

FISH ASSEMBLAGE STRUCTURE AND ASSOCIATIONS  
WITH ENVIRONMENTAL CONDITIONS IN A  
TEXAS SPRING – FED RIVER

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By

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**ABSTRACT**

FISH ASSEMBLAGE STRUCTURE AND ASSOCIATIONS WITH  
ENVIRONMENTAL CONDITIONS IN A  
TEXAS SPRING – FED RIVER

by

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Numerous spring systems in the Edwards Plateau and Trans-Pecos regions of Texas support parapatric 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 the Devils River, Texas allowed an opportunity to assess the influence of temperature and other variables (i.e., current velocity, depth, and substrate) on spatial and temporal patterns in the fish assemblage

Physical parameters (10.6%), site (4.9%), and season (1.6%) explained 19.6% (CCA,  $P < 0.01$ ) of the Devils River fish assemblage. Current velocity, depth, and vegetation were among the strongest factors explaining fish segregation. *Astyanax mexicanus* and *Cyprinella proserpina* were generally found in riffle habitats, *Etheostoma grahami*, and *Notropis amabilis* were found in runs with moderate current velocities and depths, and *Micropterus salmoides*, *Lepomis macrochirus*, and *Dionda diaboli* were more associated with deeper, vegetated pools. Water temperature influenced seasonal movement of spring associated species (i.e., *A. mexicanus*, *N. amabilis*, *C. Proserpina*, *Dionda argentosa*, and *E. graham*) into spring outflow habitats during summer and winter and resulted in a segregated assemblage. Surprisingly, the abundance and distribution of the federally threatened *Dionda diaboli*, a species listed as a spring-associate, did not correlate with spring outflows and was present throughout the Devils River. This study suggests spring flow (i.e., current velocity and depth) and constant water temperature are segregating factors and important for maintaining parapatric assemblages.

## CHAPTER 1

### INTRODUCTION

Spring-fed streams in the Edwards Plateau and Trans-Pecos regions of southwestern USA and northern Mexico are regional diversity hotspots (Myer 2000), supporting a rich concentration of endemic aquatic fauna (Mathews and Edwards 1992; Bowles and Arsuffi 1993; Valdez-Cantu and Winemiller 1997; Edwards et. al 2002) and providing refugia for riverine fauna (Rhodes and Hubbs 1992). High rates of endemism are attributed to zoogeographical isolation of these spring-fed systems and to relatively stable abiotic environments because of consistency in groundwater discharge (Warren and Burr 1994; Hubbs 1995). Endemic taxa can be extremely abundant but have limited distributions, making them susceptible to population declines and extirpations from instream modifications, groundwater depletions, and land use alterations (Brune 1981; Williams et al. 1989; Elvira 1995; Moyle 1995; Hubbs 1995, 2001; Sharp et al. 2003). Among the total fish fauna associated with spring-fed streams in the Edwards Plateau and Trans-Pecos region of Texas, 30% are either extinct (i.e., Amistad gambusia *Gambusia amistadensis*, San Marcos gambusia *Gambusia georgei*, and Maravillas red shiner *Cyprinella lutrensis blairi*) or imperiled (i.e., 18, Miller et al. 1989; Hubbs et al. 2008).

Among larger spring systems, groundwater discharge maintains perennial stream flows at constant water temperature, turbidity, conductivity, pH, and other physical and chemical parameters up to 16 km downstream (Groeger et al. 1997; Watson 2006). Groundwater discharge becomes less of an influence on the stream environment when

ambient temperatures or convergence with surface runoff (i.e., confluence with mainstem river) creates a more variable environment. Contiguous but different abiotic environments typically support two distinct fish assemblages (Gelwick 1990; Kelsey 1997; Garrett et al. 2004; Watson 2006). Endemic fishes generally are restricted to the environmentally stable portion of the stream, whereas fishes with more ubiquitous distributions generally are found in the more environmentally variable portion of the stream (Hubbs 1995). Biotic (e.g., competition, fecundity) and abiotic factors (e.g., temperature, salinity, or stream gradient) are hypothesized to regulate segregation between parapatric taxa and assemblages (Magnuson et al. 1979; Ingersoll and Claussen 1984; Taylor and Leinesch 1996; Gido et al. 1999; Garrett et al. 2004; Quist et al. 2004; de la Hoz Franco and Budy 2005). Among abiotic factors, constant temperature is most often identified as the explanatory variable for segregation (Gehlbach et al. 1978; Bonner et al. 1998). However, these conclusions were based on studies completed on systems with a single spring source and thus were ineffective in distinguishing temperature from headwater influence (Whiteside and McNatt 1972) on assemblage and species segregation. Consequently, a multiple spring source system along a stream course is needed to adequately assess the influence of water temperature on fish segregation.

Purpose of this study was to quantify parapatric fish assemblages within the Devils River of south Texas. The Devils River is a multiple spring system in the Edwards Plateau region with at least 13 known instream and near shore springs contributing discharge ranging from  $<0.1$  to  $>0.75$  cms along a 64-km course of the river (Harrell 1978; Brune 1981). Typical of many Edwards Plateau and Trans Pecos spring systems, the Devils River supports several Rio Grande basin endemic fishes of

conservation concern, including *Cyprinella proserpina*, *Dionda argentosa*, *Dionda diaboli*, *Ictalurus lupus*, *Cyprinodon eximius*, and *Etheostoma grahami*, and fishes generally recognized as spring-associated fishes, including *C. proserpina*, *D. argentosa*, *D. diaboli*, *Notropis amabilis*, *Astyanax mexicanus*, *I. lupus*, *C. eximius*, and *E. grahami* (Thomas et al. 2007; Hubbs et al. 2008). Objectives of this study were to describe fish assemblage occurrence and abundance among multiple sites within the Devils River, to assess multivariate influence of season, site location, and habitat parameters on species occurrence and abundance, and to quantify univariate associations, especially water temperature, with fish distributions across time and space. Spring systems like the Devils River are threatened by groundwater depletions and instream flow alterations with little information on how changes in water quantity and quality will affect the fish assemblage. Quantification of Devils River fish assemblage in relation to spring sources and other habitat variables through time and space will allow a better understanding of how anthropogenic alterations will impact the regionally diverse ichthyofauna.

## MATERIAL AND METHODS

The Devils River originates in northwest Sutton County, Texas and flows southeast through Val Verde County and empties into Amistad Reservoir near Del Rio, Texas. The watershed is within the Edwards Plateau region of Texas and drains approximately 10,000 km<sup>2</sup>. Mean annual precipitation is 53 cm, with greatest rainfalls occurring during the months of September and May. Upper reach of the Devils River generally has ephemeral and intermittent stream flow supported by localized and shallow alluvial aquifers (Barker et al. 1994). Lower reach of the Devils River extends 64 km

from Pecan Springs to Amistad Reservoir with perennial base flow from the Edwards-Trinity Aquifer (Brune 1981). Annual median discharge within the lower Devils River is  $8.7 \text{ m}^3/\text{s}$  (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 sand, cobble, and bedrock substrates.

