

STRUCTURE AND HABITAT ASSOCIATIONS OF
DEVILS RIVER FISH ASSEMBLAGES

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ABSTRACT—Spatial variation in the structure of fish assemblages at eight sites in the Devils River was examined seasonally over one year. Data were analyzed to explore natural variation at the mesohabitat scale. The local fish fauna was dominated by four minnows (Cyprinidae) and one mosquitofish (Poeciliidae). Overall assemblage composition in this study was similar to that reported previously, but three species were not reported before, and nine species previously reported were not observed during our study. Four threatened species ranked among the most abundant fishes encountered during our surveys. Species diversity (H') and fish abundances showed relatively large variation between mesohabitats as well as between seasons within most mesohabitats. The most species-rich mesohabitats were pools, channels, channel edges, and riffles, whereas the least species occurred in shallow, isolated pools dominated by *Cyprinodon eximius*. Spatiotemporal patterns of taxonomic composition were examined using principal components analysis. Seasonal shifts in assemblage structure were associated primarily with an axis that contrasted domination by *Moxostoma congestum*, *Etheostoma grahami*, *Cyprinodon eximius*, and *Dionda diaboli* versus domination by *Micropterus dolomieu*, *Cyprinella proserpina*, *Cyprinella venusta*, and *Cichlasoma cyanoguttatum*. Canonical correlation analysis was performed using assemblage data in combination with a set of environmental parameters. The first pair of canonical axes described a pattern in which fishes occupied a wide range of sites during summer, and in which during winter, most species were associated with shallow, channel mesohabitats with high dissolved oxygen. The Devils River is dominated by small fishes that have extended spawning periods and that scatter their eggs over open substrates.

A major issue in ecology is the causes of patterns of species distribution and abundance at different spatial and temporal scales (Shmida and Wilson, 1985; Brown and Mauer, 1989). Species assemblages can be examined from different perspectives, including taxonomic composition, trophic ecology, and reproductive guilds. The environmental factors associated with local fish diversity in streams has generated much interest (e.g., Bain et al., 1988; Matthews, 1986; Bass, 1990; Matthews et al., 1992), and models have been proposed to explain the observed patterns (Karr et al., 1986; Schlosser, 1987). However, few studies in aquatic ecology have quantified responses to both physical and biological factors simultaneously. According to Schlosser (1987), processes related to both of these factors determine community organization, and these processes are strongly influenced by spatial habitat heterogeneity, frequency and intensity of physical disturbance, and organisms' life-history attributes.

The spatial scale of observation also influ-

ences perceived assemblage stability. Most studies of fish assemblages have focused on patterns observed across large spatial scales, such as entire streams (Ross et al., 1985; Matthews et al., 1988; Meador and Matthews, 1992) or watersheds (Jenkins et al., 1972; Moyle et al., 1982). Recently, it has been suggested that the spatial scale selected for research should consider the spacing of biologically relevant habitat units, such as pools and riffles (Matthews et al., 1994). At these small spatial scales, assemblages are strongly influenced by between-habitat (beta) diversity. The strong longitudinal patterns of species association observed at large spatial scales (Vannote et al., 1980) generally are replaced by a more complex spatial configuration associated with microhabitat heterogeneity at smaller spatial scales of analysis (Gorman and Karr, 1978).

The Devils River is an important aquatic system in the desert Southwest. The free-flowing portion of the Devils River is the last remaining undammed, unpolluted major river in west

Texas (Harrell, 1978). Although the river has not been contaminated, habitat degradation and excessive water use in the region have led to a decline in range and abundance of endemic species such as *Dionda diaboli* (Devils River minnow), *Cyprinodon eximius* (Conchos pupfish), *Etheostoma grahami* (Rio Grande darter), and *Cyprinella proserpina* (proserpine shiner) to the point at which their survival is threatened (Hubbs and Garrett, 1990). Moreover, the introduction of species like *Micropterus dolomieu* (smallmouth bass), *Morone chrysops* (white bass), and *Lepomis auritus* (red breast sunfish) may impact native endemics via competition or predation.

Over recent decades, the Devils River has been sampled at irregular time intervals and at scattered locations (Harrell, 1978; Garrett et al., 1992). The basic ecological characteristics and interrelationships of fish species inhabiting this area are not well documented. The primary goal of the current study was to improve understanding of the interaction between physical and biotic environmental factors influencing fish populations in the Devils River at the Nature Conservancy's Dolan Falls Preserve. We examined the size structure, relative abundance, and habitat associations of each species in relation to habitats and seasons. In addition to documenting factors associated with assemblage spatiotemporal variation, results from this study contribute to our understanding of ecological factors controlling biodiversity in this unique ecosystem.

STUDY AREA—The Devils River is a clear, spring-fed stream that flows over a cobblestone and limestone bedrock substratum through alternating riffles and pools. It arises in northwestern Sutton County (Texas) and flows intermittently southward into Val Verde County where the river's permanent surface water is located (Belisle and Josselet, 1975). The river lies entirely within the Edwards Plateau region of Texas and drains approximately 10,000 km² (Brown, 1954). The watershed is sparsely populated, semi-arid and receives about 46 cm of rainfall annually. The water is hard (160-190 mg/l CaCO₃) with less than 250 mg/l total dissolved solids (Davis, 1980).

