

SPATIAL AND TEMPORAL VARIATION IN  
FISH ASSEMBLAGE STRUCTURE IN VILLAGE CREEK,  
HARDIN COUNTY, TEXAS

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**Abstract.**—Fish assemblages were sampled seasonally at Village Creek, a blackwater tributary of the Neches River in Hardin County, Texas. Forty-four fish species were captured from aquatic mesohabitats that included backwater pools, deep channel pools, sloping sandbanks, sandy riffles, and shallow channel margins. Associations between fish assemblage structure and mesohabitats were strong, yet also affected by seasons and discharge fluctuations. Principal components analysis (PCA based on faunal composition at sample sites across four seasons) was performed on a dataset containing the 10 species with highest site occurrence. The first PC axis identified an assemblage gradient that contrasted deep pool and backwater habitats versus shallow riffle and sandbank habitats, and the second PC axis identified a gradient between backwaters versus channel habitats. Relationships between assemblage composition and mesohabitat attributes were examined using canonical correlation analysis (CCA) based on the 10 species with the highest site occurrences and six physical parameters at each site. The first canonical correlation gradient modeled 75% of the total variation and was primarily a water temperature gradient secondarily influenced by dissolved oxygen. Seasonal variation in species relative abundances and length frequency distributions were examined according to mesohabitats. Seven fishes, including the dominant species, *Cyprinella venusta*, revealed size distribution patterns consistent with protracted spawning seasons. During winter and spring, stream discharge was high and many species increased the range of habitats occupied. Juveniles of many species tended to occupy shallower mesohabitats than adults, with backwaters being particularly important for several channel pool-dwelling species. Seasonal variation in fish relative abundances and mesohabitat associations poses problems for indices of biotic integrity, however, following Karr's index, the Village Creek fish community is classified as excellent to good.

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This study examines spatiotemporal patterns of fish assemblages in Village Creek, a relatively pristine stream in the Big Thicket region of east Texas, and contributes species assemblage and population structure data useful for ecological assessment. Patterns in community structure and the perceived degree of assemblage stability are influenced by the spatial scale of observations. Matthews et al. (1994) contended that stream investigators should select spatial scales that reflect biologically meaningful units, in contrast to *a priori* selection of linear distances for study. In a large stream, neither the watershed nor the entire stream

reach captures local species interactions, because many species would never, or rarely, come into contact with one another. At the other extreme of the spatial continuum, microhabitats would not encompass species interactions, because, theoretically, a microhabitat is occupied by a single individual in a given instance. Species interactions, life history strategies, population dynamics and habitat selection influence patterns of assemblage structure at the mesohabitat level. Most individual fishes interact and have diel movements at this mesohabitat scale; therefore, this was the spatial scale chosen for analysis of assemblage composition in Village Creek.

Matthews et al. (1994) concluded that stream pools and riffles were biologically meaningful units for spatial analysis, but the channel of Village Creek does not conform well with these units. Within the study reach, there were no shallow riffles that spanned the stream channel, however discernible habitats were visible along the banks of the stream (e.g., shallow riffle-like habitats, backwaters, gently sloping sandbanks), and these conform well with Meffe & Sheldon's (1988) mesohabitat definition. The riffle-like habitats in Village Creek were defined as fast flowing, shallow water over corrugated sand bars. These riffles normally did not span the entire width of the stream channel, yet they contained many of the physical features of a true riffle.

Village Creek is a blackwater stream of the Gulf coastal plain in east Texas. Blackwater streams have been studied less than most other stream types in North America (Hocutt & Wiley 1986; Meffe & Sheldon 1988). Blackwater streams typically are acidic (pH 3.5-6.5), have low conductivity and suspended sediments, and are stained with humic substances (e.g., fulvic and tannic acids) leached from surrounding watersheds (Meyer 1992). In the southeastern U.S., blackwater streams flow over sandy soils, have low gradients, and generally drain floodplain swamps (Meyer 1992).

#### STUDY AREA

Village Creek forms the western boundary of the Nature Conservancy of Texas' (TNCT) Larson Reserve, a 970 ha restoration and management area. The reserve is immediately west of Silsbee, 40 km north of Beaumont in Hardin County, Texas, and is situated on sandy alluvial

deposits that support a unique xerophytic plant community. In addition to the xerophytic community of the uplands, the reserve has bottomland hardwood forests and baygall communities. During the course of the study, TNCT leased an additional 162 ha along Village Creek's west bank from Temple-Inland Corporation (TNCT Annual Report 1993), so that now the entire watershed is protected from the reserve's upstream boundary (FM 418) to its downstream (HWY 327). During October 1996, the entire riparian zone of Village Creek received federal protection from landscape alterations.

Village Creek is a low gradient stream with characteristics of blackwater streams in the southeastern U.S. The stream bed is primarily sand without any gravel or rocks, and silt and leaf litter accumulates in cypress backwater sloughs. Bottomland hardwood forests (e.g., southern magnolia [*Magnolia grandiflora*], American beech [*Fagus grandiflora*]) shade both banks of the stream, and fallen limbs and trees provide cover for fishes and influence the shape of the channel, as do roots and trunks of living trees. Woody debris is characteristic of blackwater streams, and, wood provides a stable substrate in a channel of shifting sand and supports high production of benthic macroinvertebrates, a major source of food for fishes (Benke et al. 1985). Aquatic macrophytes are absent in the channel. Backwater sites are shaded by cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) and are frequently covered by water lilies (*Nymphaea odorata*). Lily coverage is greatest during summer. Channel water is clear and tea colored from dissolved organic compounds but becomes turbid during spates.

## METHODS AND MATERIALS

A 3.3 km reach of Village Creek was sampled seasonally (Summer - 29-31 July, 1993; Fall - 21-22 October, 1993; Winter - 21-22 January, 1994; and Spring - 15-16 April, 1994) from FM 418 downstream to the Gulf, Colorado and Santa Fe Railway bridge. During spring, an additional 1 km was sampled just upstream from HWY 327. Following Frissel et al. (1986), mesohabitats were defined as pools, riffles and runs. Sites were selected for quantitative sampling on the basis of two characteristics: (1) presence of a distinctive habitat type (e.g., channel pool vs. sandy riffle vs. backwater cypress slough, etc.) and (2) relative degree of homogeneity (subjectively judged) within a site. Meffe & Sheldon (1988) stated that multiple microhabitats are represented within