Sites 1 through 3 (approximately  $30^\circ 03'13.54''\text{N}$ ,  $101^\circ 9'5.57''\text{W}$ ) were located in the upper reach of the Devils River (Fig 1). Site 1 was relocated to Site 2 in February 2008 and to Site 3 in June 2008 because of stream drying. Sites 4 through 6 (Site 4,  $29^\circ 57'52.66''\text{N}$ ,  $101^\circ 08'49.34''\text{W}$ ; Site 5,  $29^\circ 54'14.41''\text{N}$ ,  $101^\circ 00'37.68''\text{W}$ ; Site 6,  $29^\circ 53'58.95''\text{N}$ ,  $100^\circ 59'52.63''\text{W}$ ) were located in the lower reach of the Devils River, upstream from Dolan Falls. Although base flows were supported by spring discharge, Sites 1 through 4 did not have immediate spring discharge within at least a 2 km of each site. Sites 5 and 6 contained areas with spring discharge.

Seine hauls and habitat measurements were taken along multiple transects, perpendicular to the shoreline, at each site (Simonson et al. 1994; Ostrand and Wilde 2002) from September 2007 through October 2008. Seine hauls proceeded in a downstream to upstream direction with transects spaced 20 to 80 m apart, depending on stream width. Seine hauls were spaced along each transect an adequate distance 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 x 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 kick were used in shallow and swift water run and riffle habitats. A minimum of 25 seine hauls were made

at each site with 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 Tricaine methanesulfonate (MS-222), and preserved in 10% formalin; otherwise, fish were released.

Current velocity (m/s), depth (m), water temperature (°C), substrate type (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. Percent substrate, vegetation cover, and woody debris were visually estimated within each seine haul. Specific conductance ( $\mu\text{S}/\text{cm}$ ), dissolved oxygen (mg/l), and pH were measured with YSI Model 85 at each site and sampling date.

Species relative abundance (%), relative abundance of spring associated and riverine species (%), taxa richness (S), diversity (H), and evenness ( $E_s$ ) were calculated for each site. Fishes generally recognized as spring associated species were *Cyprinella proserpina*, *Dionda argentosa*, *Dionda diaboli*, *Notropis amabilis*, *Astyanax mexicanus*, and *Etheostoma grahami*. Remaining fishes were collectively referred to as riverine species. Diversity was calculated using the Shannon –Wiener index ( $\log_e$  base), and evenness was calculated using Shannon evenness ( $E_s = H/H_{\text{max}}$ ). Species of the genera *Gambusia* (i.e., species *G. geiseri* and *G. speciosa*) and *Ictalurid* (i.e., species *I. lupus* and *I. punctatus*) were grouped due to difficulty in identifying morphologically

distinguishing features in the field (Rauchenberger 1989; Kelsch and Hendricks 1990; Bean et al., in review). Principal components analysis (PCA; Canoco 4.5) was performed to describe 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 loadings were plotted to illustrate habitat present at each site. Canonical correspondence analysis (CCA; Canoco 4.5) was used to analyze fish 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 ( $\alpha = 0.05$ ) of each effect.

Univariate assessments were used to further describe current velocity, depth, substrate, vegetative cover, and temperature associations for the most abundant species in the Devils River, excluding *Gambusia*. Habitat suitability estimates for each species was 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 temperature ( $^{\circ}\text{C}$ ) and standard deviation were calculated for the 12 most abundant Devils River fishes at sites without direct spring outflows (Site 1-4) and sites with direct spring outflows (Site 5-6). Temperature selection for the 12 most abundant Devils River fishes was described by plotting mean deviation in degrees ( $^{\circ}\text{C}$ ) from mean spring temperature versus mean deviation in degrees from mean river temperature and measured temperature among seine hauls (%). A t-test was used to determine significant differences in deviation ( $^{\circ}\text{C}$ ) from mean river temperature between transitional seasons (i.e., fall and spring) and extreme

seasons (i.e., winter and summer) for spring-associated species, riverine species, and *Dionda diaobli* for direct spring outflow sites (Site 5-6).

## RESULTS

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. Upper reach consisted of shallow to moderate depths (0.16 – 1.3 m) and slow current velocities (0.0 – 0.35 m/s) (Table 1). 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%; *Potamogeton* and *Justicia*) or filamentous algae (12%). 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) or bedrock (72%) and cobble (15%) substrates (Site 5 and 6). Submergent vegetation and algae coverage ranged from 25% (Sites 5 and 6) to 75% (Site 4), and consisted of *Chara*, *Potamogeton*, *Equisetum*, and *Justicia*. Water quality parameters in both reaches did not vary widely through time (range for conductivity: 447 - 488  $\mu\text{S}/\text{cm}$ ; 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

positive loadings for PC axis I were bedrock (1.73), algal cover (1.02), and spring outflows (0.60). Strongest negative loadings were vegetation (-2.42), silt (-2.40), and current velocity (-1.17). Axis II explained 11% of the variation and represented a geomorphic unit, temperature, and depth gradient. Strongest positive loadings on PC axis II were riffle (1.59), pool (1.56), and gravel (1.40). Strongest negative loadings were run (-2.01), bedrock (-1.52), and temperature (-1.32). Sites 1-3 (mean sample scores) 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 2). Cyprinidae was the most abundant family (69%), followed by Poeciliidae (13%), and Characidae (12%). Most abundant species were *Dionda argentosa* (30%) *Notropis amabilis* (17%), *Gambusia* (13%), *Astyanax mexicanus* (12%), *Cyprinella proserpina* (6.2%), and *Dionda 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* (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 Site 4-6 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.

### *Multivariate associations*

Physical parameters, site, and season explained 19.6% ( $P < 0.01$ ) of the variability in Devils River fish assemblage (Fig 3). Pure effects of environmental 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) among physical parameters, site, and season accounted for 2.5% variation. Physical parameters and site strongly associated with CCA axis I 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*, *Gambusia* sp., and *A. mexicanus* were more abundant at lower reach sites and riffle or spring outflow habitats. *Dionda argentosa* and *Cyprinus carpio* were found among available geomorphic units and sites but were most abundant over gravel substrate at Sites 1-3. *Notropis stramineus* and *Cyprinella venusta* were found among available geomorphic units but most abundant at Site 5. Three spring-associated species, *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* sp., *Micropterus* sp., and *Cichlasoma cyanoguttatum* were most abundant in pool and backwater habitats at Sites 4 and 5. A significant season effect was attributed to the capture of juvenile *Lepomis* and *Micropterus* species only during spring and summer.

