## THESIS

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## CHAPTER I

## INTRODUCTION

Seven hundred ninety fish species are found in the United States and Canada representing the most diverse temperate freshwater fish assemblage in the world (Page and Burr 1991). Among these fishes, $80 \%$ are found in the contiguous United States (Warren and Burr 1994), and the highest diversity (71\%) is found in the southern portion (Warren et al. 2000). Despite high ecological diversity, fishes of the southern U.S. are highly threatened by anthropogenic alterations; approximately $28 \%$ are extinct, endangered, threatened, or of special concern (Warren et al. 2000).

Increased habitat modification and alteration by damming, dewatering, pollution, and removal of riparian zones has contributed to extirpation and extinction of native fishes and alteration of fish assemblages (Cross and Moss 1987; Rutherford et al. 1987; Sheldon 1988; Winston et al. 1991). Impoundments likely cause the greatest collective disturbance as there are presently more than 75,000 dams at least 1.8 m in height in the U.S. (Collier et al. 1996) and decrease or eliminate longitudinal connectivity important to riverine biodiversity (Vannote et al. 1980). Modifications attributed to impoundments include altering temperature and flow regimes (Travnicheck et al. 1995; Cumming 2004), preventing or disrupting spawning behaviors (Auer 1996; Bonner and Wilde 2000), and altering other life history characteristics of native fishes (e.g., predator-prey interactions)
through physio-chemical changes (Starrett 1951; Mendelson 1975; Miner and Stein 1993; 1996; Bonner and Wilde 2002). Fishes that have evolved specific morphological adaptations yielding success in rivers with highly variable flow, high turbidity, and that are subjected to temperature extremes (obligate riverine fishes) have been replaced by or have become numerically inferior to species adapted to less dynamic conditions (habitat generalist fishes) (Anderson et al. 1983; Cross and Moss 1987; Pflieger and Grace 1987; Moss and Mayes 1993).

Decreased flow, and subsequent loss of habitat, is perhaps the most significant source of impact upon obligate riverine fishes which require the river for all aspects of their life history (Holden 1979; Cumming 2004). Accordingly, as the demand for water increases with human population size, the hydrology of major rivers will change as well. The purpose of this thesis is to compare recent and historical data for fish assemblages in portions of the Brazos, Sabine, and San Antonio Rivers and provide pertinent information about specific life-history characteristics of native and non-native larval and juvenile fishes in the Rio Grande in order to provide greater insight for species conservation policy by state and federal agencies. To perform these separate assessments, an extensive set of fish assemblage data was collected and analyzed to determine the extent to which changes in hydrology have affected fish population structure; chronological similarity within each drainage among time periods and assemblage trajectory was also measured. Individual species population trends and trophic and reproductive guild changes were determined chronologically. Rio Grande larval and juvenile fishes were collected across myriad habitats in Big Bend National Park to assess the relationship between fish assemblage structure and habitat utilization. Habitat associations were determined
among discrete geomorphic units for each species, and diet analysis was performed for all species collected. Similarity of diet among individual species and geomorphic units was measured.

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## CHAPTER II

# FISH ASSEMBLAGE CHANGES IN WESTERN GULF SLOPE DRAINAGES: AN HISTORICAL PERSPECTIVE 


#### Abstract

Hydrologic alteration from impoundments and dewatering have modified ichthyofaunal habitat in western gulf slope drainages. Historical and recent fish assemblage data for the lower Brazos River, lower Sabine River, and lower San Antonio River were compiled to assess potential impacts within these drainages. These data compared with respective hydrologic data were used to determine fish species population status. The Brazos River has sustained the greatest hydrologic alteration due to numerous impoundments in its middle reach. The Sabine River and San Antonio River have been moderately altered via Toledo Bend Reservoir and channelization (and subterranean diversion) in downtown San Antonio respectively. Population trend analysis indicated that some obligate riverine fishes declined in the lower Brazos River (i.e., $N$. oxyrhynchus and $N$. potteri), and $N$. buccula suffered extirpation. However, habitat generalist fishes increased (i.e., Cyprinella lutrensis and Pimephales vigilax). The lower Sabine River analysis indicated a decline in obligate riverine fishes (i.e., Macrhybopsis hyostoma and N. buchanani), and extirpation (C. lutrensis) and decline ( $P$. vigilax and Gambusia affinis) of habitat generalist species. The lower San Antonio River fish assemblage was relatively stable with exception of 3 increasing species (Campostoma anomalum,


Lepomis cyanellus, and L. megalotis). Non-indigenous species were uncommon except in the lower San Antonio River ( $31 \%$; $\mathrm{N}=17$ ); some species sustained high relative abundance. Trophic guild analyses indicated that invertivores composed the majority of fish fauna in each drainage. Invertivores increased in the lower Sabine River yet decreased in the lower San Antonio River. Detritivores decreased among all drainages. Omnivores increased in the lower Brazos River and lower San Antonio River whereas they declined in the lower Sabine River. Reproductive analyses suggest a decrease of pelagophilic and lithopelagophilic fishes in the lower Brazos River and lower Sabine River whereas brood-hiding speleophils, nest-spawning speleophils, or both increased in all three drainages. Viviparous fishes decreased in the lower San Antonio River due to the decline of G. affinis.

## INTRODUCTION

Anthropogenic impacts on rivers and streams directly and indirectly affect aquatic fauna (Hughes et al. 2005). These impacts alter tiered abiotic and biotic factors that determine faunal distribution, composition, abundance, and life history of fishes by limiting habitat components or by modifying biotic interactions (Deacon et al. 1979; Schlosser 1991; Daniels et al. 2005). Consequently, anthropogenic impacts on fishes worldwide range from moderate to severe (Anderson et al. 1983; Rutherford et al. 1987; Warren and Burr 1994; Tallman et al. 2005a; 2005b) and will likely continue and become more severe as the demand for surface waters for hydropower and recreation and surface and subsurface waters for municipal use increase (Baxter and Glaude 1980; Gore and Shields 1995; Collier et al. 1996; Poff et al. 1997).

The degree of change in fish assemblage composition and abundance has been used in studies examining anthropogenic impact on fishes (Pflieger and Grace 1987; Martinez et al. 1994; Anderson et al. 1995; Bonner and Wilde 2000; Edwards 2001; Contreras-Balderas et al. 2002). However, fish assemblages do not respond consistently across impact gradients because of local and regional differences in lotic environments and zoogeographical influences. Nevertheless, greater understanding of interrelationships between fish assemblage change and anthropogenic impacts is needed to assist aquatic resource management as future water demands increase (Clark 1973; Schlosser 1991; 1995; Anderson et al. 1995; Quinn and Kwak 2003).

The purpose of this study was to quantify fish assemblage changes in three riverine environments in Texas (lower Brazos River, lower Sabine River, and lower San Antonio River). These rivers represent gulf slope drainages west of the Mississippi River
drainage that collectively share similar geological histories and ichthyofauna (Conner and Suttkus 1987) but differ along precipitation and anthropogenic impact gradients (e.g., reduced discharge). Additionally, we analyzed stream flow records in these watersheds to describe relationships among hydrologic alterations, fish assemblage changes, and specific fish population changes.

## STUDY AREAS

The Brazos River watershed is $116,000 \mathrm{~km}^{2}$ and is among the most modified rivers in Texas (Anderson et al. 1983) at least in the middle reach between Possum Kingdom Reservoir and Lake Waco. The river and its tributaries compose the largest drainage basin in the state. Headwaters of the Brazos River originate near the city of Lubbock in northwest Texas. Seventeen impoundments with a total water capacity of more than 60 million $\mathrm{m}^{3}$ impede the Brazos River and tributary flow on its southeast course through the state (Osting et al. 2004), which is approximately 1,300 river km in length. I limited the scope of this assessment to the lower Brazos River, the section of river downstream from Brazos Lake Dam to the zone of tidal influence influenced by the Gulf of Mexico.

The Sabine River watershed is $18,000 \mathrm{~km}^{2}$, originating in northeast Texas and forming the border between Louisiana and Texas beginning at the northern end of Toledo Bend Reservoir. This reservoir is the largest impediment to river flow, and its dam supports a hydropower facility. Daily river flow fluctuates greatly downstream of the dam due to pulse releases for peak power generation; river depth may increase by one to four meters (Seidensticker 1980). Downstream from Toledo Bend Dam, the lower Sabine River passes through pine forest and agricultural land as it flows southward. Sand and compressed clay compose the substrate providing opportunity for geomorphic change (i.e. riffles and pools). The Sabine River flows for 645 km from the outfall of Lake Tawakoni to the Gulf of Mexico. I limited the scope of this assessment to the lower Sabine River, the section of river downstream from Toledo Dam to the tidal influence in the Sabine River.

The San Antonio River watershed is $11,000 \mathrm{~km}^{2}$ and originates in San Antonio as it emerges from the Edwards Aquifer. Anthropogenic impact on the river began as early as 1718 (Fisher 1997) with the first diversions of water for municipal use. Headwaters are now channelized through the downtown portion and through an underground bypass used for flood mitigation; base flow is maintained by pumping. The San Antonio River flows for approximately 615 km to its confluence with the Guadalupe River near the Gulf of Mexico. I limited the scope of this assessment to the lower San Antonio River, the section of river downstream from Loop 410 near the City of San Antonio (TX) to its confluence with the Guadalupe River.

## MATERIALS AND METHODS

Daily discharge records were obtained from U.S. Geological Survey gauging stations on the lower Brazos River (Waco, USGS 08096500; Richmond, USGS 08114000), lower Sabine River (Logansport LA, USGS 08022500, Burkeville TX, USGS 08026000; Ruliff TX, USGS 08030500) and lower San Antonio (Falls City, USGS 08183500; Goliad, USGS 08188500). These particular gauging stations were selected because they encompassed the greatest spatial and temporal patterns in hydrologic regime in each river. Discharge records for each site were divided into two time periods, earliest record - 1969 and $1970-2006$, to assess temporal changes in discharge within watersheds; earlier time period generally represents river discharge before major alterations (i.e., water withdrawals and reservoir filling). Earliest record was 1900 (lower Brazos River at Waco), 1955 (lower Sabine River at Burkeville), and 1925 (lower San Antonio River at Falls City). To extend the Burkeville station to an earlier time, discharge records from Logansport (1907-1969; located 100 km upstream) were used as a surrogate to infer changes in discharge downstream from Toledo Bend Dam at Burkeville.

Daily discharge data were analyzed with Indicators of Hydrologic Alteration, v. 7.0 .3 (IHA) to determine changes in number of small and large flood events and mean annual discharge. The IHA software package uses daily stream-flow data to determine a multitude of hydrologic parameters based on specified analysis metrics. Number of flood events and mean annual discharge are two of 33 parameters generated by IHA to quantify hydrologic changes through time. I selected only number of flood events and mean annual discharge to represent hydrologic changes because of their relevancy to habitat
availability and variability for fishes and to maintenance of stream morphology (Richter et al. 1996). High flow pulses were defined as all flows that exceeded 75\% of flows for the period. Small floods were defined as high flow events with recurrence time of at least 2 years; large floods had a recurrence time of at least 10 years. The water year was defined as the calendar year.

An extensive set of fish assemblage data was collected to determine the extent to which changes in hydrology have affected fish population. Fish collection records were acquired from museum records, published and unpublished data, and agency reports. Records were-compiled by location and date within each drainage. Museum records used herein were obtained from Texas Cooperative Wildlife Collection at Texas A\&M University, Texas Natural History Collection at University of Texas, Tulane Museum of Natural History, and the University of Kansas Natural History Collection. Unpublished data were taken from C. Williams and T. Bonner (Texas State University), G. Wilde and T. Bonner (Texas Tech University), and J. Rosendale (U.S. Geological Survey). Published data and agency reports used for assemblage data include TPWD (1963; 1964; 1965), Wenger (1969); Austin et al. (1975); Dames and Moore (1975); Seidensticker (1980); Twidwell (1985); Moss and Mayes (1993); Whiteside et al. (1993); Linam et al. (1994); Whiteside et al. (1995); Gonzales and Moran (1996); Findeisen (1997); Longley et al. (1998); Winemiller et al. (2000); Li (2003); Winemiller et al. (2004); Gonzales and Moran (2005); San Antonio River Authority (2006); TPWD (2006). Main stem and tributary fish collection records were acquired, but only records of main stem fish assemblages were used to assess temporal changes. Tributary fish collection records were insufficient to assess temporal changes. Native and non-native status was
determined by drainage using the collection accounts of Douglas (1974), Hubbs et al. (1991), and Fuller et al. (1999).

