

EFFECTS OF A DECLINING HYDROGRAPH ON INSTREAM HABITATS AND
FISH COMMUNITIES IN A SEMI-ARID KARSTIC STREAM

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ABSTRACT

EFFECTS OF A DECLINING HYDROGRAPH ON INSTREAM HABITATS AND FISH COMMUNITIES IN A SEMI-ARID KARSTIC STREAM

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Low to subsistence flows are natural components of riverine hydrographs, but their effects on fish communities are poorly understood. Instream habitats and fish community responses to a declining hydrograph were assessed along upper, middle, and lower reaches of the Llano River, Texas, and among tributaries. Using general stream theory, I predicted that greatest hydrological variability among reaches during a declining hydrograph would be associated with increased habitat variability, decreased species richness and diversity, and shifts in fish-habitat associations. The control was the upper reaches of the Llano River with hydrologically stable flows attributed to large outflows of a karst terrain aquifer. Hydrological variability differed ($P < 0.01$) among mainstem sites and tributaries with the greatest hydrological variability occurring in the lower reach. Biotic indices (catch per unit effort, diversity, and evenness) were inversely related, whereas taxa richness and community stability were directly related to hydrological variability. Available habitats and fish-habitat associations were independent of

hydrological variability, although riffle specialists were restricted to current velocities > 0.6 m/s and run specialists to current velocities > 0.4 m/s less than expected approaching subsistence flows. Collectively, patterns in hydrological variability, instream habitats, and fish community responses suggest that karst spring outflows alter expected patterns in hydrological variability along a river network, but hydrological variability was supported as the primary driver of instream habitats and fish communities. In addition, fish communities and habitat associations were similar as flows approached subsistence levels. Following subsistence flows, flows within the lower reach ceased and the reach rapidly dewatered. Once flows returned, the lower reach was initially recolonized by large-bodied fishes from downstream and hydrologically stable sites of the Colorado River and secondarily by small-bodied fishes from the hydrologically stable upper Llano River. Consequently, this study demonstrated that persistent flows of the upper reach contribute to the downstream community and therefore illustrates the influence of karst aquifers on communities near and distant from the spring source.

CHAPTER I

EFFECTS OF A DECLINING HYDROGRAPH ON INSTREAM HABITATS AND FISH COMMUNITIES IN A SEMI-ARID KARSTIC STREAM

INTRODUCTION

Habitat distribution and fish communities are predictable along a longitudinal gradient as a response to variation in water quantity (Gorman and Karr 1978, Horwitz 1978, Schlosser 1982, Poff and Allan 1995). Among non-karstic river systems, hydrological variability decreases in a downstream direction resulting in lower reaches (i.e. high stream order) characterized as less variable habitats and more persistent fish communities and fish-habitat associations (Gorman and Karr 1978, Horwitz 1978, Schlosser 1987). Upper reaches (i.e., low stream order) are characterized by more variable habitats, high turnover in fish communities, and transitory fish-habitat associations. Therefore, hydrological variability is inversely related to habitat stability (Shea and Peterson 2007), stream order (Whiteside and McNatt 1972, Horwitz 1978), species richness (Schlosser 1987, Herbert and Gelwick 2003), species diversity and evenness (Horwitz 1978, Schlosser 1982) and community stability (Gorman and Karr 1978, Schlosser 1987, Oberdorff et al. 2001). A notable exception to general patterns in stream theory is the inadequacy of stream order to predict habitat variability and other interrelated response variables in semi-arid karstic terrain streams of the Edwards

Plateau, where large outflows of karst terrain aquifers support abiotically stable stream flows since at least the Pleistocene (Blum et al. 1994). From portions of the Brazos River basin to large tributaries of the Rio Grande, hydrological variability is less in the upper reaches compared to streams without origins on the Edwards Plateau, and more noticeable under extreme flow conditions (i.e. high flow pulses, subsistence flows). Lower hydrological variability in the upper reaches should be associated with habitat stability, higher species richness, species diversity and community stability. However, upper reaches of streams with karst spring outflows typically have distinct spring-associated fish assemblages compared to lower reaches, but not highest species richness, diversity, evenness or habitat stability during high and medium baseflows (Bean et al. 2007, Shattuck 2010, Kollaus and Bonner 2012) within the basin. As such, a mechanism other than hydrological variability might drive community composition among Edwards Plateau streams, or confounding factors (i.e., dispersion, abiotic environment) might obscure the influence of hydrological variability.

Maintenance of hydrological variability within riverine environments (Natural Flow Paradigm: Poff et al. 1997, Propst and Gido 2004) is the prevailing theory in instream flow programs and in maintaining sound ecological environments (NRC 2005). Application of the Natural Flow Paradigm includes mimicking the timing and magnitude of flow components within riverine systems, followed by validation that recommended environmental flow tiers (i.e., subsistence and base flows, one per season high flow pulse, one per year high flow pulse) are maintaining soundness of ecological environments. Timing and magnitude of flow components are estimated from historically recorded flows (Orth and Maughan 1982) and support for the Natural Flow Paradigm in

maintaining ecological soundness is found in a number of studies (Moyle and Baltz 1985, Bonner and Wilde 2000, Propst et al. 2008, Perkin and Guido 2011, Benejam et al. 2012, Deitch and Kondolf 2012). However, as the science of instream flows progress, more information is needed to validate multi-tiered flow regimes and provide compelling support to resource managers, water regulatory agencies, and water users that often perceived complex environmental flow recommendations are necessary, or not, to maintain a sound ecological environment. A shortcoming in the contemporary instream flow recommendations is the biotic responses of the aquatic communities during declining hydrographs from low base flows to subsistence flows (Magalhaes 2002). Subsistence flows are defined as the minimum flows necessary to maintain adequate water quality and limited habitat over a short period of time and quantified as the 95th percentile (Q95) of the historical hydrograph (Colorado River BBEST 2011). However, effects of subsistence flows on fish communities and habitat associations are poorly understood and therefore necessary to quantify and validate as suitable to maintain a sound ecological environment.

To assess the apparent inadequacies of hydrological variation to predict stream communities (Gorman and Karr 1978, Horwitz 1978, Schlosser 1982) and to gain a greater understanding on how fish communities respond to low flow conditions, we assessed habitat distribution, fish community structure and habitat-fish association changes in a semi-arid karst river of the Edwards Plateau during an extremely dry period with a hydrograph declining from dry base flows to subsistence flows. We made three general predictions based on traditional stream theory that: (1) habitat variability would be related to hydrological variability during a declining hydrograph from base flows to

subsistence flows, (2) species richness and diversity would be inversely related to hydrological variability and (3) fish-habitat associations would differ between reaches with low variability in the hydrograph and reaches with high variability in the hydrograph. How communities respond, in taxa richness, diversity and habitat associations, can assist in validating subsistent flow recommendations, currently set 95Q. Objectives of this study were to quantify stream habitats, community structure, and fish-habitat associations within four locations (upper, middle, and lower reaches of the mainstem and tributaries) of the Llano River from the start of an area wide drought through the cessation of flows in the lower reach, which occurred over a one-year period (Fall 2010 – Summer 2011). In addition, we monitored the return of the fish community for one year in the lower reach and provide observations on how the fish community recolonized after total dewater of a high order stream in the Edwards Plateau, using again the prediction of general stream theory that recolonization of low order streams following dewatering will come from downstream communities (Schlosser 1987, Taylor and Warren 2001).

METHODS

Study Area

The Llano River watershed encompasses nine counties on the Edwards Plateau consisting of approximately 11,568 square kilometers (Heitmuller and Hudson 2009). The North Llano originates in Sutton County and flows 80 river kilometers (rkm) to join the 89 rkm South Llano River beginning in Edwards County. The two rivers meet in Junction, Texas (Kimble County) and continue 161-rkm east to Lake Lyndon B. Johnson

on the Colorado River (Perkin et al. 2009). The Llano River is a semi-arid spring-fed stream typical of the Edwards Plateau characterized by limestone bedrock with moderately flowing habitats and dense riparian zones in the upper reach and tributaries transitioning to granitic outcroppings with wide braided channels in the lower reach. A fairly abrupt shift in habitat occurs as the Llano flows from upstream to downstream moving from Cretaceous bedrock with substantial amounts of alluvial deposits to Precambrian bedrock with reduced alluvium in the Llano Uplift (Heitmuller and Hudson 2009). This groundwater dominated system is located in karstic terrain where spring seeps and outflows are the primary source of flow near the headwaters with increasing contribution from surface flow in the lower reach.

Sampling occurred at nine sites throughout the Llano River system. Sites were grouped into four sampling locations: upper reach, middle reach, lower reach and tributaries. The upper reach consisted of two sites on the South Llano River at County Road (CR) 150/US 377 (Site 1; 30°23'36.38"N, 99°52'54.39"W / 30°20'43.62"N, 99°54'7.36"W) and Texas Tech University-Junction (Site 2; 30°28'7.12"N, 30°32'14.75"N, 99°37'35.87"W). The middle reach consisted of two sites at county road 314 (Site 3; 30°32'14.75" N, 99°37'35.87" W) and Farm to Market (FM) 2389 (Site 4; 30°39'0.54" N, 99°15'2.62" W). The lower reach consisted of two sites at FM 2768 near Castell (Site 5; 30°42'12.96"N, 98°57'31.45"W) and on private property (Site 6; 30°42'40.15"N, 98°31'12.37"W). Tributary sites were on the North Llano River south of Roosevelt at CR 275 (30°29'26.87"N, 99°59'9.06"W), the Johnson Fork at FM 2169 (30°26'6.43"N, 99°40'27.88"W) and the James River at James River road second crossing

(30°33'54.60"N, 99°19'48.53"W) (Figure 1). Sites were selected to reflect representative reaches of the Llano River basin.