Although the Devils River is located within the Balconean biotic province, its proximity to the Chihuahuan and Tamaulipan provinces

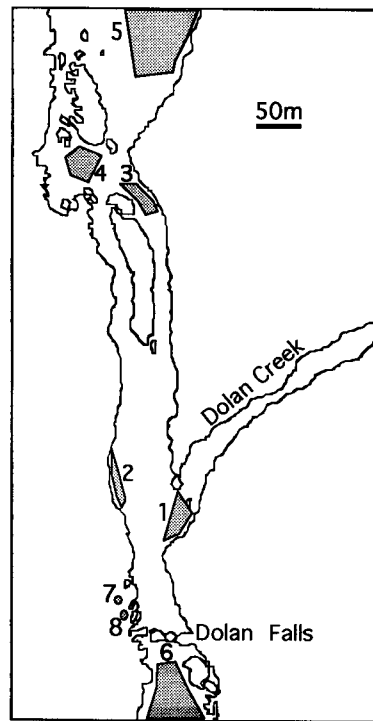


FIG. 1.—Map showing the locations of mesohabitat sampling sites with the Devils River study region at Dolan Falls Preserve.

contributes to high biotic diversity for a desert stream (Hubbs, 1957). Peripheral Mexican fishes in the Devils River include *Etheostoma grahami*, *Astyanax mexicanus* (Mexican tetra), and *Cichlasoma cyanoguttatum* (Rio Grande perch). Pondweed (*Potamogeton* sp.) and yellow cow-lily (*Nuphar luteum*) are common in pools, and water nymph (*Najas* sp.), *Chara* sp., *Spirogyra* sp., and *Cladophora* sp. often occur in spring areas (Brown, 1954). Riparian vegetation consists of interspersed stands of pecan (*Carya illinoensis*), willow (*Salix* sp.), live oak (*Quercus virginiana*), and sycamore (*Platanus occidentalis*).

The study site was located at the Texas Nature Conservancy's Dolan Falls Preserve in Val Verde County, Texas. This section of the river includes a complex of meso-habitats that are representative of those found in other portions of the river. The following sample sites were selected to represent a range of available mesohabitats (Fig. 1): 1) Dolan Creek channel at its juncture with the Devils River (N 29°53.065', W 100°59.60'; mean depth = 0.73 m; mean

width = 24.6 m), 2) shallow channel edge with bedrock bottom at the bank opposite from the mouth of Dolan Creek (N 29°53.13', W 100°59.60'; mean depth = 0.26 m; mean width = 7.8 m), 3) riffle ca. 400 m upstream from Dolan Falls (N 29°53.23', W 100°59.60'; mean depth = 0.37 m; mean width = 19.5 m), 4) marshy area along channel edge ca. 25 m west of site 3 (N 29°53.25', W 100°59.56'; mean depth = 0.22 m; mean width = 53.7 m), 5) vegetated pool edge ca. 500 m upstream from Dolan Falls (N 29°53.38', W 100°53.38'; mean depth = 1.18 m; mean width = 90 m), 6) deep pool immediately below Dolan Falls (N 29°53.029', W 100°59.60'; mean depth = 10 m; mean width = 40 m), 7) shallow isolated marginal pool 24 m upstream from Dolan Falls and 4.2 m from watered channel (N 29°53.049', W 100°59.628'; mean depth = 0.16 m; mean width = 9.9 m), 8) deep isolated marginal pool 15 m upstream from Dolan Falls and 4.2 m from watered channel (N 29°53.036', W 100°59.62'; mean depth = 0.36 m; mean width = 2.5 m).

MATERIALS AND METHODS—During summer (August 3), autumn (November 19), winter (January 25), and spring (May 17) of 1993-94, collections were made at eight stations (Fig. 1) to estimate the relative distributions and abundances of fishes. Fishes were collected with seines (6.1 m × 2.4 m, 0.95 cm mesh; 3.0 m × 1.8 m, 0.64 cm mesh) at each site, an experimental monofilament gill-net (50 m × 3 m; mesh = 2.54 cm × 5.08 cm × 7.62 cm) at site 6, and a portable handheld electrofishing unit and dip-net at sites 1 and 5. Snorkeling supplemented counts for species that managed to evade collection in the deep pool (site 6) and shore observation was used to estimate abundances in the isolated marginal pools (sites 7 and 8), respectively. The effectiveness of the latter two methods is well established for enumeration of fishes in clear streams (Lobb and Orth, 1991; Aadland, 1993).

Each site was sampled intensively with the primary goal being attainment of a sample in which all species were represented in relative proportions approximating those of the local assemblage. The use of multiple methods at some sites increased confidence that all species were documented and that relative abundance estimates were reasonably accurate. Each seasonal survey lasted from one to two days, and, except for the use of a gillnet at site 6 (set from 0900–1300 hr), the effort at a given site (=mesohabitat) was continued until 30 minutes of collecting produced no additional species for the sample. Except for four species currently listed by the state as

“threatened”, all specimens collected with seines and electroshocking were preserved in 10% formalin and taken to the laboratory. Threatened species were very quickly identified, measured, and returned to the stream. Large specimens collected with gillnets were identified, measured, and weighed on site. Preserved specimens were identified, counted, and measured for standard length (SL) in the laboratory. Fishes were identified following Hubbs et al. (1991) and Page and Burr (1991), and preserved specimens were deposited in the Texas Cooperative Wildlife Collection, Texas A&M University.

Habitat Evaluation—Physical habitat conditions were recorded on the same dates that fishes were sampled. Determinations of width and depth at each site were done to the nearest 1.0 cm with a tape measure. Temperature (°C) and dissolved oxygen (mg/l) profiles were made at each station using a YSI model 51B oxygen/temperature meter. In all but the shallowest waters, environmental measurements were taken at three different depths (top, middle, bottom) then averaged. Conductivity (μMho) was measured using a Cole-Parmer model 33 salinity-conductivity-temperature meter. Water current velocity was measured to the nearest 0.1 m/sec with a Marsh-McBirney electronic flowmeter, and pH was measured with reagent-grade pH paper. Qualitative shoreline characteristics, substrate composition, and vegetation also were recorded at each site.