All records were used to document fish occurrence whereas a subset of records were used to quantify fish abundance after passing through a series of filters. For occurrence and abundance records, questionable identifications (i.e., fishes reported outside of their reported range) were verified or refuted if voucher specimens existed. If vouchers did not exist, questionable identifications were deleted if not within the range of published distributions or re-identified as a closely related species native to the drainage (i.e., Notropis amabilis changed to Notropis atherinoides in the lower Sabine River). Collections also were omitted from abundance calculations if they did not represent a natural fish assemblage and were taken purely for voucher purposes (i.e., one or two individuals for 15-20 taxa per collection).

For abundance records, we attempted to standardize comparisons through time by collection method, but collection methods were not consistent within drainage or among time periods. Fish were taken from the lower Brazos River by seining and electroshocking, but seining was the more common technique used among collections, and therefore I only used data from collections that sampled by seining to calculate relative abundance. Seining and electroshocking techniques were used frequently in the lower Sabine River and lower San Antonio River, thus I used fish captured by both techniques to calculate relative abundance.

Relative abundance was assessed by two methods. First, relative abundances were calculated for each collection and plotted through time by species. Rare fishes, those that occurred in $<10 \%$ of the total collections within each drainage, were eliminated
from further analyses and population trend assessment except for taxa of conservation concern (i.e., Notropis buccula, Macrhybopsis marconis). Population status of rare fishes was identified as indeterminable. Among the remaining taxa, we used linear leastsquares regression (Neter et al. 1996) to model relative abundance of each species as a function of time. Relative abundance, the dependent variable, was $\log _{10}(n+1)$ transformed, and time, the independent variable, was $\log _{10}$ transformed. Time was represented as the numbers of days from January 1 of the year with the earliest collection record. For example, the earliest record in the lower Brazos River was taken in 1939. Consequently, January 1, 1939 was labeled as " 1 ", January 1, 1949 was labeled as " 3,654 ", and so on until all collection dates were assigned a number. From the results of the linear regression, I classified populations as increasing, decreasing, or stable based on significance level of positive and negative slopes. Here, I defined increasing status as significant $(\alpha=0.05)$ increases in relative abundance through time, decreasing status as significant $(\alpha=0.05)$ decreases in relative abundance through time, stable as nonsignificant ( $\alpha>0.05$ ) slopes through time.

Second, mean relative abundance was calculated by species ([sum of relative abundance in each collection / number of collections]*100) for three periods in the lower Brazos River (Period I: 1939-1969; Period II: 1970-1994; Period III: 1995-2006), two periods in the lower Sabine River (Period I: 1948-1969; Period II: 1970-2006), and two periods in the lower San Antonio River (Period I: 1950 - 1969; Period II: 1970 - 2006). As with the hydrologic assessment, time periods were assumed to reflect minimum (i.e., Period I) and maximum (i.e. Period II or III) anthropogenic alterations with period termination corresponding to the completion date of mainstem or large
tributary reservoirs within each watershed (Texas Almanac 2006). Temporal fish collections were ample for the lower Brazos River so an additional time period (Period III) was added. Taxa richness $(S)$ and Simpson's Diversity indices (1-D) were calculated for each period. Similarity matrices (Bray and Curtis 1957) were derived from mean relative abundance and tested with analysis of similarity (ANOSIM; $\alpha=0.05$; 9,999 permutations) within each watershed and among time periods using PRIMER 6.1.6 (Clarke 1993; Clarke and Warwick 2001); permutation analysis indicated the average rank dissimilarity within and between samples (Clarke and Gorley 2006). Data were fourth-root transformed to down-weight taxa with high relative abundance and increase the contribution of rare taxa (Clarke and Green 1988). Multi-dimension scaling (MDS) plots were generated to illustrate dissimilarity of fish assemblage among periods. Trajectory plots were created using mean values for Axes I and II from MDS in 5-year increments.

Relative abundances of trophic and reproduction guilds were calculated from the groomed subset of fish records. Species were assigned to trophic guilds using the classification scheme defined by Goldstein and Simon (1999) and to reproductive guilds using the classification scheme defined by Simon (1999). Literature sources for diet and feeding information were Moss and Mayes (1993), Goldstein and Simon (1999), Linam et al. (2002), Tamaru et al. (2001), Boschung and Mayden (2004), Hoover et al. (2004), and C. Williams, T. Bonner, and J. Perkin (Texas State University-San Marcos, unpublished data). Literature sources for reproductive information were Fryer and Iles (1972), Pflieger (1975), Moyle (1976), Boyer et al. (1977), Itzkowitz and Nyby (1982), Martin (1986), Sublette (1990), Heins and Machado (1993), Moss and Mayes (1993),

DeWoody et al. (1998), Platania and Altenbach (1998), Marks (1999), Simon (1999), Ross (2001), and Boschung and Mayden (2004). Guild relative abundances were calculated ([sum of individuals per guild in time period / total individuals in time period]*100) across sites and time periods. Changes in guild abundances through time were assessed within each watershed and explained by changes in fish abundance among periods. Consequently, relative abundance changes in guilds and fish among periods, which provide course assessments of temporal changes, are likely not to correspond with increasing or decreasing populations as classified with linear regression.

## RESULTS

## Hydrologic changes

Comparative analysis of the historical (1900-1969) and current (1970-2006) periods indicated that the degree of hydrologic alterations varied among and within watersheds. In upper portions of the lower Brazos River near Waco (TX), annual frequency of small ( $>1,046 \mathrm{~m}^{3} / \mathrm{s}$ ) and large ( $>2,995 \mathrm{~m}^{3} / \mathrm{s}$ ) flood events decreased from 0.57 (40 events; 1900 - 1969) to 0.03 ( 1 event; 1970 - 2006), and mean annual discharge decreased from 71 to $58 \mathrm{~m}^{3} / \mathrm{s}$ (Figure 2.1). In the lower portion of the lower Brazos River near Richmond (TX), annual frequency of small ( $>1634 \mathrm{~m}^{3} / \mathrm{s}$ ) and large ( $>2,631$ $\mathrm{m}^{3} / \mathrm{s}$ ) flood events decreased from 0.58 ( 28 events; 1922 - 1969) to 0.44 ( 16 events; 1970 - 2006) whereas the mean annual discharge increased from 204 to $222 \mathrm{~m}^{3} / \mathrm{s}$.

In upper portions of the lower Sabine River near Logansport (LA) and Burkeville (TX), annual frequency of small ( $>788 \mathrm{~m}^{3} / \mathrm{s}$, Logansport; $>833 \mathrm{~m}^{3} / \mathrm{s}$, Burkeville) and large $\left(1,154 \mathrm{~m}^{3} / \mathrm{s}\right.$, Logansport; $1,332 \mathrm{~m}^{3} / \mathrm{s}$, Burkeville) flood events were similar ( $0.42,28$ events, 1903 - 1969; 0.44, 16 events, 1970 - 2006) between periods of record (Figure 2.2). Mean annual discharge increased from 92 (Logansport) and 121 (Burkeville) to 166 $\mathrm{m}^{3} / \mathrm{s}$ at Burkeville. In lower portions of the lower Sabine River, annual frequency of small ( $>1,365 \mathrm{~m}^{3} / \mathrm{s}$ ) and large ( $>2,080 \mathrm{~m}^{3} / \mathrm{s}$ ) flood events decreased from 0.37 ( 17 events; $1925-1969$ ) to 0.27 (10 events; 1970 - 2006). Mean annual discharge increased from 230 to $240 \mathrm{~m}^{3} / \mathrm{s}$. Annual discharge hydrographs obscured changes in daily discharge patterns, which are notable in the lower Sabine River. Toledo Bend Dam releases water for hydropower power generation, producing discharges varying up to $75 \mathrm{~m}^{3} / \mathrm{s}$ per day or
up to $100 \mathrm{~m}^{3} / \mathrm{s}$ during a 5 -day period (representative sample: July through September 2000, Burkeville).

Discharge was substantially less in the lower San Antonio River than in the lower Brazos River or lower Sabine River because of San Antonio River location in more arid regions and because of its smaller drainage basin. In upper portions of the lower San Antonio River near Falls City (TX), annual frequency of small ( $>254 \mathrm{~m}^{3} / \mathrm{s}$ ) and large ( $>436 \mathrm{~m}^{3} / \mathrm{s}$ ) flood events increased from 0.22 (10 events; 1925 - 1969) to 0.31 (11 events; 1970 - 2006), and mean annual discharge increased from 9 to $20 \mathrm{~m}^{3} / \mathrm{s}$ (Figure 2.3). In lower portions of the lower San Antonio River near Goliad (TX), frequency of small ( $>404 \mathrm{~m}^{3} / \mathrm{s}$ ) and large ( $>842 \mathrm{~m}^{3} / \mathrm{s}$ ) flood events were similar ( $0.27,8$ events, 1939 1969; 0.25, 9 events, 1970 - 2006) between periods of record whereas mean annual discharge increased from 15 to $28 \mathrm{~m}^{3} / \mathrm{s}$.

## Fish assemblage changes

Sixty-seven species and 118 collections were taken from the lower Brazos River from 1939 through 2006 (Table 2.1). Cyprinidae was the most abundant family (94\%), followed by Poeciliidae (2.0\%), Ictaluridae (1.1\%), Clupeidae (0.9\%), and Centrarchidae (0.7\%). Among marine-derived taxa, Mugil curema and Alosa chrysochloris were not considered significant freshwater components of the assemblage. Seven species were non-native and composed $<0.1 \%$ of the total fish assemblage. Taxa richness increased among Period I ( $S=43$ ), Period II $(S=55)$, and Period III $(S=60)$, primarily attributed to increases in collection effort and number of individuals collected among periods. Diversity was similar between Period I (1-D=0.73) and Period II (1-D=0.75) but decreased by Period III (1-D=0.56). Overall, fish assemblage similarity differed
(ANOSIM global $\mathrm{R}=0.49, \mathrm{P}<0.01$ ) among periods; MDS trajectory indicated a shift along Axis I (Figure 2.4). Bray Curtis Similarity indices were $74 \%$ between Period I and Period II, $77 \%$ between Periods II and III, and $63 \%$ between periods I and III.

Lower Brazos River fish assemblage dissimilarities among periods were attributed in part to notable changes in relative abundance for 12 species (Figure 2.5). Eight species had declining population trends: Notropis buccula, Notropis oxyrhynchus, Notropis potteri, Carpiodes carpio, Ictalurus punctatus, Lepomis gulosus, Pomoxis annularis, and Aplodinotus grunniens. Collectively, these fishes represented $>62 \%$ of the lower Brazos River fish assemblage in Period I and $<2 \%$ in Period III. Four species had increasing population trends: Cyprinella lutrensis, Notropis buchanani, Pimephales vigilax, and Gambusia affinis. Collectively, these fishes represented $<18 \%$ of the lower Brazos River fish assemblage in Period I and $>86 \%$ in Period III. About $80 \%$ of the Period III fish assemblage consisted of Cyprinella lutrensis and Pimephales vigilax. Population trends for the remaining 55 species taken from the lower Brazos River were either stable $(N=39)$ or indeterminable ( $N=16$ ).