Field Collections

Sites were sampled from October 2010 to June 2011 four times throughout the year to represent seasonality: fall, winter, spring, and summer. Additional sampling was conducted in the lower reach roughly six months (January 2012) and one year (June 2012) post-extirpation; the Llano ceased to flow end of June 2011 and flows returned mid September 2011. Fish were sampled with the use of seines (3.0 x 1.8 m straight seine and 4.3 x 1.8 x 1.8 m bag seine with 3.2 mm mesh), a Smith-Root backpack electroshocker, and a boat mounted electroshocker. Fish abundances were quantified in available mesohabitats (i.e. riffles, runs, pools, and backwaters) per site. Mesohabitats were sampled exhaustively to best represent associations within geomorphic units (Williams and Bonner 2006). Fishes were identified to species (Hubbs et al. 2008) and counted. All fish were returned to the field except for vouchers and unidentifiable species. Fish that were retained were administered a lethal dose of tricainemethanesulfonate (MS-222) and fixed in a 10% formalin solution.

Water quality data were collected at each site using a YSI-65 and 85 consisting of temperature (°C), pH, conductivity (µS/cm), and dissolved oxygen (mg/L). Habitat data were quantified at each mesohabitat. Average depth in meters was determined by selecting five points that best represented each mesohabitat. Current velocity (m/s) was measured at each of the five points with a Marsh-McBirney Flo-mate 2000 flow meter and averaged. Length and width of each mesohabitat was measured in meters. Percent

substrate was quantified using a modified Wentworth scale consisting of silt, sand, gravel, cobble, boulder, and bedrock. Percent vegetation cover, algal cover and woody debris were visually estimated (Williams et al. 2005).

Site Assessment

Hydrological data were obtained from three U.S. Geological Survey gauge stations located on the Llano River – Junction, TX (08150000), south of Mason, TX (08150700), and Llano, TX (08151500). Coefficients of variation (CV) were calculated for the study period (October 15, 2010 – June 22, 2011) at each gauging station to assess hydrological variability across reaches within the river. Coefficients of variation were equal to the standard deviation of the mean daily discharge ($\text{m}^3\text{sec}^{-1}$) divided by the mean daily discharge. Distribution of deviation in daily discharge from mean discharge were compared among USGS station with an analysis of variance (ANOVA) to test for differences in hydrological variability between reaches. Fisher's Least Significant Difference ($\alpha = 0.05$) was used assess mean separation. Rate of change in flow ($\text{m}^3\text{sec}^{-1}\text{day}^{-1}$) was calculated by calculating the mean of the absolute value of change in flow per day. Flow duration curves and baseflow conditions were based on the Llano River HEFR (Historical Environmental Flow Regime) in the Colorado River Environmental Flow Regime Recommendations Report (Colorado River BBEST 2011). Instream flow recommendations in the Llano River are based on USGS gauging station 08151500 in Llano, TX.

Habitat types were assessed by calculating the relative abundance of each geomorphic unit per sampling location based on total coverage (m^2). Depth, current

velocity, and water quality parameters were averaged per location. Weighted means (%) were calculated for substrate type, vegetation cover, algal cover, and woody debris. Principal Component Analysis (PCA) was used to assess spatial and temporal variation between sampling locations based on physical habitat parameters and water quality data (Canoco v. 4.55 2006). Qualitative data (i.e. mesohabitat) were represented using dummy variables. Quantitative habitat data (i.e. substrate, cover, depth, current velocity and water quality data) were z-scored prior to analysis to ensure standardized weighting across all variables (Krebs 1999). Mean PC scores for each sampling location per season were graphed to assess seasonal shifts in available habitat. Mean PC scores for each reach and tributaries were graphed and encircled by one standard deviation to assess habitat variability. Levene's t-test was used to test for differences in habitat variability between the upper and lower reach (Zar 2010). Analysis of variance was performed on the mean scores to test differences in habitat across sampling location and season. Fisher's LSD ($\alpha = 0.05$) was used post-hoc to determine which locations and seasons differed.

Assemblage Structure

Fish assemblage structure was characterized by calculating total species abundance (N), relative abundance (%), catch per unit effort (CPUE; individuals/m²), richness (S), diversity (H'), and evenness (J') for each sampling location and season. Species diversity was calculated using the Shannon-Wiener index (log₁₀ base; Shannon 1948) and evenness using Pielou's evenness index (Pielou 1966). Species abundance data were fourth-root transformed (Warwick 1988) and Bray-Curtis similarity indices

(Bray and Curtis 1957) were created to assess similarity in assemblage structure (PRIMER v. 6.1.6 2006). Analysis of similarity (ANOSIM) was run on resulting matrices to determine differences across sampling locations and seasons. CLUSTER analysis (group average mode) was used to group assemblages from each location and season combination based on similarity. The SIMPROF function (9,999 permutations and 999 simulations) was then used to test ($\alpha = 0.05$) for structure within the data. The SIMPER function was used to assess individual species influence on dissimilarities among assemblages. Average percent change in assemblages across season for each sampling location was calculated as the reciprocal of Renkonen's Similarity Index to assess assemblage variability (Gorman and Karr 1978). Bray-Curtis similarity matrix was used to calculate average dissimilarity in assemblages across season for each sampling location.

Habitat Associations

Canonical Correspondence Analysis (CCA) was conducted on habitat and species data to determine environmental variables responsible for spatial and temporal trends in habitat associations at each sampling location (Canoco v. 4.55 2006). Species data were $\log(x + 1)$ transformed to reduce the influence of high species abundance. Species composing less than one percent of the total abundance per location were excluded from analysis. Rare species were downweighted and 999 Monte Carlo permutations were used to test significance ($\alpha = 0.05$) of both axes. Total variation for each sampling location was partitioned into pure effects for physical habitat parameters and season (Borcard et al. 1992).

Deviation from preferred depth and current velocity distribution was analyzed across sampling season in relation to flow to assess effects of low flow conditions on habitat use. Species that were most abundant in the upper and lower reach ($n = 8$) were selected and grouped based on typical mesohabitat preference. Shift from preferred habitat was measured by subtracting expected (upper) seasonal averages from observed (lower). Percent flow duration was calculated for each sampling event based on the Llano River HEFR (Colorado River BBEST 2011). Relationship for each functional group between deviation from preferred depth and flow was assessed with a linear regression ($\alpha = 0.05$).

RESULTS

Habitat Characterization

Water quantity and quality differed among seasons and sampling locations within the Llano River watershed with greater variation observed across seasons than locations. During the duration of this study, mean discharge ranged from 2.4 to 1.1 m^3/s in the upper reach (USGS station 08150000), 4.19 to 0.51 m^3/s in the middle reach (08150700) and 7.87 to 0.10 m^3/s in the lower reach (08151500) (Figure 2). Hydrological variability was lowest in the upper reach (mean daily discharge ± 1 SD: $1.96 \pm 0.34 \text{ m}^3/\text{s}$; coefficient of variation: 0.18; rate of change: $0.03 \text{ m}^3\text{sec}^{-1}\text{day}^{-1}$), moderate in the middle reach ($2.38 \pm 0.65 \text{ m}^3/\text{s}$, 0.27, $0.08 \text{ m}^3\text{sec}^{-1}\text{day}^{-1}$) and greatest in the lower reach ($2.34 \pm 1.06 \text{ m}^3/\text{s}$, 0.45, $0.12 \text{ m}^3\text{sec}^{-1}\text{day}^{-1}$) with mean daily discharge variability differing ($F_{2,750} = 70.85$, $P < 0.01$) among all three reaches and with differences among pairwise contrasts (Figure 3). Among collection dates, discharge was highest in the winter (upper: $2.21 \text{ m}^3/\text{s}$, middle:

2.69 m³/s, lower: 2.94 m³/s) and lowest in the summer (upper: 1.25 m³/s, middle: 0.88 m³/s, lower: 0.17 m³/s). Water temperature ranged from a low of 9.4°C during winter to a high of 34.4°C during the summer, pH ranged from 7.2 to 8.6, dissolved oxygen ranged from 5.3 to 14.1 mg/l, and specific conductance ranged from 253 to 583 µS/cm (Table 1).

Mainstem reaches were distributed along a longitudinal gradient of physical habitat parameters from upstream to downstream (Table 1). Most abundant geomorphic units were run habitats (range among reaches: 37 – 68%) and riffle habitats (13 – 33%). Upper reach consisted of shallow to moderate depths (mean: 0.44 m) and swift current velocities (0.44 m/s) with cobble (38%) and bedrock (36%) substrates. Middle reach consisted of shallow to moderate depths (0.49 m) and moderate current velocities (0.30 m/s) with cobble (38%) and bedrock (34%) substrates. Lower reach consisted of shallow to moderate depths (0.49 m) and moderate current velocities (0.22 m/s) with sand (56%) and cobble (14%) substrates. Tributaries primarily consisted of run (54%) and pool (28%) habitats with shallow to moderately deep depths (0.42 m), slow current velocities (0.12 m/s), bedrock (48%), silt (27%) and cobble (20%) substrates, and vegetation (26%).

Principal component analyses explained 47% of the total variation in physical habitat and water quality parameters among sampling locations (Figure 4). Principal component (PC) axis I (16.0% of total variation) represented a current velocity, geomorphic unit and substrate gradient with strong positive loadings for current velocity (1.98), riffle (1.89) and cobble (1.74) and strong negative loadings for silt (-1.18), backwater (-1.14) and depth (-1.04). PC axis II (12.5%) represented a water quality gradient with strong positive loadings for dissolved oxygen (1.65) and pH (1.22) and strong negative loadings for conductivity (-2.27) and temperature (-2.25). Sampling

locations differed along PC I ($F_{3,258} = 10.31, P < 0.01$) and PC II ($F_{3,258} = 27.00, P < 0.01$) with the upper reach differing from middle reach, lower reach, and tributaries along PC axis I and upper reach and middle reach differing from lower reach and tributaries along PC axis II. In general, mainstem reaches transitioned from riffle habitats with higher current velocities, conductivity and cobble substrate in the upper reach to sluggish water with sand and gravel substrates and higher pH in the lower reach. Tributaries were segregated from mainstem reaches by having larger proportions of backwater habitats and silt substrates, slower current velocities, warmer temperatures and higher conductivities. Across locations, physical habitat and water quality parameters differed among season along PC II ($F_{3,258} = 65.92, P < 0.01$) but not along PC I ($F_{3,258} = 2.36, P = 0.07$). Seasonal effects were also influenced by the declining hydrograph as discharge moved from base flow conditions towards subsistence flows (Figure 4A). In general, current velocities decreased, whereas water temperature and conductivity increased. However, variability among PC axis I scores did not differ ($t'_{0.05(1),115} = 1.64, P > 0.05$) among sampling locations, although deviation in PC I scores were slightly greater upstream (upper: ± 0.42 , lower: ± 0.35) (Figure 4B).

