

CONSEQUENCES OF LONG-TERM CHANGES IN FISH COMMUNITY  
STRUCTURE ON ECOSYSTEM FUNCTIONING  
IN A SUBTROPICAL SPRING-FED RIVER

By

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## TABLE OF CONTENTS

	<b>Page</b>
ACKNOWLEDGEMENTS.....	iv
LIST OF FIGURES .....	vii
ABSTRACT.....	viii
CHAPTER	
I.    INTRODUCTION .....	1
Introduction.....	1
II.   MATERIALS & METHODS .....	5
Study System and Hydrological Data.....	5
Historical Fish Data Compilation .....	7
Data Analysis .....	9
Determination of Fish Body Nutrient Content and Excretion .....	12
III.  RESULTS .....	16
Compositional Changes in Fish Community Structure .....	16
Contributions of Native and Non-Native Species to Community Biomass.....	17
Contributions of Native and Non-Native Species to P and N Recycling .....	18

Comparison of Spring-Associated and Riverine-Associated Fish.....	19
Comparison of Reproductive Guilds .....	20
Historical Changes in the Upper San Marcos River .....	20
IV. DISCUSSION.....	21
IV. FIGURES.....	26
APPENDIX SECTION.....	34
REFERENCES .....	48

## LIST OF FIGURES

<b>Figure</b>	<b>Page</b>
1. Map of the Upper San Marcos River .....	26
2. PERMANOVA and non-metric multi-dimensional scaling on presence-absence data, depicting 2 breaks in community structure.....	27
3. Species accumulation curve for the three time periods .....	28
4. Top 8 contributors of occurrence-weighted C, N, and P community biomass across all periods.....	29
5. Occurrence-weighted nutrient biomass of native and non-native species to C, N, and P biomass across all time periods.....	30
6. Occurrence-weighted contributions of species to the community P recycling rate of top 8 contributors, and native vs. non-native amongst all periods. ....	31
7. Occurrence-weighted contributions of species to the community N recycling rate of top 8 contributors and native vs. non-native amongst all periods .....	32
8. Mean Monthly Discharge (m <sup>3</sup> /sec) of the Upper San Marcos River.....	33

## **ABSTRACT**

In this study, I examined patterns of long-term changes in the composition of the fish community in the spring-influenced upper San Marcos River (central Texas, USA) and the ecosystem functioning implications of compositional changes in the fish community. Using a long-term historical data set of fish community composition (Perkin et al. 2011; Kollaus et al. 2015; BIO-WEST, Inc. 2013-2016) and contemporary species-specific fish excretion data from the upper San Marcos River, I examined how temporal changes in the composition and diversity of the fish community were related to changes in the rates and ratios of dissolved inorganic N and P recycled by the fish community and how the sequestration of nutrients into fish biomass changed through time. I hypothesized that temporal changes in fish community composition would lead to changes in which species function as the largest contributors to the community-wide aggregate nutrient recycling rates, as well as changes to the community-wide aggregate ratios of excreted nutrients. Accordingly, I also predicted that temporal changes in fish community composition would be associated with changes to which species sequester the largest amount of C, N, and P, and these changes will alter the community-wide aggregate C:N:P.

# CHAPTER I

## INTRODUCTION

Over the last three decades, ecologists have examined and debated the relationship between biodiversity and ecosystem functioning (e.g., Tilman 1999; Loreau et al. 2001; Naeem et al. 2002; Hooper et al. 2005; Balvanera et al. 2006; Loreau 2010; Vaughn 2010). In general, studies have found that the functional roles of species within a community affect ecosystem-level processes and that the maintenance of biodiversity affects ecosystem functioning, if functional diversity of the community is related to the ecosystem processes of interest (Hooper et al. 2005; Loreau 2010). On a global scale, loss of biodiversity in freshwater ecosystems during the Anthropocene has been large, with losses of freshwater fish species being particularly acute (Ricciardi and Rasmussen 1999; Dudgeon et al. 2006). Loss of freshwater biodiversity, including fishes, is a consequence of multiple human-associated activities including population overexploitation, introduction of pollutants, modification of flow regimes, degradation or loss of habitat, and the introduction of non-native taxa (Dudgeon et al. 2006).

Biological invasions are globally pervasive and can have potentially deleterious effects on ecosystems (Vitousek et al. 1996). In particular, introduction of some non-native species can be problematic because these taxa can establish dominance in biomass or abundance and have a detrimental impact on their introduced environment (Vitousek 1990). Some non-natives can compete with native taxa, resulting in loss of biodiversity and the alteration of abiotic and biotic factors in ecosystems due to consumption and/or ecological engineering practices (Srivastava and Vellend 2005; Strayer et al. 2006; Scott et al. 2012; Datri et al. 2015). Changes to the physical structure of an ecosystem through

the introduction of non-native taxa can be relatively slow, taking decades for the full effects of an invader to appear (Strayer et al. 2006), but the severity of the impact of non-native taxa is often dependent on its abundance and biomass in the community (Strayer et al. 2006, Capps et al. 2013b). Although the effects of non-native taxa have been examined by ecologists and conservation biologists for decades, few studies have utilized a longer-term perspective when analyzing the effects of altered community assemblages due to both natural and anthropogenic forces (e.g., Olden and Poff 2005). Indeed, shifts or changes in community structure over time are a result of multiple simultaneous processes including the immigration of new non-native species into the community, the extinction of native taxa, and stochastic variation in population sizes (Vellend 2010), but the introduction of non-native taxa often coincides with anthropogenic disturbances which impact native species (Gurevitch and Padilla 2004).

Despite the acknowledgement that the long-term loss of native species and their gradual replacement with non-native taxa can potentially alter ecosystem functioning, few studies have utilized long-term datasets (i.e., >10 years of data) to assess how changes in community composition may affect ecosystem functioning. Long-term data sets portraying community composition changes over the span of decades exist and have provided insights into how environmental change can alter communities (e.g., Shaver et al. 2001; Gardner et al. 2003; Olden and Poff 2005; Collie et al. 2008; Perkin et al. 2016). However, examination of how similarly scaled long-term changes in community structure and composition can lead to changes in ecosystem functioning are far less common. Many studies have explicitly examined how shifts in community composition are related to changes in ecosystem functioning (e.g., Tilman et al. 2001; Vaughn et al. 2015), but

most have been conducted over relatively shorter time scales (i.e., <10 years), illustrating the difficulties in obtaining both long-term data on community composition and ecosystem-level processes simultaneously.

Ecological stoichiometry is a framework which allows for examination of the roles of individual species vary in community and provides a quantifiable way to identify how animals both directly and indirectly affect a key ecosystem process: nutrient recycling (Vanni et al. 2002). Fish are among the most nutrient rich organisms in riverine ecosystems and can play a substantial role in nutrient recycling (Vanni 2002; McIntyre et al. 2010). Fish sequester nutrients such as nitrogen (N) and phosphorus (P) in biomass and excrete soluble inorganic nutrients as waste, which in turn can support nutrient requirements of primary producers (Vanni 2002; McIntyre et al. 2007; McIntyre et al. 2008). Fish species vary extensively in dissolved N and P recycling rates due to differences in body size, physiology, morphology, and growth rates (Schindler and Eby 1997; Sterner and Elser 2002; Vanni et al. 2002; McIntyre et al. 2007). Recycled nutrient rates and ratios are also dependent on the imbalance between a fish's body nutrient content relative to its primary food items (Schindler and Eby 1997; Sterner and Elser 2002). Given inter-species differences in nutrient content and recycling, changes in fish community composition over time has the potential to affect aggregate recycling rates of N and P and the available nutrient ratios of the environment, as well as patterns in the sequestration of nutrients in the fish community.

Spring-fed aquatic ecosystems often exhibit relatively high levels of organismal endemism, containing unique species assemblages (Bowles and Arsuffi 1993). However, spring-fed systems are also under threat from a variety of anthropogenic impacts,

including groundwater extraction, eutrophication and contamination from urban and agricultural runoff, alteration of surface recharge and flow regimes, and the introduction of non-native species (Bowles and Arsuffi 1993). Physicochemical consistency of many spring-fed systems make them particularly susceptible to introduction and establishment of non-native species (Moyle et al. 1996). Fish communities in some spring-fed ecosystems have been monitored for many decades (e.g., Perkin et al. 2011; Kollaus et al 2015), making the acquisition of long-term data sets portraying potential changes to community structure possible. Thus, spring-fed systems offer a unique opportunity to examine how changes in the fish community composition over time may alter nutrient recycling by fishes.

In this study, I examined patterns of long-term changes in the composition of the fish community in the spring-influenced upper San Marcos River (central Texas, USA) and the ecosystem functioning implications of compositional changes in the fish community. Using a long-term historical data set of fish community composition (Perkin et al. 2011; Kollaus et al. 2015; BIO-WEST, Inc. 2013-2016) and contemporary species-specific fish excretion data from the upper San Marcos River, I examined how temporal changes in the composition and diversity of the fish community were related to changes in the rates and ratios of dissolved inorganic N and P recycled by the fish community and how the sequestration of nutrients into fish biomass changed through time. I hypothesized that temporal changes in fish community composition would lead to changes in which species function as the largest contributors to the community-wide aggregate nutrient recycling rates, as well as changes to the community-wide aggregate ratios of excreted nutrients. Accordingly, I also predicted that temporal changes in fish

community composition would be associated with changes to which species sequester the largest amount of C, N, and P, and these changes will alter the community-wide aggregate C:N:P.

## **CHAPTER II. MATERIAL AND METHODS**

### **Study System and Hydrological Data**

The upper San Marcos River originates from a large number of artesian springs in the headwaters of the river (San Marcos Springs in Spring Lake) and flows ~8 km downstream before reaching its confluence with the Blanco River (Fig. 1). Supplied by the Edwards Aquifer, the upper San Marcos River is characterized by perennial flows, clear water, consistent temperatures (23°C), and little temporal and spatial variation in physicochemical characteristics in the upper river (Groeger et al. 1997). Although the upper San Marcos River, like many spring-fed systems, is largely considered to have relatively consistent base flows (Groeger et al. 1997; Perkin et al. 2011), I assessed changes in fish community composition over a long period of time (from 1938 – 2017; see below for fish community composition data) and wanted to examine if river discharge and/or the hydrological characteristics changed over the same time period.

Hydrological data for the upper San Marcos River were not available for the same temporal extent as the fish data set, but the United States Geological Survey (USGS) operated gage #08170500 on the upper San Marcos River for the year 1956, and the period of 1994 through 2017. In order to estimate river flows in the gap in the historical hydrological record for the upper San Marcos River from 1957 to 1993, I utilized

historical flow data from another USGS gaging station which is now non-operational (USGS gage #08170000, San Marcos Springs) which had discharge records from 1957 – 1993. The upper San Marcos River gage and the San Marcos Springs gage locations are in very close proximity (<300 m apart), share the same latitude and longitude coordinates as reported by the USGS, and both gages were operational and overlapped in daily discharge data for years 1938 – 1956 and 1994 – 2016, totaling a 40-year period of time. Ordinary least-squares linear regression was used to predict mean daily discharge at the upper San Marcos River for the 1957-1993; mean daily discharge for the two gages was highly correlated ( $r^2 = 0.52$ ,  $p < 0.0015$ ,  $n = 22,135$ ,  $y = 1.053x - 4.16$ ). Unexplained variation in the relationship between the two gaging sites is very likely related to the fact that a smaller tributary (Sessom Creek) enters the San Marcos River just upstream from the upper San Marcos River gaging site but downstream from the San Marcos Springs site; this small creek can generate runoff during storm events causing short-term variation in riverine discharge at the San Marcos River gaging site not related to changes in spring or base flows of the river.

