Habitat associations of a semi-arid fish community in a karst spring-fed stream

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ABSTRACT

Karst spring systems provide permanent water sources in semi-arid to arid environments, supporting a diverse aquatic community. Numerous karst streams in the Edwards Plateau and Trans-Pecos regions of Texas support two distinct fish assemblages, spring-associated species and riverine species. Previous studies have identified constant water temperature as the segregating factor but have lacked the ability to effectively distinguish temperature from headwater influence. Multiple spring sources along a 64-km course of a semi-arid stream allowed an opportunity to assess the influence of temperature and other environmental variables on spatiotemporal patterns in the fish assemblage. Physical parameters (10.6%), site (4.9%), and season (1.6%) explained significant variation within the Devils River fish assemblage. Current velocity, depth, and vegetation were among the strongest factors explaining fish segregation. Water temperature influenced seasonal movement of spring-associated species into spring outflow habitats during summer and winter and resulted in a segregated assemblage. This study suggests spring flow (i.e., current velocity and depth) and constant water temperature are leading segregating factors and important for maintaining parapatric assemblages.

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1. Introduction

Spring systems sustained by groundwater discharge from karst aquifers occur worldwide and are of ecological importance because of the unique aquatic communities that they support (Dikov and Zivkov, 2004; Meyer et al., 2007; Scarsbrook et al., 2007). Unlike groundwater discharge from alluvium aquifers, karst aquifers contain extensive, integrated systems of underground conduits in limestone that localize the transport of water (White, 1988). Discharges from karst aquifers are concentrated at source points rather than diffused throughout the substrate, forming large spring systems with typically higher discharge volumes and more permanent water sources than alluvium aquifers (White, 1998). Within semi-arid to arid environments, karst streams often provide permanent freshwater habitats, and while isolated from other surface waters, contribute to species radiation (Minckley and Deacon, 1968). Consequently, karst streams in semi-arid to arid regions are rich in biodiversity, providing habitat and refugia for endemic fauna and flora as well as generalist aquatic taxa (Rhodes and Hubbs, 1992; Scarsbrook et al., 2007).

Karst springs are primary contributors of base flows in upper riverine reaches of many southwestern USA drainages. As such, unique environmental gradients occur from the spring sources to downstream reaches (Hubbs, 1995). Headwater reaches near spring sources are characterized by relatively constant water temperatures and distinctive homogeneous physical and chemical parameters (e.g., Groeger et al., 1997). Heterogeneity among and within abiotic parameters increases with longitudinal distance from spring outflows because of contributions from sheet flow (e.g., tributary streams) and regional abiotic conditions (e.g., ambient temperatures) (Power et al., 1999). Longitudinal variations in abiotic parameters influence fish distributions within spring-fed streams according to species-specific physiological tolerances and habitat associations (e.g., Taylor and Lienesch, 1996). Among larger karst streams, regionally endemic fishes are generally concentrated in the stenothermal, headwater sections of streams, whereas fishes with more ubiquitous distributions are generally concentrated in the more abiotically variable, downstream sections of streams (Hubbs, 1995). Because of their limited distributions in or near a spring source, these regionally endemic fishes are often described as spring-associated; however, exact factors leading to their restricted range as well as their segregation with riverine taxa remain unclear (Garrett et al., 2004). Several biotic (e.g., competition, fecundity) and abiotic (e.g., temperature, salinity, stream order, stream gradient) factors are hypothesized to regulate fish distributions and segregation among fish assemblages (Garrett

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et al., 2004; Gido et al., 1999; Ingersoll and Claussen, 1984; Taylor and Lienesch, 1996). Among abiotic factors, constant temperature is most often identified as the explanatory variable of fish assemblage segregation in larger karst streams (Bonner et al., 1998; Gehlbach et al., 1978; Hubbs, 2001). However, reported associations between water temperature and fish segregation stem from systems with a single head spring, and are therefore ineffective in testing alternative structuring mechanisms, such as channel morphology or resource availability as predicted by the Stream Continuum Concept (Schlosser, 1982). Consequently, multiple spring sources along a stream course are needed to adequately assess the influence of water temperature on spring-associated and riverine fish distributions and segregations.

The Edwards Plateau and Trans-Pecos regions in Texas contain one of the largest concentrations of karst streams within the southwestern USA and are identified as regional biodiversity hotspots (Brune, 1981; Myers et al., 2000). Within these semi-arid regions, nearly half of all spring systems in Texas receive water from two karst aquifers (i.e., Edwards and Trinity group aquifers), supporting 90 endemic plant, invertebrate, fish, salamander, and reptile species (Bowles and Arsuffi, 1993). Among fishes, 30% of the fish fauna within the region are either imperiled (i.e., 18 taxa) or extinct (i.e., 3 taxa; Hubbs et al., 2008). Extirpations and extinctions are attributed to excessive groundwater withdrawals (e.g., *Etheostoma fonticola*; Schenck and Whiteside, 1976 and *Cyprinodon elegans*; Hubbs et al., 2008) and to reservoir construction (e.g., *Gambusia amistadensis*, Hubbs et al., 2008). Habitats of remaining taxa are threatened by continued groundwater withdrawals, instream habitat alterations, and land use alterations (Hubbs et al., 2008). Information on habitat relations of fishes among karst streams is necessary to understand mechanisms behind species persistence and to effectively manage remaining aquatic communities.

