INFLUENCE OF CONNECTIVITY AND HABITAT HETEROGENEITY ON FISHES IN THE UPPER SAN MARCOS RIVER, TEXAS

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INFLUENCE OF CONNECTIVITY AND HABITAT HETEROGENEITY ON FISHES

IN THE UPPER SAN MARCOS RIVER, TEXAS

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ABSTRACT

INFLUENCE OF CONNECTIVITY AND HABITAT HETEROGENEITY ON FISHES IN THE UPPER SAN MARCOS RIVER, TEXAS

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Fish distributions and habitat association models are useful for predicting fish community responses to anthropogenic modifications, such as reductions in water quantity and alterations of instream habitats. Among western gulf slope drainages, spring runs (i.e., from spring outflows to the confluence with larger streams) provide habitats for a large number of endemic fish fauna; however, current knowledge of fish distributions and habitat associations within spring runs is insufficient to accurately predict community changes or to assess community changes as a result of pre-existing anthropogenic modifications. Based on previous research, spring-associated fishes are distributed homogenously within spring runs and rarely in mainstem rivers, whereas riverine fishes of mainstem rivers rarely enter spring runs. Therefore, a primary prediction of this study was that spring-associated fishes of the upper San Marcos River would be homogenously distributed from spring origin (Spring Lake) to the confluence with the Blanco River. I quantified fish abundance, densities, and habitat associations during four seasons and among five reaches within the river, using multiple gear types to sample wadeable and non-wadeable habitats. Overall, spring-associated fishes were not homogenously distributed throughout the river, attributed to a lack of connectivity and likely habitat alterations. Also, riverine fishes occurred in high abundance throughout the river. Fish-habitat associations ranged from slack water specialists (i.e., endangered Fountain Darter, endemic Large Spring Gambusia) to swift water specialists (i.e., regional endemic Burrhead Chub and Guadalupe Darter). Results from this study and a companion study demonstrated that the upper San Marcos River fish community is highly persistent during a span of 100 years, have highly predictable habitat associations, and demonstrate the ecological function of habitat heterogeneity and constant water quantity.

CHAPTER I

INFLUENCE OF CONNECTIVITY AND HABITAT HETEROGENEITY ON FISHES IN THE UPPER SAN MARCOS RIVER, TEXAS

INTRODUCTION

Edwards Plateau region of Central Texas likely will increase in frequency and duration of warmer and drier conditions as the region shifts towards a more arid climate (Milly *et al*. 2005). As such, society (i.e., municipal, agriculture, industry) will place greater demands on surface and groundwater resources, which are currently inadequate to meet demands at times of below average precipitation. Concerns with limited water resources are concentrated near spring outflows of the Edwards Aquifer because of the occurrence of flora and fauna protected by Endangered Species Act (ESA; Ono *et al*. 1983; Votteler 2004). Groundwater pumping from the Edwards Aquifer reduces spring discharge, and less spring discharge reduces the amount of surface water habitat available for the threatened and endangered taxa (McCarl *et al.* 1999). Restricting pumping has socioeconomic consequences, whereas excessive pumping has ESA consequences (Blanchard-Boehm *et al*. 2009; Cox *et al*. 2009). Therefore, a balance between the two must be met to sustain current and future aquatic communities within the spring outflows.

The quantity of spring or river discharge necessary to maintain structure and function of lotic systems is predicted by a theory called Natural Flow Paradigm (Poff *et al*. 1997). The Natural Flow Paradigm states that contemporary discharge characteristics (i.e., magnitude, duration, timing, and rate of change) should be similar to historical discharge characteristics. The Natural Flow Paradigm however does not explicitly address the need to account for changes in water quantity due to climate changes within an interglacial period. If historical discharge characteristics are intact, the structure and function of biological communities and physical habitat characteristics (sediment transport, water quality) will not likely be constrained, at least by water quantity. Surplus water, water that is extracted while discharge characteristics are intact, can be captured or harvested for human consumption or use. Application of the Natural Flow Paradigm by various instream flow programs (Vaughn *et al*. 2010; Gooch *et al*. 2012) calculates central tendencies of subsistence flows, base flows, and several tiers of high flow pulses at points along a river basin and ensures that these flow targets are maintained within the channel. Among many predictions to test within systems managed by the natural flow paradigm is that habitat use and availability for fishes is sufficient when applying recommended flows that represent central tendencies of low, base, and high flows. In order to test this and other predictions, an understanding is necessary on how fish communities are assembled within a river reach, which is typically along current velocity and depth gradients (Aadland 1993; Rabeni and Jacobson 1993), and spatially along a river reach.

The upper San Marcos River is an artesian river system fed by three major fissures and nearly 200 adjacent openings of the Edwards Aquifer, located in Central

Texas, and is characterized by persistent water quantity and water quality (i.e. temperature, conductivity, pH; Groeger *et al*. 1997; Brune 1981) until it reaches the confluence with the Blanco River. Thereafter, water quantity is less immediately dependent upon spring discharge and more influenced by runoff, and reflect a greater variability in water quality parameters (Greoger *et al*. 1997). The upper San Marcos River, like many spring-fed systems of the Edwards Plateau, provides habitat for a number spring-associated fishes of conservation concern, including *Notropis chalybaeus*, *Notropis amabilis*, *Dionda nigrotaeniata*, *Gambusia geiseri*, *Percina carbonaria*, and federally listed *Etheostoma fonticola* (Hubbs *et al*. 2008). The upper San Marcos River fish community has endured over a 100 years of human influence but has been highly persistent (Kollaus *et al*. In review), meaning the majority of species within the fish community still occur at similar relative abundances through time and extirpations are low. However, habitat conditions are highly altered in at least two locations: Spring Lake area, by a lowhead dam, and in the lower reaches of the upper San Marcos River, by a lowhead dam (Capes Dam) and the large Cummings Dam in the San Marcos River downstream from the Blanco River confluence (Kollaus *et al*. In review). In a few remaining spring systems with only minimum human influence, the spring associated fish community is homogenously distributed throughout the stream as long as water quality parameters are similar (Bonner *et al*. 2005; Watson 2006). As the spring run approaches a confluence with runoff dominated flows (i.e., river), the community gradually becomes similar to the riverine community, since riverine fishes will also use the spring runs a certain times of the year (Rhodes and Hubbs 1992). Therefore, I predict that the upper San Marcos River fish community will be homogenously distributed throughout the stream, becoming similar to the Blanco River and lower San Marcos River fish community within the lower reach, and that fishes will be segregated along current velocity and depth gradients.

Objectives of this study were to quantify fish community structure and habitat associations for all fishes within the upper San Marcos River and develop sample methodology to adequately document the fish community among wadeable and non-wadeable habitats. Previous studies (Kelsey 1997; Kollaus *et al*. In review) provide occurrence and abundance information on fish communities of the upper San Marcos, but with the exception of Kelsey (1997), study objectives were biased towards the monitoring of *Etheostoma fonticola*. A variety of sampling techniques are necessary to adequately represent the fish community (Goldstein 1978; Heggenes *et al*. 1990; Roni and Fayram 2000; Mueller 2002). Habitats along the headwaters range from shallow (<1 m) to deep (6 m) but the exclusion of electroshocking in the endangered fish habitats exclude traditional stream sampling techniques, thereby making quantifiable collection methods to monitor all fishes difficult to employ.

METHODS

Study Area

Sampling occurred at eleven sites in the upper San Marcos River. Sites were grouped into 5 sampling locations: Spring Lake spring arm, Spring Lake slough arm, upper reach, middle reach and lower reach. Spring Lake spring arm consisted of five sites within Spring Lake (Site 1, 29°53’38.10”N, 97°55’48.63”W; Site 2, 29°53’35.82”N, 97°55’53.55”W; Site 3, 29°53’32.34”N, 97°55’57.26”W / 29°53’26.06”N, 97°56’03.63”W; Site 4, 29°53’27.53”N, 97°56’57.55”W; Site 7, 29°53’25.52”N, 97°55’59.94”W) and Spring Lake slough arm consisted of two sites (Site 5, 29°53’32.27”N, 97°55’43.31”W; Site 6, 29°53’39.41”N, 97°55’38.25”W). The upper reach consisted of three sites at Sewell Park (Site 8, 29°53’19.94”N, 97°56’02.73”W; Site 9, 29°53’16.35”N, 97°55’04.02”W) and Hopkins St Bridge (Site 10, 29°52’59.25”N, 97°56’06.53”W). Middle reach consisted of four sites at Rio Vista Park (Site 11, 29°53’43.72”N, 97°55’56.83”W; Site 12, 29°52’38.23”N, 97°55’59.29”W), interstate 35 (Site 13, 29°52’27.85”N, 97°55’51.72”W) and A E wood State Fish Hatchery (Site 14, 29°52’05.98”N, 97°55’39.55”W). Lower reach consisted of two sites on private property (Site 15, 29°51’34.98”N, 97°55’20.31”W; Site 16, 29°51’30.67”N, 97°53’19.12”W) and the San Marcos–Blanco River confluence (Site 17, 29°51’34.83”N, 97°54’49.03”W). A reference site was selected in the Blanco River to compare assemblage composition (Site 18, 29°51’40.83”N, 97°54’40.36”W). Sites were selected as representative subsamples of reaches (Figures 1–3).

Field Collections

Sites were sampled quarterly from January to December 2011. Sample locations included wadeable and deep-water habitats with fish surveyed by two methodologies, in wadeable habitats fish were sampled by seines (3.0 x 1.8 m strait seine) and deep-water habitats fish were sampled by underwater observation via SCUBA. Seine hauls and underwater observations were conducted along multiple line transects, with each transect treated as a unique geomorphic unit. Seine hauls were conducted in either a downstream haul or 5-m substrate kick with adequate spacing between hauls to minimize disturbance of adjacent samples. SCUBA surveys were segregated into two scales of observation with pelagic fishes observed along the entire transect (Mesohabitat) and benthically associated fishes observed along the lines of each transect (Microhabitat). Seine and SCUBA methods were segregated as well as mesohabitat and microhabitat surveys for analysis. Fishes were identified to the lowest possible taxonomic group and their abundance recorded (Hubbs *et al*. 2008). It is likely that hybrid centrarchids (i.e. *M. treculii*) were included in sample surveys, however in lieu of genetic verification; individuals were identified based on morphology and coloration (Littrell *et al.* 2007). All fish were returned to the field except those specimens taken as vouchers; vouchers were anesthetized with a lethal dose of tricaine methanesulfonate (MS-222) and preserved in 10% formalin. Water quality data were collected at each sample using a YSI-65 and a YSI-85 and included the following parameters: temperature (°C), pH, electroconductivity (µS/cm) and dissolved oxygen (mg/L). Habitat parameters were recorded for each geomorphic unit and included the following variables: type of unit (i.e., run, riffle, pool, and backwater), transect line length and width (m), percent substrate composition (silt, sand, gravel, cobble, clay, boulder, woody debris and detritus), percent vegetation cover, depth and current velocity. Current velocity (m/s) was measured with a Marsh-McBirney FLOW-MATE 2000 flow meter. In underwater observations, current velocity was measured at multiple depths along the water column and averaged prior to analysis.