Fish Community Characterization

A total of 35,138 individuals comprised of 12 families and 34 species were collected from the Llano River across all sampling locations and seasons. Cyprinidae (76%) was the most abundant family, followed by Centrarchidae (8.4%), Poeciliidae (7.2%), and Percidae (5.6%). Most abundant species were *Cyprinella venusta* (52%), *Notropis amabilis* (11%), *Gambusia affinis* (7.2%), *Lepomis auritus* (5.0%), *Notropis*

volucellus (4.4%), *Notropis stramineus* (4.1%), *Etheostoma spectabile* (3.8%) and *Campostoma anomalum* (3.8%). Species endemic to the Edwards Plateau (*Dionda nigrotaeniata*, *N.amabilis*, *Moxostoma congestum*, *Micropterus treculii*, *Etheostoma lepidum*, and *Percina carbonaria*) comprised 14% of the total fish assemblage. Spring-associated species (*D. nigrotaeniata*, *N. amabilis*, and *E. lepidum*) represented 12% of the total fish assemblage. Non-native species (*Cyprinus carpio*, *Morone chrysops*, *L. auritus*, and *Cichlasoma cyanoguttatum*) comprised 5.9% of the total fish assemblage.

Catch per unit effort, species richness, diversity, and evenness differed among sampling locations and seasons. Among sampling locations, CPUE (individuals/m²) across season ranged from 0.59 in tributaries and 0.27 in upper reach to 0.15 in the middle reach and 0.16 in the lower reach (Table 2). Species richness (S) was greatest in the lower reach (S = 32), whereas species diversity (H') and evenness (J') was greatest in upper reach (H' = 0.90; J' = 0.67). Variability in S was similar among reaches (CV of upper: 0.07, middle: 0.06, lower: 0.05), whereas variability in H' was greater in the upper (0.11) and middle (0.16) reaches than in the lower reach (0.08) (Figure 5). Among seasons, CPUE across sampling locations ranged from 0.41 in the Winter to 0.22 in the Fall. Correspondingly, winter also was greatest in S (33), H' (0.86), and J' (0.57) (Table 3).

Fish assemblage similarity did not differ among seasons (ANOSIM Global R = -0.23, *P* = 0.99) but differed among sampling locations (ANOSIM Global R = 0.95, *P* < 0.01). Among seasons, percent change in assemblage composition was 42% in the upper reach, 32% in the middle reach, 17% in the lower reach, and 19% in tributaries. Average assemblage dissimilarity was 43% in the upper reach, 29% in middle reach, 22% in the

lower reach, and 31% in the tributaries. Among sampling locations, upper reach was most dissimilar (37%) to lower reach with *N. amabilis*, *Pimephales vigilax*, *Carpiodes carpio*, *Cyprinella lutrensis*, *N. stramineus*, *Ictiobus bubalus*, *Dorosoma cepedianum*, *D. nigrotaeniata* and *Lepisosteus osseus* contributing >50% of the dissimilarity. Two distinct clusters were detected (Figure 6). Lower reach assemblages differed ($P_i = 4.1$, $P < 0.01$) from those in the other sampling locations with 10 fishes (*N. amabilis*, *P. vigilax*, *I. bubalus*, *C. lutrensis*, *Carpiodes carpio*, *N. stramineus*, *D. cepedianum*, *Cyprinus carpio*, *C. cyanoguttatum* and *E. lepidum*) contributing >50% dissimilarity. Two additional clusters ($P_i = 3.4$, $P < 0.01$) of tributary assemblages and upper and middle assemblages with *N. stramineus*, *C. venusta*, *C. anomalum*, *N. amabilis*, *Carpiodes carpio*, *G. affinis*, *Pylodictis olivaris* and *N. volucellus* contributing >50% dissimilarity were detected.

Habitat Associations

Physical habitat and season explained 65% ($P < 0.01$) of the total variation in the Llano River fish assemblage in the upper reach (habitat: 59% and season: 2.5%), 48% ($P < 0.01$) in the middle reach (habitat: 43% and season: 5.0%), 54% ($P < 0.01$) in the lower reach (habitat: 50% and season: 6.1%) and 41% ($P < 0.01$) in the tributaries (habitat: 37% and season: 3.1%) (Figure 7). Physical habitat parameters with strongest loadings for the upper reach were depth (-0.82), silt (-0.45), riffle (0.78) and current velocity (0.86) on CCA axis I and depth (-0.45), run (-0.34), silt (0.57) and backwater (0.77) on CCA axis II (Figure 7A). Physical habitat parameters with strongest loadings for the middle reach were current velocity (-0.71), riffle (-0.63), silt (0.55) and backwater (0.58) on CCA axis

I and backwater (-0.46), cobble (-0.42), run (0.38) and depth (0.58) on CCA axis II (Figure 7B). Physical habitat parameters with strongest loadings for the lower reach were current velocity (-0.47), riffle (-0.45), pool (0.34) and depth (0.75) on CCA axis I and cobble (-0.53), current velocity (-0.53), backwater (0.51) and sand (0.60) on CCA axis II (Figure 7C). Physical habitat parameters with strongest loadings for tributaries were pH (-0.47), riffle (-0.32), silt (0.50) and depth (0.76) on CCA axis I and bedrock (-0.61), backwater (-0.40), current velocity (0.84) and riffle (0.84) on CCA axis II (Figure 7D).

Habitat specialists selected relatively similar habitats among sampling locations and no noticeable changes in habitat associations were observed between fishes in upper reach with less variable hydrograph and fishes in lower reach with more variable hydrograph. Riffle habitat specialists (percids and *C. anomalum*) were associated with moderate to swift current velocities and cobble substrate, although *C. anomalum* shifted more to sand substrates in the lower reach and to bedrock in the tributaries. Run specialists (*N. amabilis*, *M. congestum*, *N. volucellus*, *N. stramineus* in tributaries) were associated with moderate depths and current velocities. Pool and slackwater specialists (*G. affinis*, *C. cyanoguttatum*, centrarchids, *D. nigrotaeniata* in upper reaches) were consistently associated with slower current velocities, silt substrates and vegetation. Among fishes common to all three mainstem sampling locations, association with current velocity differed from expected (upper reach) for riffle specialist ($R^2 = 0.49$, $P = 0.05$) and run specialist ($R^2 = 0.56$, $P < 0.01$) (Figure 8). As the hydrograph in the lower reach declined from near dry base flow towards subsistence flow (95Q), riffle specialists were increasingly restricted to current velocities ranging from 0.26 to 0.63 m/s (max: 0.70) less than riffle specialists in the upper reach, and run specialists were restricted to current

velocities ranging from 0.05 to 0.35 m/s (max: 0.41) less than run specialists in the upper reach. Association with current velocity was not different from expected for pools specialists. Likewise, association with water depth was not different from expected for riffle, run or pool specialists (Figure 9).

DISCUSSION

During a declining hydrograph from low base flow towards subsistence flow, hydrological variability was lowest and CPUE, diversity, and evenness were highest in upper reaches of the Llano River supported by spring outflows. In contrast, lower reaches of the Llano River, specifically reaches not immediately supported by spring outflows, were highest in taxa richness. Habitat variability and fish-habitat associations were similar among all reaches. Riffle and run specialists generally selected swifter waters among those available, although swifter waters differed as much as 0.60 m/sec for riffle specialists and 0.40 m/sec for run specialists during extreme low flows.

The prediction of a direct relationship between hydrological variability and habitat variability was not supported in this study. Habitat variability, defined as variation in linear combinations of physical and chemical parameters (PC scores), was not different among reaches, although discharge declined from 79 to 94Q among mainstem reaches. In contrast, habitat variability is associated with hydrological variability in non-karst streams mainly due to reduction in flow and periods of zero flow (Schlosser 1982, Shea and Peterson 2007). Schlosser (1982) attributed greater habitat variability in upper reaches to accentuated low flows in the headwater reaches and also found that habitat volume (i.e. a component of habitat diversity) was more variable than

habitat diversity itself. Among various published studies, there are no consistencies in quantifying habitat variability. Schlosser (1982) assessed habitat variability by quantifying variability in habitat diversity, and Shea and Peterson (2007) used coefficients of variation for diel change in habitat availability. I used a novel approach to quantify habitat variability but do not attribute the inability of detecting similar trends to the methodology. Instead, this study demonstrated that instream habitats among reaches were persistent under declining hydrological conditions (dry base flow to subsistence flow), which is likely typical for streams with fairly homogenous depths and current velocities throughout its course.

