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# Spring flow lost: a historical and contemporary perspective of an urban fish community

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**Abstract**
Water quality and quantity within the upper San Antonio River (Bexar County, Texas) were supported historically from spring flows of the Edwards Aquifer. Since the 1700s, water quality, quantity, physical aquatic habitats, and presumably fish communities have been altered in the upper San Antonio River, including loss of spring flow and replacement of base flow by treated wastewater. The upper San Antonio river fish community provides a unique opportunity to fill a gap in knowledge on spring-associated fish responses to spring flow loss. The purpose of our study was to describe temporal changes in the upper San Antonio River fish community in relation to increased anthropogenic alterations from reported fish collections and infer from reference conditions. Comparisons with reference conditions were necessary since anthropogenic alterations occurred before the first fish collections within the basin. We found the upper San Antonio River fish community changed through time with increases in native and introduced fishes and decreases in spring-associated fish richness and relative abundances. Decreases in spring-associated fish richness and relative abundances were attributed to decreases in spring flow and to changes in water quality; however, specific mechanisms between loss of spring flow and spring-associated fishes are unknown at this time. Quantifying historical fish community changes through time in systems with a long history of urbanization is difficult, but our assessment provides a greater understanding of how spring flow loss due to increasing water demand in highly urbanized areas can alter communities with spring-associated species.

**Keywords** Spring-associated · Urbanization · Historical · San Antonio River · Reference condition

## Introduction

Freshwater spring and spring run environments (i.e., spring complexes) are hotspots for biodiversity and endemism (Scarsbrook et al. 2007; Cantonati et al. 2012; Davis et al. 2013). Spring complexes of the karst Edwards Plateau of south-central USA are historically and contemporarily habitats for endemic and cosmopolitan flora and fauna (Bowles and Arsuffi 1999). Among fishes, many of the endemic forms are thought to have originated within the Edwards Plateau (Conner and Suttkus 1986), and those that are spring-associated fishes have a strong association with water quality (e.g., water temperature) of spring complexes that varies less than the water quality outside of spring complexes (Slade et al. 1986; Hubbs 1995; López-fernández and Winemiller 2005; Kollaus and Bonner 2012; Craig et al. 2019). As such, spring-associated fishes have greater relative abundances and densities within spring complexes compared to outside of spring complexes. Within spring complexes, species richness, relative abundance, and densities of spring-associated fishes are positively related to magnitude of spring flow (Craig et al. 2016).

Spring complexes of the Edwards Plateau differ along a gradient of anthropogenic alteration. Non-urbanized spring complexes with minimal or no evidence of anthropogenic alteration are dominated by spring-associated fishes (Watson 2006; Kollaus and Bonner 2012). Spring complexes with anthropogenic alterations (i.e., urbanized spring complexes) have minor changes in fish communities (e.g., increases in introduced fish richness) when spring flows are maintained (Garrett et al. 1992; Kollaus et al. 2015; Scanes 2016). When spring flows are not maintained and spring complex is dewatered, the fish community is extirpated (Winemiller and Anderson 1997). However, it is unclear how fish communities will respond to reductions in spring

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flows but not completely dewatered (e.g., water source replaced with wastewater return).

The upper San Antonio River (Bexar County, Texas) is an example of an Edwards Plateau spring complex that, through time, has lost spring flow but has not been dewatered. The upper San Antonio River forms from a spring complex, which at one time were considered as one of the largest within the Edwards Plateau with flows exceeding 4.5 $m^3$/s (G. Eckhardt, San Antonio Water System, San Antonio, TX, 2016 pers. comm.). Since the 1700s, the watershed surrounding the springs and upper San Antonio River has become urbanized (i.e., 38% urban land use as of 2010; Yi et al. 2017). Anthropogenic alterations consisted of changes to stream morphology, water quality, and groundwater supply (Arneson 1921; Brune 1981; Glennon 2004) which are consistent with the urban stream syndrome (Walsh et al. 2005). Median flow of the upper San Antonio River was reduced gradually to 0.36 $m^3$/s (USGS gaging station 08178000; 2013–2014) with primary source of base flow shifting from spring water to treated wastewater from San Antonio Zoo (0.13 $m^3$/s; Miertschin 2006) and City of San Antonio (G. Eckhardt, pers. comm.). Reported changes in the upper San Antonio River fish community consist of occurrences and increased abundances of introduced species (Barron 1964; Hubbs et al. 1978) and community estimates, finding that introduced fishes accounted for 61% of fish species and 62% of the fish biomass (Edwards 2001). However, it is unknown from previous studies the response of the native fish community to water quality alterations, including spring-associated fishes.

Assessment of historical fish collections and comparison of an existing fish community to reference conditions are two common methods used to quantify changes in fish communities exposed to anthropogenic alterations (e.g., Trautman 1981; Karr et al. 1985; Hughes and Noss 1992). Historical fish collections, however, can lack completeness and breadth (Davis and Simon 1994; Labay et al. 2011) and consist of fishes taken with a variety of gear and effort (Davis and Simon 1994; McManamay and Utz 2014), which influences compatibility among collections. An additional challenge in the upper San Antonio River is that fish collections in the 1800s were taken after documented anthropogenic alterations. In streams with incomplete historical fish collections or, like in the San Antonio River, collections taken after stream degradation, reference conditions can be used to provide expectations of historical conditions and enable assessment of community changes associated with anthropogenic alterations (Davis and Simon 1994). Craig et al. (2016) developed predictive models to estimate species richness, relative abundance, and density of spring-associated fishes within Edwards Plateau spring complexes based on long-term median spring flow magnitudes that naturally range from 0.06 $m^3$/s at the smallest spring complexes to 4.5 $m^3$/s at the largest. Using spring fish richness, relative abundance, and density predictions of Craig et al. (2016) as contemporary reference conditions, combined with quantification of contemporary fish community composition, can provide a more comprehensive assessment of fish community changes in the upper San Antonio River.

