water temperatures and greater water transparency, conditions observed in both rivers during late summer when flows were low. In contrast, fishes from other families such as Percidae (e.g. species of *Percina* and *Etheostoma*) spawned regardless of hydrological conditions, instead relying primarily on seasonal cues (either water temperature and/or day length). Thus, temporal variation in larval fish assemblages may be driven by synergistic effects of abiotic and biotic factors that

influence responses according to species-specific life history strategies. I caution against applying general hypotheses regarding fish responses to hydrological or environmental variables in systems with diverse fish assemblages containing divergent life history strategies.

At both study sites, water temperature was statistically significant in explaining temporal and taxonomic variation in larval fish assemblage structure. In the CCA, water temperature alone explained 38% and 61% of variation defined by relationships between larval fish assemblages and environmental gradients in the Brazos and Trinity River, respectively. This suggests seasonality as the main mechanism driving larval fish assemblage structure. Temporal patterns of family protolarvae abundance in both rivers generally agreed with previous reports in terms of seasonal temperature variations (Fuiman et al. 1983, Holland-Bartels et al. 1990). While the majority of Centrarchidae specimens were prevalent later in the summer, some individuals were captured earlier in the reproductive season. Largemouth Bass *Micropterus salmoides*, Spotted Bass *Micropterus punctulatus*, and Orangespotted Sunfish *Lepomis humilis* are reported to spawn as early as April (Vogele 1975, Holland-Bartels et al. 1990, Wallus and Simon 2008). Green Sunfish, Bluegill Sunfish *Lepomis macrochirus*, White Crappie *Pomoxis annularis*, and Longear Sunfish *Lepomis megalotis* are reported to begin spawning later in the season (Holland-Bartels et al. 1990, Wallus and Simon 2008). Small-bodied cyprinids are known to have extended reproductive seasons due to their opportunistic life history strategy and this was confirmed as they were typically the most abundant taxon throughout the reproductive season. Patterns of larval abundance in relation to

temperature appear to be a function of interspecific life history variation affecting responses to fairly predictable seasonal changes in rivers in temperate regions.

Overall, for the Brazos River samples, none of the hydrological variables used in the CCA were statistically significant in explaining variation in larval fish assemblage structure; however, in the Trinity River, discharge was significantly associated with larval fish assemblage structure, albeit to a lesser degree than water temperature (discharge, by itself, explained 9% of the variation in the Trinity River dataset, and water temperature explained 61%). The reason discharge is statistically significant in explaining larval fish assemblage in the Trinity River is likely an artifact of generally higher flows, following spring rains, happening to coincide with the early spawning season of families such as Percidae during the 2013 reproductive season. Members of the Centrarchidae family spawned during the summer while water temperatures were higher and because there was a lack of rain the discharge was generally low. Discharge and water temperature were negatively correlated ($r = -0.32$). I hypothesize that much like the pattern demonstrated in the Brazos River, temperature is the overriding mechanism determining larval fish assemblage structure at the family level in the Trinity River, but multiple years of sampling across years of varying hydrological conditions would be required to test this hypothesis.

Species-specific analyses are needed to elucidate how hydrology and other aspects of environmental variation influence fish spawning and recruitment. In practice, research involving spatial and temporal patterns of abundance of fish protolarvae is dependent on availability of illustrated guides that enable accurate identification to

species level. I could not identify protolarvae to species, therefore my research project could not provide quantitative flow estimates that meet the spawning and recruitment requirements of fluvial specialist cyprinids that should serve as useful bioindicators for environmental flow regimes in Texas Gulf Coast rivers. These minnows are sensitive to altered flow regimes and disruption of longitudinal connectivity of fluvial systems, and have declined in rivers of the prairie regions of the central United States (Luttrell et al. 1999, Perkin and Bonner 2011, Perkin et al. 2013, 2015, Worthington et al. 2014). Currently, techniques that do not require the identification of protolarvae to species provide a more efficient approach to understanding relationships between reproduction, recruitment, and hydrology. Gonadosomatic index, oocyte development and size distribution, histological examination of reproductive tissues, and the estimation of hatch dates using otoliths have been used to relate reproduction and recruitment of broadcast-spawning cyprinids to stream flow patterns (Durham and Wilde 2006, 2008b, 2014). Therefore, future research evaluating an environmental flow regime's capacity to fulfill key ecological functions should rely on reproductive analyses performed on adult and juvenile fluvial specialists.

CHAPTER III

RELATIONSHIP BETWEEN HATCH DATE AND FLOW REGIME FOR SHOAL CHUB *MACRHYBOPSIS HYOSTOMA*

Introduction

Studies by Moore (1944) and Bottrell et al. (1964) provided insights into the reproductive strategy of a group of Great Plains cyprinids by documenting that Arkansas River Shiner *Notropis girardi* and Speckled Chub *Macrhybopsis aestivalis* spawned non-adhesive, semi-buoyant ova. Further work by Platania and Altenbach (1998) confirmed that multiple species, comprising three genera of cyprinids, belong to an unrelated, evolutionarily convergent reproductive guild that broadcast-spawn non-adhesive, semi-buoyant ova in the main channel of lotic systems (Hoagstrom and Turner 2013). Early hypotheses concerning the reproductive ecology of these species proposed that high flow pulses during appropriate periods of the year could trigger spawning, and flow pulses prevent fertilized eggs from settling to the stream bottom and subsequently suffocating in sediment. Flow pulses also disperse drifting larvae longitudinally during development, after which they may move horizontally into slack-water habitats (Moore 1944, Lehtinen and Layzer 1988, Taylor and Miller 1990, Platania and Altenbach 1998, Dudley and Platania 1999). More recent studies determined that while flow pulses synchronize population-wide spawning events in this reproductive guild, individuals also exhibit asynchronous reproduction during varying hydrological conditions throughout an extended reproductive season (Durham and Wilde 2008b, 2014). Pelagic broadcast-spawning minnows have been documented to spawn in isolated pools during periods of

streamflow intermittency; however, spawning in isolated pools resulted in total recruitment failure (Bonner 2000, Durham and Wilde 2006, 2009b, Durham 2007). The opportunistic life history strategy of pelagic broadcast-spawning cyprinids is believed to be a mechanism for increasing odds of successful reproduction in highly variable lotic environments (Durham and Wilde 2009b). Extremely fast developmental rates allow individuals to take advantage of short-lived flow pulses in these systems (Moore 1944, Bottrell et al. 1964, Platania and Altenbach 1998).

Unfortunately, anthropogenic modifications of river hydrology are ubiquitous within the continental United States (Benke 1990). Two major threats to lotic ecosystems in the southern United States are dewatering and fragmentation by dams. According to Cooper (2013), there are over 19,000 barriers fragmenting stream networks in the Great Plains region, which has led to major alterations in natural flow regime. Dams have reduced regional discharge by 88%, making Great Plains streams among the most regulated in the world (Lehner et al. 2011, Costigan and Daniels 2012). Fish taxa in need of conservation in the southern United States have risen 75% in recent years (Warren et al. 2000). Due to fragmentation and desiccation in the Great Plains region, the loss of small-bodied pelagophilic and lithopelagophilic fishes has not only resulted in a loss of biodiversity, but also shifted once functionally and taxonomically diverse communities towards homogenized communities dominated by benthic reproductive guilds (Perkin et al. 2015).

The Shoal Chub *Macrhybopsis hyostoma* is a member of the *Macrhybopsis aestivalis* complex (Eisenhour 1999) of small benthic minnows that inhabit rivers in the

central United States. Other species in the *Macrhybopsis aestivalis* complex have been documented as members of the cyprinid pelagic-broadcast spawning reproductive guild (Bottrell et al. 1964, Platania and Altenbach 1998, Hoagstrom and Turner 2013). Due to similarities in morphology and close phylogenetic relationships, Shoal Chubs are hypothesized to belong to the same reproductive guild; however, no study has provided direct evidence to substantiate this claim (Perkin and Gido 2011). Shoal chubs are benthic insectivores and habitat specialists that prefer unregulated stretches of lotic environments with moderately strong currents over clean sand and gravel substrates within the main river channel (Luttrell et al. 2002, Williams 2011, Pierce et al. 2014). *Macrhybopsis* spp. have life spans that seldom exceed one year (Wilde and Durham 2008b, Williams 2011). Given their short life span, populations of these opportunistic species cannot afford even one poor year of recruitment. It has been proposed that dams, which fragment lotic systems, and alterations to the natural flow regime have contributed to Shoal Chub declines in abundance and geographic distribution (Becker 1983, Cross and Moss 1987, Winston et al. 1991, Etnier and Starnes 1993, Luttrell et al. 1999, Eisenhour 2004).

