

Habitat Associations of Fishes in the Devils River, Texas

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ABSTRACT

The Devils River is a spring-fed river that drains desert landscape in southern Texas and provides essential habitat for several endemic and threatened fish species. To evaluate potential effects of seasonal changes in physical habitat on fish distribution and abundance, we examined species-habitat associations in two reaches separated by 1.5 km. A distinct assemblage pattern existed in each of three mesohabitat types (pool, riffle, run). At the scale of stream reach, species distribution and abundance were associated more with factors related to geomorphology than physicochemistry. Similar mesohabitats had similar fish assemblages, irrespective of reach. Reaches and mesohabitats displayed seasonal variation in physicochemistry and fish assemblage structure. Assemblages associated with runs were least variable across seasons, however no species was strongly associated with runs. Because runs had comparatively little structural complexity and provided little protection from piscivorous smallmouth bass (*Micropterus dolomieu*), species probably use these areas primarily as migration corridors. Densities of two threatened species, *Etheostoma grahami* and *Cyprinella proserpina*, were negatively correlated with smallmouth bass density.

INTRODUCTION

Factors that determine fish assemblage structure in streams remain poorly understood, and the physical heterogeneity and dynamic nature of fluvial ecosystems challenge creation of robust models (Matthews and Hill 1980, Grossman et al. 1982, Angermeier and Karr 1983, Ross et al. 1985, Meffe and Sheldon 1988, Meador and Matthews 1992). Streams have unique landscapes, climates, and evolutionary histories that create variable local conditions (Gorman and Karr 1978, Horwitz 1978, Angermeier 1987, Schlosser 1987). Biotic interactions may result in dissimilar fish assemblages within similar habitat types in a given region (Cerri and Fraser 1983, Power 1987, Rahel and Stein 1988, Harvey 1991), and abiotic phenomena such as floods can, at least temporarily, alter species-habitat associations (Harrell 1978, Meffe and Minckley 1986). For example, Matthews et al. (1994) observed more variation in the fish assemblage within than among pools at the scale of a 1-km stream reach in Oklahoma.

In this study, we examined how differences in physicochemical features between habitats and seasonal fluctuations in environmental conditions influenced fish-habitat associations in the Devils River, a spring-fed river in southern Texas. The primary goal was to examine fish assemblage structure within three mesohabitats (riffles, runs, and marginal pools). To explore the influence of scale, we sampled each of these mesohabitats in two similar stream reaches separated by approximately 1.5 km. Sampling was conducted

over a 15-month period to evaluate a third component of variation, the influence of seasonal changes in physicochemical parameters on species-habitat associations.

The Devils River contains populations of four fish species listed as threatened by state and federal agencies (Hubbs and Garrett 1990, Garrett et al. 1992). The stream also supports a large population of smallmouth bass (*Micropterus dolomieu*), a non-native piscivore. Periodic floods have been shown to alter species-habitat associations in the Devils River (Harrell 1978), and the interaction between those events and the presence of an exotic predator could negatively impact native species (Taylor et al. 1984, Power et al. 1985, Mittelbach and Chesson 1997). Valdes and Winemiller (1997) found a negative association between densities of three threatened species (*Cyprinella proserpina*, *Dionda diaboli*, and *Etheostoma grahami*) and smallmouth bass density. Therefore, a second objective was to compare new findings with those of Valdes and Winemiller (1997) to evaluate further the potential impacts of smallmouth bass on native species.

METHODS AND MATERIALS

Study Area

The Devils River originates in northeastern Crockett County, Texas, and flows southward 160 km through Val Verde County. The river is intermittent along much of its length but has permanent surface flow over the final 56 km. At base flow, this spring-fed system reveals low variation in conductivity, pH and dissolved oxygen, and seasonal temperature variation is moderate (Valdes and Winemiller 1997). Infrequent flash floods scour the stream bed and can have short-term impacts on fish populations. Harrell (1978) showed how the Devils River fish assemblage regained a similar structure of relative abundance among dominant species within six months of a major flood. Over the course of our study, discharge only varied from 3 to 7 m³/s (International Boundary Water Commission stream gauge data). The only exception was an increase in discharge to 76.4 m³/s 10 days after our first survey date followed by a return to baseflow within five days.