Principle Component Analysis (PCA) was used to asses spatial variation between sample reaches based on physical habitat parameters and water quality (Canoco v. 4.55 2006). Qualitative data (i.e., reach) were represented as dummy variables, while quantitative habitat data (i.e., depth, current velocity, substrate, vegetation cover and water quality) were z-scored transformed (Krebbs 1999). Mean and standard deviation of PC scores were graphed to assess longitudinal variation in habitat characteristics across all reaches. Analysis of variance was performed on mean scored to test for differences across reaches with Fisher's LSD ($\alpha = 0.05$) post-hoc to determine specific reach differences.

Fish assemblage structure was characterized by calculating total species abundance (N), relative abundance (%), species richness (S), diversity (H'), and evenness (J') for each reach. Evenness was calculated using Pielou's evenness index and species diversity was calculated by using the Shannon-Wiener index with log10 base (Pielou 1966; Shannon 1948). Species abundance data were fourth-root transformed and Bray-Curtis similarity indices were created to assess similarity in assemblage structure (Warwick 1988; Bray-Curtis 1957). Analysis of similarity (ANOSIM) was run to determine differences in fish assemblage composition across reaches. The SIMPROF function (9,999 permutations and 999 simulations) was performed to test ($\alpha = 0.05$) for structure within the data. The SIMPER function was used to assess individual species contribution to dissimilarity in assemblage composition across reaches. CLUSTER analysis was used to determine groups of assemblages across sample reaches based on assemblage similarity. Among underwater observations, species of the genera *Gambusia* (i.e., *G. affinis, G. geiseri*) and some species of the genera *Lepomis* (i.e., *L. auritus, L. macrochirus, L. megalotis*) were grouped due to difficulty in distinguishing identifying criteria in situ.

Canonical correspondence analysis (CCA) was conducted to determine fish habitat associations with physical habitat parameters and water quality variables across all reaches (Canoco v. 4.55 2006). Species which comprised less than one percent of total abundance were excluded from analysis. Total variation was partitioned into pure effects of environmental parameters, site and season and Monte Carlo permutations were used to test significance ($\alpha = 0.05$) of both CC axes (Bochard *et al*.1992). Rare fishes were downwieghted to reduce influence on habitat parameters.

RESULTS

A total of 34 species of fishes (73% native, 27% non-native) occurred within the upper San Marcos River (Table 1). Taxa richness ranged between 18 species (53% of total) in Spring Lake (spring and slough arms; N = 16 each) to 28 species (82%) in middle and in lower reaches. Fourteen species were observed from all reaches. The number of unique species ranged between 0 in Spring Lake and the upper reach to five in the lower reach. Twenty-one species were most abundantly observed with seines, followed by 13 species observed most abundantly by mesohabitat and one species observed most abundantly by microhabitat. Across all gear types, three species were most abundant in the slough arm, eight species were most abundant in the spring arm, eight species, juvenile *Micropterus salmoides,* and *Lepomis* were most abundant in the upper San Marcos River, three species were most abundant in the middle San Marcos River, and 13 species were most abundant in the lower San Marcos River (Table 2).

Total CPUE was 4.6 fish/m^2 among all sites and gear types. Spring-associated fishes comprised 69% (3.2 fish/m^2) of total CPUE with *Gambusia geiseri* comprising

41% of total CPUE, followed by *Etheostoma fonticola* (17%), *Notropis amabilis* (4.8%), and *Astyanax mexicanus* (2.7%). Among stream-associated fishes, *Gambusia affinis* was the most abundant (12% of total CPUE), followed by *Lepomis auritus* (3.5%), *Lepomis* (2.9%), and *Lepomis miniatus* (2.2%). Among reaches and restricted to gear type most effective for capture, spring associated fishes comprised 11% of total CPUE in Spring Lake-Slough Arm, 84% in Spring Lake-Spring Arm, 81% in upper reach, 84% in middle reach, and 35% in the lower reach.

Seine

Reaches were distributed along a longitudinal gradient of physical habitat parameters. The most abundant geomorphic units were run (range among reaches: 0 – 93%) and backwater (4.9 – 100%) followed by riffle (0 – 12.6%) and pool habitats (0 – 8.1%). Spring Lake slough arm consisted of 100% backwater habitat with moderate depths (mean= 0.75 m, SE = 0.03), no measureable flow (0.0 m/s), dense vegetation (71%) of floating aquatic macrophytes, predominantly silt substrates (89%), the greatest seasonal variation in water temperature (22.9ºC; 0.33), low dissolved oxygen (3.0 mg/l; 0.27), with stable pH (7.3; 0.02), and conductivity (555µs; 7.5). The upper reach consisted of run habitats (93%), shallow to moderate depths (0.58 m; 0.02), moderate current velocity (0.24 m/s; 0.02) with moderate amounts of vegetation cover (55%; 22% Texas wildrice), silt (47%) and sand (26%) substrates, constant water temperature (22.1ºC; 0.07), moderate dissolved oxygen (7.7 mg/l; 0.11), with stable pH (7.4; 0.02) and conductivity (566µs; 4.6). The middle reach consisted of run (77%) and riffle (13%) habitats with shallow to moderate depths (0.46 m; 0.02), swift current velocities (0.66

m/s; 0.04), sparse vegetation (6.7 %), silt (35%) and gravel (37%) substrates, constant water temperature (22.9ºC; .05), moderate dissolved oxygen (8.5 mg/l; 0.1) with stable pH (7.6; 0.01) and conductivity (576µs; 3.4). The Lower reach consisted of predominantly run (87.0%) habitats, deep to moderate depths (0.73 m; 0.03), sluggish current velocities (0.12 m/s; 0.01) within with thin layer of silt (52%) and gravel (35%) substrates overlaying Taylor Marl clay, stable water temperature (23.2ºC; .017), moderate dissolved oxygen (7.0 mg/l; 0.0), and stable pH (7.7; 0.01) and conductivity (595µs; 5.2) (Table 3).

Principle component analysis explained 59% of the total variation in physical habitat and water quality parameters among sampling reaches. Principal component (PC) axis I (26% of total variation) represented a vegetation, water quality and substrate gradient with positive loadings for silt substrate (0.81), vegetative cover (0.71), and depth (0.25) and negative loadings for dissolved oxygen (-0.69), current velocity (-0.60), pH (-0.56) and gravel substrate (-0.53). PC axis II (15% of total variation) represented a temperature, water quality and substrate gradient with positive loadings for conductivity (0.78), temperature (0.74) and negative loadings for cobble substrate (-0.40), current velocity (-0.31), and sand substrate (-0.18). Reaches differed along PC I ($F_{3,565} = 316.3$, $P < 0.001$) and PC II ($F_{3,565} = 59.5$, $P < 0.001$) with significant pairwise differences across all reaches along PC axis I and lower reach differing from upper reach and slough along PC axis II (Figure 4).

Across all reaches and among 569 seine hauls, a total of 8,423 individuals representing 8 families and 31 species were surveyed from the headwaters of the San Marcos River. Poeciliidae (75%) were the most abundant family, followed by

Cyprinidae (9.6 %), Centrarchidae (8.6 %) and Percidae (3.9 %). *Gambusia geiseri* (61 %) were the most abundant species followed by *Gambusia affinis* (11 %), *Notropis amabilis* (5.4 %), *Lepomis auritus* (2.5 %), *Etheostoma fonticola* (2.4%), *Notropis chalybaeus* (2.3 %), *Poecilia lattipina* (2.2 %), and *Lepomis miniatus* (2.0 %). Spring-associated species (*Dionda nigrotaeniata*, *E. fonticola*) comprised 2.6 % of the total fish assemblage. Introduced species (*Astyanax mexicanus, Hypostomus plecostomus, Poecilia formosa, P. latipinna*, *Ambloplites rupestris, L. auritus, Herichthys cyanoguttatus*, *Oreochromis aureus*) comprised 8.5% of the total fish assemblage. Species richness (S), diversity (H') and evenness (J') increased along a longitudinal gradient with 21 species along the upper reach (H': 1.25, J': 0.28), 22 species in the middle reach (H': 1.30, J': 0.51) and 27 species in the lower reach (H': 1.37, J': 0.71). Species overlap occurred in all reaches with few exceptions including *Ameiurus natalis* exclusive to upper reach, *Macrhybopsis marconis* exclusive to middle reach, *Pimephales vigilax, P. formosa*, *Micropterus treculii* and *Etheostoma spectabile* exclusive to lower reach (Table 4).

Fish assemblages differed among reaches (ANOSIM Global R = 0.89, $P < 0.01$). Average similarity decreased along a longitudinal gradient across seasons in reach sample sites with 79% assemblage similarity in spring lake slough, 72% similarity in the upper reach, 72% similarity in the middle reach and 58% similarity in the lower reach. Among sample reaches, spring lake slough shared the least dissimilarity with the upper reach (51%) with *G. geiseri, E. fonticola, P. latipinna, L. gulosus, A. rupestris* and *N. chalybaeus* contributing over 50% of the dissimilarity between reaches. Among reaches, greatest dissimilarity occurred between upper and lower reach (49%) with *G. geiseri, A.*

mexicanus, *N. chalybaeus*, *N. amabilis*, *C. venusta*, *L. macrochirus* and *E. fonticola* contributing over 50% of the dissimilarity. Spring lake slough assemblage differed from river reaches (pi = 3.38, $P < 0.05$) with *N. amabilis, G. geiseri, N. chalybaeus, P. latipinna, E. fonticola, H. plecostomus, P. apristis* and *L. gulosus* contributing > 50% dissimilarity between clusters.

Physical habitat (15%) and reach (5%) explained 20% (P < 0.01) of the total variation of the fishes in the headwaters of the San Marcos River. Physical habitat parameters and reaches with the strongest loadings for CCA axis I were upper reach (-.87), vegetation cover (-0.37), temperature (0.42) and lower reach (0.75). Physical habitat parameters and reaches strongly associated with CCA axis II were Spring Lake slough (-0.55), silt (-0.47), cobble (0.52), middle reach (0.60) and current velocity (0.79). Among fishes associated with CCA axis I and II *G. geiseri* were most abundant and most commonly found in the upper reach in pool and backwater habitats with moderate vegetation cover, *G. affinis* were found among identical habitat parameters but were most abundant within spring lake slough and the lower reach. Riffle specialists (*P. apristis* and *P. carbonaria*) were strongly associated with gravel and cobble substrates and swift current velocities and found in greatest abundance in the middle and lower reaches. Deep bodied fishes (centrarchids) were associated with greater depths, slow current velocities and found in greatest abundance in Spring Lake Slough and the lower reach, introduced *L. auritus* was homogenously distributed along a longitudinal gradient, whereas native *L. miniatus* was most abundant and strongly associated with Spring Lake Slough. Run specialists (*C. venusta*, *N. amabilis* and *N. chalybaeus*) were associated with moderate to swift current velocities and gravel substrates and were most abundant among the middle and lower reaches. *E. fonticola* was most abundant in the upper reach and associated with slow to moderate current velocities and moderate to dense vegetation (Figure 5).