Research that targets species that are known to be sensitive to flow and that occur in multiple basins provides an effective means for gaining insights that can be extended beyond a particular location, and improved understanding of how flow pulses influence reproduction and recruitment of fluvial specialist species is needed for conservation of native biodiversity. The main objective of this study was to investigate the reproductive ecology of the Shoal Chub. Specifically, patterns of Shoal Chub recruitment were

examined for relationships with hydrology in the lower Brazos River. The lower Brazos currently maintains a relatively stable Shoal Chub population, and the unregulated segment from Waco, TX to the Gulf of Mexico provides an ideal study system for this research. Findings about relationships between fish species identified as fluvial specialists and hydrology will be useful for evaluating environmental flow regimes in Texas Gulf Coast rivers. Environmental flow regimes are an important step towards conserving fresh water resources as they attempt to balance human needs for water while maintaining flows that fulfill key ecological functions of components of the natural flow regime.

Methods

Study Locations

Field collections were made at one site on the lower Brazos River near State Highway 105 bridge near Navasota, Brazos County, Texas (30° 21' 45.1" N, 96° 09' 16.8" W) and one site on the middle Trinity River near the crossing with State Highway 7, approximately 13 miles west of Crockett, Leon County, Texas (31° 19' 08.6" N, 95° 40' 07.8" W) (Figure 10). The Brazos River is the third longest river in Texas. Originating in northwest Texas, the Brazos River flows approximately 1,700 miles southeast and discharges into the Gulf of Mexico at Freeport, Texas (Brazos Bay and Basin Expert Science Team [Brazos BBEST 2012]). Annual precipitation is 38-64 centimeters per year in the northern extent of the basin and 114-127 inches per year in the southern range of the basin (Brazos BBEST 2012). The Brazos River main stem and tributaries have been altered by the construction of 16 reservoirs for flood control and

water supply (Brazos BBEST 2012). However, the lower Brazos River maintains an unregulated 330-km stretch of river that extends from Waco, Texas, to the Gulf of Mexico. Historic flow conditions indicate winter and spring are typically associated with the highest monthly flows (Zeug and Winemiller 2008). Summer rainstorm events create unpredictable flows. High nutrient concentrations, moderate pH, and high transport of fine sediments resulting in high levels of turbidity are common physicochemical characteristics of the lower Brazos River (Roach and Winemiller 2011). The lower Brazos River fish community has maintained moderate fish assemblage integrity, notwithstanding several noticeable disappearances and population declines of fluvial specialists including Sharpnose Shiner *Notropis oxyrhynchus*, Smalleye Shiner *Notropis buccula*, Plains Minnow *Hybognathus placitus*, and Chub Shiner *Notropis potteri* (Bonner and Runyan 2007).

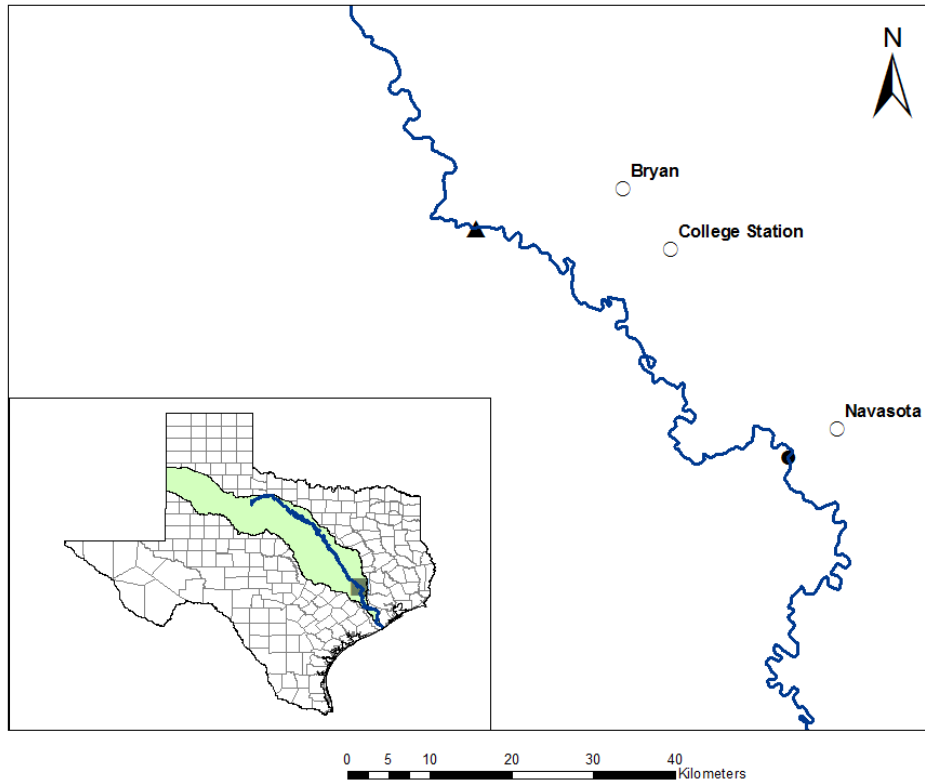


Figure 10 Site map of Brazos River survey sites. Black circle represents Brazos collection site and black triangle represents the nearest upstream USGS streamflow gauge.

Field Collections

Sampling took place over a one-year interval from March 2013 to March 2014. During the peak fish reproductive season (May-September) drift net collections were conducted every other week at the Brazos River (two surveys per month). Outside of the reproductive season (October-April), samples were collected once per month to survey for evidence of fish reproductive activity. To collect drifting larval fishes, drift nets 1 m in length, 0.45 m wide, and 0.30 m tall with a mesh size of 500 μm were set at wadeable

depths on sandbars. Drift nets were set in three arrays perpendicular to the shoreline, and each array consisted of three drift nets. Individual drift nets within an array were positioned in a straight line extending out from shore towards the middle of the channel. The distance from shore (m) was measured using a 30-m measuring tape after nets were set, and the depth (cm) and current velocity (m/s) were measured in the center of each drift net at the beginning and end of each collecting period using a meter stick and Marsh-McBirney current meter (Flo-Mate Model 2000, Frederick, MD, U.S.A). Drift net samples were standardized by total water filtered in order to calculate drift net catch per unit effort (CPUE). Total water filtered through each net was calculated at the product of mean current velocity in each net (m/s), net area (m²; width X submerged portion of net), and duration of sampling (s). Drift net samples were collected every two hours, with the first sample collected at 1800 h and the last sample collected at 0200 h (yielding a total of 36 individual driftnet samples on each date). Outside of the peak spawning period, sampling effort was reduced, with the last collections at 2200 h (yielding a total of 18 individual driftnet samples). After each 2-h interval, contents of each drift net were washed into individual Whirl-Pac® bags and stored in 95% ethanol. Samples were then transported to the lab at Texas A&M for processing.

Streamflow Data Collection

Discharge data were obtained from United States Geological Survey (USGS) surface water monitoring stations. Streamflow data for the Brazos River were obtained from USGS 8108700 near Bryan, TX. USGS 8108700 is located approximately 57 river miles upstream of our Brazos River site.

Laboratory Methods

Larval fish were separated from other contents of the Whirl-Pacs® and then counted and stored in labeled vials in 70% ethanol. Developmental stages of the larval fish were determined following characteristics given by Snyder (1998): *protolarvae*, complete absence of spines and rays; *mesolarvae*, at least one dorsal, anal, or caudal fin spine or ray, but still lacking the full set of adult soft rays in at least one median fin, or lacking pelvic fin buds; *metalarvae*, full set of principal soft rays in all median fins and pelvic fin buds or pelvic fins, with the fin fold still present; *juveniles*, full set of adult median and paired fin rays and spines with the fin fold completely absorbed. After specimens were sorted by their developmental stage, identification took place beginning with the oldest stage, juveniles, and proceeded downward to protolarvae. Larval identification was carried down to family level for each specimen based primarily on Snyder and Seal (2008) with additional references including Auer (1982) and Fuiman et al. (1983). Metalarvae and juvenile cyprinid specimens were set aside for further identification. Due to their morphological similarities to adult specimens, we were able to identify metalarvae and juvenile Shoal Chub specimens to the species level.