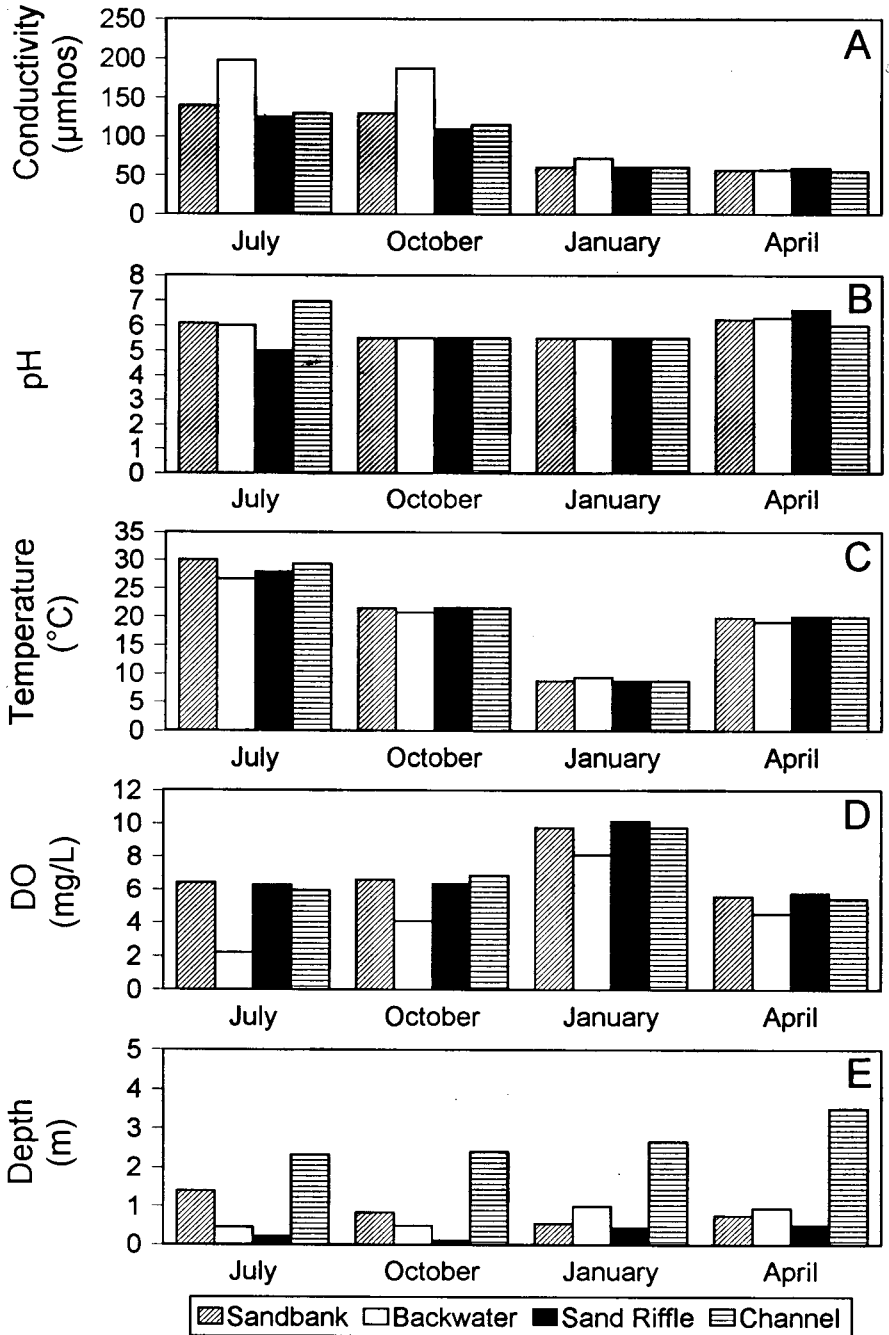


Figure 1. Seasonal variation in conductivity (A), pH (B), temperature (C), dissolved oxygen (D), and depth (E) in mesohabitats at Village Creek.

such sites, but heterogeneity at the mesohabitat scale within a site is minimized by these criteria. Site boundaries were determined by natural stream physiography and were not standardized by length (range = 5–30 m).

During each season (except fall), depth and width were measured just below the railway bridge. The depth measurement was taken in the middle of the stream, from the stream floor to the surface of the water, using a weighted measuring tape (and compensating for stream flow), or the graduated pole of the flow meter (ca. 3 m). Maximum stream depth fluctuated from 2.3 m during summer to 3.5 m during spring (Fig. 1), and maximum stream width from 29.5 m to 39.7 m.

At each site, an attempt was made to sample the entire fish assemblage, such that the sample for each species reflected its relative abundance and population size structure during each season. The collecting effort expended each season was approximately equal for each site or mesohabitat. The same sites were not used every season because sometimes sites used in a previous season were flooded. Sampling was terminated when additional effort produced no additional rare species.

During each season, 7–11 sites were sampled. Sandbanks on the edge of the stream, sand riffles, and backwaters were sampled with a 3 by 1.9 m seine (mesh = 3 mm) and a 6.2 by 1.8 m seine (mesh = 9.5 mm). Leaf litter and woody debris at the edge of the stream were sampled with dip nets and the 3 m seine. Except for large individuals (>150 mm), which were identified, measured and thrown back, all collected fishes were preserved in 10% formalin. Deep areas (>1.5 m) of the stream channel were sampled using a hand-held boat electroshocking unit and a monofilament experimental gillnet (45.7 by 2 m with 2.5 cm, 5 cm, and 7.5 cm mesh panels). The gillnet was set for a minimum of 4 hr in deep pool areas. Except for the spring when the electroshocking unit was inoperable, a 3.3 km study reach of the stream channel received one intensive electroshocking pass per seasonal sample. Four people floated downstream from FM 418 to the railway bridge and sampled deep pool areas, especially near woody debris. Electroshocking was performed between 1500–1800 hr, and total effort was approximately equal for each seasonal sampling event (>1 to 2 hr).

Samples of the deep pool/channel fish assemblage were not as

complete as those from other mesohabitats. Water column fishes were well represented, but benthic species in deep pools probably were underrepresented. Electroshocking catch-per unit effort (CPUE) was inversely associated with stream discharge. Assuming that the size of the electric field remained constant, as the depth of the water increases, the electric field no longer extends through the entire depth profile. On 30 July, 1993, the discharge was  $2.91 \text{ m}^3/\text{s}$ , or about  $0.7 \text{ m}^3/\text{s}$  more than the lowest discharge recorded during the year of study (June 1993–May 1994, Fig. 2). Electrofishing CPUE was higher during summer (70 fish/hr) than fall (14 fish/hr) and winter (6 fish/hr). On 21 January, 1994, the discharge was  $13.62 \text{ m}^3/\text{s}$ , over four times higher than the summer sample period. On 15 April, 1994, when the electroshocking unit was inoperable, the discharge was  $21.32 \text{ m}^3/\text{s}$ .

Physical and chemical features were recorded for each mesohabitat sampled. Substrate composition and the presence of submerged woody debris, aquatic vegetation, and shoreline vegetation were recorded. Channel dimensions were measured with a 50 m measuring tape. Water current velocity was measured with a portable Marsh-McBirney, Inc., Flow-Mate Model 2000 flow meter. Whatman low-range pH indicator strips (4.5–10 pH in 0.5 pH units) were used to measure pH. Dissolved oxygen and temperature were measured with a Yellow Springs Instruments portable oxygen meter (model 58), and conductivity and salinity were measured with a Yellow Springs Instruments conductivity meter (model 33).

Preserved fishes were transported to the lab for analysis. Prior to identification, the specimens were removed from the formalin solution, soaked in water for 12–24 h, and stored in 70% ethanol. Page & Burr (1991) and Eddy & Underhill (1978) were used as identification guides. Referenced specimens were deposited in the Texas Cooperative Wildlife Collection, Texas A&M University. Standard length was measured with vernier calipers. For the abundant species, a few individuals of adult size were examined, and variation in gonad condition and egg diameter, the latter measured using a dissecting scope with an ocular micrometer, were recorded.