The prediction of an inverse relationship between hydrological variability and fish community structure (CPUE, S, H' and evenness) was partially supported in this study. Fish CPUE, diversity, and evenness were highest in the upper reach with lowest hydrological variability, intermediate in the middle reach with intermediate variability, and lowest in the lower reach with highest hydrological variability. Patterns in CPUE, diversity, and evenness in relation to hydrological variability were consistent with patterns reported (Gorman and Karr 1978, Schlosser 1987, Oberdorff et al. 2001) but inconsistent with patterns observed among stream orders in non-karst streams. Specifically, low order streams (i.e. upper reaches) of the Llano River had the highest CPUE, diversity, and evenness, whereas high order streams (i.e. lower reaches) have the highest CPUE, diversity, and evenness in non-karst streams. High CPUE, diversity, and evenness in the upper reaches of the Llano River offers an independent test of the underlying mechanism (i.e., hydrological variation) driving CPUE, diversity, and evenness. As such, stream order (Whiteside and McNatt 1972, Vannote et al. 1980) is a

poor predictor of CPUE, diversity, and evenness among fish communities in areas with substantial base flows contributed by perennial springs of large aquifers, such as the Edwards-Trinity aquifer. Two, often related, biotic parameters associated with stream order and hydrological variability are species richness and community stability. Species richness generally is greatest in higher order streams (Whiteside and McNatt 1972), which often times coincides with less hydrologically variable streams (Horwitz 1978, Schlosser 1982, Herbert and Gelwick 2003). Highest richness was observed in the lower reach, consistent with trends based on stream order (Whiteside and McNatt 1972) but differed from predictions of the underlying mechanism, specifically that taxa richness would be highest in reaches with low hydrological variability. Higher richness in the lower reach of the Llano River was attributed to movement of fishes from species pools downstream. Though extirpation is more likely in hydrologically variable reaches, species in the lower reaches of the Llano River are replaced by migrants from downstream, which typically would not be available to upper reach sites in non-karstic streams. Number of taxa comprising upper assemblages (i.e. hydrologically variable) in most rivers is generally limited to available species pools downstream (Whiteside and McNatt 1972, Evans and Noble 1979, Taylor and Warren 2001); however, this scenario is not the case with stable groundwater dominated headwater streams possessing a unique pool of spring-associated assemblages (Paller 1994, Williams et. al 1996, Kollaus and Bonner 2012). Therefore, higher richness in the lower reach is an anomaly to mechanisms driving species richness.

An increase in hydrological variability negatively influences assemblage stability (Gorman and Karr 1978, Schlosser 1987, Oberdorff et al. 2001). However, shifts in fish

community structure in the Llano River were greater in areas with less hydrological variability. Variability in species richness and diversity was slightly greater in the upper reach compared to the lower reach. Assemblages in the lower reach were more closely related (percent change: 17%) than those in the upper reach (42%) where a higher degree of stability persisted. I attribute higher community stability in the lower reach to two plausible explanations: lack of sampling during extreme flows (i.e. sampling N = 4 during wadeable conditions and not across the hydrograph period of record), or greater number of more tolerant and large-bodied reservoir derived fishes and an assemblage dominated by a single species *C. venusta*. Coon (1987) found similar trends in the variation in abundance of benthic riffle fishes *Etheostoma* in a coldwater karstic stream, with populations of the more tolerant forms being more temporally stable than those of the less tolerant forms. Consequently, differences among physiological tolerances of species can obscure patterns in community assembly rules when comparing patterns among reaches.

The prediction of a relationship between hydrological variability and deviations in fish-habitat associations was partially supported in this study. Multivariate fish-habitat associations were similar among riffle, run, and pool specialists among reaches. As the hydrograph declined in the middle and lower reaches, riffle and run specialists continued to associate with swifter currents, although current velocities were considerably less than velocities in the upper reach. Consequently, deviation from expected distributions related to geomorphic units, substrate, and water depth were not detected in this study. Numerous studies demonstrate that habitat shifts are observed during flood pulse events (Matthews 1986, Perkin et al. 2009), wet versus dry base flows (TIFP – SARA 2011),

and from base flows to isolated pools (Ostrand 2000, Magoulick and Kobza 2003).

Fishes generally shift to habitats with slower current velocities under higher than average base flows (high flow pulses, wet base flows). Under no flow conditions, fish predictably are restricted to isolated pools and persist at different rates (Ostrand 2000) usually in very different habitats than expected. In this study, habitat associations were not substantially different under a hydrograph shifting from low base flow to subsistence flows. Riffle specialists still associated with riffle habitats, and run specialists still associated with run habitats. However, riffle specialists in low flow reaches were restricted to current velocities < 0.60 m/s than conspecifics in the upper reach, and run specialists were restricted to current velocities < 0.40 m/s than conspecifics in the upper reach.

Physiological effects of fish restricted to slower current velocities for extended periods are widely unknown on fish life history needs (e.g. reproduction, feeding, general physiology) and was outside the scope of this study. Ultimately, this information would be useful and necessary to further quantify the effects of subsistence flows on riffle and run specialists and provide opportunities for water managers to adjust recommended subsistence flows for a river reach. Zero-flow days are a natural part of the lower Llano River hydrograph (Colorado River BBEST 2011) and should be allowed to occur at similar frequencies and duration as the past. However, water managers can adjust water withdrawals up to current subsistence flows (55 cfs in the Llano River) with more information available on how communities respond to restrictions in extremely low flow.

Patterns in fish community structure and habitat variability associated with hydrological variability in the Llano River likely are applicable to other Edward Plateau river systems and demonstrate the ubiquity of hydrological influences on community

structure and the uniqueness of karst spring supported river systems. Persistent spring outflows in the upper reaches support diverse and often distinct communities of endemic fishes (Hubbs 1995, Kollaus and Bonner 2012); however, flows are sometimes not sufficient to support perennial flows in lower reaches of these rivers. As such, fish communities in lower reaches differ from upper reaches and depend upon recolonization events from riverine habitats upstream and downstream from the Edwards Plateau. In this study, complete dewatering of the lower reaches followed the June 2011 survey. Several precipitation events in September 2011 provided subsistence to high base flows (95 to 41Q) with several high flow pulses that were sustained through June 2012. In January 2012, we observed primarily large body and mobile fishes (*L. osseus*, *Cyprinus carpio*, *Carpoides carpio*, *I. bubalus*, *M. congestum*, *I. punctatus*, *L. auritus*, *M. salmoides* and *A. grunniens* consisting of 55% of the total assemblage) recolonizing the reach, likely from a downstream source (Lake LBJ, mainstem reservoir on the Colorado River). One year after complete dewatering (June 2012), we observed a fish community that was 40-60% similar to the community before dewatering, with successive recolonization of small body fishes likely from upstream sources (*C. anomalum*, *N. amabilis*, *N. stramineus*, *N. volucellus* and *E. spectabile* consisting of 9% of the total assemblage). Consequently, fish communities in lower reaches are resilient to complete dewatering by first being colonized by downstream forms with high mobility and with subsequent colonization by upstream forms likely due to dispersion of juveniles and age-0 individuals (Pavlov 1994, Slack et al. 2004, Williams 2011). Spring outflows are refugia for fishes during extreme environmental conditions (Sedell et. al 1990, Rhodes and Hubbs 1992) and therefore a source for the diversity of downstream communities.

Additionally, nutrients (Vannote et al. 1980), aquatic macroinvertebrates and sediments (Heitmuller and Raphael 2012) are likely transported from upper reaches to lower reaches and provide essential elements to support the diversity of downstream communities (Vannote et al. 1980). Collectively, this study demonstrates that persistent flows of the upper reach contribute to the downstream community and therefore should be a consideration in how lower reaches are influenced by changes in spring flows due to water harvest, impoundment and stream fragmentation.

Table 1. Mean physical habitat parameters across sampling locations on the Llano River from October 2010 – June 2011.

	<u>Mainstem</u>			
	<u>Upper</u>	<u>Middle</u>	<u>Lower</u>	<u>Tributaries</u>
Total area sampled (m ²)	17,700	24,129	42,668	32,992
Average mesohabitat (m ²)	347	431	646	371
<u>Habitat Type (%)</u>				
Riffle	16.8	32.7	13.0	11.1
Run	68.1	37.3	63.9	53.9
Pool	13.6	16.0	12.8	27.9
Backwater	1.5	14.1	10.3	7.2
<u>Habitat Parameters</u>				
Depth (m)	0.44	0.49	0.49	0.42
Current Velocity (m/s)	0.44	0.30	0.22	0.12
<u>Substrate (%)</u>				
Silt	5.9	13.7	5.5	27.0
Sand	1.4	0.3	56.3	0.1
Gravel	11.2	10.8	13.2	4.2
Cobble	37.8	37.9	13.8	20.4
Boulder	7.7	3.6	4.7	0.2
Bedrock	36.0	33.6	6.7	48.1
Vegetation (%)	5.8	13.4	9.3	26.1
Algal cover (%)	2.9	3.9	2.1	1.9
Woody Debris (%)	7.1	1.1	0.2	1.1
<u>Water Quality</u>				
Temperature (°C)	20.4	21.3	19.2	21.5
Dissolved Oxygen (mg/L)	8.7	8.5	8.5	7.7
Conductivity (µS/cm)	366.2	362.6	342.4	410.2
pH	7.9	8.2	8.3	8.1

Table 2. Relative abundance (%), total number of species (N), CPUE, species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across sampling locations for the Llano River from October 2010 – June 2011.