SCUBA Microhabitat

Underwater observation surveys were conducted among run (range among reaches: 0 – 100 %), pool (0 – 83.5 %) and backwater (0 – 100 %) geomorphic units. Spring Lake spring arm had the greatest mean (SE) depth among reaches (2.6 m; 0.16), low current velocity (0.03 m/s; 0.01), moderate to high vegetation density (78 %), predominantly silt (77 %) substrate, with constant water temperature (22.1ºC; 0.01), pH (7.2; 0.01) and conductivity (571µs; 1.8). Spring lake slough arm consisted of relatively shallow water depths (1.3 m; 0.07), low current velocity (0.01 m /s), dense vegetation (96 %), silt (100 %) substrate, greater seasonal variation in water temperature (22.6ºC; 1.2), stable pH (7.5; 0.02) and variable conductivity (562µs; 14.2). Upper reach consisted of shallow to deep depths (1.5 m; 0.11), swift current velocity (0.16 m/s; 0.02), with moderate vegetation cover (43%; 64% Texas wildrice), predominantly sand (33 %) and gravel (31%) substrates, with constant water temperature (21.7ºC; 0.11), pH (7.4; 0.03) and conductivity (574µs; 2.1). Middle reach consisted of moderate depths (1.6 m; 0.05), moderate current velocity (0.07 m/s; 0.01) with moderate density of vegetation (61%), predominantly silt (65%) and sand (21.7%) substrates, with constant water temperature (22.0ºC; 0.14), pH (7.6; 0.02) and conductivity (571µs; 1.9). Lower reach consisted of moderate to deep depths (1.7 m; 0.09), moderate current velocity (0.09 m/s; 0.01), and sparse vegetation (5.7%) with thin layer of silt (63%) on top of Taylor Marl clay or exposed Taylor Marl clay (7.3%) substrates, constant water temperature (21.7ºC; 0.28), pH (7.7; 0.02) and conductivity (583µs; 3.4) (Table 5).

Principle component analysis explained 66% of the total variation in physical habitat and water quality parameters among sample reaches. PC axis I (30.8% of total variation) represented a current velocity, substrate and vegetation cover gradient with positive loadings for current velocity (0.89), gravel substrate (0.63) and sand substrate (0.31) and negative loadings for silt substrate (-0.68), and vegetation cover (-0.58). PC axis II (13.4% of total variation) represented a temperature, water quality and substrate gradient with positive loadings for conductivity (0.88) and temperature (0.87) and negative loadings for sand substrate (-0.28) and cobble substrate (-0.18). Reaches differed along PC 1 ($F_{4,276}$ = 47.8, P < .001) with significant pairwise differences across all reaches along PC axis I, reaches did not differ along PC II($F_{4,276}$ = 0.90, P > .05) (Figure 6).

Across all reaches of the sample period and 281 under water observations a total of 2,409 individuals representing 10 families and 28 species were observed in the headwaters of the San Marcos River. Poeciliidae (47%) was the most abundant family, followed by Percidae (35%), Centrarchidae (13%), Loricariidae (2.8%) and Cyprinidae (1.1%). The most abundant fishes identified to genus and/or species were *Gambusia* (47 %), *E. fonticola* (33%), *Micropterus salmoides* (7.2%), *Lepomis spp.* (3.6 %), *H. plecostomus* (2.8 %), *L. auritus* (1.1 %), *A. mexicanus* (1.0%), *E. spectabile* (0.6%) and *N. chalybaeus* (0.5%). Spring associated species (*E. fonticola*, *D. nigrotaeniata*) comprised 34 % of the total fish assemblage. Introduced species (*A. mexicanus, H. plecostomus, A. rupestris, L. auritus, H. cyanoguttatus*, *O. aureus*) comprised 5.1 % of the total fish assemblage. Spring Lake spring arm had greater richness, diversity and lower evenness than Spring Lake slough arm with 16 species (H’: 0.72, J’: 0.59) and 6 species (H’:0.68, J’:0.87) respectively. Among river reaches, species richness decreased, while diversity increased and evenness increased along a longitudinal gradient with 18 species (H’: 0.51, J’:0.40) in upper reach, 16 species (H’: 0.44, J’: 0.37) in middle reach and 13 species (H’: 0.87, J’: 0.76) in lower reach (Table 6).

Fish assemblage similarity differed among reaches (ANOSIM Global R = 0.54, P <0.01). Average similarity varied among sample reaches across seasons with 65% assemblage similarity in spring arm, 6.0% similarity in the slough arm, 53% similarity in the upper reach, 64% similarity in the middle reach and 53% similarity in the lower reach. Among lake reaches, Spring Lake spring arm was 86% dissimilar to Spring Lake slough arm with *E. fonticola, Gambusia spp.,* and *M. Salmoides* contributing over 50% of the dissimilarity between reaches. Among river reaches, the greatest dissimilarity occurred between the upper and lower reachs (70%) with *H. plecostomus, P. carbonaria, E. fonticola* and *E. spectabile* contributing over 50% of the dissimilarity between reaches. Lowest dissimilarity among river reaches occurred between the upper and middle reach (45%) with *Gambusia* spp., *E. fonticola*, *A. rupestris* and *L. auritus* contributing > 50% dissimilarity. Spring Lake slough arm assemblage differed from river reaches (pi = 3.72, P < .10) with *E. fonticola, M. salmoides, H. cyanoguttatus,* and *P. apristis* contributing >50% dissimilarity between clusters.

Physical habitat and reach explained 20% (P < 0.01) of the total variation of fishes in the headwaters of The San Marcos River physical habitat parameters and reaches with the strongest loadings for CCA axis I were vegetation cover (-0.62), silt (-

0.35), clay (0.41), current velocity (0.50) and lower reach (0.92). Physical habitat and parameters and reaches strongly associated with CCA axis II were spring (-0.76), cobble (-0.66), gravel (-.34), middle reach (0.52), silt (0.52) and pH (0.68). Among fishes associated with CCA axis I and II *E. fonticola* were the most abundant species, and were observed amongst all reaches except Spring Lake slough arm where the greatest abundance occurred in the Spring Lake spring arm, followed by the middle and then upper reach. *E. fonticola* were observed amongst a variety of habitat types including gradients of shallow to deep depths, slow to moderate current velocities with low to high vegetation cover. *Gambusia* spp., were associated with slow current velocities in the upper reaches amongst moderate to high vegetation cover. Riffle specialists (*P. apristis, P. carbonaria*) were associated with middle to lower reaches and swift current velocities. Introduced *H. plecostomus* were strongly associated with the lower reach, swift current velocities and no vegetation cover (Figure 7).

SCUBA Mesohabitat

Across all reaches of the sample period in 49 mesohabitat surveys, a total of 6,767 individuals representing 10 families and 27 species were observed in the headwaters of The San Marcos River. Centrarchidae (40%) was the most abundant family, followed by Poeciliidae (24%), Cyprinidae (18%), Characidae (18%) and Loricariidae (2.8%). Most abundant fishes identified to genus and/or species were *Gambusia* (24%), *A. mexicanus* (18%), *D. nigrotaeniata* (17%), *L. auritus* (9.8%), *lepomis spp.* (8.4%), *M. salmoides* (9.7%) and *H. plecostomus* (2.8%). Introduced species (*A. mexicanus, C.* carpio, *H. plecostomus, A. rupestris, L. auritus, H. cyanoguttatus, O. aureus*) comprised 33% of the total fish assemblage. Spring Lake spring arm had greater abundance, richness and diversity than the Spring Lake slough Arm with 4,672 individuals comprised of 16 species (H': 0.86, J': 0.72) and 136 individuals comprised of 11 species (H': 0.78, J':0.75) respectively. Among river reaches, species richness, diversity and evenness was greater in the upper and middle reaches than the lower reach with 18 species (H': 0.78, J': 0.65) in the upper reach, 21 species (H': 0.91, J':0.69) in the middle reach and 13 species (H:'0.59, J':0.53) in the lower reach. 87% of the fish assemblage in the lower reach was comprised of non-native species including *C. carpio* (0.5%), *H. plecostomus* (60%) and *L. auritus* (15%) (Table 7).

Fish assemblage similarity differed among reaches (ANOSIM Global R = 0.58, P <0.01). Average similarity decreased along a longitudinal gradient among sample reaches across seasons with 86% assemblage similarity in the spring arm, 35% similarity in the slough arm, 67.1% similarity in the upper reach, 64.7% similarity in the middle reach and 51.7% similarity in the lower reach for the sample period. Among lake reaches, the spring arm was 66.7% dissimilar to slough arm with *D. nigrotaeniata*, *A. mexicanus, Gambusia* spp., and *L. auritus* contributing >50% dissimilarity between the reaches. Among river reaches, the greatest dissimilarity occurred between the upper and lower reaches (63.3%) with *Gambusia* spp., *M. congestum, M. salmoides, L. auritus, H. cyanoguttatus* and *lepomis* spp., contributing >50% of the dissimilarity between reaches. Least dissimilarity among river reaches occurred between the upper and middle reach (37.8%) with *Gambusia* spp., *D. nigrotaeniata, N. chalybaeus, M. salmoides, L. macrochirus* and *A. mexicanus,* contributing >50% dissimilarity. The lower reach fish assemblage differed from all other reaches (Pi: 8.81, $P < 0.01$) with *Gambusia* spp., *D.*

nigrotaeniata, H. *plecostomus, A. mexicanus, L. auritus, L. macrochirus, L. microlophus, H. cyanoguttatus* and *M. congestum* contributing >50% dissimilarity. Additional clusters identified differences between the slough (Pi: 3.94, $P < 0.05$) and the spring (Pi: 5.07, $P < 0.01$) assemblages with the upper and middle reaches.

DISCUSSION

Fishes were distributed longitudinally within the upper San Marcos River with spring associated fishes being the most abundant in Spring Lake-Spring Arm and the upper and middle reaches of the San Marcos River and with riverine-associated fishes being most abundant in the Spring Lake-Slough arm and lower reaches of the San Marcos River. However, distinct delineation between spring associated and riverine associated fishes was not observed. Eleven riverine-associated fishes were most abundant in Spring Lake-Spring arm and the upper and middle reaches of the San Marcos River, whereas two spring-associated fishes were most abundant in the lower reach of the San Marcos River. Heterogeneity in the upper San Marcos River fish community is attributed to differences in habitat connectivity and physical habitat characteristics among reaches.

Similarities among stream fish communities are associated with stream connectivity (Perkin and Gido 2012). The lower reach of the upper San Marcos River is bounded by a low-head dam upstream (Ed Capes dam) and the confluence with the Blanco River downstream. All species, including five species unique to the lower reach and excluding the introduced *H. plecostomus*, occur in the Blanco River (Bean *et al*. 2007) or in the San Marcos River downstream of the confluence with the Blanco River (Perkin and Bonner 2012). Fish community similarity between the lower reach and the lower Blanco River is likely attributed to unimpeded exchanges between the two connected water bodies. Fish community dissimilarity between the lower and middle to upper reaches of the upper San Marcos River is partly attributed to restricted movements upstream because of Ed Capes dam. Instream barriers, such as low-head dams, reduce connectivity between upstream and downstream fish communities (Porto *et al*. 1999; Ozburn 2007; Perkin and Gido 2012). However, impendence of upstream movement does not adequately explain why the middle and upper reach fishes are absent or reduced in abundance in the lower reach, since instream barriers minimally restrict upstream to downstream movement (Porto *et al*. 1999). Instead, my results suggest that differences in physical habitat characteristics also accounted for observed community differences among reaches.