### *Univariate associations*

Distribution of available temperatures ranged from 0 to 6.7°C deviations from mean spring water temperatures and 0 to 3.6°C deviations from available mean riverine water temperatures at sites without direct spring outflows (Sites 1 - 4) and at sites with direct spring outflows (Sites 5 & 6) (Fig 4). Among abundant species at sites without direct spring outflows, mean water temperature inhabited by species ranged from 0.85 to 3.36°C deviations of mean riverine water temperature and from 1.78 to 5.39°C deviations of mean spring water temperature (Table 3). In general, water temperature distribution of spring-associated species overlapped that of the riverine-associated species (Fig 4a). Among the abundant species at sites with direct spring outflows, mean water temperature inhabited by species ranged from 1.84 to 3.07°C deviations of mean riverine water temperature and from 0.67 to 4.24°C deviations of mean spring water temperature. Within the lower reach sites (5 & 6), ambient heating and cooling of the river and spring outflows caused larger gradients in available temperatures. Distribution of spring-associated species did not overlap with the distribution of riverine-associated species, except for one species (Fig 4b). Mean water temperature inhabited by *D. diaboli* was similar to that of riverine-associated species.

Seasonal associations with water temperature differed ( $P = 0.04$ ) among the spring-associated species but not the riverine-associated species ( $P = 0.48$ ) at Sites 5 and 6 (Fig 5). During the Fall and Spring seasons, spring-associated species were taken at water temperatures that deviated on average 0.94°C from mean water temperature. During riverine water temperature extremes in the Winter and Summer seasons, spring-associated species were taken at water temperatures that deviated on average 1.78°C from

mean water temperature, indicating that spring-associated species were seeking thermal refuge (warmer or cooler) temperatures during the extreme water temperatures. In contrast, riverine-associated species were within  $-1.27^{\circ}\text{C}$  deviations of mean river temperature independent of seasonal. Likewise, *D. diaboli* was within  $-2.18^{\circ}\text{C}$  deviations of mean river temperature during water temperature extremes, attributed primarily with the collection 37% of *D. diaboli* captured during the summer with water temperatures ranging from  $21.7$  to  $30.6^{\circ}\text{C}$ .

Distribution of available current velocities ranged from  $0$  to  $1.54$  m/s among sites. Species with greatest relative abundances in lower current velocities (i.e.,  $0 - 0.2$  m/s, 76% of total available) included *C. venusta* (89% relative abundance), *D. argentosa* (94%), *D. diaboli* (94%), and *N. amabilis* (94%); whereas, species with greater relative abundances in higher current velocities (i.e.,  $0.21 - 1.54$  m/s; 24% of total available) included *C. proserpina* (31%), *E. grahami* (43%) and *A. mexicanus* (55%) (Fig 6). Species with relative abundances proportional to current velocity availability included *N. stramineus* and *C. cyanoguttatum*. Distribution of available depths ranged from  $0.1$  to  $1.52$  m among sites. Species with greater relative abundances in  $0.1 - 0.3$  m (i.e., 37% of total available) included *C. venusta* (44%), *D. argentosa* (55%), and *C. proserpina* (80%); whereas, species with greater relative abundances in deeper depths (i.e.,  $>0.3\text{m}$ ; 63% of total available) included *N. amabilis* (74%), *E. grahami* (77%), and *D. diaboli* (90%) (Fig 7). Species with relative abundances proportional to depth availability included *A. mexicanus*, *N. stramineus*, and *C. cyanoguttatum*. Among substrates, species more abundant over silt substrate (29% of total available) included *C. cyanoguttatum* (37%), *E. grahami* (41%), and *D. diaboli* (62%), whereas species more abundant over

bedrock substrate (34% of total area) were *N. amabilis* (49%), *C. proserpina* (60%), *N. stramineus* (62%), and *A. mexicanus* (63%) (Fig 8). *Dionda argentosa* was the only species with a higher relative abundance (48%) over gravel and cobble substrates (36% of total available). Species with higher relative abundances relative to available vegetative cover (39%) included *E. grahami* (67%), *C. cyanoguttatum* (69%), and *D. diaboli* (74%), whereas species with lower relative abundances associated with vegetative cover included *A. mexicanus* (30%), *C. venusta* (30%), *C. proserpina* (17%), and *N. stramineus* (13%).

## DISCUSSION

Devils River fishes demonstrated typical patterns in habitat use and longitudinal distribution (Matthews and Styron 1981; Taylor et al. 2006; Lapointe et al. 2007; Buisson et al. 2008). Current velocity, depth, and vegetation explained the largest percent of the variation in fish occurrence and distribution. *Astyanax 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 *Micropterus salmoides*, *Lepomis macrochirus*, and *D. diaboli* were more associated with deeper, vegetated pools. Species segregation among 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); despite previous suggestions on the lack of species segregation in the Devils River (Harrell 1978; Ross 1985). Occurrences in species segregation are attributed to a numerous factors, including predator avoidance patterns, swimming speed capabilities, and differences in feeding behavior (Power 1984; Harvey and Stewart 2001; Leavy and

Bonner 2009). A few Devils River fishes demonstrated distributional patterns along a longitudinal gradient. Upstream sites (Sites 1 – 4) contained more *D. argentosa*, *D. diaboli*, and Ictalurids than downstream sites. Downstream sites (Sites 5 & 6) contained more *C. venusta*, *N. stramineus*, *A. mexicanus*, *C. cyanoguttatum*, and *Oreochromis aurea*. Consequently, species diversity and evenness increased longitudinally along the Devils River, typical among river systems (Horwitz 1978; Belliard et al. 1997; Ibanez et al. 2007) and attributed to increased habitat heterogeneity and stability (Jackson et al. 2001).

Although water temperature was not identified as a major influence in multivariate fish assemblage distribution, seasonal occurrence and abundance of some fishes were associated with water temperature gradients created by spring outflows. Based on the results of this study, taxa generally recognized as spring associated fishes (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. Fish seeking thermal refugia is common during seasonal ambient temperature extremes (i.e., winter and summer) for warm water fishes (Peterson and Rabeni 1996; Magalhaes et al. 2002). However, results of this study suggested that only spring associated fishes moved into spring outflow habitats under the conditions observed during the study period. Consequently, parapatric assemblages were detected between most of the generally recognized spring associated fishes and riverine fishes. Season-dependent parapatric distributions are reported elsewhere (Jackson et al. 2001). Mechanisms for the observed segregation and movement are unclear, but attributed to competition or predator avoidance (Ingersoll and

Clausen 1984), physiological advantages (Ohlberger et al. 2008), and increased foraging efficiency (Persson 1984).

Surprisingly, occurrence of the federally threatened *D. diaboli* (CANABIO 1997; USFWS 1999), a species listed as a spring-associate, 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 (Hubbs and Garrett 1990; Mayden et al. 1992; Schonhuth et al. 2008). Additionally, *D. diaboli* were taken in the upper reach of the Devils River, an area where *D. diaboli* were previously reported as extirpated (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 fishes 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 fishes and is consistent with season-dependent parapatric distributions (Jackson et al. 2001). Specifically spring-associated fishes 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; Garrett 1992; Valdez – Cantu and Winemiller 1998; Robertson and Winemiller 2001) with only slight differences in species occurrence and abundance ranks. Among studies, six species (*D. argentosa*, *N. amabilis*, *Gambusia* sp., *A. mexicanus*, *C.*

*proserpina*, and *C. venusta*) remained dominant in the Devils River. Only four species previously reported (i.e., *Cyprinodon eximius*, *Ameiurus melas*, *Aplodinotus grunniens*, and *Morone chrysops*) (Valez-Cantu and Winemiller 1997) were not observed in this study and is likely attributable to different sampling sites or technique. Relative abundance of *D. diaboli* was notably higher in this study than more recent studies (Valdez – Cantu and Winemiller 1997; Robertson and Winemiller 2001), and closely resembled Harrell's (1978) findings.