Species	Mainstem			
	Upper	Middle	Lower	Tributaries
<i>Lepisosteus osseus</i>	-	<0.1	0.3	<0.1
<i>Dorosoma cepedianum</i>	-	-	0.6	<0.1
<i>Campostoma anomalum</i>	0.6	1.4	0.5	6.2
<i>Cyprinella lutrensis</i>	-	-	1.2	<0.1
<i>Cyprinella venusta</i>	37.2	51.3	65.5	50.8
<i>Cyprinus carpio</i>	-	-	0.3	-
<i>Dionda nigrotaeniata</i> **	1.9	0.5	<0.1	0.3
<i>Macrhybopsis hyostoma</i>	-	0.1	-	-
<i>Notropis amabilis</i> **	11.7	7.2	0.1	15.4
<i>Notropis stramineus</i>	-	1.0	1.2	6.7
<i>Notropis volucellus</i>	10.3	3.4	3.0	3.6
<i>Pimephales vigilax</i>	-	0.3	1.8	-
<i>Carpionodes carpio</i>	-	<0.1	1.3	0.2
<i>Ictiobus bubalus</i>	-	-	1.1	-
<i>Minytrema melanops</i>	<0.1	-	-	-
<i>Moxostoma congestum</i> *	0.2	0.3	0.1	0.3
<i>Ictalurus punctatus</i>	1.1	0.3	0.5	<0.1
<i>Pylodictis olivaris</i>	0.2	0.2	<0.1	-
<i>Fundulus zebrinus</i>	-	-	<0.1	<0.1
<i>Gambusia affinis</i>	10.7	7.2	5.6	7.0
<i>Morone chrysops</i>	-	-	<0.1	-
<i>Lepomis auritus</i>	5.8	6.1	8.3	3.4
<i>Lepomis cyanellus</i>	<0.1	0.2	0.5	<0.1
<i>Lepomis gulosus</i>	0.2	0.3	0.1	<0.1
<i>Lepomis macrochirus</i>	0.2	1.3	1.7	0.7
<i>Lepomis megalotis</i>	1.9	5.0	0.4	0.6
<i>Lepomis microlophus</i>	<0.1	0.1	<0.1	<0.1
<i>Micropterus salmoides</i>	0.1	<0.1	0.2	0.2
<i>Micropterus treculii</i> *	1.7	1.1	0.9	0.5
<i>Etheostoma lepidum</i> **	0.4	0.4	<0.1	0.6
<i>Etheostoma spectabile</i>	10.4	5.5	3.4	2.0
<i>Percina carbonaria</i> *	4.0	5.0	0.5	0.3
<i>Aplodinotus grunniens</i>	-	-	0.2	-
<i>Cichlasoma cyanoguttatum</i>	1.4	1.5	0.1	0.9

Table 2-Continued: Relative abundance (%), total number of species (N), CPUE, species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across sampling locations for the Llano River from October 2010 – June 2011.

Total N =	4,866	3,673	6,974	19,625
CPUE (individuals/m ²)	0.27	0.15	0.16	0.59
Richness (S)	22	26	32	26
Diversity (H')	0.90	0.83	0.67	0.76
Evenness (J')	0.67	0.59	0.44	0.54

* Endemic to the Edwards Plateau

** Endemic to the Edwards Plateau and spring associated species

Table 3. Relative abundance (%), total number of species (N), CPUE, species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across seasons for the Llano River from October 2010 – June 2011.

Species	Season			
	Fall	Winter	Spring	Summer
<i>Lepisosteus osseus</i>	0.1	<0.1	<0.1	<0.1
<i>Dorosoma cepedianum</i>	0.1	0.2	0.1	0.3
<i>Campostoma anomalum</i>	2.5	3.8	6.3	0.7
<i>Cyprinella lutrensis</i>	0.3	0.5	0.2	0.1
<i>Cyprinella venusta</i>	55.3	47.1	48.7	59.8
<i>Cyprinus carpio</i>	<0.1	0.1	<0.1	<0.1
<i>Dionda nigrotaeniata</i> **	0.6	0.1	0.2	1.4
<i>Macrhybopsis hyostoma</i>	<0.1	<0.1	<0.1	-
<i>Notropis amabilis</i> **	6.2	11.0	15.6	9.2
<i>Notropis stramineus</i>	5.9	3.7	3.5	3.2
<i>Notropis volucellus</i>	3.2	3.2	6.5	3.4
<i>Pimephales vigilax</i>	0.5	0.2	0.2	0.8
<i>Carpionodes carpio</i>	0.2	0.3	0.4	0.8
<i>Ictiobus bubalus</i>	0.2	0.5	<0.1	0.2
<i>Minytrema melanops</i>	-	-	<0.1	-
<i>Moxostoma congestum</i> *	0.3	0.5	0.1	0.1
<i>Ictalurus punctatus</i>	0.3	0.2	0.3	0.5
<i>Pylodictis olivaris</i>	<0.1	<0.1	<0.1	<0.1
<i>Fundulus zebrinus</i>	<0.1	<0.1	<0.1	-
<i>Gambusia affinis</i>	9.6	9.9	5.1	4.3
<i>Morone chrysops</i>	-	<0.1	-	-
<i>Lepomis auritus</i>	4.8	4.0	4.8	6.9
<i>Lepomis cyanellus</i>	0.2	0.2	0.1	0.2
<i>Lepomis gulosus</i>	<0.1	<0.1	0.1	<0.1
<i>Lepomis macrochirus</i>	1.1	0.9	0.5	1.0
<i>Lepomis megalotis</i>	1.6	0.5	1.2	1.7
<i>Lepomis microlophus</i>	<0.1	<0.1	<0.1	<0.1
<i>Micropterus salmoides</i>	0.3	0.3	0.1	0.2
<i>Micropterus treculii</i> *	0.6	0.7	0.5	1.8
<i>Etheostoma lepidum</i> **	0.4	0.8	0.2	0.2
<i>Etheostoma spectabile</i>	2.2	7.9	3.4	1.2
<i>Percina carbonaria</i> *	1.3	1.7	1.2	1.3
<i>Aplodinotus grunniens</i>	<0.1	<0.1	<0.1	<0.1
<i>Cichlasoma cyanoguttatum</i>	1.7	1.4	0.2	0.4

Table 3-Continued: Relative abundance (%), total number of species (N), CPUE, species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of species across seasons for the Llano River from October 2010 – June 2011.

Total N =	8,749	8,602	11,667	6,120
CPUE (individuals/m ²)	0.22	0.41	0.38	0.23
Richness (S)	32	33	33	30
Diversity (H')	0.79	0.86	0.80	0.74
Evenness (J')	0.53	0.57	0.53	0.50

* Endemic to the Edwards Plateau

** Endemic to the Edwards Plateau and spring associated species

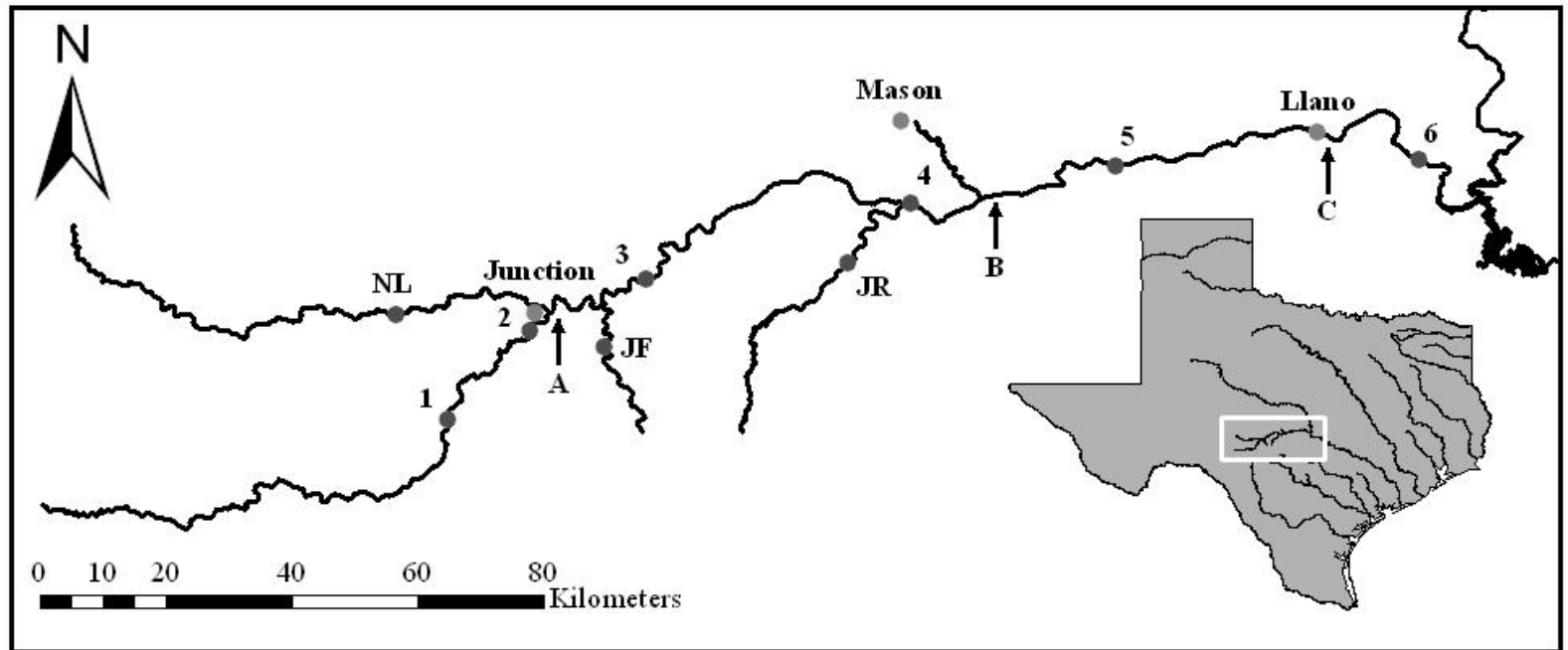


Figure 1. Site map of the Llano River: upper reach = sites 1 – 2, middle reach = sites 3 – 4, lower reach = sites 5 – 6, NL = North Llano River, JF = Johnson Fork, JR = James River, A = USGS 08150000, B = USGS 08150700 and C = USGS 08151500.