With 28 native species, the Devils River fish community is particularly diverse for a desert stream. Three species are endemic to the region – the Devils River minnow (*Dionda diaboli*), the proserpine shiner (*Cyprinella proserpina*), and the Rio Grande darter (*Etheostoma grahami*). In addition, several peripheral Mexican fish species are on the edge of their ranges in this area, including the Conchos pupfish (*Cyprinodon eximius*), the Mexican mosquitofish (*Gambusia speciosa*), the blotched mosquitofish (*Gambusia senilis*), the Mexican tetra (*Astyanax mexicanus*), the Rio Grande cichlid (*Herichthys cyanoguttatus*), and the headwater catfish (*Ictalurus lupus*). *Gambusia senilis* is considered extirpated from the area (Harrell 1978, Hubbs and Garrett 1990, Hubbs et al. 1991).

Sampling procedures

Two 250-m reaches of the Devils River were studied. One reach was located within the Devils River State Natural Area and the second, approximately 1.5 km downstream, was immediately above Dolan Falls within the Dolan Falls Preserve of the Texas Nature Conservancy (TNC). The two reaches had similar physical attributes (i.e., similar substrates and channel morphology), but a spring-fed creek (Dolan Creek) flows into the lower reach from the west.

Within each reach, fishes were surveyed in six mesohabitat units (two riffles, two runs, two marginal pools) every other month from June 1997 to August 1998. Run habitats were 10–30 m in length with relatively uniform depth, bedrock substrate, and little aquatic vegetation. Riffles (4–9.5 m length) had greater water velocities and were shallower than runs. Riffles substrate was cobble and gravel and often contained dense patches of submersed aquatic macrophytes. Marginal pools (5–13 m length) were deep areas, usually adjacent to one bank, that had lower water velocity than the other two mesohabitats. Substrate in pools was dominated by silt-covered cobble that tended to be larger than cobble in riffles. Pools contained variable amounts of submersed aquatic, emergent, and overhanging terrestrial vegetation. In each mesohabitat, we recorded maximum depth and used a Hydrolab datasonde to measure pH, dissolved oxygen, conductivity, and temperature. Water velocity was measured with a Marsh-McBirney digital flowmeter.

Fishes were sampled during daylight hours using a 3.0 m x 1.8 m straight seine with 0.6 cm mesh for runs and pools and a 4.9 m x 1.8 m bag seine with 0.6 cm mesh for riffles. The bag seine was held stationary below the riffle, and then a series of kick sweeps of the substrate drove the fishes toward the seine. Sampling was conducted throughout the entire area of each mesohabitat, and effort was terminated when the total catch on a per-seine-haul or kick-sweep basis declined to <5% of the cumulative catch. The surface area of each habitat was determined by measuring perpendicular dimensions in the field with a tape measure. Fishes were identified, counted, measured (standard length, SL, to the nearest 0.1 mm using dial calipers), and then returned to their habitats (except for smallmouth bass that were removed from the TNC reach and voucher specimens of each species that were deposited in the Texas Cooperative Wildlife Collection at Texas A&M University).

Data Analysis

Multivariate ordinations were used to examine fish assemblage composition among the three mesohabitat types and between reaches. Only the 11 most abundant fish species (of 17 surveyed) were included in these analyses; uncommon species (those comprising <1% of total abundance) were omitted. Principal components analysis (PCA) was first used to compare sites for differences in depth, flow, temperature, pH, and dissolved oxygen (DO) in order to examine physicochemical variation between reaches and among mesohabitat types within a reach. This analysis also allowed examination of seasonal fluctuations in these variables. Due to equipment difficulties, three dates were excluded from this analysis (June 1997, June 1998, and August 1998).