Lack of fish assemblage changes in the Devils River during a 30 year period differs from other similar size streams in the western gulf slope and Rio Grande drainages, which have experienced substantial shifts in fish assemblage structure (Hubbs et al. 1997; Calamusso et al. 2005; Runyan 2007). In impacted streams and rivers, habitat specialists (e.g., native and endemic species) declined in abundance, whereas habitat generalists (e.g., cosmopolitan species and exotic species) increased in abundance and distribution. Habitat loss and degradation attributed to dam construction and dewatering are among the leading causes for this observed trend (Rinne et al. 2005). Currently, the Devils River is without extensive anthropogenic alterations, but increasing pressure for groundwater extraction might threaten the future of the Devils River fish assemblage, similar to other areas altered by groundwater extraction (Mercado-Silva et al. 2006). Reductions in base flow and water quality result in declines of native fishes and increases in taxa tolerant in more variable water temperatures and other water quality parameters (Mercado-Silva et al. 2006). Based on the results of this study, reduced base flow in the Devils River and other spring-supported streams and rivers throughout the Edwards Plateau would likely decrease the 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. Consequently, occurrence and abundance of at least five Rio Grande endemic fishes could become restricted in the Devils River.

Table 1. Mean ( $\pm$ SD) physical parameters across sites for Devils River during September 2007 – October 2008 collection.

	Site 1-3	Site 4	Site 5	Site 6
	<u>Mean</u>	<u>Mean</u>	<u>Mean</u>	<u>Mean</u>
Depth (m)	0.4 (0.3)	0.5 (0.3)	0.5 (0.2)	0.5 (0.3)
Current Velocity (m/s)	0.1 (0.2)	0.3 (0.3)	0.1 (0.1)	0.1 (0.2)
Temperature (°C)	20.9(5.80)	21.8 (3.7)	22.0 (5.4)	23.4 (2.9)
Substrate Type (%)				
Silt	17.0	65.1	12.7	7.8
Sand	0.2	2.6	0.1	0.1
Gravel	30.2	13.2	1.7	1.1
Cobble	47.3	17.2	25.4	4.2
Boulder	3.2	1.1	0.3	1.3
Bedrock	2.0	0.2	57.4	85.1
Woody Debris	0.0	0.6	0.0	0.0
Aquatic vegetation (%)	15.4	75.4	25.3	24.9
Algal cover (%)	12.0	1.4	2.6	8.9

Table 2. Relative abundance (%), relative abundance of spring associated and river species (%), taxa richness, Shannon-Weiner diversity, and Shannon evenness of fishes collected from Devils River (September 2007 – October 2008).

Species	Site				
	Site 1-3	Site 4	Site 5	Site 6	Total
<i>Lepisosteus oculatus</i>	-	-	-	<0.1	<0.1
<i>Cyprinella proserpina</i> *	3.7	3.6	9.2	8.7	6.2
<i>Cyprinella venusta</i>	2.6	1.7	15.5	2.8	4.8
<i>Cyprinus carpio</i>	4.9	-	-	<0.1	1.7
<i>Dionda argentosa</i> *	50.6	29.9	11.8	18.0	30.3
<i>Dionda diaboli</i> *	3.4	12.7	4.6	2.7	5.1
<i>Dionda sp.</i> *	0.1	0.4	1.4	0.2	0.4
<i>Notropis amabilis</i> *	8.2	27.6	6.5	28	17.3
<i>Notropis stramineus</i>	<0.1	-	16.7	2.2	3.6
<i>Carpionodes carpio</i>	<0.1	-	-	-	<0.1
<i>Moxostoma congestum</i>	-	0.1	0.2	-	<0.1
<i>Astyanax mexicanus</i> *	5.1	14.7	15	17.7	12.3
<i>Ictalurid sp.</i> **	<0.1	0.6	<0.1	-	0.1
<i>Pylodictis olivaris</i>	-	<0.1	-	-	<0.1
<i>Gambusia sp.</i> ***	18.9	1.1	8.5	15.9	13
<i>Lepomis auritus</i>	0.2	1.2	0.8	0.2	0.5
<i>Lepomis cyanellus</i>	0.1	-	-	-	<0.1
<i>Lepomis macrochirus</i>	0.4	0.2	1.2	0.08	0.4
<i>Lepomis miniatus</i>	-	<0.1	<0.1	<0.1	<0.1
<i>Lepomis megalotis</i>	0.9	0.1	0.9	0.8	0.7
<i>Lepomis sp.</i>	0.1	-	0.1	<0.1	<0.1
<i>Micropterus dolomieu</i>	<0.1	<0.1	0.4	<0.1	0.1
<i>Micropterus salmoides</i>	0.2	0.7	0.5	0.1	0.3
<i>Etheostoma grahami</i> *	0.2	3.6	1.6	0.7	1.2
<i>Cichlasoma cyanoguttata</i>	0.3	1.5	4.8	1.1	1.6
<i>Oreochromis aurea</i>	-	-	<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 =	5,399	2,726	2,749	4,730	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	

\* Spring associated species

\*\* *Ictalurid sp* includes species of *I. lupus* and *I. punctatus*

\*\*\* *Gambusia sp* includes species of *G. geiseri* and *G. speciosa*

Table 3. Deviation (Abs °C ( $\pm$ SD)) from mean spring temperature and mean river temperature for spring associated and riverine species at non direct spring outflow sites and direct spring outflow sites from the Devils River (September 2007 – October 2008).