The purpose of this study was to describe the fish community of the upper San Antonio River and to evaluate temporal changes in this community using estimated reference conditions from Craig et al. (2016). Study objectives were to (1) quantify contemporary fish community species richness and relative abundance, and for spring-associated fish, the richness, relative abundance, and density among four sites in 2013 and 2014, (2) compare fish community species richness, diversity, evenness, and relative abundance between contemporary collections and published and unpublished fish collections taken from 1853 to 2015, and (3) compare spring-associated fish richness, relative abundance, and density from Objective 1 and Objective 2 to reference conditions. Using reference conditions, we developed two predications: (1) the upper San Antonio River fish community was dominated by spring-associated fishes (i.e., 7 species, 77% in relative abundance, and 1.8 fish/$m^2$) before anthropogenic alterations and at earliest spring baseflow estimate of 4.5 $m^3$/s; and (2) the contemporary fish community would be dominated by spring-associated fishes (i.e., 5 species, 57% in relative abundance, and 0.3 fish/$m^2$) with flows being reduced to 0.36 $m^3$/s because of anthropogenic alterations.

## Materials & methods

Groundwater of the Edwards Aquifer discharges 4.6 million $m^3$ of water annually (Hamilton et al. 2003) and provides surface waters in six major river basins of Texas (Rio Grande, Nueces River, San Antonio River, Guadalupe River, Colorado River, and Brazos River; Worthington 2003). Perennial portions of the upper San Antonio River historically began within the city of San Antonio at San Antonio Springs (29°28′7.73″N 98°28′2.80″W) and San Pedro Springs (29°26′49.55″N 98°30′5.86″W) (Fig. 1). Outflows of San Pedro Springs join the San Antonio River about 10 km downstream from San Antonio Springs (Brune 1981). Upper San Antonio River, defined by Texas Commission of Environmental Quality as Segment 1911, continues downstream and through the City of San Antonio until merging with the Medina River approximately 30 km downstream. After the confluence, the lower San Antonio River flows into the Guadalupe River before discharging into San Antonio Bay.

Within the upper San Antonio River, anthropogenic alterations began in the early 1700s with the construction of canals and aqueducts to transport water from the river to Spanish

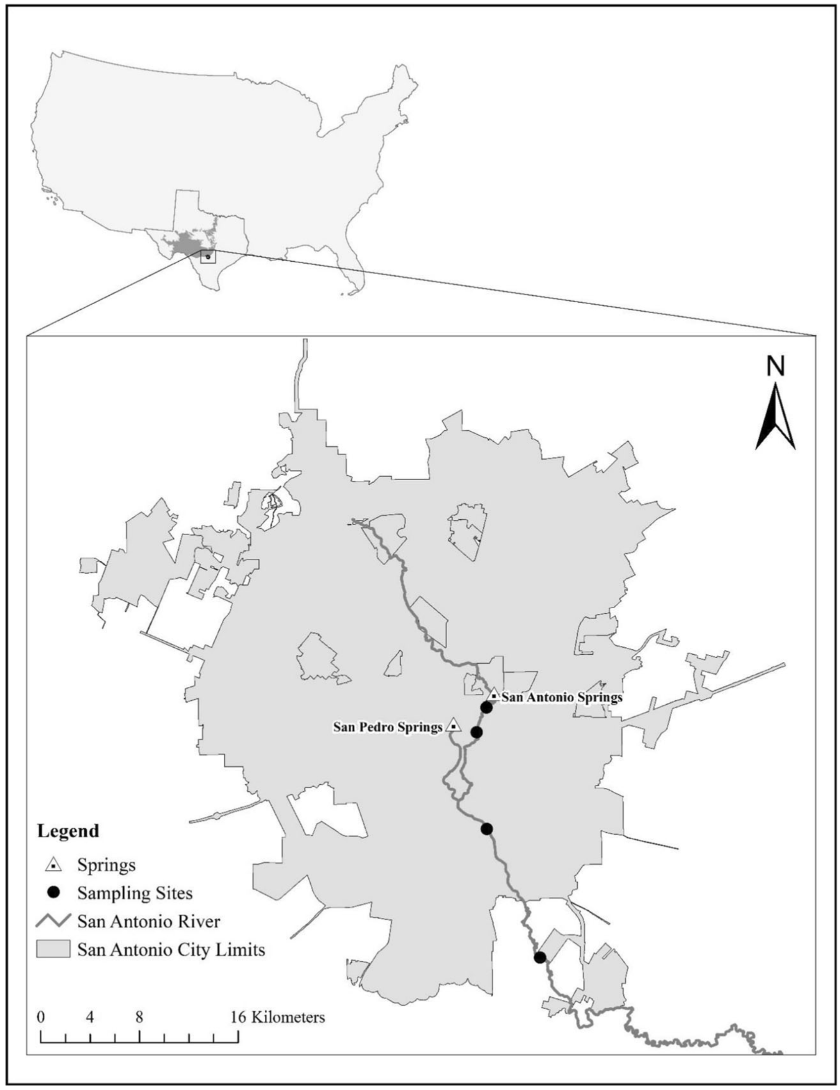


**Fig. 1** Shaded area of the United States represents the Edwards-Trinity aquifer system in Texas. Inset map illustrates the locations of the two major springs and sampling locations in the upper San Antonio River (Bexar County). Shaded area of inset map denotes the city limits of San Antonio. Sampling locations were used to estimate contemporary fish community 2013–2014

