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# Influence of urbanization on a karst terrain stream and fish community

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**Abstract** Effects of catchment urbanization described as the urban stream syndrome generally result in an altered fish community with headwater stream fish communities particularly vulnerable to changes associated with urbanization. In this study, we considered how the fish community in a Central Texas headwater karst stream changed with catchment urbanization. Paleohistory and a narrative on urbanization within the upper San Marcos River were compiled and qualitatively related to historical fish changes from 1880 to 2011 to test predictions of the urban stream syndrome. Our predictions of decreases in native fish community and species abundances were largely unsupported despite 170 years of urbanization, specifically anthropogenic alterations to instream and catchment habitats, water quantity and water quality, stream morphology, and introduced species. Overall, the upper San Marcos River supports a persistent (>60 %) fish community through time with observed native species declines and extirpations not attributed solely to urbanization within the catchment. As such, we conclude that upper San Marcos River is largely an exception to the urban stream syndrome, which we attribute to two mechanisms; 1) paleohistory of the upper San Marcos River suggests a dynamic stream system with decreasing stream flow and increasing water temperatures since the last glacial maximum, and 2) water quantity of the San Marcos River is much greater than water quantity of other headwater streams used to assess urban stream syndrome. Nevertheless, the lower portion of the upper San Marcos River is indicative of an altered system, in both habitat and fish community, and represents a target area for rehabilitation.

**Keywords** Urbanization · Karst stream · Historical narrative · Long-term fish community changes

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## Introduction

Effects of catchment urbanization on stream ecosystems arise from an array of interrelated factors and are described as the urban stream syndrome (Hughes et al. 2014; Kaushal and Belt 2012; O'Driscoll et al. 2010; Walsh et al. 2005). Although variable in level of disturbance, urban stream syndrome is associated with changes in hydrology (Roy et al. 2009; Konrad and Booth 2005), altered stream morphology (Brown et al. 2005), and increased nutrients and contaminants (Brown et al. 2009). Combined effects of expanding impervious surfaces and transport of runoff via man-made structures (e.g., culverts, pipes, and concrete ditches) increase the frequency and magnitude of stream flows (Weaver and Garman 1994; Brown et al. 2005), whereas excessive groundwater pumping and decreased direct recharge areas can lower base flows (Finkenbine et al. 2000; Roy et al. 2009). Modification of a stream's hydrology alters streambed composition and stream morphology, resulting in stream channelization and reduced habitat complexity (Walsh et al. 2005). Urban runoff and treated wastewater, often returned to the stream near urban areas, elevate water temperatures and increase concentrations of chemical pollutants, suspended sediments, and nutrients such as phosphorus and nitrates (Nelson and Palmer 2007). An amalgamation of these abiotic changes generally results in an altered aquatic community with reduced biotic richness and increased abundance of tolerant taxa (Morgan and Cushman 2005).

Headwater streams (i.e., 1st order – 3rd order) support diverse and distinct aquatic communities that often contain rare or endemic taxa (Meyer et al. 2007); however, these streams are particularly susceptible to changes associated with urbanization (Morgan and Cushman 2005; Smith and Lamp 2008). Headwater streams constitute the largest fraction of stream length and occur across a wide variety of geological landscapes (Clarke et al. 2008) while their generally smaller size and inconspicuous nature make them more vulnerable to urban disturbances (Meyer and Wallace 2001). Small streams are prone to stream burial (i.e., streams are entirely converted into pipes, culverts, or drainage ditches), resulting in natural stream destruction and aquatic habitat fragmentation (Elmore and Kaushal 2008). Excessive groundwater pumping or increases in impervious surfaces within urban areas decrease stream flow and, in some regions, cause cessation of flows, which is important as headwater streams often originate as groundwater discharge (Winter 2007; Sharp 2010). Stream burial and reduced groundwater discharge restrict or eliminate available habitat for rare or endemic taxa within headwater streams through habitat alteration, fragmentation, and loss, increasing the risk of localized extirpations or extinctions (Warren and Burr 1994; Hubbs 1995; Gage et al. 2004).

The Edwards Plateau region in Texas contains one of the most productive karst aquifers (i.e., Edwards Aquifer) in North America, serving as a major water source for a rapidly growing urban population and several headwater streams supporting distinct biological communities (Loáiciga 2009; Maxwell 2012). Currently, four of the 100 fastest growing counties and the second and 16th fastest growing metropolitan areas in the USA are located within the Edwards Plateau region (2012 U.S. Census). Within the last several decades, catchment urbanization among Edwards Plateau watersheds has been an increasing concern (Sung and Li 2010). Small springs and headwater streams have ceased flowing with larger streams experiencing deceased base flows from lowered groundwater levels (Brune 1981) with increases in impervious cover, groundwater extraction, and stream burial listed among contributing factors (Zektser et al. 2005; Sung and Li 2010). Springs and headwater streams originating from the Edwards Aquifer have historically demonstrated relatively constant water quality and quantity, providing habitat for 90 endemic aquatic species of invertebrates, fish, reptiles, and amphibians (Bowles and Arsuffi 1993; Maxwell 2012). Among native fishes in the region, 30 % (i.e., 20 species) of the fish fauna are endemic with 34 % (i.e., 23 species) of the native fishes listed as imperiled (Thomas et al. 2007; Hubbs et al. 2008). Several studies document fish community changes within urbanized headwater streams of Edwards Plateau, primarily reporting occurrence of introduced species (Whiteside and Berkhouse 1992; Edwards 2001; Lopez-Fernandez and Winemiller 2005) but also long-term (e.g., ~70 years) shifts in community structure (Labay et al. 2011; Perkin and Bonner 2011). However, the latter two studies did not directly assess the effects of fish community change related to urbanization other than alterations of hydrology (Perkin and Bonner 2011).

Purpose of this study was to assess long-term changes in a fish community associated with catchment urbanization in a representative Edwards Plateau headwater karst stream. Urbanization within the Edwards Plateau will increase into the foreseeable future. As such, understanding relationships among urbanization, instream habitat, and biotic responses are necessary to mitigate and manage anthropogenic alterations (Hughes et al. 2014) within the catchment basin and within streams of Edwards Plateau headwater streams. We selected the upper San Marcos River for this assessment, because of its long record of fish collections (130 years) and urbanization (170 years) and designation as critical habitat for five federally listed taxa, using the urban stream syndrome model (Walsh et al. 2005) to establish predictions. Specifically, we predict that native fish richness and diversity (Shannon-Wiener) have decreased through time, associated with increasing urbanization, and that community structure has shifted towards increasing abundances of tolerant native taxa or introduced fishes. To test these hypotheses, we calculated fish community indices (taxa richness, diversity, and persistence), assessed fish community shifts through time using similarity matrices, and examined abundance changes in individuals species as well as habitat guilds and reproductive guilds during the period of fish collection records. To relate detectable changes in the fish community to urbanization, we 1) qualitatively describe paleohistory of the upper San Marcos River, providing a working model on the natural variation of the river as the context to measure changes relating to urbanization, and 2) qualitatively describe history and effects of urbanization within the upper San Marcos River, with effects relating specifically to reported alterations in instream and catchment habitats, water quantity and quality, and stream morphology. Steedman et al. (1996) offers compelling justification for the use of narrative prose (qualitative rather than quantitative) to assess relationships between human activity and ecosystems in retrospective analysis, such as this study. Briefly, the authors argue that human effect on ecosystems is multi-dimensional, consisting of numerous inter-related factors; isolating individual factors is rarely successful, if even possible. Instead the authors recommend assessing cumulative effects in aggregate with "qualitative generalization".

## Methods

### Study area

The upper San Marcos River originates from groundwater discharge of the Edwards Aquifer at San Marcos Springs in the City of San Marcos, southeast Hays County, Texas and flows approximately 8 km southeast before reaching its confluence with the Blanco River (Fig. 1). Characterized by relatively constant temperature and flow (Groeger et al. 1997), the upper San Marcos River is a major aquatic recreational area and source of surface water or groundwater for the City of San Marcos, Texas State University-San Marcos, and the Texas Department of Parks and Wildlife A. E. Wood Fish Hatchery and supports nine regionally endemic fishes and fishes of conservation concern (Hubbs et al. 2008; Behen 2013). The upper San Marcos