PCA then was used to ordinate species density data ($\log_{10}(N+1)$ transformed) and examine species composition patterns between reaches and habitat types. A second multivariate test, canonical correlation analysis (CANCOR), was used to ordinate sites based on a model that integrates species abundance ($\log_{10}(N+1)$) and physicochemical data. All statistical analyses were performed using SAS (SAS Institute Inc. 1985).

RESULTS

Physicochemical parameters from both reaches tended to cluster by dates (seasons) relative to the total multivariate space occupied by all sample sites (Fig. 1). The first PCA axis was strongly influenced by temperature (variable loading -0.99) followed by pH (0.42) and DO (0.25). The second axis

was strongly influenced by DO (-0.97) and pH (-0.51). Physicochemical variables also varied between reaches during most sampling periods; samples within the same reach tended to cluster together irrespective of mesohabitat type. The winter sample (February) was the one exception to this trend when the two reaches revealed high overlap.

A total of 3,840 individual fishes representing 17 species was captured during the study (Table 1). PCA based on species density by site yielded four axes with eigenvalues >1.0 that together accounted for 67.5% of the variation (Table 2). The correlation matrix revealed highly ($r > 0.45$) positive correlations between *E. grahami*, *H. cyanoguttatus*, and *A. mexicanus*; *I. punctatus*, *E. grahami* and *H. cyanoguttatus*; and *N. amabilis* and *N. venusta* (Table 3). *Cyprinella proserpina* and *E. grahami*, two threatened species, were weakly but negatively correlated with the introduced piscivore *M. dolomieu* ($r = -0.13$ and $r = -0.08$, respectively). *Moxostoma congestum* ($r = -0.10$) and *I. punctatus* ($r = -0.115$) also were negatively associated with *M. dolomieu*. *Cyprinella venusta* was the only species with a high positive association with *M. dolomieu* ($r = 0.53$) and also was highly and positively correlated with *N. amabilis* ($r = 0.64$). There were no high negative correlations between any species pair.

The first two principal components were both dominated by variation associated with habitat type. On the first axis, *E. grahami*, *H. cyanoguttatus*, *A. mexicanus*, and *I. punctatus* all loaded high, whereas *C. venusta*, *N. amabilis*, *M. dolomieu*, *G. speciosa*, and *M. congestum* loaded near zero (Table 2). This axis portrays a gradient separating species found predominately in riffles (high loadings) from species generally associated with marginal pools (low loadings). Cichlids are usually associated with deeper slow-moving habitats, but the species loaded high on axis 1 because a large number of juveniles were captured in riffles. The second axis also was associated with habitat, but it had a greater association with season. Species with high loadings on the second axis (*C. venusta* and *N. amabilis*) were associated with marginal pools and were captured most frequently during summer.

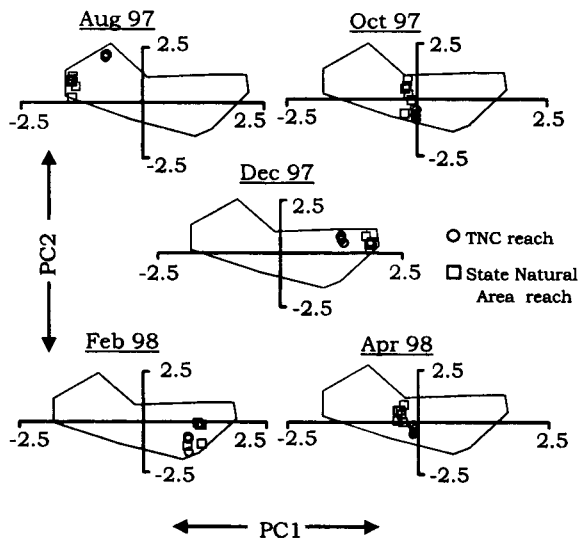


Figure 1. Scatterplots of sites across the principal component axes PC1 and PC2 based on physicochemical data; each individual graph represents one sample date.