Data Analysis—Spatiotemporal patterns of taxonomic composition were examined using principal components analysis (PCA), a form of multivariate analysis that produces independent orthogonal axes from a multivariate cluster of data points (James and McCulloch, 1990). Catch data for each species were compiled by site, and sample totals were converted to species relative abundances. To reduce distribution skewedness, species relative abundance and environmental data were log-transformed [$\log_{10}(N+1)$] prior to ordination. PCA was performed on the full 27 species data set, for both the matrix of relative abundances [$\log_{10}(N+1)$ -transformed] and the matrix of raw numerical abundances [$\log_{10}(N+1)$ -transformed]. This analysis resulted in site 6 (summer) being an extreme outlier on PC axis 1. Therefore, only the 12 most common species were included to prevent uncommon taxa from having a disproportionate effect. Uncommon taxa were defined as those rare species whose combined numerical abundances comprised 3% of the total collection, and common taxa as those abundant species comprising 97% of the total collection. In addition to the PCA, canonical correlation analysis (CANCOR) was performed. CANCOR is a multivariate technique that ordines sites using information from both species abundances and a corresponding set of environmental variables (Ter Braak, 1986). For

CANCOR, the 12 common species were used in combination with the following environmental parameters: channel width, depth, water temperature, current velocity, conductivity, pH, and dissolved oxygen. Species diversity at each site was calculated as the Shannon and Weaver (1963) index, H' . Species richness was defined as the total number of species present at a given site, and abundance was considered as the total number of individuals documented at each site.

RESULTS—Habitat Attributes—No major physico-chemical differences were observed between sites, or between seasons within sites. Salinity approximated 0 ppt at all sites, and was essentially constant across all seasons, except for sites 2 and 6 that measured 2.5 and 4 ppt, respectively, during fall. Dissolved oxygen was near or above saturation (>7.0 mg/l) at all sites during each period, and pH ranged from 6 to 7.5. Physical features varied considerably between sites and over time. Channel width, depth and current were the most important components of spatial variation, and water temperature contributed the most to seasonal variation. Water temperature varied little between mesohabitats within seasons, but ranged seasonally from 14°C at site 8 during fall, to 27.9°C at site 6 during summer. Current velocity varied from 0 m/sec at sites 5, 7 and 8 to 1.57 m/sec at site 1.

Species Diversity and Abundances—During our surveys, 4,740 specimens were collected, representing 13 families and 27 species (Table 1). Based on this collective sample, *Cyprinella venusta*, *Dionda argentosa*, *Notropis amabilis*, *Cyprinella proserpina*, and *Gambusia affinis* were the most abundant species and comprised 85.5% of the total number of fish collected. Four rare species, *Lepomis auritus*, *Ameiurus melas*, *Morone chrysops*, and *Oreochromis aureus* (nonindigenous tilapia) were represented by single individuals. Community composition in this study was similar to that reported previously (Harrell, 1978; Garrett et al., 1992; Hubbs, unpublished data). Although differences in sampling methods and effort among studies prevented quantitative comparisons, generally, the same species were common or rare in each dataset. Three rare species found during our survey, (*Ameiurus melas*, *Aplodinotus grunniens*, and *Cyprinus carpio*) have not been reported from previous studies. During his 1986 survey, Hubbs (unpublished) obtained nine species that were

TABLE 1—Total number and percentage abundances of fish species collected from the Devils River at the Texas Nature Conservancy's Dolan Falls Preserve.

Species	Total number	%
<i>Cyprinella venusta</i>	1,580	33.33
<i>Dionda argentosa</i>	1,332	28.10
<i>Notropis amabilis</i>	568	11.98
<i>Cyprinella proserpina</i>	312	6.58
<i>Gambusia affinis</i>	261	5.50
<i>Etheostoma grahami</i>	151	3.18
<i>Notropis stramineus</i>	128	2.70
<i>Cyprinodon eximius</i>	108	2.27
<i>Lepomis megalotis</i>	60	1.26
<i>Cichlasoma cyanoguttatum</i>	44	0.92
<i>Moxostoma congestum</i>	39	0.82
<i>Micropterus dolomieu</i>	37	0.78
<i>Dionda diaboli</i>	28	0.59
<i>Micropterus salmoides</i>	25	0.52
<i>Lepisosteus osseus</i>	17	0.35
<i>Ictalurus punctatus</i>	14	0.29
<i>Carpiodes carpio</i>	8	0.16
<i>Cyprinus carpio</i>	6	0.12
<i>Lepomis auritus</i>	5	0.10
<i>Astyanax mexicanus</i>	5	0.10
<i>Dorosoma cepedianum</i>	4	0.08
<i>Pylodictis olivaris</i>	2	0.04
<i>Aplodinotus grunniens</i>	2	0.04
<i>Lepomis macrochirus</i>	1	0.02
<i>Ameiurus melas</i>	1	0.02
<i>Morone chrysops</i>	1	0.02
<i>Oreochromis aureus</i>	1	0.02
Total collection	4,740	

not observed during our study, however, all of them, with the exception of *Campostoma anomalum* and *Pimephales vigilax*, were rare.

Species richness differed between sites and seasons, ranging from 14 (site 6—summer) to zero (site 7—winter; site 8—fall and winter) (Fig. 2). For the majority of mesohabitats, the number of species by site was highest during summer and lowest during spring. However, there were two exceptions: site 1 (pool near Dolan Creek) which was lowest during fall, and site 3 (riffle) which was highest during fall and winter. Site 2 (shallow channel edge) had the greatest inter-seasonal consistency for species richness, and site 6 (deep channel pool) was the most variable (Fig. 2). Both species diversity (H') and fish abundance showed relatively large variation between mesohabitats and be-