In order to assess hydrological characteristics of the upper San Marcos River during the study period, I utilized the USGS's Hydrologic Assessment Tool (HAT) software (Henriksen et al. 2006) that has been customized for Texas rivers and streams (i.e., TXHAT) to quantify changes in hydrologic characteristics of the river during the time periods determined by analysis of the fish community data set (see analysis of fish community composition data below). The HAT tool calculates 171 statistical hydrological indices (reviewed in Olden and Poff 2003) for a river based upon USGS stream flow data and I assessed all 171 indices for the upper San Marcos for each time

period.

During the period covered by the fish community data set, the upper San Marcos River has undergone a number of modifications both in the river and in the surrounding watershed. An historical perspective of many of these changes is reviewed in Kollaus et al. (2015). Several low head dams were constructed in the upper San Marcos River in the mid-1930s by Civilian Conservation Corps (CCC) and by private landowners during the 1950s. Additionally, there were several flood retention structures installed in the upstream portions of two of the major tributaries (Purgatory Creek and Sink Creek) of the San Marcos River by the Natural Resources Conservation Service in the 1980s (Woods and Earl, 2002). These tributaries typically do not provide sustained perennial flows to the upper San Marcos River, but can generate runoff contribution to the river during substantial storm events. Data on temporal changes in land use and land cover for the period covered by the fish data and are not readily available, thus I accessed human population census data via the United States Census Bureau (USCB) for the city of San Marcos for this period.

### **Historical Fish Community Data Compilation**

I compiled fish community data for the upper San Marcos River spanning the years 1938 – 2016. The majority of data on fish community composition for the upper San Marcos River (from 1938 – 2000) was acquired from Perkin et al. (2011) who obtained historical fish data from published literature, museum collections and agency reports (see original paper for detailed data compilation and censoring methods). The study presented here utilized fish community data for the portion of the San Marcos River

from below the river's headwaters (Spring Lake) to its the confluence of the Blanco River (hereafter, referred to as the "upper San Marcos River"). Fish data in these collections are from seining and reported as relative abundances for each species. Fish community data for the year 2011 were obtained from Behen (2013) and Kollaus et al. (2015); fish surveys in these studies were conducted via a combination of seining and SCUBA transect counts and reported as the relative abundance of each species. Fish community data for the years 2013 – 2016 were obtained from the Edwards Aquifer Authority's (EAA) Biological Monitoring Program of the Edwards Aquifer Habitat Conservation Plan (BIO-WEST, Inc. 2014-2016). Fish community sampling efforts were performed quarterly every year by using seines in shallower areas and SCUBA transect counts in deeper habitats and reported as relative abundance of species in the community. I again restricted data from these sources to include only data from the upper San Marcos River.

Data obtained from Perkin e al. (2011) were derived from only seining surveys and the data for the 2011-2016 period utilized both seining and SCUBA transect counts, therefore, I ascertained if a specific gear type (seining *versus* SCUBA) was associated with species-specific detection biases in the 2011 – 2016 collections. To do this, the percent composition of different species collected solely via seining was compared to the percent composition of different species counted with SCUBA transects (see Appendix D). Comparison of the data using both methods revealed that the relative abundance of the most common fish species encountered during concurrent SCUBA and seine samples in general did not significantly differ between methods and the relative abundance of native vs. non-native fish in concurrent seine and SCUBA counts did not differ either (Appendix I). Thus, for this study, I utilized the fish community data for the 2013 – 2016 period that

included both gear types.

Using the groomed data set, each fish species found in the community data set across the entire time interval was categorized as native to the drainage or non-native to the drainage using Hubbs (2008). Fish species were also classified as either being spring-associated (i.e., typically found in and around springs or in spring-influenced reaches of rivers) or surface water-associated using Hubbs et al. (1953), Gilbert (1980), Perkin et al. (2012), Birkhead (1980), Stevens (1977), Bonner and McDonald (2005), Robbins and Page (2007), Linam and Kleinsasser (1998). Fish species were additionally grouped into reproductive guilds using a classification method derived from Goldstein and Meador (2004), in which individual species were categorized as livebearers, broadcast spawners, brood hidiers, or nesters.

### **Data Analysis**

After compilation and grooming of the data, I assembled a 76-year data set composed of 59 (individual fish community sampling events (see Appendix 2). All fish community data across the study interval were reported as the relative abundance of each species in each collection and many of the individual sampling events did not record the number of seine hauls, the total number of fish caught or the surface area of the site in the river that was sampled. In addition, the Upper San Marcos River morphology and surface area has likely varied over the 76-year time interval. Thus, it is not possible to express fish densities (number/m<sup>2</sup>) or the total population size of each fish species in the Upper San Marcos River. Thus, I elected to use an approach in which the 76-year community dataset was converted from relative abundance to presence-absence or

detection-nondetection data, where a value of 1 indicated presence, and a value of 0 indicated absence for each sampling event. Use of presence-absence data takes into account the unavoidable bias in the variation of animal abundance or  $n$  for each sampling event (Royle and Nichols, 2003) and a similar presence/absence approach has been utilized by other studies assessing long-term, multi-decadal changes in fish communities (e.g., Gido et al. 2010). I separated fish data into six approximately decade-long periods: 1940-1949 (including a 1938 sampling event), 1950-1959, 1960-1969, 1980-1989 (including a 1977 sampling event), 1990-1999 (including a 2001 sampling event) and 2011-2016. Decades with just one sampling event were included in the closest relative period. Separation of data into decades was performed because it is a commonly used period length in long term studies (i.e., Gido et al. 2010) and grouping collections into these periods ensured that each decade had the same approximate number of sampling events (mean = 12 collections per decade, range = 5 – 22 collections per decade).

Changes in the fish community composition (presence/absence data for each species) over the entire historical data set were assessed with permutational analysis of variance (PERMANOVA) and non-metric dimensional scaling (NDMS). PERMANOVA tests the null hypothesis that centroids and dispersion of the community composition (based on presence – absence data) for each time period (decade) are equivalent across decades and rejection of the null hypothesis indicates that the centroid and/or the spread of the data is different between decadal periods. NDMS was used to present community composition data from the various decadal periods. PERMANOVA was run in R using the vegan package (version 1.1.383) on the presence-absence data to determine the strongest break points in community composition across the data set

decadal periods. NDMS was also run in R using the vegan package. Separate PERMANOVAs were run on a data set that included both gear types (seine and SCUBA) and the data only representing the seine data.

Using PERMANOVA results, I separated the community composition decadal time series data into several longer periods in which the community composition was consistently similar in composition (see RESULTS). If fish species diversity differed among the community composition defined time periods, I utilized a rarefaction approach; this approach is appropriate because the time periods in the data set did not have identical sampling effort, and I wanted to avoid potential bias associated with differences in sampling effort among time periods (Gotelli and Graves 1996; Gido et al. 2010). I assessed the change in cumulative species richness with increasing number of samples in each time period by first randomizing the sampling effort in each time period, then running  $n = 10,000$   $p^*$  iterations in time period to estimate uncertainty. The initial increase in the relationship between species richness and number of samples (i.e., the slope of the relationship) should be steeper with greater sampling intensity and/or sampling efficiency of each collection, but the asymptote of this relationship should occur at the same point if enough samples were taken to depict the fish species richness during each period. I then compared the cumulative species richness among the community-defined periods using the minimum number of collections ( $n=19$ ) in each period with the fewest collections.

In order to examine how the occurrence of species in the San Marcos fish community varied among the composition-defined periods, I used a randomization procedure to determine which species were more likely to occur within and across

periods (Gido et al. 2010). In this procedure, a subset of the collections from each period was randomly drawn without replacement, and the percent of collections with that species was calculated. The number of samples drawn was 80% of the number of collections in the period with the fewest number of collections ( $n = 19$  collections in the period with the fewest collections; Appendix 2). Thus, I randomly selected 15 collections from each community composition-defined period to calculate the percent of collections in which each species occurred. This randomization process was repeated 1000 times for each period, and the median percent occurrence of each species and associated 95% confidence intervals were calculated to assess whether species significantly increased or decreased in their probability of occurrence across periods.

### **Determination of Fish Body Nutrient Content and Excretion Rates**

The major goal of this thesis research was to determine if the contribution of the various fish species in the upper San Marcos River to the recycling rate of nutrients and the sequestration of nutrients into fish biomass changed throughout the historical record. Obviously, historical estimates of fish body nutrient content and excretion rates for the various species in the upper San Marcos community are not available. However, I utilized contemporaneous species-specific estimates of fish nutrient content and dissolved nutrient excretion rates in the upper San Marcos River and then linked these data to the historical fish data. Using this approach, I assumed that species-specific nutrient excretion rates (dissolved inorganic N and P) and body nutrient composition [carbon I, N and P] remained consistent across the study period. As stated previously, fish excretion rates can vary substantially with several factors. Both per capita and mass-specific

excretion rates of fish vary with body size (Schindler and Eby, 1997; Vanni, 2002) and I assumed that the mean body size of the populations of different species in the upper San Marcos have not changed over the study period. Most of the historical fish surveys of the upper San Marcos River do not report the body size distributions of the fish they collected. Factors such as intense size-selective predation by members of the fish community (Nowlin et al. 2007) and anthropogenic fish harvest (Pauly et al. 1998) can reduce the mean body size and trophic position of species in the community. However, the San Marcos River has not had an intense commercial fishery and based upon examination of the data sets of long-term fish community composition, I have no reason to *a priori* suspect that predation rates by members of the community have changed substantially in the upper San Marcos River food web over the data set time interval.

Fish excretion rates may also vary with the diet of a species and with water temperature (Schindler and Eby, 1997; Vanni, 2002). Fish species are to a large extent limited in their principle diet due to morphological constraints on feeding (e.g., Wainright and Richard 1995), thus I assumed that fish species in the community did not significantly alter their diet throughout the study period. In addition, it is highly unlikely that the water temperature in the upper San Marcos River have substantially changed over the study period. Historical data for the upper San Marcos River indicate that water temperatures have exhibited limited seasonal and inter-annual variation and are consistently around 22.5 – 23.0°C; data on water temperatures of the upper San Marcos River show that water temperatures have been approximately 23°C since at least the late 1950s (Hannan and Dorris 1970; Guyton et al. 1979; Ogden et al. 1985; Groeger et al. 1997).

