LONG-TERM CHANGES IN FLOW REGIME AND FISH ASSEMBLAGE COMPOSITION IN THE GUADALUPE AND SAN MARCOS RIVERS OF TEXAS

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ABSTRACT

Riverine flow regimes are naturally dynamic, but become increasingly homogenized following anthropogenic flow alteration. Loss of dynamism disrupts naturally occurring structuring mechanisms within the associated biotic communities, at times causing shifts in composition. Here we considered how stream fish assemblages in two Central Texas rivers changed after alteration of flow regime by either construction of a mainstem, deep storage reservoir or flood-retaining structures. Following impoundment, number of large and small floods increased from 0.81 to 1.07 floods per year (FPY) in the upper Guadalupe River, decreased from 0.84 to 0.42 FPY in the lower Guadalupe River and decreased from 0.87 to 0.7 FPY in the San Marcos River. Historical ichthyofauna data ranging from 1938 to 2006 were used to assess changes in assemblage composition and species abundance. Assemblages did not differ in the upper Guadalupe River (Bray–Curtis index = 37.4%; ANOSIM global $R = 0.079$, $p = 0.08$), but did differ in the lower Guadalupe River (25%; global $R = 0.409$, $p < 0.01$) and San Marcos River (27%; global $R = 0.19$, $p < 0.01$). In general, habitat generalist species dominated assemblages during periods of reduced flood frequencies (i.e. drought of record; following impoundment), whereas regionally endemic species ($N = 3$) and substrate and broadcast spawning species ($N = 5$) declined ($b_1 < 0$; $\alpha = 0.05$). Based on the results from this study, managing flows in the lower Guadalupe River to mimic historical timing of flood pulses might attenuate contemporary disruption of natural assemblage composition. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: fish assemblage changes; hydrologic alteration; Guadalupe River; San Marcos River; flood frequency

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INTRODUCTION

A suite of biotic and abiotic structuring mechanisms influence the natural occurrence and abundance of warm-water stream fishes through time and space (Matthews, 1998). Anthropogenic alterations of riverine environments disrupt these structuring mechanisms, causing minor and major changes to stream fish assemblages (Winston *et al.*, 1991; Aadland, 1993; Rinne *et al.*, 2005b; Poff *et al.*, 2007). Major changes to stream fish assemblages include the extinction or imperilment of endemic freshwater fishes (Keenlyne, 1997; Haro *et al.*, 2000; Garrett *et al.*, 2002; Adams *et al.*, 2006). Per cent of extinct or imperiled native freshwater fishes is 39% in North America (Jelks *et al.*, 2008), 28% in southeastern USA (Warren *et al.*, 2000) and 48% in southwestern USA (Warren and Burr, 1994). In Texas, 44% of native freshwater fishes are considered imperiled (Hubbs *et al.*, 2008). Despite the alarming rate of species imperilment and the subsequent increasing trend of fish homogenization (Rahel, 2000), successful conservation of warm-water stream fishes can be enhanced with water quality and quantity management (Angermeier, 1995; Pister, 1999; Richter *et al.*, 2003; Petts *et al.*, 2006).

Water quantity management in southwestern United States streams is necessary due to increasing aridity (Martin and Menringer, 1965) and demand for water (McCarl *et al.*, 1999). Low-head dams and deep storage reservoirs are common practices for securing adequate year-round water supply and hydroelectric power for urbanized or industrialized areas (Baxter, 1977). Detrimental effects of reservoirs on aquatic biota are well documented (Richter *et al.*, 1997); among others, a notable effect of reservoir construction is alteration of natural flow regime (Poff *et al.*, 1997). Reservoirs can cause drastic reduction or elimination of small and large floods (Runyan, 2007) and therefore alter numerous biotic (e.g. spawning cues; Bonner and Wilde, 2000) and abiotic (e.g. stream morphology; Poff *et al.*, 1997) factors for considerable distances downstream (Edwards, 1978). Furthermore, detrimental effects continue upstream of impounds by inundation of habitat, conversion of lotic to lentic water (Edwards, 1978) and disruption of migration patterns (Bonner and Wilde, 2000).

A growing body of literature exists for historical changes in stream fish assemblages in relation to anthropogenic stream alteration (see Rinne *et al.*, 2005a). However, additional research is necessary since streams are among the most negatively impacted environments by human activity

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(Helfman, 2007) and stream fish assemblage changes have been poorly documented with regard to the degree of existing alteration (Quinn and Kwak, 2003). Analysis of long-term trends in stream-dwelling fish assemblages provides several benefits including better understanding of the extent and magnitude of anthropogenic alteration (Calamusso *et al*., 2005), identifying species decline prior to imperilment (Runyan, 2007), consideration of changes over broad time scales (e.g. >60 years; Gido *et al*., 2002) and quantifying species loss due to extirpation or extinction (Mercano-Silva *et al*., 2006). Quantifying stream fish assemblage changes following stream alteration is limited by availability of baseline data collected prior to alteration (Gido *et al*., 2002), a limitation that has enhanced the value of historical museum collections (Suarez and Tsutsui, 2004).

Purpose of this study was to assess the effects of a deep storage, hydroelectric reservoir as well as tributary impoundments and watershed flood retarding and retention dams on fish assemblages of the Guadalupe River basin, Texas. More specifically, we sought to assess changes in mean annual flow, frequency of flood events, fish assemblage structure, abundance of specific taxa, and reproductive and trophic guild abundances following anthropogenic alteration of flow regimes within a semi-arid watershed.

STUDY AREA

The Guadalupe River originates at the confluence of the North Fork Guadalupe River and South Fork Guadalupe River near the City of Hunt, Kerr County, Texas (Figure 1). The total drainage area is 15 700 km^2 as it flows about 370 km southeast towards the Gulf of Mexico. Among the seven mainstem impoundments on the Guadalupe River, Canyon Lake reservoir was constructed in 1964. With a maximum depth of about 40 m and with a surface area of 3300 ha, Canyon Lake reservoir is the only deep storage reservoir within the Guadalupe River basin, representing the most significant alteration of mainstem discharge (Young *et al*., 1972; Edwards, 1978). Remaining mainstem reservoirs are impounded by low-head dams (maximum height: 12 m), constructing from 1928 to 1931 in the lower Guadalupe River (Young *et al*., 1972).

The San Marcos River, among the largest tributaries of the Guadalupe River, originates from artesian springs in the City of San Marcos, Hays County, Texas and flows about 120 km before reaching its confluence with the Guadalupe River near Gonzales, Gonzales County, Texas. The San Marcos River has seven low-head dams (maximum height: 6 m) and numerous low water crossings constructed between 1849 and 1901 (Taylor, 1904). Several low-head dams were constructed in the upper Blanco River, a tributary of the San Marcos River by Civilian Conservation Corps in mid-1930s and by private landowners through the 1950s. Flood retarding structures were constructed by the Natural Resource Conservation Service (NRCS) in the Plum Creek and York Creek drainages of the lower San Marcos River in the mid-1960s and 1970s. Flood retention structures were constructed by NRCS in the upper San Marcos River watershed in the 1980s (Woods and Earl, 2002).