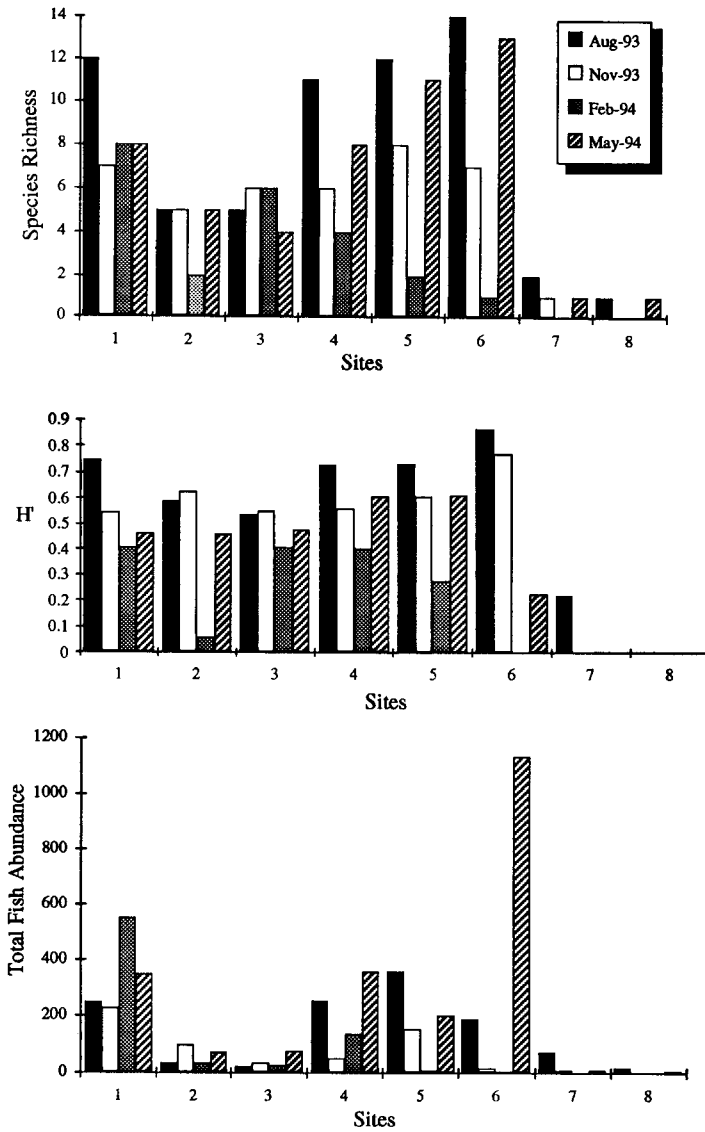


FIG. 2—Frequency histograms showing between-site and seasonal variation in fish species richness, species diversity, and total fish abundance in the Devils River.

tween seasons within mesohabitats (Fig. 2). When data for all seasons were aggregated by site, site 6 had the greatest fish diversity (0.86) and abundance (1,137 individuals), and site 8 (small isolated pool) had the lowest diversity (0) and abundance (0). Species diversity tended to be highest during summer and lowest during winter, except for sites 2 and 3 which had the highest diversity in the fall collection.

Population Structure—Small fishes (maximum SL < 50 mm) numerically dominated all sites,

however large fishes, such as *Lepisosteus osseus* and *Micropterus dolomieu*, contributed to most to the fish biomass of the deep pool below the falls. The largest individual recorded from the total collection was *Pylodictis olivaris* (700 mm SL), and *Etheostoma grahami* and *Cichlasoma cyanoguttatum* had the smallest individuals (15 mm SL).

The blacktail shiner (*Cyprinella venusta*), the most abundant species in the total collection, attained a maximum SL of 59.7 mm. With the

exception of sites 7 and 8 (isolated marginal pools), this species was present in all mesohabitats. Blacktail shiners were most abundant in vegetated sites near the channel margin (e.g., sites 1, 4, and 5). Many small individuals (SL < 15 mm) were collected during the fall and spring, whereas numerous large individuals were collected during summer and winter. Size data indicate at least two annual reproductive periods by *C. venusta*, with at least some spawning during winter.

The second most abundant species, the roundnose minnow (*Dionda argentosa*), had a maximum SL of 75.9 mm. *Dionda argentosa* occurred in most mesohabitats, except for the isolated pools and site 6 (deep pool), and its absence from the latter possibly indicates avoidance of large predators. Small individuals of this species (SL < 15 mm) were collected from fall through spring, with the highest incidence in winter, a pattern that suggests peak reproduction during the fall.

Notropis amabilis, the third most abundant species, also was found in most of the mesohabitats, with the exception of the two isolated pools, and it was spatially segregated according to size. Small individuals (SL < 15 mm) had a strong association with channel areas, whereas larger individuals (SL > 25 mm) were more abundant in riffles, especially during winter. Small individuals were collected during the entire year, indicating year-round recruitment. The largest individual was 52.3 mm SL.

Cyprinella proserpina, the fourth most abundant species (maximum SL = 53.4 mm), was present in most mesohabitats, with the exception of the two isolated pools. The proserpine shiner was most abundant in the marshy area (site 4) and vegetated channel edge mesohabitats. Small individuals (SL < 15 mm) were found only during summer and fall, indicating reproduction from late spring to early fall.

The mosquitofish, *Gambusia affinis*, was the fifth most abundant species (maximum SL = 43.4 mm). Unlike the minnows, mosquitofish were only collected from shallow vegetated areas, especially the marsh and the channel edges. It was the only species, other than the pupfish (*Cyprinodon eximius*), observed in the isolated pools. Small individuals (SL < 15 mm) were collected year-round and were always more abundant than large individuals. This species matures at approximately 19–35 mm

SL (Lee et al., 1980) and seems to reproduce throughout the year at this location.

Assemblage Patterns—Correlations between all pairwise combinations of species abundances [$\log_{10}(N+1)$ -transformed] are given in Table 2. High positive correlations indicate frequent species co-occurrence in mesohabitats (e.g., *Etheostoma grahami* with *Moxostoma congestum*), whereas high negative correlations indicate species that do not commonly coexist (e.g., *Cyprinodon eximius* with all other species). Non-indigenous smallmouth bass were negatively correlated with *Dionda argentosa*, *Etheostoma grahami*, *Cyprinella proserpina*, and *Cyprinodon eximius* (Table 2).