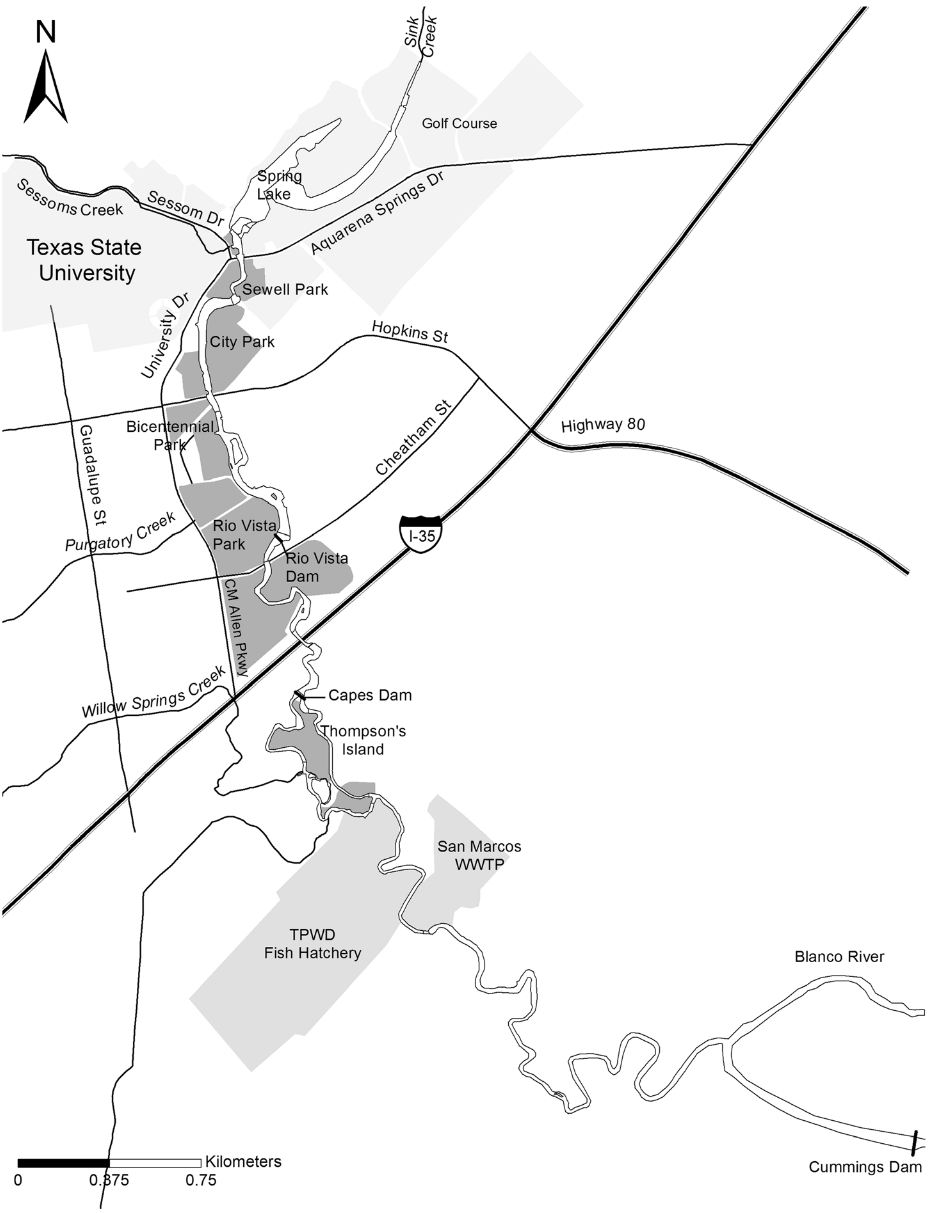


**Fig. 1** Site map of the upper San Marcos River, Hays County, Texas. *Dark gray polygons* denote San Marcos city parks

catchment drains approximately 250 $km^2$ and receives a mean annual precipitation of 86 cm. Two major ecoregions of Texas conjoin in the upper San Marcos catchment, a result from faulting in the underlying bedrock, with the Edwards Plateau rising sharply to the west and the Blackland Prairie sloping gently to the east. Soils in the Upper San Marcos catchment consists of predominantly exposed cretaceous limestone and shallow Holocene soils on top of cretaceous limestone at higher elevations, and Quaternary alluvium deposits overlaying cretaceous limestone at lower elevations (Nickels and Bousman 2010). Census of European settlement began in the late 1800s and is used herein as a baseline for measuring urbanization. Since founded in 1881, the City of San Marcos has exponentially increased at a rate of 3 % over 129 years and was listed as the fastest growing large city in USA by the US Census Bureau in 2012.

## Data compilation

Historical and contemporary narratives of the upper San Marcos River watershed were developed from published literature, agency reports, and city records obtained from the public library. We compiled historical conditions of the upper San Marcos River including the paleohistory of the San Marcos River and habitat characterization prior to census of European settlement (i.e., 1881). Effects of urbanization post European settlement were categorized based on their disturbance of the upper San Marcos system (i.e., stream morphology, water quantity, water quality, riparian alteration, and biological alteration) and a category (i.e., protection) was included to document watershed and species protection policies (e.g., city ordinances, federal listing of threatened or endangered species, habitat conservation plans, groundwater use restrictions, and establishment of non-governmental organizations or NGOs).

Historical fish data (1880–2000) were obtained from Perkin and Bonner (2011) and supplemented by 2011 collections (Behen 2013). Perkin and Bonner (2011) obtained historical fish data from published literature, museum collections, and agency reports and inspected data to minimize uncertainties and excluded any questionable data sets. See Perkin and Bonner (2011) for a detailed description of data censoring. Behen (2013) sampled eighteen sites within the upper San Marcos River quarterly from January to December 2011 as part of a fish-habitat association study. At each site, fish were quantified among multiple line transects using common seines (3.0×1.8 m strait seine) within wadeable habitats and underwater observation within deep-water habitats. For the purposes of this study, we grouped Behen (2013) fish community data by river reach (i.e., upstream of I-35, and downstream of I-35), season, and gear type (i.e., seine or underwater observation).

## Statistical analysis

Inferring community and species responses through time is challenging given that species were collected by multiple collectors, for various purposes, with possibly incomplete reporting of fish captures, using a variety of sampling techniques, and often without reporting effort. As such and similar to the acknowledgment by Perkin and Bonner (2011), we acknowledge limitations of a historical collation of fish collections and are aware of the increased likelihood of spurious and aberrant results, but emphasize that limitations do not necessarily preclude quantitative assessments. Nevertheless, we were limited in the type of response variables to include in our assessment, namely fish densities, since reporting of effort per site and collection date was rarely given. Given our awareness of spurious and aberrant results, we analyzed the data set in three ways in order to assess and understand different aspects and scales of the data set and to identify potentially misleading or unusual data: 1) we assessed community response variables (i.e., taxa richness, diversity, and persistence) with general linear models, 2) assessed community structure (occurrence and abundances) with non-metric multidimensional scaling and ANOSIM, an analogue of univariate ANOVA, and 3) assessed species responses with general linear models.

Community response variables were calculated within each decade, rather than Julian date, to simplify our analyses and increase sample size for the response variables spanning a decade rather than specific dates. Due to the paucity of fish collections prior to 1900, we grouped fish collections from 1880 and 1890 into one (1890). Taxa richness, rather than species richness, was calculated because of grouping of two congener (*Gambusia geiseri* and *Gambusia affinis*) in most past collections, taxonomic uncertainties with *Hypostomus* (Nico and Martin 2001), and grouping of larval and juvenile *Lepomis*. Diversity was calculated with the Shannon-Weiner Diversity index (Spellerberg and Fedor 2003), and persistence was calculated from an index of species turnover rates using the formula provided in Meffe and Minckley (1987). Index of fish community persistence ranged from zero (i.e., no persistence) to one (i.e., complete persistence). We calculated taxa richness, diversity, and persistence for the entire fish community (introduced and native fishes) and native taxa richness, native diversity, and native persistence for native fishes only, but only tested response variables of native fishes among decades. Justifications for testing native fishes, rather than the introduced and native fishes, include a priori knowledge that numbers of introduced species have increased through time in the upper San Marcos River (Hubbs et al. 2008; Perkin and Bonner 2011) and our primary interest is assessing changes to native fish species.

Before testing linear relationships among response variables and decade, we sought to understand and minimize the influence of confounding factors that might relate independently with taxa richness, diversity, and persistence. Number of fish collections by decade (hereafter effort) ranged from 2 to 26 collections, and number of individuals collected by decade (hereafter Total N) ranged from 184 to 19,964.

We assessed relatedness among effort, Total N, and response variables with correlation analysis. If significant correlations ($\alpha$=0.05) were not detected (statistical tests not shown), we interpreted this as effort or Total N had minimal or no influence on the response variables and were dropped from further analyses. If significant correlations were detected, multiple regression models were constructed to test the partial relationships between a response variable, decade (1890–2010; independent variable of interest), confounding variables (effort or Total N), and interaction terms. All interaction terms were not significant and removed from the final regression models.

Changes in the upper San Marcos River fish community among decades was assessed by Bray-Curtis similarity matrices created in Primer 6.1.6 and tested with an analysis of similarity (ANOSIM; $\alpha$=0.05; 9,999 permutations) using permutations to assess average rank dissimilarity among decades. Rare species (i.e., <0.1 % relative abundance) and species reported only once among collections were removed from analyses. Data were fourth-root transformed to standardize contribution of low and high abundant species and illustrated using a multidimensional scaling (MDS) plot by plotting the centroids of fish collections for each decade. Within Primer, the similarity percentage option (SIMPER) was used to identify percent fish community dissimilarities among decades and to determine which species constituted the majority of dissimilarity among decades.