Daily growth increments (circuli) formation in the otoliths of young-of-the-year cyprinids in the Brazos River have been validated as a reliable means to estimate hatch dates (Durham and Wilde 2008a). Total length (mm) and standard length (mm) were recorded for each Shoal Chub specimen prior to otolith examination. Procedures for otolith preparation and daily growth estimation generally followed those of Campana (1992) and Secor et al. (1992). Asteriscus otoliths, the largest otoliths in Cyprinidae

(Secor et al. 1992), were removed using a dissecting microscope with two polarizing filters, one mounted between the light source and the otolith, and one mounted between the objective lens and otolith. After removal, otoliths were fixed to a glass slide using thermoplastic cement. Before reading, a drop of immersion oil was placed on the slide, and daily growth rings were counted with the aid of a compound light microscope at 40x magnification. Counts of daily growth rings on each otolith were made independently by two readers. Age estimates from the two readers that were within 10% were accepted as valid and retained for analysis. The daily age estimate was recorded as the mean of the two estimates (Durham and Wilde 2006, 2009b). The number of usable Shoal Chub otoliths was 68 (3% were excluded). We limited our analysis to include only specimens < 20 mm standard length (SL), because agreement between readers declined markedly for larger specimens. To check the validity of daily age estimates, linear regression was used to determine relationships between otolith diameter, daily growth ring counts and fish SL. Linear regressions of our estimated age on otolith diameter, age on SL, and SL on otolith diameter were all highly significant ($r^2 = 0.82$, $P < 0.00001$, $r^2 = 0.87$, $P < 0.00001$, $r^2 = 0.94$, $P < 0.00001$, respectively). Strong relationships among these variables indicate consistent patterns of otolith formation and have been used to validate daily growth rings as reliable indicators of age (Miller and Storck 1982, Durham and Wilde 2006). To determine birth dates from age estimates, 1 day was added to the final daily growth ring count, and this was based on as Bottrell et al.'s (1964) determination that eggs of *Macrhybopsis aestivalis*, a closely related species to Shoal Chub, hatch within 28 hours of spawning.

Statistical Analysis

The χ^2 goodness-of-fit test was used to determine if there was a significant relationship between daily stream flows categorized as flow pulses and the number of Shoal Chub larvae that hatched and survived. The χ^2 goodness-of-fit test was also used to test surviving Shoal Chub hatch dates in relation to periods with increasing, decreasing, or constant flows. The χ^2 goodness-of-fit test measures discrepancies between an observed frequency distribution and a distribution expected under a null hypothesis generated by a simple probability model (Whitlock and Schluter 2015). Mean daily flow statistics from USGS 8108700 (state highway 21 gage) were used to classify components of the flow regime. Daily streamflows were classified as subsistence, base, high flow pulse, or overbanking flow regime components. Flow separation was performed using parameters developed by the Brazos River Basin and Bay Expert Science Team (Table 3.3 in Brazos BBEST 2012). Subsistence flows were determined to be flows that occurred in the 5th percentile of the historical flow record. Daily mean flow was classified as subsistence if it was less than 299 CFS (cubic feet per second). The minimum flow for pulse flows was 833 CFS, and the maximum flow for base flows was 5,370 CFS. For discharge values between minimum and maximum values for base and pulse flows; percent change of discharge determined how to categorize the flow. If the previous day was a base flow and there was an increase greater than 25% in discharge, the flow was classified as a pulse flow. If the previous day was a pulse flow and the decrease in discharge was less than 5%, the flow was classified as base flow. To count as an overbank flow, discharge had to exceed 41,200 CFS. For the χ^2 goodness-of-fit test

analyzing flow trends, a flow was categorized as increasing if the percent change in discharge was greater than 1% from the previous days flow. The flow was considered decreasing if the percent change was less than -1%. Constant flows were determined to be flows where the percent change was between -1% and 1% compared to the previous days flow. The expected frequencies for the null hypothesis were calculated by counting the number of days the river was classified into various streamflow components and dividing each one by the total number of days in the reproductive season (April to October (Williams 2011) then multiplying by the number of Shoal Chub individuals included in the analysis. Additionally, multiple linear regression, in the form of polynomial regression, was used to calculate a coefficient of determination to investigate a potential relationship between the numbers of surviving Shoal Chubs hatched and the magnitude of discharge.

Results

Mean length (SL, mm) and age (days) of Shoal Chub young-of-year for which otoliths were analyzed were 10.1 mm (range = 7.1-18.8 mm) and 11 days (range = 7-34 days), respectively. During the 2013 reproductive season (214 total days) base flows occurred on 148 days, flow pulses on 49 days, and subsistence flows occurred for 5 days. There were no overbanking flows between April and October. The χ^2 goodness-of-fit test analyzing surviving Shoal Chub hatch dates at discrete flow levels was significant ($\chi^2 = 150.18$, $df = 2$, $P < 0.00001$). More of the surviving Shoal Chub larvae were hatched on pulse flow dates than expected at random, and less surviving Shoal Chub larvae were hatched on base and subsistence flow dates. During the 2013 reproductive

season, increasing flows occurred on 72 days whereas decreasing and constant flows occurred on 111 and 31 days, respectively. The χ^2 goodness-of-fit test analyzing surviving Shoal Chub hatch dates and the hydrological trend of stream discharge also was significant ($\chi^2 = 13.54$, $df = 2$, $P = 0.001$). More of the surviving Shoal Chub larvae were hatched on increasing flows than would be expected at random, and fewer surviving Shoal Chub larvae were hatched on days with decreasing or constant discharge values compared to the day before (Figure 11). The relationship between surviving Shoal Chubs hatched and mean daily discharge was significant and non-linear ($R^2 = 0.46$, $P = 0.048$) (Figure 12). I overlaid the environmental flow standards for USGS 8108700 near Bryan, TX on the scatterplot between Shoal Chubs hatched and discharge (Figure 13). Environmental flow recommendations differ across seasons; thus, I used the “summer” environmental flow standards in this plot because the Shoal Chub hatch dates in my sample were from the defined summer season (June-October). Based on my limited samples the two-per-season flow pulse recommendation appears to promote the highest Shoal Chub recruitment.

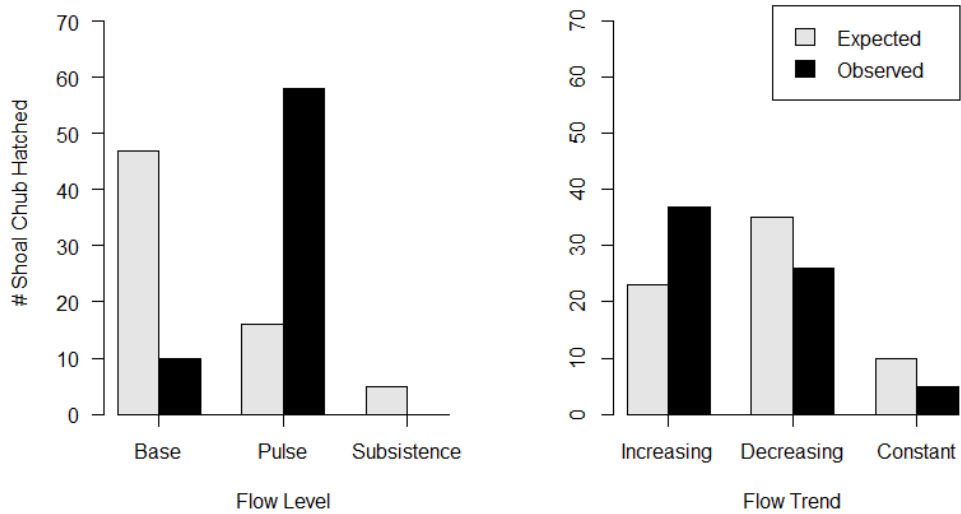


Figure 11 Shoal Chub hatch dates in relation to hydrological categories. The expected frequency is the number of Shoal Chubs expected to be hatched based on the null hypothesis model. The observed frequencies were the actual number of Shoal Chubs hatched that corresponded to various flow levels and trends. Results for both χ^2 goodness-of-fit tests were significant.