Ninety species and 183 collections were taken from the lower Sabine River from 1948 through 2006 (Table 2.2). Cyprinidae was the most abundant family (93\%), followed by Centrarchidae ( $2.2 \%$ ), Poeciliidae (1.4\%), Ictaluridae ( $0.8 \%$ ), and Percidae (0.7\%). Among marine-derived taxa, nine fishes (i.e., Elops saurus, Alosa chrysochloris, Brevoortia patronus, Anchoa mitchilli, Ariopsis felis, Strongylura marina, Mugil curema, Paralichthys lethostigma, and Trinectes maculatus) were not considered a significant freshwater component of the assemblage. Four species were non-native and composed $<0.1 \%$ of the total fish assemblage in Period I or II. Taxa richness was higher in Period I
( $S=75$ ) than in Period II $(S=70)$ whereas collection effort and number of individuals collected were greater in Period II than in Period I. Diversity was higher ( $1-D=0.84$ ) in Period I than in Period II ( $1-D=0.78$ ). Fish assemblage similarity differed (ANOSIM global $\mathrm{R}=0.16, \mathrm{P}<0.01$ ) between periods; MDS trajectory indicated a shift along Axis II (Figure 2.4). Bray Curtis Similarity Index was 74\% between Period I and Period II.

Lower Sabine River fish assemblage dissimilarity between periods was attributed in part to the large number taxa unique to either Period $\mathrm{I}(N=16)$ or Period II $(N=12)$ and to changes in relative abundance of 17 species (Figure 2.6; 2.7). Collective relative abundances of unique taxa were $<2 \%$ in Period I and $<0.1 \%$ in Period II, suggesting rare natural occurrence of 28 unique taxa. Consequently, their detection in either time period was likely haphazard and not associated with species distribution expansions or extirpations. Nine species had declining population trends: Cyprinella lutrensis, Hybognathus nuchalis, Macrhybopsis hyostoma, Notropis atherinoides, Notropis buchanani, Pimephales vigilax, Aphredoderus sayanus, Gambusia affinis, and Lepomis gulosus. Eight species had increasing population trends: Cyprinella venusta, Fundulus olivaceus, Menidia beryllina, Lepomis macrochirus, Lepomis megalotis, Micropterus punctulatus, Ammocrypta vivax, and Percina sciera. Notable population changes included the apparent extirpation of Cyprinella lutrensis by 1973, population decline in Notropis atherinoides from a maximum relative abundance of $40 \%$ before 1969 to <1\% after 1969, population decline in Notropis buchanani from a maximum relative abundance of $23 \%$ before 1969 to $6 \%$ after 1969, and a population increase in Cyprinella venusta from a relative abundance maximum of 54\% before 1969 to 83\%
relative abundance in 2006. Population trends for the remaining 73 species taken from the lower Sabine River were either stable $(N=23)$ or indeterminable $(N=50)$.

Fifty-seven species and 73 collections were taken from the lower San Antonio River from 1950 through 2006 (Table 2.3). Cyprinidae was the most abundant family (62\%), followed by Poeciliidae (21\%), Ictaluridae (9.4\%), Centrarchidae (2.7\%), and Cichlidae ( $2.2 \%$ ). Seventeen species were non-native and composed $11 \%$ of the total fish assemblage. Taxa richness was lower in Period I $(S=23)$ than in Period II $(S=55)$ as were collection effort and number of individuals collected. Diversity was lower (1-D= 0.62 ) in Period I than in Period II ( $1-D=0.80$ ). Overall, fish assemblage similarity was not different (ANOSIM global $\mathrm{R}=0.12, \mathrm{P}=0.072 ;$ Fig. 4) between periods although Bray Curtis Similarity index was $47 \%$ between Period I and Period II. Multi-dimensional scaling trajectory indicated that little change occurred between the earliest and latest collections (Figure 2.4).

Failure to detect between period differences in the lower San Antonio River fish assemblage was likely a result of low collection effort in Period I. Nevertheless, notable changes in occurrence and abundance were found for several fishes or groups of fishes (Figure 2.7). The number of non-native taxa increased from 4 in Period I to 17 in Period II. Native taxa with increasing population trends were Campostoma anomalum, Lepomis cyanellus, and Lepomis megalotis whereas Opsopoeodus emiliae and Gambusia affinis declined. Population trends for the remaining 52 native species taken from the lower San Antonio River were either stable $(N=18)$ or indeterminable ( $N=34$ ).

## Guild Changes

Trophic structure changed in all three drainages among periods; however, changes were not consistent among drainages or periods except for the decline of detritivores (Table 2.4). Detritivore abundance decreased in the three drainages among periods. Decreases were related to population declines in Carpiodes carpio in the lower Brazos River, Hybognathus nuchalis in the lower Sabine River, and Opsopoeodus emiliae in the lower San Antonio River. Omnivore abundance increased in the lower Brazos River, related primarily to population increase in Pimephales vigilax, and in the lower San Antonio River, related to population increases in Pimephales vigilax and Poecilia latipinna, whereas omnivore abundance decreased in the lower Sabine River, related to population decrease in Pimephales vigilax. Invertivore abundance, the most common trophic guild across drainages, decreased in the lower San Antonio River (related to fewer Gambusia affinis taken in Period II) and increased in the lower Sabine River (related to the population increase in Cyprinella venusta), yet was remained constant in the lower Brazos River. Piscivore abundance decreased in the lower Brazos River, related to population decreases in Notropis potteri and Pomoxis annularis, but increased in the lower San Antonio River. However, the increase in the lower San Antonio River piscivore abundance was not attributed to fish assemblage change, but rather to the detection of several native piscivores (Lepisosteus and Micropterus) only during Period II. Herbivore abundance increased in the San Antonio River, related to population increases of Dorosoma cepedianum and Campostoma anomalum. Planktivore abundance decreased in the Sabine River, related to population decreases in Notropis atherinoides and to the lack of collection of Brevoortia patronus during Period II.

As with trophic guilds, shifts in reproductive guilds were not consistent among drainages (Table 2.4). Reproductive guilds with greatest shifts in relative abundance were speleophils, both brood hiders and nest spawners, and open substrate pelagophils. Speleophil abundance increased in the lower Brazos River, lower Sabine River, and lower San Antonio River, related to population increases of Cyprinella lutrensis (brood hider) and Pimephales vigilax (nest spawner) in the lower Brazos River, Cyprinella venusta (brood hider) in the lower Sabine River, and catfishes (native and exotic; nests spawner) in the lower San Antonio River. Pelagophil abundance decreased in the lower Brazos River, related to population declines in Notropis buccula, Notropis oxyrhynchus, Notropis potteri, Carpiodes carpio, and Aplodinotus grunniens. Additional shifts in reproductive guild abundance were found (i.e., decrease in viviparous fishes due to decline of Gambusia affinis in the lower San Antonio River), but not all of these were attributed to population declines. They were instead attributed to abundance differences through time among stable populations.

## DISCUSSION

Fish occurrence (i.e., taxa richness), assemblage structure (i.e., relative proportions by families) and function (i.e., measured here as trophic and reproductive guilds) remained fairly intact within all drainages, despite changes in some populations through time. Taxa richness generally increased, but increases were generally associated with capture of native taxa with greater sampling efforts in recent periods rather than associated with non-native fish introductions. Cyprinidae historically and currently was the most abundant family in the lower Brazos River (94\%), lower Sabine River (93\%) and lower San Antonio River (62\%). Consequently, trophic structure historically and currently was dominated by invertivores. Other families of fishes and trophic guilds persisted with few exceptions (i.e., detritivores declined) through time. Although the study reaches represented a small portion of the western gulf slope drainages, these three study reaches encompassed fairly broad ranges in geography, precipitation, and anthropogenic impacts, yet they collectively indicated and inferred a prevalence of relatively intact fish assemblages at least in lower reaches of gulf slope watersheds. This is in contrast to other watersheds and rivers throughout the USA, where an estimated $81 \%$ of water bodies are negatively affected by anthropogenic modifications (Judy et al. 1984), $>70 \%$ of wadeable streams and non-wadeable rivers are in sub-optimal condition in eastern Atlantic slope drainages (USEPA 2003; Hughes et al. 2005), and nonindigenous fishes and cosmopolitan sportfishes introductions are contributing to largescale fish assemblage homogenizations (Rahel 2002). Nevertheless, apparent extirpations were found in two of the river reaches: two obligate riverine fishes (Notropis buccula and Hybognathus placitus) in the lower Brazos River, and five marine fishes and
perhaps Cyprinella lutrensis in the lower Sabine River. Among these, the apparent extirpation of $N$. buccula in the lower Brazos River is significant from a species conservation perspective. Notropis buccula is a Brazos River endemic and now restricted to the upper reaches of the Brazos River in west Texas. It is presently a candidate for listing under the Endangered Species Act (USFWS 2006).

Statistically significant shifts in fish assemblages were attributed primarily to changes in species abundance through time. Among all drainages and excluding extirpated fishes, 17 historically abundant fishes became rare whereas 14 historically rare fishes became common or abundant. Abundance declines in Brazos River endemic Notropis oxyrhynchus (another candidate for listing under the Endangered Species Act) and Notropis potteri (endemic to the Brazos River and Red River) are ecologically important from a species conservation perspective. These fishes along with Notropis buccula, Hybognathus placitus, Carpiodes carpio, and Aplodinotus grunniens in the lower Brazos River and Notropis atherinoides and Notropis buchanani in the lower Sabine River comprised $64 \%$ of the extirpated or declining taxa and are pelagophilic or lithopelagophilic open substrate spawners. However, one population of pelagophilic spawners (Notropis buchanani in the lower Brazos River) increased in abundance through time. Others with large abundance increases included Cyprinella lutrensis and Pimephales vigilax in the lower Brazos River and Cyprinella venusta in the lower Sabine River, which all are speleophils, although Cyprinella lutrensis apparently was extirpated in the lower Sabine River.

Linkages among hydrologic alterations, species extirpations or population declines, and reproductive strategy of open substrate spawning are well established for
prairie streams and large rivers in the central USA. Stream fishes such as most species in the genera Notropis, Macrhybopsis, and Hybognathus broadcast spawn semi-buoyant eggs that disperse downstream (Moore 1944; Lehtinen and Layzer 1988; Bestgen et al, 1989; Taylor and Miller 1990; Platania and Altenbach 1998). After drifting for several days, larvae move out of the currents, seeking refuge in offchannel, slack water, or backwater habitats (Platania and Altenbach 1998; Porter and Massong 2004). These fishes eventually migrate upstream for spawning (Cross et al. 1985). Duration and distance of upstream migration likely are species specific (Bonner 2000). The broadcast spawning strategy is an adaptation to variable riverine environments with fluctuating stream flows and substantial sediment deposition, which reduces success of eggs spawned in nests or crevices (i.e., speleophils) (Platania and Altenbach 1998). Dams, channel dewatering, and associated hydrological changes disrupt this reproductive cycle and upstream migration on multiple levels. Dams block potamodromous migration routes and downstream dispersal (Cross et al. 1985; Wilde and Ostrand 1999; Bonner 2000) and alter stream flows needed for successful rearing of larvae (Durham and Wilde 2006). Likewise, altered stream flows (i.e., fewer small and large flood events, timing and duration of floods) affect physical (i.e., geomorphology, turbidity) and chemical conditions of the riverine environment (Baxter 1977; Stanford and Ward 1979; Bonner and Wilde 2002). Numerous broadcast spawning fishes and other obligate riverine fishes have consequently declined in abundance or have been extirpated (Cross et al. 1985; Cross and Moss 1987; Larson et al. 1991; Limbird 1993; Bonner and Wilde 2000), whereas speleophils, such as Cyprinella lutrensis, have increased in abundance because of less variable flows that benefit their reproduction and that minimize downstream
displacement of individuals (Minckley and Meffe 1987; Cross and Moss 1987; Larson 1991; Bonner and Wilde 2000).

