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Spatial and temporal patterns in fish assemblages of upper coastal plain streams, Mississippi, USA*

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Abstract

We assessed spatial, seasonal, and annual variation in fish assemblages over 17 months in three small- to medium-sized, incised streams characteristic of northwestern Mississippi streams. We sampled 17 962 fish representing 52 species and compared assemblages within and among streams. Although annual and seasonal variability in assemblage structure was high, fish assemblages maintained characteristics unique to each stream. High variability in fish catch-per-unit-effort (CPUE) was exemplified in one site where total CPUE increased an order of magnitude from July 1993 to 1994. Species turnover and percent dissimilarity were often higher seasonally than annually, consistent with a period of change in spring to early summer and a return to similar species compositions between summers. Temporal variability was also high at the individual species level, and no species were classified as 'stable'. We found little evidence for correlation between changes in fish assemblage structure and measured habitat conditions. The fish characteristics fit the profile of 'colonizing assemblages', which probably resulted from both natural and anthropogenic causes. Flashy hydrographs, created in part by stream channelization and incision and watershed deforestation, may play a large role in structuring these fish assemblages. Extreme interannual variability in assemblages in the absence of detectable habitat change has important implications for the statistical power of fish monitoring programs designed to detect trends in fish assemblages over time.

Introduction

Spatial and temporal variation in stream fish assemblages occur at scales from microhabitat to basin and diel to decadal or longer. Understanding and quantifying temporal variation is valuable for (1) clarifying sources of assemblage regulation (e.g. biotic versus abiotic) across stream types and regions (Grossman et al., 1998), (2) identifying species or assemblages with high rates of immigration and emigration, indicating dependence on habitat connectivity (Gowan et al., 1994), (3) designing appropriate monitoring and research approaches (Maxell, 1999), and (4) correctly interpreting time-series data on fish assemblages (Schlosser, 1990). Comparison of spatial and temporal variation can guide decisions regarding the most efficient distribution of sampling effort (e.g. greater temporal versus greater spatial coverage, Matthews, 1990). Monitoring data used to examine the influence of human actions or natural events on fish assemblages generally cannot be interpreted reliably without knowledge of temporal variation in the assemblage prior to an event (Schlosser, 1990).

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Fish assemblage variability is a function of many interacting factors, including geoclimatic region, hydrologic regime, channel type, species composition, biotic versus abiotic regulation, and disturbance history, frequency, and magnitude (natural and anthropogenic) (Schlosser, 1985; Grossman et al., 1998). Because assemblages respond in diverse ways to these factors, quantification of variability must be repeated under many different conditions. Spatio-temporal variability in fish assemblage structure has received little attention in channelized, incised, sand-bottom streams of the upper Gulf of Mexico Coastal Plain, USA, (but see Shields et al., 1995), although some studies addressed the issue in other Coastal Plain streams (e.g. Ross et al., 1987). Because channelization and resultant incision represent profound and fundamental alterations of stream structure and function, we expected that variability in channelized streams would not mimic that in other Coastal Plain or upland streams.

Temporal variability tends to be high in warmwater streams and higher still in anthropogenically disturbed streams (Schlosser, 1982). Human alteration of watersheds and stream channels in northwestern Mississippi has led to extreme channel degradation and simplification as well as channel instability. We predicted that these changes would lead to high temporal variability in the warmwater fish assemblages.

We studied fish assemblages in three, small- to medium-sized streams in northwest Mississippi over 17 months to quantify spatial and temporal patterns in persistence and stability at both assemblage and species levels and to compare those to results from other systems. We focused on among-stream, among-season, and between-year variations. Our assemblage-level objectives were to (1) quantify and compare assemblage characteristics among streams using metrics of total number of species, species dominance, and catch per unit effort (CPUE), (2) qualitatively and quantitatively address whether assemblages were more similar over space or over time, (3) identify the degree and timing of changes in assemblage composition and structure, (4) evaluate synchrony in assemblage metrics among streams, and (5) test whether assemblage changes were correlated with stream habitat changes. At the individual species level, objectives included (1) comparing stability of CPUE to that in other stream systems, and (2) determining the contribution of spatial versus temporal effects to the variation in CPUE.

Study areas

We studied three tributary streams of the Little Tallahatchie River, upper Yazoo River basin, northwestern Mississippi (Fig. 1, Table 1), that differed in size, condition, land use, and connectivity to the mainstem. Hotopha and Cypress creeks were comparably-sized, channelized streams, whereas Buckhorn Creek was smaller and not channelized at the study site. All had flashy hydrographs (e.g. Fig. 2) and moderate to extreme channel incision (Hotopha Creek: Shields & Cooper 1994). Channelization and construction of small, headwater flood-control reservoirs were widespread in the watersheds prior to the mid-1960s (Hotopha Creek: Simon & Darby, 1997). The Cypress Creek watershed retained considerably more forest cover than did the other two watersheds (Table 1), and nearly all of the Cypress

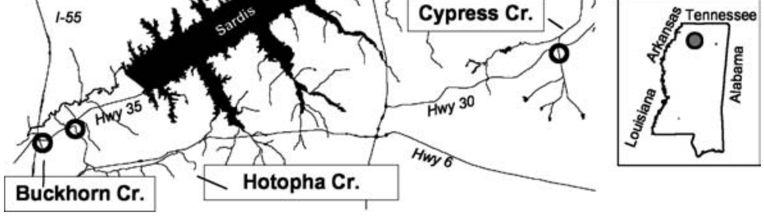

Figure 1. Location of study sites in Panola and Lafayette counties, Mississippi, USA.