Longitudinal habitats in the upper San Marcos River ranged from lentic-like habitats in Spring Lake (Spring arm and Slough arm) with silt substrates, greater depths, and high vegetative cover to lotic-like habitats in the upper, middle, and lower reaches with more heterogeneous substrates, shallow to moderate depths, and little to high vegetative cover. Within lotic-like habitats, reaches differed primarily along sluggish (upper and lower reaches) to swift (middle reach) current velocities, moderate (upper and middle reaches) to deep (lower reach) water depth, and low (middle) to high (upper) vegetative cover gradients. Correspondingly, slackwater fishes (*Dionda*, *Etheostoma*, *Lepomis*, *Micropterus*, *Herichthys*) were associated with Spring Lake-Spring arm, lotic (*Notropis*, *Moxostoma*) and lentic (*Gambusia geiseri*, *Lepomis*) fishes were associated with the upper reach, riffle and shallow run specialists (*Macrhybopsis*, *Percina apristis*) were associated with the middle reach. Fishes inhabiting the lower reach were lentic

(*Lepomis*, *Poecilia*) and lotic (*Notropis*, *Cyprinella*) fishes, including two species typically associated with spring systems (*Notropis amabilis, Percina carbonaria*). Among water quality gradients, variation in water temperature differed between Spring Lake-Spring Arm and Spring Lake-Slough Arm. Spring-associated fishes and riverine-associated fishes were more abundant in the Spring Arm, which has less diel and seasonal variation in water temperature, whereas only riverine-associated fishes were more abundant in the Slough Arm, which has greater diel and seasonal variation in water temperature. However, abundances of spring-associated fishes increased in the slough arm during the summer months, when water temperatures were warmer, and riverine-associated fishes increased in the spring arm during winter months, when water temperatures were cooler in the slough arm (Behen, unpublished data). Longitudinal patterns in species distributions related to water quality gradients were not observed among river reaches, likely attributed to homogeneity of water quality throughout the upper San Marcos River (this study, Groeger *et al*. 1997). High abundance of two spring associated fishes (*Notropis amabilis* and *Percina carbonaria*) in the lower reach supports this observation. Based on these collective findings, we (Kollaus *et al*. In review) propose that habitat of the lower reach, which currently represents an altered condition, is too dissimilar from the upper, middle, and the historical lower reaches in water depth, current velocity, substrate composition, and vegetation coverage and therefore no longer providing adequate habitat for slackwater surface and benthic specialists (i.e., *Gambusia geiseri*, *Etheostoma*, *Dionda*) and lotic riffle specialists (*Macrhybopsis).* Mechanisms of habitat alteration in the lower reach are identified and discussed in Kollaus *et al*. (In review).

Across all reaches and Spring Lake, the fish community in the upper San Marcos River is similar to the fish communities in the adjacent Blanco River and spring systems throughout the Edwards Plateau. Among a total of 40 species of fish, 26 species occur in both the upper San Marcos River and Blanco River system (including two tributaries that are supported by springs) with 8 unique species in the San Marcos, including four introduced species, and 6 unique species in the Blanco River, including one (*M. dolomieu*) and likely another (*P. promelas*; commonly used baitfish) introduced species. Among the four unique native fishes within the upper San Marcos River, *Lepisosteus oculatus* is widely distributed in the Guadalupe-San Antonio River basin (Runyan 2007; Perkin 2009), coastal streams of Texas, and central North America (Hubbs *et al*. 2008), *Notropis chalybaeus* is a glacial relict within the San Marcos River (Swift 1970; Perkin *et al*. 2012) and widely distributed throughout eastern North American drainages, and *Etheostoma fonticola* and *Gambusia geiseri* occur naturally in the upper San Marcos River and nearby Comal River, though *Etheostoma fonticola* likely was extirpated from the Comal River in 1950s and reintroduced in the 1970s (Schneck and Whiteside 1976), and *Gambusia geiseri* is introduced in the upper Colorado River and throughout the Rio Grande drainage (Hubbs *et al*. 2008). Among the four unique native fishes of the Blanco River, all (*Campostoma anomalum, Cyprinella lutrensis, Notropis stramineus*, and *Fundulus notatus*) historically occurred in the upper San Marcos River (Kollaus *et al*. in review). Consequently, spring run habitats of the upper San Marcos River is a contribution to the regional ichthyofauna by providing resources for 3 unique species (*N. chalybaeus, G. geiseri, E. fonticola*). As such, upper San Marcos River is similar to many other spring-fed systems of the Edwards Plateau in providing habitats for unique spring-associated fishes, such as *Notropis amabilis*, *Etheostoma lepidum* and *Dionda nigrotaeniata* in the South Llano River (Curtis 2012); *Notropis amabilis, Cyprinella proserpina*, *D. argentosa*, and *Etheostoma grahami* in the upper Devils River (Kollaus and Bonner 2012), Independence Creek (Bonner *et al*. 2005), and San Felipe Creek (Lopez-Fernandez and Winemiller 2005), as well as habitat for many riverine-associated fishes.

Spring run habitats of the upper San Marcos River support persistent populations of three unique fishes (*Notropis chalybaeus*, *Gambusia geiseri*, *Etheostoma fonticola*; Kollaus *et al*. In review). Another endemic species of the upper San Marcos River (*Gambusia georgei*) is extinct (Hubbs and Peden 1969; Hubbs *et al*. 2008). Habitat associations of *N. chalybaeus* in the upper San Marcos River are similar to conspecifics elsewhere (Robison 1977), associating with moderate levels of depths, current velocities, and vegetative cover. Habitat associations of *G. geiseri* are similar to those reported for this species previously in the upper San Marcos River and for the congenera in general (Hubbs and Peden 1969), associating with high amounts of vegetation in slackwater habitats. Habitat associations of *E. fonticola* ranged from slackwater habitats with moderate vegetative cover in wadeable habitats (19% of the total number observed) to slackwater habitats with low to high amounts of vegetative cover, including water depths up to 5 m and habitats with sand to cobble substrates without vegetative cover, in SCUBA surveys (81% of the total number observed). Among wadeable habitats, habitat associations observed in this study were similar to previous studies (Schenck and Whiteside 1976; Crowe and Sharp 1997). *Etheostoma fonticola* is associated with vegetative cover but also taken from habitats without vegetative cover in the Comal River

(Crowe and Sharp 1997), whereas Schenck and Whiteside (1976) found *E. fonticola* exclusive to habitats with vegetation. Among SCUBA habitats within Spring Lake-Spring Arm and upper and middle reaches of the upper San Marcos River including wadeable and non-wadeable habitats, *E. fonticola* were among the most abundant and ubiquitously distributed fishes and observed in all benthic habitat types (lentic and lotic mesohabitats, shallow to deep depths, silt to cobble substrates, short to tall growing vegetation), except swift flowing waters. Other fishes within Subgenus *Microperca* (*E. microperca* and *E. proeliare*; Near *et al*. 2011) also are associated with slackwater to run habitats consisting of detrital terrestrial leaves, woody debris, and dense vegetation (Burr and Page 1978; Paine *et al*. 1981; Johnson and Hatch 1991).

Abundant and persistent non-native plants, a trematode, mollusks, and fishes within the upper San Marcos River are well documented (Owens *et al*. 2001; Mitchell 2000; Pound *et al*. 2011; Kollaus *et al*. In review) and follow similar patterns as other stenothermal spring runs (Nico *et al*. 2012), which provide year round thermal refuge for many tropical nonnatives. Among the upper San Marcos River fish communities, the number of non-native fishes observed during this study is 9 (27% of the total S), representing 18% of the total number of individuals and 10% of CPUE (using CPUE for most effective gear type). *Lepomis auritus* and *Astyanax mexicanus* have the highest observed densities among introduced fish. Recent establishment of suckermouth catfish is a potential concern within the upper San Marcos River (Pound *et al*. 2011) and other spring systems throughout the Edwards Plateau (Edwards 2001; Lopez-Fernandez and Winemiller 2005) and elsewhere (Nico *et al*. 2012), although detailed diet study and stable isotope analysis suggest that suckermouth catfish within the upper San Marcos

River are consuming detrital alga with no indication on the consumption macrophytes, macroinvertebrates, or fish eggs (i.e., fountain darter) deposited on macrophytes and algae (Pound *et al*. 2011). Likewise, occurrence of *Centrocestus formosanus*, a digenetic trematode within the upper San Marcos River, is attributed to the introduction of a nonnative mollusk (Mitchell 2000) with the long term effects on fish host populations potentially alarming (McDonald *et al*. 2006; McDonald *et al*. 2007; Fleming *et al*. 2011) but yet evident. Collectively, risk perception (Gozlan 2008) of nonnative fishes and fish parasite in the upper San Marcos River is high. Nevertheless, the native fish community is persistent in the upper San Marcos River, despite the occurrence of nonnative fishes in the upper San Marcos for over 70 years (Kollaus *et al*. In review) or fish parasite for over 10 years (Mitchell 2000). Lack of noticeable effects among several nonnative fishes in the upper San Marcos River is not surprising given that few introduced fishes are demonstrated to have adverse consequences on existing communities (Gozlan 2008), despite high risk perception. The tendency of nonnative fishes to have none to negligible effects on existing communities is consistent with unsaturated aquatic systems, whereby biological invasions are sustainable (Hugueny and Paugy 1995).

Appropriateness of multiple gear types to sample aquatic systems, ranging in habitats from wadeable to nonwadeable, and fishes, ranging from small and benthic to large body and pelagic, was evident in this study. Also evident is that one technique or gear type alone would not convey the spatial structure of the upper San Marcos fish community. Appropriate sample technique is paramount for precise and accurate inference of trends among sample populations (Andrew and Mapstone 2006), and observations in population dynamics are strongly influenced by the adequacy of sample methodology (Sissenwine and Kirkley 1982; Willis and Murphy 1996; Pelrik and Levin 1999; Andrew and Mapstone 2006; Dickens *et al.* 2011). Consequently, multiple sample methodologies are recommended for future sampling within the upper San Marcos River and elsewhere (Amour and Boisclair 2004; Jordan *et al.* 2007) to adequately assess community structure, especially in the upper San Marcos River as monitoring protocols are developed to satisfy conditions of the newly accepted Habitat Conservation Plan (Edwards Aquifer Recovery Implementation Program; www.eahcp.org/). However, gear effectiveness among underwater observations is potentially limited because of topography, vegetation density, current velocity, water clarity, field identification skills of observer, number of species, and number of individuals in sample area. As such, skills of observers must be sufficient to appropriately conduct underwater observations.

Since the most recent glacial maximum, persistent water quantity from the Edwards Aquifer is likely the major contributing factor explaining the unique ichthyofauna of the upper San Marcos River (Kollaus *et al.* in review). High proportions of endemism in West and Central Texas stream fish communities are positively correlated with decreased connectivity between main-stem water bodies and persistent water availability (Maxwell 2012). Furthermore, differences in geophysical characteristics of habitat occupied by main-body and disjunct relict *Notropis chalybaeus*, suggest habitat selectivity of spring environments may play less of role determining population distribution than water permanency (Perkin *et al*. 2012). Since listing in 1970, fountain darter *Etheostoma fonticola* and Texas wildrice *Zizania texanus*, are the most intensely studied aquatic organisms within the Edwards Plateau (Jordan and Gilbert 1886; Evermann and Kendal 1894; Schenck and Whiteside 1976, 1977; Linam *et al*.