Species changes and guild changes in the upper San Marcos fish community were assessed using simple linear regression models. Relative abundance of dominant taxa (i.e., >1 % relative abundance) and species of special concern were calculated for each collection date within each decade and were further Z-score transformed to standardize relative abundance distributions among collection events (Perkin and Bonner 2011). Julian date rather than decade was the independent variable to obtain the lowest possible level of resolution for species. Habitat (i.e., lentic tolerant and fluvial specialist) and reproductive guilds (i.e., nest, brood hiders, internal bearer, open substratum, and substratum chooser) were determined for each dominant species and species of concern by decade using the reproduction classification scheme of Simon (1999) and habitat associations listed in Thomas et al. (2007). Simple linear regressions were used to test if slope (b) of individual species relative abundances and relative abundance of each habitat and reproductive guild differed ($\alpha$=0.05) through time from zero and were classified as increasing ($b$>0.01), decreasing ($b$<0.01), or stable ($b$=0) in abundance. Status for species in low abundance (i.e., <1.0 % relative abundance among all collections) were classified as indeterminable.

## Results

### Paleohistory of the upper san marcos river narrative

Near the end of the last glacial maximum (14,000 to 11,000 B.P.), Edwards Plateau valleys consisted of vast alluvial deposits and laterally mobile streams (Blum et al. 1994), especially in areas east and south of the Balcones Escarpment where higher gradient streams of the plateau exit onto the lower gradient coastal plains of Texas (Sylvia and Galloway 2006). Laterally mobile streams with voluminous discharges up to four times of that in contemporary times (Sylvia and Galloway 2006) provided sufficient erosive capabilities to down-cut confining limestone layers of the Edwards Aquifer, creating the major portion of the Edwards Aquifer (Deike 1990) and artesian springs along the southeastern edge of the Edwards Plateau (Woodruff and Abbott 1979; Grimshaw and Woodruff 1986). Eventually, laterally mobile streams migrated away from the newly tapped spring openings and abandoned the eroded stream channel to create oxbows. Newly created spring outflows of the Edwards Aquifer maintained connectivity to the mobile main channel, forming a spring run rather than a more traditional oxbow. This sequence of events likely describes the origin of the San Marcos springs and San Marcos River by down cutting from a former channel of the Blanco River (Grimshaw and Woodruff 1986). Timing is supported by the age of the alluvial deposits on top of the confining limestone layer near San Marcos springs (11,500 B. P.; Bousman and Nickels 2003) and rates of dolomite dissolution within the Edwards Aquifer (11,000 B. P. during early Holocene; Deike 1990).

From early Holocene to pre-European settlement, the San Marcos River and contributing watershed sustained variable climates and changes in stream characteristics. Paleoclimate cycled between more mesic and cooler temperatures (3 to 6 °C cooler than present; Toomey et al. 1992) to more xeric and warmer temperature conditions (Toomey et al. 1992; Russ et al. 2000; Al-Rabab'ah and Williams 2004). Substrate of the newly formed San Marcos River, or former channel of the Blanco River, was likely similar to contemporary substrates of the Blanco River: a mix of sand, gravel, cobbles, and boulders (Bean et al. 2007) overlaying limestone bedrock on the escarpment (<0.5 km from spring outflows) or overlaying Taylor Marl east of the escarpment. The relatively smaller watershed of the San Marcos River reduced scouring of the stream bed and allowed sediment aggradation throughout the spring run, which likely continued to be laterally mobile. The area of the spring outflows formed a large bog during more mesic conditions but was reduced in volume about 7,000 B.P. (Bousman and Nickels 2003), coinciding with climate shifts towards more xeric conditions. With sediment aggradation and lateral mobility caused by less frequent but intense tropical spates (Baker 1975), stream morphology became more sinuous, forming islands (Sanborn 1944) and heterogeneous mix of water depths, current velocities, and exposed Taylor marl, silt, gravel, and cobble substrates (Saunders et al. 2001). Among spring runs of the Edwards Plateau, periodic large floods (>150 $m^3$/s; Baker 1975; O'Connor and Costa 2004) generated from monsoonal and frontal precipitation and runoff radically alter stream morphology. Riffle-run-pool mesohabitats with heterogeneous substrates shift to riffle-run mesohabitats with gravel, cobble, and bedrock substrates (Baker 1975; Watson 2006). Through time, spring runs transition back to more pool habitats with sediment aggradation before the next large flood. As sediments are added, mesohabitats and substrate heterogeneity increased with large floods resetting the stream morphology.

## History and effects of urbanization in the upper san marcos river

Records of European settlement in the upper San Marcos River watershed date to the 17th century, but anthropogenic alterations to instream and catchment habitats in the upper San Marcos River are generally documented after the founding of the City of San Marcos in 1846. The earliest record of stream alterations is the construction of Spring Lake dam in 1849, raising water elevation up to 3.5 m over the spring outflows (Appendix 1). Low head dams (i.e., Ed Cape's Dam, 1867) and mill races were constructed for irrigation purposes, stream channels were dredged to alter water flow, riparian and bottomland timbers were harvested, and a National Fish Hatchery was located near the headwaters (i.e., present day Texas State University – San Marcos campus) during the latter half of the 19th century. During the 20th century, additional dams were constructed and water diverted from the main channel within the spring run reach (e.g., Rio Vista Dam and Resort, 1904) and downstream of the San Marcos River and Blanco River confluence (Cummings Dam, 1914). Effluents from wastewater treatment plants entered near the headwaters (i.e., present day City Park) beginning in 1907, but water quality concerns, including warnings about contact recreation in the 1930s, eventually led City of San Marcos to relocate the wastewater treatment plant farther downstream to its current location and near another wastewater effluent (Texas Parks and Wildlife State Fish Hatchery, 1949). Recreational value of the San Marcos River prompted dredging, adding gravel and rock substrates, and constructing retaining walls along stream margins to form Sewell Park beginning in 1917. A golf course and hotel, predecessor of the Aquarena Springs Theme Park (1950), were located adjacent to Spring Lake in 1928. From 1944 through 1970, the property of Aquarena Springs Theme Park operated an aquatic vegetation business, harvesting at times up to 700 kg of vegetation per day and cultivating exotic vegetation to raise and harvest. Sediments were dredged and vegetation removed periodically in Spring Lake and in the San Marcos River through the late 1980s. Meanwhile, watershed flood retentions dams were constructed in the mid-1980s within the watershed to prevent catastrophic flooding (Earl and Wood 2002). By the late 1980s, regulation and management of species listed under Endangered Species Act in the 1970s limited instream changes in channel morphology and aquatic habitats, and federal, state and local agencies and NGOs become more aware and involved in groundwater, surface water, and watershed monitoring and protection.

Some alterations in water quantity and water quality are evident in the upper San Marcos River. Decreases in water quantity are not detectable in San Marcos Springs discharge (USGS Gage #08170000; period of record: 1956–1998; Saunders et al. 2001), despite an estimated 46,600 ha m pumped annually from the Edwards Aquifer from 1955 through 2007 (Edwards Aquifer Authority 2011). Period of record (1994–2011) is insufficient to quantify long term changes in San Marcos River surface flows (USGS Gage #08170500; Fig. 2). A longer period of record exists for USGS Gage #08170500, but the original location of this gage did not support accurate measurement of surface water discharge. Historical and contemporary surface water diversions (235 hectare-meter/year authorized use; mean water use = 8.4 hectare-meter/year, SE=0.72; 1994–2008) for municipal and agriculture purposes in the upper San Marcos River potentially can reduced base flows by <0.1 % on average, and flood retention dams (i.e., watershed structures constructed by the Soil Conservation Service) likely have attenuated small flood pulses as these and other retention dams have done in the lower San Marcos River

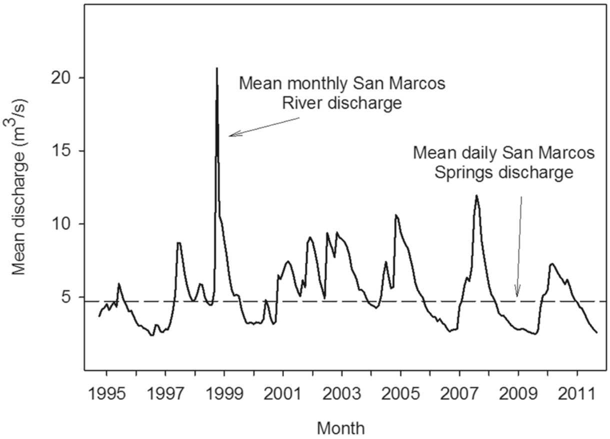


**Fig. 2** Hydrograph of San Marcos River discharge from earliest period of record (1994) through 2011 (USGS Gage #08170500). *Dashed line* represents mean San Marcos Springs discharges (USGS Gage #08170000) from 1956 through 1998 (Saunders et al. 2001)

(Perkin and Bonner 2011). Water is considered very high quality (Groeger et al. 1997) and assigned as exceptional aquatic life use and primary contact recreation use by TCEQ water quality standards (TCEQ 2010). However, degradation of water quality occurs frequently in the urbanized area of the San Marcos River, including abnormal rates of sedimentation and non-point source pollution, riparian vegetation degradation, turbidity and redistribution of sediments because of recreation, nutrient enrichment from the state fish hatchery (EARIP Habitat Conservation Plan, Recon Environmental Inc. et al. 2012) and City of San Marcos (Groeger et al 1997), and accidental releases of wastewater and chemicals into the river from Texas State University and City of San Marcos (Houston Chronicle 10/01/2000; San Marcos Daily Record 10/31/2010, San Marcos Daily Record 5/30/2013).