Principal components analysis (PCA) was used to examine patterns of covariation in species abundances by sites and dates. This approach is

relevant to the more general question of temporal stability of assemblage structure. An  $m \times n$  data matrix was constructed, where  $m$  represents species and  $n$  represents samples taken over time or space. Using an eigenvector solution, the analysis produces  $m$  principal components; the first component explains the maximum amount of variance in the dataset along a single axis, and all subsequent components iteratively explain the maximum amount of variance remaining. Loadings of each variable on each PCA axis indicates the degree to which that variable contributes to modeling total variation by that axis (Gauch 1982). A database was generated with columns ( $m$ ) being made up of species and rows ( $n$ ) of mesohabitats/sites. The raw numerical abundance data approximated a lognormal distribution, as did the converted relative abundance data. Both databases were  $\log_e(x+1)$ -transformed to reduce skewness. Components were considered interpretable if their eigenvalues were greater than 1.0 (Grossman et al. 1991).

Thirty four samples were obtained, but five samples yielded no fish, thus reducing the effective sample number to 29, from which 44 fish species were collected (Table 1). Grossman et al.'s (1991) demonstrated that an increase in the number of observations (samples) improved the performance of the eigenvalue tests regardless of the number of independent variables (species). Provided that the number of samples ( $n$ ) was at least 3 times the number of species ( $3 \times m$ ), the eigenvalue tests generally operated at the 0.05 level. With  $n = 29$ ,  $m$  should equal approximately 10 (i.e.,  $n = 3 \times m$ ). Therefore, the 10 species with the highest site occurrence were used for PCA (Table 2). When the database was reduced to 10 species, the summer channel edge sample fell out. Fishes in this sample tended to be rare (e.g., *Aphredoderus sayanus* and *Elassoma zonatum*).

Two databases were generated for PCA. One was made up of  $\log_e(x+1)$ -transformed raw abundance data, and the other of  $\log_e(x+1)$ -transformed relative abundances. The interpretations of the gradients produced by the two methods (both using the dominant 10 species) were virtually the same, although the variable loadings were not identical. Raw abundance PCA is reported here, because the relative abundance database (relative proportions for species within sites) could bias results, in that an abundant species at a site might be much less abundant than another species at that site and thus be assigned a low relative abundance.

Table 1. Fish species, total number of specimens and number of sites collected at Village Creek, presented in descending order of site occurrence.

Species	Number	Sites Present
<i>Cyprinella venusta</i>	1148	16
<i>Pimephales vigilax</i>	583	15
<i>Gambusia affinis</i>	263	14
<i>Fundulus olivaceus</i>	137	14
<i>Notropis sabiniae</i>	194	13
<i>Notropis texanus</i>	153	11
<i>Lepomis macrochirus</i>	61	11
<i>Etheostoma vivax</i>	118	10
<i>Labidesthes sicculus</i>	98	10
<i>Micropterus punctulatus</i>	31	10
<i>Lythrurus fumeus</i>	327	9
<i>Lepomis megalotis</i>	45	8
<i>Esox americanus vermiculatus</i>	7	7
<i>Centrarchus macropterus</i>	64	6
<i>Etheostoma proeliare</i>	21	6
<i>Hybognathus nuchalis</i>	18	6
<i>Lepomis punctatus</i>	9	6
<i>Aphredoderus sayanus</i>	19	5
<i>Opsopoeodus emiliae</i>	16	5
<i>Etheostoma chlorosomum</i>	14	5
<i>Noturus nocturnus</i>	9	5
<i>Percina sciera</i>	5	5
<i>Hybopsis amnis</i>	30	4
<i>Pomoxis annularis</i>	21	4
<i>Moxostoma poecilurum</i>	15	4
<i>Notropis atrocaudalis</i>	11	4
<i>Etheostoma fusiforme</i>	8	4
<i>Elassoma zonatum</i>	22	3
<i>Minytrema melanops</i>	10	3
<i>Etheostoma clarum</i>	7	3
<i>Lepisosteus oculatus</i>	3	3
<i>Phenacobius mirabilis</i>	3	3
<i>Notemygonus crysoleucas</i>	8	2
<i>Fundulus blairae</i>	8	2
<i>Etheostoma gracile</i>	6	2
<i>Lepomis gulosus</i>	3	2
<i>Lepomis microlophus</i>	2	2
<i>Notropis vollucellus</i>	45	1
<i>Mugil cephalus</i>	9	1
<i>Ictalurus punctatus</i>	3	1
<i>Aplodontiis grunniens</i>	1	1
<i>Etheostoma histrio</i>	1	1
<i>Pylodictus olivaceus</i>	1	1
<i>Dorosoma petenense</i>	1	1

Canonical correlation (CCA) was performed on a database containing the log-transformed ( $\log_e[x + 1]$ ) raw abundances of the 10 species with highest site occurrences, and six physical parameters measured at each site: water temperature, dissolved oxygen, conductivity, pH, depth, and



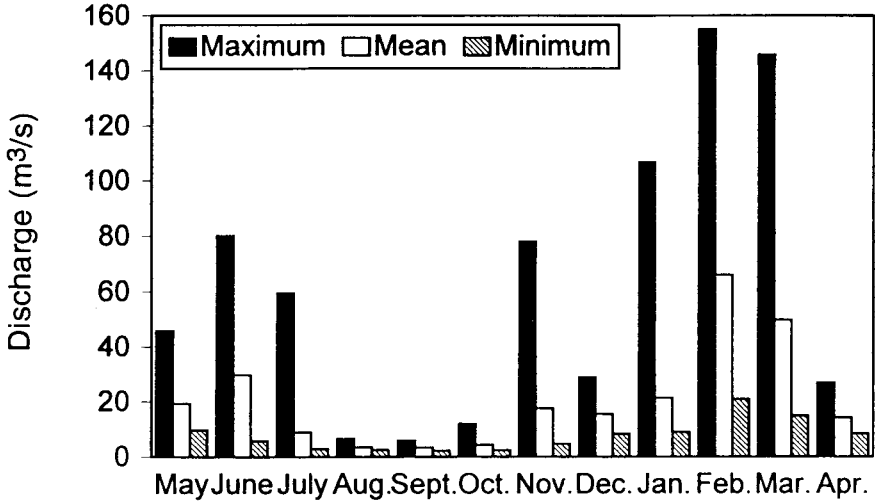


Figure 2. Maximum, mean and minimum monthly discharge at Village Creek from May 1993 to April 1994.

current velocity. CCA identifies relationships between two sets of variables by finding the linear combinations of the variables in the first set that are most highly correlated with the linear combinations of the variables in the second set (Lebart et al. 1984) or the regression of one vector on another vector (Kshirsagar 1972). By considering only the first few dominant canonical variables, CCA reduces the complexity of a multiple variable problem (Kshirsagar 1972). After derivation of the canonical vectors, correlations of the original variables with these vectors (loadings) were computed. The resulting canonical structure served as the basis for biological interpretation (Page & Swofford 1984). Bartlett's test for the equality of eigenvalues was used to test the significance of canonical correlations; a pair of canonical vectors was considered only if a test of equality of the remaining eigenvalues (squared canonical correlation coefficients) was significant at  $P < 0.05$ . Both PCA and CCA were performed using PCSAS. Species abundance and environmental data were log-transformed ( $\log_e[x+1]$ ) prior to canonical correlation. To examine how individual species responded to spatiotemporal variation in stream habitat, length-frequency distributions were plotted by seasons and mesohabitats.