missions (Arneson 1921). By the late 1800s, water was contaminated with human waste and garbage; waterborne disease was pervasive (Brune 1981). Municipal water wells were drilled and accessed the same groundwater source as the artesian springs (Ewing 2000). In 1891, the city began to rely on wells rather than the aqueducts for its water supply, and the artesian springs began to decline. Soon after, Hill and Vaughan (1896) recognized that water well extraction was linked to reductions in artesian spring flows, based on a greater understanding of the Edwards Aquifer hydrogeology. As the City of San Antonio expanded rapidly from the 96th largest city in USA in 1880 to 54th by 1910, municipal water well use increased and artesian springs became intermittent by 1897 (Livingston et al. 1936). Additional water wells were drilled and diverted into the upper San Antonio River for the specific purpose of providing base flow to the river and to avoid complete dewatering of the stream channel. By 1918, artesian wells were the primary source of base flows in the river (Livingston et al. 1936). Beginning around 1930, additional artesian wells were drilled in downtown San Antonio for the purpose of single pass air conditioning systems; after use, water was returned to upper San Antonio River and contributed to base flow (Livingston et al. 1936). Up to 1 $m^3$/s of well water was used and returned daily to the upper San Antonio River (Call 1953). Through time, wells were abandoned or capped, with the last remaining artesian well capped in 2004. In 2000, treated wastewater was pumped into the upper reaches to supplement well water base flow. By 2004, base flows were dependent upon treated wastewater discharges, although spring outflows from San Antonio Springs and San Pedro Springs can contribute to base flows briefly following precipitation events. Currently, the upper San Antonio River drainage area (325 $km^2$) is highly urbanized (60% impervious cover, Kreuter et al. 2001; annual growth rate of 2.4% between 1970 and 2011; Zhao et al. 2016).

Earliest records of flow monitoring by USGS began in 1915 with gage station 08178000 (upstream gage) and was continuously monitored with few exceptions from 1929 to 1997. USGS gage station 08178050 (downsteam gage), located about 3 km downstream, began in 1992 and continuously monitored with few exceptions. Mean daily flow during the shared period of record (1992–1997) were correlated ($r^2$ = 0.90) with downstream gage having slightly greater (<0.1 $m^3/s$) mean daily flow. A composite hydrograph was constructed, using mean daily flows from the upsteam gage (1915–1997) and mean daily flows from the downsteam gage (1997–2015) (Fig. 2). Median of mean daily flows was 0.74 $m^3/s$ from 1915 through 2015. Median of mean daily flows was 0.36 $m^3/s$ (range: 0.01–5.4) during contemporary fish community collections.

To estimate contemporary community structure, we sampled four sites within the City of San Antonio four times from June 2013 to April 2014. Site 1 (29°27′32.23″N 98°28′25.75″ W) was the most upstream site and located 2.5 km downstream from San Antonio Springs. Site 1 was within a forested city park, consisted of run, riffle, and pool mesohabitats, and was straddled by the upstream and downstream city wastewater discharge sites (located at 29°27′41.4″N 98°28′05.9″W and 29°26′48.2″N 98°28′49.1″W respectively). Site 2 (29°26′26.71″N 98°28′56.62″W) was located near downtown San Antonio and 2.5 km downstream from Site 1. Site 2 was artificially channelized and consisted of run mesohabitat. Site 3 (29°21′52.47″N 98°28′18.68″W) was located within another city park and located 12 km downstream from Site 2 and 1.4 km downstream from the upstream gage. Efforts (San Antonio River Improvements Project, 2009–2012) to create mesohabitats in this area provided riffle, run, and pool habitats, riparian vegetation, and a reconfigured low head dam. Site 4 (29°16′31.55″N 98°26′5.84″W) was located 11 km downstream from Site 3. Site 4 was the least physically altered site (i.e., meandering stream, dense riparian vegetation) with run, pool riffle, and backwater mesohabitats.

Fishes were sampled from available mesohabitats (i.e., riffles, pools, runs, and backwaters; Bain et al. 1999) within 200–500 m reach at each site using a combination of multiple single pass seining (3.2 mm mesh), bag seining (3.2 mm mesh), barge electrofishing (Smith-Root Model 2.5 GPP), and backpack electrofishing (Smith-Root Model 12-b POW). Seines were used at each site in slow moving, wadeable habitats, and barge and backpack electrofishing were used near woody debris, in shallow riffle habitats, or in deeper waters. Sampling techniques were standardized by area. All fishes were identified to species (Craig and Bonner 2019) and enumerated. Juvenile species of the genus *Lepomis* <15 mm in total length were grouped due to difficulty in confidently