Anthropogenic alterations to steam morphology are quantified by Saunders et al. (2001). Briefly, low-head dams convert run type habitats with sandy and gravel substrates to pool habitats with more silt substrates; flood retention dams reduce frequency and intensity of flushing flows to suspend and move fine substrates. Low head dams in the upper San Marcos River trap sediments and provide slackwater habitats (Saunders et al. 2001; Behen 2013). Spring Lake, Rio Vista, and Capes dams trap substantial amounts of substrates upstream, creating a heterogeneous mix of mesohabitat and substrates interspersed between runs and some riffle habitats (Fig. 3). With sediments retained upstream, mesohabitats and substrates are cumulatively less heterogeneous downstream of Capes Dam (Hudson 2012). Along with greater water depths attributed to Cummings Dam and lower water quality and reduced clarity associated with treated wastewater discharges (City of San Marcos and TPWD state fish hatchery; Groeger et al. 1997), greatest deviations from natural spring run conditions exist downstream from Capes Dam to the confluence with the Blanco River.

## Quantification of fish community changes (1880–2011)

A total of 40,966 individuals consisting of 12 families and 56 fish species was taken in 102 collections from the upper San Marcos River (Table 1). Across decades, Poeciliidae were the most abundant (36 %) followed by Cyprinidae (23 %), Centrarchidae (23 %), and Percidae (11 %). Most abundant species were *Gambusia* spp. (30.5 %), Spotted Sunfish *Lepomis*

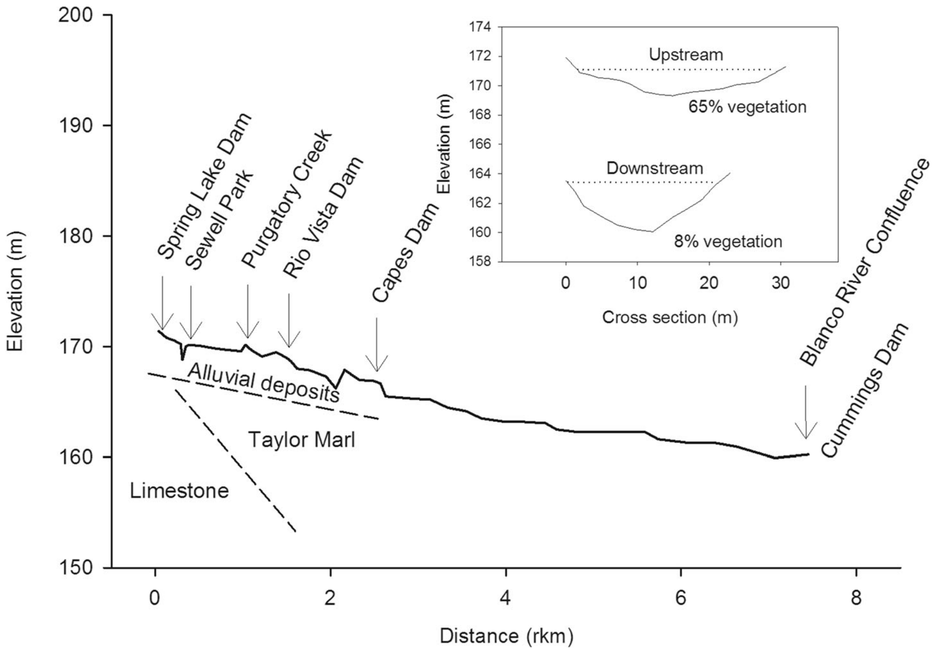


**Fig. 3** Longitudinal profile and river cross sections upstream and downstream of Capes Dam for the upper San Marcos River. We used bathymetry and physical habitat estimates collected in 2009 (Hardy et al. 2012) to document contemporary stream elevation profile, cross sections, and aquatic vegetation and substrate composition for the upper San Marcos River

*miniatus* (9.3 %), Texas Shiner *Notropis amabilis* (7.7 %), Fountain Darter (7.2 %), and Bluegill Sunfish *Lepomis macrochirus* (4.7 %). Native fishes comprised 86 % (range: 69 % in 1960 to 100 % in 1890). Native richness differed ($P<0.01$) with effort ($\beta_1=0.95$; SE=0.235; $P<0.01$) but not among decades ($\beta_2=0.05$; SE=0.038; $P=0.25$). Native diversity did not differ ($P>0.05$) among decades ($\beta_1>-0.01$; SE=0.004; $P=0.61$) and Total N ($\beta_2>-0.01$; SE <0.001; $P=0.09$), and native persistence did not differ ($P>0.05$) among decades ($\beta_1<0.01$; SE=0.002; $P=0.23$) and Total N ($\beta_2<0.001$; SE: <0.001; $P=0.48$) (Fig. 4).

Upper San Marcos River fish community similarity differed among decades (ANOSIM global $R=0.273$, $P<0.01$) with greatest dissimilarity observed between 1890 and following decades (1930–2010; Fig 5). The fish community in 1890 was >50 % dissimilar (range 58–95 %) to other decades, whereas succeeding decades (1930–2010) generally demonstrated <50 % dissimilarities in fish community composition (Table 2). Absence of introduced species and high abundance of fluvial specialists (i.e., Burrhead Chub and Guadalupe Darter *Percina apristis*) and Red Shiner *Cyprinella lutrensis* among 1890 collections contributed to high fish community dissimilarity among 1890 and later decades. Contributing to community dissimilarities among 1930 and other decades were low species richness, low abundance of fluvial specialists (e.g., Texas Shiner and Blacktail shiner *Cyprinella venusta*), and lack of introduced species (i.e., *Poecilia* spp. and redbreast sunfish *Lepomis auritus*). The 1950 collections contained high abundances of Fountain Darter (31 %) and 1960 was the only decade to document occurrence of San Marcos Gambusia. Absence of *Gambusia* spp., Fountain Darter, and Texas Shiner among 1970 collections contributed to fish community dissimilarities among 1970 and other decades. The 1990 fish community was slightly dissimilar from other decades

**Table 1** Native status, mean relative abundance per decade and overall, population trend and associated *p*-value for species collected in the upper San Marcos River

| Species | Status | Decade | | | | | | | | | | Overall | Population trend | *p*-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1890 | 1930 | 1940 | 1950 | 1960 | 1970 | 1980 | 1990 | 2000 | 2010 | | | |
| *Lepisosteus oculatus* | N | | | | | | 0.05 | | 0.29 | | 0.04 | 0.04 | – | |
| *Lepisosteus osseus* | N | | | | | | | | 0.04 | | | <0.01 | – | |
| *Dorosoma cepedianum* | N | | | | | | | | 1.65 | | | 0.17 | – | |
| *Campostoma anomalum* | N | | | | 0.04 | 0.05 | | 1.76 | 0.99 | 0.01 | | 0.29 | – | |
| *Carassius auratus* | I | | | | | | | 1.03 | | | | 0.10 | – | |
| *Cyprinella lutrensis* | N | 22.83 | 0.24 | 9.40 | 0.54 | | | 1.32 | | | | 3.43 | −0.012 | <0.01 |
| *Cyprinella venusta* | N | | | 11.91 | 4.17 | 0.38 | 0.81 | 11.03 | 11.54 | 0.08 | 1.17 | 4.11 | S | |
| *Cyprinus carpio* | I | | | | | | | | 0.17 | | 0.01 | 0.02 | – | |
| *Dionda nigrotaeniata* | N | | | 1.34 | 0.61 | 0.65 | 2.33 | 3.53 | 1.16 | 0.14 | 0.96 | 1.07 | S | |
| *Macrhybopsis marconis* | N | 14.67 | | | 0.27 | | | | 0.21 | | 0.02 | 1.52 | −0.042 | <0.01 |
| *Notemigonus crysoleucas* | N | | | | 0.04 | 0.32 | | 0.44 | 0.08 | | | 0.09 | – | |
| *Notropis amabilis* | N | 7.61 | 22.99 | 7.89 | 7.35 | 1.58 | | 8.16 | 15.35 | 0.16 | 5.94 | 7.70 | S | |
| *Notropis chalybaeus* | N | | 0.47 | | 0.08 | | | | 0.95 | 0.27 | 1.40 | 0.32 | +0.008 | <0.01 |
| *Notropis stramineus* | N | | | | 0.08 | | | 1.76 | | | | 0.18 | – | |
| *Notropis volucellus* | N | 10.87 | | 0.50 | 1.03 | | | 3.24 | 11.63 | 0.03 | 0.39 | 2.77 | S | |
| *Pimephales vigilax* | N | 4.89 | | | | | | 0.07 | 0.12 | 0.01 | 0.02 | 0.51 | – | |
| *Ictiobus bubalus* | N | | | | | | | | 0.04 | | | <0.01 | – | |
| *Moxostoma congestum* | N | 0.54 | | | | | 0.11 | 0.15 | 1.99 | 0.02 | 0.45 | 0.33 | – | |
| *Astyanax mexicanus* | I | | 2.37 | 0.84 | 0.50 | 0.22 | 12.60 | 8.31 | 1.86 | 0.11 | 1.03 | 2.78 | S | |
| *Ameiurus melas* | N | | | | | 0.75 | 0.05 | | 0.17 | 0.01 | | 0.10 | – | |
| *Ameiurus natalis* | N | | | 1.68 | 1.34 | 0.38 | 0.16 | 1.10 | 0.33 | 0.33 | 0.15 | 0.55 | – | |
| *Ictalurus lupus* | N | | | 0.34 | | | | | | | | 0.03 | – | |
| *Ictalurus nebulosus* | N | | | | | | 0.05 | | | | | 0.01 | – | |