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

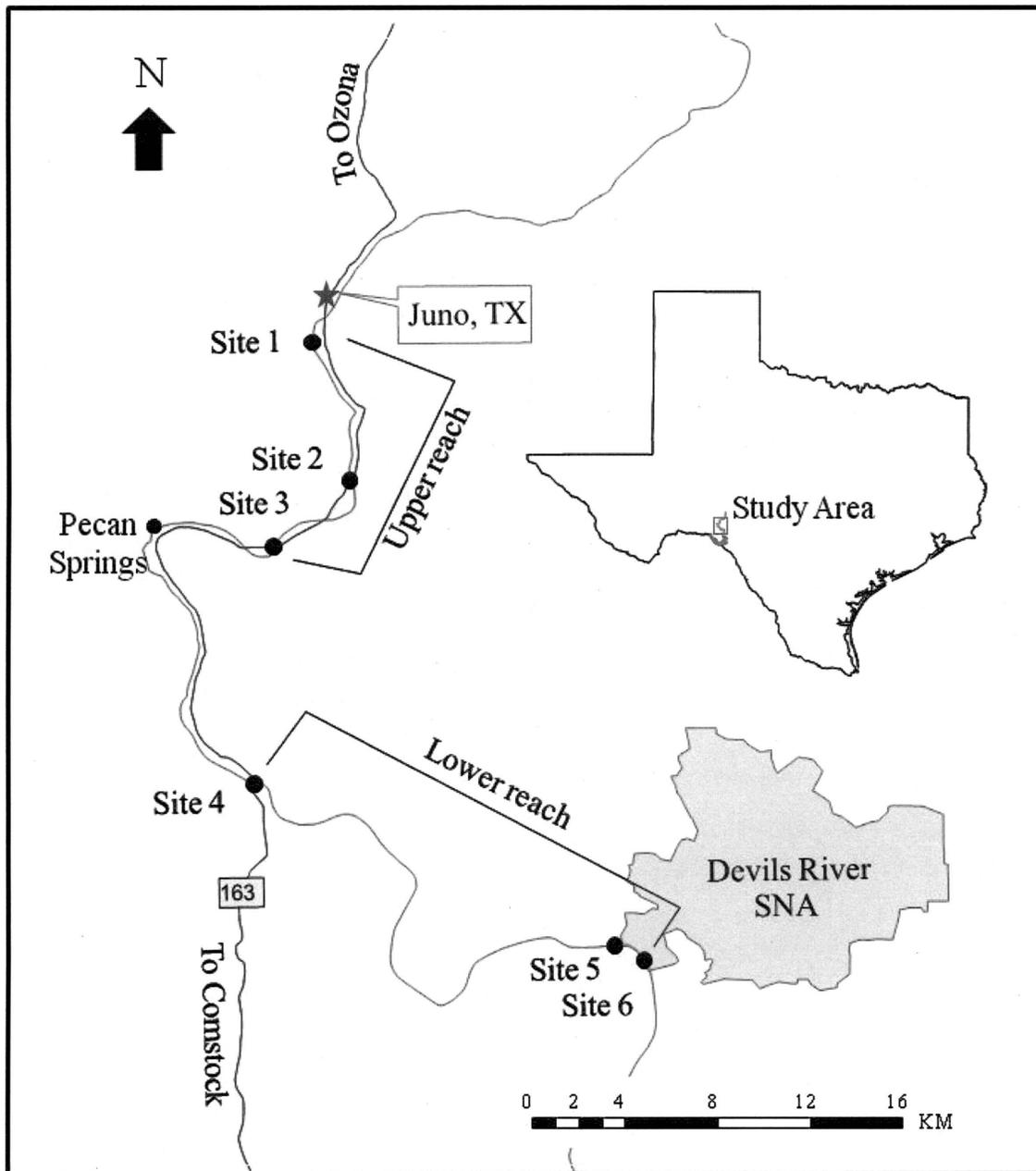


Figure 1. Site map of Devils River, Val Verde County, TX.

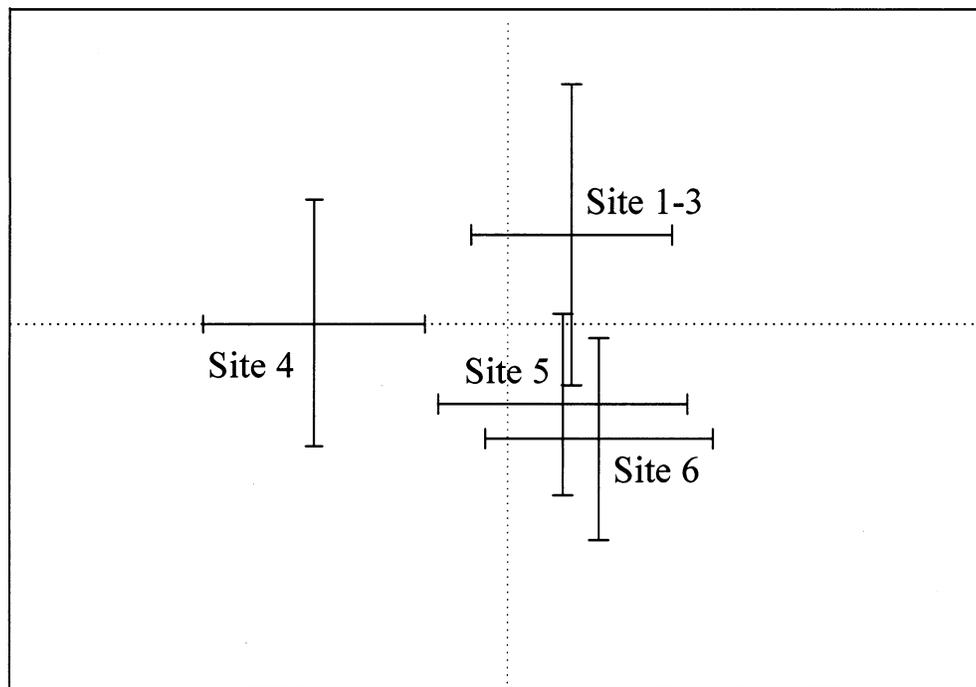
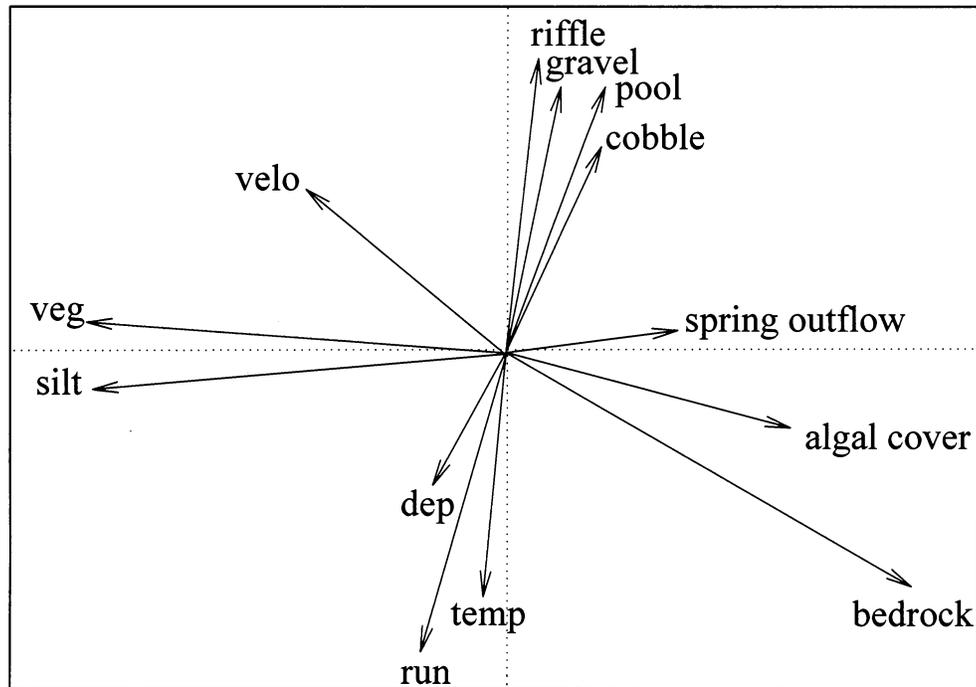


Figure 2. Principal component ordination plots for measured environmental parameters and general habitat characteristics from Devils River (September 2007 – October 2008).