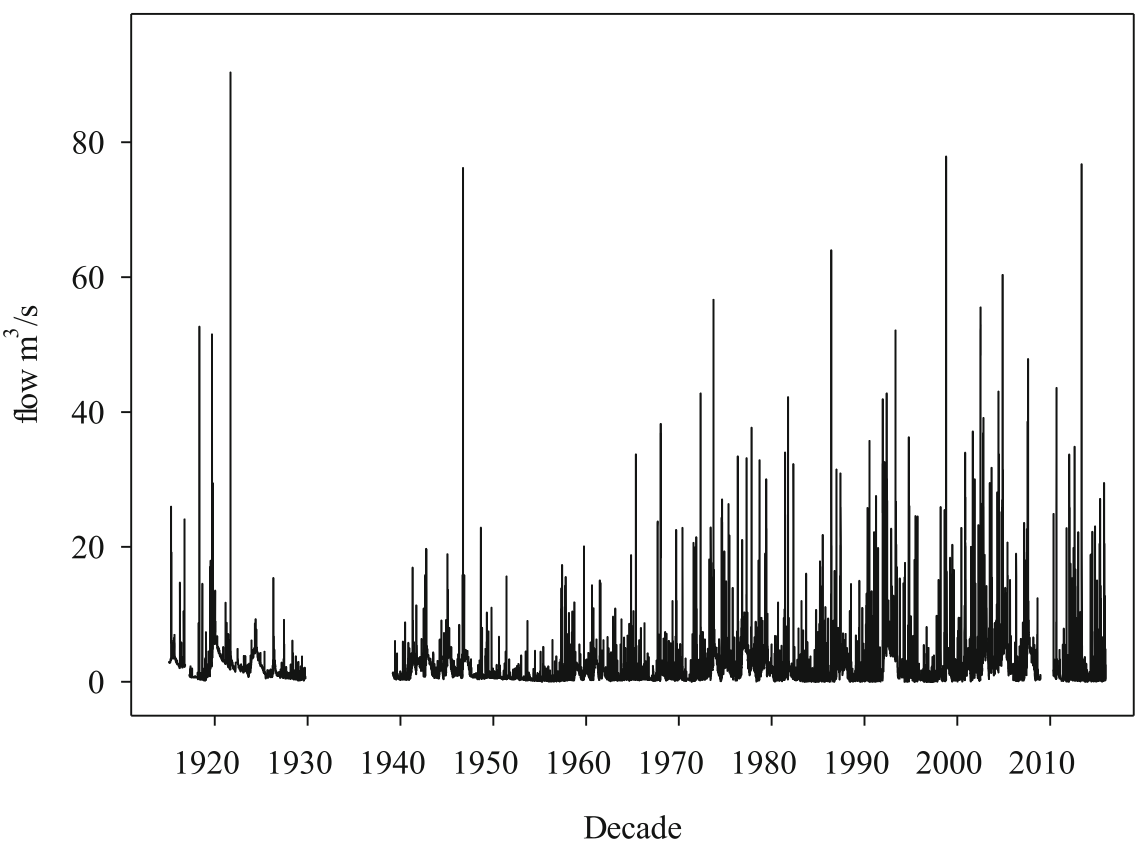


**Fig. 2** Composite hydrograph of mean daily flow for USGS gaging station 08178000 and 8178050 ($r^2$ = 0.90). Period of record from February 1915 through December 2015

identifying morphologically distinguishing features. Fishes were taken in accordance with Texas State University Animal Use and Care protocol 1207-0109-01 and Texas Parks and Wildlife Scientific Permit SPR-0601-159.

Fish collections from the four sampled sites sampled quarterly were combined for analysis (Table 1). Species richness (S), relative abundance (%), diversity (H), and evenness (E) were calculated by combining quarterly samples by site. Diversity was calculated using the Shannon-Wiener index, and evenness was calculated using Shannon's evenness index. Species richness, Shannon-Weiner diversity index ($\log_e$), and evenness ($E = H/H_{max}$) were calculated by site. Additional fish community data were obtained for the upper San Antonio River main stem from published and unpublished collections taken between 1853 and 2015 (Table 2). Collections were grouped by time periods. Fish records from 1853 through 1979 were obtained from museum records (Hendrickson and Cohen 2015), Barron (1964), and Hubbs et al. (1978). Earliest records contained partial reporting of fish collections and represent a conservative estimate of historic fish community. Therefore, we included several decades and only retained and combined species occurrences to represent the earliest time period. For the 1980s (1980–1989), fish occurrences and counts were obtained from Twidwell (1984) and Gonzales (1988) and used seines, trawls, rotenone, gillnets, and electrofishing. For the 1990s (1990–1999), fish occurrences and counts were obtained from San Antonio River Authority (1996) which used seines and electrofishing, and museum records (Hendrickson and Cohen 2015). For the 2000s (2000–2009), fish occurrences and counts were obtained from Edwards (2001), Hoover et al. (2004), Gonzales and Moran (2005) which used seines, gillnets, and electrofishing. For the 2010s (2010–2015), fish occurrences and counts were obtained from BIO-WEST (2012), Texas Commission on Environmental Quality (2015), and this study which used seines and electrofishing. Species identified among published and unpublished literature were accepted as reported, except for *Pimephales notatus* and *Oreochromis niloticus* (Hoover et al. 2014) since neither species were recorded as vouchered specimens and not previously known from the drainage (Hendrickson and Cohen 2015). Fish names were revised according to Page et al. (2013). Fish occurrences and counts were summed among collections by time period to calculate relative abundances. Fish sampling, when provided, ranged from one technique to multiple, and from one to multiple locations within the upper San Antonio River. Combining fish occurrences and summing collections by time period have limitations, when fishes were sampled for different purposes and by different collectors, techniques, and efforts. We acknowledge potential limitations in compiling and interpreting fish community changes through time, as others (Perkin and Bonner 2011; Kollaus et al. 2015),have also done; however, limitations do not preclude use of these data, because these data, at the very least, are a summary of the fish community reported within the upper San Antonio River.