1993; Brandt *et al*. 1993; Labay and Brandt 1994; Bergin *et al.* 1997; Bonner *et al*. 1998; Dwyer *et al.* 2004; McDonald *et al*. 2006, 2007; Dammeyer 2010). Current research and management plans of the upper San Marcos fish population are not surprisingly biased towards ESA species. A multi-year study by Texas Parks and Wildlife to quantify fountain darter habitat availability in the upper San Marcos River determined that severe reductions in spring discharge may result in substantial habitat loss (Saunders *et al.* 2001). Reduced flow may have little effect on abundance of fountain darter, given they demonstrate strong association for slackwater habitats with no to slow current velocities (Schenck and Whiteside 1976). Not surprisingly *E. fonticola* and sister taxa (*E. proeliare*) are slackwater specialists in small streams and creeks, further evidence that water permanency may play a stronger role in population distribution than selectivity for spring environments. Measures of ecosystem health are often inferred from population status of a few sensitive taxa (Pikitch *et al*. 2004; Leslie and Mcleod 2007; Levin *et al.* 2009). However, seemingly sensitive taxa (i.e., fountain darter) in the San Marcos River do not adequately measure the habitat requirements of all endemic and species of conservation concern. A holistic management approach, which incorporates considerations of habitat requirements of swift and slack water fishes will ensure greater adequacy of management plans to successfully maintain both biodiversity and sustainability of the water resource (Pikitch *et al*. 2004).

Table 1. Total number of species (N), Gear type of greatest CPUE, number of individuals for gear type specified, CPUE, and relative abundance (%) by reach across all sample methods from January – December 2011. (*) denotes non-native taxa. X represents documented occurrence with a different gear type

						Spring Lake		Upper San Marcos River		
Species	Total N	Gear type	N for gear type	CPU (m^2)	Percent of total CPUE	Slough arm	Spring arm	Upper	Middle	Lower
Lepisosteus oculatus	19	Meso	17	0.002	<0.1		67		33	
Cyprinella venusta	120	Seine	97	0.050	1.1				15	85
*Cyprinus carpio**	1	Meso	1	<0.001	<0.1					100
Dionda nigrotaeniata	1,178	Meso	1,151	0.121	2.6	X	82	8.2	9.3	X
Macrhybopsis marconis	2	Seine	2	0.001	0.0				100	
Notropis amabilis	589	Seine	562	0.225	4.8			2.9	23	74
Notropis chalybaeus	146	Seine	90	0.033	0.7			67	33	
Notropis volucellus	37	Seine	37	0.020	0.4				3.9	96
Pimephales vigilax	2	Seine	2	0.001	<0.1					100
Moxostoma congestum	44	Meso	41	0.016	0.4			82	18	
*Astyanax mexicanus**	1,348	Meso	1,221	0.123	2.7	0.5	90	8.9	0.5	
Ameiurus natalis	15	Seine	13	0.005	0.1			100		
Ictalurus punctatus	4	Seine	2	0.001	<0.1		X		41	59
*Hypostomus plecostomus**	353	Meso	187	0.062	1.3	0.3		12	20	68
Gambusia	8,824									
Gambusia affinis		Seine	339	0.538	11.6	48	X	20	1.3	30
Gambusia geiseri		Seine	4,319	1.882	40.6	2.6	X	82	15	0.5
*Poecilia formosa**	19	Seine	19	0.010	0.2			42	8.3	49
*Poecilia latipinna**	182	Seine	182	0.079	1.7					100
*Ambloplites rupestris**	45	Seine	34	0.014	0.3			53	8.2	38
*Lepomis auritus**	897	Meso	663	0.164	3.5	0.9	19	63	10	6.6

Table 1. Continued.

Species	Total N	Gear type	N for gear type	CPU (m^2)	Percent of total CPUE	Spring Lake: Slough arm	Spring Lake: Spring arm	Upper San Marcos River: Upper	Upper San Marcos River: Middle	Upper San Marcos River: Lower
Lepomis cyanellus	6	Seine	5	<0.001	<0.1		X	100	X	
Lepomis gulosus	65	Seine	60	0.044	1.0	93		0.8		6.1
Lepomis macrochirus	291	Meso	161	0.024	0.5	3.3	49	43	4.4	X
Lepomis megalotis	19	Seine	14	0.008	0.2	28		X	X	72
Lepomis microlophus	191	Meso	169	0.017	0.4	4.6	84	8.6	2.4	X
Lepomis miniatus	185	Seine	169	0.104	2.2	77	X	17	4.0	1.6
Lepomis spp.	656	Meso	569	0.133	2.9	6.3	14.3	49	27	2.8
Micropterus salmoides A	456	Meso	327	0.050	1.1	3.8	46	35	10	4.5
Micropterus salmoides J	477	Meso	329	0.058	1.3	8.8	35	47	8.4	0.6
Micropterus treculli	1	Seine	1	0.001	<0.1					100
Etheostoma fonticola	1,048	Micro	844	0.765	16.5	X	64	7.6	27	1.8
Etheostoma spectabile	19	Seine	15	<0.001	<0.1					100
Percina carbonaria	58	Seine	45	0.022	0.5			3.2	17	80
Percina apristis	91	Seine	75	0.030	0.6			9.7	78	13
*Cichlisoma cyanoguttatum**	226	Meso	157	0.026	0.6	8.7	36	33	22	X
*Oreochromis aureus**	30	Meso	23	0.004	0.1	3.8	22	24	51	X
Total	17,644			4.638						
Numbeer of Species (S)	34					16	16	25	28	28
Number of unique species						0	0	0	1	5

Table 2. Species list of fishes within each reach which comprised the highest CPUE (>45%) of total catch by gear type specified in Table 1. Bold type denotes species with small sample sizes (< 30 individuals).

Spring Lake				
Slough arm	Spring arm	Upper	Middle	Lower
Lepomis gulosus	*Astyanax mexicanus*	***Ameiurus natalis***	***Macrhybopsis marconis***	***Cyprinus carpio***
Lepomis miniatus	*Lepomis microlophus*	***Lepomis cyanellus***	*Percina apristis*	***Pimephales vigilax***
Gambusia affinis	*Dionda nigrotaeniata*	*Gambusia geiseri*	*Oreochromis aureus*	*Poecilia latipinna*
	Lepisosteus oculatus	*Moxostoma congestum*		***Micropterus treculli***
	Etheostoma fonticola	*Notropis chalybaeus*		***Etheostoma spectabile***
	Lepomis macrochirus	*Lepomis auritus*		*Notropis volucellus*
	Micropterus salmoides	*Ambloplites rupestris*		*Cyprinella venusta*
	Cichlisoma cyanoguttatum	*Lepomis spp.*		*Percina carbonaria*
		Micropterus salmoides juv		*Notropis amabilis*
		Lepomis macrochirus		***Lepomis megalotis***
				Hypostomus plecostomus
				Ictalurus punctatus
				Poecilia formosa

Table 3. Mean (±SE) physical habitat parameters across all sample reaches for seine hauls on the San Marcos River from January – December 2011.

	Slough	Upper Reach	Middle Reach	Lower Reach
Total Area Sampled (m^2)	1,305	2,790	2,610	1,845
Habitat type (%)				
Riffle	0.0	0.5	12.6	0.0
Run	0.0	92.5	77.0	87.0
Pool	0.0	0.0	3.4	8.1
Backwater	100.0	7.0	6.9	4.9
Habitat Parameters				
Current Velocity (m/s)	0.00	0.2 (0.01)	0.66 (0.04)	0.11 (0.01)
Depth (m)	0.75 (0.02)	0.58 (0.02)	0.46 (0.02)	0.73 (0.02)
Substrate (%)				
Silt	89.4	46.7	35.0	52.1
Sand	0.5	16.8	24.5	8.8
Gravel	9.0	26.6	37.1	35.3
Cobble	1.0	9.6	30.0	3.7
Clay	0.0	0.1	15.7	0.1
Boulder	0.1	0.1	10.9	0.1
Vegetation cover (%)	70.7	54.8	6.7	29.3
Texas Wild Rice (%)	0.0	22.2	1.1	0.0
Woody Debris (%)	1.9	0.2	2.1	2.4
Detritus (%)	2.8	0.9	0.5	0.7
Water Quality				
Temperature (°C)	21.9 (0.33)	22.1 (0.07)	22.9 (0.05)	23.2 (0.16)
pH	7.3 (0.02)	7.4 (0.01)	7.7 (0.01)	7.7 (0.01)
Conductivity (µS/cm)	554.9 (7.5)	566.3 (4.6)	576.9 (3.4)	595.6 (5.3)
Dissolved Oxygen (mg/L)	3.0 (0.27)	7.7 (0.11)	8.5 (0.1)	7.04 (0.05)

Table 4. Relative abundance (%), total number of species (N), species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across all sample reaches for seine hauls in the San Marcos River from January – December 2011.

Species	San Marcos River Headwater			
	Slough	Upper Reach	Middle Reach	Lower Reach
Cyprinella venusta	-	-	1.6	6.3
Dionda nigrotaeniata	0.3	-	0.8	0.4
Macrhybopsis marconis	-	-	0.2	-
Notropis amablis	-	0.3	11.5	24.8
Notropis chalybaeus	-	1.2	2.4	8.2
Notropis volucellus	-	-	0.2	2.8
Pimephales vigilax	-	-	-	0.2
*Astyanax mexicanus***	2.2	1.5	0.8	-
Ameiurus natalis	-	0.2	-	-
Ictalurus punctatus	-	-	0.1	0.1
*Hypostomus plecostomus***	-	0.2	7.1	0.5
Gambusia affinis	46.4	5.8	1.5	24.4
Gambusia geiseri	8.6	82.0	60.5	1.4
*Poecilia formosa***	-	-	-	1.5
*Poecilia latipinna***	-	1.8	1.4	5.8
*Ambloplites rupestris***	-	0.4	0.3	0.8
*Lepomis auritus***	6.6	1.2	2.0	5.8
Lepomis cyanellus	-	<0.1	-	-
Lepomis gulosus	7.4	<0.1	-	0.4
Lepomis macrochirus	1.6	0.2	0.9	7.2
Lepomis megalotis	0.4	-	-	0.9
Lepomis microlophus	1.2	<0.1	-	0.2
Lepomis miniatus	14.4	0.9	0.9	0.2
Micropterus salmoides	6.6	0.5	0.8	1.6
Micropterus treculii	-	-	-	0.1
*Etheostoma fonticola**	-	3.4	1.0	1.0
Etheostoma spectabile	-	-	-	0.2
Percina carbonaria	-	<0.1	0.8	2.7
Percina apristis	-	0.2	5.0	0.6
*Herichthys cyanoguttatus***	4.1	0.2	0.2	1.6
*Oreochromis aureus***	0.1	0.0	0.1	0.2

Table 4-Continued. Relative abundance (%), total number of species (N), species richness (S), Shannon-Wiener diversity (H’), and Pielou’s evenness (J’) of species across all sample reaches for seine hauls in the San Marcos River from January – December 2011.

Total N =	730	5,269	1,191	1,233
Richness (S)	13	21	22	27
Diversity (H')	1.08	1.25	1.30	1.39
Evenness (J')	0.69	0.28	0.51	0.71

* Federally listed

** Introduced

Table 5. Mean (±SE) physical habitat parameters across all sample reaches for microhabitat survey in the San Marcos River from January – December 2011.