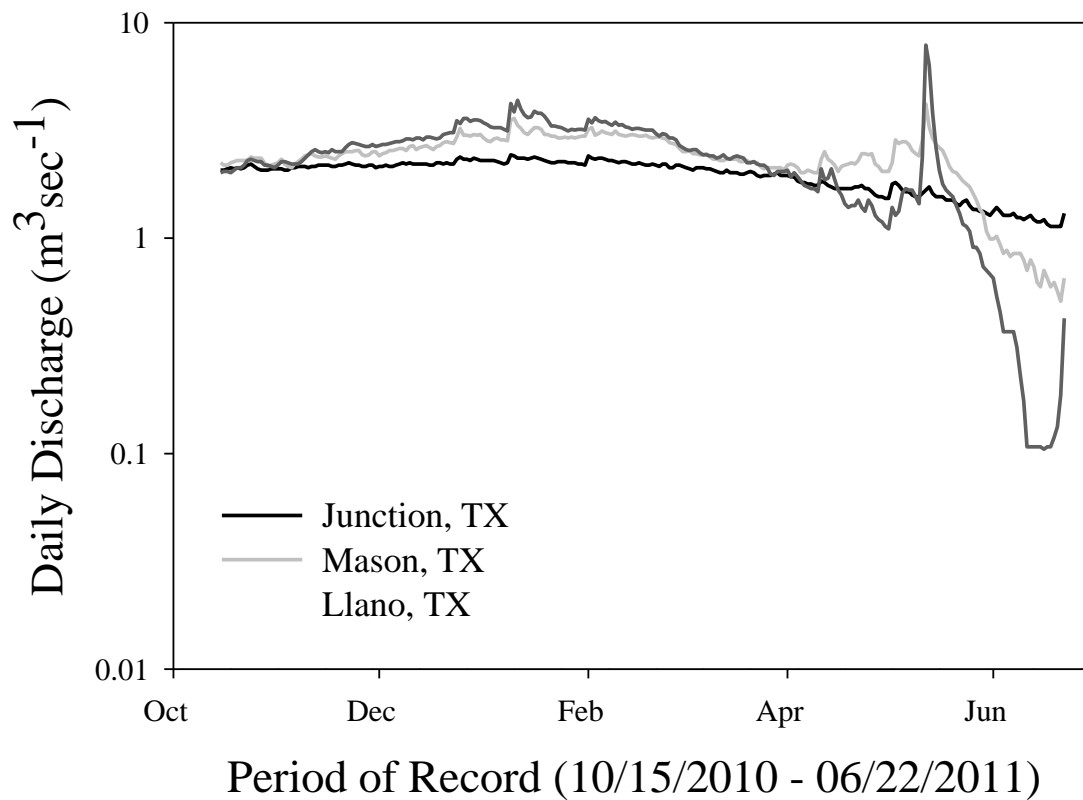


Figure 2. Daily discharge for three USGS gage stations near Junction, TX (USGS 08150000), Mason, TX (USGS 08150700) and Llano, TX (USGS 08151500) located on the mainstem Llano River between 10/15/2010 – 06/22/2011.

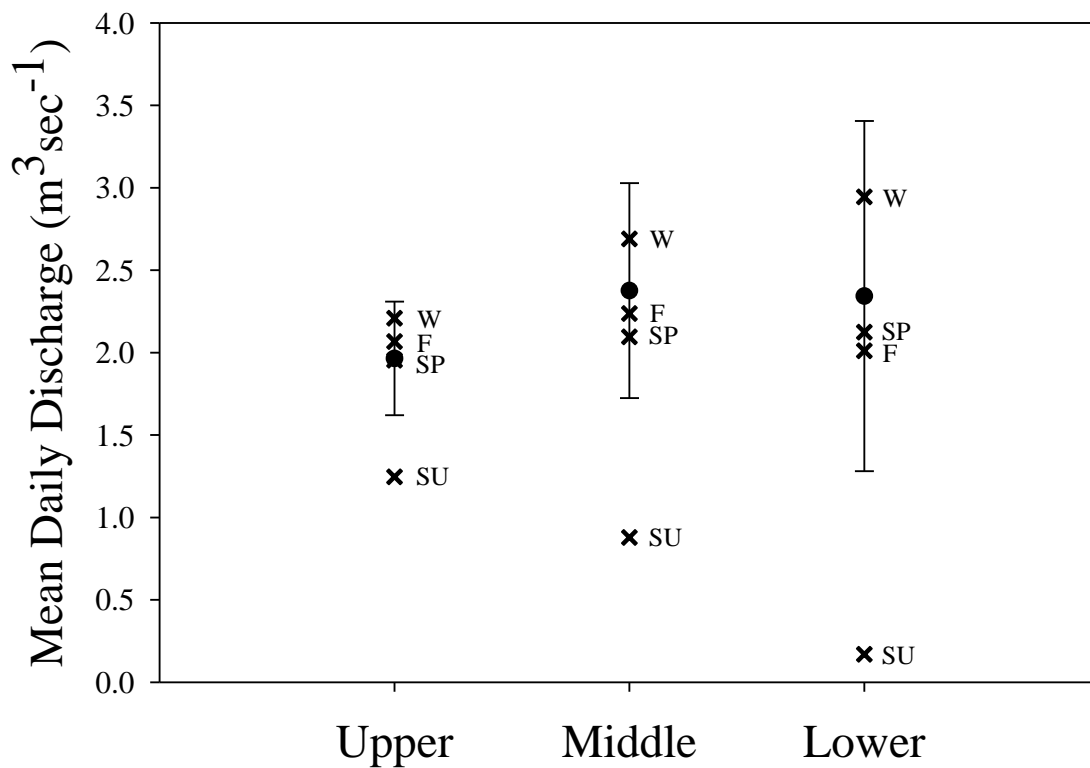


Figure 3. Mean daily discharge \pm SD for three USGS gage stations (upper: 08150000, middle: 08150700, lower: 08151500) on the mainstem Llano River between 10/15/2010 – 06/22/2011. Flow during seasonal sampling events represented with an X.

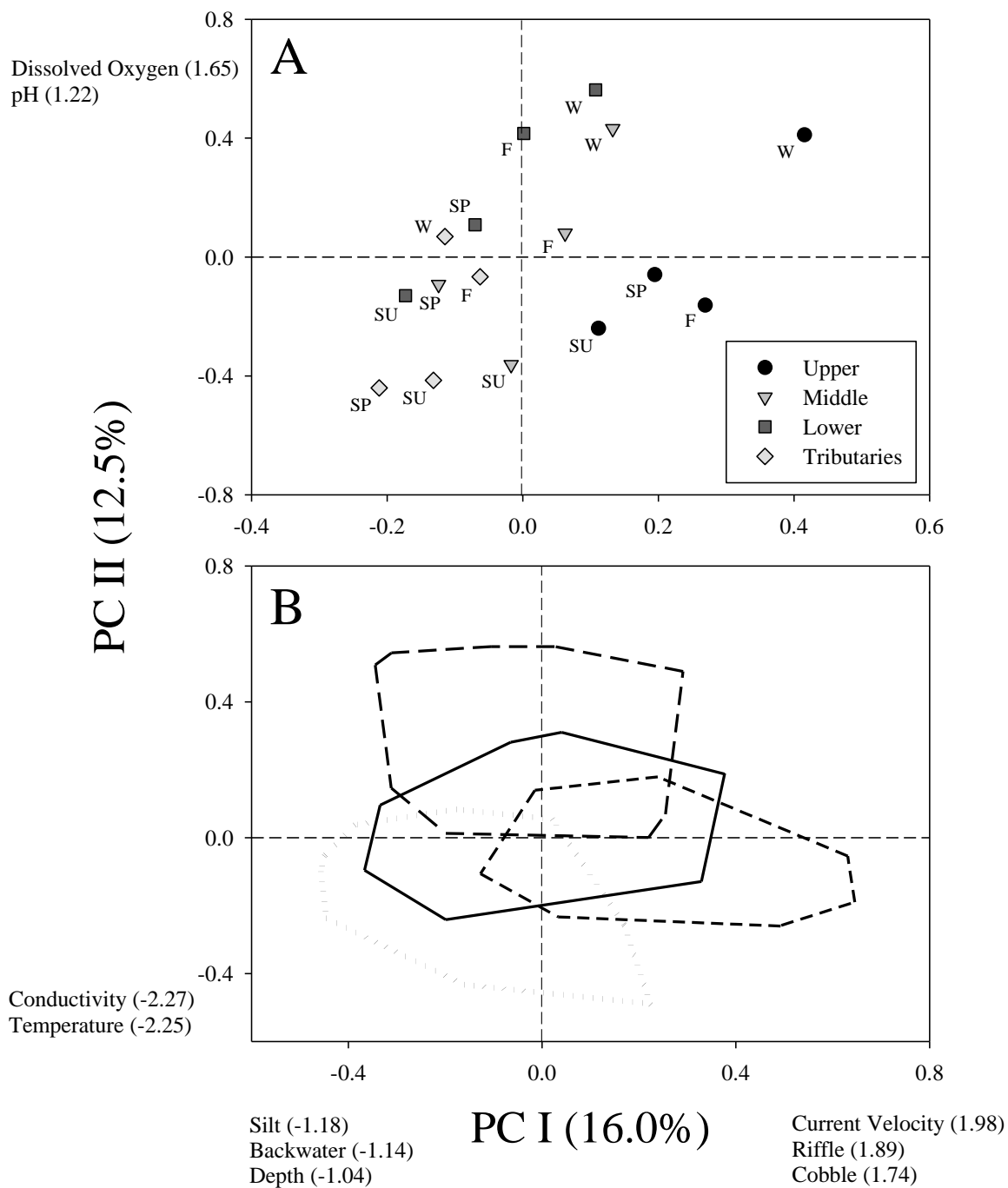


Figure 4. Principal Component Analysis of A) mean physical habitat parameters for each sampling location by season and B) mean scores for each reach and tributaries circled by one standard deviation: upper reach = short dash, middle reach = solid line, lower reach = long dash, and tributaries = dotted line on the Llano River from October 2010 – June 2011. Total variation explained = 47%.