**Table 1** (continued)

| Species | Status | Decade | | | | | | | | | | Overall | Population trend | *p*-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1890 | 1930 | 1940 | 1950 | 1960 | 1970 | 1980 | 1990 | 2000 | 2010 | | | |
| *Ictalurus punctatus* | N | 1.63 | | | 0.69 | 0.22 | | | 0.21 | 0.02 | 0.05 | 0.28 | – | |
| *Noturus gyrinus* | N | | 2.13 | 0.84 | 7.19 | 0.05 | | | | | | 1.02 | −0.008 | <0.01 |
| *Noturus nocturnus* | N | | | | 0.15 | | | | | | | 0.02 | – | |
| *Hypostomus sp.* | I | | | | | | | | | 0.09 | 3.55 | 0.36 | – | |
| *Fundulus notatus* | N | | | | 0.04 | | | 0.07 | 0.37 | 0.02 | | 0.05 | – | |
| *Gambusia georgei* | N | | | | | 3.77 | | | | | | 0.38 | – | |
| *Gambusia* spp. | N | 5.43 | 35.78 | 14.60 | 17.21 | 46.20 | 0.00 | 23.82 | 11.09 | 83.67 | 67.05 | 30.49 | +0.011 | <0.01 |
| *Poecilia formosa* | I | | | | | 15.99 | 0.06 | 3.31 | 0.58 | 0.01 | 0.18 | 2.01 | S | |
| *Poecilia latipinna* | I | | | 4.03 | 4.09 | 9.71 | 0.05 | 3.16 | 2.77 | 0.65 | 1.74 | 2.62 | S | |
| *Cyprinodon variegatus* | I | | | | 0.04 | | | | | | | <0.01 | – | |
| *Ambloplites rupestris* | I | | | 1.34 | 0.92 | 0.12 | 2.54 | 2.28 | 1.45 | 1.52 | 0.44 | 1.06 | S | |
| *Lepomis auritus* | I | | | | 0.69 | 0.22 | 6.81 | 2.35 | 10.96 | 0.25 | 4.76 | 2.61 | 0.014 | <0.01 |
| *Lepomis cyanellus* | N | | | | 0.23 | 0.49 | 0.11 | 1.10 | 0.37 | 0.03 | 0.05 | 0.24 | – | |
| *Lepomis gulosus* | N | | 0.95 | | 0.46 | 0.11 | 2.60 | 0.29 | 1.08 | 0.12 | 0.03 | 0.56 | – | |
| *Lepomis macrochirus* | N | | 1.90 | 12.08 | 3.21 | 1.63 | 17.79 | 3.53 | 5.46 | 0.35 | 1.22 | 4.72 | S | |
| *Lepomis megalotis* | N | 8.70 | | | 0.31 | 0.05 | 0.00 | 0.07 | 1.37 | 0.02 | 0.12 | 1.06 | S | |
| *Lepomis microlophus* | N | | 5.21 | | 0.50 | 0.76 | 5.79 | 0.59 | 0.25 | 0.01 | 0.09 | 1.32 | S | |
| *Lepomis miniatus* | N | | 9.95 | 22.48 | 5.93 | 1.57 | 35.79 | 7.72 | 6.41 | 2.86 | 0.51 | 9.32 | S | |
| *Lepomis* spp. | N | | | | 0.54 | | | | | 0.55 | 0.13 | 0.12 | – | |
| *Micropterus dolomieu* | I | | | | | | | 0.29 | 0.21 | | | 0.05 | – | |
| *Micropterus punctulatus* | N | | | | | | 0.27 | | 0.12 | | | 0.04 | – | |
| *Micropterus salmoides* | N | 1.63 | 0.71 | 2.35 | 0.61 | 3.03 | 7.57 | 1.40 | 3.39 | 0.19 | 2.15 | 2.14 | +0.007 | 0.04 |
| *Micropterus treculii* | N | | | 0.17 | | | | | 0.58 | | 0.02 | 0.08 | – | |

**Table 1** (continued)

| Species | Status | Decade | | | | | | | | | | Overall | Population trend | *p*-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1890 | 1930 | 1940 | 1950 | 1960 | 1970 | 1980 | 1990 | 2000 | 2010 | | | |
| *Pomoxis annularis* | N | | | | 0.04 | | | | | | | <0.01 | – | |
| *Etheostoma fonticola* | N | 0.54 | 15.17 | 4.87 | 31.14 | 6.73 | | 0.88 | 0.70 | 8.07 | 3.70 | 7.18 | S | |
| *Etheostoma spectabile* | N | 3.26 | | 0.17 | 0.15 | | 0.11 | 1.54 | 0.74 | 0.01 | 0.18 | 0.62 | – | |
| *Percina carbonaria* | N | 0.54 | | 0.17 | 0.50 | 0.06 | | 0.15 | 0.12 | 0.01 | 0.58 | 0.21 | – | |
| *Percina macrolepida* | N | | | | | | | 0.15 | 0.08 | | | 0.02 | – | |
| *Percina apristis* | N | 16.85 | | 1.51 | 5.81 | 0.12 | | 2.79 | 0.87 | 0.09 | 0.88 | 2.89 | −0.012 | <0.01 |
| *Cichlasoma cyanoguttatum* | I | | 2.13 | 1.51 | 2.60 | 4.85 | 3.79 | 1.62 | 1.82 | 0.20 | 0.79 | 1.93 | S | |
| *Cichlasoma nigrofasciatum* | I | | | | | | | | 0.04 | | | <0.01 | – | |
| *Oreochromis aureus* | I | | | | | | 0.12 | 0.44 | 0.12 | 0.02 | 0.19 | 0.09 | – | |
| *Oreochromis mossambicus* | I | | | | | | 0.43 | | 0.04 | | | 0.05 | – | |
| Collections during decade: | | 5 | 2 | 4 | 26 | 10 | 2 | 13 | 17 | 7 | 16 | 102 | | |
| Individuals collected: | | 184 | 422 | 596 | 2,614 | 1,864 | 1,849 | 1,360 | 2,417 | 19,964 | 9,696 | 40,966 | | |
| SE[a] | | 2.15 | 11.22 | 4.00 | 9.83 | 2.97 | 29.99 | 3.28 | 2.90 | 26.00 | 5.85 | | | |
| Taxa richness: | | 14 | 14 | 22 | 35 | 28 | 23 | 35 | 45 | 34 | 36 | 56 | | |
| Native richness: | | 14 | 12 | 18 | 29 | 22 | 15 | 26 | 34 | 26 | 25 | | | |
| Diversity (H'): | | 2.20 | 1.81 | 2.36 | 2.45 | 1.91 | 2.02 | 2.76 | 2.80 | 0.96 | 1.15 | | | |
| Native Diversity (H'): | | 2.20 | 1.64 | 2.07 | 2.11 | 1.21 | 1.32 | 2.00 | 2.18 | 0.77 | 1.05 | | | |
| Persistence: | | | 0.36 | 0.61 | 0.71 | 0.81 | 0.65 | 0.65 | 0.80 | 0.82 | 0.86 | | | |
| Native Persistence: | | | 0.40 | 0.57 | 0.67 | 0.78 | 0.56 | 0.55 | 0.79 | 0.84 | 0.87 | | | |

[a] Standard error for number of individuals collected among collection events in each decade

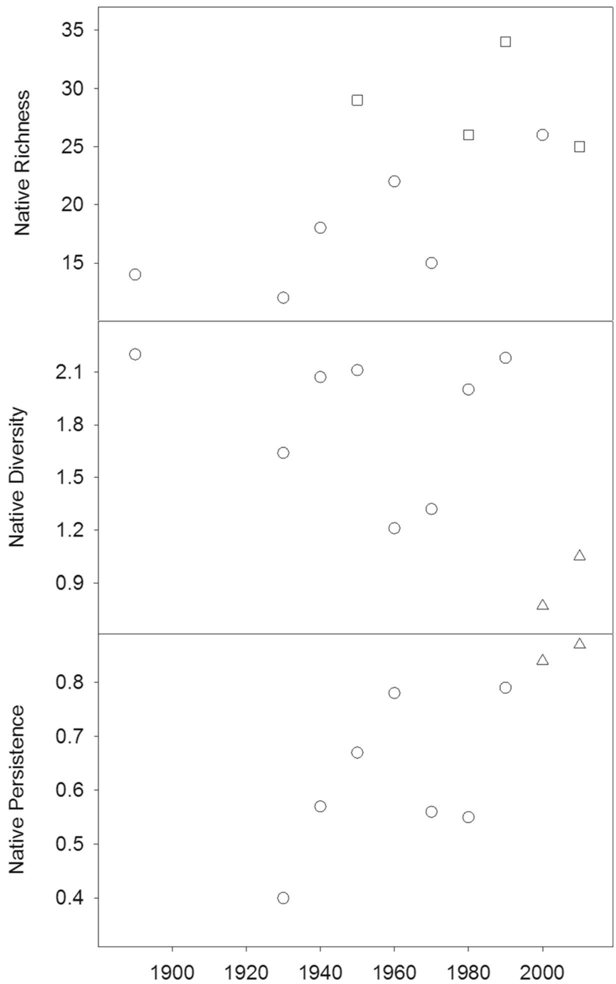


**Fig. 4** Scatterplots of the upper San Marcos River fish community parameters among decades. Native richness was positively associated with effort (*circles* represent <10 and *squares* represent >10 collection events per decade) but independent of decade. Native diversity was negatively associated with Total N (*circles* represent <3,000 and *triangles* represent >9,600 individuals) but independent of decade. Native persistence was positively associated with Total N but independent of decade. See "Results" for statistical reporting

due to higher occurrence and abundance of riverine fishes (e.g., mimic shiner *Notropis volucellus* and gizzard shad *Dorosoma cepedianum*).