Abundance changes in this study are consistent with species declines and replacements in prairie streams and large rivers of central USA. Pelagophilic or lithopelagophilic open substrate spawners have decreased in abundance or have been extirpated likely due to dams and changes in flow regime that fragment riverine habitats (i.e., source-sink relationships; Dunning et al. 1992), alter available habitats (i.e., turbidity), impact reproductive success, or facilitate speleophil abundance, which in turn affects biotic interactions with open substrate spawners (Pflieger and Grace 1987; Scott and Helfman 2001). Not all open substrate spawners are affected, as with Macrhybopsis, likely because of species-specific adaptations in life history patterns. Apparent extirpations of speleophils Cyprinella lutrensis was surprising given that this species is rarely reported as declining in abundance. Cyprinella lutrensis extirpation in the lower Sabine River might be caused by fragmentation effects of Toledo Bend dam, eliminating upstream sources of downstream dispersants, or associated with flow alterations related to hydropower generation where flows fluctuate up to $100 \mathrm{~m}^{3} / \mathrm{s}$ within a few days.

Non-indigenous fishes represented only a minor component of the lower Brazos River and lower Sabine River fish assemblages in taxa richness and relative abundance, but a larger component in the lower San Antonio River where 17 species ( $31 \%$ of taxa) composed $13 \%$ of the relative abundance in recent collections. Edwards (2001) reported occurrence of nine of these non-indigenous species (Astyanax mexicanus, Hypostomus sp., Poecilia latipinna, P. formosa, Xiphophorus helleri, Cichlasoma cyanoguttatum, Oreochromis mossambicus, O. aureus, and Tilapia zillii) in the upper San Antonio River.

In contrast, Hubbs et al. (1978) reported only six non-indigenous species in the upper reach. Established populations of non-indigenous fishes in the upper portion of the San Antonio River likely will spread downstream with unknown ecological consequences; however, dispersion downstream beyond the influence of spring discharges was impeded in the winter of 2007 by cold temperatures that caused a major fish kill of tropical and semi-tropical non-indigenous fishes. Therefore, abundance and distribution of nonindigenous fishes might be regulated by natural means.

It is critical to note that assemblage composition and structure differed among drainages although our study streams and western gulf slope watersheds in general share a common geological history with numerous interconnections and physicochemical characteristics (Conner and Suttkus 1986). Taxa richness, number of basin endemics, pervasiveness of cyprinids ( $>90 \%$ ), and differences therein are shaped historically by factors such as proximity to adjacent species pools (i.e., Mississippi River drainage), precipitation and temperature gradients, drainage basin size, and flow rates. These collectively or independently regulate fish dispersion and extinctions, facilitate rates of endemism, and develop evolutionary relationships between fish and habitat. My analysis indicated that anthropogenic impacts can have varying effects on the resident fish assemblages depending on the type and uniqueness of the assemblage. For example, I consider lower Brazos River fish assemblage imperiled because of the number of endemic and semi-endemic forms that are decreasing in abundance. Yet, if we exclude consideration of these taxa (or they never existed), the lower Brazos River fish assemblage would appear exceptional because the majority of the fish assemblage is intact. The San Antonio River is the most anthropologically impacted system in this
study yet the fish assemblage showed the least change. This is likely because its relatively small drainage size and distance from Mississippian-type fishes precluded endemic taxa instead selecting a more generalist fish assemblage that is more adept to withstand flow alterations and water quality problems associated with highly urbanized watersheds.

Twenty-eight percent of fishes in the southern USA (Warren et al. 2000) and 38\% of Texas freshwater fishes considered imperiled, thus greater understanding of relationships between discharge and species, and assemblage sustainability is critical for proper management of water resources and native fishes. Anthropogenic impacts, on both local (i.e., dam) and watershed (i.e., urbanization, introduced taxa) scales, have altered the natural fish assemblage of the studied drainages; however, the ecological and biodiversity consequence of the impact depends on the fish assemblage and degree of endemism. Assemblage changes appear predictable and therefore likely avoidable with adequate planning and management. For example, several stream segments in Texas support a large number of diverse fish assemblages containing many of the Texas imperiled fishes such as Big Bend reach of the Rio Grande (Edwards et al. 2002), San Marcos River (Kelsey 1997), Independence Creek (Bonner et al. 2005), upper Brazos River (Hubbs et al. 1991), upper Red River (Hubbs et al. 1991), and Canadian River (Bonner and Wilde 2000). These streams have all been impacted at some level; however, future anthropogenic modifications should be minimized to maintain the high biodiversity each sustains. Alternatively, biologically unique assemblages that are already stressed (i.e., lower Brazos River) can be maintained and even restored by a suite of techniques that were developed, designed, and tested to balance water needs between
humans and the riverine community (Richter et al. 2003). The science of river ecology is slowly moving past basic research and understanding towards sustainable use management and riverine restoration, which imparts an optimistic future for water resource management.


Figure 2.1: Hydrographs of the Brazos River at Waco and Richmond, Texas USGS gauging stations.


Figure 2.2: Hydrographs of the Sabine River at Logansport, Louisiana and Burkeville and Ruliff, Texas USGS gauging stations.


Figure 2.3: Hydrographs of the lower San Antonio River at Falls City and Goliad, Texas USGS gauging stations.

Table 2.1: Relative abundance, population status, and reproduction and trophic guilds of fishes in the lower Brazos River, Texas. Status refers to native ( N ), non-indigenous ( I ), or present ( X ) during period but in an unused collection. Mean relative abundance is presented for Period I (1939-1969), Period II (1970-1994), and Period III (1995-2006). Population trend is indicated as increasing ( $\uparrow$ ), decreasing ( $\downarrow$ ), stable (S), or indeterminable ( - ). Reproductive guilds follow Simon (1999) classification scheme. Trophic guilds are detritivore (DT), herbivore (H), invertivore (IF), omnivore (O), piscivore (P), and planktivore (PL).

| Species | Status | Period I | Period II | Period III | Population Trend | Primary Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Atractosteus spatula* | N |  |  | <0.01 | - | Open Substrate | Phytophil | P |
| Lepisosteus oculatus | N | 0.55 | 0.51 | 0.02 | $\downarrow$ | Open Substrate | Phytophil | P |
| Lepisosteus osseus | N | 0.03 | 0.28 | 0.36 | S | Open Substrate | Phytolithophil | P |
| Amia calva | N |  | 0.03 | <0.01 | S | Nest Spawner | Phytophil | P |
| Anguilla rostrata ${ }^{* \dagger}$ | N | X |  |  | - | Catadromous | Catadromous | P |
| Alosa chrysochloris | N |  |  | 0.02 | - | Open Substrate | Phytolithophil | PL |
| Dorosoma cepedianum | N | 0.97 | 4 | 1 | S | Open Substrate | Lithopelagophil | H |
| Dorosoma petenense | N | 0.12 | 0.97 | 0.36 | S | Open Substrate | Phytophil | PL |
| Campostoma anomalum* | N |  |  | <0.01 | - | Brood Hider | Lithophil | H |
| Cyprinella lutrensis | N | 15 | 35 | 58 | $\uparrow$ | Brood Hider | Speleophil | IF |
| Cyprinella venusta | N | 0.04 | 0.14 | 0.58 | S | Brood Hider | Speleophil | IF |
| Cyprinus carpio | I | $<0.01$ | 0.20 | <0.01 | S | Open Substrate | Phytolithophil | O |
| Hybognathus nuchalis | N | 0.17 | 0.25 | 0.08 | S | Open Substrate | Lithopelagophil | DT |
| Hybognathus placitus | N | 0.02 | 0.24 |  | - | Open Substrate | Pelagophil | H |
| Hybopsis amnis | N | 0.01 | 0.07 | <0.01 | S | Open Substrate | Lithophil | IF |
| Lythrurus fumeus | N |  | 0.02 | 0.02 | S |  |  | IF |
| Macrhybopsis hyostoma | N | 1 | 2 | 3 | S | Open Substrate | Pelagophil | IF |
| Macrhybopsis storeriana | N | 0.21 | 0.39 | 0.18 | S | Open Substrate | Lithopelagophil | IF |

Table 2.1 Continued

| Species | Status | Period I | Period II | Period III | Population <br> Status | Primary Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Notemigonus crysoleucas | N |  | 0.05 | $<0.01$ | S | Open Substrate | Phytophil | IF |
| Notropis buccula | N | 3 | 0.43 |  | $\downarrow$ | Open Substrate | Pelagophil | IF |
| Notropis buchanani | N | 1 | 0.90 | 5 | $\uparrow$ | Open Substrate | Pelagophil | IF |
| Notropis oxyrhynchus | N | 22 | 4 | 0.04 | $\downarrow$ | Open Substrate | Pelagophil | IF |
| Notropis potteri | N | 11 | 4 | 0.05 | $\downarrow$ | Open Substrate | Pelagophil | P |
| Notropis shumardi | N | 6 | 11 | 3 | S | Open Substrate | Pelagophil | IF |
| Notropis volucellus | N |  | 0.03 | 0.02 | S | Open Substrate | Phytophil | O |
| Opsopoeodus emiliae | N | 0.02 | 0.14 | 0.01 | S | Nest Spawner | Speleophil | DT |
| Pimephales promelas | I | X | <0.01 | <0.01 | S | Nest Spawner | Speleophil | O |
| Pimephales vigilax | N | 1 | 12 | 21 | $\uparrow$ | Nest Spawner | Speleophil | O |
| Carpiodes carpio | N | 4 | 6 | 0.57 | $\downarrow$ | Open Substrate | Lithopelagophil | DT |
| Ictiobus bubalus | N | 0.02 | 0.17 | 0.03 | S | Open Substrate | Lithopelagophil | O |
| Moxostoma congestum | N |  |  | <0.01 | - | Open Substrate | Lithophil | IF |
| Ameiurus melas | N |  |  | $<0.01$ | - | Nest Spawner | Speleophil | IF |
| Ameiurus natalis ${ }^{* \dagger}$ | N | X |  |  | - | Nest Spawner | Speleophil | IF |
| Ictalurus furcatus | N | 1 | 0.91 | 0.92 | S | Nest Spawner | Speleophil | P |
| Ictalurus punctatus | N | 17 | 6 | 0.62 | $\downarrow$ | Nest Spawner | Speleophil | O |
| Noturus gyrinus | N | 0.04 | 0.03 | 0.10 | S | Nest Spawner | Speleophil | IF |
| Pylodictis olivaris | N | 0.01 | 0.25 | 0.01 | S | Nest Spawner | Speleophil | IF |
| Aphredoderus sayanus | N | 0.29 | 0.04 | 0.02 | S | Bearer | Mouth brooder | IF |
| Fundulus notatus | N | 0.04 | $<0.01$ | 0.01 | S | Open Substrate | Phytophil | H |
| Fundulus olivaceus* | I | 4 |  |  | - | Open Substrate | Phytophil | IF |

Table 2.1 Continued

| Species | Status | $\begin{gathered} \text { Period } \\ \text { I } \\ \hline \end{gathered}$ | $\begin{gathered} \text { Period } \\ \text { II } \\ \hline \end{gathered}$ | $\begin{gathered} \text { Period } \\ \text { III } \\ \hline \end{gathered}$ | Population Status | Primary Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Cyprinodon variegatus* | N |  | 0.12 |  | - | Nest Spawner | Polyphil | O |
| Gambusia affinis | N | 0.24 | 5 | 3 | $\uparrow$ | Bearer | Viviparous | IF |
| Poecilia latipinna | N |  |  | 0.11 | - | Bearer | Viviparous | 0 |
| Labidesthes sicculus | I |  | 0.06 | 0.07 | S | Open Substrate | Phytolithophil | IF |
| Menidia beryllina | N |  | 0.05 | 0.15 | S | Open Substrate | Phytophil | IF |
| Morone chrysops | I |  | $<0.01$ | 0.06 | S | Open Substrate | Phytolithophil | P |
| Lepomis cyanellus | N | 0.05 | 0.35 | 0.10 | - | Nest Spawner | Polyphil | IF |
| Lepomis gulosus | N | 0.55 | 0.23 | 0.04 | $\downarrow$ | Nest Spawner | Lithophil | IF |
| Lepomis humilis | N | 0.13 | 0.88 | 0.14 | S | Nest Spawner | Lithophil | IF |
| Lepomis macrochirus | N | 0.30 | 0.50 | 0.12 | S | Nest Spawner | Polyphil | IF |
| Lepomis marginatus | N |  |  | <0.01 | - | Nest Spawner | Polyphil | IF |
| Lepomis megalotis | N | 0.19 | 0.69 | 0.15 | S | Nest Spawner | Polyphil | IF |
| Lepomis microlophus | N | $<0.01$ | 0.01 | 0.07 | S | Nest Spawner | Polyphil | IF |
| Lepomis miniatus | N | 2 | 0.27 | 0.02 | - | Nest Spawner | Polyphil | IF |
| Lepomis symmetricus | N | 0.53 |  | $<0.01$ | S | Nest Spawner | Polyphil | IF |
| Micropterus punctulatus | N |  | 0.05 | 0.06 | S | Nest Spawner | Polyphil | IF |
| Micropterus salmoides | N | 0.02 | 0.05 | 0.04 | S | Nest Spawner | Polyphil | P |
| Pomoxis annularis | N | 3 | 1 | 0.11 | $\downarrow$ | Nest Spawner | Phytophil | P |
| Pomoxis nigromaculatus | N |  | $<0.01$ | 0.02 | S | Nest Spawner | Phytophil | IF |
| Etheostoma chlorosomum | N | 0.76 | X | $<0.01$ | S | Substratum Chooser | Phytophil | IF |
| Etheostoma gracile | N | 0.17 | 0.07 | 0.02 | S | Substratum Chooser | Phytophil | IF |
| Percina caprodes | I |  | X | $<0.01$ | - | Brood Hider | Lithophil | IF |