Fishes were categorized as native or introduced (Hubbs et al. 1978; Edwards 2001; Hubbs et al. 2008). Spring-associated fishes (i.e., *Dionda nigrotaeniata*, *Notropis amabilis*, *Astyanax mexicanus*, *Percina carbonaria*) were defined based on the range-wide distributions (Craig et al. 2016). *Astyanax mexicanus* is considered introduced into San Antonio River (Brown 1953), but was retained as a spring-associated fish because *A. mexicanus* is native in two drainages within the Edwards Plateau reported by Craig et al. (2016) and associate with minimally-disturbed spring systems. Other introduced fishes (e.g., *Hypostomus*, *Oreochromis aureus, Oreochromis mossambicus*) are associated with spring complexes within the Edwards Plateau. These introduced fishes were not retained as spring-associated fishes because of their certainty as introduced species within the Edwards Plateau. Species richness, relative abundance, Shannon-Weiner diversity index, and Shannon's evenness were calculated for each time period after 1979.

Reference conditions for fish community structure of the upper San Antonio River were obtained from models developed by Craig et al. (2016), which predicted spring-associated fish communities related to spring flow. Models were developed from six independent and minimally disturbed spring complexes within the Edwards Plateau and represent expectations of spring complex fish communities (i.e., spring-associated fish richness, relative abundance, and density) with median spring flow. The three spring complex fish community regression models suggested that spring fishes were positively correlated to spring flow quantity. Specifically, spring-associated fish richness ($r^2 = 0.83$) and relative abundance ($r^2 = 0.87$) had an asymptotic relationship with historical median spring flow, while spring-associated fish density ($r^2 = 0.84$) had a linear relationship with historical median spring flow (Craig et al. 2016; Fig. 5)

Estimated historical median spring flow ($x$) of the upper San Antonio River (4.5 $m^3/s$; maximum flow assessed in reference conditions) was used to calculate expected spring-associated fish richness ($y = 0.203\ (1 - e^{(-3.13x)})$). Expected spring-associated fish relative abundance and density were not calculated, because relative abundances were not available in the earliest time period (1853–1979) and densities were not available from additional fish collections. Observed spring-associated fish richness were taken from contemporary (2013–2014) and additional (1853–2015) fish collections. Median flow (0.36 $m^3/s$) was used to calculate expected spring-associated fish richness ($y = 0.203(1 - e^{(-3.13x)})$, relative abundance ($y = 82.53(1 - e^{(-3.35x)})$, and density ($y = 0.203 + 0.352x$). Observed spring-associated fish richness, relative abundance, and density were taken from contemporary fish collections, combined among the four sites. Differences in species richness, relative abundance, and density between expected and observed were assessed by estimating the probability of the standard residual z-score [$Z_{residual} = (y_{observed} - \hat{y}_{expected}) / SD_{residual}$] with N – 2 DF. Standard deviation of the residuals (SD residual) is a measure of variation in between the regression line and measured values and was calculated as the square root of the mean of the squared residual values found in Craig et al. (2016). Expected species richness was rounded to a whole number.

## Results

A total of 34,326 fishes, representing 13 families and 52 species, was collected from the upper San Antonio River between 1853 and 2015. The most abundant families were Cyprinidae (range among time periods: 17–54%), Poeciliidae (19–35%), and Cichlidae (5.5–32%). Species richness ranged from 24 species in the 1980s to 41 species in the 2000s, diversity ranged from 1.89 in the 1980s to 2.32 in the 2000s, and evenness ranged from 0.59 in the 2010s to 0.70 in the 1990s. Diversity increased though time from 1.89 in the 1980s to 2.18 in the 2010s, whereas evenness remained similar between the 1980s and the 2010s. Both spring-associated fish species richness (S = 3) and introduced species richness (S = 15) were greatest in the 2000s. Spring-associated fish relative abundances were 21% in the 1980s and decreased to 2.0% in 2010s. Relative abundances of introduced species were 52% in the 1980s and decreased to 17% in the 2010s.

A total of 5806 fishes, representing 10 families and 31 species, were collected among four sites from June 2013 through April 2014. The most abundant families were Cyprinidae (55%) followed by Poeciliidae (18%), Centrarchidae (16%), and Cichlidae (8.8%). Two spring-associated fishes (*Astyanax mexicanus* and *Percina carbonaria*) were found within the upper San Antonio River. Spring-associated fishes were most abundant at Site 1 (11.3%) followed by Site 3 (1.8%) and had a combined relative abundance of 1.5% and a combined density of 0.02 fish/m$^2$. By contrast, introduced species richness was 10.

The Craig et al. (2016) model predicted a species richness of seven spring-associated fishes (95% CI = ± 2.1) at the earliest spring flow estimate of 4.5 m$^3$/s. Among 1853 through 2015 fish collections, observed spring-associated fish richness of four (i.e., *Dionda nigrotaeniata*, *Notropis amabilis*, *Astyanax mexicanus*, and *Percina carbonaria*) was less than expected ($P < 0.01$; Table 3). At median flow of 0.36 m$^3$/s, models predicted a species richness of five spring-associated fishes (95% CI = ± 2.03) with a relative abundance of 57% (95% CI = ± 15.7) and a density of 0.33 fish/m$^2$ (95% CI = ± 0.4). Within the contemporary community, observed spring-associated fish richness of two (i.e., *Astyanax mexicanus*, and *Percina carbonaria*) was less than expected ($P < 0.01$), relative abundance of 1.5% was less than expected ($P < 0.01$), and density of 0.02 fish/m$^2$ was not different ($P = 0.15$) from expected.

## Discussion

Based on assessments of collections taken from 1853 through 2015 and comparing upper San Antonio River fish community to reference conditions, we observed differences in the fish community through time. Spring-associated fish richness among 1853 through 2015 collections was less than the reference condition at historical spring flow of 4.5 m$^3$/s, and spring-associated fish richness and relative abundance of contemporary community (2013–2014) were less than reference conditions at reduced spring flow of 0.36 m$^3$/s. Since the 1980s, species richness of native fishes increased, species richness of introduced species increased, and spring-associated fish relative abundance decreased.