Because per capita and mass-specific excretion rates are dependent upon the body size of individuals, I needed to estimate the average body size of individual fish of each species in the upper San Marcos River. For a majority of species, including the most common/abundant species in the upper San Marcos River, the mean body size (g wet weight) of an individual of each fish species was determined using data previously collected from the upper San Marcos River (Pray 2009; Nowlin *unpubl. Data*); mean body size of each species was estimated as the mean body size of a species in these data sets. For the remaining species, individual body size was estimated using genus or species-specific data and length-weight regressions from Schneider et al. (2000) and Carlander (1969).

To estimate dissolved inorganic N (as  $\text{NH}_4^+$ ) and P (as  $\text{PO}_4^{3-}$ ) excretion rates for each fish species in the community, I utilized contemporaneous estimates of excretion rates as reported by Pray (2009) and Nowlin (*unpubl. Data*); these data consists of  $n = 99$  independent N and P excretion weight estimates from fish in the upper San Marcos River, representing 17 species, 13 genera, and 8 families. For these 17 species, I estimated the mean per-capita and mass-specific N and P excretion rates using the data from Pray (2009) and Nowlin (*unpubl. Data*); these data sets measured N and P excretion rates from as broad a body size range as possible for each species. For the remaining fish species community which did not have body size ranges or excretion rates measured by these data sets, I estimated the per capita N and P excretion rates using a body size scaling relationship and associated regression equations generated for the fish species which I had both body size and excretion rates (Appendix 1). Each fish species that had its estimated per capita N and P excretion rates determined from scaling equations from the

most closely related group represented in the data set in decreasing order from genus, to family, to all data. For example, the excretion rates of goldfish (*Carrasius auratus*) were determined using the equation for Cyprinidae because the data set contained no other species in the genus (Appendix 1) (McIntyre et al. 2008, Vaughn et al. 2015). Across all species, the per capita excretion rates were determined for the mean body size of each species in the river (see above).

Body nutrient content (% N, %C, and %P of body mass) for each species was predicted using the data sets of Pray (2009) and Nowlin (*unpub. Data*) on body nutrient composition for 17 species in the San Marcos River. I estimated the %N, %C, and %P for the remaining fish species not included the above data sets by using the %N, %C, and %P from the Pray and Nowlin data sets, in decreasing order of preference: genus, family, order, all data (Appendix 1). Fish body stoichiometry is largely phylogenetically constrained, with fish body %P, N and C being similar across fish species within taxonomic groups (Vanni et al. 2002). The mean body size of an individual of each species (see above) was then multiplied by the proportion of N, P, and C to the overall body mass of that species in order to calculate the N, P and C biomass in an individual of each species.

The percent contribution of each species to the overall community-wide N and P excretion rate was determined by first multiplying the per capita excretion rate of each species to the median probability of occurrence during a given time period, yielding an occurrence-weighted excretion rate, known hereafter as OWER. The community-wide OWER was estimated by summing the OWER for all species and the percent contribution of each species to the community-wide rate was calculated by dividing each

species-specific OWER by the overall community-wide rate. Similarly, the contribution of each species to the total amount of C, N and P sequestered into fish biomass was determined by multiplying the C, N, and P in an individual of each species to the median probability of occurrence of the species, yielding an occurrence-weighted C, N, and P biomass of that species. Community-wide C, N, and P biomass was calculated by summing all nutrient biomasses across species and the percent contribution of each species to the community-wide C, N, and P biomass was calculated by dividing each species-specific occurrence-weighted biomass by the overall community-wide biomass.

## **CHAPTER III. RESULTS**

### **Compositional Changes in Fish Community Structure**

Two significant breaks were apparent in the PERMANOVA and NDMS, indicating three distinct periods: 1938 – 1959, 1960-1989, and 1990 – 2016 (hereafter Periods, I, II and III, respectively; Fig. 2A). It is critical to note that these breaks occur between the same time periods for data collected using seine data only, and for all types of fish collection (Fig. 2B). NMDS plots similarly show a separation of these periods when comparing across these three periods (Fig. 2C and D).

Comparison of species accumulation curves among the three time periods indicated that species richness in the upper San Marcos River fish community varied across periods (Fig. 3). The fastest rates of species accumulation occurred in Period III (1990 – 2016) and this period also had the highest cumulative species richness after 15 collections. Periods I (1938 – 1949) and II (1960 – 1989) had similar rates of species accumulation, but Period II had the lowest cumulative species richness when compared to the other time periods.

### **Contribution of Native and Non-Native Species to Community Biomass**

The eight top contributors to the occurrence-weighted C biomass accounted for 87% of the total community biomass in Period I, 86% in Period II, and 78% in Period III (Fig. 4A). In Period I, the top contributors to overall community biomass were native to the drainage and the species with the largest contributions to occurrence weighted C biomass were channel catfish (*Ictalurus punctatus*), several native *Lepomis* species and two native *Micropterus* species (*M. treculi* and *M. salmoides*) (Fig. 5). The only non-native species in the top eight was rock bass (*Ambloplites rupestris*) (Fig. 5). In Period II, native fish species again made up the majority of top fish species contributing to C biomass, but non-native smallmouth bass (*M. dolomieu*) was the largest contributor to C biomass. In addition, non-native rock bass and redbreast sunfish (*Lepomis auritus*) were among the top C biomass contributors. By Period III, however, smallmouth bass, rock bass, and redbreast sunfish were no longer in the top contributors to C biomass, but spotted gar (*Lepososteus oculatus*) and grey redhorse (*Moxostoma congestum*) and several centrarchids were the largest were important native contributors to C biomass. Interestingly, the tropical and non-native armored catfish (*Hypostomus plecostomus*) and common carp (*Cyprinus carpio*) were now included in the top contributors to C biomass in this period.

Patterns in N biomass followed the same species pattern through each period as C biomass (Fig. 4B). Species contributions for P biomass were also similar, with the only difference being that armored catfish making a larger percent contribution to the total community-wide P biomass (ranked 3<sup>rd</sup> overall) during Period III than it did for C and N

biomass (ranked 5<sup>th</sup> for C and N; Fig. 4C).

The overall contribution to native versus non-native species to the community-wide C, N, and P biomass varied across the three periods (Fig. 5A – C). Native species comprised a majority of the C, N, and P biomass in the fish community across all three time periods, with native species making up >90% of the C, N, and P biomass in Period I (Fig. 5A). However, in Period II, non-native fishes accounted for just under half of the C, N, and P biomass (Fig. 5B). By Period III, non-native species made substantially smaller contributions to fish community C, N, and P biomass, but this contribution had not returned to Period I values (Fig. 5C).

### **Contributions of Native and Non-Native Species to P and N Recycling**

The relative importance of different fish species' contribution to the occurrence-weighted community wide P recycling rates followed the same general pattern as the results for the sequestration of nutrients in to biomass, with a few notable differences (Fig. 6A – C). In Period I, the largest contributors to the community-wide P excretion rates were dominated by native species (with the only exception being rock bass), with several sunfish species, channel catfish, and largemouth bass being the top contributors (Fig. 6A). During Period II, community P recycling was again dominated by native taxa, but the non-native Mexican tetra (*Astyanax mexicanus*), smallmouth bass, and rock bass were among the more important species (Fig. 6B). By Period III, the number of non-native species contributing to community-wide P recycling declined, but armored catfish and redbreast sunfish were in the top group of contributors (Fig. 6C). Overall, non-native species contributed ~12.37% of the community-wide rate in Period I, this contribution

increased to ~30.02% by Period II, and then subsequently declined to ~21.91% by Period III (Fig. 6D).

Species' contributions to community-wide N recycling followed a similar pattern to that observed with P recycling (Fig. 7A-C). In general, the same species were also the largest contributors to the overall N recycling rate with rock bass being the only non-native species in the top group in Period I (Fig. 7A) and rock bass, smallmouth bass, and redbreast sunfish being the non-native species in the top group of contributors in Period II (Fig. 7B). In Period III, armored catfish had a more prominent role in N recycling (when compared to its contribution to P recycling) and was the second largest contributor to community-wide N recycling (Fig. 7C). Overall, native versus non-native contributions over the three periods followed a similar trend as that observed for P recycling (Fig. 7D).

### **Comparison of Spring-Associated and Riverine-Associated Fish**

Out of the 59 species reported in the historical dataset, 11 were categorized as spring-associated, and 48 were classified as riverine-associated. The contribution of native spring-associated fish to community-wide P recycling and N recycling declined across periods (Appendix 3). The contribution of spring-associated species to community-wide P recycling decreased from 14.82% in Period I to 13.63% in Period II, and 9.70% in Period III. Similarly, the contribution of spring-associated species to community-wide N recycling decreased from 7% in Period I to 3% in Period III. Overall, there was an increase in non-native spring-associated and riverine-associated percent contribution in all nutrient cycling and body content in Period II, but this contribution

decreased in Period III (see Appendix 3). Patterns in the proportional contribution of spring-associated species to community-wide biomass of C, N, and P followed a similar declining contribution.

### **Comparison of Reproductive Guilds**

Out of the 59 species in the historical data set, 8 were classified as livebearers, 27 were classified as broadcast spawners, 7 were classified as brood hidiers, and 17 were classified as nesters. Occurrence of livebearers consistently increased across periods, thereby increasing the relative importance and percent contribution of these fishes to community-wide P and N recycling across periods (Appendix 4). The contribution of broadcast spawners decreased from Period I to Period II for community-wide N and P recycling, yet substantially increased in Period III. Brood hidiers contribution to community-wide N and P recycling consistently decreased across periods, although this reproductive guild had the lowest number of species ( $n = 7$ ). Nest building species had an increase in their contribution to community-wide N and P recycling from Period I to Period II, but this contribution precipitously decreased in Period III.

### **Historical Changes in the Upper San Marcos River**

For the periods of time covered by the hydrological data (Periods II and III), the mean daily discharge of the Upper San Marcos River ranged from 169.92 cfs (Period II), and 192.15 cfs (Period III) (Fig. 8A). The five-year running average of annual discharge for the upper San Marcos River generally increased over the same time period (Fig. 8B), suggesting that the overall baseflows supported by groundwater increased from the late

1950s to 2017. Indeed, examination of the various indices determined by the TXHAT, indicated that mean annual flow increased between Period II and Period III from 172.37 cfs to 192.78 cfs. However, some of the largest differences between Periods II and III were in the variability of flows experienced within each period. Between Period II and Period III, the variability of maximum flows substantially increased. In addition, the variability in the daily fall rate in the hydrograph increased by 1100% from Period II to Period III and variability in rise rate of the daily hydrograph also increased by 764% from Period II to Period III. Both the specific mean annual maximum flow and daily maximum flow increased by 236% from Period II to Period III and the annual coefficient of variation in discharge increased from 18.66 to 36.81 between the two time periods.

In addition to the changes in hydrological characteristics of the river, the population of the San Marcos area and practices in the watershed also changed. According to US Census statistics, the population of the city of San Marcos increased from 6,006 in 1940 to 61,980 in 2016, a 932% increase in population size. Undoubtedly, this kind of population increase is likely associated with an increase in impervious cover and changes in storm water runoff characteristics.