Table 2.1 Continued

| Species | Status | Period I | $\begin{gathered} \text { Period } \\ \text { II } \end{gathered}$ | Period III | Population Status | Primary Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Percina sciera | N |  | 0.12 | 0.03 | S | Brood Hider | Lithophil | IF |
| Aplodinotus grunniens | N | 2 | 1 | 0.04 | $\downarrow$ | Open Substrate | Pelagophil | IF |
| Oreochromis aureus | I |  | 0.01 | <0.01 | S | Bearer | Mouth Brooder | O |
| Agonostomus monticola* | N |  | $<0.01$ |  | - | Catadromous |  | 0 |
| Mugil cephalus | N | 0.01 | 0.15 | 1 | S | Catadromous |  | DT |
| Mugil curema | N |  | $<0.01$ | $<0.01$ | S | Catadromous |  | O |
| Collections During Period: |  | 18 | 36 | 64 |  |  |  |  |
| Individuals Collected: |  | 7,259 | 28,807 | 257,782 |  |  |  |  |
| Taxa Richness: |  | 43 | 55 | 60 |  |  |  |  |
| Diversity: |  | 0.73 | 0.75 | 0.56 |  |  |  |  |

* Species represented by one collection.
$\dagger$ Species not used for richness and diversity.


Figure 2.4: Multi-dimensional scaling (MDS) plots and trajectories for the lower Brazos River, lower Sabine River, and lower San Antonio River. Data was standardized by relative abundance and fourth-root transformed for similarity matrices (Bray-Curtis). X's represent Period I, shaded circles Period II, and open circles Period III. Trajectory plots were created using mean values for Axes I and II from MDS in 5-year increments.


Figure 2.5: Relationship of $\log 10(n+1)$ relative abundance through time with linear least-squares regression and associated P-value for lower Brazos River fishes.

Table 2.2: Relative abundance, population status, and reproduction and trophic guilds of fishes in the lower Sabine River, Texas. Mean relative abundance is presented for Period I (1948-1969) and Period II (1970-2006). Abbreviations presented in Table 2.1.

| Species | Status | Period I | Period II | Population Trend | Primary <br> Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Ichthyomyzon castaneus | N | 0.08 | $<0.01$ | S | Brood Hider | Lithophil | Parasitic |
| Ichthyomyzon gagei ${ }^{\text {* }}$ | N |  | X | - | Brood Hider | Lithophil | PL |
| Atractosteus spatula ${ }^{* \dagger}$ | N | X |  | - | Open Substrate | Phytophil | P |
| Lepisosteus oculatus | N | $<0.01$ | 0.17 | S | Open Substrate | Phytophil | P |
| Lepisosteus osseus | N | 0.02 | $<0.01$ | S | Open Substrate | Phytolithophil | P |
| Amia calva | N |  | 0.13 | S | Nest Spawner | Phytophil | P |
| Elops saurus* | N |  | $<0.01$ | - | Anadromous | Anadromous |  |
| Alosa chrysochloris* | N | $<0.01$ |  | - | Anadromous | Anadromous | PL |
| Brevoortia patronus | N | 0.40 |  | - | Catadromous | Catadromous | PL |
| Dorosoma cepedianum | N | 0.20 | 0.37 | S | Open Substrate | Lithopelagophil | H |
| Dorosoma petenense | N | 0.19 | 0.60 | S | Open Substrate | Phytophil | PL |
| Anchoa mitchilli | N | 1 |  | - | Anadromous | Anadromous |  |
| Cyprinella lutrensis | N | 20 | 19 | $\downarrow$ | Brood Hider | Speleophil | IF |
| Cyprinella venusta | N | 15 | 41 | $\uparrow$ | Brood Hider | Speleophil | IF |
| Cyprinus carpio | I |  | 0.03 | - | Open Substrate | Phytolithophil | 0 |
| Hybognathus hayi* | N |  | $<0.01$ | - |  |  |  |
| Hybognathus nuchalis | N | 10 | 4 | $\downarrow$ | Open Substrate | Lithopelagophil | DT |
| Hybopsis amnis | N | 0.83 | 0.27 | S | Open Substrate | Lithophil | IF |
| Lythrurus fumeus | N | 0.08 | 0.10 | S |  |  |  |
| Lythrurus umbratilis | N | 0.02 |  | - | Open Substrate | Lithophil | IF |
| Macrhybopsis hyostoma | N | 0.79 | 0.09 | $\downarrow$ | Open Substrate | Pelagophil | IF |
| Notemigonus crysoleucas | N | 0.25 | 0.01 | - | Open Substrate | Phytophil | IF |

Table 2.2 Continued

| Species | Status | Period I | Period II | Population Status | Primary <br> Reproductive Guild | Secondary <br> Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Notropis atherinoides | N | 3 | 0.01 | $\downarrow$ | Open Substrate | Pelagophil | PL |
| Notropis atrocaudalis | N | 0.03 |  | - |  |  |  |
| Notropis blennius | I | 0.41 |  | - | Open Substrate | Pelagophil | IF |
| Notropis buchanani | N | 2 | 0.28 | $\downarrow$ | Open Substrate | Pelagophil | IF |
| Notropis sabinae | N | 7 | 8 | S | Open Substrate | Pelagophil | 0 |
| Notropis shumardi ${ }^{*}$ | N | 0.13 |  | - | Open Substrate | Pelagophil | IF |
| Notropis texanus | N | 4 | 3 | S |  |  | DT |
| Notropis volucellus | N | 4 | 3 | S | Open Substrate | Phytophil | O |
| Opsopoeodus emiliae | N | 0.34 | 0.31 | S | Nest Spawner | Speleophil | DT |
| Phenacobius mirabilis | N | 0.03 | 0.02 | S |  |  |  |
| Pimephales vigilax | N | 15 | 9 | $\downarrow$ | Nest Spawner | Speleophil | 0 |
| Semotilus atromaculatus ${ }^{*+}$ | N | X |  | - | Brood Hider | Lithophil | P |
| Carpiodes carpio | N | 0.26 | 0.32 | S | Open Substrate | Lithopelagophil | DT |
| Cycleptus elongatus* ${ }^{*}$ | N |  | X | - |  |  |  |
| Erimyzon oblongus | N | 0.07 | $<0.01$ | - | Open Substrate | Lithopelagophil | IF |
| Erimyzon sucetta* ${ }^{*+}$ | N |  | X | - | Open Substrate | Phytolithophil | IF |
| Ictiobus bubalus* | N | $<0.01$ |  | - | Open Substrate | Lithopelagophil | 0 |
| Minytrema melanops | N | 0.01 | 0.05 | S | Open Substrate | Lithopelagophil | IF |
| Moxostoma poecilurum | N | 0.02 | 0.11 | - | Open Substrate | Lithophil | IF |
| Ameiurus melas* | N | 0.04 |  | - | Nest Spawner | Speleophil | IF |
| Ameiurus natalis | N | 0.16 | $<0.01$ | - | Nest Spawner | Speleophil | IF |
| Ictalurus furcatus | N | $<0.01$ | $<0.01$ | - | Nest Spawner | Speleophil | P |
| Ictalurus punctatus | N | 2 | 0.60 | - | Nest Spawner | Speleophil | O |

Table 2.2 Continued

| Species | Status | Period I | Period II | Population Status | Primary <br> Reproductive Guild | Secondary <br> Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Noturus gyrinus* | N |  | $<0.01$ | - | Nest Spawner | Speleophil | IF |
| Noturus nocturnus | N | 0.02 | 0.03 | - | Nest Spawner | Speleophil | IF |
| Pylodictis olivaris | N | $<0.01$ | $<0.01$ | - | Nest Spawner | Speleophil | IF |
| Ariopsis felis* | N | 0.12 |  | - | Bearer | Mouth Brooder | O |
| Esox americanus | N | 0.05 | $<0.01$ | - | Open Substrate | Phytophil | P |
| Aphredoderus sayanus | N | 0.11 | $<0.01$ | $\downarrow$ | Bearer | Mouth Brooder | IF |
| Strongylura marina | N | <0.01 | 0.02 | - | Open Substrate | Phytolithophil | P |
| Fundulus chrysotus | N | 0.35 | $<0.01$ | - | Open Substrate | Phytophil | IF |
| Fundulus notatus | N | 0.60 | 0.29 | S | Open Substrate | Phytophil | H |
| Fundulus olivaceus | N | 0.02 | 0.23 | $\uparrow$ | Open Substrate | Phytophil | IF |
| Gambusia affinis | N | 4 | 1 | $\downarrow$ | Bearer | Viviparous | IF |
| Labidesthes sicculus | N | 0.34 | 0.31 | S | Open Substrate | Phytolithophil | IF |
| Menidia beryllina | N | 0.01 | 0.77 | $\uparrow$ | Open Substrate | Phytophil | IF |
| Morone mississippiensis | N |  | 0.03 | - | Open Substrate | Phytolithophil | IF |
| Centrarchus macropterus | N | 0.36 | <0.01 | - | Nest Spawner | Lithophil | IF |
| Lepomis cyanellus | N | 0.02 | $<0.01$ | - | Nest Spawner | Polyphil | IF |
| Lepomis gulosus | N | 0.11 | 0.06 | $\downarrow$ | Nest Spawner | Lithophil | IF |
| Lepomis humilis | N | 0.03 | $<0.01$ | - | Nest Spawner | Lithophil | IF |
| Lepomis macrochirus | N | 0.27 | 2 | $\uparrow$ | Nest Spawner | Polyphil | IF |
| Lepomis marginatus | N |  | 0.02 | - | Nest Spawner | Polyphil | IF |
| Lepomis megalotis | N | 0.43 | 0.50 | $\uparrow$ | Nest Spawner | Polyphil | IF |
| Lepomis microlophus | N | 0.74 | 0.54 | S | Nest Spawner | Polyphil | IF |
| Lepomis miniatus | N | $<0.01$ | 0.04 | - | Nest Spawner | Polyphil | IF |