## RESULTS

*Water quality.*—Village Creek water was soft (conductivity 15–197

Table 2. PCA Statistics for the Village Creek fish data matrix based on  $\log_e$ -transformed abundances of 10 species with highest site occurrence and 25 sites. Variable loadings (eigenvectors) on the first three PC axes that were between -0.150 and 0 are listed as —, and those between 0 and 0.350 are listed as +.

	PC1	PC2	PC3
Eigenvalue	4.032	2.336	1.159
% variance	40.3	23.4	11.6
<b>Variable</b>			
<i>C. venusta</i>	0.440	—	-0.233
<i>P. vigilax</i>	0.466	—	—
<i>G. affinis</i>	+	0.465	-0.555
<i>F. olivaceus</i>	+	+	+
<i>N. sabiniae</i>	0.407	-0.185	-0.263
<i>N. texanus</i>	+	+	0.430
<i>L. macrochirus</i>	-0.172	0.510	+
<i>E. vivax</i>	0.439	+	+
<i>L. sicculus</i>	+	0.557	-0.175
<i>M. punctulatus</i>	+	+	0.546

$\mu$ mhos; Fig. 1) and acidic (pH 5–6.95; Fig. 1). During the sampling year, water temperatures ranged from 8.7°C in the winter to 30°C in the summer (Fig. 1), and, except for backwater habitats during the warmer months, DO was never recorded below 5 mg/L (Fig. 1). Discharge fluctuated from 2.2 m<sup>3</sup>/s to 155.19 m<sup>3</sup>/s (Fig. 2; gauging station #08041500 at the downstream side of the FM 418 bridge and 2.56 km upstream from the Gulf, Colorado, and Santa Fe Railway bridge; Gandara et al. 1994).

*Assemblage structure.*—The first three axes of the 10-species PCA accounted for 40.3, 23.4 and 11.6%, respectively, and 75.3% collectively, of the total variance (Table 2). Figure 3 shows the distribution of 25 sites across all seasons on PCA axes I and II, plus the highest and lowest species loadings associated with each axis. In each panel, identical scatterplots are bounded by the open polygon, but each panel contains a different filled polygon bounding the total space occupied by a given mesohabitat throughout the sample year. Because the space occupied by each mesohabitat was small relative to the total space occupied by all mesohabitats, mesohabitat assemblages were relatively small subsets of the total fauna.

The first PC axis identified an assemblage gradient that contrasted pool and backwater habitats versus riffle and sandbank habitats. The

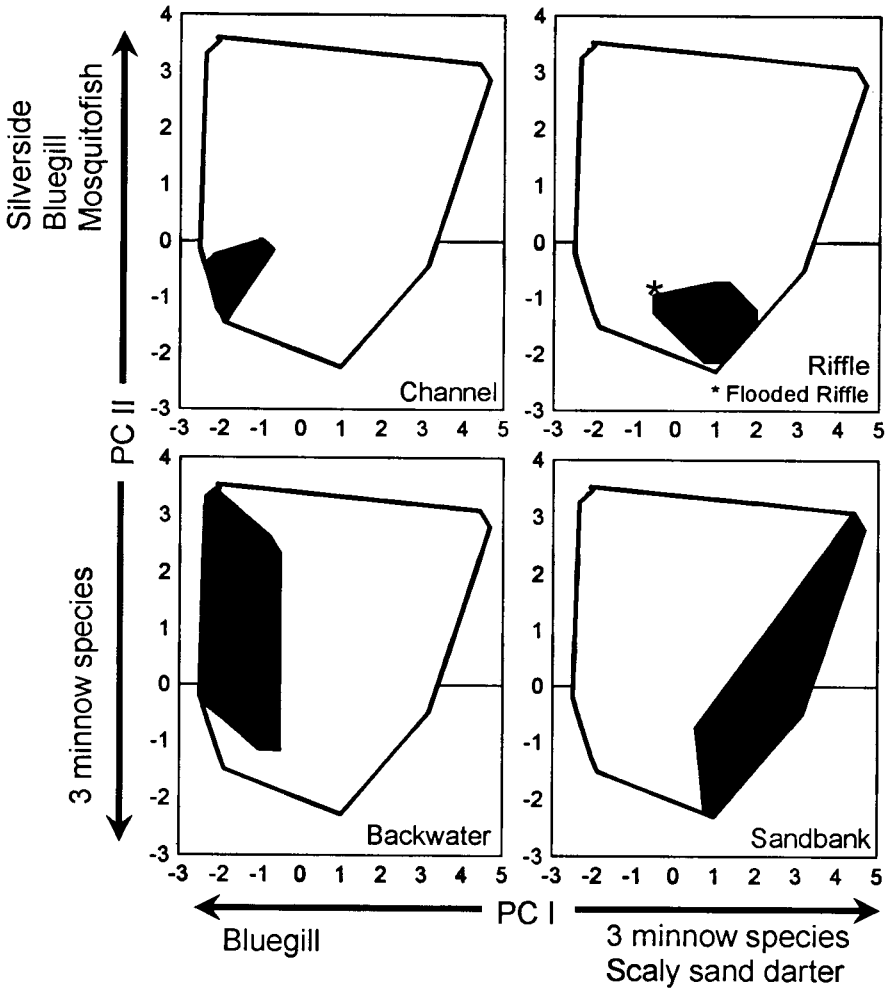


Figure 3. Scatterplots of principal component axes I and II for 25 sample sites across time in Village Creek, with the total multivariate space occupied by all samples enclosed by the large polygon (which is identical in each case), and the total multivariate space occupied by each mesohabitat across all survey dates depicted by the solid polygon.

stream channel and backwaters were dominated by *Lepomis macrochirus*, and riffle and sandbank habitats were dominated by cyprinids (*Notropis sabinae*, *Pimephales vigilax*, *Cyprinella venusta*) and *Etheostoma vivax* (Table 2, Fig. 3). The second PC identified a gradient that contrasted backwaters versus the stream channel, sandbank and riffle habitats (Table 2, Fig. 3). The latter habitats were dominated by