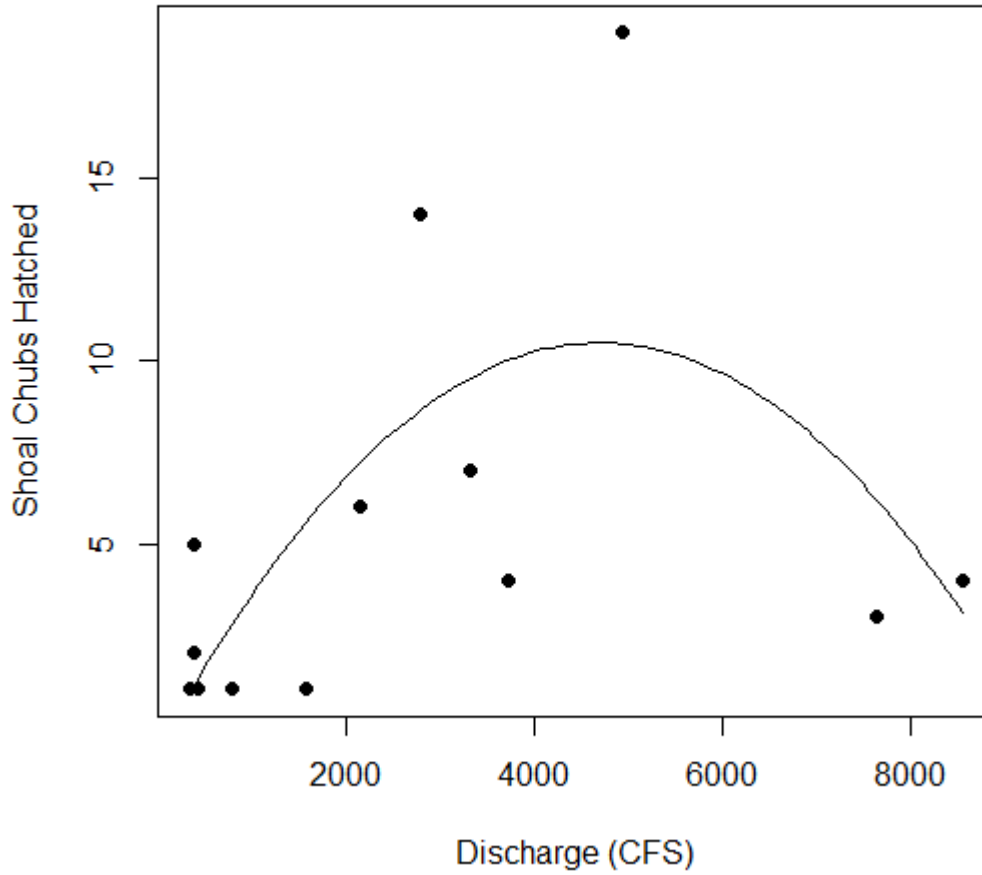


Figure 12 Numbers of surviving Shoal Chubs hatched and discharge. Non-linear relationship was significant ($R^2 = 0.46$, $P = 0.048$). Equation for the regression line was $y = -5E-07x^2 + 0.0047x - 0.604$.

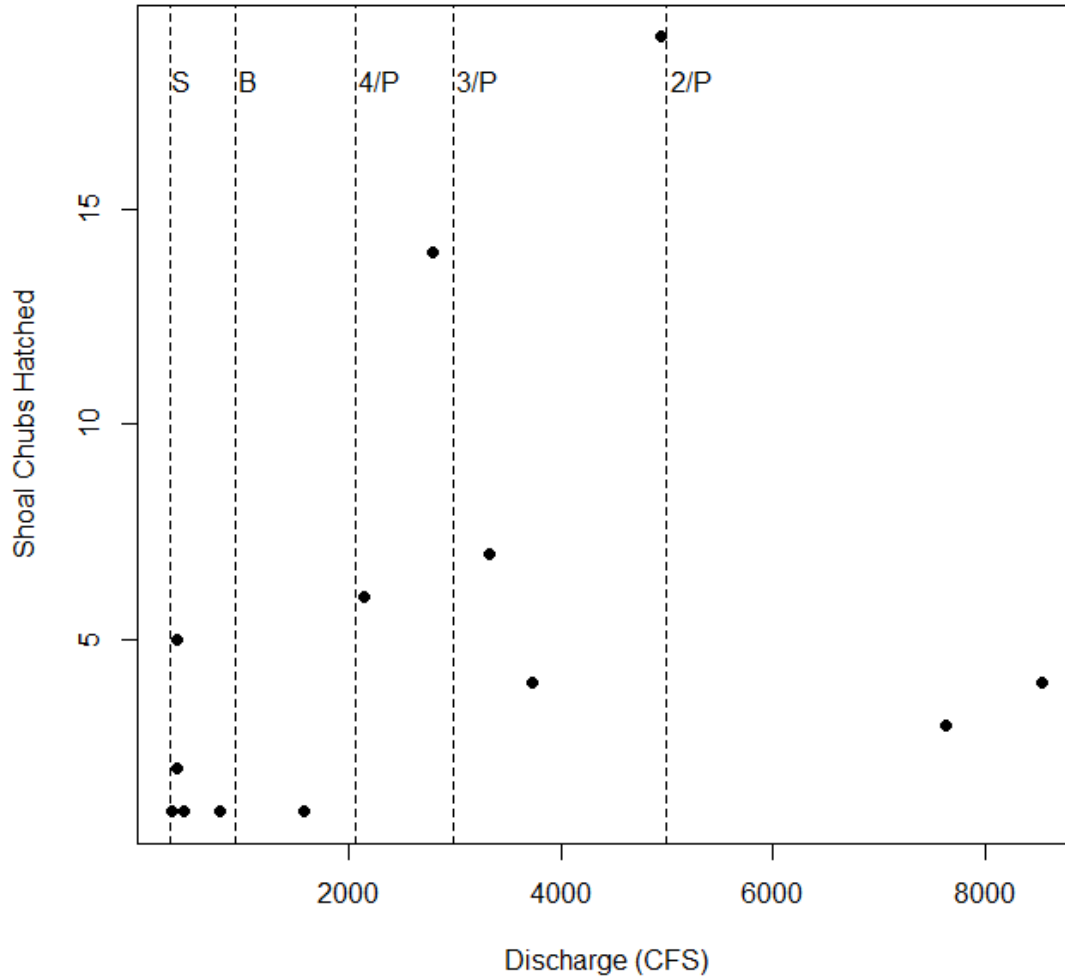


Figure 13 Shoal Chub hatches and environmental flow standards. Environmental flow recommendations, from the summer period (June-October), are based on USGS streamflow gauge near Bryan, TX. S = subsistence flow, B = base flow, 4/P = four-per-season flow pulse, 3/P = three-per-season flow pulse, 2/P = two-per-season flow pulse.

Discussion

Initial studies concerning relationships between flow pulses and cyprinid broadcast spawning in prairie rivers yielded contradictory results (Durham and Wilde 2006, 2009b). More recent studies, that analyzed a suite of reproductive parameters, have documented the unique reproductive ecology of pelagic broadcast-spawning cyprinids whereby asynchronous individual recruitment events are continuous throughout the reproductive season, but flow pulses stimulate population-wide synchronized spawning (Durham and Wilde 2009b, 2014). While spawning is not restricted to any particular aspect of the hydrological regime, flow pulses result in marked increases in the number of drifting pelagic broadcast-spawning cyprinid propagules. My research did not provide means to estimate the number of Shoal Chub protolarvae produced in relation to hydrology, but instead focused on understanding the relationship between successful recruitment and streamflow patterns. My findings concerning the reproductive ecology of Shoal Chub compliment the aforementioned studies by demonstrating that aside from an increase in spawning effort, pelagic broadcast-spawning cyprinids may experience greater recruitment when hatched during flow pulses. In the lower Brazos River, surviving Shoal Chubs hatched on both base and pulse flows, and at times of increasing, decreasing, and consistent discharge trends. However, significantly more surviving Shoal Chubs were hatched during flow pulses, especially when discharge was increasing. Thus the rising limb of a flow pulse appears to promote greater recruitment of Shoal Chub in the lower Brazos River compared to base or subsistence flows.

There are benefits to spawning during elevated periods of discharge compared to subsistence or base flow conditions for pelagic broadcast-spawning cyprinids. Reliance on advection for propagule transport (passive dispersal) is more energetically efficient than adult migration for spawning in or near nursery habitats. An extended reproductive season and continuous recruitment probably hedge against risks of relying on unpredictable flows for larval transport (Durham and Wilde 2009b, Hoagstrom and Turner 2013). For successful recruitment, larval fish require nursery habitats that provide optimum conditions for growth and survival. Flow pulses enhance larval fish nursery habitats through nutrient enrichment and nutrient concentration (Hoagstrom and Turner 2013). Additionally, propagule retention within favorable nursery habitats increases during flow pulse attenuation (Medley et al. 2007, Widmer et al. 2012, Hoagstrom and Turner 2013). Biotic interactions, such as predation and competition, are influenced by flow pulses as well. Predator density decreases and competition is reduced due to increases in water volume and larval dispersion (Hoagstrom and Turner 2013).

I detected a significant non-linear relationship between the magnitude of discharge and the number of surviving Shoal Chub larvae. This provides evidence, albeit on a limited sample size, that Shoal Chub recruitment is positively associated with increased discharge values, but perhaps only to a certain threshold. The “maximum discharge threshold” hypothesis postulates that the greatest reproductive investment by pelagic broadcast-spawning minnows will be associated with moderate flow pulses. High magnitude flow pulses might be detrimental to survival of propagules; therefore, reproductive effort would be reduced under these conditions. This optimum threshold

matched quite well with the two-per-season flow pulse recommendation for the USGS gauge near Bryan, TX (Figure 13). Further research involving larger samples is needed to validate the flow pulse magnitudes associated with greatest spawning activity and recruitment. Future studies will also need to determine optimum frequencies of these flow pulses for maintaining stable populations of pelagic broadcast-spawning cyprinids.

To maintain a stable local population, pelagic broadcast-spawning cyprinids either need to take advantage of hydrologic conditions that reduce downstream transport of larvae, or else undergo upstream movements during the juvenile and/or adult stage to balance downstream drift of larvae, the latter being much more energetically expensive. Since flow pulses tend to be brief in prairie rivers, (Hoagstrom and Turner 2013), this explains the tendency for species in this reproductive guild to initiate spawning on the rising limb of a flow pulse (Medley et al. 2007). Upstream migrations can be reduced if spawning occurs during short-lived flow pulses of moderate magnitude that also facilitate retention of drifting propagules in nearby nursery habitats following pulse subsidence (Medley et al. 2007, Widmer et al. 2012). Higher magnitude discharge events should result in greater downstream transport distances of drifting propagules.