The first three PCA axes accounted for 36.3, 17.5, and 11.1% of the total variation, respectively, or 64.9% collectively (Table 3). The first PCA axis describes a species richness gradient running from the narrow isolated pool (site 8) containing only one species (*C. eximius*), to larger, main-channel mesohabitats containing many species (with *C. eximius* absent). *Notropis amabilis*, *Lepomis megalotis*, *Cyprinella venusta*, and *Gambusia affinis* had the highest positive loadings on axis 1, and only *Cyprinodon eximius* loaded negatively. The second PCA axis contrasted shallow, fast-moving channel edge mesohabitats with deep, nonflowing, pool edge mesohabitats. *Moxostoma congestum*, *Etheostoma grahami*, *Cyprinodon eximius*, and *Dionda argentosa* had large positive loadings on axis 2, whereas *Micropterus dolomieu*, *Cyprinella proserpina*, *Cyprinella venusta*, and *Lepomis megalotis* had large negative loadings. The third axis was more difficult to interpret, but seemed to ordinate species according to seasonal abundances with positive values indicating high abundances during fall and winter, and negative values indicating high abundance during summer. Only *Cyprinella proserpina*, and *Notropis stramineus* loaded strongly on axis 3.

A means of illustrating variation in fish assemblages across time and space is to create scatterplots of sample scores from the PCA (Angermeier, 1987). Figure 3 shows each site grouped across seasons in relation to the space occupied by the total assemblage on PCA-axes 1 and 2. Seven of the eight sites occupied relatively small spaces within the scatterplot (depicted by solid polygons) relative to the total space occupied by all sites (represented by the large polygon identical in each case). The only

TABLE 2—Correlation matrix of fish species abundances [$\log_{10}(N + 1)$ -transformed] by site for the 12 most abundant species.

	1	2	3	4	5	6	7	8	9	10	11
1 <i>Gambusia affinis</i>	1.000										
2 <i>Cyprinella venusta</i>	0.379	1.000									
3 <i>Cyprinella proserpina</i>	0.155	0.389	1.000								
4 <i>Notropis amabilis</i>	0.408	0.710	0.353	1.000							
5 <i>Notropis stramineus</i>	0.608	0.132	-0.194	0.373	1.000						
6 <i>Dionda argentosa</i>	0.451	0.308	0.267	0.346	0.469	1.000					
7 <i>Micropterus dolomieu</i>	0.037	0.358	-0.004	0.438	0.076	-0.189	1.000				
8 <i>Lepomis megalotis</i>	0.594	0.664	0.189	0.836	0.454	0.249	0.342	1.000			
9 <i>Cichlasoma cyanoguttatum</i>	0.454	0.394	-0.014	0.356	0.337	0.400	0.290	0.291	1.000		
10 <i>Moxostoma congestum</i>	0.190	0.207	-0.095	0.265	0.152	0.576	0.047	0.089	0.446	1.000	
11 <i>Etheostoma grahami</i>	0.416	0.272	-0.046	0.334	0.061	0.536	-0.146	0.357	0.361	0.702	1.000
12 <i>Cyprinodon eximius</i>	-0.014	-0.295	-0.233	-0.279	-0.150	-0.025	-0.216	-0.325	-0.170	0.095	0.122

exception was site 4, which occupied more than half the total space occupied by all sites collectively. Sites 1 and 6 occupied the region associated with dominance by *Micropterus dolomieu*, *Cyprinella proserpina*, *Cyprinella venusta*, and *Lepomis megalotis*. Sites 7 and 8 occupied the region associated with dominance by *Cyprinodon eximius*. Sites 2 and 3 occupied the region associated with dominance by *Micropterus dolomieu*, *Cyprinella proserpina*, *Cyprinella venusta*, *Lepomis megalotis*, and *Cyprinodon eximius*. Site 5 occupied the region dominated by *Notropis amabilis*, *Lepomis megalotis*, *Cyprinella venusta*, and *Gambusia affinis*. Site 4 occupied the region associated with the presence of most of the 12 most abundant species, with the exception of *Cyprinodon eximius*.

To show how the multivariate space occupied by all sites during each season relates to the multivariate space occupied by all sites across all seasons, a second series of scatterplots was created (Fig. 4) based on the same PCA results, but with solid polygons representing all sites for a single season. Most seasonal variation in assemblage structure was associated with axis 2. Summer is the only season that occupied a relatively large multivariate space within the scatterplot, indicating the presence of most of the 12 species. The fall and spring regions were associated with dominance by *Cyprinodon eximius*, *Micropterus dolomieu*, *Cyprinella proserpina*, *Cyprinella venusta*, and *Lepomis megalotis*. Winter occupied the region associated with dominance by *Moxostoma congestum*, *Etheostoma grahami*, *Cyprinodon eximius*, and *Dionda argentosa*.

Canonical Correlation Analysis—The first three axes from CANCOR, based on sets of assemblage and environmental variables, accounted for 90.7% of the total variance (Table 4). *Cyprinella proserpina*, *Notropis stramineus*, *Micropterus dolomieu*, and *Etheostoma grahami* had highest positive loadings on assemblage axis 1, whereas *Notropis amabilis* and *Moxostoma congestum* had largest negative loadings. The first environmental axis described a mesohabitat gradient running from narrow, shallow sites with high oxygen concentration, to wide, deep sites with low oxygen concentration. Highest loadings on environmental axis 1 were for channel width, dissolved oxygen, and channel depth. The coefficient of determination for the relationship between assemblage axis 1 and environmental

TABLE 3—Eigenvalues, proportion of variance explained, cumulative proportions, and species' variable loadings (eigenvectors) for the first four axes from PCA performed on the 12 most abundant species based on fish species abundance [$\log_{10}(N + 1)$ -transformed].