#### **CHAPTER IV. DISCUSSION**

Occurrence of the various fish species in the upper San Marcos River changed substantially throughout the 78-year time period covered by this study. Across all of the fish community-defined study periods, the proportion of non-native taxa increased considerably during Period II (1959 – 1989). In particular, there were several native fish

species which had a zero occurrence rate during this period, including the sand shiner (*Notropis stramineus*), the headwater catfish (*Ictalurus lupus*), Chihuahua catfish (*Ictalurus sp.*), and the freckled madtom (*Noturus nocturus*) and one additional native species was had a zero occurrence rate in Period III (tadpole madtom; *Noturus gyrinus*). This pronounced loss of native species during Period II could be due to a series of modifications and management practices in the upper San Marcos River and the establishment of several non-natives in the river, which included smallmouth bass and redbreast sunfish.

It is critical to note that even in the earliest period (Period I), non-native fishes were already present in the upper San Marcos River, including rock bass. It is likely that many of these species were introduced to the river via to sport-fish introductions or bait-fish releases (Hubbs, 1982; Bowles & Bowles, 2001). However the relatively large increase in non-native species during Period II (9 non-native species were reported), including the Amazon molly (*Poecilia formosa*) and blue tilapia (*Oreochromis aureus*), and common goldfish (*Carassius auratus*) and these introductions were likely due to accidental hatchery release or via aquaculture release. Smallmouth bass and redbreast sunfish also had higher occurrence rates during Period II and were likely introduced for sport-fishing; these introductions may have occurred as early as the 60s (Bowles & Bowles, 2001). By Period III, 10 non-native species were occurring in the community, but two additional non-native species appeared: Common carp and armored catfish. Armored catfish are often introduced due to aquarium releases (Hubbs, 1982) and can have profound effects on nutrient recycling in ecosystems (Datri et al. 2015).

In the present study, the relative importance of non-native species to various measures of ecosystem function varied across periods. In particular, the relative importance of non-native fishes was greatest in Period II. Occurrence-weighted contribution of non-native species to community-wide C, N and P in fishes was ~8% in Period I and this increased to ~40% in Period II, an approximate 5x increase. Similarly, occurrence-weighted contribution of non-native species to community-wide recycling of P increased from 12% in Period I to 30% in Period II and non-native contribution to N recycling increased from 12% in Period I to 37% in Period II, an increase of ~3x. However, the relative importance of non-native taxa notably declined in Period III, with contributions of non-natives to community-wide nutrient biomass declining to 18-19% and contributions to community recycling decreasing to 22-23% by Period III.

It is important to note, however, that the contribution of the various individual species to occurrence-weighted community biomass and to community-wide P recycling were not entirely congruent. For example, channel catfish were the largest contributor to Period I community biomass but was ranked 3<sup>rd</sup> overall in its contribution to community P recycling. In addition, armored catfish in Period III accounted for a greater proportion of community-wide P biomass than its occurrence-weighted biomass would along predict. Armored catfish in the family Loricariidae have large body plates on their bodies containing relatively large amounts of P (Vanni et al. 2002; Scott et al. 2012; Datri et al. 2014). Both of these examples illustrate that species-specific variation in body stoichiometry and nutrient excretion rates play an important role in determining the relative importance of species within a community (McIntyre et al. 2007).

Identification of the precise mechanisms leading to the temporal changes in species composition and the relative importance of different taxa in ecosystem functioning is extremely difficult to identify, but the upper San Marcos River has a long history of natural and anthropogenic disturbances and alterations which may have led to shifts in community composition over time. From 1934-1976, the Aquarena Springs theme park managed an aquatic plant business, harvesting up to 680 kg daily and sediments and vegetation were regularly removed from the upper portion of the river through dredging through the 1980s (Kollaus et al. 2014). Removal of sediments and vegetation can result in the habitat loss and homogenization, resulting in the changes in species diversity and abundances and community restructuring (Plaska et al. 2016). In addition, a relatively large and persistent drought period occurred from 1950 – 1957, and discharge from the San Marcos River reached a record low in the summer of 1956, dropping to slightly below 50 cfs (Saunders et al. 2001). The end of this drought of record was temporally associated with one of the identified period shifts in fish community composition (transition from Period I to Period II) in which there was an increase in the relative importance of non-native species in community nutrient biomass and nutrient recycling.

Other anthropogenic alterations also coincided with transitions in fish community structure. The city of San Marcos had a wastewater treatment plant discharge located in the upper portion of the river that was eventually removed (after a lawsuit) and relocated in the late 1980s, approximately at the end of Period II. There were also a large number of small dams constructed in the upper river. Spring Lake dam was built in 1849, Cape's Dam in 1867, Rio Vista Dam in 1904, Cummings Dam in 1914 and five flood control

dams were built from 1981-1991 on several tributaries of the upper San Marcos. Cumulatively, the installation of these structures is thought to have led to smaller magnitude storm flow events in the upper river (Earl and Wood 2002) and changes to frequency of small and large flood events are linked to changes in fish community assemblage (Perkin et al. 2009), and dams have been shown to be a significant cause of altered stream flows with reduced flow variability, which can lead to significant loss of native fishes and create new niche opportunities for non-native taxa (Mims and Olden, 2013). Interestingly, analysis of river hydrology indicates that there was an increase in variability of flood events and an increase in riverine “flashiness” in Period III, but if these changes in hydrological characteristics are associated with alterations of community structure in the upper San Marcos River remain unknown.

The decline in non-native species observed in Period III may be associated with a suite of environmental protection efforts initiated in the late 1980s and early 1990s. As mentioned previously, the San Marcos waste water treatment plant was upgraded and moved in the early 1990s and the Edwards Aquifer Authority was created in 1993 to issue permits and regulate groundwater withdrawals from the Edwards Aquifer. Consequently, more intense regulation of water usage from the aquifer and habitat protection and restoration efforts starting in the late 1980s may have facilitated declines in non-native species and recovery of native fishes.

## V. FIGURES

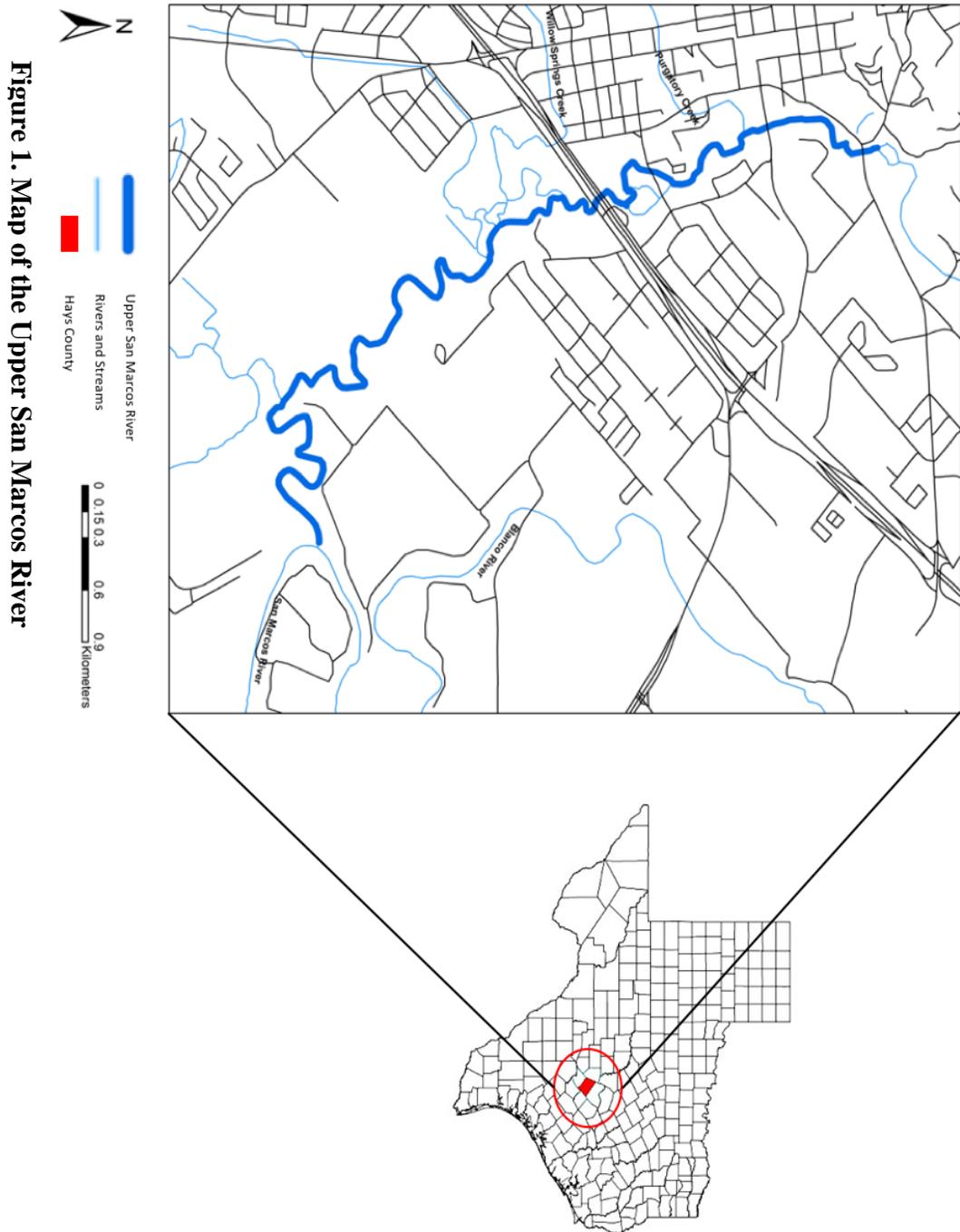
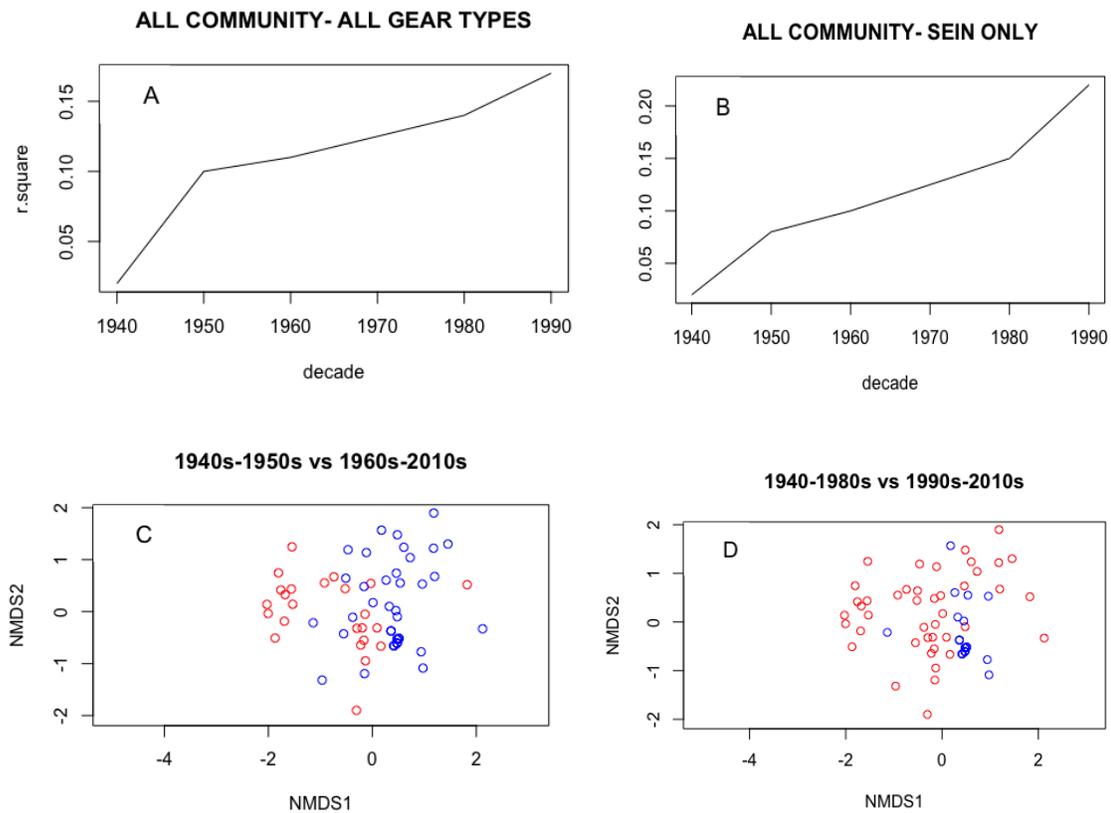
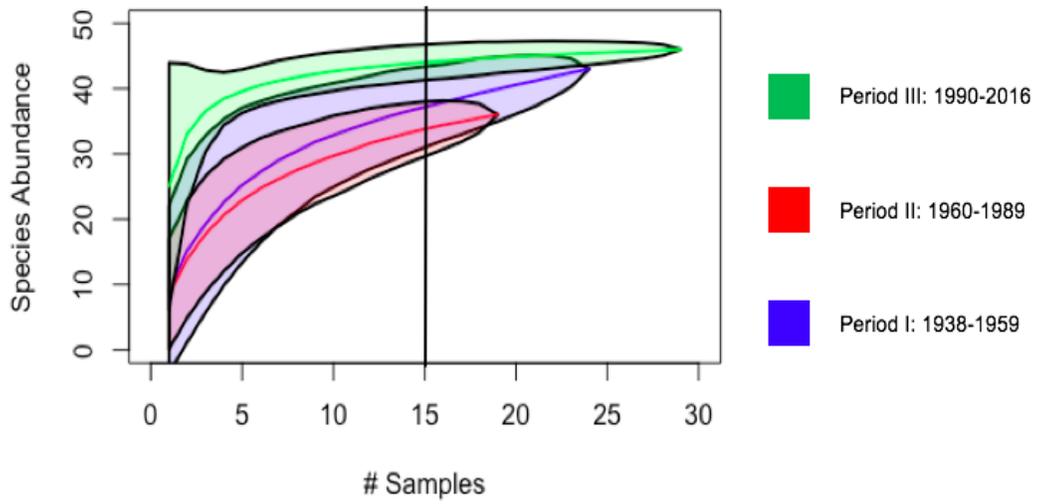