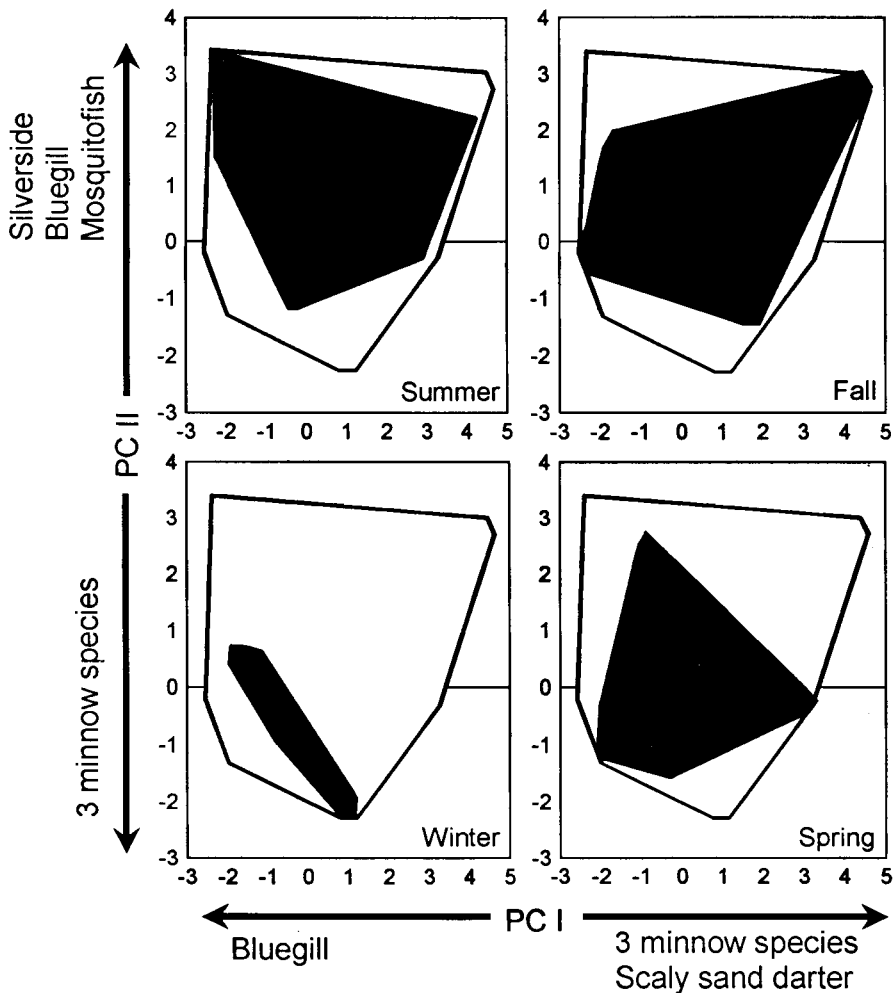


Figure 4. Scatterplots of PC axes I and II as in Figure 3, but with solid polygons bounding the total multivariate space occupied by all mesohabitats during each season.

cyprinids (*N. sabiniae*, *P. vigilax*, *C. venusta*); the backwater habitats by *Labidesthes sicculus*, *L. macrochirus* and *Gambusia affinis*. Two sandbank habitats were strongly influenced by *L. macrochirus*, and had high scores on PC2. The third PC identified an assemblage gradient aligned along the lateral stream gradient of channel pools versus shallow marginal regions and backwater habitats (Table 2). Sites with high

Table 3. Correlations of habitat variables and species abundances with the first two canonical vectors from CCA.

Variable	Canonical vector	
	I	II
<u>Physical Parameter</u>		
Water temperature	0.922	-0.223
Dissolved oxygen	0.429	0.873
Conductivity	-0.052	-0.241
pH	0.260	-0.010
Depth	0.111	0.091
Current	0.351	0.179
<u>Species</u>		
<i>Cyprinella venusta</i>	0.352	0.116
<i>Pimephales vigilax</i>	-0.213	0.224
<i>Gambusia affinis</i>	0.267	-0.798
<i>Fundulus olivaceus</i>	0.020	-0.076
<i>Notropis sabiniae</i>	-0.505	0.319
<i>Notropis texanus</i>	-0.283	0.452
<i>Lepomis macrochirus</i>	-0.420	-0.038
<i>Etheostoma vivax</i>	0.546	-0.245
<i>Labidesthes sicculus</i>	-0.199	-0.029
<i>Micropterus punctulatus</i>	0.855	-0.187
Canonical correlation (r)	0.974	0.892

scores on PC3 were dominated by centrarchids (*Micropterus punctulatus*) and cyprinids (*Notropis texanus*); sites with low PC3 scores were dominated by *G. affinis*. The two winter backwater sites were outliers relative to backwater sites during other seasons, as was the winter flooded riffle sample. Backwaters served as refugia for several channel-dwelling species during the high stream discharge of winter (e.g., *N. texanus*). Two sandbank habitats were also strongly influenced by *N. texanus*, and had high scores on PC3.

To examine seasonal variation in assemblage structure, the same PCA data were plotted with the shaded polygons representing the total multivariate space occupied by all sampled mesohabitats during a given season (Fig. 4). Assemblages showed more spatial structure (Fig. 3) than temporal structure (Fig. 4), which means that mesohabitat assemblages remained fairly distinct year round. This pattern had two exceptions. The winter sample had low between-mesohabitat variation in assemblage structure compared with the other seasonal samples. The other exception was the spring sample, where the polygon in Figure 4 is distorted by a single backwater sample. If that sample were omitted