Table 2.2 Continued

| Species | Status | Period I | Period II | Population Status | Primary <br> Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lepomis symmetricus | N | 0.63 |  | - | Nest Spawner | Polyphil | IF |
| Micropterus punctulatus | N | 0.34 | 2 | $\uparrow$ | Nest Spawner | Polyphil | IF |
| Micropterus salmoides | N | 0.32 | 0.43 | S | Nest Spawner | Polyphil | P |
| Pomoxis annularis | N | 0.96 | 0.07 | - | Nest Spawner | Phytophil | P |
| Pomoxis nigromaculatus | I | 0.24 | 0.14 | - | Nest Spawner | Phytophil | IF |
| Elassoma zonatum | N | 0.32 |  | - | Substratum Chooser | Phytophil | IF |
| Ammocrypta clara | N | 0.02 | 0.03 | - | Open Substrate | Psammophil | IF |
| Ammocrypta vivax | N | 0.46 | 0.49 | $\uparrow$ | Open Substrate | Psammophil | IF |
| Etheostoma asprigene | N |  | 0.05 | - | Substratum Chooser | Phytophil | IF |
| Etheostoma chlorosoma | N | 0.06 | 0.09 | S | Substratum Chooser | Phytophil | IF |
| Etheostoma gracile | N | 0.47 | 0.02 | - | Substratum Chooser | Phytophil | IF |
| Etheostoma histrio | N | $<0.01$ | $<0.01$ | - | Substratum Chooser | Phytophil | IF |
| Etheostoma proeliare | N | 0.02 | $<0.01$ | - | Substratum Chooser | Phytophil | IF |
| Etheostoma artesiae ${ }^{\dagger}$ | N | X | X | - | Substratum Chooser | Phytophil | IF |
| Percina caprodes* | I | <0.01 |  | - | Brood Hider | Lithophil | IF |
| Percina macrolepida | N | $<0.01$ | $<0.01$ | S | Brood Hider | Lithophil | IF |
| Percina sciera | N | 0.11 | 0.15 | $\uparrow$ | Brood Hider | Lithophil | IF |
| Percina shumardi | N | $<0.01$ | $<0.01$ | - | Brood Hider | Lithophil | IF |
| Mugil cephalus | N | 0.13 | 0.54 | S | Catadromous |  | DT |
| Mugil curema* | N | <0.01 |  | - | Catadromous |  | O |
| Paralichthys lethostigma* | N |  | $<0.01$ | - | Marine |  |  |

Table 2.2 Continued

| Species | Status | Period I | Period II | Population | Primary <br> Status | Secondary <br> Reproductive Guild | Trophic <br> Reproductive Guild |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Trinectes maculatus | N | 0.06 | $<0.01$ | S | Anadromous |  | IF |
| Collections During Period: |  | 59 | 124 |  |  |  |  |
| Individuals Collected: | 57,442 | 111,693 |  |  |  |  |  |
| Taxa Richness: | 75 | 70 |  |  |  |  |  |
| Diversity: | 0.84 | 0.78 |  |  |  |  |  |

* Species represented by one collection.
$\dagger$ Species not used for richness and diversity.


Figure 2.6: Relationship of $\log 10(n+1)$ relative abundance through time with linear least-squares regression and associated P -value for fishes with decreasing populations in the lower Sabine River.


Figure 2.7: Relationship of $\log 10(n+1)$ relative abundance through time with linear least-squares regression and associated P -value for fishes with increasing populations in the lower Sabine River.

Table 2.3: Relative abundance, population status, and reproduction and trophic guilds of fishes in the lower San Antonio River, Texas. Mean relative abundance is presented for Period I (1950-1969) and Period II (1970-2006). Abbreviations presented in Table 2.1.

| Species | Status | Period I | Period II | Population Trend | Primary Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Atractosteus spatula* | N |  | <0.01 | - | Open Substrate | Phytophil | P |
| Lepisosteus oculatus | N |  | 0.97 | - | Open Substrate | Phytophil | P |
| Lepisosteus osseus | N |  | 1 | - | Open Substrate | Phytolithophil | P |
| Dorosoma cepedianum | N | 0.35 | 3 | S | Open Substrate | Lithopelagophil | H |
| Dorosoma petenense | N |  | 0.02 | - | Open Substrate | Phytophil | PL |
| Campostoma anomalum | N |  | 2 | $\uparrow$ | Brood Hider | Lithophil | H |
| Cyprinella lutrensis | N | 45 | 29 | S | Brood Hider | Speleophil | IF |
| Cyprinella venusta | N |  | 0.63 | - | Brood Hider | Speleophil | IF |
| Cyprinus carpio | I |  | 2 | S | Open Substrate | Phytolithophil | O |
| Macrhybopsis marconis | N | 0.01 | 0.13 | S | Open Substrate | Pelagophil | IF |
| Notropis amabilis | N |  | 0.02 | - | Open Substrate | Pelagophil | IF |
| Notropis buchanani | N | X | 0.33 | - | Open Substrate | Pelagophil | IF |
| Notropis stramineus | N |  | 0.02 | - | Open Substrate | Lithophil | IF |
| Notropis volucellus | N |  | 0.36 | S | Open Substrate | Phytophil | 0 |
| Opsopoeodus emiliae | N | 8 | X | $\downarrow$ | Nest Spawner | Speleophil | DT |
| Pimephales promelas | I | 0.02 | 0.02 | S | Nest Spawner | Speleophil | O |
| Pimephales vigilax | N | 5 | 10 | S | Nest Spawner | Speleophil | 0 |
| Carpiodes carpio* | N |  | $<0.01$ | - | Open Substrate | Lithopelagophil | DT |
| Ictiobus bubalus | N | 0.01 | 2 | S | Open Substrate | Lithopelagophil | O |
| Ictiobus niger* | N |  | $<0.01$ | - | Open Substrate | Lithopelagophil | O |
| Moxostoma congestum | N |  | 0.21 | S | Open Substrate | Lithophil | IF |

Table 2.3 Continued
$\left.\begin{array}{lccccccc}\hline & & & & & & \text { Primary } & \begin{array}{c}\text { Secondary } \\ \text { Reproductive }\end{array} \\ \text { Species } & & & \text { Population } & \text { Trophic } \\ \text { Reproductive }\end{array}\right]$

Table 2.3 Continued

| Species | Status | Period I | Period II | Population Status | Primary Reproductive Guild | Secondary Reproductive Guild | Trophic Guild |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lepomis megalotis | N | 0.03 | 2 | $\uparrow$ | Nest Spawner | Polyphil | IF |
| Lepomis microlophus* | N |  | <0.01 | - | Nest Spawner | Polyphil | IF |
| Lepomis miniatus | N |  | 0.14 | - | Nest Spawner | Polyphil | IF |
| Micropterus dolomieu* | I |  | 0.03 | - | Nest Spawner | Polyphil | P |
| Micropterus punctulatus | N |  | 0.78 | - | Nest Spawner | Polyphil | IF |
| Micropterus salmoides | N | 0.27 | 0.72 | S | Nest Spawner | Polyphil | P |
| Micropterus treculii* | N |  | 0.06 | - | Nest Spawner | Polyphil | P |
| Pomoxis annularis | N | 0.01 | 0.13 | - | Nest Spawner | Phytophil | P |
| Percina carbonaria | N |  | 0.02 | - | Brood Hider | Lithophil | IF |
| Cichlasoma cyanoguttatum | I | 0.35 | 4 | S | Substratum Chooser | Lithophil | IF |
| Oreochromis aureus | I |  | 0.01 | - | Bearer | Mouth Brooders | O |
| Oreochromis mossambica | I |  | 0.49 | - | Bearer | Mouth Brooders | O |
| Tilapia zillii | I |  | 0.03 | - | Nest Spawner | Lithophil | O |
| Mugil cephalus | N | 0.33 | $<0.01$ | - | Catadromous |  | DT |
| Collections During Period: |  | 10 | 63 |  |  |  |  |
| Individuals Collected: |  | 7,639 | 26,652 |  |  |  |  |
| Taxa Richness: |  | 23 | 55 |  |  |  |  |
| Diversity: |  | 0.62 | 0.80 |  |  |  |  |

* Species represented by one collection.
$\not \ddagger$ Pending voucher confirmation; probable misidentification.


Figure 2.8: Relationship of $\log 10(n+1)$ relative abundance through time with linear least-squares regression and associated P-value for lower San Antonio River fishes.

Table 2.4: Trophic and reproduction guilds for the lower Brazos River, lower Sabine River, and lower San Antonio River by time period.

|  | Brazos |  |  | Sabine |  | San Antonio |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Period I | Period II | Period III | Penod I | Period II | Period I | Period II |
| Trophic Guild |  |  |  |  |  |  |  |
| Detritivore | 3 | 3 | 0.99 | 11 | 6 | 6 | 0.33 |
| Herbivore | 1 | 3 | 0.51 | 0.15 | 0.2 | 0.79 | 3 |
| Invertivore | 78 | 73 | 78 | 59 | 68 | 89 | 61 |
| Omnıvore | 14 | 18 | 20 | 28 | 24 | 4 | 32 |
| Piscivore | 5 | 3 | 0.49 | 0.31 | 0.35 | 0.38 | 3 |
| Planktıvore | 0.01 | 0.62 | 0.12 | 2 | 0.42 |  | 003 |
| Reproductive Guild |  |  |  |  |  |  |  |
| Non Guarders: |  |  |  |  |  |  |  |
| Open substrate |  |  |  |  |  |  |  |
| Pelagophrl | 30 | 19 | 13 | 11 | 9 | 0.09 | 2 |
| Lithopelagophll | 4 | 5 | 0.91 | 9 | 4 | 0.13 | 2 |
| Lithophil |  |  |  | 0.73 | 0.36 |  | 0.15 |
| Phytoluthophil | 0.21 | 0.2 | 0.22 | 0.33 | 0.28 |  | 1 |
| Phytophll | 0.51 | 0.91 | 0.19 | 4 | 4 | 0.76 | 0.96 |
| Psammophil |  |  |  | 0.39 | 0.45 |  |  |
| Brood Hiders |  |  |  |  |  |  |  |
| Lithophll |  | 0.15 | 0.02 | 0.12 | 0.18 |  | 2 |
| Speleophll | 48 | 45 | 63 | 49 | 65 | 48 | 39 |
| Guarders: |  |  |  |  |  |  |  |
| Substrate Chooser |  |  |  |  |  |  |  |
| Lithophil |  |  |  |  |  | 0.37 | 3 |
| Phytophal | 0.28 | 0.01 | $>0.01$ | 0.16 | 0.1 |  |  |
| Nest Spawners |  |  |  |  |  |  |  |
| Polyphil | 1 | 2 | 0.21 | 1 | 2 | 1 | 3 |
| Lithophil | 0.54 | 2 | 0.05 | 0.12 | 0.03 |  | 0.17 |
| Phytophtl | 0.48 | 0.35 | 0.09 | 0.34 | 0.14 | 0.01 | 0.06 |
| Speleophil | 14 | 19 | 20 | 20 | 14 | 10 | 32 |
| Bearers: |  |  |  |  |  |  |  |
| Glll brooder | 0.03 | 0.03 | 0.01 | 0.1 | $<0.01$ |  | 0.25 |
| Viviparous | 0.69 | 6 | 2 | 3 | 0.48 | 40 | 14 |
| Anadromous: |  |  |  | 0.03 | $<0.01$ |  |  |
| Catadromous: | 0.01 | 0.12 | 0.64 | 0.7 | 0.09 | 0.04 | $<0.01$ |

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## CHAPTER III

## DISTRIBUTION AND DIET OF LARVAL AND JUVENILE FISHES IN THE RIO GRANDE, TEXAS


#### Abstract

Fishes of the Rio Grande in the Big Bend region of Texas represent an imperiled fauna because of direct anthropogenic alterations and continued growth of municipalities upstream. Fish species once populous are now extirpated and several are now extinct as a product of habitat modification. The larval and juvenile fish assemblage was assessed by sampling discrete geomorphic units at three mainstem Rio Grande sites and two tributary sites in Big Bend National Park. Cyprinella lutrensis comprised 75\% of the overall assemblage followed by Notropis braytoni (14\%), Carpiodes carpio (5\%), and Gambusia affinis (3\%). Specific habitat associations were determined that suggest at least 12 fish species found therein utilized slackwater habitats (i.e., backwaters) predominantly. Fishes were not evenly distributed among sites, geomorphic units, or chronologically and Canonical Correspondence Analysis explained $21 \%(P=0.044)$ of the total variation. Variance partitioning to asséss pure effects of first order interactions explained all but 2\% of the total variation. Stomach content analysis of fishes indicated opportunistic feeding of Diptera and other aquatic insects. No chronological difference in diet was found among time periods using Analysis of Similarity ( $\mathrm{R}: 0.096, \mathrm{P}=0.13$ ).