Alterations to lotic flow regimes through dam construction and water withdrawals can reduce historic discharge levels and homogenize flow regimes by removing the natural variability (Lytle and Poff 2004, Lehner et al. 2011, Costigan and Daniels 2012). Sustained reservoir releases increase transport distances of drifting semi-buoyant eggs (Dudley and Platania 2007). Recolonization of upstream reaches by young-of-the-year pelagic broadcast-spawning cyprinids could be hindered if during

higher flows eggs or larvae are transported beyond physical barriers that block upstream migration. Also, sustained high flows could transport propagules long distances into degraded riverine habitats and reservoirs (Dudley and Platania 1999, 2007). Pelagic broadcast-spawning cyprinids in highly regulated lotic environments have been extirpated or experienced large reductions throughout much of their native range (Cross and Moss 1987, Winston et al. 1991, Platania and Altenbach 1998). In unregulated river reaches transport distances of propagules are lessened due to naturally complex heterogeneous habitats (Medley et al. 2007). The lower Brazos River remains mostly unregulated, and this is likely a major factor contributing to the persistence of the Shoal Chub population, as well as other fluvial specialists.

Without cyprinid pelagic broadcast-spawners, the functionally diverse fish assemblages in Texas rivers would become more homogenous. A large body of research has illustrated the important role that discharge magnitude and intra-annual variation in discharge magnitude play in preserving populations of this reproductive guild of fishes (Durham and Wilde 2006, 2008b, 2009b, 2009a, 2014, Wilde and Durham 2008b). Conservation of Shoal Chub and other members of the cyprinid pelagic broadcast-spawning guild require environmental flow regimes that maintain adequate discharge variability to promote synchronized spawning and successful recruitment. During a 6-year period of below average discharge in the Canadian River, Texas, Peppered Chub *Macrhybopsis tetranema* abundance declined by about 80% (Wilde and Durham 2008b). Other studies also have linked declines of pelagic broadcast-spawning cyprinids with recruitment failure under altered flow regimes (Durham and Wilde 2006, 2008b, 2009b,

Wilde and Durham 2008a). To determine a more precise relationship between discharge and reproductive effort, research is needed that incorporates larger samples of Shoal Chub juveniles to estimate hatch dates and patterns of abundance across a wide range of discharge magnitudes. Environmental flow regimes that maintain numerous moderate flow pulses during the reproductive season provide the best chance for protecting populations of native pelagic broadcast-spawning cyprinids in the Brazos River and other prairie rivers of North America.

CHAPTER IV

LITTORAL FISH ASSEMBLAGE STRUCTURE IN RELATION TO INTRA-ANNUAL HYDROLOGIC VARIATION IN THE LOWER BRAZOS RIVER

Introduction

Mechanisms that structure fish communities operate on two very different scales. Regional scale processes such as: historical biogeography, evolution, colonization, and extinction structure fish community assemblages temporally and spatially on broad scales. Different mechanisms operate to structure local species assemblages. Contemporary species assemblages at local scales are influenced by biotic interactions, such as predation and competition, as well as species' morphological and physiological adaptations to local environmental variables (Grossman et al. 2010, Winemiller 2010). In lotic systems, hydrology has a pervasive influence on local assemblages. Streamflow has been deemed a "master environmental variable" because biology, habitat diversity, physical processes, and numerous physicochemical characteristics of water are ultimately linked to the hydrologic regime (Poff and Ward 1989, Poff et al. 1997, Bunn and Arthington 2002). Flow velocity can constrain fish habitat use due to differences in critical swimming velocities of fish, thus high flows can limit upstream dispersal by some species (Grossman et al. 2010). Discharge variability and predictability also can structure lotic fish assemblages, and alteration to natural flow regimes is expected to change lotic fish assemblages (Poff and Allan 1995, Marchetti and Moyle 2001, Olden and Kennard 2010, Kiernan et al. 2012). Studies in the southern Appalachian region of

the United States demonstrated that hydrologic variation among years was the dominant mechanism determining species richness, assemblage structure, and fish abundance along a longitudinal gradient (Grossman et al. 1998). However, much of the research on mechanisms structuring lotic fish assemblages has concentrated on inter-annual variation among years of varying hydrological conditions (Seegrist and Gard 1972, Schlosser 1985, Bonner and Wilde 2000, Propst and Gido 2004, Perkin and Bonner 2011, Kiernan et al. 2012, Stanley et al. 2012) or among streams differing in natural flow regimes (Poff and Allan 1995, Scheidegger and Bain 1995, Freeman et al. 2001, Shea and Peterson 2007, Olden and Kennard 2010, Erős et al. 2012). While some studies have looked at community shifts following major disturbance events, little work has been done to explore variation in fish assemblages in relation to intra-annual variation in discharge (Harrell 1978).

Highly variable flow regimes may result in temporally variable fish assemblages, especially in rivers with oxbow lakes in their floodplains. Oxbow lakes are highly productive, eutrophic habitats common in the floodplain of lowland rivers worldwide. Oxbow lakes have spatiotemporal environmental variability (related to the age of the oxbow) that influences fish assemblage structure. Newly formed oxbows are deep and lie close to the river channel, but over time they receive sediments and become shallower. Channel meandering in response to erosion and sediment deposition leaves some older oxbows positioned at greater distances from the active channel (Winemiller et al. 2000). These productive habitats can maintain high densities of fish and serve as important nursery habitats for juveniles of some species (Winemiller et al. 2000, Zeug et

al. 2009). Most oxbows provide conditions that promote growth and survival of diverse fishes (Winemiller et al. 2000). Research on the lower Brazos River has shown that assemblage structure in oxbow lakes are distinct from those in the adjacent river channel, even though many species are shared (Zeug et al. 2005). For example, several species inhabiting the lower Brazos River maintain high numbers in oxbow lakes, but are rarely captured in the river channel and vice versa (Winemiller et al. 2000, Zeug et al. 2005). During periods of elevated discharge, oxbow lakes connect with the river channel, which allows for the exchange of resources and aquatic organisms.

Objectives of this study were to investigate mechanisms responsible for structuring fish assemblages within littoral zones of a Texas Gulf Coast river. Specifically, I wanted to determine what role intra-annual hydrologic variation played in regulating fish assemblage structure within the littoral zone over a one year period. I hypothesized that after periods of high flows, river-channel littoral assemblages would be different than assemblages surveyed during base or subsistence flow conditions. This is because species typically found in oxbows disperse into the river channel during periods of lateral connection. I further hypothesize that fish species classified as ‘oxbow specialists’ would have positive relationships with river discharge. Understanding how environmental variation influences species assemblages should facilitate development of frameworks that predict responses to anthropogenic disturbances, including alteration of the natural flow regime. This study emphasizes the role of intra-annual hydrologic variability in maintaining biodiversity of Texas Gulf Coast rivers.

Methods

Study Locations

Field collections were made at one site on the lower Brazos River near State Highway 105 bridge near Navasota, Brazos County, Texas (30° 21' 45.1" N, 96° 09' 16.8" W) (Figure 14). The Brazos River is the third largest river in Texas. Originating in northwest Texas, the Brazos River flows approximately 1,700 miles southeast and discharges into the Gulf of Mexico at Freeport, Texas (Brazos Bay and Basin Expert Science Team [Brazos BBEST 2012]). Annual precipitation is 38-64 centimeters per year in the northern extent of the basin and 114-127 inches per year in the southern range of the basin (Brazos BBEST 2012). The Brazos River main stem and tributaries have been altered by the construction of 16 reservoirs for flood control and water supply (Brazos BBEST 2012). However, the lower Brazos River maintains an unregulated 330-km stretch of river that extends from Waco, Texas, to the Gulf of Mexico. Historic flow conditions indicate winter and spring are typically associated with the highest monthly flows (Zeug and Winemiller 2008). Summer rainstorm events create unpredictable flows. High nutrient concentrations, moderate pH, and high transport of fine sediments resulting in high levels of turbidity are common physicochemical characteristics of the lower Brazos River (Roach and Winemiller 2011). The lower Brazos River fish community has maintained moderate fish assemblage integrity, notwithstanding several noticeable disappearances and population declines of fluvial specialists including Sharpnose Shiner *Notropis oxyrhynchus*, Smalleye Shiner *Notropis buccula*, Plains Minnow *Hybognathus placitus*, and Chub Shiner *Notropis potteri* (Bonner and Runyan 2007).