We attributed differences in observed versus expected spring-associated richness and abundance to changes in water quantity and quality, which are interrelated and difficult to parse into independent variables (Hellwig et al. 2017, Lind and Davalos-Lind 2002), as are other anthropogenic alterations (e.g., altered channel morphology) associated with urban stream syndrome (Meyer et al. 2005; Walsh et al. 2005). Per reference condition, we expected seven spring-associated fishes existing at the historical flow of 4.5 m$^3$/s, but only four spring-associated fishes were reported in the historical record. An expectation of seven spring-associated fishes is feasible for the upper San Antonio River, given that the Guadalupe-San Antonio River drainage supports nine spring-associated fishes (Kollaus et al. 2015, Scanes 2016) and the Medina River, a spring complex tributary of the San Antonio River with a historical median flow of 1.4 m$^3$/s, supports five spring-associated fishes (Hendrickson and Cohen 2015). As such, we presumed that spring-associated fish richness was greater in the upper San Antonio River but not reported in the historical record because of changes in water quantity and quality before the first collection of fishes in the 1850s.

We attributed the difference in spring-associated fish richness, relative abundance, and density between expected (S = 5; 57% in relative abundance; 0.33 fish/m$^2$ in density; reference conditions) and observed (S = 2; 1.5%; 0.02 fish/m$^2$; contemporary community; Table 3) at 0.36 m$^3$/s, primarily to changes in water quality associated with loss of spring flow and replacement with wastewater. In particular, replacement water within the upper San Antonio River (mean ± 1SD: 22.9 °C ± 4.96, min: 8.8 °C; max: 33.3 °C period of record: 2015–2020; San Antonio River Authority station at Mitchell Street) lacks the stenothermal character of spring flows (e.g., San Marcos River, Station 2; mean ± 1SD: 21.5 °C ± 1.66, min: 18.3 °C; max: 26.1 °C, period of record: 1994–1997; Saunders et al. 2001), which potentially have fitness benefits

**Table 1** Upper San Antonio River occurrences and abundances of fishes collected by site from 2013 through 2014. Status identified fishes as native (N) or introduced (I). Asterisk denotes spring-associated species identified by (Craig et al. 2016). Juvenile individuals of the genus *Lepomis* <15 mm in total length were grouped together and not counted towards species richness. Species within genus *Hypostomus* and *Pterygoplichthys* were counted as two species in species richness calculations. Likely each genus contains multiple species, but taxonomic status of species is uncertain (Cook-Hildreth et al. 2016). Diversity was calculated using the Shannon-Wiener index, and evenness was calculated using Shannon evenness

| | Status | Site 1 | Site 2 | Site 3 | Site 4 | Combined |
|---|---|---|---|---|---|---|
| *Dorosoma cepedianum* | N | | | <0.1 | 1.2 | 0.6 |
| *Dorosoma petenense* | N | | | | <0.1 | <0.1 |
| *Campostoma anomalum* | N | | | 0.9 | <0.1 | 0.3 |
| *Cyprinella lutrensis* | N | | 10.4 | 66.0 | 39.3 | 43.4 |
| *Cyprinus carpio* | I | | | | 0.2 | 0.1 |
| *Notropis volucellus* | N | 3.1 | 19.7 | <0.1 | <0.1 | 1.7 |
| *Pimephales promelas* | N | | | | <0.1 | <0.1 |
| *Pimephales vigilax* | N | | | 2.5 | 17.2 | 9.8 |
| *Astyanax mexicanus** | I | 11.3 | 0.7 | 1.8 | <0.1 | 1.5 |
| *Ameiurus melas* | N | | | 0.7 | | 0.2 |
| *Ameiurus natalis* | N | 0.2 | | | <0.1 | <0.1 |
| *Ictalurus punctatus* | N | | 0.5 | 0.6 | | 0.2 |
| *Noturus gyrinus* | N | | | | <0.1 | <0.1 |
| *Hypostomus* | I | 0.5 | | | | <0.1 |
| *Pterygoplichthys* | I | | 0.5 | | | <0.1 |
| *Menidia audens* | N | | | | <0.1 | <0.1 |
| *Gambusia affinis* | N | 46.0 | 13.7 | 12.7 | 7.4 | 12.4 |
| *Poecilia formosa* | I | 0.7 | 0.7 | 0.5 | 0.9 | 0.7 |
| *Poecilia latipinna* | I | 1.2 | 1.2 | 0.8 | 7.6 | 4.4 |
| *Lepomis auritus* | I | 6.0 | 23.9 | 0.4 | 5.9 | 5.4 |
| *Lepomis cyanellus* | N | | | 0.4 | 0.8 | 0.6 |
| *Lepomis gulosus* | N | | | <0.1 | 0.1 | 0.1 |
| *Lepomis macrochirus* | N | 16.6 | 0.9 | 1.8 | 6.9 | 5.4 |
| *Lepomis megalotis* | N | 1.2 | 0.7 | 0.9 | 4.4 | 2.7 |
| *Lepomis microlophus* | N | | 0.2 | | | <0.1 |
| *Lepomis* | | 0.5 | 0.7 | 0.1 | 1.3 | 0.8 |
| *Micropterus salmoides* | N | 4.3 | 0.9 | 0.2 | 0.4 | 0.6 |
| *Pomoxis annularis* | N | | | <0.1 | | <0.1 |
| *Percina carbonaria** | N | | | | <0.1 | <0.1 |
| *Herichthys cyanoguttatus* | I | 7.5 | 3.3 | 3.4 | 6.1 | 5.1 |
| *Oreochromis aureus* | I | 0.7 | 21.8 | 6.3 | <0.1 | 3.8 |
| *Tilapia zillii* | I | | | <0.1 | | <0.1 |
| Individuals collected | | 415 | 422 | 1949 | 3020 | 5806 |
| Species richness | | 13 | 15 | 21 | 24 | 31 |
| Introduced species richness | | 7 | 7 | 7 | 7 | 10 |
| Diversity (Shannon-Weiner) | | 1.73 | 1.93 | 1.35 | 1.94 | 2.05 |
| Evenness | | 0.67 | 0.71 | 0.44 | 0.61 | 0.59 |