METHODS

Daily discharges were obtained from three locations on the Guadalupe River (United States Geological Survey Station
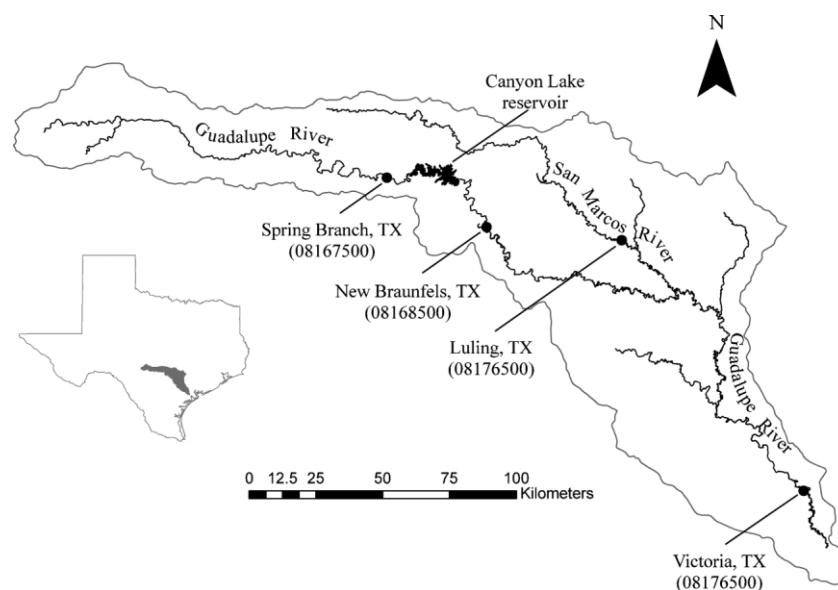

Figure 1. Guadalupe River basin of Texas. Dots represent USGS stream flow gauge locations (station I.D. number) used in Indicators of Hydrologic Alteration (IHA) analysis

08168500, New Braunfels, Texas; USGS Station 08176500, Victoria, Texas; USGS Station 08167500, Spring Branch, Texas) and one location on the San Marcos River (USGS Station 08172000, Luling, Texas; Figure 1). These locations encompass the largest available spatiotemporal range in drainage discharge (1927–2007 for Station 08168500; 1934–2007 for Station 08176500; 1922–2007 for Station 08167500 and 1938–2007 for Station 08172000). For each Guadalupe mainstem site, discharge data were divided into Period I (1938–1963) and Period II (1965–2007), using the completion of Canyon Lake reservoir (1964) as the environmental impact. For the San Marcos River, a break in ichthyological data during 1963–1976 was used to define Period I (1927–1963) and Period II (1976–2007), which generally corresponds with pre- and post-construction of water retarding and retention dams developed in the upper and lower watershed from late 1950s to early 1980s. Changes in frequency of small and large floods and mean annual discharge between periods were assessed with Indicators of Hydrologic Alteration, v. 7.0.3 (IHA). Flood frequency and mean annual discharge were used because of strong interrelationship among these parameters, fish habitat availability and stream morphology (Richter *et al*., 1996; Runyan, 2007). Small floods were defined as high flow events (i.e. exceeding 75% of discharge in Period I) with recurrences of at least 2 years. Large floods were defined as high flow events with recurrences of at least 10 years.

Historical ichthyofaunal collections from the Guadalupe River and San Marcos River drainages were obtained from museum collections, agency reports and published documents. Museum collections were obtained from the Texas Natural History Museum (TNHC; University of Texas), Texas Cooperative Wildlife Collection (TCWC; Texas A&M University), Tulane Museum of Natural History (Tulane), University of Kansas Natural History Museum (KU), University of Michigan Museum of Zoology (UMMZ), Field Museum of Natural History (FMNH; Chicago, Illinois), San Noble Oklahoma Museum of Natural History (OMNH; University of Oklahoma) and the National Museum of Natural History (NMNH; Smithsonian). Agency reports and published data included Texas Game and Fish Commission (TGFC, now Texas Parks and Wildlife, 1956, 1958, 1962, 1973), U.S. Fish and Wildlife Service (1976), Underwood and Dronen (1984), Longley *et al*. (1996), Terre and Magnilia (1996), Kelsey (1997) and Longley *et al*. (1998). Species occurrences and abundances, date and location of collection, principal collector and methods of collection were obtained from all collections (see Appendices I–III in Perkin, 2009).

There are uncertainties associated with using disparate data sets that span time and space to infer fish assemblage changes, especially among data sets where voucher specimens were incomplete or not taken. Uncertainties include comparability of data sets taken for different purposes (i.e.

targeting specific habitats or species vs. targeting available habitats and assemblages), from different locations within a watershed, at different seasons, by different collectors and with different gear types. We attempted to minimize these uncertainties by careful inspection of each data set and liberal exclusion of questionable data sets. Species lists were compared to expected ichthyofaunal list for the Guadalupe River drainage (Conner and Suttkus, 1986; Thomas *et al*., 2007; Hubbs *et al*., 2008) and questionable identifications were confirmed or refuted with available voucher specimens. Others were noted and removed when voucher specimens were not taken or available. Spatiotemporal variation in assemblage composition was addressed by assessing upper (upstream of Canyon Lake reservoir) and lower (downstream of Canyon Lake reservoir) segments of the Guadalupe River mainstem independently among time periods (as defined above). Museum collection data were retained if the collection had >5% of the total taxa found in the drainage and if the collection had >0.1% of the total number of individuals collected to improve the likelihood of the collection being a representative sample of the fish assemblage on a given date. Published literature and state agency reports were included if objectives of each study or report included assessing total assemblage composition (i.e. studies of specific species were excluded). Among 284 collections retained for analyses, 52% were obtained from museum collections, 31% from published literature and 17% from state agency reports (see Appendices I–III in Perkin, 2009). Among periods, 42% of all collections utilized (80% of museum collections) were supervised by a single individual, Clark Hubbs (see biography by Hendrickson and Stewart, 2000). Approximately equal sampling among seasons occurred within the final data set retained for analysis and consisted of fall (32% Period I, 22% Period II), winter (19% Period I, 21% Period II), spring (17% Period I, 32% Period II) and summer (32% Period I, 25% Period II). Among collections retained for analyses, gear types were limited to seining or electrofishing combined with seining. Because of advances in fisheries techniques during the time period of our study, Period I collections consisted only of seining ($n = 145$ collections), whereas Period II collections consisted of only seining in some cases ($n = 40$) and electrofishing combined with seining for others ($n = 99$). We acknowledge the potential for changes in gear type to confound results, but emphasize that limitations imposed by changes in sampling gear do not necessarily preclude quantitative assessment of assemblage changes through time.