The purpose of this study was to examine fish distribution and habitat associations related to karst spring outflows of fishes within an Edwards Plateau stream. The Devils River is a karst stream in the Edwards Plateau region with multiple springs (i.e., at least 13 known instream and near-shore springs) contributing discharges ranging from <0.1 to >0.75 cms along a 64-km course of the river (Brune, 1981; Harrell, 1978). Typical of many Edwards Plateau and Trans-Pecos karst streams, the Devils River supports several endemic fishes of conservation concern and species recognized as spring-associated fishes, including *Cyprinella proserpina*, *Dionda argentosa*, *Dionda diaboli*, *Ictalurus lupus*, *Cyprinodon eximius*, *Etheostoma grahami*, *Notropis amabilis*, and *Astyanax mexicanus* (Hubbs et al., 2008). Objectives of this study were to: (1) describe spatiotemporal patterns and habitat associations among fish assemblages within the Devils River through multivariate analysis, (2) quantify univariate associations (i.e., current velocity, depth, and substrate) with fish distributions across time and space, and (3) quantify temperature distribution for spring-associated and riverine species. Quantification of the Devils River fish assemblage in relation to spring sources and other habitat variables through time and space will allow a better understanding of natural structuring mechanisms within these unique aquatic habitats and greater predictability on how anthropogenic alterations will affect the ichthyofauna.

2. Material and methods

2.1. Study area

The Devils River originates in southwest Texas and flows southeast before emptying into Amistad Reservoir near Del Rio, Texas. The watershed is within the Edwards Plateau region

(Balconian biotic province) of Texas and drains approximately 10,000 km². Mean annual precipitation is 53 cm, with precipitation occurring primarily during September and May. Upper reaches of the Devils River generally have ephemeral and intermittent stream flow supported by localized and shallow alluvial aquifers (Barker et al., 1994). The lower reach of the Devils River extends 64 km from Pecan Springs to Amistad Reservoir, with perennial base flow supported by karst springs from the Edwards-Trinity Aquifer (Brune, 1981). Annual median discharge within the lower Devils River is 8.7 m³/s (period of record: 1978 to 1995; US Geological Survey Station 08449400). In the upper and lower reaches, the Devils River is a heterogeneous mix of run, riffle, and pool habitats with silt, cobble, and bedrock substrates.

Six sampling sites were selected along a 53 km stretch of the Devils River. Study sites 1 through 3 (approximately 30°03′13.54″ N, 101°9′5.57″ W) were located in the upper reach of the Devils River (i.e., upstream of Pecan Springs; Fig. 1) and were relocated due to stream desiccations. Sites 1−3 were grouped for analysis because of their close proximity (i.e., <5 km apart) to one another and because the three sites are in areas supported by alluvial aquifers. Sites 4 through 6 (site 4, 29°57′52.66″ N, 101°08′49.34″ W; site 5, 29°54′14.41″ N, 101°00′37.68″ W; site 6, 29°53′58.95″ N, 100°59′52.63″ W) were located in the lower reach of the Devils River, downstream from Pecan Springs and upstream from Dolan Falls. Sites 5 and 6 were less than 2 km apart but treated as independent samples because they are separated by a natural fish barrier (i.e., cascading waterfall).

To asses fish distribution based on temperature, sampling sites were grouped according to annual temperature variability. Sites 1−3 and site 5 were selected to represent the environmentally variable riverine segments of the Devils River. Although base flows were supported by groundwater discharge from a shallow alluvial aquifer (sites 1−3) or by a small (<0.5 cms), unnamed Edwards-Trinity spring (site 5), water temperatures (mean = 21.5 °C; SD = 5.7; range: 9.6−32.4 °C for $N = 360$ daytime measurements)
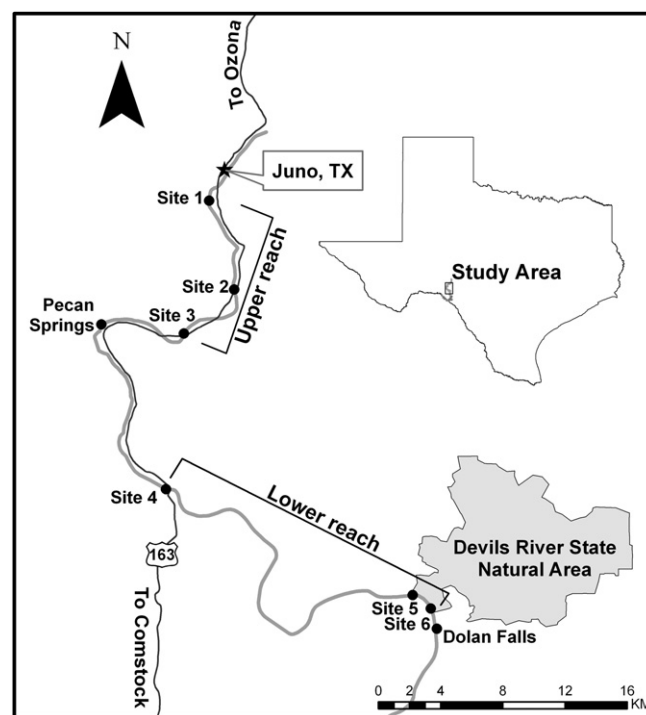

Fig. 1. Site map of Devils River, Val Verde County, TX.

among available habitats were strongly influenced by ambient temperature conditions (e.g., daytime heating and winter cooling). Sites 4 and 6 were selected to represent environmentally stable spring run segments of the Devils River. Base flows at site 4 were supported by two large springs (i.e., Pecan Springs, located 10 km upstream and Hudspeth Springs, located 3 km upstream; Brune, 1981; Harrell, 1978) and Site 6 included spring outflows from Finnegan Springs, a defuse series of fissured springs (Brune, 1981). Mean water temperatures (mean = 22.0 °C; SD = 3.4; range: 15.6–32.2 °C for N = 432 daytime measurements) among available habitats deviated less from spring outflow conditions (mean = 21.7 °C; SD = 1.45; range: 20.8–23.0 °C). However, spring run segments did contain backwater and run habitats that were hydrologically disconnected from the spring flows so water temperatures within those areas were influenced by ambient temperature conditions, causing a wider temperature gradient than expected for a spring run segment (Groeger et al., 1997).