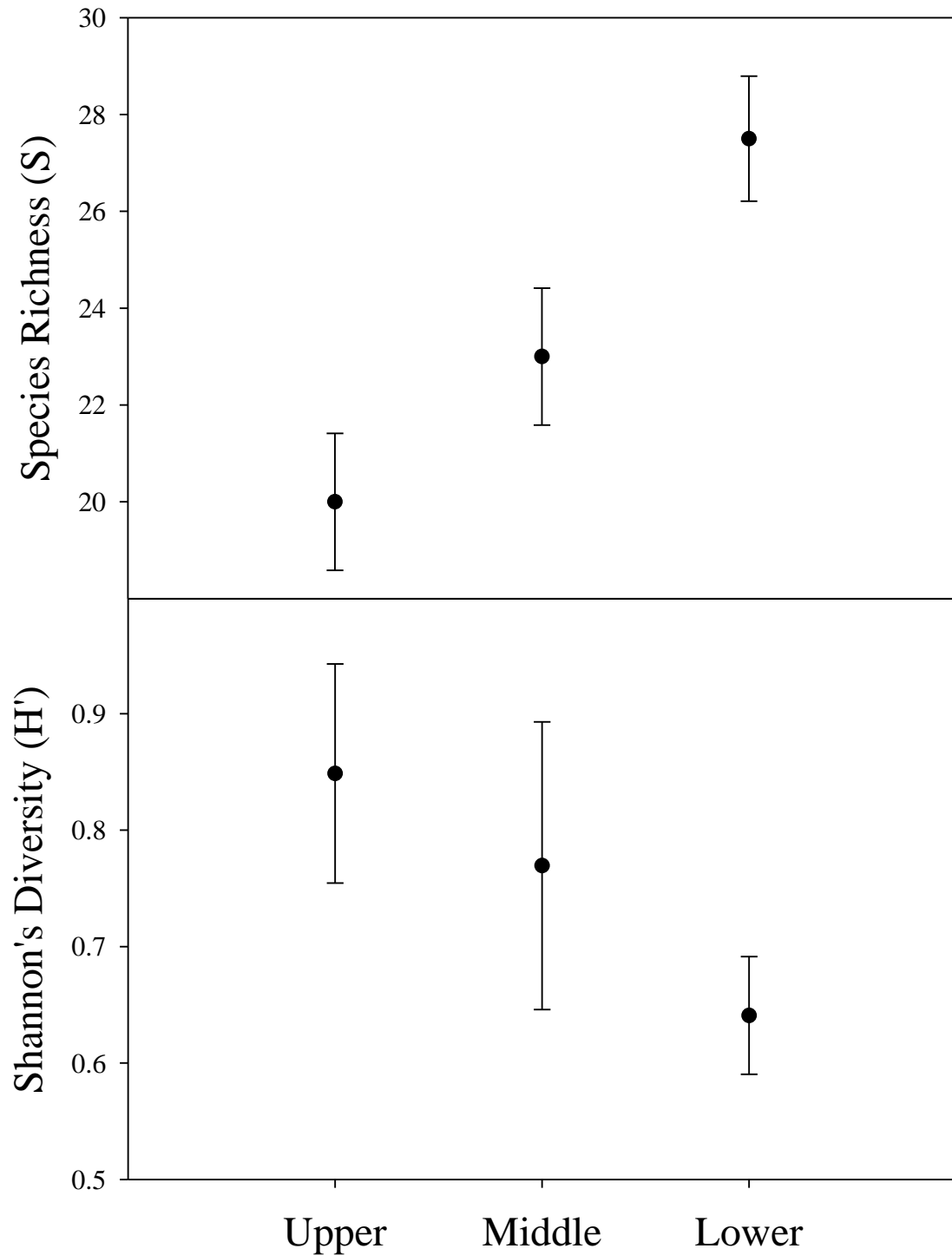


Figure 5. Mean species richness (S) and diversity (H') \pm SD for each sampling location across all seasons on the Llano River from October 2010 – June 2011.

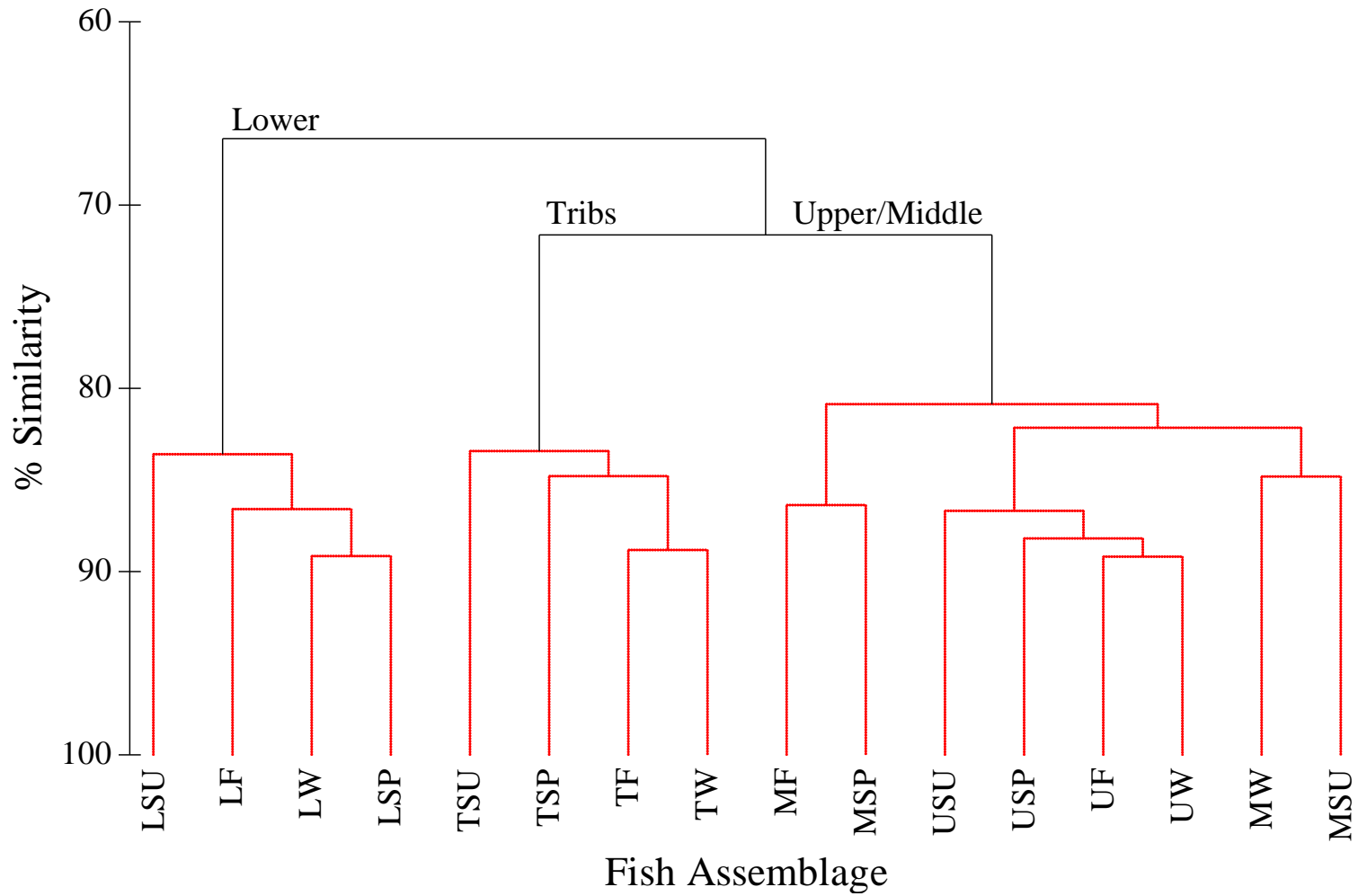


Figure 6. CLUSTER analysis for fish assemblages across all combinations of sampling location and season for the Llano River from October 2010 – June 2011. Solid black lines represent significant structure ($P < 0.05$). Abbreviations as follow: U = upper reach, M = middle reach, L = lower reach, T = tributaries, F = fall, W = winter, SP = spring and SU = summer.