## Species and guild changes

Some notable changes were observed among species in the Upper San Marcos River within the period of collections. Two species, San Marcos Gambusia and Headwater Catfish *Ictalurus lupus* were only reported in one decade (1960, 1940, respectively) among collections (Table 1). Relative abundances of two fluvial specialists listed as species of concern (Burrhead Chub and Guadalupe Darter), one other cyprinid (Red Shiner), and one ictalurid (Tadpole Madtom *Noturus gyrinus*) decreased through time, whereas *Gambusia* spp. and

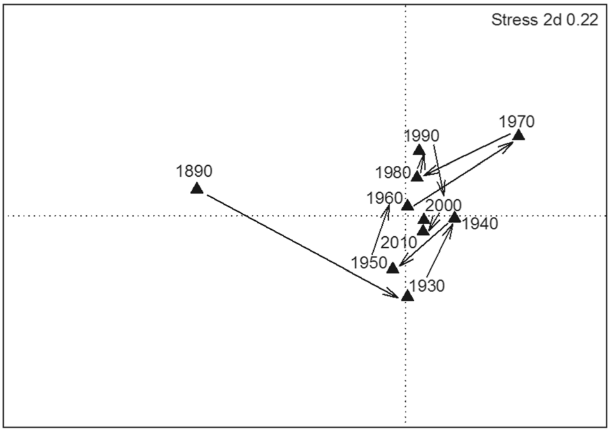


**Fig. 5** Multi-dimensional scaling (MDS) plot for upper San Marcos River fish community 1890–2011. *Points* represent centroids of ichthyological collections for each decade and were plotted following fourth root transformation of relative abundances

Largemouth Bass *Micropterus salmoides* increased through time. Among other species of concern, Ironcolor Shiner *Notropis chalybaeus* increased through time (Relative abundance mean = 0.25; range = 0.27–0.95), Guadalupe Roundnose Minnow *Dionda nigrotaeniata* generally increased through time (RA mean = 1.8; range 0.61–8.23), and the abundance of the federally endangered Fountain Darter varied greatly (ranging from 0.54 in 1890 to 31 in 1950), but did not differ through time. Occurrence of introduced species increased among decades ranging from 0 species in 1890 to 13 species in 1990 with relative abundance increasing (range 0 % in 1890 to 31.1 % in 1960). In particular, relative abundances of two introduced species, Redbreast Sunfish and Armored Catfish *Hypostomus*, increased through time.

No detectable trends occurred among habitat guilds and reproduction guilds in the upper San Marcos River among decades. Among all decades, lentic tolerant species were generally higher in abundance than fluvial specialist species. However, relative abundance of either guild did not differ ($P>0.05$) through time. Among the four fishes with increasing abundances through time, reproductive guilds consisted of two nest builders (Redbreast Sunfish and

**Table 2** Fish community dissimilarity percentages (SIMPER) among decades in the upper San Marcos River

| | 1890 | 1930 | 1940 | 1950 | 1960 | 1970 | 1980 | 1990 | 2000 |
|---|---|---|---|---|---|---|---|---|---|
| 1890 | | | | | | | | | |
| 1930 | 75 | | | | | | | | |
| 1940 | 61 | 43 | | | | | | | |
| 1950 | 58 | 41 | 58 | | | | | | |
| 1960 | 75 | 46 | 41 | 32 | | | | | |
| 1970 | 95 | 58 | 52 | 53 | 50 | | | | |
| 1980 | 61 | 52 | 33 | 27 | 36 | 45 | | | |
| 1990 | 61 | 57 | 41 | 33 | 40 | 43 | 24 | | |
| 2000 | 70 | 47 | 43 | 36 | 32 | 52 | 40 | 42 | |
| 2010 | 59 | 50 | 35 | 31 | 34 | 46 | 32 | 28 | 26 |

Largemouth Bass), one open substrate spawner (i.e., Ironcolor Shiner) and one internal bearer (*Gambusia* spp.). Among the four fishes with decreasing abundances, reproductive guilds consisted of two brood hiders (Red Shiner and Guadalupe Darter), one open substrate spawner (Burrhead Chub), and one nest builder (Tadpole Madtom).

## Discussion

Our predictions of decreases in native fish community and species abundances were largely unsupported despite 170 years of urbanization, specifically anthropogenic alterations to instream and catchment habitats, water quantity and water quality, stream morphology, and introduced species. As such, we conclude that upper San Marcos River is currently an exception to the urban stream syndrome model, though acknowledging that lag times in introduce species effects (Crooks and Soulé 1999) and other aspects of urbanization might change our conclusion in the future. Our conclusion is surprising given that the upper San Marcos River is considered a stable system with respect to water quality and quantity (Hubbs 1995; U.S. Fish and Wildlife Service 1996, Groeger et al. 1997; White 1998), and slight to moderate deviations in water quality, quantity, and instream habitats are predicted to shift biological communities (Hubbs 1995) and reduce viability of spring-associated species (Hubbs and Peden 1969; Tolley-Jordan and Powers 2007). We attribute lack of conformity to the urban stream syndrome, at least in the upper 2.5 km of the river, to two primary mechanisms: 1) Paleohistory of the upper San Marcos River suggests a dynamic stream system with decreasing stream flow and increasing water temperatures since the last glacial maximum and with heterogeneous mix of substrates and mesohabitats often reset by periodic and extensive flooding and flushing, and 2) water quantity of the San Marcos River is much greater than water quantity of other headwater streams used to assess urban stream syndrome (Walsh et al. 2005). As such, the native fish community was persistent and resilient through time with no detectable changes in native species richness, native species diversity, habitat guilds, and reproductive guilds attributed solely to urbanization. Observed differences in native species and community similarities among decades, when noted, were attributed to sampling issues (e.g., increased detectability of rarer native species with greater effort) and presumed selective reporting of catch (e.g., absence of *Gambusia* spp., Fountain Darter, and Texas Shiner in 1970s). However, some changes in the fish community were detected through time.

The likely extinction of San Marcos Gambusia in the San Marcos River and extirpations of Headwater Catfish and Guadalupe Bass are reported previously. San Marcos Gambusia was described in 1960s with an estimated population size of 1,000 individuals (Hubbs and Peden 1969). The last wild specimen was taken in the 1980s (U.S. Fish and Wildlife Service 1996). Hubbs and Peden (1969) provided qualitative habitat preferences for San Marcos Gambusia and concluded that minor alterations to existing slackwater habitats without dense aquatic vegetation and silt substrate could cause extirpation. However, this conclusion is inconsistent with the historical dynamic character of the upper San Marcos River; therefore, association between minor habitat alterations and extirpation of San Marcos Gambusia is tenuous. An alternative explanation is equally speculative, but the San Marcos Springs are not the only spring system within the upper San Marcos River drainage. Willow Springs and Purgatory Springs, which currently are ephemeral, were historically and periodically connected to the upper San Marcos River. Either of the springs could have supported endemic fauna, especially a species of Gambusia given their high rates of speciation within the basin and across the Edwards Plateau and Trans-Pecos regions (Hubbs et al. 2008). Headwater Catfish are associated with headwater reaches of streams from the Colorado River drainage of Texas to the Rio

Grande (Kelsch and Hendricks 1990), and Guadalupe Bass are associated with flowing waters of Edwards Plateau streams (Hubbs et al 1953; Hurst et al. 1975). Extirpations in urbanized and non-urbanized areas are attributed to introgression with congeners stocked for recreational purposes (Channel Catfish *Ictalurus punctatus*: Kelsch and Hendricks 1990; McClure-Baker et al. 2010; Bean et al. 2011; Smallmouth Bass *Micropterus dolomieu*: Morizot et al. 1991; Littrell et al. 2007; Bean et al. 2013). Consequently, localized urbanization effects are not solely responsible for at least two, but possibly three extirpations, observed in the upper reaches of the San Marcos River.