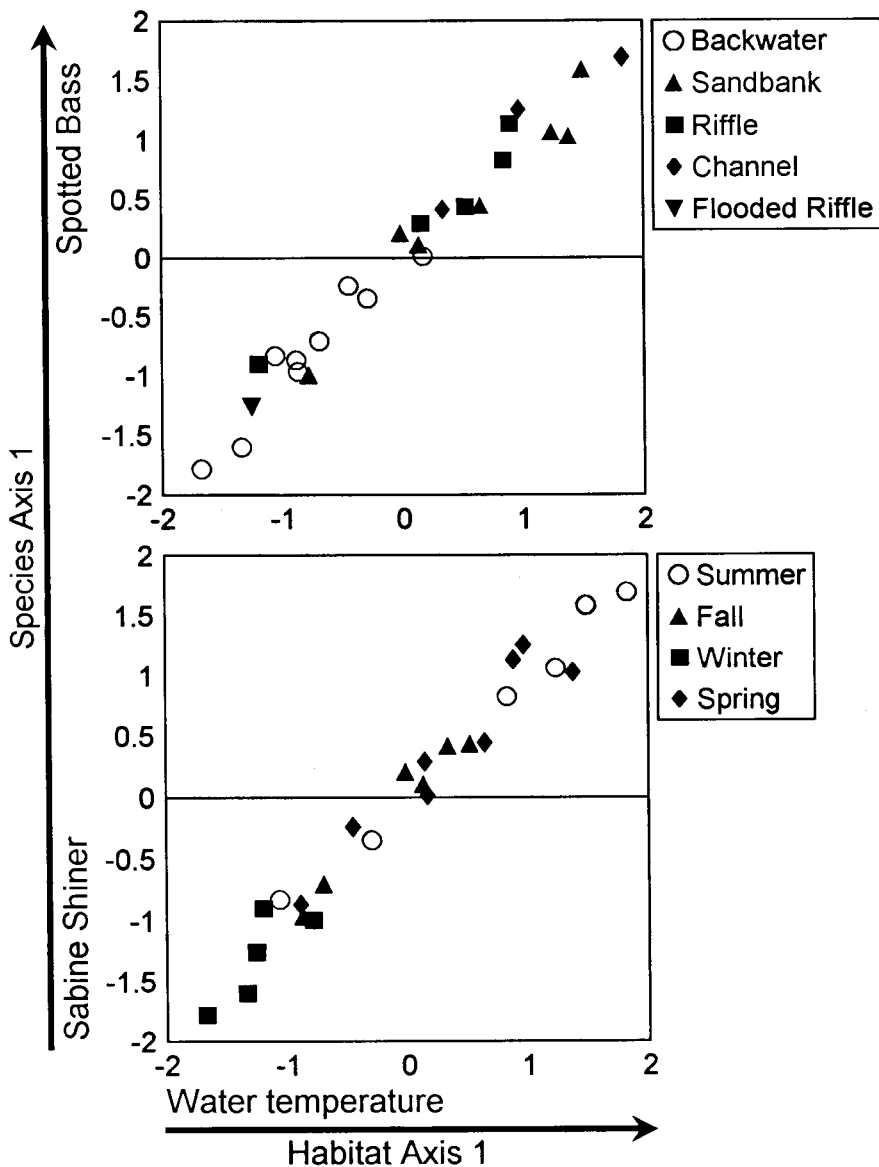


Figure 5. Locations of mesohabitats and seasonal samples in the space determined by the first pair of canonical vectors (species and physical parameter variables) of CCA.

from the spring polygon, the new polygon area would be below the abscissa, which would indicate that between-mesohabitat variation in

assemblage structure was low compared with the summer and fall samples.

The canonical structure for the first two pairs of axes from CCA analysis is shown in Table 3. The first axis explained 75% of the variance (eigenvalue = 29.3, Bartlett's test  $P < 0.0001$ ). The channel and sandbank mesohabitats had high scores on both linear combinations, whereas backwater mesohabitats had low scores (Fig. 5). Water temperature, dissolved oxygen and current had high loadings on the first gradient axis, as did *M. punctulatus*, *E. vivax*, and *N. sabiniae*. The winter sandbank, flooded riffle and low-water riffle samples were influenced by cold water temperatures, and shared certain backwater characteristics, such as cooler temperatures. As in the PCA, winter backwater sites showed high similarity to several of the lotic habitats. During winter, the physical environment of the overall stream reach tended to be more homogeneous, and many channel-dwelling species (e.g., *N. texanus*) occupied backwaters.

The second CCA gradient (eigenvalue = 6.33, variation explained = 16% of the total variance, Bartlett's test  $P = 0.057$ ) indicated an assemblage association with dissolved oxygen, and contrasted backwaters against riffle and sandbank mesohabitats (Table 3). *Gambusia affinis* and *N. texanus* had highest loadings on axis 2 (Table 3).

*Species mesohabitat use.*—*Cyprinella venusta* occurred year-round in riffle and sandbank habitats (Fig. 6). During the summer, most individuals were captured from sandbank habitats. *Cyprinella venusta* also were found in deep channel and riffle habitats, although no individual  $> 47$  mm SL occurred in riffles. Individuals  $< 17$  mm SL were found predominantly in riffle habitats during fall and winter. During spring, juveniles were found almost exclusively in the sandbank mesohabitat. *Pimephales vigilax* was captured almost exclusively from sandbank habitats, except during winter when individuals were collected from riffle and flooded riffle habitats. *Notropis sabiniae*'s mesohabitat-size relationships were much like those observed for *C. venusta*; with small individuals in shallow riffles and larger individuals in deeper parts of sand bars. This species occurred almost exclusively in riffle and sandbank habitats, except for six individuals that were found in a backwater sample during the high stream discharge of spring. *Fundulus*

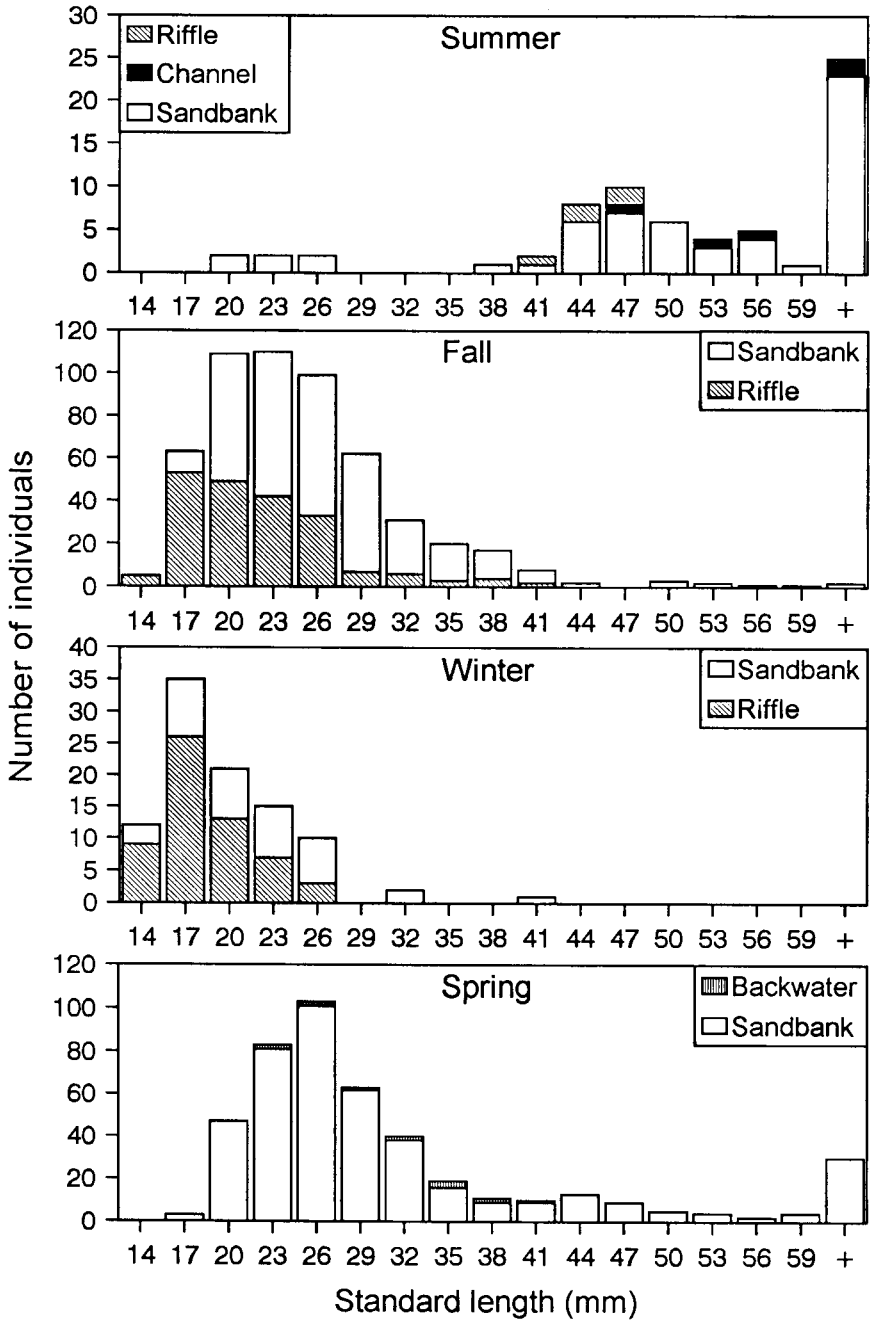


Figure 6. Length frequency distributions of *Cyprinella venusta* by mesohabitat and season.