A scatterplot of site scores across the first two axes shows the pattern of assemblage variation associated with each mesohabitat (Fig. 2). Run assemblages revealed little variation on either axis, indicating relatively stable species composition across seasons. In contrast, the multivariate space occupied by riffle assemblages revealed much greater variation, particularly on the first axis. Pool assemblages were more variable on the second PC axis.

Even though temperature, pH and DO varied seasonally, distribution of species among sites was relatively stable over time. PCA based on species density data revealed that on most sample dates, local assemblages occupied similar areas within multivariate space, with some among-site divergence during August, and convergence during October and February (Fig. 3).

CANCOR resulted in two highly significant axes ($p < 0.0001$, $p = 0.0024$; Table 4). *Cyprinella venusta*, *N. amabilis*, *A. mexicanus*, *G. speciosa*, and *M. dolomieu* loaded high (>0.30) and positively on the first assemblage axis (V1), whereas *C. proserpina* loaded high and negatively. These species associations can be interpreted in relation to the first environmental axis (W1, Fig. 4) which was dominated by mesohabitat-associated differences. Flow and temperature tended to have the greatest influence on site ordination along axis W1, but depth was also important. This axis describes a gradient from shallow sites with low temperature and high flow (riffles), to deep sites with high temperature and low flow (pools), with most of the run habitat samples falling in between. Run habitats varied less in relation to the first environmental axis than the other two mesohabitats.

The first environmental axis was influenced by season in addition to mesohabitat variation. For instance, several summer riffle samples clustered with marginal pools. Seasonal variation had an influence on species associations that sometimes overshadowed the influence of habitat type. *Etheostoma grahami* was sampled only in riffles but had an axis-1 loading similar to those of species found primarily in run habitats. *Dionda argentosa* was most common in marginal pools, but many individuals were captured from riffles during warmer weather, which yielded an intermediate loading. *Cyprinella venusta* also was captured from pools and riffles during warmer

Table 1. Fish species collected from the Devils River and overall abundances based on seine captures summed across all sampling dates and sites.

Common name	Species	Abundance TNC Preserve	Abundance State Nat. Area
Blacktail shiner	<i>Cyprinella venusta</i>	1,040	888
Proserpine shiner	<i>Cyprinella proserpina</i>	257	382
Texas shiner	<i>Notropis amabilis</i>	183	151
Rio Grande cichlid	<i>Herichthys cyanoguttatus</i>	201	75
Roundnose minnow	<i>Dionda argentosa</i>	148	64
Rio Grande darter	<i>Etheostoma grahami</i>	84	13
Mexican tetra	<i>Astyanax mexicanus</i>	73	20
Mosquitofish	<i>Gambusia speciosa</i>	70	13
Smallmouth bass	<i>Micropterus dolomieu</i>	20	25
Channel catfish	<i>Ictalurus punctatus</i>	32	8
Grey redhorse	<i>Moxostoma congestum</i>	37	2
Sunfish	<i>Lepomis</i> spp.	4	24
Sand shiner	<i>Notropis stramineus</i>	7	4
Flathead catfish	<i>Pylodictis olivaris</i>	10	1
Devils River minnow	<i>Dionda diaboli</i>	0	3
Largemouth bass	<i>Micropterus salmoides</i>	2	0

Table 2. Summary data of PCA performed on species density data including variable loadings (eigenvectors) of the 11 most abundant fish species for the first three axes.