	Spring	Slough	Upper Reach	Middle Reach	Lower Reach
Total Area Sampled (m^2)	1,165	274	658	877	877
Habitat type (%)					
Riffle	0.0	0.0	0.0	0.0	0.0
Run	14.1	0.0	83.3	100.0	100.0
Pool	83.5	0.0	0.0	0.0	0.0
Backwater	2.4	100.0	16.7	0.0	0.0
Habitat Parameters					
Current Velocity (m/s)					
Bottom	0.02	0.01	0.08	0.04	0.05
Middle	0.02	0.01	0.15	0.05	0.07
Top	0.04	0.01	0.18	0.08	0.11
Open Water	0.04	0.01	0.21	0.11	0.14
Average	0.03 (0.0)	0.01 (0.0)	0.16 (0.13)	0.07 (0.01)	0.09 (0.01)
Depth (m)	2.6 (0.16)	1.3 (0.08)	1.5 (0.11)	1.6 (0.05)	1.7 (0.09)
Substrate (%)					
Silt	76.6	100.0	25.3	65.2	62.9
Sand	7.8	0.0	32.9	21.7	7.9
Gravel	6.2	0.0	31.4	8.3	4.8
Cobble	9.0	0.0	8.6	3.2	12.8
Clay	0.0	0.0	0.0	1.2	7.3
Boulder	0.4	0.0	1.8	0.1	0.5
Vegetation(%)	78.1	95.5	43.2	61.2	5.7
Texas Wild Rice (%)	1.4	0.0	63.9	0.1	0.0
Woody Debris (%)	0.1	0.0	0.6	0.2	5.9
Detritus (%)	1.4	0.0	12.5	3.0	7.5
Water Quality					
Temperature (°C)	22.1 (0.01)	22.4 (1.2)	21.8 (0.11)	22.0 (0.14)	21.8 (0.3)
pH	7.2 (0.02)	7.6 (0.02)	7.5 (0.03)	7.6 (0.02)	7.7 (0.02)
Conductivity (µS/cm)	571.7 (1.8)	562.3 (14.2)	574.3 (2.1)	571.9 (1.9)	583.6 (3.5)

Table 6. Relative abundance (%), total number of species (N), species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across all sample reaches for microhabitat surveys in the San Marcos River from January – December 2011.

Species	San Marcos River				
	Spring	Slough	Upper Reach	Middle Reach	Lower Reach
Lepisosteus oculatus	0.1	-	0.4	-	-
Cyprinella venusta	-	-	-	0.3	-
Dionda nigrotaeniata	0.5	-	-	0.2	3.5
Notropis chalybaeus	-	-	-	1.3	-
Moxostoma congestum	-	-	0.4	0.2	-
*Astyanax mexicanus***	2.2	-	-	-	-
Ameiurus natalis	-	-	0.4	-	-
Ictalurus punctatus	0.1	-	-	-	-
*Hypostomus plecostomus**	-	15.8	0.4	1.8	40.9
Gambusia spp.	24.7	-	71.6	72.3	-
Ambloplites rupestris	-	-	1.1	0.4	0.9
Lepomis auritus	1.1	5.3	2.3	0.4	2.6
Lepomis gulosus	0.4	-	-	0.1	-
Lepomis macrochirus	0.8	-	0.4	-	-
Lepomis megalotis	-	-	0.4	-	-
Lepomis microlophus	0.7	5.3	0.4	-	-
Lepomis miniatus	0.1	-	0.4	0.1	-
Lepomis spp.	4.0	36.8	4.2	1.9	7.0
Micropterus salmoides	0.9	10.5	1.1	-	8.7
Micropterus salmoides	12.8	26.3	-	-	1.7
*Etheostoma fonticola**	51.5	0.0	14.4	19.9	10.4
Etheostoma spectabile	-	-	-	-	13.0
Percina carbonaria	-	-	-	0.1	7.8
Percina apristis	-	-	0.8	0.8	1.7
*Herichthys cyanoguttatus**	0.1	-	1.1	0.1	0.9
*Oreochromis aureus***	-	-	0.4	-	-
Total N =	1098	19	264	913	115
Richness (S)	16	6	18	16	13
Diversity (H')	0.72	0.68	0.51	0.44	0.87
Evenness (J')	0.59	0.87	0.40	0.37	0.76

* Federally listed

** Exotic species

Table 7. Relative abundance (%), total number of species (N), species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across all sample reaches for mesohabitat surveys in the San Marcos River from January – December 2011.

Species	San Marcos River				
	Spring	Slough	Upper Reach	Middle Reach	Lower Reach
Lepisosteus oculatus	0.3	-	-	0.3	-
Cyprinella venusta	-	-	-	-	10.6
Cyprinus carpio	-	-	-	-	0.5
Dionda nigrotaeniata	23.1	-	2.2	6.2	-
Notropis amabilis	-	-	-	3.1	-
Notropis chalybaeus	-	-	-	5.1	-
Moxostoma congestum	-	-	3.0	1.6	-
*Astyanax mexicanus***	25.5	2.9	2.4	0.3	-
Ameiurus natalis	-	-	-	-	0.5
Ictalurus punctatus	0.0	-	-	-	-
*Hypostomus plecostomus***	-	0.7	1.6	6.7	60.1
Gambusia spp.	20.7	0.7	38.0	35.8	0.5
Ambloplites rupestris	-	-	0.2	0.1	-
Lepomis auritus	7.3	6.6	22.8	9.1	15.4
Lepomis cyanellus	<0.1	-	0.3	0.1	-
Lepomis macrochirus	2.8	3.7	2.3	0.6	-
Lepomis megalotis	-	-	0.2	0.2	-
Lepomis microlophus	3.4	3.7	0.3	0.2	-
Lepomis miniatus	0.2	-	-	0.3	-
Lepomis spp.	4.4	38.2	14.4	19.9	5.3
Micropterus salmoides	5.4	8.8	3.8	2.8	3.2
Micropterus salmoides	4.7	23.5	6.0	2.7	0.5
Micropterus treculli	-	-	-	-	0.5
*Etheostoma fonticola**	-	-	0.1	-	-
Etheostoma spectabile	-	-	-	-	0.5
Percina carbonaria	-	-	-	-	1.6
Percina apristis	-	-	0.1	0.3	0.5
*Herichthys cyanoguttatus**	2.1	10.3	1.9	3.1	-
*Oreochromis aureus***	0.2	0.7	0.2	1.2	-
Total N =	4672	136	911	860	188
Richness (S)	16	11	18	21	13
Diversity (H')	0.86	0.78	0.78	0.91	0.59
Evenness (J')	0.72	0.75	0.65	0.69	0.53

* Federally listed

** Exotic species

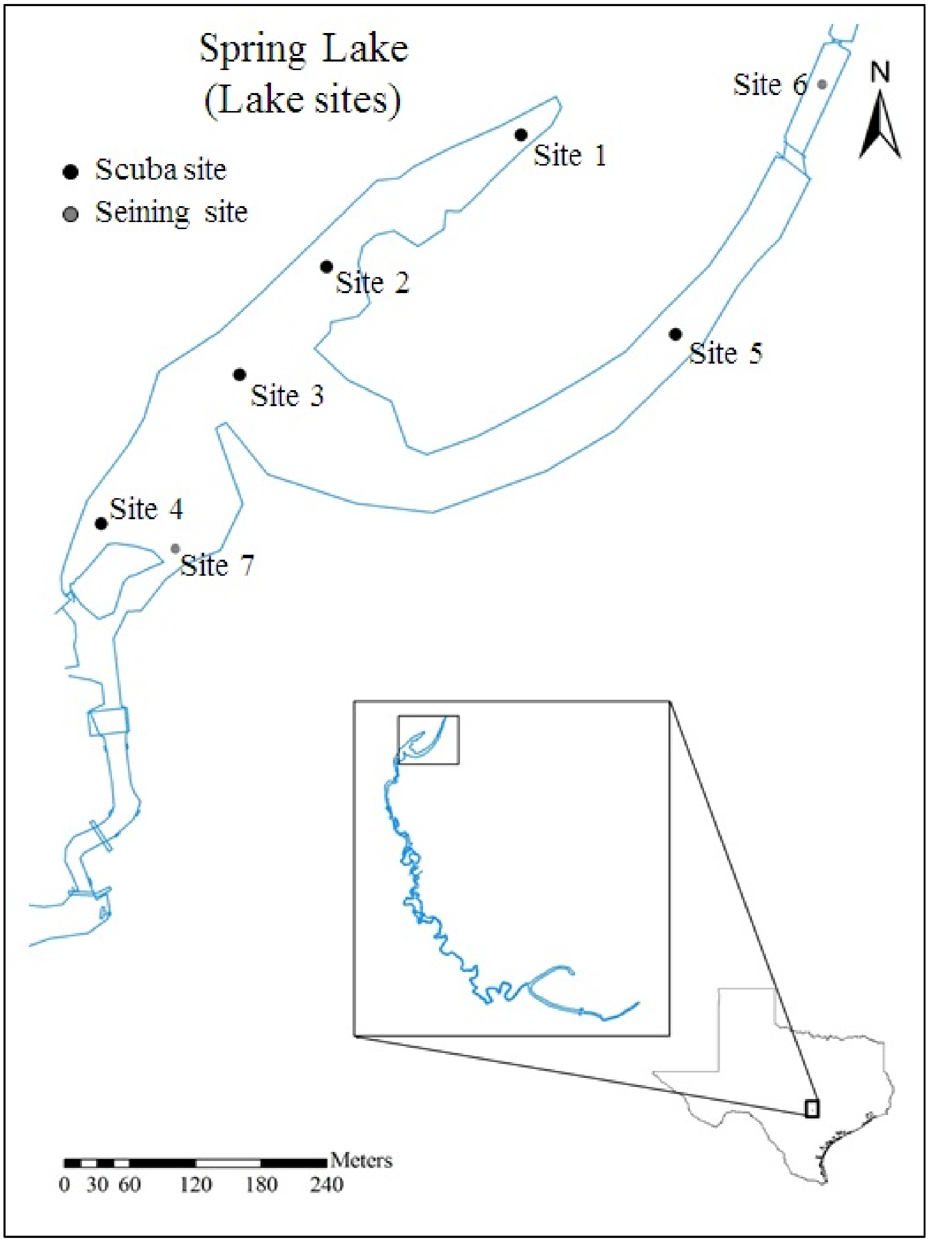

Figure 1. Site map of the San Marcos River: Spring Lake spring arm = sites 1 – 4, 7, Spring Lake slough arm = sites 5 – 6.