## INTRODUCTION

The study of age-0 fishes (larval and juvenile) is an essential component in understanding species-specific information regarding reproductive success, year-class strength, and habitat associations (Snyder et al. 2005). Furthermore, fish assemblages are a good indicator for instream flow as they comprehensively incorporate aspects of an aquatic community (Osting et al. 2004). In the southwestern USA and Chihuahuan desert region of northern Mexico, many aquatic habitats are endangered as a result of modern development of municipalities and increased demand upon limited water resources (Edwards et al. 2002). A high degree of endemism among aquatic fauna exists in this region as a result of physiographic isolation and its arid nature (Smith and Miller 1986). Fishes found in headwater springs, streams, and large rivers of this region are under great threat from anthropogenic alteration (Minckley and Deacon 1968; Karges 2003).

Native fishes of the Rio Grande drainage represent imperiled fauna (Edwards et al. 2002); at least $50 \%$ are of conservation concern (Hubbs et al. 1991). Many species once prevalent in the Chihuahuan desert and Trans Pecos regions are now extinct or extirpated, and several more are endangered or threatened (Hubbs et al. 1991; Dudley and Platania 1997). Alteration of fish assemblages here are largely attributed to habitat degradation and loss (Karges 2003) as flow has been reduced substantially in the Rio Grande and Río Conchos (confluence upstream of study area). Studies of faunal composition and abundance change in major rivers of this region suggest a shift from dominance of obligate riverine fishes, to an assemblage dominated by habitat generalists (Hoagstrom 2001; Edwards et al. 2003).

Preservation of habitat via maintenance of river flow is vital for conservation of many species in the Rio Grande (e.g., Hybognathus amarus and Macrhybopsis aestivalis) as their spawning behavior requires adequate flow for longitudinal distribution and development of larvae (Richter et al. 1996; Dudley and Platania 1997; Platania and Altenbach 1998). Obligate riverine fishes such as H. amarus often have specific habitat requirements for larval development (Dudley and Platania 1997). Natural river flows (variable intra-annual discharge, pulse floods) are required to create, maintain, and alter these habitats (Collier et al. 1996; Richter et al. 1996). Protection of larval and juvenile fish habitats as well river flow is necessary in order to maintain faunal integrity (Scheidegger and Bain 1995). The objectives of this study were to determine larval and juvenile fish distribution among discrete geomorphic units and to investigate diets across the larval and juvenile fish assemblage.

## STUDY AREA

Five sites, three main-stem and two tributary locales, were selected in the Big Bend region of the Rio Grande. The region's arid climate, sandy soil, and mountainous physiography resulted in a river system subject to rapid hydrologic changes and geomorphic alteration; its course through the study area alternates between deep canyons and lowland floodplains. Santa Elena and its tributary influence, Terlingua Creek, Johnson Ranch, and Hot Springs and its tributary, Tornillo Creek, were sites utilized in this study. The most upstream site, Santa Elena, and Hot Springs, furthest downstream, are separated by approximately 115 river km . A series of alternating narrow, deep canyons and meandering river stretches separate these sites.

Santa Elena and Hot Springs provided ample opportunity for sampling myriad habitats due to tributary influence and the cobble, gravel, sand, and silt substrates in constant flux; however, Johnson Ranch exhibited the least geomorphic change throughout the sampling period maintaining a long continuous run with shifting gravel and sand bars. Both tributary sites are characterized by intermittent flow from springs and flash flooding from intense rainfall, and the oft temperate waters flow over gravel and sand to their main-stem confluence.

## MATERIALS AND METHODS

Monthly collections started with the first occurrence of age-0 fishes in April 2006 and extended through December 2006. At each main stem site, I selected geomorphic units (e.g., backwater, eddy, channel margin) where larval and juvenile Rio Grande fishes are known to occur (Dudley and Platania 1997). Geomorphic units were not proportionally represented by sampling. Instead, an effort was made to sample all and replicates of the available geomorphic units. At each tributary site, all geomorphic units (i.e., pool, runs, and riffles) were sampled up to 100 m upstream from the confluence. Fish collections consisted of multiple passes with a larval fish seine ( $1.2 \times 1.8 \mathrm{~m} ; 800 \mu \mathrm{~m}$ mesh size) or a small aquarium dipnet (on one occasion amidst boulder substrate) until a large number of fishes were captured. Consequently, sampling effort was not consistent among geomorphic units. Likewise, numbers of seine hauls in geomorphic units without fish were not recorded. Captured fishes were anesthetized with a lethal dose of MS-222 $(80 \mathrm{mg} / \mathrm{L})$ to prevent regurgitation of stomach contents (Mendelson 1975) and fixed in $10 \%$ buffered formalin. For each collection, geomorphic unit type was recorded along with substrate type, and current velocity was determined using an ordinal scale (no flow, low flow, and moderate flow).

In the laboratory, fishes were identified, measured (total length; mm), and enumerated. Only fishes less than specific size limits were considered for further analyses to maintain a strictly larval and juvenile assemblage based on estimated total length at sexual maturation. Cyprinella lutrensis (Laser and Carlander 1971; Farringer et al. 1979) and Notropis braytoni and N. chihuahua (length inferred from C. lutrensis) were retained if less than 30 mm , Macrhybopsis aestivalis if less than 45 mm (inferred
from M. hyostoma; C. S. Williams pers. comm. 2007), Astyanax mexicanus if less than $50^{\prime}$ mm (Estrada 1999), Fundulus zebrinus if less than 25 mm (Bohnam 1962), Gambusia affinis if less than 10 mm (Haynes and Cashney 1995), and Lepomis megalotis if less than 45 mm (Jennings and Philipp 1992). Lepisosteus osseus (Haase 1969), Cyprinus carpio (Farabee 1979; Ross 2001), Carpiodes carpio (Bass and Riggs 1959), and Ictalurus sp. (Appelgate and Smith 1950; Jenkins 1956) mature at lengths exceeding those I collected thus all individuals were retained for analyses.

Habitat analyses consisted of determining relative abundance of species that occurred in geomorphic units by time period, by site, and modeling species and habitat parameters throughout the sampling period using Canonical Correspondence Analysis (CCA; ter Brack 1986). Variance partitioning was used to determine the pure effects of environmental variables, sites, and time period and Monte Carlo simulation tests (999. permutations) were run to test significance (Williams et al. 2005). Species richness ( $S$ ) was determined by site and geomorphic unit.

Samples were separated for diet analysis into two time periods, Period I (AprilAugust) and Period II (September-December), combined together by geomorphic unit maintaining species integrity within each time period, and up to 5 vouchers were retained for each sample when possible. Five individuals of each species were randomly drawn from combined samples for diet analysis. Fish were eviscerated and gut contents from the most anterior end of the stomach to the first turn of the large intestine were examined (Heins and Clemmer 1975; Bowen 1996). Carpiodes carpio was an exception to this rule because of its long coiled intestine; the anterior $25 \%$ of the gut tract was examined.

Stomach contents were identified to the lowest practical taxonomic level and recorded as occurrence by food item for each species (Hyslop 1980; Bowen 1996). Similarity matrices (Bray and Curtis 1957) were determined from relative abundance of food items and tested with analysis of similarity (ANOSIM; $\alpha=0.05 ; 9,999$ permutations) across time periods using PRIMER 6.1.6 (Clarke 1993; Clarke and Warwick 2001). Permutation analysis indicated average rank dissimilarity within and between samples (Clarke and Gorley 2006). Species that occurred only during one period, Lepisosteus oculatus, $N$. chihuahua, Ictalurus sp. and Lepomis megalotis, were excluded from this analysis because their inclusion generated specious significance. Additionally, these species composed only a minor portion of the overall relative abundance across periods.

## RESULTS

A total of 8,364 individuals was collected between April and December 2006. Among these, 6,928 fishes were determined to be larval or juvenile fishes and were retained for analyses. Eight families consisting of 12 species were represented by the larval and juvenile assemblage from 75 geomorphic units. Among all larval and juvenile fishes taken, Cyprinella lutrensis was the most abundant ( $75 \%$ in relative abundance) followed by Notropis braytoni (14\%), Carpiodes carpio (5\%), and G. affinis (3\%) (Table 3.1).

Larval and juvenile fishes ( $N=5,325$ ) were taken from 38 geomorphic units during Period I (Table 3.2). Channel margins was the most speciose with 11 species of fishes, followed by backwaters ( $S=7$ ), tributaries $(S=5$ ), and eddies ( $S=3$ ). Among the 11 taxa, two (C. lutrensis and N. braytoni) were taken from all geomorphic unit types, three were taken from three geomorphic unit types, three were taken from two geomorphic units, and three were taken from only one geomorphic unit (channel margins).

Larval and juvenile fishes were taken from all geomorphic unit types during Period II ( $N=1,603$ ). Channel margins were again the most speciose with 8 species, followed by eddies and tributaries $(S=6)$ and backwaters $(S=4)$. Among the 9 fishes collected, two species (C. lutrensis and A. mexicanus) were taken from all geomorphic units. Three species were taken from three geomorphic units, two species were taken from two geomorphic units, and two species taken from only one geomorphic unit.

Multivariate ordination of site, habitat parameters, and time period explained $21 \%$ ( $P=0.04$ ) of fish assemblage variation (Figure 3.1). Using variance partitioning, pure
effect of site explained $11 \%(P=0.017)$ of assemblage variation, pure effect of habitat variables explained 7\% ( $P=0.266$ ), and time period explained $1 \%(P=0.543)$. Two percent of the total variation was not explained by first order interactions. Significant site effects were attributed to the occurrence or high abundance of a few species at only one site location (i.e., L. megalotis and Ictalurus at Johnson Ranch site; F. zebrinus at Tornillo Creek site). Lack of significance among environmental variables was attributed to ubiquitous habitat associations of few, dominate taxa (e.g., C. lutrensis and $N$. braytoni). Nevertheless, some taxa (i.e., L. megalotis, G. affinis, L. osseus, and A. mexicanus) were strongly associated with habitat parameters.

Environmental factors with the greatest positive biplot scaling scores on Axis I were gravel substrate ( 0.52 ) and current velocity ( 0.50 ). The greatest negative biplot scores among environmental variables were silt substrate ( -0.45 ) and vegetation ( -0.13 ).

Fish species with high positive biplot scaling scores were F. zebrinus (1.9), N. chihuahua (1.5), and $A$. mexicanus (1.0). Fishes with the greatest negative biplot scores were $G$. affinis (-1.2), Lepomis megalotis (-1.1), Lepisosteus osseus (-0.96), Carpiodes carpio (-0.76), and Ictalurus sp. (-0.70). Sites with positive biplot scaling scores were Tornillo Creek (0.66), Hot Springs (0.17), and Terlingua Creek (0.14). Sites with negative biplot scores were Johnson Ranch ( -0.63 ) and Santa Elena ( -0.04 ).

Differences in species diets between time periods were not different (ANOSIM; Global R: $0.096, P=0.13$ ); species-specific diets of most fishes were similar between periods (Figure 3.2). Consequently, diet information was combined for both periods. Among nine food categories (Copepoda, insect parts, Ephemeroptera, Coleoptera, Hemiptera, Diptera, fish, organic detritus, and silt), Diptera were the most common food
item consumed by all taxa ranging from $13 \%(N=8)$ to $100 \%(N=6)$ (Table 3.3). Unidentifiable insect parts, due to mastication or digestion or both, was also common and occurred in all but 2 species. Other notable diet contents included silt consumed by Carpiodes carpio (88\%; $N=26$ ), Cyprinus carpio ( $25 \% ; N=16$ ), and $N$. braytoni $(22 \%$; $N=45$ ), Coleoptera were consumed by Lepomis megalotis ( $25 \% ; N=4$ ), $N$. braytoni $(16 \% ; N=7)$, and $A$. mexicanus $(13 \% ; N=8)$. Fishes were only consumed by Lepisosteus osseus whereas Hemiptera were only consumed by Lepomis megalotis. Across taxa and grouped by geomorphic unit, fishes from margin and tributary geomorphic units consumed the most diverse food items (Table 3.4). Diptera and insect parts were consumed among all geomorphic units whereas copepods and ephemeropterans were consumed only in the margins and tributaries, and hemipterans were consumed only in the margins.