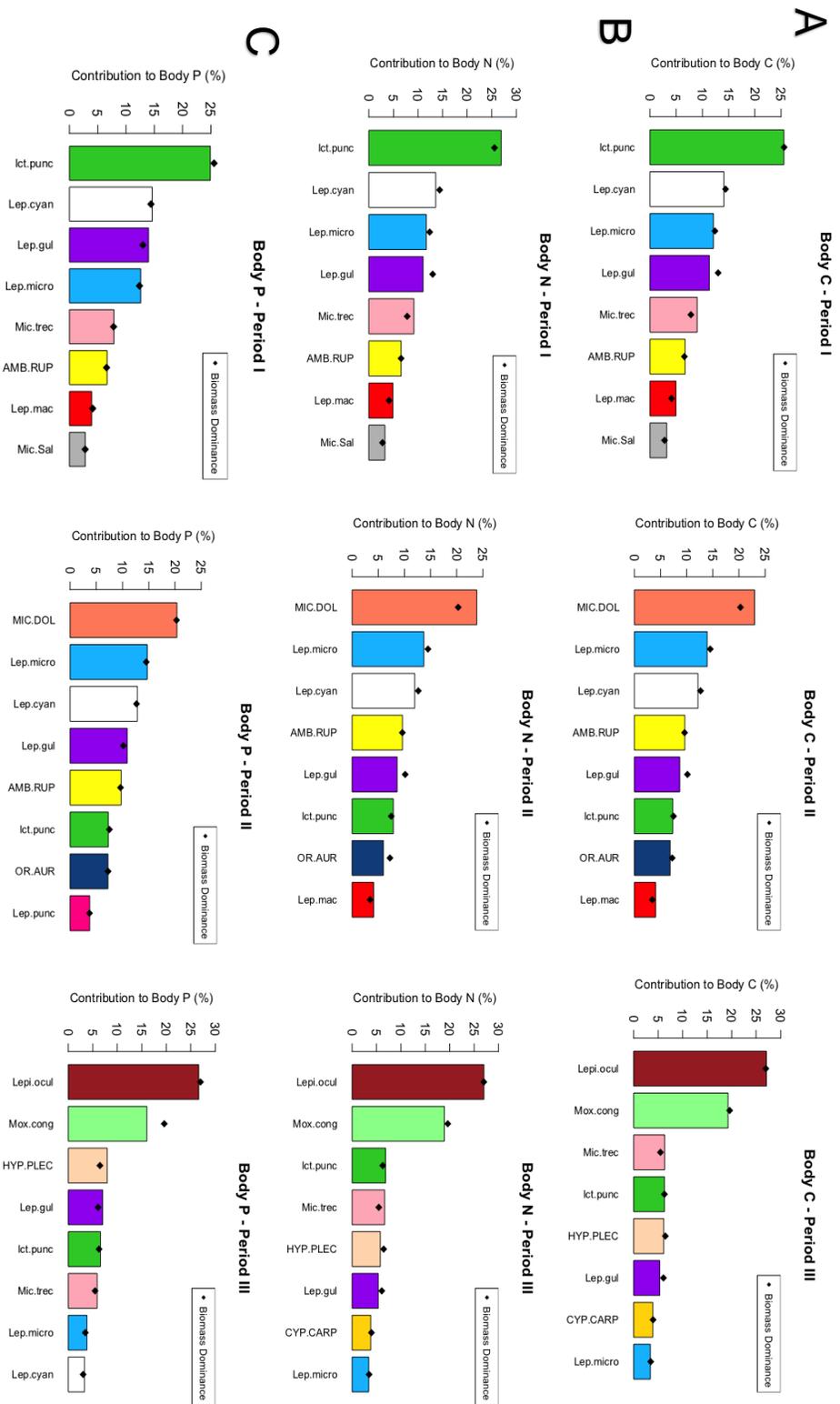
Figure 1. Map of the Upper San Marcos River



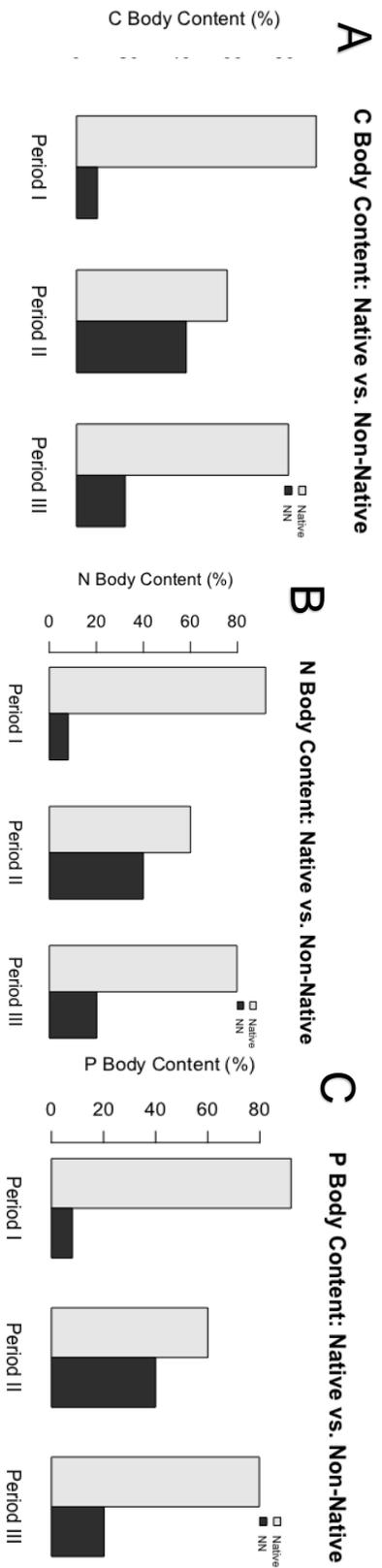
**Figure 2. PERMANOVA and non-metric multi-dimensional scaling on presence-absence data depicting 2 breaks in community structure.** PERMANOVA using all gear types versus (2A) PERMANOVA using solely seine gear type in sampling events for years 2013-2016 (2B). NMDS plot of species occurrence separation of the 1940s and 1950s relative to all future decades (2C), and 1990s and 2010s (2D) compared to all prior decades. Red circles represent the former time period vs. the blue circles which are the latter time period relative to each image.