	PC1	PC2	PC3
Eigenvalue	2.726	2.407	1.182
Total variation explained	0.248	0.219	0.107
Cumulative variation	0.248	0.467	0.574
<i>C. venusta</i>	0.030	0.560	-0.163
<i>C. proserpina</i>	0.121	-0.053	0.165
<i>N. amabilis</i>	0.039	0.525	0.352
<i>D. argentosa</i>	0.163	0.224	-0.345
<i>E. grahami</i>	0.531	-0.147	0.005
<i>M. dolomieu</i>	0.021	0.355	-0.542
<i>M. congestum</i>	-0.006	-0.130	0.215
<i>H. cyanoguttatus</i>	0.531	0.060	-0.069
<i>A. mexicanus</i>	0.488	0.083	0.081
<i>G. speciosa</i>	0.025	0.376	0.590
<i>I. punctatus</i>	0.391	-0.204	0.052

periods, yet it had a higher loading than *D. argentosa*. *Astyanax mexicanus* loaded within the range of species associated with marginal pools, yet it was more common in riffles during warmer periods. *Notropis amabilis*, *M. dolomieu*, and *G. speciosa* had high loadings on axis 1 and were found most frequently in marginal pools, whereas *C. proserpina* and *I. punctatus* had relatively high negative loadings and were most common in riffles. No species occurred exclusively in run habitats.

DISCUSSION

Our study revealed strong associations between individual species and mesohabitats in the Devils River, and these associations were, for the most part, replicated in two separate reaches. Despite the relative stability of physicochemical attributes and fish assemblage in runs, no species was strongly associated with this habitat. The shallow depth and lack of cover in runs probably inhibits use of this habitat by small species vulnerable to piscivores, especially smallmouth bass that occupy a range of habitats in the Devils River. Few fishes were observed over broad stretches of open water over limestone bedrock in runs. Most of the small fishes captured in runs were near rocks, patches of vegetation, or adjacent riffles. Although many species seem to avoid runs, these habitats undoubtedly serve as corridors for fishes moving between more structurally complex mesohabitats.

Riffle fish assemblages in the Devils River were relatively diverse. The only species of darter in the river, *E. grahami*, was strongly associated with riffles. This species is reported to move into deep vegetated pools (deep pools were not present in the river reaches we surveyed) for a portion of the year and then into riffles to spawn (Kuehne and Barbour 1983, Page 1983). Other species closely associated with riffles included *C. proserpina* and juvenile size classes of *I. punctatus* and *H. cyanoguttatus*. Valdes and Winemiller (1997) found *C. proserpina* associated with mesohabitats we defined as marginal pools, yet most individuals sampled in the present study were captured in riffles. A shift in habitat use could be the result of any number of changes in hydrology or community dynamics. Harrell (1978) showed species may change

Table 3. Correlation matrix of species densities the 11 most abundant species.

	1	2	3	4	5	6	7	8	9	10
1 <i>N. venusta</i>										
2 <i>C. proserpina</i>	0									
3 <i>N. amabilis</i>	0.64	0								
4 <i>D. argentosa</i>	0.31	0.02	0.18							
5 <i>E. grahami</i>	-0.16	0.16	-0.10	0.15						
6 <i>M. dolomieu</i>	0.53	-0.13	0.17	0.13	-0.08					
7 <i>M. congestum</i>	-0.13	-0.11	-0.03	-0.07	0.02	-0.10				
8 <i>H. cyanoguttatus</i>	0.09	0.07	0.09	0.16	0.67	0.15	-0.09			
9 <i>A. mexicanus</i>	0.13	0.11	0.13	0.17	0.61	0.03	0.05	0.69		
10 <i>G. speciosa</i>	0.29	-0.03	0.57	0	-0.07	0.05	-0.08	0.06	0.11	
11 <i>I. punctatus</i>	-0.17	0.09	-0.14	0.03	0.58	-0.11	0.09	0.45	0.26	-0.08