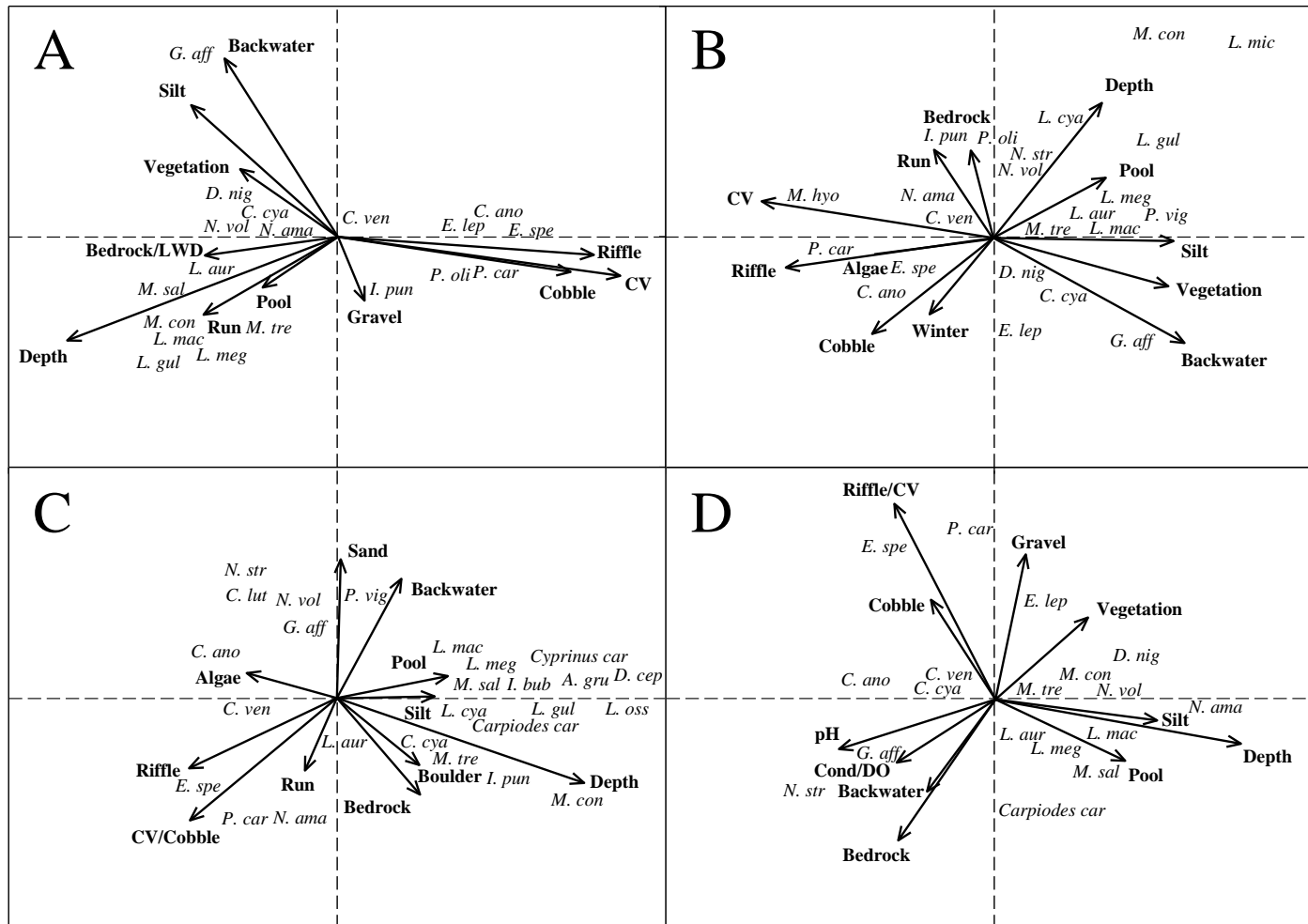


Figure 7. Canonical Correspondence Analysis of physical habitat parameters and season for the A) upper reach, B) middle reach, C) lower reach and D) tributaries on the Llano River from October 2010 – June 2011.

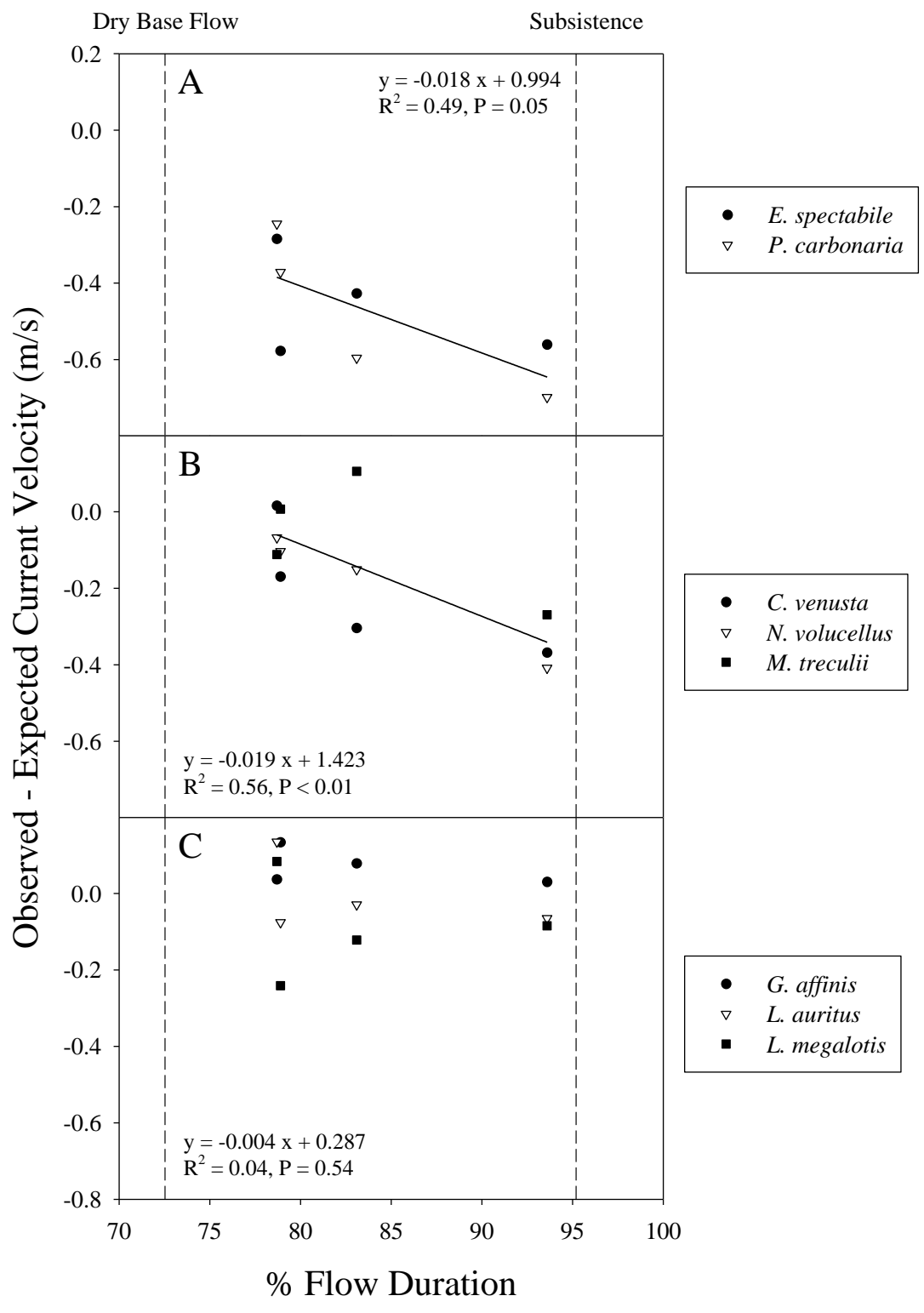


Figure 8. Deviation from expected current velocity for A) riffle, B) run and C) pool species in relation to percent flow duration; classifications of instream flow recommendations for the Llano River taken from Colorado River BBEST Report.

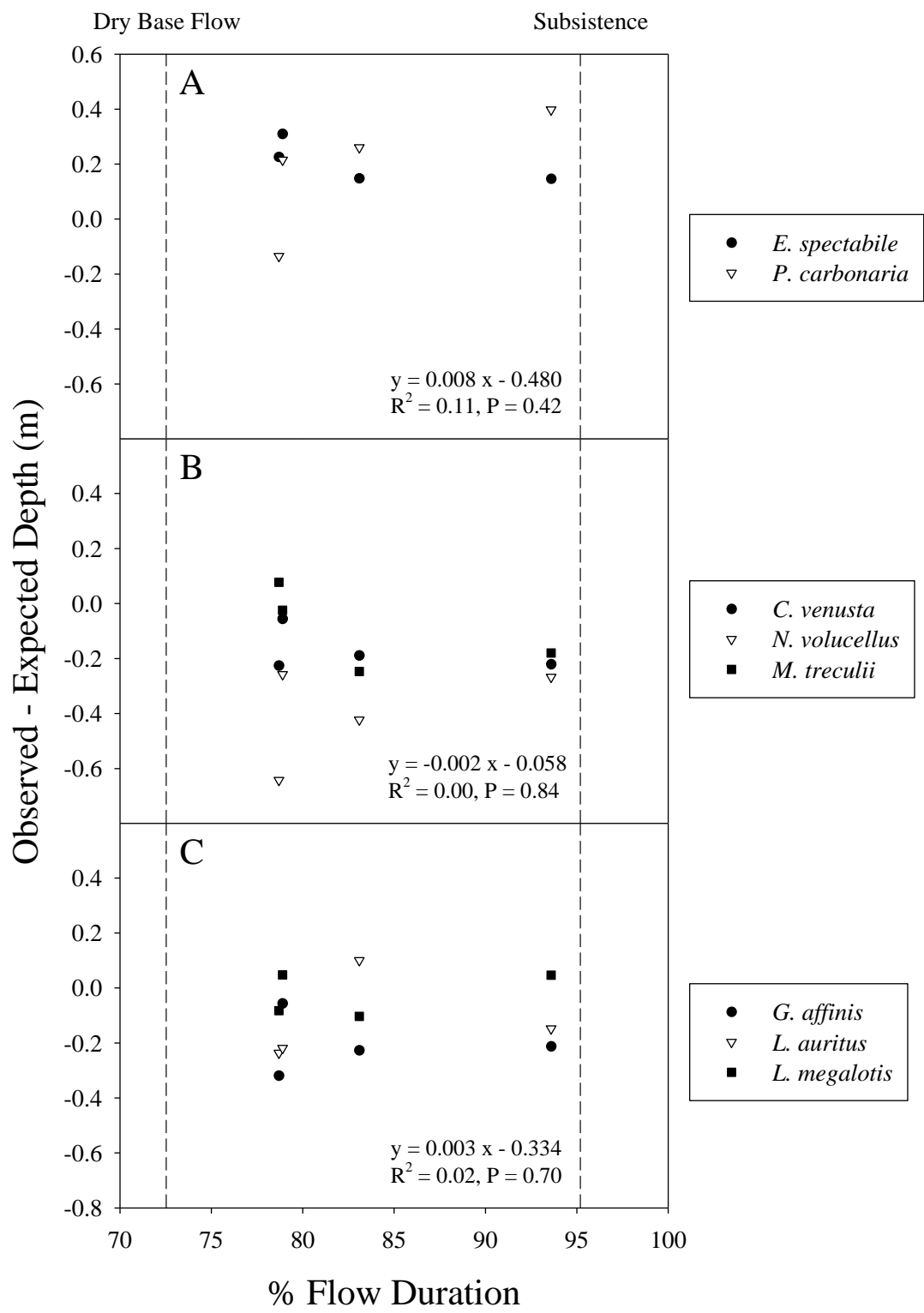


Figure 9. Deviation from expected depths for A) riffle, B) run and C) pool species in relation to percent flow duration; classifications of instream flow recommendations for the Llano River taken from Colorado River BBEST Report.

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