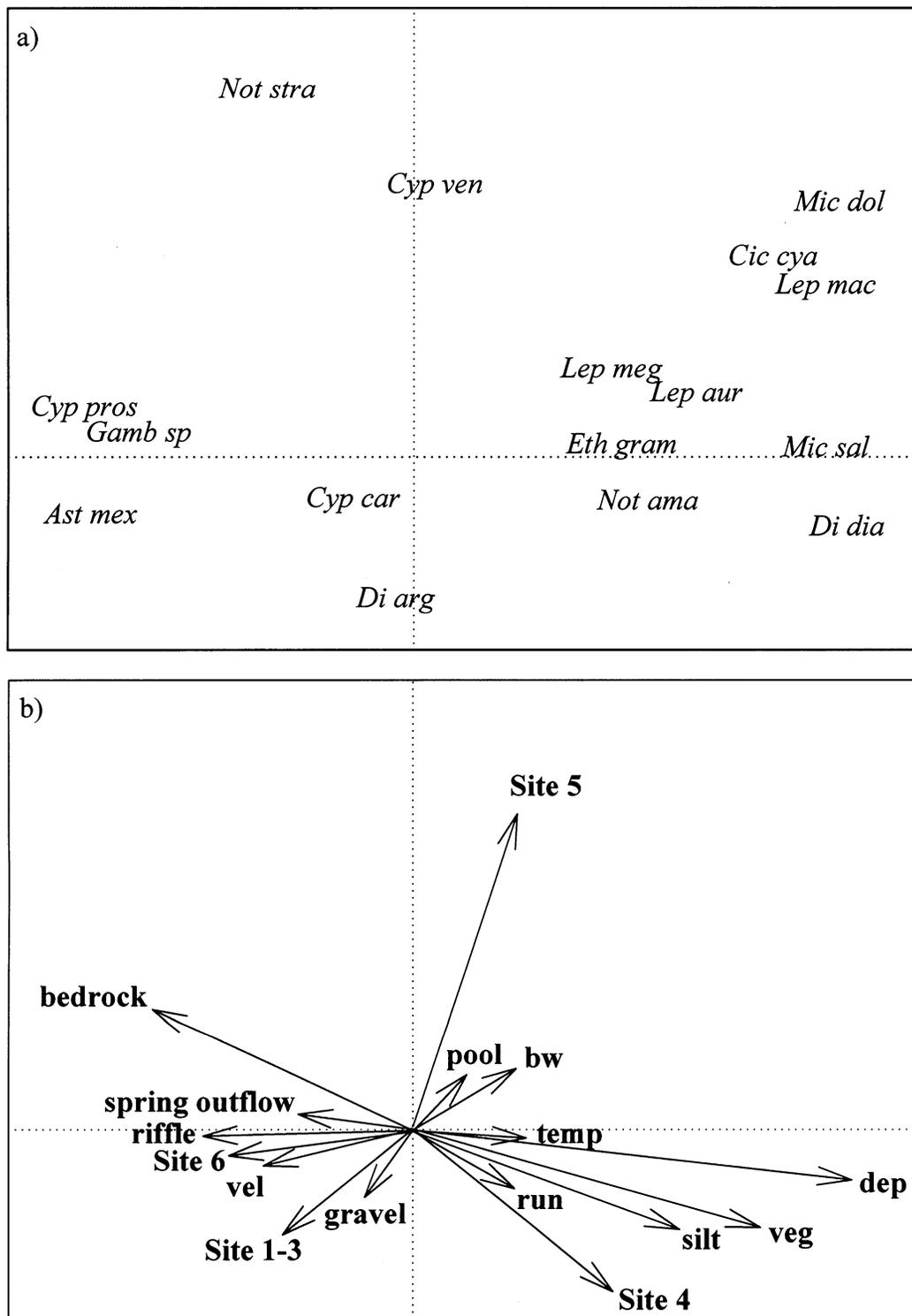


Figure 3. Canonical correspondence ordination plots for a) fishes and b) environmental parameters and sites from Devils River (September 2007 – October 2008).