To further assess temperature distribution among fishes, sites were additionally grouped based upon the presence or absence of a direct spring outflow. Sites with direct spring outflows (i.e., riverine site 5 with the unnamed spring and spring run site 6 with Finnegan Springs), provided areas where fish have a choice between water temperatures predominately influenced by ambient conditions or by spring outflow conditions. The remaining two sites (i.e., riverine sites 1–3 and spring run site 4) did not contain a direct spring outflow and were used to assess temperature distribution without the option or no choice to select water temperature other than the conditions offered at the site level.

2.2. Field sampling

Seine hauls and habitat measurements were taken along multiple transects arranged perpendicular to the shoreline at each site (Simonson et al., 1994) with sites sampled every two months from September 2007 through October 2008. Transects proceeded from downstream to upstream and were spaced 20–80 m apart depending on maximum stream width at each site. Multiple habitats were sampled along each transect with seine hauls spaced at least 0.5 m apart to minimize disturbing adjacent seine hauls. Fishes were captured within a geomorphic unit (i.e., riffle, run, pool, backwater) with downstream 5-m seine (3 m × 1.8 m, mesh size = 3.2 mm) haul or a 5-m downstream substrate kick into a seine. Downstream seine hauls were used for slow run or pool habitats, whereas downstream substrate kicks were used in shallow and swift water run and riffle habitats. Number of seine hauls ranged from 25 to 45 for each site and date depending on available habitats. Captured fish were identified, enumerated, and total length (TL) measured to the nearest millimeter (up to 30 specimens per species per seine haul). Voucher specimens were taken for each taxon, anesthetized in a lethal dose (80 mg/l) of tricaine methanesulfonate (MS-222), and preserved in 10% formalin. All other individuals were released.

Current velocity (m/s), depth (m), water temperature (°C), substrate type (i.e., sand, silt, gravel, cobble, boulder, or bedrock), percent vegetative cover, and percent woody cover were recorded at the location of each seine haul. Water depth was measured to the nearest 0.01 m and current velocity at 60% depth was recorded in two evenly distributed points across the width of the area seined using a Marsh-McBirney FLOW-MATE™ Model 2000 flow meter. Water temperature was measured using a YSI Model 85 m. Percent substrate, vegetation cover, algal cover, and woody debris were visually estimated within each seine haul. Specific conductance (µS/cm), dissolved oxygen (mg/l), and pH were measured with a YSI Model 85 m at each site and sampling date.

2.3. Statistical analysis

Species relative abundance (%), relative abundance of spring-associated and riverine species (%), taxa richness (S), diversity (H), and evenness (Es) were calculated for each site. Diversity was calculated using the Shannon–Wiener index (log$_e$ base), and evenness was calculated using Shannon evenness (Es = H/Hmax). Species of the genera *Gambusia* (i.e., species *Gambusia geiseri*, *Gambusia speciosa*, and possibly *Gambusia affinis*) and *Ictalurus* (i.e., species *Ictalurus lupus* and *Ictalurus punctatus*) as well as juvenile individuals (i.e., total length <18 mm) of the genera *Lepomis* and *Dionda* were grouped due to difficulty in confidently identifying morphologically distinguishing features in the field, taxonomic uncertainty, or introgression (Hubbs et al., 2008). Group genera were excluded from multivariate and univariate analyses since described patterns or habitat associations would not be representative of any particular species.

Bray–Curtis similarity matrices were created in Primer 6 using log(x+1) transformed species abundance data and tested with one-way analysis of similarities (ANOSIM = 0.05, 10,000 permutations) to identify differences in Devils River fish assemblage between environmental stable spring sites and riverine sites. The similarity percentage option (SIMPER) was used to identify contributions of individual species to the total dissimilarity among sites. Renkonen similarity index was used to assess differences in fish assemblages between seasons [i.e., transitional seasons (fall/spring) and extreme seasons (winter/summer)] at each site. Principal component analysis (PCA; Canoco 4.5, Microcomputer Power 2002) was used to assess linear combinations of habitat characteristics at each site. Qualitative data (e.g., geomorphic units) were denoted as dummy variables, whereas quantitative data (e.g., current velocity, depth, temperature) were z-transformed (Krebs, 1999). The resulting PCA loadings were plotted to assess habitat variability within and among sites. Canonical correspondence analysis (CCA; Canoco 4.5) was used to assess patterns in habitat associations for Devils River fishes. Total variation was partitioned into pure effects of environmental parameters, site, and season (Borcard et al., 1992), and Monte Carlo tests (10,000 permutations) were used to determine the significance (α = 0.05) of each effect.

Univariate assessments were used to describe current velocity, depth, substrate, vegetative cover, and temperature associations for abundant fishes in the Devils River. Temperature associations and distributions were assessed on additional riverine species (i.e., *Micropterus salmoides*, *Lepomis megalotis*, and *Lepomis macrochirus*) to examine temperature segregation between spring-associated and riverine species. Kolmogorov–Smirnov (KS) tests were used for continuous data to test for differences between expected and observed fish abundances among current velocity (0.1 m/s), depth (0.01 m), and temperature (1 °C) gradients. A Chi-square goodness of fit test was used for ratio data to test differences between expected and observed fish abundances for substrate classifications and vegetative cover. Values for KS and goodness of fit tests were determined by pooling species abundance and habitat data across sites and seasons, calculating percent available current velocity, depth, substrate, and vegetative cover, and multiplying by the total number of species collected.

Mean (±SD) water temperature associations (°C) were calculated for the 12 most abundant Devils River fishes at sites without direct spring outflows (sites 1–3 and site 4) and sites with direct spring outflows (sites 5 and 6). Temperature distribution for the 12 most abundant Devils River fishes was illustrated by plotting mean deviation in degrees (°C) from mean spring temperature versus mean deviation in degrees from mean river temperature, along with water temperature measured among seine hauls (i.e., percentage of available temperatures). Deviation from mean spring-outflow temperature and mean river temperature was used to remove the influence of

seasonal variation in available temperature and allowed for the comparison of species temperature selection among seasons. A *t*-test was used to test for differences in mean deviation (°C) from mean river temperature between transitional seasons [i.e., fall (September–November) and spring (March–May)] and extreme seasons [i.e., winter (December–February) and summer (June–August)] for spring-associated species, riverine species, and *D. diaboli* at direct spring outflow sites (sites 5 and 6).