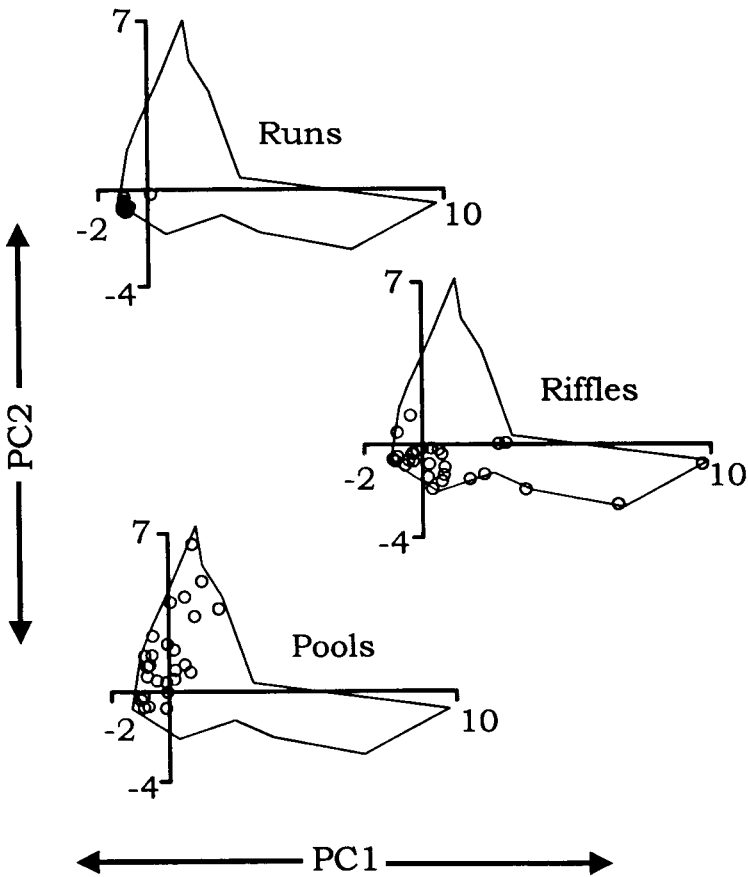


Figure 2. Scatterplots of sample scores from PCA based on species density data showing mesohabitat categories; the polygon encompasses the total multivariate space occupied by all samples.

habitat use in response to major floods; however, no major floods occurred between the two studies. Change in resource availability resulting from species introductions and altered community dynamics is another potential cause of the apparent habitat shift by *C. proserpina*.

Like Valdes and Winemiller (1997), we found that threatened fish species (*E. grahami* and *C. proserpina*) were negatively (though weakly) correlated with nonindigenous smallmouth bass. Although all three species had positive loadings on the first axis of the PCA ordination, *E. grahami* and *C. proserpina* tended to be found in riffles (where smallmouth bass were infrequently captured). The impact of smallmouth bass on native fishes of the Devils River should be further evaluated.

Species most closely associated with marginal pools were *N. amabilis*, *G. speciosa*, *C. venusta* (also in riffles during warmer months), and *M. dolomieu*. *Cyprinella venusta* was the only species that was highly positively correlated with smallmouth bass, which may be due in part to the length attained by the former. Robertson and Winemiller (2001) found that *C. venusta* within this segment of the Devils River had a mean body length greater than the optimal