Population declines were detected among four species (Red Shiner, Burrhead Chub, Tadpole Madtom and Guadalupe Darter). Red Shiner, Burrhead Chub, and Tadpole Madtom are not typically associated with spring communities. Red Shiner is ubiquitously distributed throughout south central North America (Hubbs et al. 2008) and are often associated with low gradient streams and are abundant within lowland rivers of the Guadalupe-San Antonio River basins (Runyan 2007; Perkin and Bonner 2011). Burrhead Chub is endemic to the Guadalupe-San Antonio River and Colorado River basins of central Texas (Eisenhour 2004) and currently persists in minimally fragmented reaches of these drainages (Perkin et al. 2013). Tadpole Madtom is distributed throughout central and eastern USA (Hubbs et al. 2008) and associated with slackwater habitats and aquatic vegetation (Rohde 1980). Riverine-associated fishes marginally or temporarily inhabit spring outflows but primarily reside in the more riverine habitats (Edwards and Contreras-Balderas 1991; Rhodes and Hubbs 1992; Hubbs 1995; Bonner et al. 2005; Watson 2006). Riverine populations of the three species are considered in decline throughout the San Marcos River and are attributed to hydrological alterations and stream fragmentation (Perkin and Bonner 2011). Since river populations likely serve as the source for spring populations, we attribute population declines in the upper San Marcos River to declines in the source populations within the lower San Marcos River. Though declines in the source population are ultimately attributed to anthropogenic effects (i.e., construction of instream dams and watershed dams outside of urban areas), we do not attribute population declines of Red Shiner, Burrhead chub, and Tadpole Madtom to the proximate effects of urbanization within the upper San Marcos River. Guadalupe Darter, however, is generally restricted to spring outflows of the Guadalupe River basin and is associated with riffle habitats (Hubbs 1954). Reduction in riffle habitats has occurred in the lower 6 km of the upper San Marcos River since the construction of Ed Capes Dam (1867) and Cummings Dam (1917). Population declines were detected much later, from 1990 through 2010, which might be a legacy effect of the dam construction within the upper San Marcos River. Another species previously reported to be declining in the San Marcos River, including upper and lower reaches, is the Fountain Darter (Perkin and Bonner 2011). In the upper San Marcos River, we found that the population was stable through time. Fountain Darter is generally restricted to spring outflows of the upper San Marcos River and neighboring Comal River, but is historically found in the San Marcos River downstream from the San Marcos and Blanco River confluence and outside of the spring outflows. Fountain Darter numbers have decreased in the lower San Marcos River (Perkin and Bonner 2011), likely attributed to instream barriers (Cummings Dam) that fragments upper San Marcos River (source population) from the lower San Marcos River and inhibits downstream movements.

Except for introduced species and a few detectable native species extirpations and population declines, the upper San Marcos fish community was persistent (>60 %) through time despite increasing urbanization influences. Persistence and noted changes in the upper San Marcos fish community reported herein are similar to fish communities in other Edwards Plateau karst systems within urbanized and non-urbanized areas. San Felipe Creek (Val Verde County, Texas) is located within the city limits of Del Rio and historically and currently serves as a municipal water source and a recreational area, bordered by green spaces, a golf course, and commercial development. The San Felipe Creek native fish community and spring habitats have persisted through time with increasing urbanization and introduction of non-native species (Garrett et al. 1992; Lopez-Fernandez and Winemiller 2005). Among several non-urbanized karst systems, native fish communities and habitats persist (Phantom Lake Springs, Winemiller and Anderson 1997; Pinto Creek, Garrett et al. 2004; Independence Creek, Bonner et al. 2005; upper Devils River, Kollaus and Bonner 2012; South Llano River, Curtis 2012), but have experienced noted declines in species richness of riverine-associated taxa (Bonner et al. 2005), introgression of headwater catfish with the introduced Channel Catfish in Independence Creek and Devils River (McClure-Baker et al. 2010), introgression of Guadalupe Bass with the introduced Smallmouth Bass in the South Llano River (Bean et al. 2013), and potential threats of competition and introgression with introduced fishes (Winemiller and Anderson 1997).

Despite being historically dynamic systems with resilient fish communities, karst spring systems are not immune to anthropogenic modifications and dewatering, either by natural means (White et al. 2009) or man-induced. Partial or complete extirpations of native, spring-associated fishes are reported in karst streams in urbanized areas (Comal Springs, Schenck and Whiteside 1976; upper San Antonio River, Edwards 2001; Barton Creek, Labay et al. 2011), low to moderate urbanized areas (Comanche Springs, Echelle and Miller 1974; Las Moras Creek, Garrett et al. 1992), and non-urbanized areas (Goodenough Springs, Hubbs and Jenson 1984). Biotic interactions between native and introduced species are often suggested as possible mechanisms in native, spring-associated fish declines, but introduced species occur in most, if not all, of the spring systems. Instead, partial or complete extirpations were associated with obliteration of spring habitats, such as complete or nearly complete dewatering in Comal Springs, Comanche Springs, Las Moras Creek or inundation of Goodenough Springs by a reservoir, conversion of spring habitats into recreational areas with chlorination (Las Moras Creek), fragmentation of spring habitats in Barton Creek with instream dams (Labay et al. 2011), and numerous urbanized effects, including point and non-point water pollution, bank stabilization, nutrient enrichment, fragmentation, and periodic cessation of spring flows in the upper San Antonio River (Edwards 2001; Roark et al. 2001).

Although urbanization is an array of inter-related factors, impervious cover is used as surrogate for discriminating levels of urbanization (Paul and Meyer 2001). Degradation of fish habitat is typically observed when impervious cover reaches near 10 % (Schiff and Benoit 2007); however, lower levels of impervious cover can cause degradation in sensitive water bodies (Booth and Jackson 1997). Currently, impervious cover in the upper San Marcos River is 4.5 %. The San Antonio River, an Edwards Aquifer headwater stream of comparable size and water quantity to the upper San Marcos River, is located in a highly urbanized watershed in San Antonio, Texas. Despite the San Antonio River's high water quantity initially, though current spring outflows are now ephemeral, watershed alterations, including a high percentage of impervious cover (i.e., 10-20 %), are related to alterations in the fish community with introduced species comprising 61 % of the fish community (Edwards 2001). Use of impervious cover as an indicator of urbanization used elsewhere (Schiff and Benoit 2007) appears sufficiently applicable to urbanized karst streams and therefore could be used to predict future changes in the Upper San Marcos fish community structure as urbanization increases.

## Mitigating urbanization effects in the upper san marcos river

Although the upper San Marcos River displayed high fish community persistence overall, hydrologic and channel morphology changes in the lower 6 km of the upper San Marcos River have altered the fish community within this reach (Behen 2013). More consistent with historical conditions, the upper 2.5 km of the San Marcos River is characterized by dense aquatic vegetation and coarse substrates over a broader channel with shallower depths and higher current velocities, whereas the lower 6 km is characterized by a stream channelized into the underlying Taylor Marl Clay with increased depths and slower current velocities and a general absence of aquatic vegetation. We attributed these changes to three likely factors: 1) sediment degradation downstream from Cape's Dam (Brandt 2000), which excludes necessary fine sediments for aquatic vegetation establishment; 2) the backwater effect of Cumming's Dam, creating unnaturally deep water habitats; and 3) nutrient enrichment from a fish hatchery and waste water treatment plant resulting in eutrophication, decreased water clarity, and reduced light penetration, especially in the deeper waters and slower current velocities created by the backwater effect (Groeger et al. 1997; Santucci et al. 2005). Other factors, such as stream shading and channel incision, likely contribute to decreased aquatic vegetation (Kurtz et al. 2003). Within this reach, lentic tolerant species are predominant (e.g., *Lepomis* spp.), whereas fluvial specialists species (e.g., Burrhead Chub and Guadalupe Darter), endemic headwater species (e.g., and Fountain Darter and Guadalupe Roundnose Minnow), and downstream riverine species (i.e., Red Shiner) are rare or presumed extirpated. Similar fish community changes due to low head dams are well documented and have been attributed to altered temperature and habitat preferences (Walters et al. 2005; Meador et al. 2005), increased turbidity from eutrophication and suspended sediments (Walters et al. 2009), and fragmentation from source populations (Catalano et al. 2007).

Ecological rehabilitation attempts to recover elements of the natural range of ecosystem processes within degraded systems, such as urbanized streams (Hughes et al. 2014), and urbanized streams provide unique opportunities to test aspects of rehabilitation theory and practice (Paul and Meyer 2001). Rehabilitation approaches in urban streams include improvements to hydromorphology (Niezgoda and Johnson 2005) with removal of low head dams suggested as a potential mechanism for restoring the natural dynamic state of a stream channel and corresponding ecological processes (Doyle et al. 2005). Low head dam removal increases bed sloping often resulting in reduced water depths and increased current velocities (Hart et al. 2002). Shallower depths and more heterogeneous current velocities reduce water retention time and therefore nutrient accumulation and concentration, increase water clarity, and increase sedimentation transport (Bednarek 2001), thus leading to increases in vegetation growth (Rybicki et al. 2001). The lower reach of the upper San Marcos River offers an opportunity to test rehabilitation theory related to low head dams. We predict the proposed removal of two low head dams (i.e., Capes Dam and Cummings Dam) would restore the natural dynamic state of the stream channel including reduced depths, increase current velocities, heterogeneous substrates, and vegetation, thereby expanding current distributions of several endemic species that are associated with more heterogeneous habitats. However, expanding rehabilitation efforts beyond the lower reach and into the catchment is likely needed to mitigate continuing urbanization (Hughes et al. 2014; Violin et al. 2011). Even with proper management, improvement practices, and rehabilitation efforts, the upper San Marcos River likely cannot sustain its unique fish community and associated habitat without the continued supply of groundwater from the Edwards Aquifer.