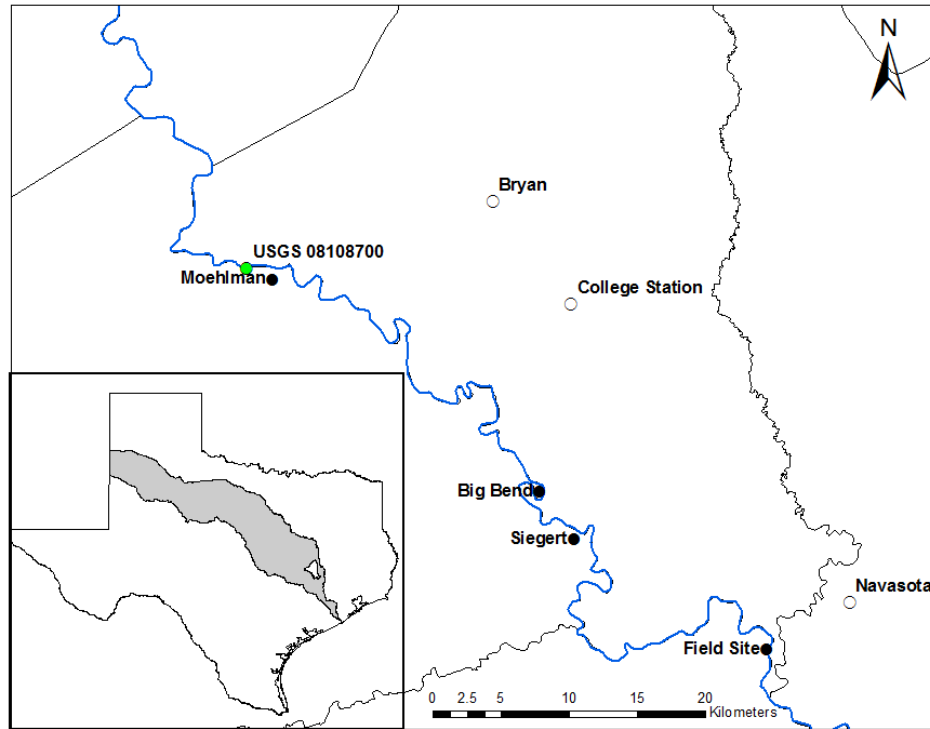


Figure 14 Site map of Brazos River survey site and upstream oxbows. Inset map depicts the Brazos River basin in light grey and Brazos County is outlined within the basin. Brazos River is depicted by the blue line on the main map, solid circles represent locations of the survey site and nearby oxbows, green dot represents USGS streamflow gauge.

Field Collections

Sampling took place over a one-year interval from March 2013 to March 2014. Seine nets were used to collect fish within littoral habitat, defined here as areas adjacent to the river bank with shallow depth (0-1 m) and slow to moderate current velocity (0-0.45 m/s). The location of littoral habitat at a given location and date varied depending on discharge. At higher magnitude discharge, the littoral zone was positioned at higher elevation along the channel margin. Collections were conducted every other week at the survey site (two surveys per month) from May through September. The survey site was sampled once per month from October to April. The number of seine hauls among sampling trips varied, and this effort was standardized by recording the number of seine hauls and the length of individual seine hauls, and then calculating catch per unit effort (CPUE) based on total area sampled. Seine samples were collected using seines of two different sizes. A straight seine (5.75 m in length, 3.95 m tall, with 2 mm mesh) was used to collect fishes along a path perpendicular to the main channel. A smaller seine (3.55 m in length, 1.35 m tall, with 2 mm mesh) was used to sample along a path parallel to the shoreline. Large catches of common species were identified and enumerated in the field, and specimens were returned alive to the river. Remaining fish specimens were euthanized, preserved in 10% formalin solution, and transported to the lab at Texas A&M for identification and enumeration. Environmental parameters measured on each date, at each survey site, using a YSI 85 meter included: water temperature (°C), dissolved oxygen (mg/L), conductivity ($\mu\text{mhos/cm}$), and salinity (ppt). Water transparency (cm) was measured using a Secchi disk, and pH was measured using a Multi-parameter PCSTestr 35.

Fish Classification

The species present in the seine samples were classified as either oxbow (primarily occurring in oxbow systems), main channel (primarily occurring in river channel) and generalists (commonly occurring in both systems) using frequency of occurrence data reported in Zeug et al. (2005). In that study, fish surveys were conducted quarterly over a 3-year period in three Brazos River oxbows with varying lateral connection frequencies plus one location within the Brazos River active channel. Only species that were present in the data set provided by Zeug et al. (2005) were included in this analysis. If a species was never reported from an oxbow, it was classified as a 'channel species'; those never reported from the channel but present in at least one oxbow were classified as 'oxbow species'. For species that were sampled in both habitats, a numerical gradient was devised by dividing the percent occurrence in oxbow habitats by the percent occurrence in main channel habitats. Species with a ratio near 1 were sampled approximately equally in both habitats and were classified as generalists. Species with low ratios of oxbow to main channel occurrences (ratio < 0.4) were classified as 'channel species'. Species with high ratios of oxbow to main channel occurrences (ratio > 2.5) were classified as 'oxbow species' (Appendix A).

Streamflow Data

Discharge data were obtained from the nearest United States Geological Survey (USGS) surface water monitoring stations located upstream from each survey site. Streamflow data for the Brazos River were obtained from USGS 8108700 near Bryan, TX. USGS 8108700 is located approximately 57 river miles upstream of our Brazos

River site. Mean daily flow statistics were used to classify components of the flow regime. Daily streamflows were classified as subsistence, base, high flow pulse, or overbanking flow regime components. Flow separation was performed using parameters developed by the Brazos River Basin and Bay Expert Science Team (Table 3.3 in Brazos BBEST 2012).

Statistical Analysis

To examine seasonal variation in fish species assemblages, sampling dates were categorized as spring (March-May), summer (June-September) or winter (October-February). These divisions were based primarily on predictable, temporal variation in water temperature. Bray-Curtis similarity matrices were constructed based on fish abundance data (CPUE) at each site on each survey date. One-way analysis of similarities (ANOSIM; $\alpha = 0.05$; 999 permutations) was then used to test for significant differences in assemblage structure among seasons. The seine net CPUE's (individuals/100m²) for all species sampled were $\log(x+1)$ transformed prior to analysis to approximate a normal distribution (Clarke and Warwick 1994, Kerezszy et al. 2011). Both the statistical analysis and calculation of distance matrices was done in R using the vegan package (Oksanen et al. 2015).

A partial canonical correspondence analysis (pCCA) was used to ordinate larval fish assemblage structure and environmental variables in the Brazos River, and to determine associations between assemblage gradients and environmental gradients. Environmental variables included in this analysis were total discharge (cfs), fluctuation of discharge (%), maximum increase of discharge (%), maximum decrease of discharge

(%), water temperature ($^{\circ}\text{C}$), and water transparency (cm). Of these six variables, four (total discharge, fluctuation of discharge, maximum increase of discharge, and maximum decrease of discharge) were calculated from data collected over the 3-days period prior to the sampling date. This time period was used because hydrological conditions in these rivers are highly variable and the conditions present on sampling days are not always indicative of the recent state of the river. Total discharge was the total water volume passing the USGS gage station during the 3-day period. Daily mean discharges (cfs) during the 3-day interval were multiplied by 86,400 (number of seconds in a day) and these values were then summed across the entire 3-day period to yield total volume of discharge for the period. Fluctuation of discharge was calculated as the average absolute value of percent change in the mean daily discharge from the previous day's discharge. This variable gives an indication of the magnitude of variation in discharge levels, but does not indicate whether the overall trend was increasing or decreasing. Maximum increase of discharge was the largest positive percent change in mean daily discharge relative to the previous day's discharge during the 3-day period. Similarly, the maximum decrease of discharge was the largest negative percent change in mean daily discharge relative to the previous day's discharge during the 3-day period. Water temperature and transparency were both measured on each sampling date and were not averaged over a 3-day window.

Canonical correspondence analysis (CCA) is a statistical method commonly employed by aquatic ecologists to elucidate patterns that associate species occurrence with environmental variables potentially influencing assemblage composition. pCCA is

similar to CCA, except it includes a covariable which is used to factor variation from specific variables (ter Braak and Verdonschot 1995). A Monte Carlo permutation test (999 permutations) was used to identify statistically significant ($p \leq 0.05$) environmental variables and constrained ordination axes. Only the first two canonical axes from the CCA (dominant axes) were interpreted. The seine net CPUE (individuals/100m²) were $\log(x+1)$ transformed prior to analysis to reduce the effect of dominant species, and rare species (present in < 10% of survey dates) were removed from the CCA analysis to reduce the effect of rare species (Legendre and Legendre 1998). Multivariate ordination was carried out in R using the vegan package (Oksanen et al. 2015).

Results

Fish Classification

We classified 28 fish species from the Brazos River according to frequency of occurrence data reported in Zeug et al. (2005). In the Brazos River, river specialists made up the largest percentage at roughly 46% (n=13), generalist species made up approximately 36% of the species sampled (n=10), and the remaining 18% comprised five species classified as oxbow specialists. Common oxbow species included: Bluegill *Lepomis macrochirus*, Inland Silverside *Menidia berrylina*, Golden Shiner *Notemigoneus crysoleucas*, Pugnose Minnow *Opsopoeodus emiliae*, and White Crappie *Pomoxis annularis*.