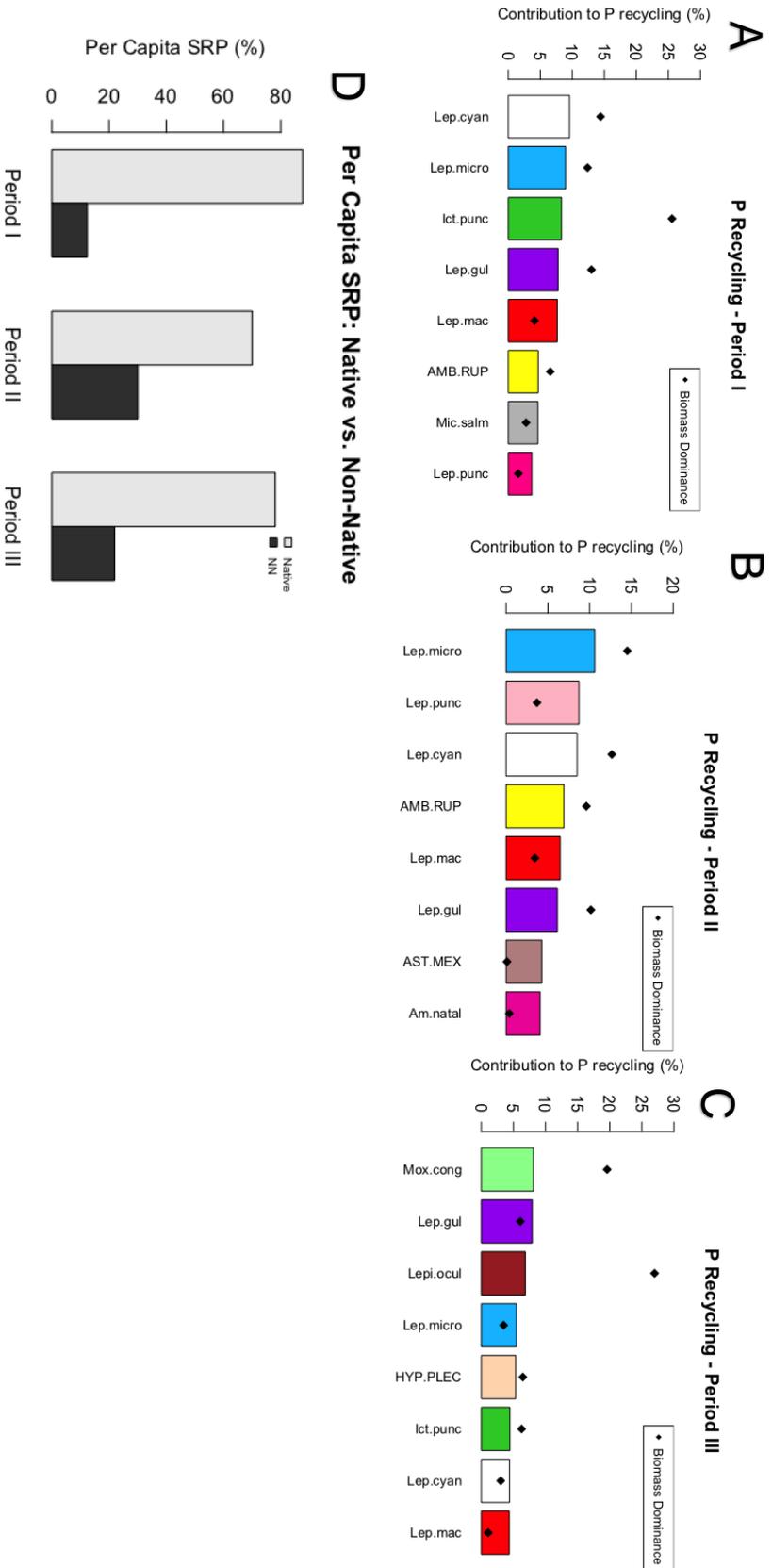
**Figure 3. Species accumulation curve for the three time periods.** Vertical line represents the mean number of species collected after 15 samples.



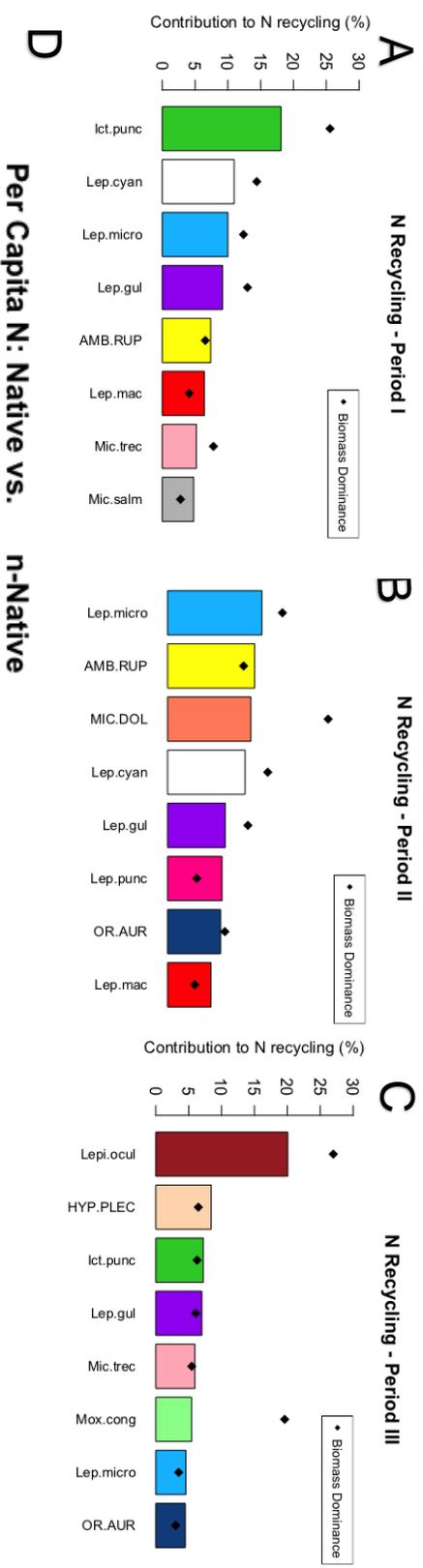
**Figure 4. Top 8 contributors of occurrence weighted C (4A), N (4B), and P community biomass (4C) across all Periods.** Individual species are represented by color and taxonomic abbreviations. Note the differences in rank order of C, N, and P body content amongst periods. Bars reflect % contribution to the overall community, whereas diamonds reflect only biomass. Differences between bars and diamonds represent influence of species identity.



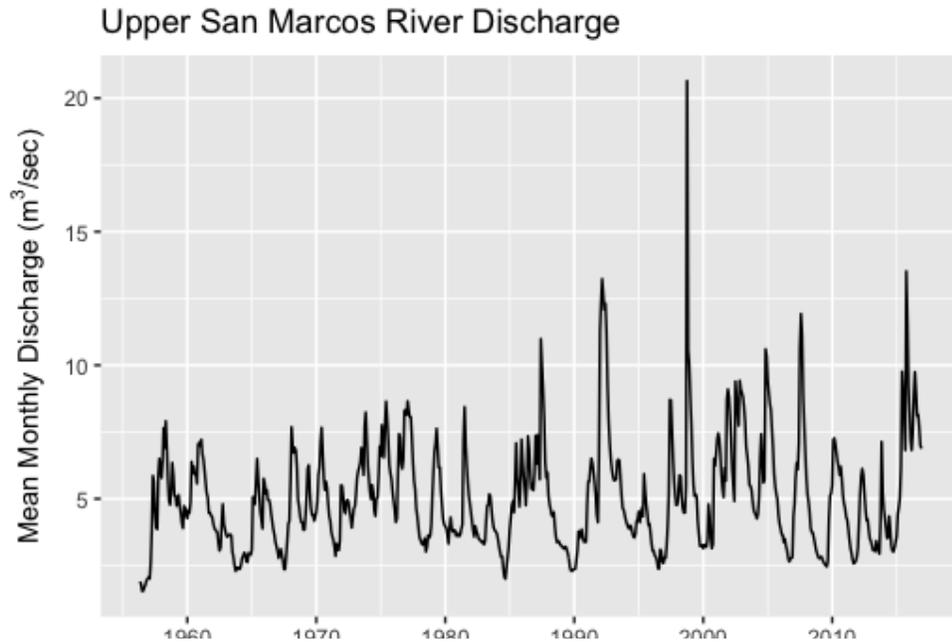
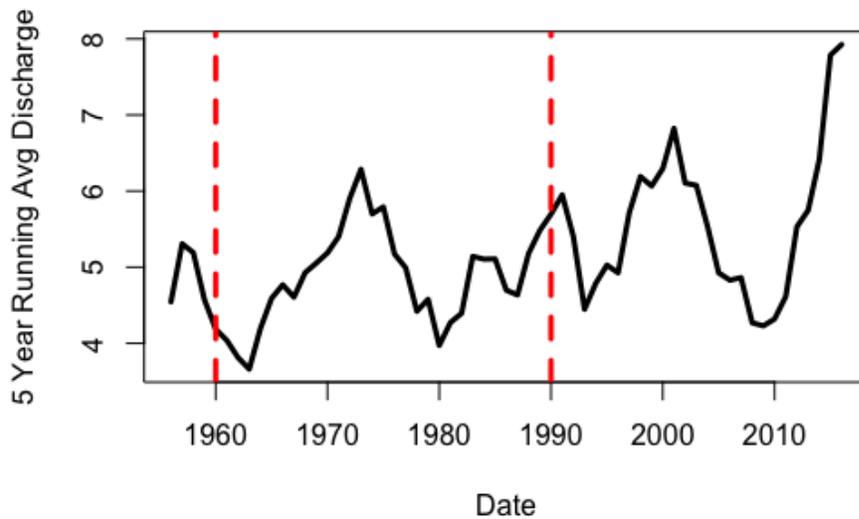
**Figure 5. Occurrence-weighted nutrient biomass of native and non-native species to C (6A), N (6B), and P biomass (6C) across all time periods.**



**Figure 6. Occurrence-weighted contributions of species to the community P recycling rate of top 8 contributors (8A-8C) and native vs. non-native amongst all periods (8D). Bars reflect occurrence weighted % P recycling rates, whereas diamonds reflect only biomass dominance. Non-Natives are represented in all capital letters.**



**Figure 7. Occurrence-weighted contributions of species to the community N recycling rate of top 8 contributors (7A-7C) and native vs. non-native amongst all periods (7D). Bars reflect occurrence weighted P recycling rates, whereas diamonds reflect only biomass dominance. Non-Native are represented in all capital letters.**

**A****B**

**Figure 8. Mean Monthly Discharge ( $\text{m}^3/\text{sec}$ ) of the Upper San Marcos River (USGS Gage #08170500, estimated using USGS Gage #08170000 for years 1956-1994) (Fig. 8A). Temporal changes in 5-yr running average annual discharge ( $\text{m}^3/\text{sec}$ ) for the Upper San Marcos River ((USGS Gage #08170500, estimated using USGS Gage #08170000 for years 1956-1994) (Fig. 8B). Vertical dashed lines represent time periods used in analysis of fish communities.**

APPENDIX SECTION

**Appendix 1.** Complete list of fish species included in the study, with indication of whether nutrient excretion was measured directly, the method for estimating per capita excretion, the method for estimating body stoichiometry, and trophic guild designations. Underlined species indicate NNIS.