Axis	Eigenvalue	Proportion	Cumulative proportion	
PC1	4.358	0.363	0.363	
PC2	2.099	0.175	0.538	
PC3	1.330	0.111	0.649	
PC4	1.198	0.100	0.749	
Species	PC1	PC2	PC3	PC4
<i>Gambusia affinis</i>	0.343	0.100	-0.212	-0.349
<i>Cyprinella venusta</i>	0.353	-0.212	0.234	0.112
<i>Cyprinella proserpina</i>	0.126	-0.253	0.620	-0.326
<i>Notropis amabilis</i>	0.396	-0.233	0.076	0.067
<i>Notropis stramineus</i>	0.264	0.075	-0.567	-0.355
<i>Dionda argentosa</i>	0.310	0.334	0.175	-0.250
<i>Micropterus dolomieu</i>	0.147	-0.374	-0.223	0.544
<i>Lepomis megalotis</i>	0.385	-0.238	-0.098	-0.085
<i>Cichlasoma cyanoguttatum</i>	0.307	0.114	-0.160	0.273
<i>Moxostoma congestum</i>	0.247	0.425	0.146	0.389
<i>Etheostoma grahami</i>	0.276	0.406	0.221	0.177
<i>Cyprinodon eximius</i>	-0.133	0.368	-0.007	0.057

axis 1 was $r^2 = 0.91$. *Lepomis megalotis* and *Dionda argentosa* had large positive loadings for assemblage axis 2, and *Etheostoma grahami* and *Micropterus dolomieu* had the largest negative loadings. The coefficient of determination for assemblage axis 2 and environmental axis 2 was $r^2 = 0.84$. The second environmental axis described a seasonal mesohabitat gradient that contrasts wide, shallow, warm sites with narrow, deep, cool sites. Highest loadings on environmental axis 2 were for depth, pH, and channel width.

To illustrate the variation of fish assemblages and environmental conditions across sites and seasons, scatterplots contrasting the first pair of assemblage and environmental axes were plotted with polygons enveloping mesohabitats and seasons (Fig. 5). Most sites occupied a relatively small space within the polygon that enveloped the full complement of data points (Fig. 5). The exception was site 4 which occupied more than half of the total space occupied by all sites collectively (similar to results from PCA). When seasonal trends were compared, summer occupied the largest space and winter the smallest (Fig. 6). During the summer, fishes tended to occupy all mesohabitats, whereas during winter, most species occupied

narrow, channel mesohabitats with high oxygen concentration.

DISCUSSION—Five species (four minnows and one mosquitofish) dominated the fish assemblages in the Devils River at Dolan Falls preserve, with the other 22 species comprising just 14.5% of the total fishes. This type of pattern, where just a few species numerically dominate an assemblage, seems to be common in animal community studies (May, 1975). Although species composition in this study was found to be similar to that found in previous studies (Harrell, 1978; Garrett et al., 1992), some of the differences in abundance ranks are important. Endemics such as *Cyprinella proserpina*, *Etheostoma grahami*, and *Cyprinodon eximius*, that are listed as endangered species by the Texas Organization for Endangered Species and the Texas Parks and Wildlife Department, ranked among the eight most abundant fishes in our study area. In contrast, previous surveys of the Devils River (Harrell, 1978; Garrett et al., 1992; Hubbs, unpublished data) found these three species ranking among the least abundant. Due to reductions in their limited geographic ranges, all three of these species are currently being evaluated for listing as either federally

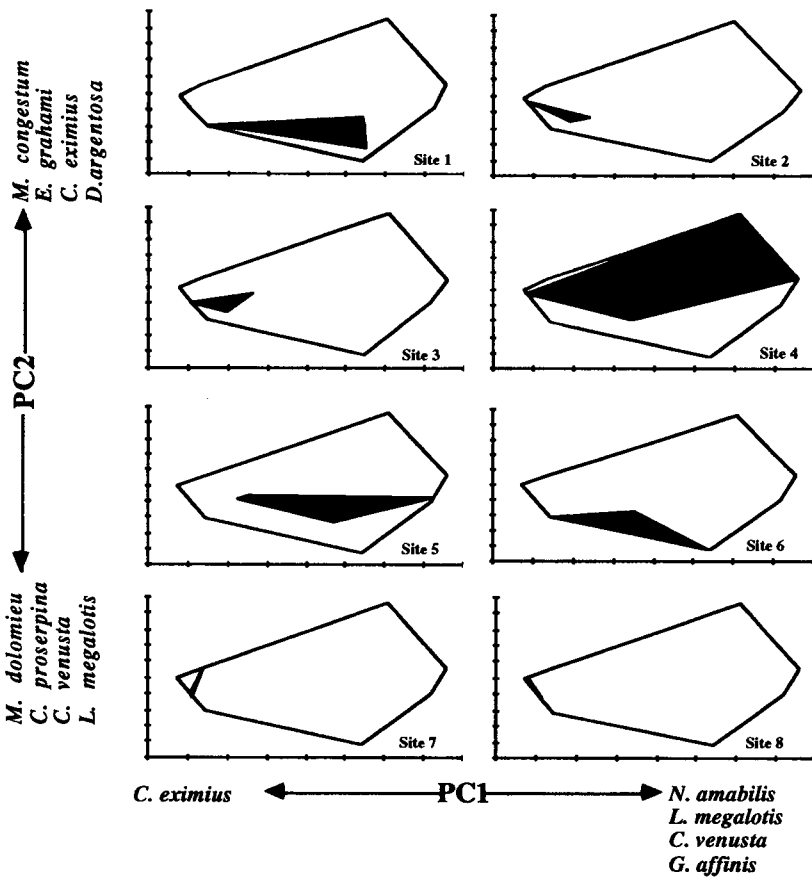


FIG. 3—Scatterplots highlighting mesohabitat variation on PCA axes 1 and 2 derived from fish assemblage data based on the abundances of the 12 most common species. The large polygon encloses the total multivariate space based on all sites and seasons (which is identical in each case), and the space occupied by each site across all 4 survey dates is shaded.

“threatened” or “endangered” species (G.P. Garrett, personal comm.). On the other hand, a few species previously considered abundant in the area, such as *Pimephales vigilax* and *Compostoma anomalum*, were not encountered during our surveys.