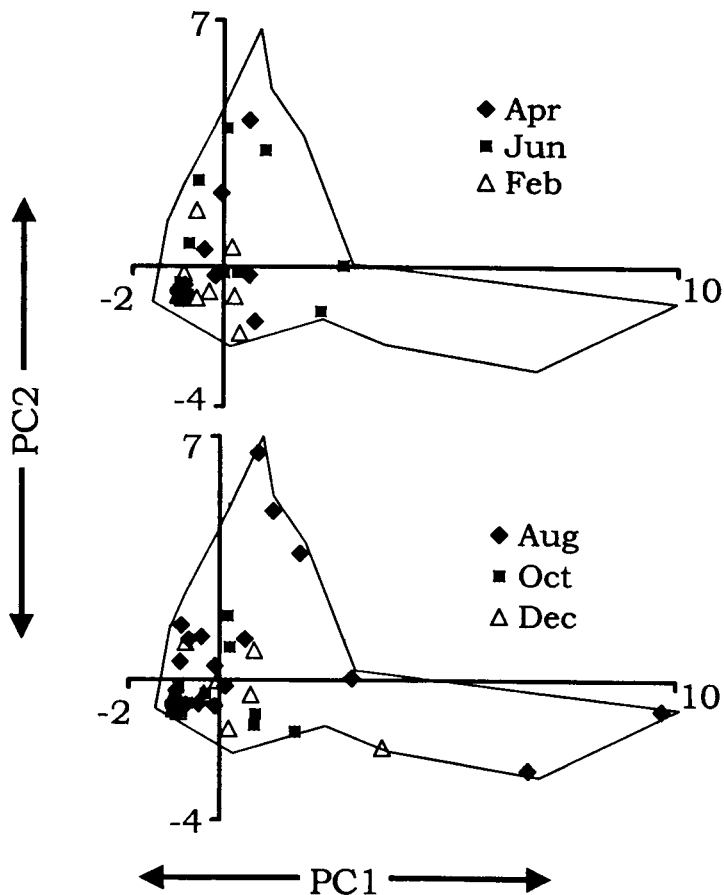


Figure 3. Scatterplots of sample scores from PCA based on species density data showing sampling periods; open symbols= winter months, filled symbols= warm months; the polygon encompasses the total multivariate space occupied by all samples.

forage size for smallmouth bass. *Astyanax mexicanus* was collected in pools during summer. In Texas, *A. mexicanus* occupies the northern extent of its range (Mayden 1992), and Harrell (1978) noted a close association of *A. mexicanus* with springs which provide thermal buffers during winter.

Associations of individual species with mesohabitats in the Devils River were influenced by season. While this suggests movement between mesohabitats in response to seasonal changes in environmental conditions, fish assemblage structure did not correlate strongly with physicochemical variation. The wintertime reduction in multivariate space occupied by sample sites in both the fish and water quality data sets implies a biotic response to changes in the abiotic environment. This is consistent with the observations of Valdes and Winemiller (1997) who also found variation in mesohabitat use was smaller during winter. During winter, many species probably moved into deep pools, the only major habitat type not sampled in our study. Winter shifts in habitat use were most likely a function of warmer temperatures in deeper habitats and sites adjacent to springs (Valdes and Winemiller 1997); however, factors such as available cover (vegetation cover was reduced in shallow habitats during winter) and prey abundance also may influence seasonal shifts in habitat use.

Differences in physicochemical attributes between the two study reaches were not sufficient to influence species associations with mesohabitat. PCA indicated that variation in physicochemical attributes was greater between reaches than within reaches (i.e., among mesohabitat types) for most sample periods, yet variation in assemblage structure tended to be greater among habitat types within reaches than between reaches. If differences in physicochemistry were driving habitat choice among runs, riffles, and marginal

Table 4. Summary data for CANCOR analysis with variable loadings on the first three axes for community (V) and environment (W) variables.

	Axis 1	Axis 2	Axis 3
Squared canonical correlation	0.539	0.504	0.233
Eigenvalue	1.169	1.016	0.305
Proportion of total variation explained	0.438	0.380	0.114
<u>Community variables (V)</u>			
<i>C. venusta</i>	0.449	-0.286	-0.104
<i>C. proserpina</i>	-0.309	0.269	-0.087
<i>N. amabilis</i>	0.343	-0.174	0.013
<i>D. argentosa</i>	0.186	-0.099	0.205
<i>E. grahami</i>	0.079	0.445	0.089
<i>M. dolomieu</i>	0.379	-0.184	-0.086
<i>M. congestum</i>	0.109	0.343	0.083
<i>H. cyanoguttatus</i>	0.165	0.105	0.202
<i>A. mexicanus</i>	0.312	0.382	0.059
<i>G. speciosa</i>	0.355	0.005	0.127
<i>I. punctatus</i>	-0.174	0.238	0.231
<u>Environmental variables (W)</u>			
Temperature	0.472	0.218	-0.173
pH	0.006	0.342	0.066
DO	0.082	0.355	0.284
Depth	0.344	-0.490	-0.144
Flow	-0.549	0.366	-0.172