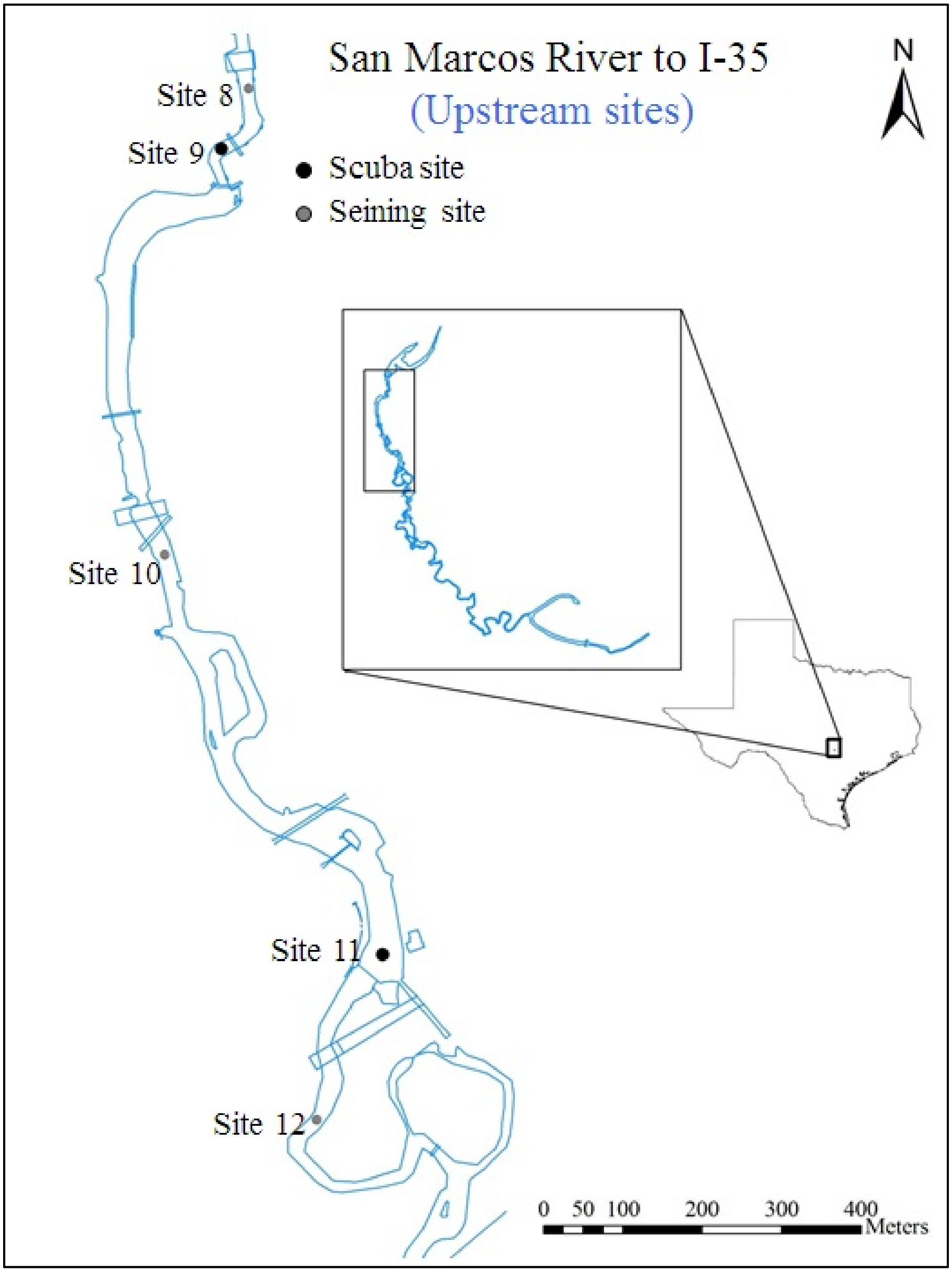

Figure 2. Site map of the San Marcos River: Upper reach = sites 8– 10, middle reach = sites 11 – 12.

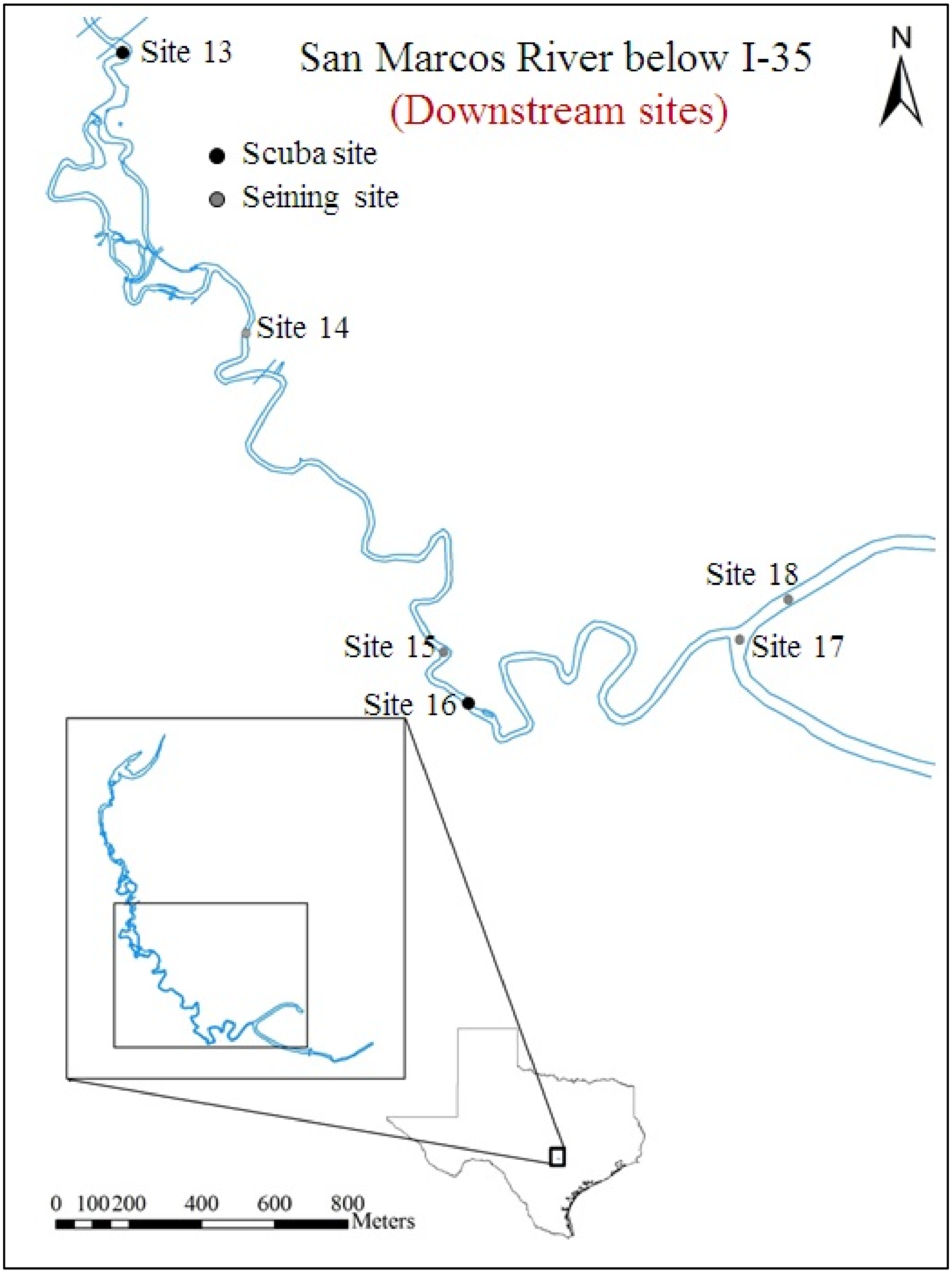

Figure 3. Site map of the San Marcos River: middle reach = sites 13 – 14, lower reach = sites 15 – 17, reference collection = site 18.

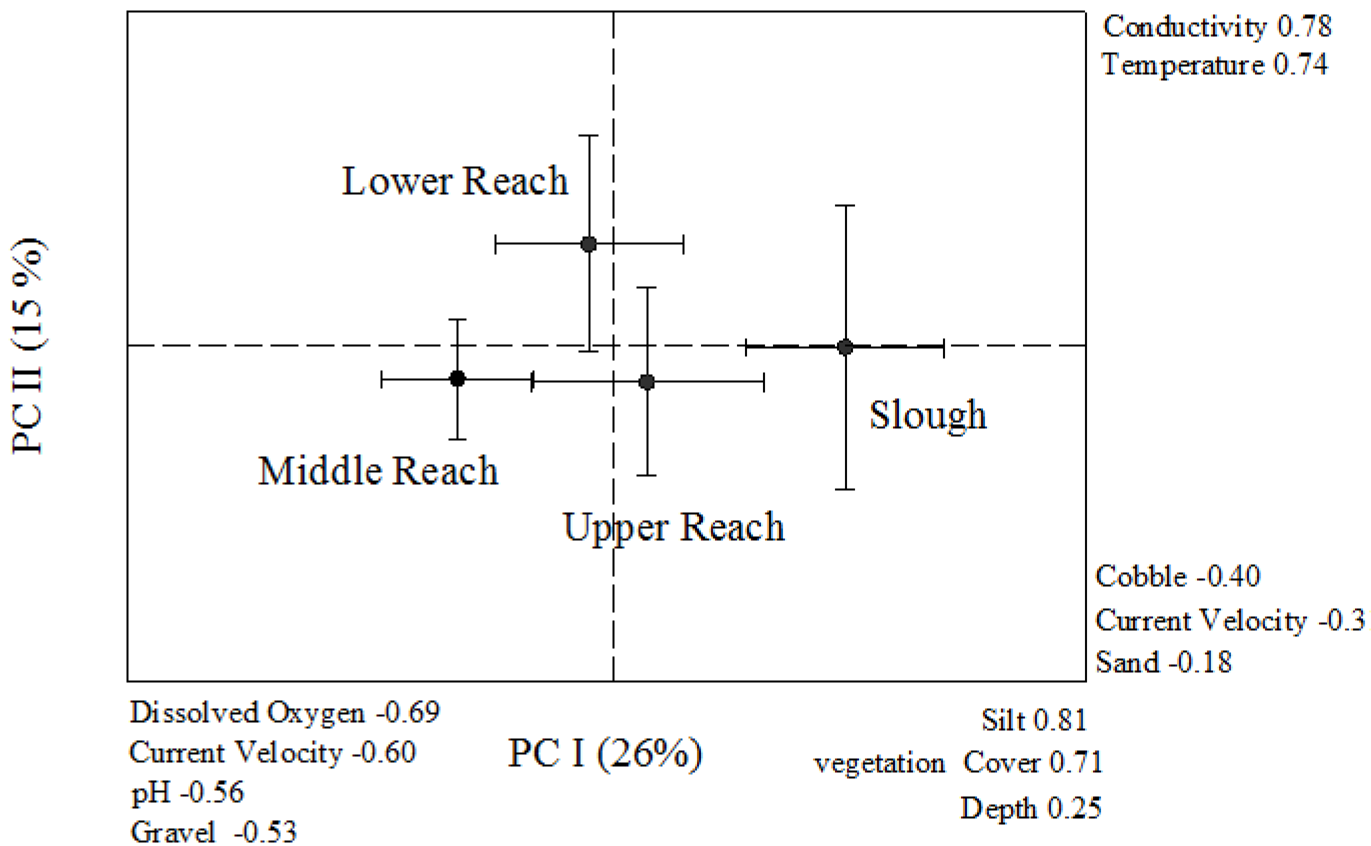

Figure 4. Principle Component Analysis ordination plot of mean ± SE for physical habitat parameters within each reach of sites sampled by seine in the San Marcos River from January – December 2011