3. Results

3.1. General characteristics

Stream flows were ephemeral in the upper reach (sites 1–3) and perennial in the lower reach (sites 4–6) of the Devils River from September 2007 through October 2008. The upper reach consisted of shallow to moderate depths (0.16–1.3 m) and slow current velocities (0.0–0.35 m/s). Common geomorphic units within the upper reach were runs (57%), pools (27%), and riffles (10%) with cobble (47%), gravel (30%), and silt (17%) substrates. Approximately 27% of the geomorphic unit areas contained submergent macrophytes (15%; i.e., *Potamogeton* and *Justicia*) or filamentous algae (12%). The lower reach (sites 4–6) consisted of shallow to moderate depths (0.06–1.4 m) and sluggish to swift current velocities (0.0–1.5 m/s). Common geomorphic units within the lower reach were runs (74%), backwaters (15%), and riffles (5.7%) with silt (up to 65% at site 4), bedrock (72%) and cobble (15%) substrates (sites 5 and 6). Submergent vegetation and algae coverage ranged from 25% (sites 5 and 6) to 75% (site 4), and consisted of *Chara*, *Ceratophyllum*, and *Justicia*. Water quality parameters in both reaches did not vary widely through time (range for conductivity: 447–488 μS/cm; dissolved oxygen: 7.8–10.7 mg/l; pH: 7.9–8.6), except for water temperature (upper reach: 9.6–26.7 °C; lower reach: 13.8–33.8 °C).

Principal component axes I and II explained 23% of variation in qualitative and quantitative habitat measurements taken among 792 seine hauls (Fig. 2). Axis I explained 12% of the variation and described a vegetation and substrate gradient. Strongest loadings for PC axis I were bedrock (1.73), algal cover (1.02), spring outflows (0.60), vegetation (−2.42), silt (−2.40), and current velocity (−1.17). Axis II explained 11% of the variation and represented geomorphic units, temperature, and depth gradient. Strongest loadings on PC axis II were riffle (1.59), pool (1.56), gravel (1.40), run (−2.01), bedrock (−1.52), and temperature (−1.32). Sites 1–3 [mean sample scores and (±SD)] were positively associated with PC axis II, site 4 was negatively associated with PC axis I, and sites 5 and 6 were positively associated with PC axis I and negatively associated with PC axis II.

Among the 792 seine hauls, 15,604 fishes, representing 27 species and nine families were taken from sites 1–6 (Table 1). Cyprinidae was the most abundant family (69%), followed by Poeciliidae (13%), and Characidae (12%). Most abundant taxa were *D. argentosa* (30%) *N. amabilis* (17%), *Gambusia* spp. (13%), *A. mexicanus* (12%), *C. proserpina* (6.2%), and *D. diaboli* (5.1%), comprising 84% of the Devils River fish assemblage. Among all sites, spring-associated species were most abundant (73%) followed by riverine species (14%) and *Gambusia* spp. (13%). Site 4 had the highest relative abundance of spring-associated species (93%), whereas site 5 had the highest relative abundance of riverine species (41%). Species richness ranged from 19 at sites 4 and 6 to 20 at site 1–3, diversity ranged from 1.65 at sites 1–3 to 2.37 at site 5, and evenness ranged from 0.53 at sites 1–3 to 0.77 at site 5.

3.2. Multivariate associations

Fish assemblage differed between sites (Bray–Curtis similarity index = 24%; ANOSIM global R = 0.792, P = 0.01) with five taxa
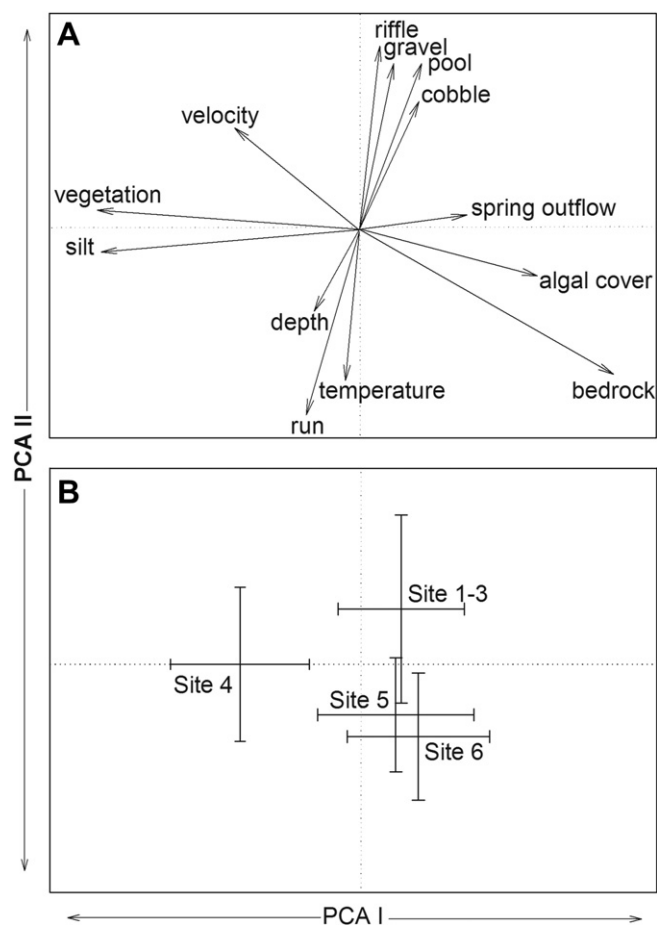