Fish relative abundance was calculated for each collection retained for analyses. Among collections, relative abundances of a species were $\log_{10}(N + 1)$ transformed and plotted through time. Time represented the number of days from the first collection (23 June 1938). Simple linear

regression was used to test if slope of relative abundance differed ($\alpha = 0.05$) through time. Populations were classified as increasing ($b_1 > 0$) or decreasing ($b_1 < 0$) in abundance. Populations were classified as stable if slope did not differ from zero ($b_1 = 0$). Population status of rare species (i.e. occurring in $<10\%$ of total collections) and populations of species reported only once were classified as indeterminable. Native status of each species was determined using Conner and Suttkus (1986), Thomas *et al.* (2007) and Hubbs *et al.* (2008). Primary and secondary reproductive guilds were determined for each species using the classification scheme of Simon (1999), and trophic guilds after Goldstein and Simon (1999). Mean relative abundance of each species, excluding rare species, for Periods I and II was determined (sum of relative abundance in each collection/number of collections) to facilitate direct comparison of species abundance between periods. Functional changes within the assemblage were addressed using the relative abundance of each reproductive and trophic guild for each period (sum of individuals in each guild for given period/total individuals in given period).

For each period, taxa richness (S) and Simpson's Index of Diversity ($1 - D$) were calculated along with similarity matrices. Bray–Curtis similarity matrices (Bray and Curtis, 1957) created in Primer 6.1.6 were tested with analysis of similarity (ANOSIM; $\alpha = 0.05$; 9999 permutations) using permutations to assess average rank dissimilarity between periods (Runyan, 2007). Data were fourth-route transformed to standardize the contribution of high and low abundance species and illustrated using a multi-dimensional scaling (MDS) plot. Within Primer, the similarity percentage (SIMPER) tool was used to obtain contributions of individual species to total dissimilarity among periods and species constituting the majority (i.e. $>50\%$) of dissimilarity were listed. To compare collective trends in increasing or decreasing species through time, relative abundances of increasing and decreasing populations were Z-scored transformed to standardized relative abundance distributions (mean $= 0$; SD $= 1$) of each species. Z-score transformed abundances were averaged across all increasing or decreasing species by year (dependent variable) and regressed against time (independent variable) with piecewise regression model. Least-squares regression and joinpoint analyses to detect significant changes in rate through time (i.e. test for appropriate piecewise models) were performed with the program JOINPOINT (Joinpoint Regression Program, Version 3.0, National Cancer Institute, 2005), a program designed to use grid-search methods for optimizing model parameters (Brendon and Bence, 2008). Parsimonious joinpoint models were selected following permutation testing ($N = 5000$; default) rather than BIC selection approach (Brendon and Bence, 2008).

RESULTS

Mean annual flows increased between periods in the Guadalupe River and San Marcos River with frequency of small and large flood events increasing only in the upper Guadalupe River and decreasing in the lower Guadalupe River and San Marcos River. Mean annual flow in the upper Guadalupe River (Spring Branch, Texas) increased from $7.3 \, m^3 \, s^{-1}$ in Period I (1927–1964) to $14.0 \, m^3 \, s^{-1}$ in Period II (1965–2007) with annual frequency of small ($95 \, m^3 \, s^{-1}$) and large ($837 \, m^3 \, s^{-1}$) flood events increasing from 0.81 to 1.07 between periods (Figure 2). In the lower Guadalupe River, mean annual flow at New Braunfels, Texas, increased from $9.7 \, m^3 \, s^{-1}$ in Period I (1927–1964) to $17.7 \, m^3 \, s^{-1}$ in Period II (1965–2007) with annual frequency of small ($120 \, m^3 \, s^{-1}$) and large ($949 \, m^3 \, s^{-1}$) floods decreasing from 0.84 to 0.42. Also in the lower Guadalupe River, mean annual flow at Victoria, Texas, increased from $48.1 \, m^3 \, s^{-1}$ in Period I (1938–1964) to
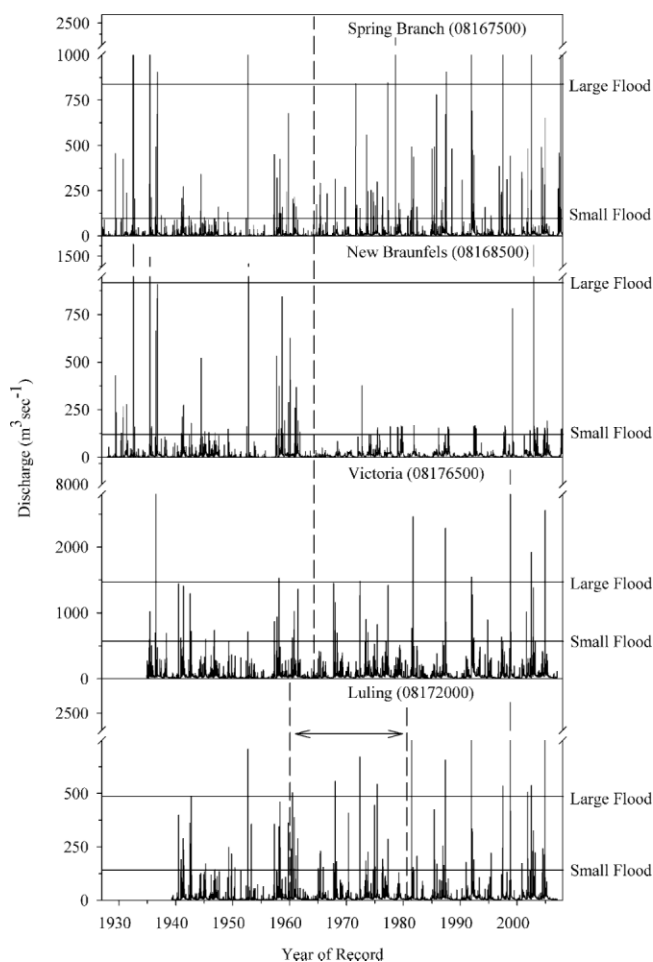

Figure 2. Hydrographs for the Guadalupe River at Spring Branch, New Braunfels and Victoria, and San Marcos River at Luling, Texas USGS gauging stations. Indicators of Hydrologic Alteration (IHA) was used to assess thresholds of large and small floods, vertical dashed lines indicate hydrologic disturbances (see text)

$64.0 \, m^3 \, s^{-1}$ in Period II (1965–2007) with annual frequency of small ($569 \, m^3 \, s^{-1}$) and large ($1461 \, m^3 \, s^{-1}$) floods decreasing from 0.56 to 0.42. In the San Marcos River, mean annual flow at Luling, Texas increased from $9.6 \, m^3 \, s^{-1}$ in Period I (1938–1963) to $13.3 \, m^3 \, s^{-1}$ in Period II (1976–2007) with annual frequency of small ($143 \, m^3 \, s^{-1}$) and large ($490 \, m^3 \, s^{-1}$) floods decreasing from 0.87 to 0.70.