for spring-associated fish reproduction (Hubbs 1995) and performance (Craig et al. 2019). Additional water quality stressors on the fish community in the upper San Antonio River include periodic reports of low dissolved oxygen, acute selenium levels, acute and chronic organics levels, and high levels of *E. coli* and fecal coliform (Texas Commission on Environmental Quality 2002). Therefore, water quality, in addition to water quantity (Craig et al. 2016), influences spring-associated fishes, although at least some of the spring-associated fishes will persist even with changes to the stenothermal character of riverine flows.

Fish communities within urbanized streams differ along a gradient of anthropogenic alteration (Wang et al. 2000; Meyer et al. 2005), ranging in extremes from fish community extirpation (Klein 1979) to less abundance in sensitive fishes (Miltner et al. 2004). Based on our assessment, the upper San Antonio River is not meeting the expectations of an Edwards Plateau spring-fish community but supports a speciose native fishes

**Table 2** Occurrences and abundances of fishes reported from contemporary (2013–2014) and additional (1853–2015) fish collections from the upper San Antonio River. Status identified fishes as native (N) or introduced (I). "X" denotes reported occurrence where quantity was not specified. Asterisk denotes spring-associated species identified by (Craig et al. 2016). Juvenile individuals of the genus *Lepomis* <15 mm in total length were grouped together and not counted towards species richness. Species within genus *Hypostomus* and *Pterygoplichthys* were counted as two species in species richness calculations. Likely each genus contains multiple species, but taxonomic status of species is uncertain (Cook-Hildreth et al. 2016). Genus *Tilapia* counted towards introduced species richness when *T. zillii* was not observed in a time period. Number of collectors represents the number of independent collections within a time period. Diversity was calculated using the Shannon-Wiener index, and evenness was calculated using Shannon evenness. Median flows were calculated from mean daily flows by time period

| | Status | 1853–1979 | 1980s | 1990s | 2000s | 2010–2015 |
|---|---|---|---|---|---|---|
| *Lepisosteus oculatus* | N | | | <0.1 | <0.1 | <0.1 |
| *Lepisosteus osseus* | N | | <0.1 | | | |
| *Dorosoma cepedianum* | N | X | | | <0.1 | 0.5 |
| *Dorosoma petenense* | N | | | | | <0.1 |
| *Campostoma anomalum* | N | | | 0.5 | 4.2 | 2.2 |
| *Carassius auratus* | I | | | | <0.1 | |
| *Cyprinella lutrensis* | N | X | 28.0 | 15.5 | 32.6 | 41.8 |
| *Cyprinella venusta* | N | X | <0.1 | | 0.8 | 1.1 |
| *Cyprinus carpio* | I | | | | <0.1 | <0.1 |
| *Dionda nigrotaeniata** | N | | <0.1 | | | |
| *Notemigonus crysoleucas* | I | | | | 0.2 | |
| *Notropis amabilis** | N | X | | | 1.3 | |
| *Notropis buchanani* | N | | | | 0.8 | |
| *Notropis stramineus* | N | | | | 0.3 | 0.1 |
| *Notropis texanus* | N | X | | | <0.1 | <0.1 |
| *Notropis volucellus* | N | X | 6.1 | 0.1 | 0.1 | 1.6 |
| *Pimephales promelas* | N | | 0.2 | 0.3 | | <0.1 |
| *Pimephales vigilax* | N | X | | 0.6 | 5.4 | 7.6 |
| *Moxostoma congestum* | N | | | 0.2 | 0.3 | 0.2 |
| *Astyanax mexicanus** | I | X | 20.8 | 5.7 | 5.9 | 1.8 |
| *Ameiurus melas* | N | | | | <0.1 | 0.2 |
| *Ameiurus natalis* | N | X | 0.3 | 1.7 | 0.4 | 0.4 |
| *Ictalurus furcatus* | N | | 0.1 | 0.5 | | |
| *Ictalurus punctatus* | N | X | 0.2 | 4.8 | 0.9 | 0.4 |
| *Noturus gyrinus* | N | X | | <0.1 | <0.1 | 0.2 |
| *Hypostomus* | I | X | 0.6 | 4.2 | 1.6 | <0.1 |
| *Pterygoplichthys* | I | | | | 0.4 | <0.1 |
| *Menidia audens* | N | X | | | <0.1 | <0.1 |
| *Lucania parva* | N | X | | | | |
| *Belonesox belizanus* | I | X | | | | <0.1 |
| *Gambusia affinis* | N | X | 11.7 | 7.9 | 19.2 | 15.0 |
| *Poecilia formosa* | I | X | | | 3.5 | 0.7 |
| *Poecilia latipinna* | I | X | 23.2 | 19.8 | 10.5 | 3.5 |
| *Poecilia reticulata* | I | X | | | <0.1 | |
| *Xiphophorus helleri* | I | | | 0.5 | <0.1 | |
| *Lepomis auritus* | I | | 2.2 | 2.7 | 0.7 | 4.4 |
| *Lepomis cyanellus* | N | X | 0.5 | 2.6 | 0.5 | 0.5 |
| *Lepomis gulosus* | N | X | <0.1 | <0.1 | <0.1 | <0.1 |
| *Lepomis macrochirus* | N | X | 0.4 | 0.5 | 0.5 | 4.1 |
| *Lepomis megalotis* | N | X | 0.3 | 0.5 | 0.8 | 3.7 |
| *Lepomis microlophus* | N | | <0.1 | | | <0.1 |
| *Lepomis miniatus* | N | X | 0.1 | | 0.2 | 0.7 |
| *Lepomis* | | | <0.1 | | | 0.6 |