Fig. 2. Principal component analysis bi-plots for measured environmental parameters (A) and general habitat characteristics by site (B) for habitats sampled at four sites on the Devils River during September 2007–October 2008.

contributing approximately 40% of observed dissimilarity [i.e., *N. amabilis* (16%), *Cyprinella venusta* (8%), *A. mexicanus* (6%), *Notropis stramineus* 6% and *D. diaboli* (4%)] between environmentally stable spring sites (sites 4 and 6) and environmentally variable riverine sites (sites 1–3 and site 5). Among the five taxa, relative abundances of three spring-associated species (i.e., *N. amabilis*, *A. mexicanus*, and *D. diaboli*) were greater at spring sites, whereas relative abundance of two riverine species (i.e., *C. venusta* and *N. stramineus*) were greater at riverine sites. Riverine sites demonstrated greater fish assemblage dissimilarities (RSI = 0.59 at sites 1–3; RSI = 0.62 at site 5) between transitional (i.e., fall/spring) and extreme seasons (i.e., winter/summer) than stable spring sites (RSI = 0.81 at site 4; RSI = 0.74 at site 6). Lower fish assemblage similarities within riverine sites were attributed to higher relative abundances of spring-associated taxa (e.g., *A. mexicanus* increased from 3% during winter/summer to 15% during fall/spring at sites 1–3 and *C. proserpina* increased from 8% during winter/summer to 16% during fall/spring at site 5); at the riverine sites during transitional seasons.

Axes I and II from CCA analysis explained 19.6% (P < 0.01) of the spatiotemporal variability in the Devils River fish assemblage from physical parameters, site, and season (Fig. 3). Pure effects of physical parameters explained 10.6% (P < 0.01), site explained 4.9% (P < 0.01), and season explained 1.6% (P < 0.01) of assemblage variation. Shared effects (two-and three-way interactions) among physical parameters, site, and season accounted for 2.5% variation. Physical parameters and sites strongly associated with CCA axis I

Table 1
Relative abundances by species (%), relative abundance of spring-associated and riverine species (%), taxa richness, Shannon-Weiner diversity, and Shannon evenness for fishes collected from the Devils River during September 2007–October 2008. Single astericks denote spring-associated species.

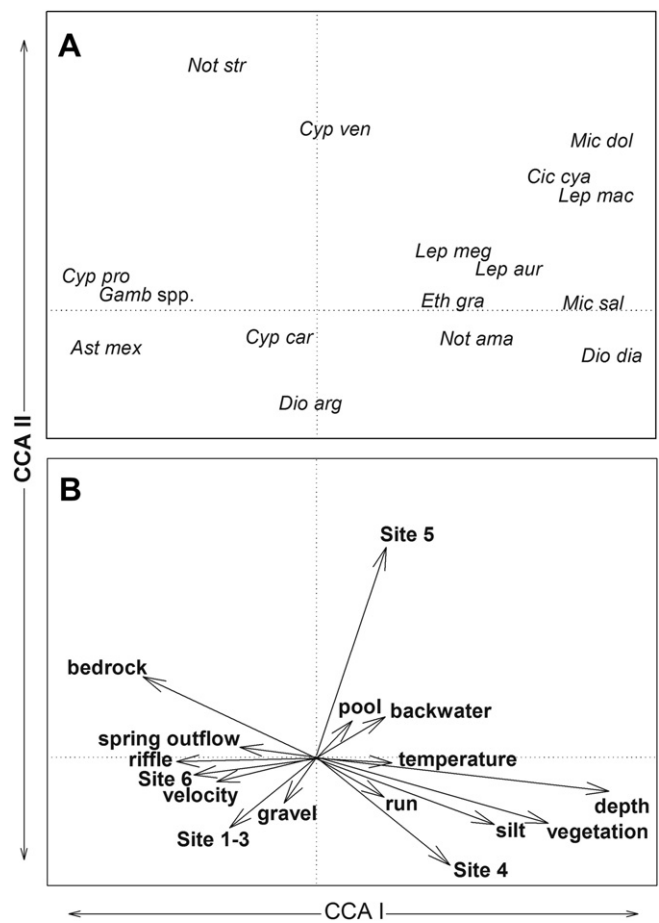| Species	Site				
	Site 1–3	Site 4	Site 5	Site 6	Total
Lepisosteus oculatus	–	–	–	<0.1	<0.1
*Cyprinella proserpina**	3.7	3.6	9.2	8.7	6.2
Cyprinella venusta	2.6	1.7	15.5	2.8	4.8
Cyprinus carpio	4.9	–	–	<0.1	1.7
*Dionda argentosa**	50.6	29.9	11.8	18.0	30.3
*Dionda diaboli**	3.4	12.7	4.6	2.7	5.1
Dionda spp.[a]	0.1	0.4	1.4	0.2	0.4
*Notropis amabilis**	8.2	27.6	6.5	28	17.3
Notropis stramineus	<0.1	–	16.7	2.2	3.6
Carpiodes carpio	<0.1	–	–	–	<0.1
Moxostoma congestum	–	0.1	0.2	–	<0.1
*Astyanax mexicanus**	5.1	14.7	15	17.7	12.3
Ictalurus spp.[b]	<0.1	0.6	<0.1	–	0.1
Pylodictis olivaris	–	<0.1	–	–	<0.1
Gambusia spp.[c]	18.9	1.1	8.5	15.9	13
Lepomis auritus	0.2	1.2	0.8	0.2	0.5
Lepomis cyanellus	0.1	–	–	–	<0.1
Lepomis macrochirus	0.4	0.2	1.2	0.08	0.4
Lepomis miniatus	–	<0.1	<0.1	<0.1	<0.1
Lepomis megalotis	0.9	0.1	0.9	0.8	0.7
Lepomis spp.[d]	0.1	–	0.1	<0.1	<0.1
Micropterus dolomieu	<0.1	<0.1	0.4	<0.1	0.1
Micropterus salmoides	0.2	0.7	0.5	0.1	0.3
*Etheostoma grahami**	0.2	3.6	1.6	0.7	1.2
Cichlasoma cyanoguttatum	0.3	1.5	4.8	1.1	1.6
Oreochromis aurea	–	–	<0.1	0.7	0.2
Spring-associated*	87.9	94.1	54.7	90.3	83.7
Riverine	12.1	5.9	45.3	9.7	16.3
N=	5399	2726	2749	4730	15,604
Taxa richness	20	19	19	19	27
Diversity	1.65	1.87	2.37	1.97	
Evenness	0.53	0.62	0.77	0.65	