Fish assemblage changes – Guadalupe River

A total of 78 species were reported in the Guadalupe River mainstem. Among the 190 collections retained for analysis, 69 species and 41 869 individuals were taken from the Guadalupe River mainstem from 1938 to 2000. Cyprinidae were most abundant (69% relative abundance), followed by Centrarchidae (11%), Poeciliidae (6%), Percidae (5%), Catostomidae (2%) and Ictaluridae (2%). Among marine-derived taxa, *Mugil cephalus*, *Mugil curema* and *Achirus lineatus* were not considered significant freshwater components of the assemblage. Guadalupe River mainstem assemblage consisted of two basin endemics (*Dionda nigrotaeniata* and *Percina apristis*), disjunct populations of two fishes (*Erimyzon sucetta* and *Percina shumardi*), south-western natural distributional extent, along with the adjacent and connected San Antonio River, of seven species (*Macrhybopsis marconis*, *Fundulus notatus*, *Lepomis humilis*, *Micropterus punctulatus*, *Micropterus treculii*, *Etheostoma chlorosoma* and *Etheostoma spectabile*), and 15 introduced species (or 22 introduced species of $N = 78$ fishes reported in the drainage; Perkin, 2009). Relative abundance of introduced fishes was <6% of the total fish assemblage.

Within the upper Guadalupe River, Cyprinidae were most abundant (73% relative abundance), followed by Percidae (8.1%), Poeciliidae (7.3%) and Centrarchidae (7.1%). Taxa richness decreased between Period I ($S = 42$) and Period II ($S = 41$), and diversity decreased between Period I ($1 - D = 0.86$) and Period II ($1 - D = 0.74$). Whereas fish assemblage similarity did not differ between periods (Bray–Curtis index $= 37.4$%; ANOSIM global $R = 0.079$, $p = 0.08$), 14 taxa collectively contributed >50% of observed dissimilarity (Table I; Figure 3). Among the 14 taxa, relative abundances of three cyprinids (*Cyprinella venusta*, *Notropis amabilis* and *Notropis volucellus*), two centrarchids (*M. treculii* and *Lepomis auritus*) and one catostomid (*Moxostoma congestum*) significantly increased through time, whereas relative abundances of three cyprinids (*Cyprinella lutrensis*, *M. marconis* and *Pimephales vigilax*) and one percid (*E. spectabile*) significantly decreased through time (Table II). Among the remaining four taxa, abundance of one cyprinid (*Campostoma anomalum*) generally was higher during Period II, and abundances of one poeciliid (*Gambusia affinis*), one centrarchid (*Lepomis megalotis*) and one ictalurid (*Ictalurus punctatus*) were lower during Period II, although significant shifts in abundances were not

detected with linear regression (see Table I). Two joinpoints were the most parsimonious models for increasing ($p < 0.01$) and decreasing ($p < 0.01$) populations. For increasing taxa, two joinpoints in 1961 denoted two distinct regression models with independent variables ranging from 1938 to 1961 and 1961 to 1997 (Figure 4). Relative abundances were not associated with either time interval ($b_1 \neq 0$, $p > 0.75$). For decreasing taxa, a joinpoint in 1950 and one in 1961 denoted three distinct regression models with independent variables ranging from 1938 to 1950, 1950 to 1961 and 1961 to 1997. Relative abundance was negatively associated ($b_1 = -0.000259$, $p < 0.01$) with time period 1950–1961.

Within the lower Guadalupe River, Cyprinidae were most abundant (68%), followed by Centrarchidae (13%), Poeciliidae (4.8%) and Catostomidae (3.0%). Taxa richness increased between Period I ($S = 40$) and Period II ($S = 62$), and diversity decreased between Period I ($1 - D = 0.92$) and Period II ($1 - D = 0.82$). Fish assemblage similarity differed between periods (Bray–Curtis index $= 25$%; ANOSIM global $R = 0.409$, $p < 0.01$) with 18 taxa contributing >50% of observed dissimilarity. Among the 18 taxa, relative abundances of three centrarchids (*Lepomis macrochirus*, *L. megalotis* and *Micropterus salmoides*), one clupeid (*Dorosoma cepedianum*) and one catastomid (*Ictiobus bubalus*) significantly increased through time, whereas relative abundances of two poeciliids (*G. affinis* and *Poecilia latipinna*), two percids (*Percina carbonaria* and *P. apristis*), one cyprinid (*Notropis buchanani*) and one fundulid (*F. notatus*) significantly decreased through time. Among the remaining seven taxa, abundances of two cyprinids (*Pimephalis vigilax* and *C. lutrensis*), one catastomid (*M. congestum*) and one cichlid (*Cichlasoma cyanoguttatum*) generally were higher in Period II, and abundances of two cyprinds (*M. marconis* and *N. volucellus*) and one ictalurid (*I. punctatus*) generally were lower in Period II, although significant shifts in abundances were not detected with linear regression. Two joinpoints was the most parsimonious model for increasing populations ($p < 0.01$), whereas one linear regression model (i.e. no joinpoint) was the most parsimonious model for decreasing populations ($p = 0.04$). For increasing taxa, one joinpoint in 1995 and another in 1997 denoted three distinct regression models with independent variables ranging from 1950 to 1995, 1995 to 1997 and 1997 to 2000. Relative abundance was positively associated ($b_1 = 0.000715$, $p < 0.01$) with time only during 1995–1997. For decreasing taxa without a joinpoint, relative abundance was negatively associated ($b_1 = -0.000063$, $p < 0.01$) with time during 1950–2000.

Fish assemblage changes – San Marcos River

Sixty-six species and 58 727 individuals were taken in 94 collections from the San Marcos River from 1938 to 2006 (Table II). Poeciliidae were most abundant (66%), followed

Table I. Similarity percentage (SIMPER) results for species collectively contributing to the majority (i.e. >50%) of dissimilarity between periods

Upper Guadalupe River	
Period I	Period II
Cyprinella lutrensis **(7.79)**	*Cyprinella venusta* **(6.48)**
Etheostoma spectabile **(4.98)**	*Notropis amabilis* **(6.30)**
Gambusia affinis (4.93)	*Notropis volucellus* **(6.30)**
Lepomis megalotis (4.16)	*Lepomis auritus* **(4.54)**
Pimephales vigilax **(3.05)**	*Campostoma anomalum* (3.99)
Macrhybopsis marconis **(3.00)**	*Micropterus treculii* **(3.93)**
Ictalurus punctatus (3.01)	*Moxostoma congestum* **(3.75)**

Lower Guadalupe River	
Period I	Period II
Pimephales vigilax (4.44)	*Lepomis megalotis* **(4.61)**
Gambusia affinis **(4.30)**	*Cyprinella lutrensis* (4.24)
Notropis buchanani **(3.38)**	*Lepomis macrochirus* **(3.89)**
Macrhybopsis marconis (3.35)	*Micropterus salmoides* **(3.51)**
Ictalurus punctatus (3.17)	*Dorosoma cepedianum* **(3.06)**
Poecilia latipinna **(3.00)**	*Moxostoma congestum* (2.97)
Notropis volucellus (2.97)	*Cichlasoma cyanoguttatum* (2.74)
Percina apristis **(2.77)**	*Ictiobus bubalus* **(1.65)**
Percina carbonaria **(2.68)**	
Fundulus notatus **(1.90)**	

San Marcos River	
Period I	Period II
Etheostoma fonticola **(4.25)**	*Notropis amabilis* **(3.77)**
Gambusia geiseri (4.20)	*Cyprinella venusta* (3.64)
Gambusia affinis (3.70)	*Lepomis miniatus* **(3.64)**
Cyprinella lutrensis **(3.62)**	*Lepomis auritus* **(3.54)**
Pimephales vigilax **(2.60)**	*Lepomis macrochirus* **(3.28)**
Cichlasoma cyanoguttatum **(2.59)**	*Notropis volucellus* **(3.26)**
Noturus gyrinus **(2.23)**	*Micropterus salmoides* **(2.84)**
Macrhybopsis marconis **(2.00)**	*Ambloplites rupestris* **(2.45)**