*olivaceus* most often occurred in sandbank and riffle habitats during periods of low discharge (summer and fall). During the high stream discharge of winter, they were taken from backwater and riffle habitats, and during spring from backwater and sandbank habitats.

*Gambusia affinis* was primarily associated with backwaters during summer and spring, but during fall, 56% were captured from the sandbank mesohabitat. *Etheostoma vivax* only occurred in sandbank and riffle habitats, and there appeared to be a slight preference for the riffle habitat among individuals <30 mm SL during fall and spring. Small *L. macrochirus* (<55 mm SL) generally were found in backwater habitats, especially during times of high discharge, and larger individuals were found in the channel.

Most *Lythrurus fumeus* in the summer sample were from sandbank habitats. During fall, most *L. fumeus* were captured from backwater habitats. According to Robison & Buchanan (1988), *L. fumeus* prefers lentic pools and backwaters, but it was also found in slow to moderate current. Perhaps this species did not occupy its preferred habitat during summer, because reduced backwater habitats resulted in greater per-unit-area densities of competitors and predators there. No *L. fumeus* were captured during winter. During spring only three large individuals were taken, one from a backwater and two from sandbank habitats.

During summer and fall, *N. texanus* was associated primarily with sandbank habitat, but as discharge increased during winter, they were found in backwaters and flooded riffles. The spring sample was too small to be conclusive. *Hybopsis amnis* occupied habitats ranging from backwaters to sandbanks. *Hybognathus nuchalis*, was taken almost exclusively from riffle and sandbank habitats. *Opsopoeodus emiliae* was mainly captured in backwater habitats; however, because few of these species were captured, inferences to their habitat preferences remain speculative.

*Lepomis megalotis* was a habitat generalist when small. Individuals <75 mm SL were found in sandbank, backwater, edge and channel habitats, however, all individuals >75 mm SL were from the summer channel sample. *Pomoxis annularis* were captured from backwaters during summer and fall when discharge was low. *Pomoxis* may have

been dispersed within inundated riparian habitats during the winter and spring. *Micropterus punctulatus* < 100 mm SL were primarily associated with sandbanks, and larger individuals were found exclusively in the deep channel.

*Labidesthes sicculus*, the ninth most abundant species, tended to occur in backwaters, but a few larger individuals were captured from sandbanks. *Aphredoderus sayanus* and *Elassoma zonatum* were captured from the channel edge during summer and from backwaters during fall. These species apparently prefer shallow water with macrophytes and leaf litter. This habitat virtually disappeared from the channel area during periods of high discharge, which may explain why the two species were not collected during winter and spring.

*Etheostoma proeliare* was only captured during summer and winter. During summer, it was found mainly in backwater habitats. During winter, *E. proeliare* was found in flooded riffles and backwater habitats. At high stream discharge, these two habitats intergraded, and thus, it appears that *E. proeliare* may prefer backwater habitats. This was a rare species, and over the four seasons, only 21 individuals were caught. *Moxostoma poecilurum* was captured primarily from channel pools, and no individuals were caught during winter or spring due to the high stream discharges. Smaller individuals were captured from backwater and sandbank habitats, where they probably avoid larger predators such as *M. punctulatus*. *Centrarchus macropterus* was relatively rare and found exclusively in backwaters, and none were collected during winter.

*Length frequency distributions.*—Length frequency distributions indicated nearly year-round recruitment in *C. venusta*, *P. vigilax*, *N. sabiniae* and *F. olivaceus*. Most of *C. venusta* in the summer samples were > 35 mm SL, but six individuals were < 26 mm SL. Juveniles < 26 mm SL were found during all four seasons, so at least some spawning probably occurred within a month or two prior to each of the sampling periods (Fig. 6). Juveniles dominated the fall and winter samples. Juvenile *P. vigilax* (SL < 30 mm) and *N. sabiniae* (SL < 24 mm) were present during fall, winter, and spring. *Fundulus olivaceus* 15-40 mm SL dominated both the summer and winter samples.

Oocytes from the ovaries of several adult female *C. venusta*, *P. vigilax*, *N. sabiniae* and *F. olivaceus* captured during each season were examined. Most of these ovaries closely matched Heins & Dorsett's (1986) description for *C. venusta cercostigma* ovaries, with two size classes of yolk-bearing eggs, large mature and smaller maturing eggs. This bimodal distribution of yolk-bearing oocytes is indicative of a protracted reproductive season during which multiple egg cohorts are released (Heins & Dorsett 1986; Heins & Rabito 1986).

Five minnows showed length-frequency distributions consistent with late spring-early summer (May-June) spawning (*L. fumeus*, *N. texanus*, *H. amnis*, *H. nuchalis* and *O. emiliae*). Unimodal distributions of these species tracked the growth of same-age cohorts. *Lythrurus fumeus* was the third most abundant species captured at Village Creek, but it was only found at nine sample sites. Ten less-abundant species occurred in a greater number of samples. High predation mortality apparently followed a summer increase in *L. fumeus* density, and relatively few individuals survived to adult size classes during the spring. Except for *L. macrochirus*, the channel pool-dwelling centrarchids appeared to be late spring spawners, (e.g., *L. megalotis*, *P. annularis* and *M. punctulatus*).

## DISCUSSION

Fish assemblages at Village Creek were strongly patterned in space and across seasons. The first CCA gradient was primarily a water temperature gradient secondarily influenced by dissolved oxygen and current velocity. Because dissolved oxygen concentration and temperature are inversely proportional, even the most oxygen-poor mesohabitats had higher dissolved oxygen levels during winter than the relatively oxygen-rich mesohabitats during warmer seasons. Matthews & Hill (1980) found that fishes restricted their habitat use during periods of physicochemical stress in an Oklahoma river. During summer at Village Creek, low dissolved oxygen levels might be a physicochemical stressor in backwater mesohabitats. Mesohabitat use by individual species was more restricted during the summer. This is consistent with Felley & Felley's (1987) observation that, during drier periods, common species had smaller distributional variances and clustered around their preferred habitats.

During winter and spring, many species expanded their use of meso-habitat types. In streams where seasonal variation in discharge is substantial, fish habitat availability is a direct function of discharge. Many fishes moved into newly inundated areas to exploit new food resources and habitats (Ross & Baker 1983). Patterns from PCA (Fig. 3, 4) revealed that fishes moved into backwater habitats during winter, and the physical homogeneity of the winter stream was indicated by patterns from CCA (Fig. 5). The homogeneity of habitats during the high spring discharge was not evident in PCA, however, the spring polygon in Figure 4 was distorted by a single backwater sample. Except for that sample, the spring samples were all negative on PC2. Fish movement into inundated areas (backwaters) was not obvious from PCA, but in many cases, it was indicated by species' length-frequency distributions plotted by habitats.