[a] *Dionda* spp. includes juvenile individuals (total length < 18 mm).
[b] *Ictalurus* spp. includes species of *I. lupus* and *I. punctatus*.
[c] *Gambusia* spp. includes species of *G. geiseri*, *G. speciosa*, and *G. affinis*.
[d] *Lepomis* spp. includes juvenile individuals (total length <18 mm).

Fig. 3. Canonical correspondence analysis bi-plots for fish species (A) and environmental parameters and sites (B) from Devils River (September 2007–October 2008). Species labels follow the first three letters of genus and species.

were depth (0.85), vegetation (0.58), silt (0.43), bedrock (−0.42), and site 4 (0.35). Physical parameters and sites strongly associated with CCA axis II were site 5 (0.84), site 4 (−0.46), bedrock (0.31), site 1–3 (−0.27), and vegetation (−0.26). Among fishes associated with CCA axes I and II, *C. proserpina*, and *A. mexicanus* were more abundant at lower reach sites and riffle or spring outflow habitats. *D. argentosa* and common carp were found among available geomorphic units and sites but were most abundant over gravel substrate at sites 1–3. *N. stramineus* and *C. venusta* were found among available geomorphic units but most abundant at site 5. *E. grahami*, *N. amabilis*, and *D. diaboli*, were found in slow run or pool habitats with *D. diaboli* generally associated with greater depths and higher percent vegetation. *Lepomis* spp., *Micropterus* spp., *Cichlasoma cyanoguttatum* were most abundant in pool and backwater habitats at sites 4 and 5. The significant season effect was attributed, in part, to the capture of juvenile sunfish and black bass individuals only during spring and summer.

3.3. Univariate associations

Species distribution among available current velocity, depth, substrate, and temperature gradients are described in detail within the Appendix.

Distribution of available temperatures ranged from 0 to 6.7 °C deviations (i.e., degrees) from mean spring water temperature (i.e., 21.7 °C) and 0–3.6 °C deviations from available mean riverine water

temperatures (i.e., 15.7–26.9 °C, mean range) (Fig. 4). Among abundant species at sites without direct spring outflows (sites 1–3 and site 4), mean water temperature inhabited by species ranged from 0.9 to 3.4 °C deviations from mean riverine water temperature and from 1.8 to 5.4 °C deviations from mean spring water temperature (Table 2). Among the abundant species at sites with direct spring outflows (sites 5 and 6), mean water temperature inhabited by species ranged from 1.8 to 3.1 °C deviations from mean riverine water temperature and from 0.7 to 4.2 °C deviations from mean spring water temperature. In general, temperature distributions of spring-associated species overlapped that of riverine species at sites without direct spring outflow (i.e., sites 1–3 and site 4, Fig. 4A). However, temperature distributions of spring-associated species at sites with direct spring outflow (i.e., sites 5 and 6) deviated less from mean spring temperatures, whereas riverine species deviated away from mean spring temperatures and occupied more of the extreme temperatures (Fig. 4B). Consequently, spring-associated species and riverine species were segregated at sites 5 and 6 based on temperature distribution, except for one species. Mean water temperature inhabited by *D. diaboli* was similar to that of riverine-associated species.

Among sites with direct spring outflow (i.e., sites 5 and 6), temperature distributions of spring-associated species were seasonally influenced, whereas temperature distributions of riverine species remained relatively consistent across seasons. Mean deviation from mean river temperature for spring-associated species differed (*t*-test, $P < 0.01$) between transitional (i.e., spring
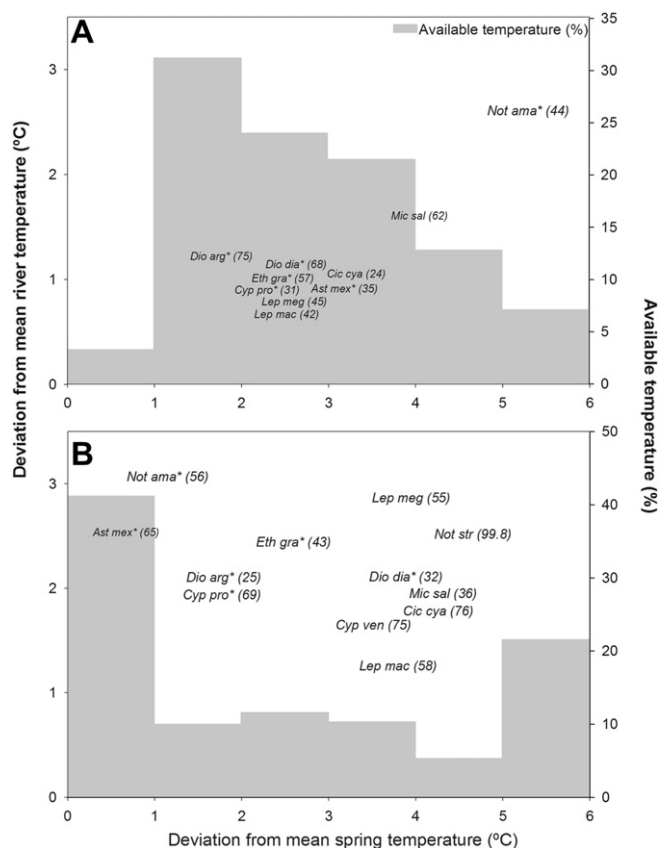
Fig. 4. Mean deviation from spring temperature (i.e., 21.7 °C, x-axis) versus mean deviation from riverine temperatures (i.e., mean range = 15.7–29.9 °C, left y-axis) for the six most abundant spring-associated (*) and riverine species at non-direct spring outflow sites (A) and direct spring outflow sites (B) sampled from the Devils River September 2007–October 2008. Parenthetical values next to species represent the percent of each species occurring at non-direct and direct spring outflow sites (i.e., values in A and B sum to 100 for each species). Shaded histogram represents the frequency distribution (%, right y-axis) of available temperatures among mean deviations from spring temperature (i.e., 21.7 °C, x-axis). Species labels follow the first three letters of genus and species.