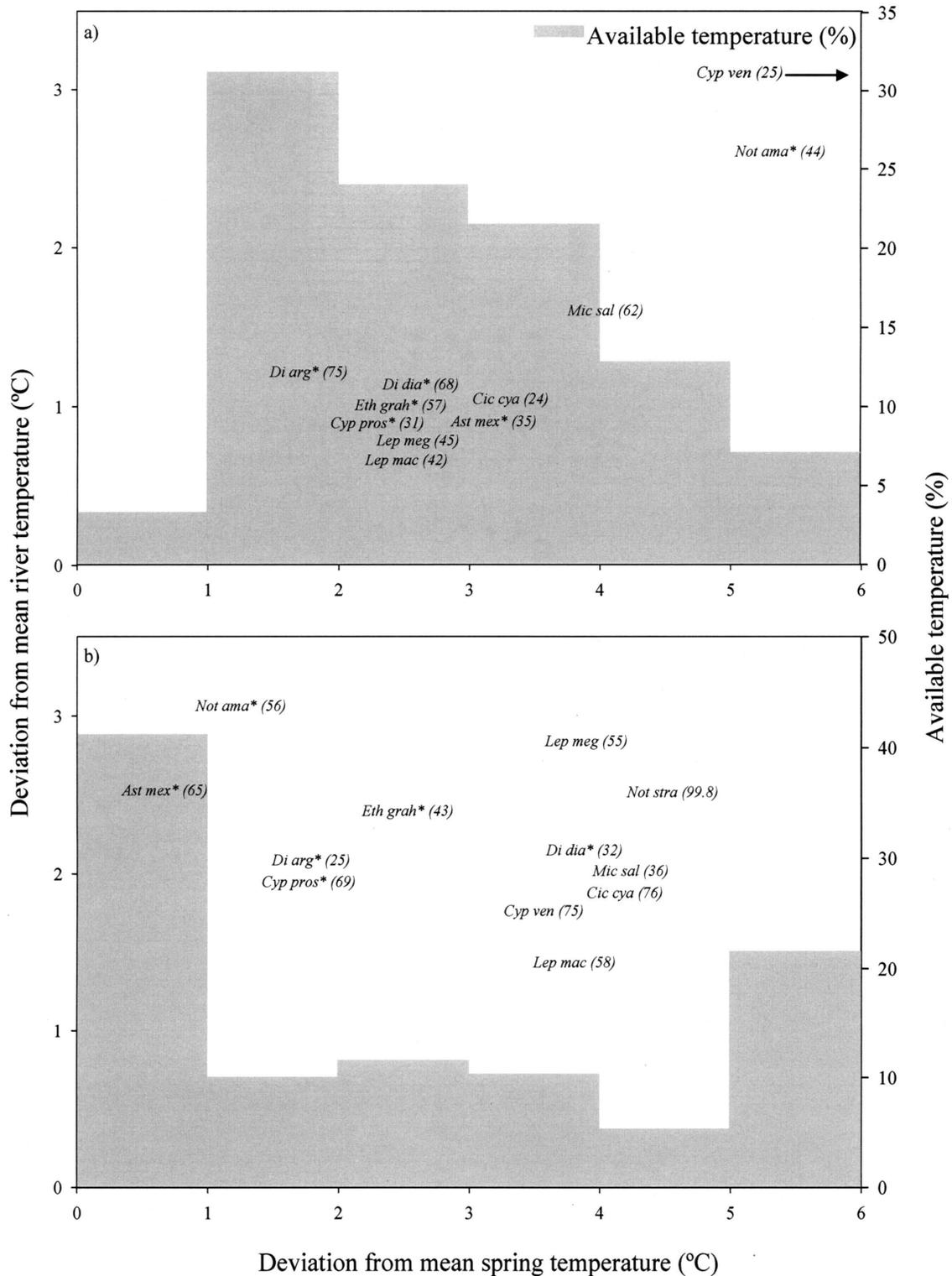


Figure 4. Mean deviation of spring associated species (\*) (Relative abundance) and six most abundant riverine species (Relative abundance) from mean spring temperature (°C) and mean river temperature (°C) at a) non-direct spring outflow sites and b) direct spring outflow sites from Devils River (September 2007 – October 2008).

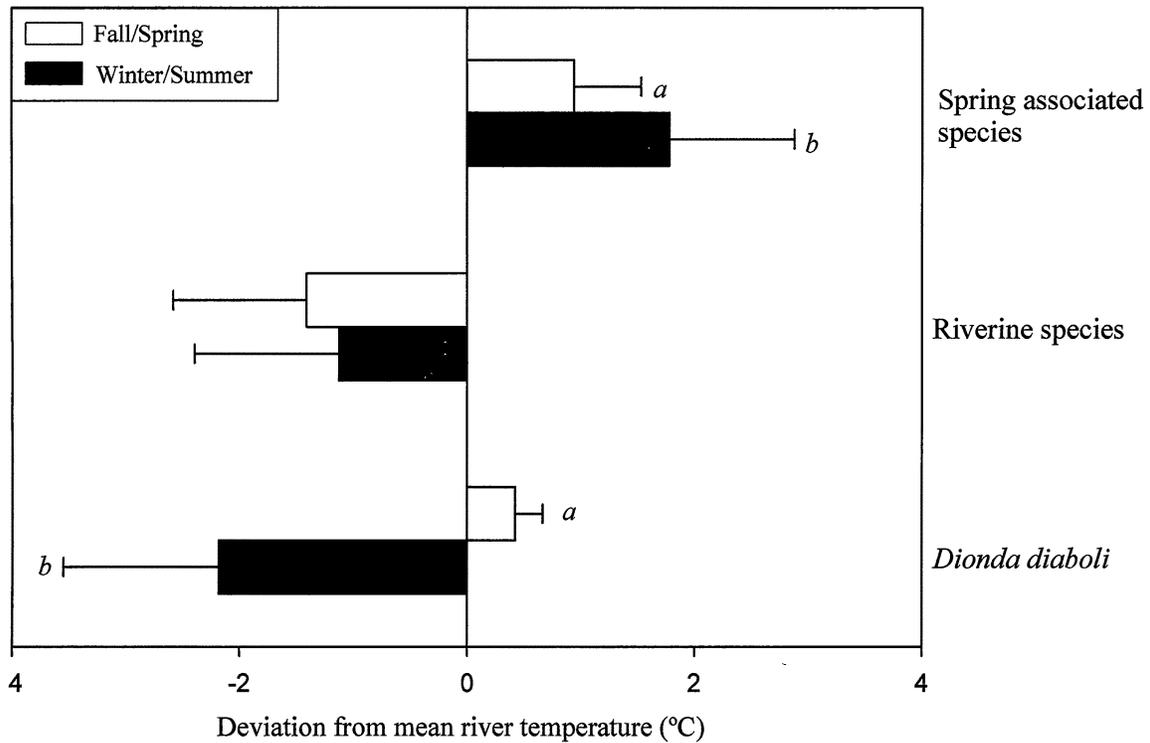


Figure 5. Mean deviation and standard deviation of spring associated species, six most abundant riverine species, and *Dionda diaboli* from mean river temperature (°C) for spring/fall and winter/summer in Devils River (September 2007 – October 2008).

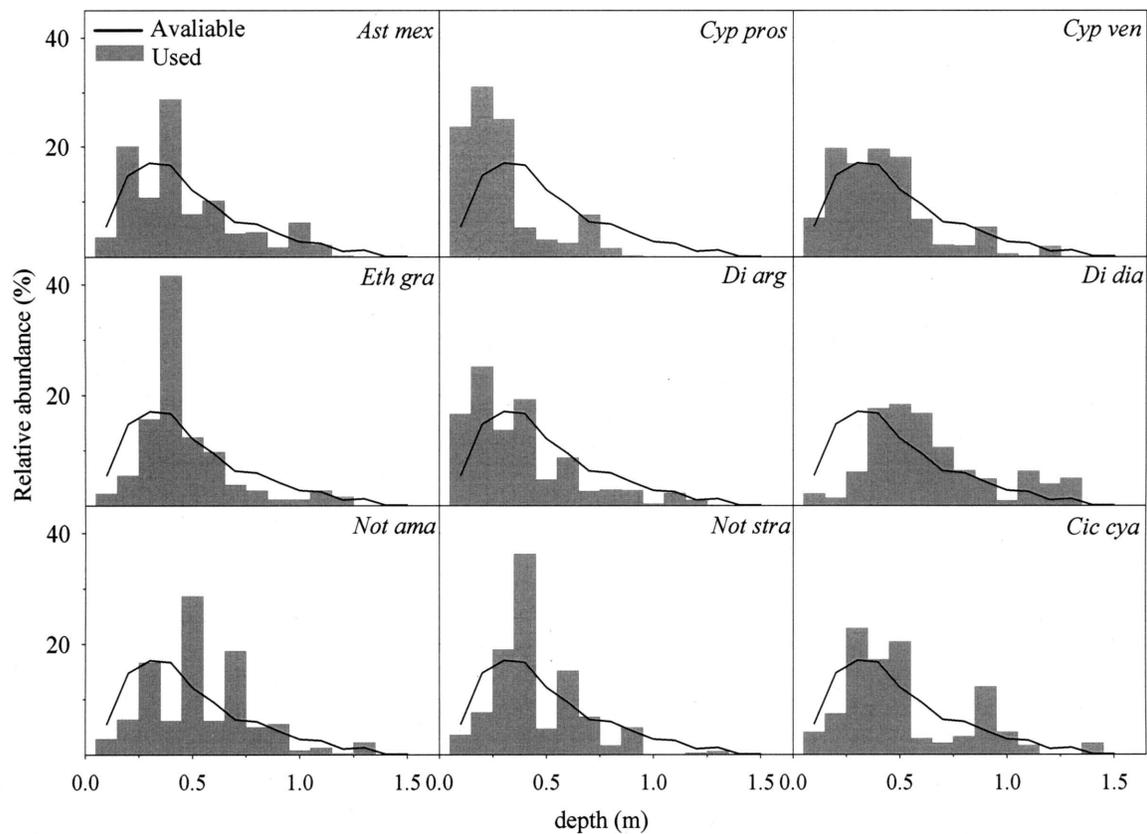


Figure 6. Available depth (%) and relative abundance (%) for the most abundant species from Devils River (September 2007 – October 2008).