## DISCUSSION

Larval and juvenile fishes captured in this study represented the more common adult taxa found in the Rio Grande (concurrent study; T. Heard, unpublished data). The use of slackwater habitats as nursery areas is common among riverine fishes (Floyd et al. 1984; Grift et al. 2003) and verified for Rio Grande-Big Bend area fishes by this study. One unexpected result was lower taxonomic diversity in tributary streams compared to mainstem sites. Tributaries provide stable refugia for larvae and juveniles of many main stem taxa (Clark 1973; Sheldon 1988) but did not necessarily support more age-0 Rio Grande fishes than main stem slackwater areas. This might be attributed to few perennially flowing tributaries in arid reaches of the Rio Grande, or that the Rio Grande, especially in the Big Bend area and downstream from the confluence with the Devils River, historically was much wider and shallower (Contreras-Balderas et al. 2002; Calamusso et al. 2005); consequently, sufficient areas of slackwater occurred within the main channel and refugia in tributaries were not necessary. Conversely, many tributaries have been altered by anthropogenic modifications and no longer suitable as nursery habitats (Edwards et al. 2002). The latter explanation is somewhat supported by fish assemblage changes in Terlingua Creek, which historically supported a unique fish assemblage (Hubbs and Wauer 1973) but currently supports an assemblage similar to the Rio Grande main stem (Edwards et al. 2002).

Fishes were not equally distributed among main stem geomorphic units or sites, and abundance differed among time periods. Target-sampling, as done in this study, prevented predictions of species-habitat association; however, CCA was useful in conveying larval and juvenile distributions among sites and environmental parameters.

The pure effects of site and environment each explained about one half of the total variation in the complete CCA model. These results were further supported by observed differences in fish species richness and individual species abundance among sites. Taxa richness was greatest at Johnson Ranch. Lepisosteus osseus, M. aestivalis, Carpiodes carpio, Ictalurus sp., G. affinis, and Lepomis megalotis were associated with Johnson Ranch and its predominately silt substrate. Species associated with more intermediate environmental variables, those with centroids near the origin, cobble, sand, and vegetation, and sites, Santa Elena, Terlingua Creek, and Hot Springs, were primarily the most abundant taxa in this study, C. lutrensis and N. braytoni, but also included Cyprinus carpio. Fundulus zebrinus was largely associated with Tornillo Creek, gravel substrate, and moderate current velocity.

Little variation in occurrence of food items examined was observed between periods for each species. Using ANOSIM to wholly compare data suggested significant similarity of prey items among the fish assemblage and commonality of individual food items by species. All fishes examined appeared to feed opportunistically; prey selectivity could not be determined and was not an objective of this study though Diptera and other insects were the most commonly ingested and likely the most available food items. Diet of all species aligned with published analyses of larval and juvenile fishes. Some species ontogenetic shifts in diet preference (e.g., Lepisosteus osseus shift from invertivory to piscivory; Echelle and Riggs 1972); however, the immature fishes examined herein were mostly classified as invertivores. Cyprinella lutrensis (Simon 1999), M. aestivalis (inferred from M. hyostoma; Starrett 1950), A. mexicanus (Edwards 1977), Ictalurus sp. (inferred from I. punctatus; Bailey and Harrison 1945), F. zebrinus (Bonham 1962), G.
affinis (Simon 1999), and Lepomis megalotis (Applegate 1966) were all classified as invertivores. Cyprinus carpio (Simon 1999) and Carpiodes carpio (Ross 2001) were classified as omnivorous, which was evidenced herein by a relatively high occurrence of silt.

Numerous large-bodied and small-bodied fishes have suffered from declines in abundance, and were extirpated from or are now extinct in the Rio Grande. Atractosteus spatula is extirpated above Falcon Reservoir (Garrett 2002), Scaphirhynchus platorynchus once ranged as far upstream as Albuquerque, New Mexico, but is now extirpated from the Rio Grande and much of Texas (Hubbs et al. 1991), Cycleptus elongatus has been reported as rare to abundant and is likely unique in the drainage (summarized by Garrett 2002), and Ictalurus furcatus, which may also be endemic (Hubbs et al. 1991), has recently suffered from a fish kill of unknown cause (pers. observ. at Santa Elena Canyon, December 2006). Additionally, Hybognathus amarus, N. orca, and $N$. simus simus are extirpated or extinct, and abundance of $N$. jemezanus and Etheostoma grahami has substantially declined (Hubbs et al. 1991). Fishes in the Rio Grande and other large rivers rely on specific habitats maintained by both pulse and base flows for reproduction and foraging (Platania and Altenbach 1998; Grift et al. 2003). To what extent that population declines in the Rio Grande are associated with the lack nursery habitats is unknown, but dewatering, main stem impoundments, channelization, and invasive riparian vegetation collectively have decreased slackwater habitats and floodplain connectivity throughout Rio Grande, especially in areas where Rio Grande endemics are extirpated, extinct, or in rare abundance (Contreras-Balderas et al. 2002; Calamusso et al. 2005). To maintain current assemblage and endemic taxa (i.e., $N$.
braytoni, M. aestivalis), main stem slackwater habitats should be maintained by flow regime or by mechanical alterations (Porter and Massong 2004a, 2004b). In addition, maintenance of these slackwater habitats likely would benefit repatriation efforts of $H$. amarus in the Big Bend reach of the Rio Grande (USFWS 2006), which seems to be a limiting factor for their successful reproduction in the upper reaches of the Rio Grande in New Mexico (Porter and Massong 2004a, 2004b).

Table 3.1: Relative abundance of Rio Grande drainage larval and juvenile fishes in Big Bend National Park collected throughout the sampling period.

| Species | Relative <br> Abundance |
| :--- | :---: |
| Cyprinella lutrensis | 75 |
| Notropis braytoni | 14 |
| Carpiodes carpio | 5 |
| Gambusia affinis | 3 |
| Fundulus zebrinus | 2 |
| Cyprinus carpio | 0.36 |
| Ictalurus sp. | 0.26 |
| Lepisosteus osseus | 0.22 |
| Astyanax mexicanus | 0.16 |
| Macrhybopsis aestivalis | 0.12 |
| Lepomis megalotis | 0.07 |
| Notropis chihuahua | 0.01 |
| $N$ | 6,928 |

Table 3.2: Relative abundance of larval and juvenile fishes by time period and geomorphic unit.

| Period I |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Species | Backwater | Eddy | Margin | Riffle | Tributary |
| Lepisosteus osseus | 0.08 |  | 1 |  |  |
| Cyprinella lutrensis | 81 | 64 | 67 | 1 | 75 |
| Cyprinus carpio | 0.06 |  | 0.87 |  |  |
| Macrhybopsis aestivalis |  |  | 0.09 |  |  |
| Notropis braytoni | 8 | 35 | 11 | 99 | 16 |
| Notropis chihuahua |  |  |  |  |  |
| Carpiodes carpio | 6 |  | 12 |  | 2 |
| Astyanax mexicanus |  | 2 | 0.09 |  |  |
| Ictalurus sp. |  |  | 2 |  |  |
| Fundulus zebrinus | 0.61 |  | 2 |  | 5 |
| Gambusia affinis | 4 |  | 4 |  | 2 |
| Lepomis megalotis |  |  | 0.44 |  |  |
| Total $N$ : | 3,586 | 55 | 1,149 | 139 | 396 |
| Geomorphic Unit $N$ : | 10 | 1 | 20 | 1 | 7 |
| Period II |  |  |  |  |  |
| Lepisosteus osseus |  |  |  |  |  |
| Cyprinella lutrensis | 78 | 97 | 65 | 100 | 76 |
| Cyprinus carpio |  |  | 0.71 |  | 1 |
| Macrhybopsis aestivalis |  | 0.85 | 0.85 |  |  |
| Notropis braytoni | 16 |  | 31 |  | 15 |
| Notropis chihuahua |  | 0.85 |  |  |  |
| Carpiodes carpio |  | 0.85 | 0.57 |  | 0.56 |
| Astyanax mexicanus | 1 | 0.85 | 0.57 |  | 0.42 |
| Ictalurus sp. | , |  |  |  |  |
| Fundulus zebrinus | 4 |  | 2 |  | 7 |
| Gambusia affinis |  |  | 0.14 |  |  |
| Lepomis megalotis |  |  |  |  |  |
| Total $N$ : | 67 | 118 | 707 | 2 | 709 |
| Geomorphic Unit $N$ : | 3 | 3 | 18 | 1 | 11 |



Figure 3.1: Canonical Correspondence Analysis of species and environmental variables (A) and habitat polygons (B) inferred from biplot scaling scores. Sites, Santa Elena (SE), Terlingua Creek (TER), Johnson Ranch (JR), Hot Springs (HS), and Tornillo Creek (TOR), and current velocity (CV) were abbreviated for clarity.


Figure 3.2: Multi-dimensional scaling plot of species and relative abundance of stomach contents. Period I species are represented by inverted triangles and are outlined by the dotted line. Period II species are represented by solid circles and are outlined by the solid line.

Table 3.3: Percent occurrence of food items by species combined by time period. Total length (TL) range for dissected fishes is given in millimeters.

|  | Species |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Food Item | L. osseus | C. <br> lutrensis | Cy. carpio | M. aestivalis | $N$. braytoni | $N$. chihuahua | Ca. carpio | A. mexicanus | Ictalurus $s p$. | $\begin{gathered} F . \\ \text { zebrinus } \end{gathered}$ | G. affinis | $L$. megalotıs |
| Copepoda |  | 7 |  |  |  |  | 4 | 13 |  |  | 20 |  |
| Insect parts |  | 68 | 44 | 33 | 33 | 100 | 35 | 75 | 60 | 25 | 40 |  |
| Ephemeroptera | 13 | 2 |  |  |  |  |  |  |  | 3 |  | 100 |
| Coleoptera |  |  |  |  | 16 |  |  | 13 |  | 3 | 7 | 25 |
| Hemiptera |  |  |  |  |  |  |  |  |  |  |  | 25 |
| Diptera | 13 | 34 | 81 | 100 | 49 | 100 | 69 | 50 | 80 | 83 | 73 | 75 |
| Fish | 88 |  |  |  |  |  |  |  |  |  |  |  |
| Detritus |  | 11 |  |  | 18 |  | 8 |  |  | 3 | 20 |  |
| Silt |  | 18 | 25 |  | 22 |  | 88 |  | 20 | 3 |  |  |
| TL Range | 27-74 | 9-29 | 13-81 | 9-29 | 12-58 | 29 | 12-58 | 9-49 | 24-51 | 9-24 | 7-10 | 11-27 |
| $N$ | 8 | 44 | 16 | 6 | 45 | 1 | 26 | 8 | 5 | 38 | 15 | 4 |

Table 3.4: Percent occurrence of food items by geomorphic unit combined by time period.

|  | Geomorphic Unit |  |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Backwater | Eddy | Margin | Riffle | Tributary |  |  |  |  |
| Copepoda |  |  |  |  |  |  | 7 |  | 4 |
| Insect parts | 43 | 63 | 38 | 33 | 31 |  |  |  |  |
| Ephemeroptera |  |  | 6 |  | 4 |  |  |  |  |
| Coleoptera |  | 10 | 1 | 33 | 8 |  |  |  |  |
| Hemiptera |  |  | 1 |  |  |  |  |  |  |
| Diptera | 77 | 50 | 65 | 22 | 63 |  |  |  |  |
| Fish | 7 |  | 5 |  |  |  |  |  |  |
| Detritus | 16 | 10 | 4 |  | 12 |  |  |  |  |
| Silt | 30 | 23 | 17 | 44 | 18 |  |  |  |  |
| $N$ | 44 | 30 | 84 | 9 | 49 |  |  |  |  |

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