Species	Common Name	Nutrient Excretion		Body Stoichiometry		Trophic Group	
		Directly Measured Y/N	Per capita P Estimation Method	Per capita N Estimation Method	Directly Measured Y/N		Estimation Method
<u><i>Lepisosteus oculatus</i></u>	Spotted Gar	N	all fish	all fish	N	all fish	Carnivore
<u><i>Lepisosteus osseus</i></u>	Longnose Gar	N	all fish	all fish	N	all fish	Carnivore
<u><i>Dorosoma cepedianum</i></u>	Gizzard shad	N	all fish	all fish	N	all fish	Herbivore
<u><i>Campostoma anomalum</i></u>	Central stoneroller	Y	all fish	Family	Y	species	Herbivore
<u><i>Carassius auratus</i></u>	Goldfish	N	all fish	Family	N	Family	Omnivore
<u><i>Cyprinella lutrensis</i></u>	Red shiner	N	all fish	Family	N	Family	Omnivore
<u><i>Cyprinella lutrensis X venusta</i></u>	Blacktail shiner	N	all fish	Family	N	Family	Omnivore
<u><i>Cyprinella venusta</i></u>	Common shiner	Y	all fish	Family	Y	Species	<u>Invertivore</u>
<u><i>Cyprinus carpio</i></u>	Common carp	N	all fish	Family	N	Family	<u>Invertivore</u>

Species	Common Name	Nutrient Excretion		Body Stoichiometry		Trophic Group	
		Directly Measured Y/N	Per capita P Estimation Method	Per capita N Estimation Method	Directly Measured Y/N		Estimation Method
<i>Diomda nigrotaeniata</i>	Guadalupe roundnose minnow	Y	all fish	Family	Y	Species	Herbivore
<i>Macrhybopsis marconis</i>	Burthead chub	N	all fish	Family	N	Family	Carnivore
<i>Notemigonus crysoleucas</i>	Golden Shiner	N	all fish	Family	N	Family	Invertivore/Herbivore
<i>Notropis amabilis</i>	Texas Shiner	Y	all fish	Family	Y	Species	Invertivore/Herbivore
<i>Notropis chalybaeus</i>	Ironcolor shiner	N	all fish	Family	N	Genus	Invertivore
<i>Notropis stramineus</i>	Sand shiner	N	all fish	Family	N	Genus	Invertivore
<i>Notropis volucellus</i>	Mimic shiner	N	all fish	Family	N	Genus	Invertivore/Herbivore
<i>Notropis</i> sp.		N	all fish	Family	N	Genus	Invertivore/Herbivore
<i>Pimephales vigilax</i>	Bullhead minnow	N	all fish	Family	N	Family	Omnivore
<i>Maxostoma congestum</i>	Gray redborse	N	all fish	Order	N	Order	Invertivore
<i>Astyanax mexicanus</i>	Mexican tetra	Y	all fish	all fish	Y	Species	Carnivore

Species	Common Name	Nutrient Excretion		Body Stoichiometry		Trophic Group	
		Directly Measured Y/N	Per capita P Estimation Method	Per capita N Estimation Method	Directly Measured Y/N		Estimation Method
<i>Ameiurus melas</i>	Black bullhead	N	Order	Order	N	Genus	Invertivore/Carnivore
<i>Ameiurus natalis</i>	Yellow bullhead	Y	Order	Order	Y	Species	Invertivore/Carnivore
<i>Ictalurus lupus</i>	Headwater catfish	N	Order	Order	N	Family	Invertivore/Herbivore
<i>Ictalurus punctatus</i>	Channel catfish	N	Order	Order	N	Family	Invertivore/Carnivore
<i>Ictalurus sp.</i>	Chihuahua catfish	N	Order	Order	N	Family	Invertivore/Carnivore
<i>Nothurus surinus</i>	Tadpole madom	N	Order	Order	N	Family	Invertivore
<i>Nothurus nocturnus</i>	Freckled madom	N	Order	Order	N	Family	Invertivore
<i>Hypostomus sp./Loricariidae</i>	Armored sucker with catfish Blackstrip	Y	Species	Family	Y	Species	Herbivore
<i>Eurubius notatus</i>	topminnow	N	all fish	all fish	N	Order	Invertivore/Herbivore
<i>Gambusia affinis</i>	Mosquitofish	Y	all fish	all fish	Y	Species	Carnivore

Species	Common Name	Nutrient Excretion		Body Stoichiometry		Trophic Group
		Directly Measured Y/N	Per capita P Estimation Method	Directly Measured Y/N	Estimation Method	
<i>Gambusia gelsei</i>	Largesprin g gambusia San Marcos	Y	all fish	Y	Species	Carnivore
<i>Gambusia georgei</i>	gambusia	N	all fish	N	Genus	Carnivore
<i>Gambusia</i> sp.	Amazon molly	N	all fish	N	Genus	Carnivore
<i>Poecilia formosa</i>	Sailfin molly	N	all fish	N	Genus	Omnivore
<i>Poecilia latipinna</i>	Sheepshea d minnow Inland	Y	all fish	Y	Species	Omnivore
<i>Cyprinodon variegatus</i>	silverside	N	all fish	N	Order	Omnivore
<i>Menidia beryllina</i>	Rock bass	N	all fish	N	All fish	Invertivore
<i>Ambloplites rupestris</i>	Redbreast sunfish	N	all fish	N	Family	Invertivore/Carni vore
<i>Lepomis auritus</i>	Green sunfish	Y	Species	Y	Species	Invertivore
<i>Lepomis cyanellus</i>	sunfish	N	Genus	N	Genus	Invertivore/Carni vore
<i>Lepomis gulosus</i>	Warmouth	Y	Genus	Y	Species	Invertivore/Carni vore

Species	Common Name	Nutrient Excretion		Body Stoichiometry		Trophic Group	
		Directly Measured Y/N	Per capita P Estimation Method	Per capita N Estimation Method	Directly Measured Y/N		Estimation Method
<i>Lepomis macrochirus</i>	Bluegill Longear sunfish	Y	Genus	Genus	Y	Species	Invertivore Invertivore/Carnivore
<i>Lepomis megalotis</i>	Redear sunfish	N	Genus	Genus	N	Genus	Invertivore
<i>Lepomis microlophus</i>	Redspot sunfish	N	Genus	Genus	N	Genus	Invertivore
<i>Lepomis miniatus</i>	Redspotted sunfish	N	Genus	Genus	N	Genus	Invertivore
<i>Lepomis punctatus</i>	Spotted sunfish	N	Genus	Genus	N	Genus	Invertivore Invertivore
<i>Lepomis</i> sp.		N	Genus	Genus	N	Genus	Invertivore
<i>Micropterus dolomieu</i>	Smallmouth bass	N	all fish	all fish	N	Genus	Invertivore/Carnivore
	Largemouth bass	Y	all fish	all fish	Y	Species	Invertivore/Carnivore
<i>Micropterus salmoides</i>		N	all fish	all fish	N	Genus	Invertivore
<i>Micropterus</i> sp. X sp.		N	all fish	all fish	N	Genus	Invertivore
<i>Micropterus treculii</i>	Guadalupe bass	N	all fish	all fish	N	Genus	Invertivore
	Fountain darter	N	all fish	all fish	N	Family	Invertivore
<i>Etheostoma fonticola</i>		N	all fish	all fish	N	Family	Invertivore
<i>Etheostoma lepidum</i>	Greenthroated darter	N	all fish	all fish	N	Family	Invertivore

Species	Common Name	Nutrient Excretion		Body Stoichiometry		Trophic Group	
		Directly Measured Y/N	Per capita P Estimation Method	Per capita N Estimation Method	Directly Measured Y/N		Estimation Method
<u><i>Etheostoma spectabile</i></u>	<u>Orangethr oat darter</u> Texas	N	all fish	all fish	N	Family	<u>Invertivore</u>
<u><i>Percina carbonaria</i></u>	<u>logperch</u> Guadalupe	Y	all fish	all fish	Y	Species	<u>Invertivore</u>
<u><i>Percina apristis</i></u>	darter	Y	all fish	all fish	Y	Species	<u>Invertivore</u>
<u><i>Percina sp.</i></u>	Rio Grande	N	all fish	all fish	N	Family	<u>Invertivore</u>
<u><i>Cichlasoma cyanocuttatum</i></u>	perch Blue	Y	all fish	all fish	Y	Species	Herbivore
<u><i>Oreochromis aureus</i></u>	tiapia	N	all fish	all fish	N	Family	Omnivore

**Appendix 2.** Median probability of occurrence percent for all detected species per time period. Lowercase letters indicate significant change in distribution. Periods that share a letter are not different. Underlined species indicate NNIS.

Family	Species	Common Name	Period I:			Period II:			Period III:		
			1938-1957	1960-1986	1992-2016	1938-1957	1960-1986	1992-2016	1938-1957	1960-1986	1992-2016
<u>Lepisosteidae</u>	<u><i>Lepisosteus oculatus</i></u>	Spotted Gar	0% <sup>a</sup>	0% <sup>a</sup>	53.33% <sup>b</sup>	0% <sup>a</sup>	0% <sup>a</sup>	0% <sup>a</sup>	0% <sup>a</sup>	0% <sup>a</sup>	
	<u><i>Lepisosteus osseus</i></u>	Longnose Gar	0.0%	0.0%	6.67%	0.0%	0.0%	0.0%	0.0%	0.0%	
<u>Clupeidae</u>	<u><i>Dorosoma cepedianum</i></u>	Gizzard shad	0.0%	0.0%	6.67%	0.0%	0.0%	0.0%	0.0%	0.0%	
	<u><i>Compostoma anomalum</i></u>	Central stoneroller	6.7% <sup>a</sup>	6.7% <sup>a</sup>	13.33% <sup>b</sup>	6.7% <sup>a</sup>	6.7% <sup>a</sup>	13.33% <sup>b</sup>	6.7% <sup>a</sup>	13.33% <sup>b</sup>	
	<u><i>Carassius auratus</i></u>	Goldfish	0.0% <sup>a</sup>	13.3% <sup>b</sup>	0.00% <sup>a</sup>	0.0% <sup>a</sup>	0.0% <sup>a</sup>	13.3% <sup>b</sup>	0.0% <sup>a</sup>	0.00% <sup>a</sup>	
	<u><i>Cyprinella lutrensis</i></u>	Red shiner	20.0% <sup>a</sup>	13.3% <sup>b</sup>	0.00% <sup>c</sup>	20.0% <sup>a</sup>	0.0% <sup>b</sup>	0.00% <sup>c</sup>	20.0% <sup>a</sup>	0.00% <sup>c</sup>	
	<u><i>Cyprinella lutrensis</i></u> X <u><i>venusta</i></u>		6.7%	0.0%	0.00%	6.7%	0.0%	0.00%	6.7%	0.00%	
	<u><i>Cyprinella venusta</i></u>	Blacktail shiner	26.7% <sup>a</sup>	20.0% <sup>a</sup>	80.00% <sup>b</sup>	26.7% <sup>a</sup>	20.0% <sup>a</sup>	80.00% <sup>b</sup>	26.7% <sup>a</sup>	80.00% <sup>b</sup>	
	<u><i>Cyprinus carpio</i></u>	Common carp	0.0% <sup>a</sup>	0.0% <sup>a</sup>	20.00% <sup>b</sup>	0.0% <sup>a</sup>	0.0% <sup>a</sup>	20.00% <sup>b</sup>	0.0% <sup>a</sup>	20.00% <sup>b</sup>	
	<u><i>Diionda nigrotaeniata</i></u>	Guadalupe roundnose minnow	26.7% <sup>a</sup>	33.3% <sup>a</sup>	60.00% <sup>b</sup>	26.7% <sup>a</sup>	33.3% <sup>a</sup>	60.00% <sup>b</sup>	26.7% <sup>a</sup>	60.00% <sup>b</sup>	

Family	Species	Common Name	Period		
			I: 1938- 1957	II: 1960-1986	III: 1992-2016
	<i>Macrhybopsis marconis</i>	Burhead chub	6.7% a	0.0% a	26.67% b
	<i>Notemigonus crysoleucas</i>	Golden Shiner	6.7%	6.7%	0.00%
	<i>Notropis anabilis</i>	Texas Shiner	33.3% a	40.0% a	86.67% b
	<i>Notropis chalybaeus</i>	Ironcolor shiner	6.7% a	0.0% a	66.67% b
	<i>Notropis stramineus</i>	Sand shiner	6.7%	0.0%	0.00%
	<i>Notropis volucellus</i>	Mimic shiner	26.7% a	13.3% b	53.33% c
	<i>Notropis sp</i>		6.7%	6.7%	0.00%
	<i>Pimephales vigilax</i>	Bullhead minnow	6.7% a	6.7% a	26.67% b
Catostomidae	<i>Moxostoma congestum</i>	Gray redborse	0.0% a	0.0% a	80.00% b
Characidae	<i>Astyanax mexicanus</i>	Mexican tetra	26.7% a	60.0% b	80.00% c
Ictaluridae	<i>Ameiurus melas</i>	Black bullhead	0.0% a	0.0% a	13.33% b
	<i>Ameiurus natalis</i>	Yellow bullhead	20.0% a	46.7% b	73.33% c