Parenthetical values indicated per cent contribution of individual species to overall dissimilarity among periods; species are listed under period in which abundances were greater. Time periods for upper and lower Guadalupe are Period I (1938–1963) and Period II (1965–2000); time periods for the San Marcos River are Period I (1938–1969) and Period II (1970–2006). Species names in bold indicate correspondence with significant population changes detected by linear regression (see Table II for linear regression results and native status).

by Cyprinidae (17%), Centrarchidae (10%) and Percidae (<7%). San Marcos River fish assemblage consisted of one endemic (*Gambusia georgei*), three basin endemics (*D. nigrotaeniata*, *P. apristis* and *Etheostoma fonticola*), disjunct populations of two fishes (*P. shumardi*, sympatric with those in the Guadalupe River, and *Notropis chalybaeus*), five fishes with southwestern natural distributional extent in the Guadalupe River drainage (*M. marconis*, *F. notatus*, *M. punctulatus*, *M. treculii* and *E. spectabile*), and 16 introduced species of fish. Relative abundance of introduced fishes represented <7% of the total fish assemblage. Currently, one species (*Ictalurus lupus*) is reported as extirpated (Kelsch and Hendricks, 1990) and another (*G. georgei*) is considered extinct (Miller *et al*., 1989).

Within the San Marcos River, taxa richness increased between Period I ($S = 48$) and Period II ($S = 58$), and diversity decreased between Period I ($1 - D = 0.91$) and Period II ($1 - D = 0.80$). Fish assemblage similarity differed between periods (Bray–Curtis index = 27%; ANOSIM global $R = 0.19$, $p < 0.01$) with 16 taxa contributing to >50% of observed dissimilarity. Among the 16 taxa, relative abundances of two cyprinids (*N. amabilis* and *N. volucellus*) and five centrarchids (*Ambloplites rupestris*, *L. auritus*, *L. macrochirus*, *Lepomis miniatus* and *M. salmoides*) significantly increased through time, whereas relative abundances of three cyprinids (*C. lutrensis*, *M. marconis* and *P. vigilax*), one ictalurid (*Noturus gyrinus*), one cichlid (*C. cyanoguttatum*) and one percid (*E. fonticola*) significantly decreased through time. Among the remaining three taxa, abundance of one cyprinid (*C. venusta*) generally was higher during Period II, and abundances of two poecillids (*G. affinis* and *G. geiseri*) generally were lower during Period II, although significant shifts in abundances were not detected with linear regression. Additionally, although per cent contribution to dissimilarity was small, linear regression detected significant increases in relative abundance through

Upper Guadalupe River

o Period I
• Period II   Stress = 0.26

Lower Guadalupe River

o Period I
• Period II   Stress = 0.19

San Marcos River

o Period I
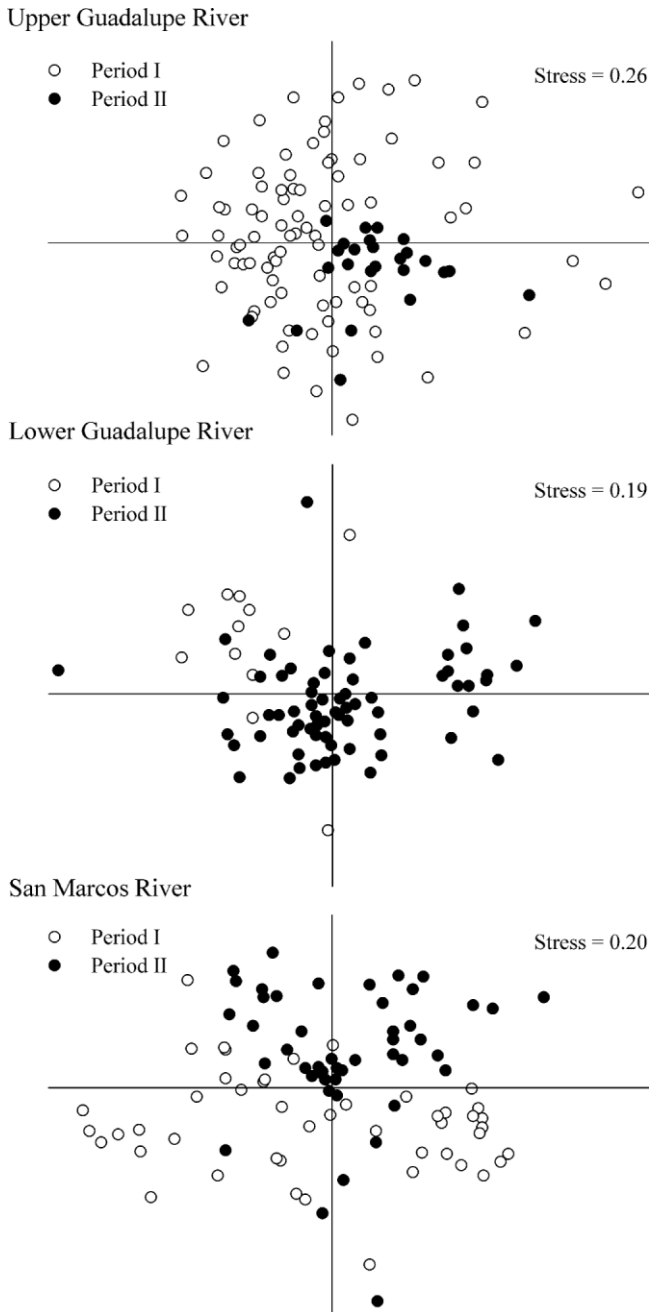• Period II   Stress = 0.20

Figure 3. Multi-dimensional scaling (MDS) plots for upper Guadalupe, lower Guadalupe and San Marcos River fish assemblages. Points represent ichthyological collections during Period I (open dots) and Period II (closed dots) and are plotted following fourth root transformation of relative abundances

time for four centrarchids (*Micropterus dolomieu*, *M. punctulatus*, *M. treculii* and *Lepomis gulosus*), two cyprinids (*C. anomalum* and *N. chalybaeus*), one catostomid (*M. congestum*), one characid (*Astyanax mexicanus*), one ictalurid (*I. punctatus*), one clupeid (*D. cepedianum*), one percid (*E. spectabile*) and one loricarid (*Hypostomus* sp.), whereas relative abundances significantly decreased through

time for one percid (*P. carbonaria*). Two joinpoints were the most parsimonious model for increasing populations ($p < 0.01$) and one joinpoint was the most parsimonious model for decreasing populations ($p < 0.01$). For increasing taxa, two joinpoints in 1993 denoted two distinct regression models with independent variables ranging from 1938 to 1993 and 1993 to 2006. Relative abundance was positively associated ($b_1 = 0.000021$, $p < 0.01$) with time during 1938–1993 and negatively associated ($b_1 = -0.000040$, $p < 0.01$) with time during 1993–2006. For decreasing taxa, one joinpoint in 1950 denoted two distinct regression models with independent variables ranging 1938–1950 and 1951–2006. Relative abundance was negatively associated ($b_1 = -0.000029, p < 0.01$) with time only during 1951–2006.