Niches may expand and contract in response to variation in the strength of competition (Schoener 1982). During periods of resource scarcity, species may specialize on resources or retreat to habitats that give them a competitive advantage. At low discharge, assemblages are more distinct, perhaps because niches are compressed in response to more intense competition for available resources. Periods of low discharge at Village creek were associated with spawning by many species, so that interspecific differences in spawning habitat selection could have contributed to patterns of niche segregation. Seasonal variation in discharge was substantial at Village Creek, and fish habitat availability varied accordingly. A species might prefer a particular mesohabitat, but the degree of selection and the kind of habitat selected may vary between years and study reaches (Angermeier 1987). Thus observed species-habitat associations, even if well defined in a given place and time, might not be sustained over larger spatiotemporal scales.

*Cyprinella venusta* and *P. vigilax* were most abundant during fall, as were many of the other small fishes (<100 mm), both common and uncommon. The presence of *C. venusta* <20 mm during winter and spring (in addition to fall; Fig. 6) appears to be inconsistent with Baker et al.'s (1994) contention that most spawning by this species takes place during May-July. During winter, there was an apparent reduction in the abundances of small common (e.g., *C. venusta*, *P. vigilax*, *N. texanus* and *G. affinis*), less common (e.g., *L. sicculus*) and rare (e.g., *O.*

*emiliae*) species. During spring, *C. venusta* increased in samples to levels nearly as high as those taken during fall. *Pimephales vigilax*'s spring recovery was not as pronounced. The samples of common and rare small fishes (minnows, topminnows, darters and mosquitofish) generally increased from winter to spring. The apparent low abundances of small fishes during winter were likely due to the combined effects of poor sampling efficiency during high waters, predation, and reduced reproductive effort.

*Cyprinella venusta* and *P. vigilax* occurred in the same three mesohabitat types during summer (i.e., sandbank, riffle, channel), as did the second and third most abundant centrarchids, *M. punctulatus* and *L. megalotis* (except the latter was not found in the riffle habitat). All *M. punctulatus* and *L. megalotis* from the sandbank mesohabitat were < 80 mm SL. Small centrarchids (< 100 mm SL) consume small prey (< 30 mm SL), and since *C. venusta* and *P. vigilax* were the most abundant species during summer, they may serve as major food resources for piscivorous *M. punctulatus*.

During periods of high discharge, aquatic habitats expand, and fishes frequently occupy a greater range of habitats (Ross & Baker 1983; Felley & Felley 1987). Several species displayed intraspecific body size/water depth relationships. For example, small *M. punctulatus* and *L. macrochirus* (< 80 mm SL) occupied shallow mesohabitats, whereas adults generally were found in deep channel areas. Small *L. macrochirus* (< 55 mm SL) were strongly associated with backwater habitats, but *M. punctulatus* and *L. megalotis* < 80 mm SL were largely associated with sandbank mesohabitats. Backwaters appear to function as nurseries (i.e., areas containing appropriate juvenile resources and refuges from predation) for several species.

Minnows also showed size segregation by mesohabitats along a depth gradient. Juvenile (< 30 mm SL) *C. venusta* and *N. sabiniae* were generally found in shallow riffles during fall and winter, and larger individuals occurred in deeper water over sandbanks. *Notropis texanus* and the killifish, *F. olivaceus*, had similar patterns of habitat use and seemed to respond primarily to water depth. During summer and fall (lower discharge), both species were found primarily in sandbank habitats, but as discharge increased during winter, they occupied

backwaters, riffles and flooded riffles. During spring, the two species occupied sandbank and backwater habitats.

*Biotic integrity.*—As defined by Karr & Dudley (1981), biotic integrity is indicated by a community of organisms having a species composition, diversity and functional organization comparable to that of the natural habitat of the region. Karr (1981) developed the index of biotic integrity (IBI), a tool for environmental impact assessment. This method assumes that a pristine natural habitat can be identified within a given region and used as a reference point. Village Creek is not without human perturbations; during summer, it is used heavily by anglers and canoers. The former may impact piscivorous fishes, one of the metrics for the index. IBI metrics classify Village Creek as "excellent" to "good". One of the metrics is species richness. Village Creek's fish species richness of 44 is high (in midwestern streams > 16 species falls into the "best" category), however, seasonally, species richness was not consistent (summer = 42, fall = 37, winter = 16, and spring = 29). Compared to midwestern streams, all of these values indicate excellent integrity.

The number of darter, sucker, and sunfish species are also metrics in the IBI (>4 species = "best" category). Over the sample year, eight darter species were captured at Village Creek, and all seasons would fall into the "best" category, except for spring, when only three darter species were captured. Eight sunfish species were captured, and each season would fall into the "best" category, except for winter when only three sunfish species were captured. Only two sucker species were captured during summer and fall, which corresponds to the midrange for this IBI category. During winter and spring, no suckers were captured at Village Creek, a likely artifact of inefficient sampling in channel pools during the floods.

The final species richness metric, is the number of intolerant species. Species that Karr (1981) considered intolerant in the midwest with ranges that extend to Village Creek, include *L. megalotis*, *M. melanops* and *P. mirabilis*. The latter two were only captured during summer and fall, but *L. megalotis* was captured year-round. At Village Creek, additional intolerant species would be *Etheostoma vivax*, *E. clarum* and *L. fumeus*. Except for winter, all seasons would fall into the "best"

category (> 4 intolerant species).

The remaining seven metrics of the IBI are the percentage of individuals that fall into six functional categories: green sunfish 0%, omnivores  $\pm 20\%$ , insectivorous cyprinids,  $\pm 60\%$ , top carnivores  $\pm 2\%$ , hybrids 0%, and diseased fishes  $\pm 0.1\%$ . Except for the top carnivore percentage (middle category), all of these correspond to the "best" category again. Karr (1981) found samples with fewer than 20% omnivores to be "good", while those with over 45% omnivores to be "badly degraded". This category is difficult to quantify because an omnivore's feeding pattern is dependent on food availability, so that an omnivore (e.g., sucker) may be a functional herbivore during some times, and a functional insectivore during others.

Age structure, growth, recruitment rates and measures of fish condition can be valuable in assessing the environmental quality of a site (Karr 1981). Overall, Village Creek appeared to have good to excellent biotic integrity, but, depending on the season, the IBI would vary considerably. According to Schlosser (1987), good sites show less variability in IBI rankings over time than do poor sites, thus, degraded sites are more likely to be overrated than good sites are likely to be underrated.

Karr et al. (1987) suggested sampling during early summer after most fishes have spawned but before young-of-the-year recruitment (Schlosser 1985; Angermeier & Karr 1986). For many species at Village Creek, reproduction does not occur during spring-early summer exclusively, hence there is no optimal sampling period for application of the IBI. Schlosser (1987) maintained that continued movement of fishes into upstream areas throughout the summer inflates estimates of species richness and population abundances at species-poor sites, because many of these species cannot persist without continual immigration. The high species richness at Village Creek during summer may have been due partially to immigration from other habitats in the longitudinal gradient. Evans & Noble (1979) examined fish assemblage structure in Big Sandy Creek, a tributary that enters Village Creek 77 km from its origin. The unusually diverse fish assemblage in the headwater region of Big Sandy Creek was hypothesized to be related to soil characteristics, but their samples (collected intermittently from 16 June to 24 January) could have been influenced by seasonal movements as well. Since stream discharge

fluctuates both seasonally and inter-annually, streams like Village Creek require long-term sampling, perhaps spanning several years, to integrate natural temporal variation into assessments of biotic integrity.

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