Table 2
Mean observed temperature deviation [°C (±SD)] from mean spring temperature (Spring, 21.7 °C) and mean river temperature (river, mean range = 15.7–29.9 °C) for the six most abundant spring-associated and riverine species at non-direct spring outflow and spring outflow sites sampled in the Devils River September 2007–October 2008.

Species	Non-direct spring outflow sites		Spring outflow sites	
	Spring	River	Spring	River
Spring-associated				
Cyprinella proserpina	2.49 (1.5)	0.94 (1.0)	1.77 (2.1)	1.98 (1.2)
Dionda argentosa	1.78 (1.1)	1.21 (0.6)	1.79 (1.9)	2.08 (1.2)
Dionda diaboli	2.64 (1.7)	1.14 (1.1)	3.88 (2.6)	2.15 (1.3)
Notropis amabilis	5.39 (3.9)	2.61 (2.3)	1.25 (1.8)	3.07 (1.6)
Astyanax mexicanus	2.93 (1.3)	0.9 (0.6)	0.67 (1.0)	2.53 (0.8)
Etheostoma grahami	2.49 (1.1)	1.01 (0.8)	2.53 (2.5)	2.40 (1.5)
Riverine				
Cyprinella venusta	6.9 (3.5)	3.36 (2.0)	3.57 (2.2)	1.84 (1.2)
Notropis stramineus	–	–	4.56 (2.4)	2.5 (1.1)
Lepomis macrochirus	2.52 (1.1)	0.85 (0.6)	3.80 (2.2)	1.44 (1.0)
Lepomis megalotis	2.61 (1.5)	0.96 (0.8)	3.90 (2.6)	2.84 (1.5)
Micropterus salmoides	4.04 (2.0)	1.61 (1.5)	4.24 (2.2)	1.94 (1.2)
Cichlasoma cyanoguttatum	3.31 (1.3)	1.01 (0.9)	4.19 (2.5)	1.88 (1.1)

and fall, mean = 0.94, SD = 0.59) and extreme (i.e., winter and summer, mean = 1.78, SD = 1.10) seasons (Fig. 5). In contrast, mean deviation from mean river temperature for riverine species did not differ ($P = 0.48$) between transitional (mean = −1.41, SD = 1.17) and extreme (mean = −1.13, SD = 1.27) seasons. Deviation from mean river temperature for *D. diaboli* differed ($P < 0.01$) between transitional (mean = 0.43, SD = 0.24) and extreme (mean = −2.18, SD = 1.37) seasons, attributed primarily with the collection 37% of *D. diaboli* captured during the summer with water temperatures ranging from 21.7 to 30.6 °C.

4. Discussion

Devils River fishes did not follow the expected spatial pattern of a spring-associated assemblage being replaced downstream by a riverine fish assemblage (Hubbs, 1995), but instead exhibited a heterogeneous assemblage structure associated with location of spring sources. Although the Devils River fish assemblage was dominated by spring-associated species, shifts in assemblage composition were observed relating to site spring influence. Sites with greater spring influence (i.e., lower annual temperature variation; sites 4 and 6) supported a fish assemblage with a higher proportion of spring-associated species (i.e., *A. mexicanus* and *N. amabilis*) and demonstrated little temporal dissimilarity in assemblage composition, whereas the more riverine sites (i.e., greater annual temperature variation; sites 1–3, 5) contained a fish assemblage with an increased abundance of riverine species (i.e., *C. venusta* and *N. stramineus*) and demonstrated greater temporal dissimilarity in assemblage composition. Dispersion of spring-associated species outside of spring sources occurred during spring and fall seasons, which accounted for the greater temporal variation in assemblage composition at riverine sites and coincided with mean river temperature reaching approximately mean spring outflow temperature. Movement during spring and fall seasons is a common behavior of fishes, often corresponding with changes in water temperature (Mills, 1991) and attributed to fishes searching for suitable spawning areas (Lucas and Batley, 1996), increasing feeding opportunities (Peterson and Rabeni, 1996), and changes in stream environment (Montgomery et al., 1983). These findings suggest a relationship exists between spring-associated species distribution and temperature stability provided by spring sources outside of any stream order influence; though, it may be seasonally dependent.
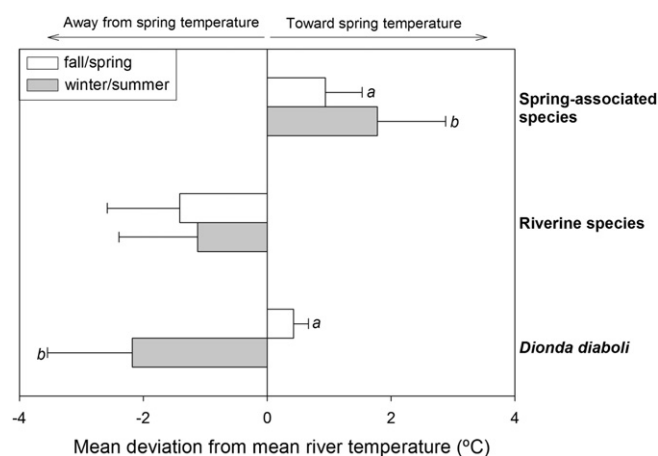
Fig. 5. Mean (±SD) deviation from mean river temperature (°C) during transitional (spring and fall) and extreme (winter and summer) seasons for six most abundant spring-associated and riverine species, as well as federally threatened *Dionda diaboli* collected from the Devils River during September 2007–October 2008. Lowercase letters indicate significant differences ($P < 0.05$) within a group.