Reproductive and trophic guilds changes

Changes in reproductive guilds and trophic guilds were assessed for the lower Guadalupe River and San Marcos River, which were the two fish assemblages that showed significant assemblage differences between periods according to ANOSIM. Among the 24 fishes with increasing populations through time, reproductive guilds consisted of 59% nest builders, 33% open substrate spawners and 8% brood hiders; trophic guilds consisted of 54% invertivores, 17% predators, 13% omnivores, 12% herbivores and 4% detrivores. Among the 13 fishes with decreasing populations through time, reproductive guilds consisted of 30% brood hiders, 23% open substrate spawners, 15% nest builders, 15% internal bearers and 16% substrate choosers; trophic guilds consisted of 77% invertivores, 15% omnivores and 8% herbivores.

DISCUSSION

Occurrence and abundance of fishes changed in the Guadalupe River and San Marcos River during a span of about 70 years. During this same time period, characteristics of river discharge were modified; specifically, mean annual flow increased and frequency of small and large flood events generally decreased. Increases in mean annual flows among all three reaches of this study were attributed to computational effects of low water years in 1950s, often described as the drought of record (1949–1959; Loaiciga *et al.*, 2000), and to the effects of Canyon Lake reservoir. Discharge during the drought of record represented 25–35% of daily discharge records in Period I, lowering mean annual flow estimates. Consequently, we suspect that mean annual flows have not meaningfully increased in the upper Guadalupe River or San Marcos River. In contrast, detected increases in mean annual flows are meaningful in the lower Guadalupe River because of water releases at Canyon Lake reservoir. Canyon Lake reservoir, operated by US Army Corp of Engineers, regulates discharge releases as part of the

Table II. Native status, mean relative abundance per time period, population trend and associated *p*-value for species collected in the upper Guadalupe River, lower Guadalupe River and San Marcos River

Species	Status	Upper Guadalupe River				Lower Guadalupe River				San Marcos River			
		Period I	Period II	Population trend	*p*-Value	Period I	Period II	Population trend	*p*-Value	Period I	Period II	Population trend	*p*-Value
Dorosoma cepedianum	N	1.38	1.86	S		0.34	3.27	→	0.013	0.17	2.20	↑	0.01
Campostoma anomalum	N							S		0.13	1.33	↑	0.01
Cyprinella lutrensis	N	21.53	1.10	→	<0.001	22.16	35.15	S		14.33	1.45	→	<0.01
Cyprinella venusta	N	23.12	47.41	↑	<0.001	0.24	3.86	S					
Macrhybopsis marconis	N	1.80	0.27	→	0.025	3.87	1.51	S		2.43	0.37	→	<0.01
Notropis amabilis	N	3.24	10.48	↑	<0.001	3.54	7.39	S		3.73	7.82	↑	0.03
Notropis chalybaeus	N									0.09	0.50	↑	0.01
Notropis buchanani	N	0.07		—		5.34	0.68	→	0.001				
Notropis volucellus	N	2.71	12.20	↑	<0.001	4.74	3.39	S		1.02	6.89	↑	0.02
Pimephales vigilax	N	3.16	0.40	→	0.027	7.86	3.43	S		4.68	1.49	→	0.02
Ictiobus bubalus	N			—			1.02	↑	0.017				
Moxostoma congestum	N	1.22	1.29	↑	0.001	0.57	3.73	S		0.04	1.63	↑	<0.01
Astyanax mexicanus	I									0.48	2.01	↑	0.03
Ictalurus punctatus	N									0.54	1.08	↑	0.04
Noturus gyrinus	N									2.95		→	<0.01
Hypostomus sp.	I										0.02	↑	<0.01
Fundulus notatus	N	8.81		—		2.18	0.21	→	0.011				
Gambusia affinis	N		3.81	S		6.90	3.07	→	0.026				
Poecilia latipinna[a]	N/I	0.05		—		5.29	0.60	→	0.013				
Ambloplites rupestris	I									0.27	1.50	↑	<0.01
Lepomis auritus	I	1.12	2.19	↑	<0.001		2.90	S		0.39	5.48	↑	<0.01
Lepomis gulosus	N									0.21	0.66	↑	0.02
Lepomis macrochirus	N	0.66	1.73	S		0.74	4.52	↑	0.001	2.64	5.19	↑	<0.01
Lepomis megalotis	N	1.97	1.84	S		1.95	5.98	↑	<0.001				
Lepomis miniatus	N									3.78	5.37	↑	0.01
Micropterus dolomieu	I										0.21	↑	0.01
Micropterus punctulatus	N										0.31	→	<0.01
Micropterus salmoides	N	0.71	1.39	S	<0.001	0.25	2.24	↑	<0.001	1.50	2.12	↑	0.01
Micropterus treculii	N	0.54	1.44	↑		1.25	0.82	S		0.16	0.57	↑	0.04
Etheostoma fonticola	N									15.45	2.33	→	0.03
Etheostoma spectabile	N	11.03	2.91	→	0.028	1.58	0.37	S		0.13	0.71	↑	0.01
Percina carbonaria	N	2.05	1.32	S		4.60	0.09	→	<0.001	0.39	0.09	→	0.03
Percina apristis	N	0.42		—		2.12	0.16	→	<0.001				
Cichlasoma cyanoguttatum	I									3.83	1.47	→	0.03
Collections during period:		86	24			12	68			47	47		
Individuals collected:		12 266	6626			1390	21 587			10 695	48 031		
Taxa richness:		42	41			40	62			48	57		
Diversity:		0.86	0.74			0.92	0.82			0.91	0.80		