One-way Analysis of Similarities

Littoral fish assemblage structure in the Brazos River was significantly related to season (ANOSIM: $R = 0.261$, $P = 0.007$). For this reason, I used pCCA to remove

variation due to water temperature (i.e. water temperature provides a surrogate for seasonality) from the gradients derived by pCCA. This was done to examine variation in assemblage structure associated with hydrological variables independent of the effect of seasonality.

Multivariate Ordination of Brazos River CPUE and Environmental Data

Axis 1 (CCA1) described a general discharge gradient, with higher discharges represented by negative values and lower discharges represented by more positive values (discharge loading on CCA1 = -0.70). CCA1 also represented a gradient in percent decreases in discharge values with larger percent decreases represented by more positive values (max increase loading on CCA1 = 0.65). CCA1 alone explained 39.9% of the variation in the ordination and was the only constrained axis that significantly explained variation within the ordination diagram (Monte Carlo permutation test, $n=999$, $p=0.006$). Positive values on CCA axis 2 (CCA2) were associated with higher transparency (transparency loading on CCA2 = 0.64). CCA2 modeled an additional 25.6% of variation, resulting in a total of 65.5% of variation explained by the first two axes. Discharge was the only environmental variable included in the pCCA that yielded a statistically significant relationship (Monte Carlo permutation test, $n=999$, $p=0.044$) with the model. Ordination of Brazos River samples revealed separation associated mostly with flow level; fish assemblage structure in the littoral zone of the Brazos River during pulse flows was different compared with structure during base and subsistence flows (Figure 15). This is illustrated by the division of sampling dates along the CCA1 gradient. Except for one base flow sampling date characterized by high discharge and

one pulse flow sampling date which had lower magnitudes of discharge, pulse flow sampling dates plotted in the same region of ordination space associated with increased discharge. Three oxbow specialists (White Crappie, Bluegill, and Pugnose Minnow) had large negative loadings on CCA1, indicating that these species were most abundant in the river channel during high discharge sampling events (Figure 16). The fourth oxbow species included in the analysis, Inland Silverside, had a negative loading on CCA1 as well, albeit to a lesser degree.

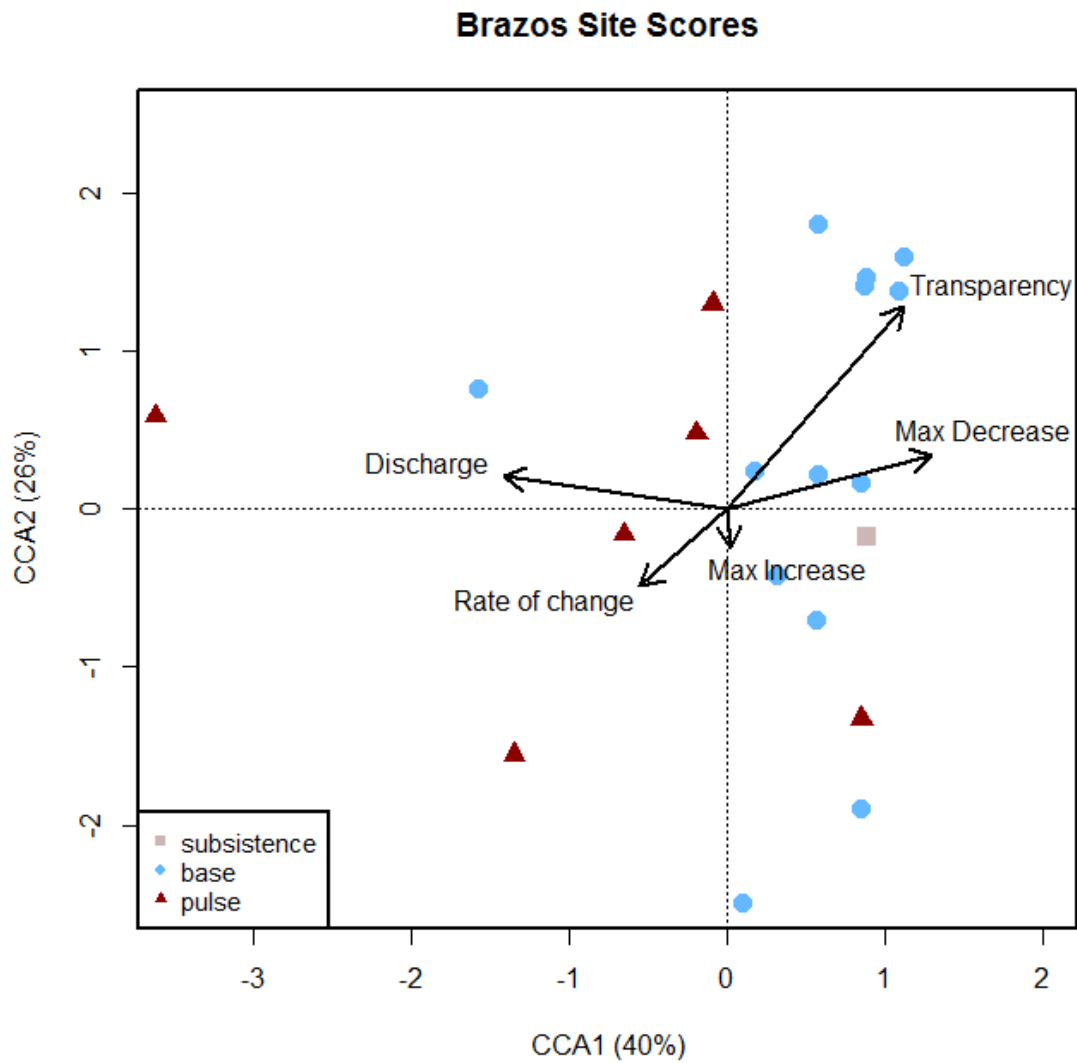


Figure 15 Brazos River sample score pCCA ordination. Each point in the ordination diagram represents a sampling date. Points sharing similar ordination space had similar assemblages. Sampling dates were categorized as subsistence, base, or pulse flows. Discharge was statistically significant $P = 0.044$.

Brazos Species Scores

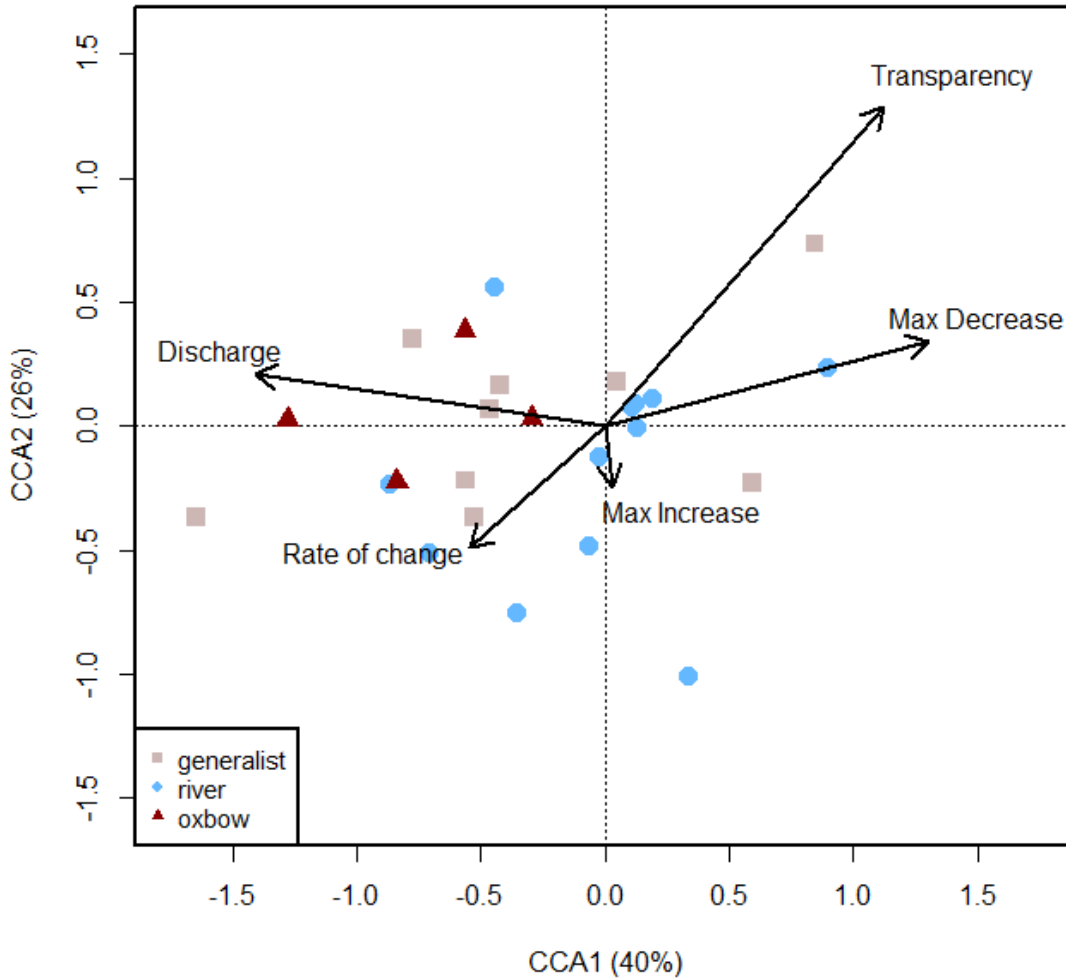


Figure 16 Brazos River species score pCCA ordination. Each point in the ordination diagram represents a one of the species (n=28) used in the analysis. Points sharing similar ordination space were constrained by similar environmental variables. Species were categorized as generalist, river, or oxbow. Discharge was statistically significant $P = 0.044$.