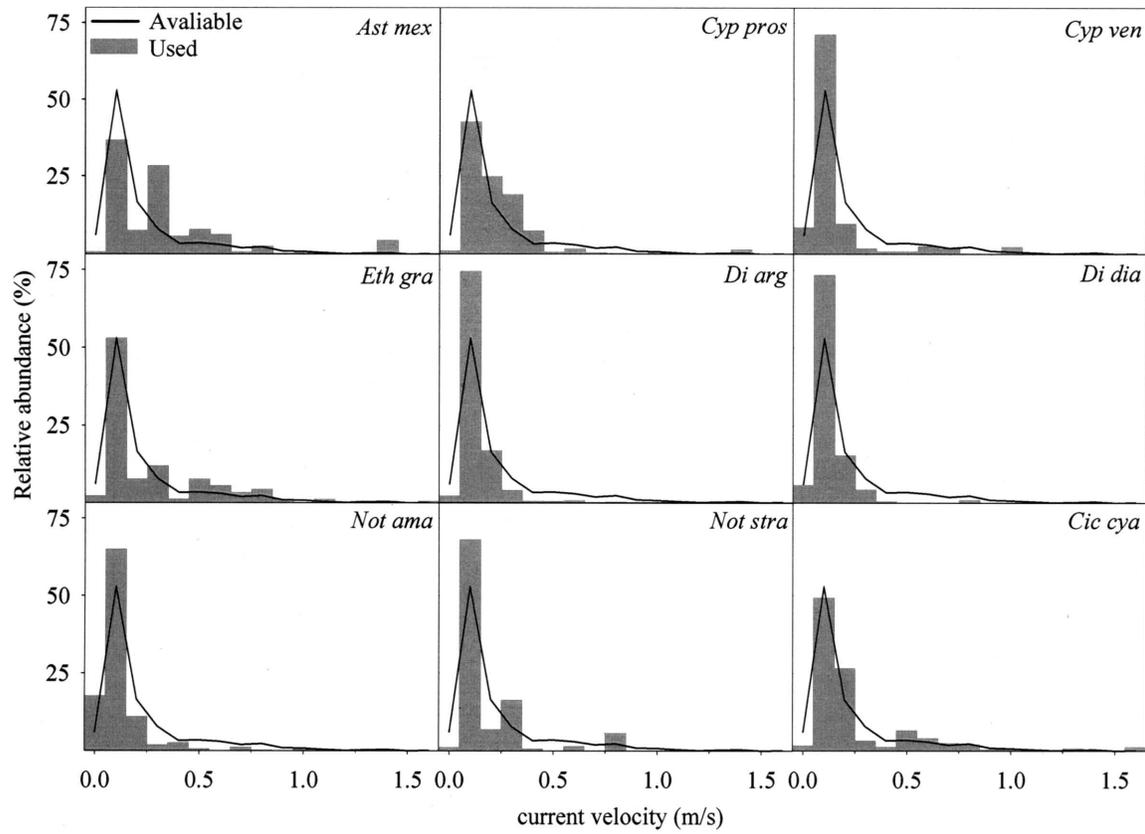


Figure 7. Available current velocity (%) and relative abundance (%) for the most abundant species from Devils River (September 2007 – October 2008).

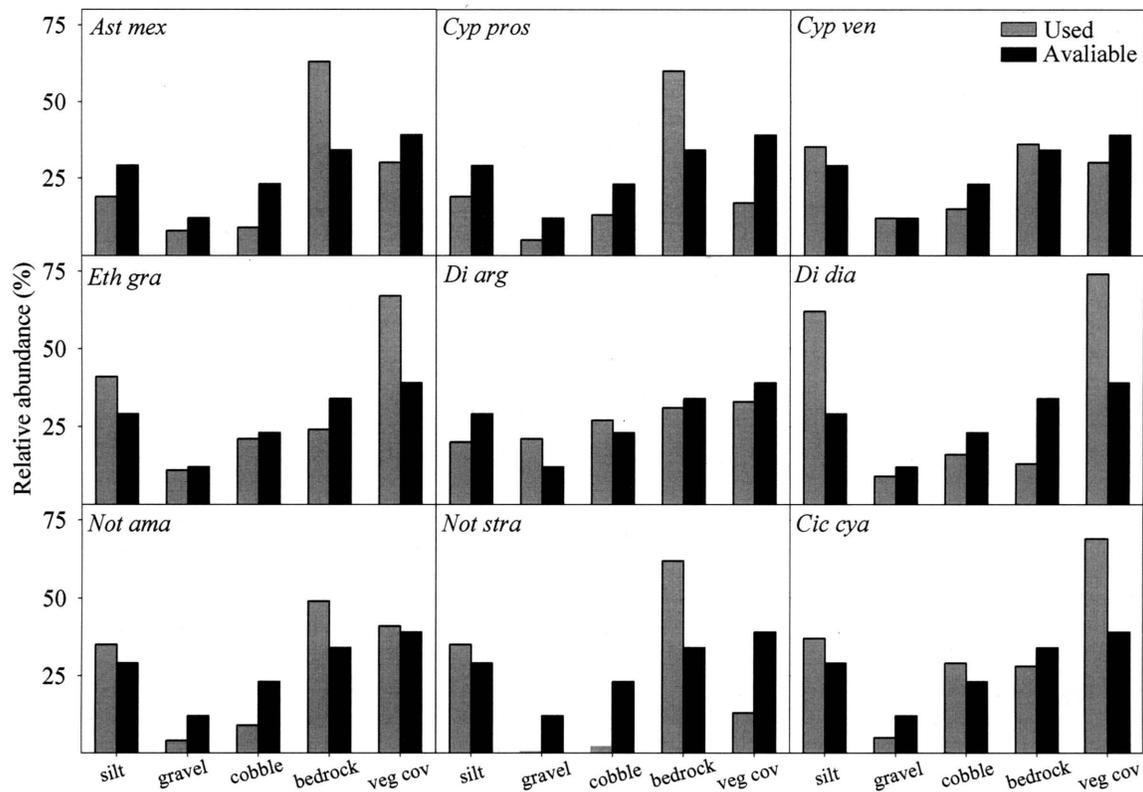


Figure 8. Available substrate and vegetation cover (%) and relative abundance (%) for the most abundant species from Devils River (September 2007 – 2008).

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## VITA

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