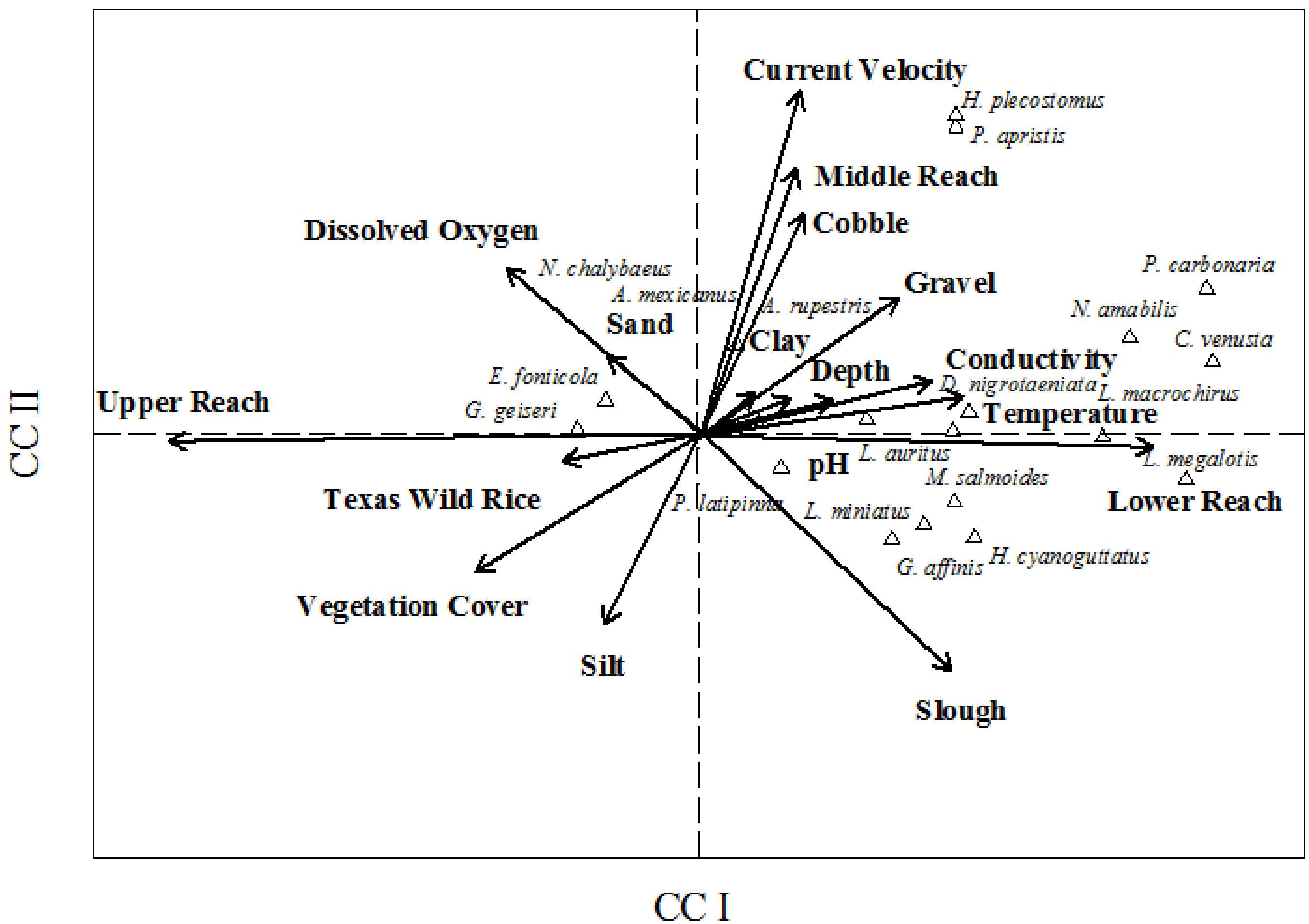

Figure 5. Canonical Correspondence Analysis ordination plot of fishes and physical habitat parameters and reach of sites sampled by seine in the San Marcos River from January – December 2011

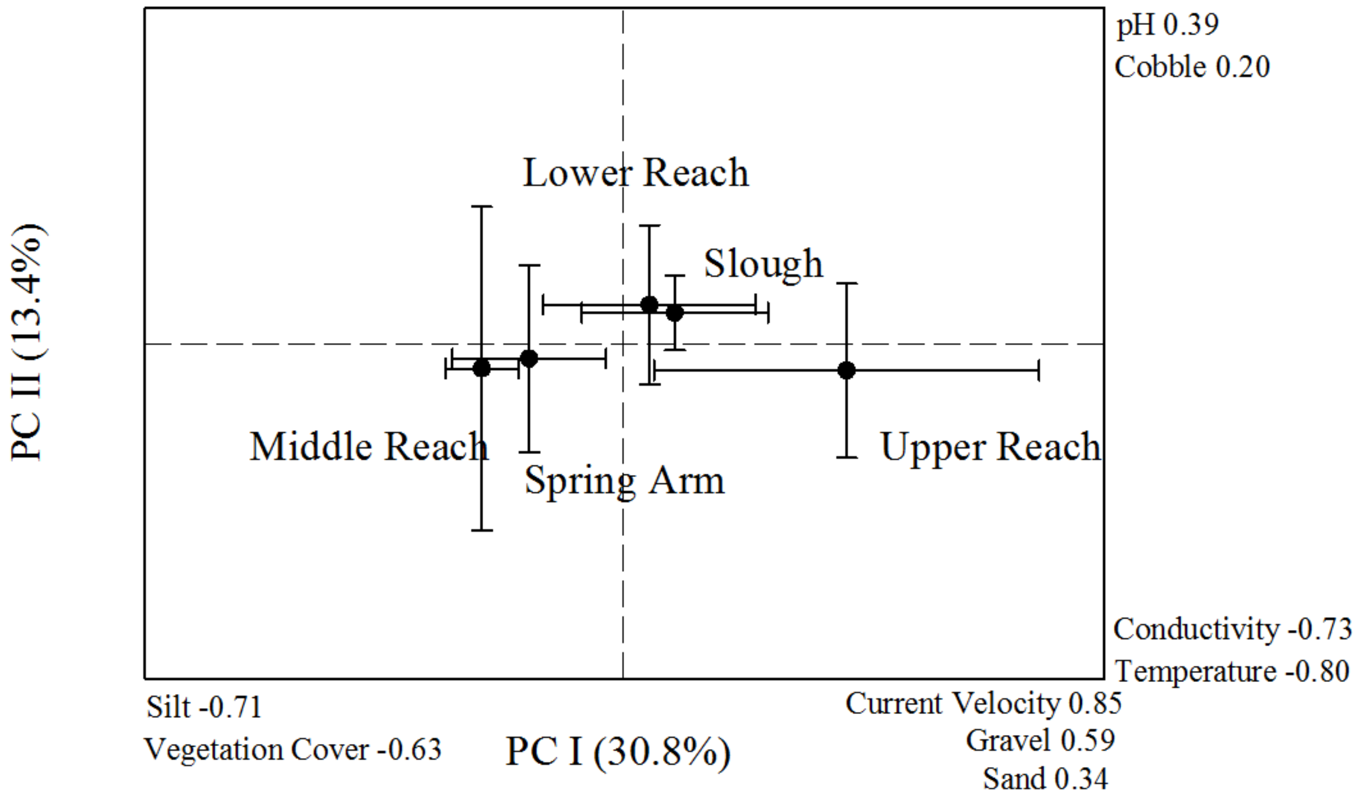

Figure 6. Principle Component Analysis ordination plot of mean ± SE for physical habitat parameters within each reach of microhabitat surveys in the San Marcos River from January – December 2011

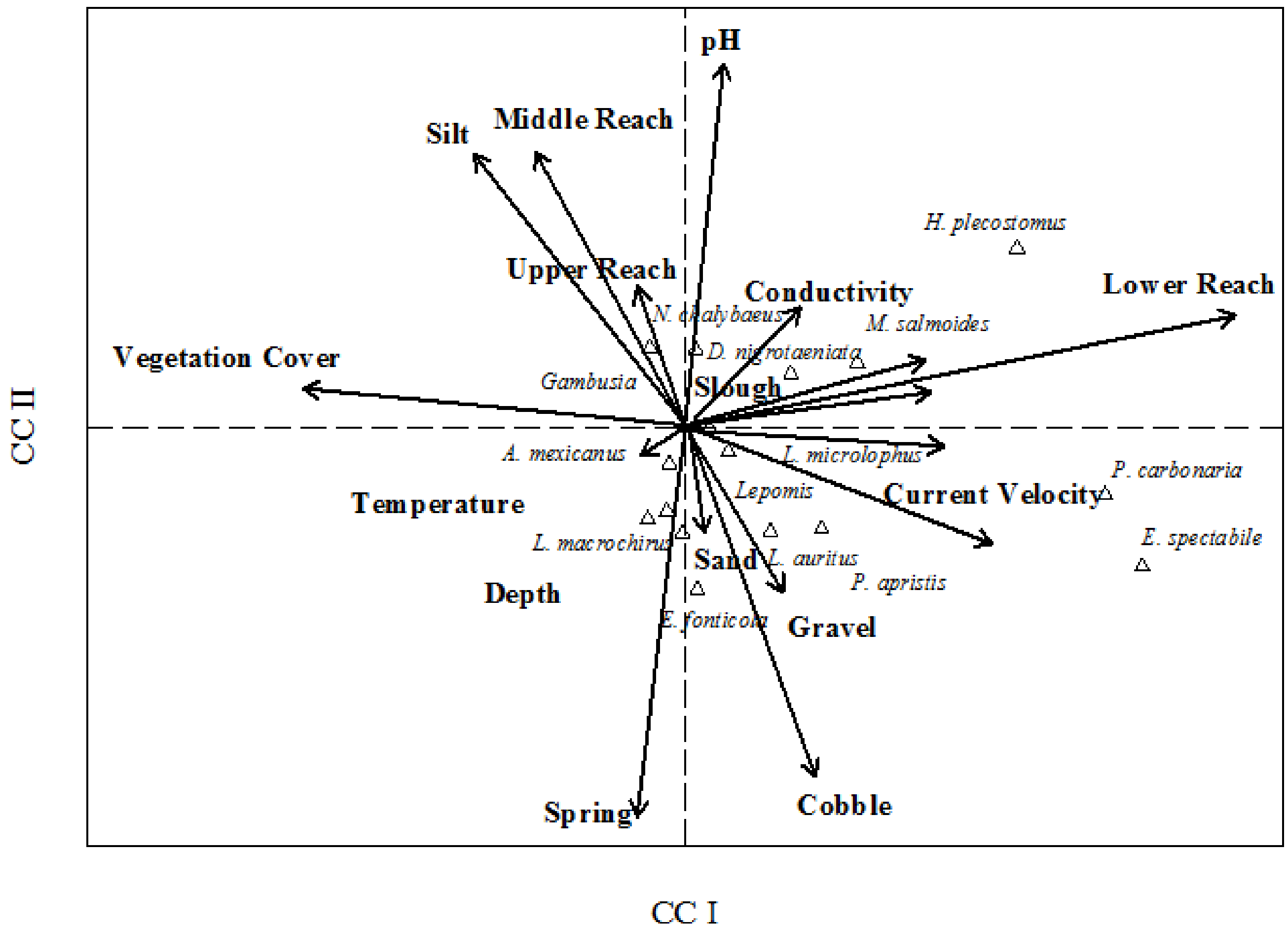

Figure 7. Canonical Correspondence Analysis ordination plot of fishes and physical habitat parameters and reach of microhabitat surveys in the San Marcos River from January – December 2011

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