pools in the Devils River, one would expect variation in community structure to be greater between reaches than among habitat types, but this was not the case. These findings demonstrate that fine-scale geomorphological variation (i.e., substrate composition, cover, water velocity) has a greater influence on habitat use than water quality variation in the Devils River. Sites with similar mesohabitat tend to have a similar fish assemblages.

Other studies have yielded conflicting results regarding the influence of spatial and environmental variation on stream fish assemblages. Matthews et al. (1994) observed, as we did, that variation in the composition of the fish assemblage was greater within than among individual mesohabitats (in this case pools) at the scale of a 1-km stream reach. In Sister Grove Creek, north-central Texas, Meador and Matthews (1992) observed that spatial variation among sites separated by 2.5 to 10 km had a greater influence on community composition than temporal changes in environmental conditions. Gelwick (1990) found conflicting patterns in a prairie stream in which pools showed more spatial than temporal differences while fishes in riffles had the opposite trend. Matthews and Hill (1980) observed that species use of mesohabitats in the South Canadian River, Oklahoma was transitory and frequently depended on environmental conditions.

The different conclusions of these studies are likely due to differences in disturbance regimes. For example, environmental stochasticity with high disturbance frequency characterizes the prairie stream studied by Matthews and Hill (1980). In contrast, the Devils River experiences relatively little environmental variation beyond large flood events that are infrequent. Abiotic conditions in the Devils River undergo relatively subtle seasonal changes and large-scale disturbances that disrupt fish-habitat associations are rare (Harrell 1978). In response to frequent fluctuations in hydrology, fishes in prairie streams may be forced to use a wider range of microhabitats to optimize foraging, predator avoidance, and reproduction. Low water discharge variation in the Devils River probably allows fishes to specialize to some degree on particular mesohabitats.

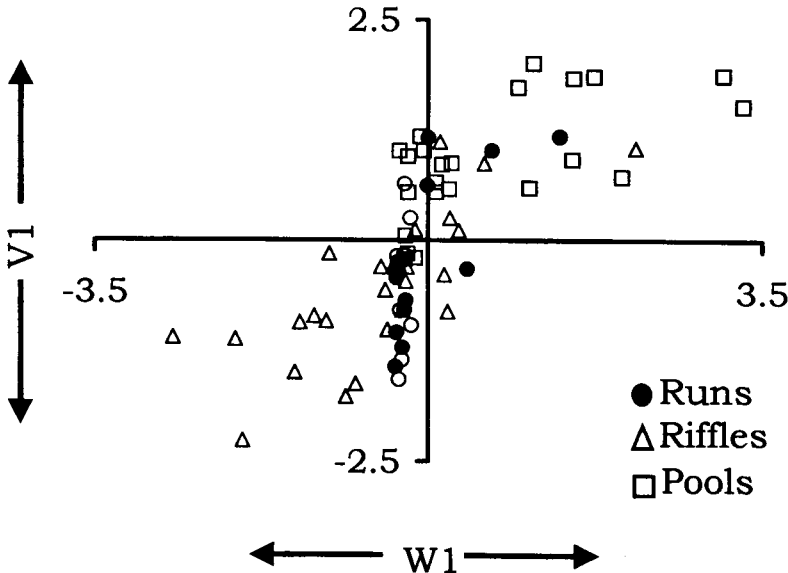


Figure 4. Scatterplot of sample scores on the first environmental axis (W1) and first community axis (V1) from CANCOR analysis.

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