Despite previous suggestion for lack of species segregation in the Devils River (Harrell, 1978), Devils River fishes demonstrated patterns in habitat use and distribution that are typical of stream fish assemblages (Taylor et al., 2006). Among environmental factors, current velocity, depth, and vegetation explained the largest percent of the variation in fish occurrence and distribution. *A. mexicanus* and *C. proserpina* were associated with riffle habitats, *E. grahami*, and *N. amabilis* were found in runs with moderate current velocities and depths, and *M. salmoides*, *L. macrochirus*, and *D. diaboli* were associated with deeper, vegetated pool habitats. Species segregation by current velocity, depth, and geomorphic units is common for run-off dominated rivers (Gillette et al., 2006) and spring-dominated rivers (Watson, 2006, this study), and is attributed to numerous factors, including predator avoidance patterns, swimming speed capabilities, and differences in feeding behavior (Harvey and Stewart, 1991; Leavy and Bonner, 2009; Power, 1984). Additionally, species diversity and evenness increased longitudinally along the Devils River, a pattern typical of river systems (Horwitz, 1978) that is associated with increased habitat heterogeneity and stability downstream (Jackson et al., 2001).

Although water temperature was not initially identified as a major influence in multivariate fish distribution, univariate analysis revealed variation in occurrence and abundance of some species was associated with water temperature gradients created by spring outflows on a seasonal basis. Based on the results of this study, taxa generally recognized as spring-associated species (i.e., *A. mexicanus*, *N. amabilis*, *C. proserpina*, *D. argentosa*, and *E. grahami*) moved into spring outflow habitats during summer and winter when mean river temperature was greater than or less than spring water temperature. Seeking thermal refugia is a common behavior of fishes during seasonal ambient temperature extremes (i.e., winter and summer) for warm water fishes (Peterson and Rabeni, 1996; Power et al., 1999). However, only spring-associated fishes moved into spring outflow habitats under the conditions observed during this study period. Consequently, parapatric assemblages were detected between most of the generally recognized spring-associated species and riverine species. Parapatric distribution in fishes has been described elsewhere in which two species shared a common boundary, but maintained two adjacent distributions (Taylor and Lienesch, 1996). Exact mechanisms for observed parapatric assemblages are often difficult to isolate, but are believed to be a form of competition or predator avoidance (Ingersoll and Claussen, 1984), increased physiological advantages (Ohlberger et al., 2008), and increased foraging efficiency (Persson, 1984).

Surprisingly, occurrence of the federally threatened *D. diaboli*, a species listed as a spring-associate (CONABIO, 1997; USFWS, 1999), was not associated with spring outflows or constant temperature. Instead, *D. diaboli* was associated with moderate to greater depths of vegetated runs to backwater habitats, even in areas of extreme temperature. These findings conflict with previous reports of *D. diaboli* and other species of *Dionda* known to inhabit shallow depths and swifter currents, often restricted to areas near spring runs (Garrett et al., 1992; Schonhuth et al., 2008). Additionally, *D. diaboli* were observed in the upper reach of the Devils River, an area that frequently experiences dewatering and causes local extirpations of *D. diaboli* and other Devils River fishes to occur (Garrett et al., 1992). Ample precipitation in the drainage prior to the start of this study provided sufficient alluvial aquifer discharge. Consequently, *D. diaboli* and other spring-associated and riverine species dispersed upstream into areas currently considered no longer suitable (USFWS, 2005). Recolonization into areas previously without wetted areas demonstrates dispersion capabilities of both spring-associated and riverine species and is consistent with season-dependent distributions (Jackson et al., 2001). Specifically,

spring-associated species will move back and forth from spring outflows over a distance of at least several kilometers.

Species composition was similar to previous studies on the Devils River (Harrell, 1978; Robertson and Winemiller, 2003) with only slight differences in species occurrence and abundance ranks. Among studies, six species (*D. argentosa*, *N. amabilis*, *Gambusia* spp., *A. mexicanus*, *C. proserpina*, and *C. venusta*) remained dominant in the Devils River. Only four species previously reported (i.e., *C. eximius*, *Ameiurus melas*, *Aplodinotus grunniens*, and *Morone chrysops*; Valdes-Cantu and Winemiller, 1997) were not observed in this study, likely attributable to different sampling sites or this study's limited sampling technique (i.e., Seining generally targets small-bodied species and is depth limited). Relative abundance of *D. diaboli* was notably higher in this study compared to recent studies (Robertson and Winemiller, 2003) but closely resembled Harrell's (1978) findings.

Karst streams have experienced general declines in base flows as a result of lowering groundwater levels caused by human groundwater extraction (Bowles and Arsuffi, 1993). Such pumping has become increasingly prevalent due to human populations growth in areas adjacent to karst aquifers. Currently, the Devils River is without extensive anthropogenic alterations, but increasing pressure for groundwater extraction from the Edwards Aquifer might threaten the future of the Devils River fish assemblage, similar to other streams altered by groundwater extraction (Mercado-Silva et al., 2006). This study demonstrated spring flows serve as refugia for spring-associated species during winter and summer months and maintain environmentally variable areas downstream for riverine species, which collectively support a diverse fish assemblage. Reduced spring flow in the Devils River and other karst spring-supported streams and rivers throughout the Edwards Plateau and Trans-Pecos regions would decrease refugia areas, number of riffle and run habitats with shallow depths and swift current velocities, increase pool habitats, and promote habitats more susceptible to ambient temperature heating and cooling.

Acknowledgments

Appendix. Supplementary data

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2011.08.013.

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