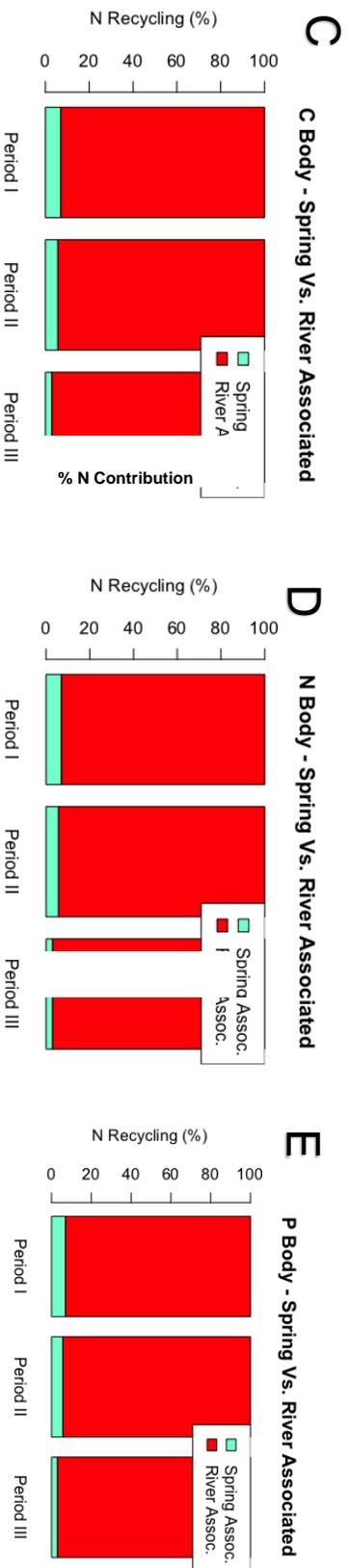
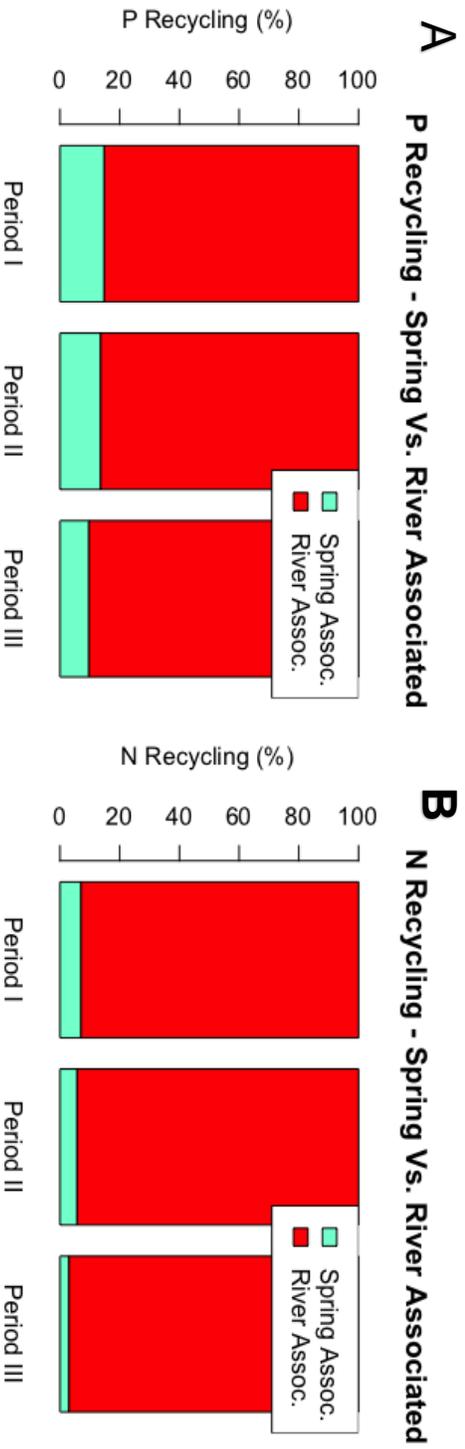
Family	Species	Common Name	Period		
			I: 1938- 1957	II: 1960-1986	III: 1992-2016
	<i>Ictalurus lupus</i>	Headwater catfish	6.7%	0.0%	0.00%
	<i>Ictalurus punctatus</i>	Channel catfish	26.7% a	6.7% b	46.67% c
	<i>Ictalurus</i> sp.	Chihuahua catfish	6.7%	0.0%	0.00%
	<i>Noturus sylvius</i>	Tadpole madtom	66.7% a	6.7% b	0.00% b
	<i>Noturus nocturnus</i>	Freckled madtom	6.7%	0.0%	0.00%
		Armored suckermouth catfish			
Loricariidae	<i>Hypostomus</i> sp./ <i>Loricariidae</i>	Blackstripe topminnow	0.0% a	0.0% a	66.67% b
Fundulidae	<i>Fundulus notatus</i>		6.7%	6.7%	0.00%
Poeciliidae	<i>Gambusia affinis</i>	Mosquitofish	40.0% a	40.0% a	86.67% b
	<i>Gambusia geiseri</i>	Largespring gambusia	60.0% a	60.0% a	80.00% b
	<i>Gambusia georgei</i>	San Marcos gambusia	0.0% a	20.0% b	0.00% a

Family	Species	Common Name	Period		
			I: 1938- 1957	II: 1960-1986	III: 1992-2016
	<i>Gambusia</i> sp.		6.7% a	0.0% a	66.67% b
	<i>Poecilia formosa</i>	Amazon molly	0.0% a	60.0% b	33.33% c
	<i>Poecilia latipinna</i>	Sailfin molly	33.3% a	46.7% a	66.67% b
	<i>Cyprinodon variegatus</i>	Sheepshead minnow	6.7% a	0.0%	0.00%
	<i>Atherinopsidae</i>				
	<i>Menidia beryllina</i>	Inland silverside	0.0% a	0.0% a	13.33% b
	<i>Centrarchidae</i>				
	<i>Ambloplites rupestris</i>	Rock bass	26.7% a	33.3% a	60.00% b
	<i>Lepomis auritus</i>	Redbreast sunfish	13.3% a	20.0% a	93.33% b
	<i>Lepomis cyanellus</i>	Green sunfish	26.7% a	20.0% a	40.00% b
	<i>Lepomis gulosus</i>	Warmouth	20.0% a	13.3% a	66.67% b
	<i>Lepomis macrochirus</i>	Bluegill	46.7% a	33.3% b	86.67% c
	<i>Lepomis megalotis</i>	Longear sunfish	13.3% a	6.7% a	66.67% b
	<i>Lepomis microlophus</i>	Redear sunfish	26.7% a	26.7% a	53.33% b
	<i>Lepomis miniatus</i>	Redspotted sunfish	20.0% a	0.0% b	66.67% c

Family	Species	Common Name	Period		
			I: 1938- 1957	II: 1960-1986	III: 1992-2016
	<i>Lepomis punctatus</i>	Spotted sunfish	26.7% a	53.3% b	26.67% a
	<i>Lepomis</i> sp.		6.7% a	0.0% a	66.67% b
	<i>Micropterus dolomieu</i>	Smallmouth bass	0.0%	6.7%	6.67%
	<i>Micropterus salmoides</i>	Largemouth bass	40.0% a	26.7% b	93.33% c
	<i>Micropterus</i> sp. X sp.		6.7%	0.0%	0.00%
	<i>Micropterus treculii</i>	Guadalupe bass	6.7% a	0.0% a	33.33% b
Percidae	<i>Etheostoma fonticola</i>	Fountain darter	80.0% a	20.0% b	80.00% a
	<i>Etheostoma lepidum</i>	<del>Greenthroat</del> darter	0.0%	0.0%	6.67%
	<i>Etheostoma spectabile</i>	<del>Orangethroat</del> darter	20.0% a	6.7% b	73.33% c
	<i>Percina carbonaria</i>	Texas <del>logperch</del>	20.0% a	0.0% b	66.67% c
	<i>Percina apristis</i>	Guadalupe darter	53.3% a	13.3% b	80.00% c
	<i>Percina</i> sp.		0.0% a	0.0% a	26.67% b

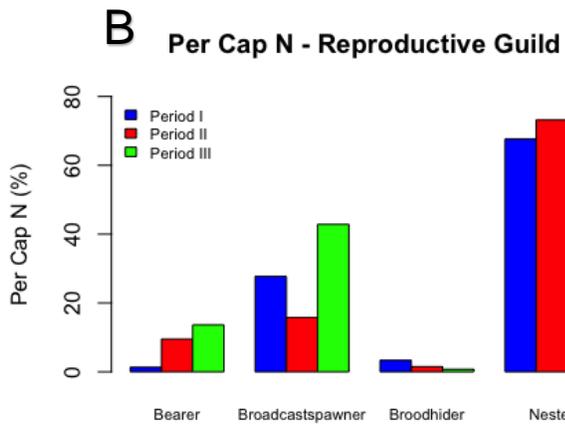
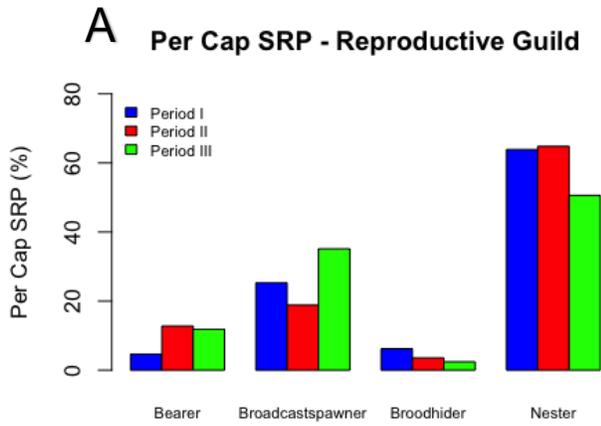
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Family	Species	Common Name	Period		
			I: 1938- 1957	II: 1960-1986	III: 1992-2016
<u>Cichlidae</u>	<u><i>Cichlasoma cyanoguttatum</i></u>	Rio Grande perch	53.3% a	46.7% a	80.00% b
	<u><i>Oreochromis aureus</i></u>	Blue tilapia	0.0% a	13.3% b	46.67% c



**Appendix 3.** Occurrence-weighted contributions of spring vs. riverine associated species across the three time periods: %P recycling (A), %N recycling (B), and %C,N,P body content (C-E).

**Appendix 4.** Contributions of different reproductive guilds to % P recycling (A) and N recycling (B).



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