Native status was determined by Conner and Suttkus (1986) and Hubbs *et al.* (2008) as native (N) or introduced (I). Time periods for upper and lower Guadalupe River are Period I (1938–1963) and Period II (1965–2000); time periods for the San Marcos River are Period I (1938–1969) and Period II (1970–2006). Population trends are increasing (↑), decreasing (↓), stable (S) and indeterminable (—); *p*-Values are reported only for species indicating significant population change.
[a]Native to lower Guadalupe River (Conner and Suttkus, 1986); Introduced to upper Guadalupe River (Stevens *et al.*, 2007).
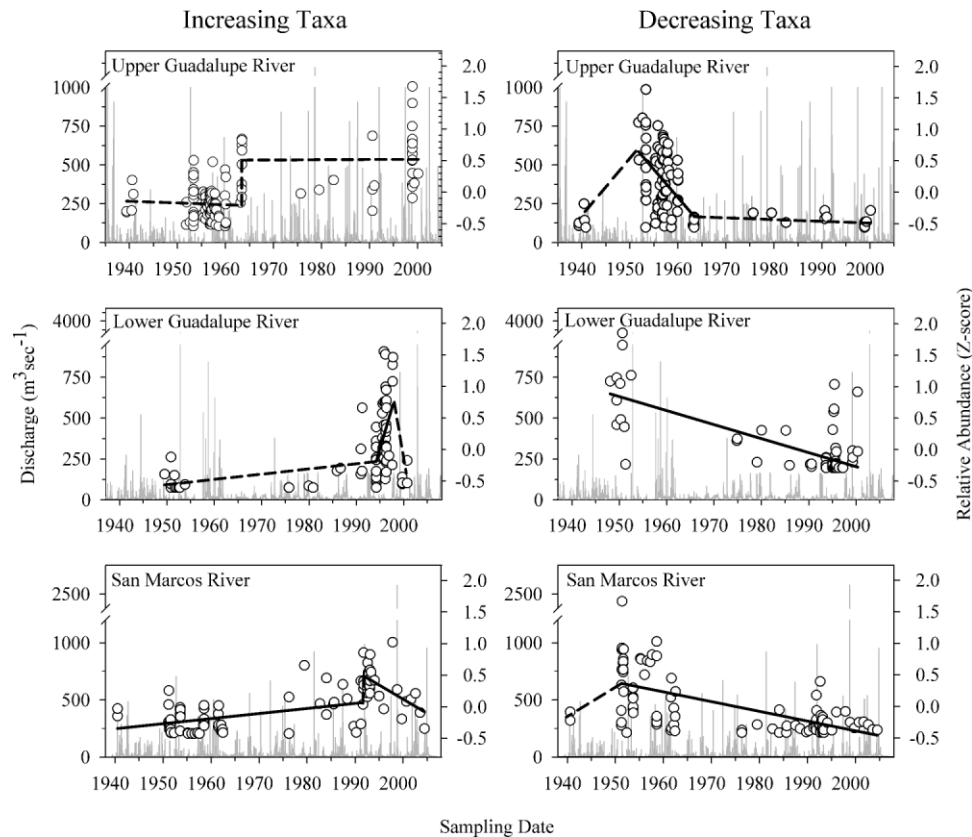
Figure 4. Hydrographs overlaid with joinpoint regressions for mainstem Guadalupe River and San Marcos River fish assemblages. Open circles represent Z-score transformed mean relative abundance for all species demonstrating significant increasing or decreasing populations. Solid lines indicate significant slopes ($b_1 \neq 0$) and dashed lines indicate non-significant slopes ($b_1 = 0$)

reservoir management plan for flood control and recreational activities (Gillig *et al.*, 2001). Likewise, decreases in frequency of small and large flood events were attributed to Canyon Lake reservoir in the lower Guadalupe River, with effects more noticeable at the nearest downstream Station (New Braunfels, 08168500). In the San Marcos River, decreases in frequency of small flood events were attributed to flow retarding and retention structures in the San Marcos watershed (Woods and Earl, 2002). Interestingly, significant differences in fish assemblage similarities were associated with river reaches that experienced decreases in frequency of small and large flood events (i.e. lower Guadalupe River and San Marcos River). This conclusion is consistent with other findings that report long-term (i.e. 1953–1986) changes within Texas freshwater fish assemblages corresponded with anthropogenic stream alteration, most notably changes in flow regime (Anderson *et al.*, 1995).

Fish assemblage changes associated with reductions in frequency of small and large flood events are well documented in temperate and tropical rivers, streams and small tributaries (Gehrke *et al.*, 1999; Bunn and Arthington, 2002; Agostinho *et al.*, 2004; Roy *et al.*, 2005; Mercano-Silva *et al.*, 2006). Reduction in flood frequency affects

stream geomorphology, causing a shift towards lentic-type habitat (Poff *et al.*, 1997), contributing to a replacement effect of fluvial specialist with lentic-type, generalist species (Scott and Helfman, 2001; Haxton and Findlay, 2008). Decreasing abundance of fluvial specialist species occurs through numerous mechanisms, including reduced reproductive success (Durham and Wilde, 2006), loss of spawning cues (Bunn and Arthington, 2002), barriers to dispersion (Luttrell *et al.*, 1999) and competitive exclusion from resources (Higgins and Strauss, 2008). Subsequent replacement by generalist species occurs through numerous mechanisms as well, including refugia from flood displacement (Stevens *et al.*, 2007), fulfilment of void niches (Winston *et al.*, 1991) and increased sedimentation (Poff *et al.*, 1997; Scott and Helfman, 2001). Abundances of generalist species typically increase at near-exponential rates flowing flow alteration (Scott and Helfman, 2001), whereas declining abundances of fluvial specialists occur over longer periods and is likely related to reduced reproductive success (Durham and Wilde, 2006).

Assemblage changes in the lower Guadalupe River and San Marcos River are consistent with general trends in generalist fish replacements. Within and outside of Western

Gulf Slope drainages, generalist fishes are those typically becoming more abundant in areas of flow alterations and include clupeids, some cyprinids, catostomids, poeciliids and centrarchids, whereas fluvial species tend to become less abundant, such as several species of cyprinids, percids and catostomids (Winston *et al.*, 1991; Kinsolving and Bain, 1993; Travnichek *et al.*, 1995; Scott and Helfman, 2001; Li and Gelwick, 2005; Mercano-Silva *et al.*, 2006; Runyan, 2007). In this study, abundances of one clupeid, four cyprinids, two catostomids, one characid, one ictalurid, one loricariid, 10 centrarchids and one percid increased through time in the lower Guadalupe River and San Marcos River. Correspondingly, abundances of fluvial specialist (i.e. three percids and four cyprinids) decreased through time in the lower Guadalupe River and San Marcos River. These patterns in change reflect those reported by Anderson *et al.* (1995), wherein changes in Texas freshwater fish assemblage composition between 1953 and 1986 were assessed using data collected by the same principal collector using similar sampling gear at similar sites. The authors noted decline of numerous cyprinids and percids (including many classified as declining herein) across Texas and concluded changes in flow regime, accompanied by other environmental changes, contributed to replacement of fluvial specialist species with generalist species. Exact mechanisms of these replacements are not known, but likely related to changes in fluvial specialist habitats and reductions in displacement floods as reported in other studies (Valdez *et al.*, 2001; Herbert and Gelwick, 2003; Holden *et al.*, 2005; Watson, 2006). Effects of displacement floods on generalist fishes were demonstrated by the results of this study. In the San Marcos River, taxa considered increasing from 1938 to 1993, specifically generalist fishes (i.e. *L. auritus*, *L. gulosus*, *L. macrochirus*, *M. salmoides* and *I. punctatus*), abruptly decreased from 1993 to 2006. These abundance declines occurred during a period of six large flood events including a catastrophic flood in 1998, which resulted in contemporary abundances characteristic of pre-impoundment abundances. A similar trend occurred in the lower Guadalupe River, where taxa that were considered increasing between 1993 and 1997 abruptly decreased following the largest flood on record since the impoundment of Canyon Lake reservoir, thereafter abundances were characteristic of pre-impoundment abundances.