Another difference between this study and previous studies is the reporting of large species that were not reported before, such as *Ameiurus melas*, *Aplodinotus grunniens*, and *Cyprinus carpio*; plus the greater abundance of predatory species, like *Micropterus dolomieu*. A nonindigenous fish introduced into Amistad Reservoir in the 1960s, *Micropterus dolomieu* was not reported at all by Harrell (1978), and it was reported to be among the least abundant species by Hubbs (unpublished data) and Gar-

rett et al. (1992). *Micropterus dolomieu* was found to be among the most abundant species in our study. Density changes in endemics and certain minnows (e.g., *Compostoma anomalum*) might be related to the changes in abundance of the predatory species, however this hypothesis needs to be tested directly. Variation in sampling techniques probably accounts for many of the between-study differences in species relative abundances. No single sampling technique is completely effective in all mesohabitats under all conditions. In order to examine community structure within mesohabitats, we estimated species relative abundances using a combination of different sampling methods (i.e., experimental gillnet, seining, electroshocking, in situ observations). Whereas

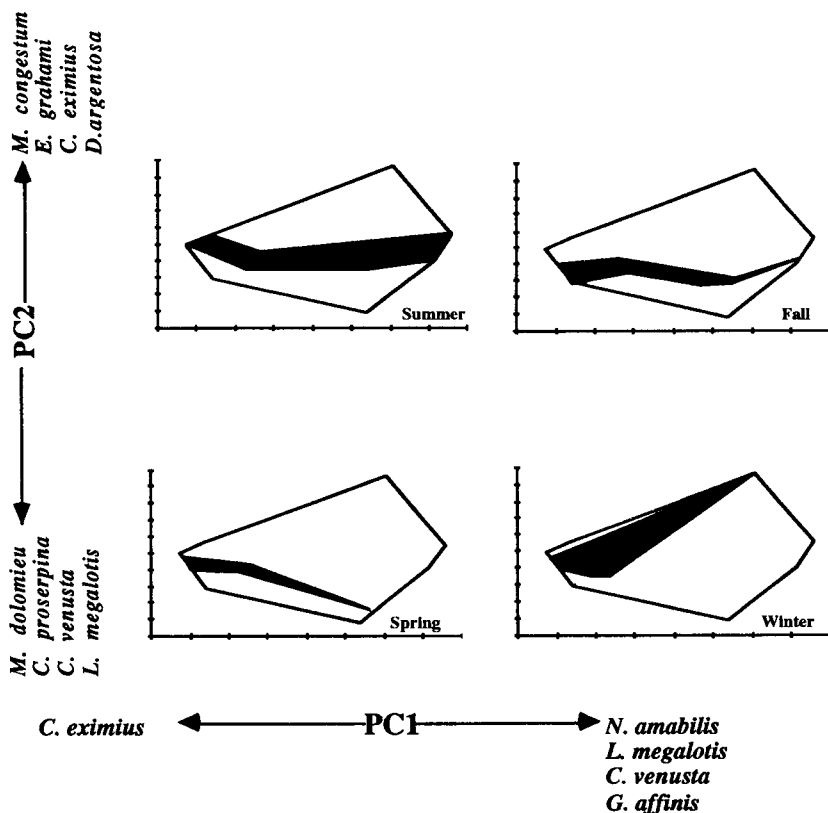


FIG. 4.—Scatterplots highlighting seasonal variation on PCA axes 1 and 2 derived from fish assemblage data. The large polygon encloses the total multivariate space based on all sites and seasons, and the space occupied by each season across all 8 sample sites is shaded.

total sampling effort was not the same for all sample sites, the criterion for establishing effort was always the same (i.e., sample until 30 minutes of effort yielded no new species).

Stream fish species richness and diversity are hypothesized to be positively related to habitat area or volume (Schlosser, 1987; Oberdorff et al., 1995). Patterns generated by this study are only partially consistent with this hypothesis. The riffle, which was smaller than most of the other mesohabitats sampled (e.g., deep pool), had a relatively large number of species (11 during summer) and relatively high diversity ($H' = 0.75$ during summer). Substantial temporal variation occurred in both species richness and species diversity. As expected for most of the mesohabitats, larger numbers of species and greater diversity were found during summer and spring when environmental conditions tend to be more conducive for reproduc-

tion and growth. Site 3 (riffle) was the only exception to this rule, with species richness being slightly higher during the fall and winter.

The movement of fishes to and from Amistad Reservoir located downstream also contributes to seasonal differences in fish structure in the Devils River. For example, *Dorosoma cepedianum* was collected from the deep pool during spring, and many of these likely were migrants from the reservoir. During the winter, many of the large species were absent (with the exception of gars, *Lepisosteus osseus*, in the pool), probably as a result of migration to deeper warmer waters of the reservoir. Reservoirs have been shown to influence the faunas of tributary rivers (Meador and Matthews, 1992). Additionally, smaller-scale, seasonal migrations at our site might have been associated with Dolan Creek. *Notropis stramineus* disappeared from the study reach during fall and

TABLE 4—First three axes from canonical correlation analysis for fish assemblages and associated environmental variables, with their corresponding canonical correlations, eigenvalues, and proportions of variance modeled.

	1	2	3
Canonical correlation	0.913	0.837	0.685
Eigenvalue	5.032	2.354	0.887
Proportion	0.552	0.258	0.097
Assemblage variables			
<i>Gambusia affinis</i>	-0.117	0.014	-0.626
<i>Cyprinella venusta</i>	-0.029	0.012	0.726
<i>Cyprinella proserpina</i>	0.638	0.008	0.015
<i>Notropis amabilis</i>	-0.716	-0.390	-0.190
<i>Notropis stramineus</i>	0.568	-0.308	0.073
<i>Dionda argentosa</i>	0.059	0.807	0.286
<i>Micropterus dolomieu</i>	0.531	-0.565	0.222
<i>Lepomis megalotis</i>	0.365	1.082	-0.116
<i>Cichlasoma cyanoguttatum</i>	0.412	-0.227	-0.508
<i>Moxostoma congestum</i>	-0.396	0.872	-0.256
<i>Etheostoma grahami</i>	0.496	-1.237	0.498
<i>Cyprinodon eximius</i>	-0.135	0.257	-0.509
Environmental variables			
Channel width	0.591	0.666	0.597
Depth	0.492	-0.737	-0.388
Water temperature	0.091	0.327	-0.346
Current velocity	0.039	-0.069	0.880
Conductivity	-0.195	-0.151	-0.194
pH	0.073	-0.676	0.702
Oxygen concentration	-0.515	-0.091	-0.632

winter, and may have moved into the spring-fed Dolan Creek in search of a warmer environment. The warmest winter temperatures were recorded at site 1 just below the mouth of Dolan Creek.