**Table 2** (continued)

| | Status | 1853–1979 | 1980s | 1990s | 2000s | 2010–2015 |
|---|---|---|---|---|---|---|
| *Micropterus dolomieu* | I | X | | | | |
| *Micropterus punctulatus* | N | | | | 0.2 | 0.5 |
| *Micropterus salmoides* | N | X | 0.2 | 0.2 | 0.6 | 0.9 |
| *Pomoxis annularis* | N | | | | | <0.1 |
| *Percina carbonaria** | N | | | | <0.1 | 0.2 |
| *Herichthys cyanoguttatus* | I | X | 3.7 | 24.8 | 4.4 | 4.2 |
| *Oreochromis aureus* | I | | 0.3 | <0.1 | 0.4 | 2.8 |
| *Oreochromis mossambicus* | I | X | 1.5 | 6.0 | 2.6 | |
| *Tilapia zillii* | I | X | | | 0.4 | <0.1 |
| *Tilapia* | | | | 0.8 | | |
| Number of collectors | | 15 | 2 | 2 | 5 | 4 |
| Individuals collected | | 819 | 7146 | 3536 | 15,014 | 7811 |
| Species richness | | 29 | 24 | 26 | 41 | 39 |
| Introduced species richness | | 10 | 7 | 8 | 15 | 11 |
| Diversity (Shannon-Weiner) | | | 1.89 | 2.24 | 2.32 | 2.18 |
| Evenness | | | 0.60 | 0.70 | 0.62 | 0.59 |
| Median flows ($m^3/s$) | | 0.85 | 0.51 | 0.57 | 1.95 | 0.36 |

community including some sensitive fishes. The upper San Antonio River contemporarily supports 28 native fishes including three species (i.e., *Notropis volucellus, Noturus gyrinus,* and *Percina carbonaria*) considered as intolerant by Linam et al. (2002) per water quality standards. Detected changes in the fish community were largely consistent with other urbanized streams (e.g., increases in introduced fishes; Walsh et al. 2005). However, one inconsistency between the upper San Antonio River and other urbanized stream were the increases in native fishes through time. We found increases in native fishes, which is an uncommon finding but similar to findings of Morgan and Cushman (2005). Morgan and Cushman (2005) attributed increases in native fishes to potential changes in food web structure or habitats that allowed for invasion of opportunistic fishes. We attributed increase in native fishes within the upper San Antonio River through time to increases in sampling effort. However, it is possible that connectivity to downstream non-urbanized reaches could have increased the number of native fish moving into our study reach (Pretty et al. 2003, Morgan and Cushman 2005) and might be attributed to improvements in upper San Antonio River water quality (Miertschin et al. 2006).

Researchers struggle to quantify historical fish community changes in rivers with a long history of urbanization. Observations of the fish community changes are anecdotal (e.g., River Thames, United Kingdom; Carter and England 2004) or take place long after anthropogenic alterations occur (e.g., Seine River, France; Beslagic et al. 2013). In this study, challenges in quantifying fish community changes included fish records taken after anthropogenic alterations, incomplete records since first fish collections, inferring expected fish communities from reference conditions, and uncertainty in historical flow. Despite the challenges, our analysis of upper San Antonio River fish community can contribute to a greater understanding of urbanization effects on spring complexes. Specifically, we quantified the gap in spring-associated fish responses to loss of spring flows without dewatering of the spring complex. With declines and loss of spring flow, spring-

**Table 3** Standard residual z-score ($Z_{residual}$), degrees of freedom (DF), and *P* value for Craig et al. (2016) expected model parameters and observed for fish communities during two time periods in the upper San Antonio River

| Fish community | Parameter | Flow ($m^3/s$) | $y_{observed}$ | $\hat{y}_{expected}$ | SD | $Z_{residual}$ | DF | P value |
|---|---|---|---|---|---|---|---|---|
| 1853–2015 | Species richness | 4.5 | 4 | 7 | 1.06 | −2.84 | 4 | <0.01 |
| Contemporary | Species richness | 0.36 | 2 | 5 | 1.06 | −2.84 | 4 | <0.01 |
| | Relative abundance (%) | 0.36 | 1.5 | 57 | 11.30 | −4.91 | 4 | <0.01 |
| | Density (fish/$m^2$) | 0.36 | 0.02 | 0.33 | 0.296 | −1.05 | 4 | 0.15 |

associated fishes decline. In contrast, spring complexes are resistant to urbanization when spring flows are maintained (Kollaus et al. 2015). Spring flow, similar to river flow (Poff et al. 1997), is likely the master variable maintaining spring complex fish communities by regulating physical, chemical, and biological processes (Whiting and Stamm 1994; Bowles and Arsuffi 1999). Our study suggests that replacement of spring flows with alternative water sources is not sufficient to maintain the spring-associated fish community because water quality in addition to quantity (Craig et al. 2016) of the spring water influences richness, relative abundance, and density of spring-associated fishes. This is in contrast with the use of treated wastewater in non-spring systems, where relatively small shifts in community structure are observed (Porter and Janz 2003; Brown et al. 2011).

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