Discussion

Discharge was significantly correlated with fish assemblage structure in littoral habitat in the Brazos River, and discharge explains a major portion of intra-annual variation in littoral fish assemblages. This finding adds to a large body of research that has revealed how hydrology influences river biota at multiple spatial and temporal scales (Seegrist and Gard 1972, Schlosser 1985, Poff and Allan 1995, Grossman et al. 1998, 2010, Olden and Kennard 2010). Multivariate ordination showed distinct differences in fish assemblages during flow pulses compared to base and subsistence flows. One base flow sampling date had fish assemblages similar to those documented during flow pulses. This date had relatively high and stable flows; therefore, it was classified as a base flow according to the flow separation methodology. Due to the high level of base flow, there could have been lateral connectivity associated with that date.

Oxbow species were more prevalent in the river channel during higher flows. These species include White Crappie, Bluegill, and Pugnose Minnow. Positive relationships with discharge supports prior research that hypothesized flow pulses create hydrological connectivity, which in turn facilitates exchange of species between these distinct habitats (Zeug et al. 2005). Inland Silverside had a minor positive relationship with increased discharge in the Brazos River. The Inland Silverside can be common in both reservoir and river channel habitats, so the lack of a major relationship with discharge magnitude is not surprising (Middaugh and Hemmer 1992).

Oxbow lakes support fish assemblages distinct from those in the main river channel; and some species rarely sampled in lotic habitats are common in oxbows

(Winemiller et al. 2000, Zeug et al. 2005). Variable flows conserve native biodiversity in Texas Gulf Coast rivers, because large flow pulses create lateral connectivity that periodically replenishes populations of oxbow species within the river channel. Without oxbow lakes serving as metapopulation sources for the river, important game species such as White Crappie and Bluegill could become locally extirpated in these river reaches. At the same time, the river channel is important as a source of colonists for oxbow lakes. Desiccation of oxbows occurs during periods of drought (Zeug and Winemiller 2007). Alterations to the natural flow regime, that reduce high flow events, could result in a loss of lateral connectivity between oxbow lakes and the river channel. This could lead to the isolation of populations, failed recruitment, and ultimately local extinction of oxbow residents. Besides playing a critical role in maintaining biodiversity in Texas Gulf Coast rivers, large flow pulses also maintain the integrity of lotic systems through their role in sediment transport, their ability to create new habitat, export and import nutrients, and increase productivity by connecting floodplain and channel habitats (Poff et al. 1997). Therefore, large flow pulses are critical components of environmental flow regimes for Texas Gulf Coast rivers.

CHAPTER IV

CONCLUSION

Environmental flow regimes seek to identify and protect key components of natural hydrologic regimes that strongly influence ecological dynamics. This thesis has demonstrated that flow pulses, of both small and large magnitude, serve important ecological functions. Smaller magnitude flow pulses resulted in greater recruitment of Shoal Chub *Macrhybopsis hyostoma*. My analysis showed that, among the surviving metalarvae and juvenile Shoal Chub, more hatch dates were associated with increasing discharge and flow pulses. Additionally, a non-linear relationship between discharge and surviving larval and juvenile Shoal Chubs suggests there is a maximum discharge threshold. Based on my limited samples, the highest survival rates of Shoal Chub young-of-year were associated with an optimum level of discharge. Higher and lower discharge magnitudes apparently resulted in lower recruitment. Two-per-season flow pulses, as outlined in the environmental flow regime for the summer months at the USGS gauge near Bryan, TX, appeared to yield the highest Shoal Chub recruitment. Further research involving larger samples is needed to validate the flow pulse magnitudes associated with greatest spawning activity and recruitment. Future studies also are needed to determine optimum frequencies of these flow pulses for maintaining stable populations of pelagic broadcast-spawning cyprinids.

Larger magnitude flow pulses create and maintain the dynamics between in-channel and floodplain habitats in the lower Brazos River. Species in the Brazos River classified as “oxbow specialists” were Bluegill *Lepomis macrochirus*, Golden Shiner

Notemigoneus crysoleucas, Inland Silverside *Menidia beryllina*, Pugnose Minnow *Opsopoeodus emiliae*, and White Crappie *Pomoxis annularis*. The four oxbow species included in the multivariate analysis were positively correlated with discharge. These species contributed to differences in species assemblages among varying levels of flow in the Brazos River. This research reinforced previous findings of the importance of lateral connectivity associated with larger flow pulses for maintenance of native biodiversity in Texas Gulf Coast rivers.

Unfortunately, species-specific relationships between protolarvae abundance and hydrology could not be elucidated during research conducted for this thesis. Further work developing means to accurately identify larval fish assemblages in the southern United States is needed. With the means to identify protolarvae to species, analysis of larval trends could yield a productive path for evaluating environmental flow regimes. My analysis conducted at the family level demonstrated that water temperature (i.e., seasonality) explained most of the variation in protolarvae assemblages in both the Brazos and Trinity Rivers. Hydrological variables had relatively weak associations with assemblage structure of fish larvae at the family level. Based on findings from Chapter III, it seems likely that the same analysis, carried out at the species level, could reveal significant differences in species' responses to hydrological variables and other environmental factors.

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APPENDIX A

FISH HABITAT CLASSIFICATIONS

| Species | Oxbow | River | Ratio | Classification |
|--------------------------------|-------|-------|-------|----------------|
| <i>Hybognathus nuchalis</i> | 0 | 8 | 0.00 | River |
| <i>Macrhybopsis hyostoma</i> | 0 | 62 | 0.00 | River |
| <i>Micropterus punctulatus</i> | 0 | 23 | 0.00 | River |
| <i>Notropis buchanaani</i> | 0 | 54 | 0.00 | River |
| <i>Percina sciera</i> | 0 | 31 | 0.00 | River |
| <i>Cyprinella venusta</i> | 3 | 38 | 0.08 | River |
| <i>Notropis shumardi</i> | 14 | 92 | 0.15 | River |
| <i>Cyprinella lutrensis</i> | 30 | 100 | 0.30 | River |
| <i>Lepisosteus osseus</i> | 16 | 54 | 0.30 | River |
| <i>Pimephales vigilax</i> | 35 | 100 | 0.35 | River |
| <i>Mugil cephalus</i> | 3 | 8 | 0.38 | River |
| <i>Pylodictis olivaris</i> | 3 | 8 | 0.38 | River |
| <i>Lepomis megalotis</i> | 32 | 85 | 0.38 | River |
| <i>Noturus gyrinus</i> | 5 | 8 | 0.63 | River |
| <i>Carpiodes carpio</i> | 35 | 38 | 0.92 | Generalist |
| <i>Dorosoma petenense</i> | 32 | 31 | 1.03 | Generalist |
| <i>Ictalurus furcatus</i> | 24 | 23 | 1.04 | Generalist |
| <i>Dorosoma cepedianum</i> | 68 | 62 | 1.10 | Generalist |
| <i>Micropterus salmoides</i> | 27 | 23 | 1.17 | Generalist |
| <i>Ictaluris punctatus</i> | 59 | 46 | 1.28 | Generalist |
| <i>Gambusia affinis</i> | 97 | 57 | 1.70 | Generalist |
| <i>Lepomis cyanellus</i> | 16 | 8 | 2.00 | Generalist |
| <i>Lepomis humilis</i> | 84 | 38 | 2.21 | Generalist |
| <i>Opsopoeodus emiliae</i> | 68 | 23 | 2.96 | Oxbow |
| <i>Menidia beryllina</i> | 68 | 15 | 4.53 | Oxbow |
| <i>Lepomis macrochirus</i> | 78 | 15 | 5.20 | Oxbow |
| <i>Pomoxis annularis</i> | 92 | 15 | 6.13 | Oxbow |
| <i>Notemigonus crysoleucas</i> | 24 | 0 | NA | Oxbow |