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## Appendix 1

**Table 3** Date, General Topic, Description, and Reference of alterations to the upper San Marcos River associated with increasing urbanization (1849–2012)

| Date | General topic | Details | Reference |
|---|---|---|---|
| 1849 | Stream morphology | Construction of Spring Lake dam, created head of 3.5 m | Kimmel, J (2006) The San Marcos: A River's Story. College Station, Texas |
| 1850 | Stream morphology | Thompson island mill race constructed for irrigation | Kimmel 2006 |
| 1866 | Stream morphology | Construction of dam near Cheatham Street for irrigation, later destroyed by flood | San Marcos Daily Record (3/3/1966) |
| 1867 | Stream morphology | Construction of Capes dam, created head of 3 m | Kimmel 2006 |
| 1872 | Biological alteration | Harvesting of trees for home building | Kimmel 2006 |
| 1876 | Stream morphology | Creation of Fromme's Ditch for irrigation; dam was built to direct water down artificial channel | Kimmel 2006 |
| 1893 | Water quantity | Creation of the U.S. Fish Hatchery | Kimmel 2006 |
| 1899 | Riparian alteration | Founding of Southwest Texas State Normal School (Texas State University - San Marcos) near the headwaters of the San Marcos River | Kimmel 2006 |
| 1904 | Stream morphology | Construction of Rio Vista dam for irrigation and provide power for a mill. Rio Vista Resort provided water sports and lodging. | Kimmel 2006 |
| 1905 | Stream morphology/ water quantity | Construction of additional dams for irrigation of farm land and city water supply | Kimmel 2006 |
| 1907 | Water quality | First sewage treatment plant formed, effluent released into cultivated land, but house waste still ended up in the river | Kimmel 2006 |
| 1914 | Stream morphology | Completion of Cummings dam (started in 1905) for irrigation of 10,000 acres | Kimmel 2006 |

**Table 3** (continued)

| Date | General topic | Details | Reference |
|---|---|---|---|
| 1914–1924 | Riparian alteration | Introduction of elephant ears as a possible replacement for Irish potatoes | Kimmel 2006 |
| 1916 | Stream morphology | River split downstream of Aquarena Bridge, west channel was originally a millrace but a flood moved main river flow into this channel, forming an island | Sanborn, CW (1944) The Story of Riverside. Thesis, Texas State University |
| 1916 | Water quality | City of San Marcos installed an activated sludge wastewater treatment plant | Kimmel 2006 |
| 1917 | Stream morphology | Summer dredging of silt and trees with introduction of gravel and rock and wooden walls constructed in Sewell Park | Sanborn 1944 |
| 1920s | Biological alteration | A cutterboat assembled in U.S. Fish Hatchery to clear Spring lake surface of vegetation; species introduced (e.g., *Cichlasoma cyanoguttatum* and *Cabomba*) | San Marcos Daily Record (9/17/1989) |
| 1924–1970s | Biological alteration | Harvesting of river moss | Kimmel 2006 |
| 1928 | Stream morphology | Construction of concrete retaining walls in Sewell Park | Sanborn 1944 |
| 1929 | Riparian alteration | Construction of Spring Lake Hotel and Golf Course | San Marcos Daily Record (9/16/1973) |
| 1930s | Water quality | Swimming in Sewell Park area was not recommended due to polluted waters | Kimmel 2006 |
| 1934–1976 | Biological alteration | Establishment of aquatic plant business, harvesting as much as 680 kg daily | San Marcos Daily Record 1962 |
| | | January–May. During this time, Rodgers planted a variety of exotic vegetation species | Kimmel 2006 |
| 1935 | Riparian alteration | Concrete slab poured in Sewell Park. Surrounding area used as a bedding ground for cattle drives | Sanborn 1944 |
| 1949 | Stream morphology | Dredging in Spring Lake occurred to provide greater depths for underwater theater for Aquarena Springs Theme Park, opening in 1950 | San Marcos Daily Record (9/16/1973) |
| 1949 | Water quality | Creation of Texas Parks and Wildlife A.E. Wood Fish Hatchery | Texas Parks and Wildlife (2013) A. E. Wood Fish Hatchery. http://www.tpwd.state.tx.us/ |

**Table 3** (continued)

| Date | General topic | Details | Reference |
|---|---|---|---|
| | | | fishboat/fish/management/hatcheries/aewood.phtml. Accessed 19 Mar 2013 |
| 1964&1965 | Stream morphology | Area from Sewell Park to City park was dredged | Hannan, HH, Dorris, TC (1970) Succession of a macrophyte community in a constant temperature river. Limnol Oceanogr 1970: 442–453 |
| 1967 | Biological alteration | First record of introduced vegetation species, *Hydrilla verticillata* | San Marcos Daily Record (04/14/1977) |
| 1968 | Water quality | Polluted water from Sessoms drive, detergents from septic tanks and sewer lines after flood | San Marcos Daily Record (1/1968) |
| 1970 | Protection | *Etheostoma fonticola* listed under USFWS protection, status endangered | USFWS (1970) Appendix D – United States list of endangered species and other fish or wildlife. Federal Register 35:16047–16048 (13 Oct 1970) |
| 1970s | Water quality | Polluted water from wastewater treatment plant ruined irrigation system at Cummings dam | Kimmel 2006 |
| 1970s | Protection | Establishment of river clean up days with first official fall river clean up occurring in 1989 | San Marcos Daily Record (10/4/1989) |
| 1973–1990 | Water quantity | Construction of three retention dams on Sink Creek and two on Purgatory Creek | Earl RA, Wood CR (2002) Upstream changes and downstream effects of the San Marcos River of central Texas. Tex J Sci 54(1):69–88 |
| 1977 | Protection | Recreational diving prohibited in Spring Lake to protect environmental sensitive area | San Marcos Daily Record (9/27/1977) |
| 1978 | Protection | *Zizania texana* listed under USFWS protection, status endangered | USFWS (1978) Determination that 11 plant taxa are endangered species and 2 plant taxa are threatened species. Federal Register 43:17910–179?? (26 Apr 1978) |
| 1980 | Protection | *Gambusia georgei* listed under USFWS protection, status endangered | USFWS (1978) Proposed listing and critical habitat determination for a fish and a salamander. Federal Register 43:30316–30319 (14 Jul 1978) |
| 1982 | Riparian alteration | Reconstruction of river walk (first built in 1974) along upper 2 km of the San Marcos River | San Marcos Daily Record (3/14/1982) |

**Table 3** (continued)

| Date | General topic | Details | Reference |
|---|---|---|---|
| 1982 | Water quality | Upper San Marcos River quarantined due to dangerous levels of fecal coliform from a sewage line break on university campus, river reopened in December 1982 | San Marcos Daily Record (10/6/1982) San Marcos Daily Record (12/21/1982) |
| 1982 | Stream morphology/ Water quality | City dredging operation removed sandbar near City Park, caused increased turbidity and potential contamination downstream | San Marcos Daily Record (10/6/1982) |
| 1984 | Water quality | Unsafe water conditions, high levels of fecal coliform found in Sewell Park area | San Marcos Daily Record (9/30/1984) |
| 1984 | Protection | Establishment of San Marcos River Community Trust Fund, founding the San Marcos River Foundation in 1985 | San Marcos Daily Record (12/7/1984) |
| 1985 | Protection | River Corridor Ordinance Adopted by City of San Marcos, preventing >30 % of riverfront lots to be impervious cover | San Marcos Daily Record (8/02/1985) |
| 1990s | Water quality | Waste water treatment plant was upgraded | Kimmel 2006 |
| 1993 | Protection | Texas Legislature in May passed Senate Bill 1477 creating The Edwards Aquifer Authority who is authorized to issue permits and regulate groundwater withdrawals | Eckhardt, G (2013) Texas Senate Bill 1477. The Edwards Aquifer website. http://www.edwardsaquifer.net/1477.html. Accessed 20 Mar 2013 |
| 2000 | Stream morphology | Section of Capes dam slipped, dropping water levels temporarily | Austin American Statesman (1/04/2000) |
| 2000 | Water quality | High fecal coliform levels detected in river; cause unknown | Houston Chronicle (10/01/2000) |
| 2002–2008 | Stream morphology | Channel dredging occurred within the lower 2.9 km of the upper San Marcos River to remove exotic water plant, *Cryptocoryne beckettii*. Dredging removed approximately 3,3320 $yd^3$ of sediment with no indication of accelerated stream bed adjustment. | Hudson PF (2012) Geomorphic monitoring of the upper San Marcos River, Texas to assess channel adjustment in response to removal of an invasive exotic water plant, *Cryptocoryne beckettii*. Report submitted to Texas Parks and Wildlife (12 Mar 2012) |
| 2006 | Protection | Edwards Aquifer Recovery Implementation Program established to develop a plan that contributes to the protection and recovery of federally-listed species | Edwards Aquifer Authority (2013) History. http://www.eahcp.org/index.php/about _eahcp/history. Accessed 08 Apr 2013 |
| 2010 | Water quality | Texas State University - San Marcos chemical spill into river (approx. 446 gal of sulfuric acid) | San Marcos Daily Record (10/31/2010) |
| 2011 | Protection | Habitat Conservation Plan approved for the upper San Marcos River | Austin American Statesman (10/21/2011) |

**Table 3** (continued)

| Date | General topic | Details | Reference |
|---|---|---|---|
| 2012 | Protection | Upper San Marcos River designated as State Scientific Area, prohibits uprooting of *Zizania texana* | San Marcos Daily Record (4/05/2012) |

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