Small fishes dominated almost all of the mesohabitats, a finding similar to those from studies of other southwestern streams. Numerical abundance tended to decline with increasing body size. The only site that presented a different pattern was the deep pool (site 6) dominated by large species. Larger fish may seek deeper water where they are less vulnerable to terrestrial and avian predators (Power, 1984). Most of the small species were not very abundant in the deep pool, which suggests piscivore avoidance. Only two minnows, *Cyprinella venusta* and *Notropis amabilis*, were abundant at that site. This pattern seems to agree with a previous community study that included the same two species (Matthews et al., 1994), in which, as in this case, the two species coexisted in pools with potential predators. By so doing,

these small, drift-feeding fishes may benefit from reduced competition because of lower densities of small heterospecific fishes that might be less proficient at evading predator attacks.

A relatively small subset of environmental variables contributed to a CANCOR model that described fish community structure at the mesohabitat spatial scale. This model indicated strong seasonal patterns of variation in which the broadest range of mesohabitats were used during the summer, and mesohabitat occupation collapsed towards narrower, shallower, more oxygenated sites during the winter.

Diverse reproductive strategies are represented among Devils River fishes, but small opportunistic species that spawn year-round were dominant. Out of 4,740 fishes collected, 4,468 (94.3%) had traits associated with Winemiller's (1992; Winemiller and Rose, 1992) opportunistic strategy, 190 (4%) with the equilibrium strategy, and 82 (1.7%) with the periodic strategy. Following Balon's (1975) classification of

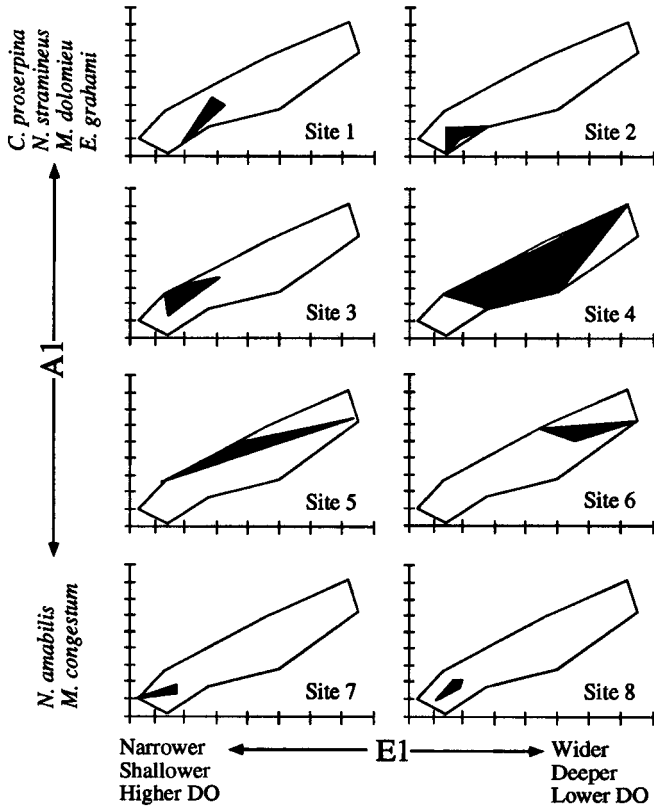


FIG. 5—Scatterplots highlighting mesohabitat variation on the first pair of canonical assemblage and environmental axes derived from CANCOR with 12 common fish species and 7 environmental variables. The large polygon encloses the total multivariate space based on all sites and seasons, and the space occupied by each site across all 4 survey dates is shaded.

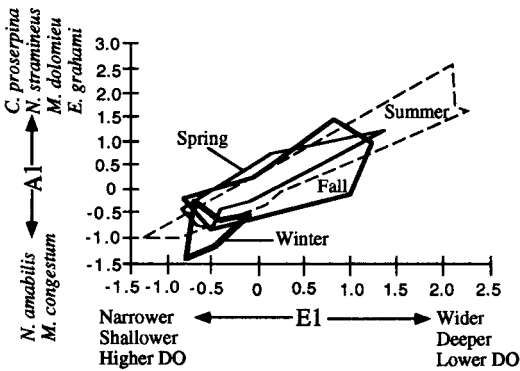


FIG. 6—Scatterplot highlighting seasonal variation on the first pair of canonical assemblage and environmental axes derived from CANCOR. The large polygon encloses the total multivariate space based on all sites and seasons, and the space occupied by each season across all 8 sample sites is shaded.

reproductive guilds, 4,037 fishes were non-guarding, open-substrate spawners, 260 were non-guarding, brood hiders (*Cyprinodon*), 14 were guarding, substrate choosers, 154 were guarding nest spawners, and 274 were internal bearers (*Gambusia*). The majority of Devils River fishes seem to be well equipped to repopulate habitats following natural disturbances, such as scouring flash floods (Harrell, 1978; Matthews, 1986), or in the face of continuous high mortality during the adult stage (e.g., predation mortality). Dominance by opportunistic strategists is logical for aquatic assemblages of desert rivers where conditions are highly variable and at times very harsh (flash flooding, desiccation, temperature extremes) (Meffe and Mickley, 1986). If the natural hydrology, water quality, and riparian habitats of the Dev-

ils River are protected and impacts from non-indigenous species minimized, the threatened native fishes appear well-suited to rapidly repopulate habitats in the event of population reductions following natural disturbances.

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