There were inconsistencies with general trends in generalist fish replacements in the lower Guadalupe River and San Marcos River. Poeciliid abundances are expected to increase with decreases in frequency of flood events in Western Gulf Slope drainages (Ward *et al.*, 2003), but they actually decreased through time in the lower Guadalupe River. Similar trends of decreasing abundance through time were observed for *G. affinis* in the San Antonio River (Runyan, 2007) and for *P. latipinna* in the upper Guadalupe River (Stevens *et al.*, 2007; this study). Stevens *et al.* (2007)

suggested that a single flood was responsible for population declines, if not extirpation, of *P. latipinna* in the upper Guadalupe River. As the authors noted, a similar response occurred with another poeciliid during a flood in a Sonoran Desert stream (Collins *et al.*, 1981). Another inconsistency in general trends in generalist fish replacements is that abundances of several fluvial specialists (*N. amabilis*, *N volucellus* and *N. chalybaeus*) increased through time, whereas abundances of taxa typically associated with flow altered systems, generalist species with broad tolerances (*C. lutrensis*, *P. vigilax* and *E. spectabile*; Matthews, 1985; Greenburg, 1989; Li and Gelwick, 2005; Runyan, 2007) decreased through time in the San Marcos River. Similar results were observed in the upper Guadalupe River; *C. lutrensis*, *P. vigilax* and *E. spectabile* decreased through time, specifically 1950 through 1961. Based on the timing of abundance declines in these more tolerant taxa in the upper Guadalupe River, we propose that fish collections during the drought of record reflected a stressed system with an abundance of tolerant taxa. With the return of average precipitation and consequently average stream discharge post-1959, fluvial specialists again proliferated whereas tolerant taxa declined. Proliferation of the natural fish assemblage does occur in streams once the natural environment returns or is restored, assuming source populations exist and recolonization is not impeded by instream structures (Kinsolving and Bain, 1993; Doyle *et al.*, 2005).

Despite detectable changes through time, fish assemblages within all three reaches of this study remain relatively intact. Relative to streams with similar alteration, the worldwide pattern of loss of diversity and ecosystem function, decline in fluvial specialist abundance and replacement by generalist species are of lower magnitude in the lower Guadalupe River and San Marcos River. For example, the Petit-Saut Dam on the Sinnamary River in French Guiana significantly altered assemblage diversity and trophic structure downstream (de Merona *et al.*, 2005), over-exploitation of water in the Laja River of central Mexico caused significant alteration of assemblage composition with a 20–22% increase in exotic species (Mercano-Silva *et al.*, 2006), and hydrologic alteration in the Virgin-Moapa River System of the southwestern USA resulted in decline of native fish fauna and virtually complete replacement by *C. lutrensis* in some portions (Holden *et al.*, 2005). However, in the Guadalupe River and San Marcos River, we found few changes in trophic structure, exotic species constituted relatively small proportions of assemblages (i.e. <7% Guadalupe River, <6% San Marcos River), and increases in habitat generalist species did not result in complete replacement in any reach of our study. Instead, changes in the Guadalupe River and San Marcos River were similar to changes reported in the Big Blue River of Kansas, a prairie stream with similar drainage size to the Guadalupe River (i.e. 24 900 km^2). In the Big Blue River,

habitat generalist species increased (e.g. *P. vigilax* and *G. affinis*), fluvial specialist species decreased (e.g. *Macrhybopsis hyostoma*) and exotic fishes were sportfish; however, despite these changes, the fish assemblage remained relatively stable during a 40-year period (Gido *et al.*, 2002). Effects of flow alteration on fish assemblages in the Sinnamary River, Laja River and Virgin-Moapa River were intensified by other factors directly tied to impoundment (i.e. stream drying due to dam closure, hydropower production and elevated water temperature, and lack of refugia from degraded mainstem conditions), which likely contributed to greater shifts in assemblage composition (de Merona *et al.*, 2005; Holden *et al.*, 2005; Mercano-Silva *et al.*, 2006).

Although flow modifications explained many of the observed fish assemblage shifts within the Guadalupe River basin, other anthropogenic effects related or unrelated to flow modifications were not tested in this study and therefore cannot be excluded as possible contributory factors of assemblage shifts. Water quality throughout the basin generally is considered exceptional because of the large amount of base flows derived from the karst Edwards Aquifer (Bowles and Arsuffi, 1993; Groeger *et al.*, 1997). However, localized impacts of water pollution on flora and fauna have been reported from petroleum exploration and extraction (Hubbs and Strawn, 1956) and waste water discharge (Terrell *et al.*, 1978; Fries and Bowles, 2002). Changes in water temperature because of hypolemnetic discharge from Canyon Lake reservoir contributed to abundance decline in a localized population of *M. treculii* (Edwards, 1978). Introduced sportfish and subsequent introgression have led to possible extirpation of *I. lupus* (Kelsch and Hendricks, 1990) and reduced distribution of genetically pure *M. treculii* (Koppelman and Garrett, 2002). Stenothermal artesian springs throughout the basin provide refugia for a number of non-native taxa introduced by illegal dumping of ornamental organisms and by other means, including a parasitic trematode (Mitchell *et al.*, 2005), molluscs (Karatayev *et al.*, 2009) and fishes (Thomas *et al.*, 2007). Potential effects of introduced organisms on aquatic systems and fishes within the basin only recently have been explored (McDonald *et al.*, 2006, 2007; Cohen, 2008; Pray, 2009; Scott, 2009). Collectively, water quality and introduced taxa have caused localized problems within the basin, and their contribution to fish assemblage changes through time cannot be easily separated from flow modifications. In fact, they might not be separated issues; instead, issues with water quality and introduced taxa are exacerbated by basin-wide modifications of flow (Anderson *et al.*, 1995). Regardless, stream flow is the master variable within lotic aquatic ecosystems (Poff and Ward, 1989), and therefore should be considered a top conservation priority in riverine management of the basin.

Proposed low-head dam removal in the San Marcos River watershed and an adaptive management approach to regulating flows downstream from Canyon Lake reservoir might act to mitigate contemporary disruption of natural assemblage composition (Marchetti and Moyle, 2001; Taylor *et al.*, 2008). Anthropogenic disturbances such as impoundments effectively limit abundance and distribution of stream-adapt species in and outside of Western Gulf Slope drainages (Detenbeck *et al.*, 1992; Aarts *et al.*, 2004; Doyle *et al.*, 2005; Runyan, 2007; Jelks *et al.*, 2008; this study). However, naturally occurring disturbances such as floods and droughts have driven the evolution of stream-adapt species and are critical for the persistence of diverse riverine fish assemblages and aquatic biodiversity (DeAngelis *et al.*, 1985; Pearsons *et al.*, 1992; Lytle and Poff, 2004). Consequently, the need for experimental manipulation of regulated flows and continued monitoring of ecosystem response is becoming increasingly necessary as human demand for water increases while supply and availability diminish (Bunn and Arthington, 2002; Richter *et al.*, 2003; Dudgeon *et al.*, 2006; Sansom, 2008). Mimicry of natural flow regime within contemporary constraints has emerged as a point of origin for watershed management actions that target conservation of aquatic biodiversity as well as regional cultural and natural heritage (Propst and Gido, 2004; Taylor *et al.*, 2008). Finally, continued monitoring of ecosystem responses to anthropogenic stream alteration on both short- and long-term scales is necessary for further understanding the consequences associated with large-scale alteration.

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