Table 1. Study site locations in Mississippi, USA, and watershed, channel, and stream characteristics

Stream	Watershed area (km^2)	Distance to confluence (km)[a]	Mean wetted widths (m)[b]	Average depths (cm)[c]	Dominant substrates	Watershed land use (%)			Study site location[d]	County	Latitude, longitude
						Row crops	Pasture	Forest			
Cypress Creek	74	8.2	7.2	16–27	Sand	6[e]	9[e]	85[e]	Hwy. 30	Lafayette	34° N 26′ 32″, 89° W 17′ 25″
Hotopha Creek	91	2.0	13.8	16–37	Sand	8[f]	40[f]	50[f]	Hwy. 35	Panola	34° N 21′ 52″, 89° W 52′ 45″
Buckhorn Creek	15	1.2	3.2	20–31	Sand, gravel	8[g]	39[g]	53[g]	Hwy. 35	Panola	34° N 21′ 04″, 89° W 54′ 47″

[a] Distance to downstream confluence with larger river.

[b] Cypress and Buckhorn creek values are means from one transect where discharge was measured during each sample. Hotopha Creek mean is from multiple transects each spring and fall, 1992–1995 from Shields et al. (1998).

[c] Water depths; range of averages measured throughout study.

[d] Highway (Hwy.) crossing.

[e] Estimated from 1:24 000 US Geological Survey (USGS) black and white digital orthophoto quadrangles, 1992, and 1:24 000 US Department of Agriculture color aerial photography, 1996 and 1999.

[f] Shields et al. (1994).

[g] Estimated from 1:24 000 USGS black and white digital orthophoto quadrangles, 1992.

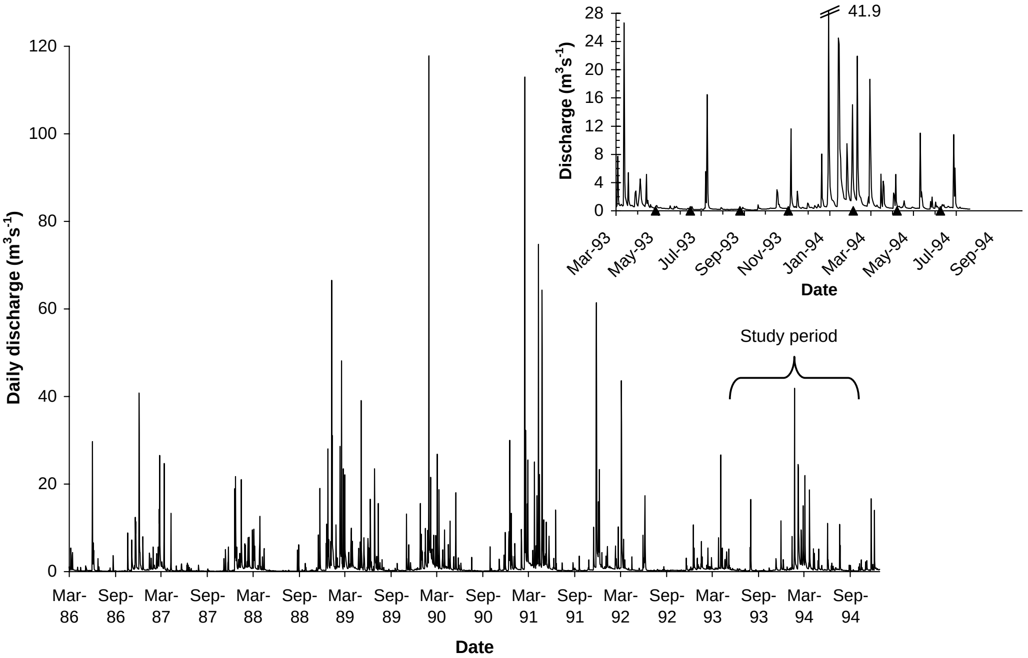

Figure 2. Hydrograph of Hotopha Creek, Mississippi, from 1986 to 1994 and detail of hydrograph during the study (inset). Black triangles in inset indicate the dates we sampled in Hotopha Creek.

Creek headwaters drained forested watersheds of the Holly Springs National Forest.

Channelization and incision have profoundly influenced riparian, channel, and in-stream characteristics of most streams in the area. In Hotopha and Cypress creeks, the mainstems and major tributaries became deeply incised (3–7 m) after channelization (Shields et al., 1993; Shields & Cooper, 1994). Mean top channel widths in Hotopha Creek increased from 17 to 42 m between 1953 and 1985 (Shields et al., 1993), and the Cypress Creek channel widened similarly. Flows, although extremely flashy, rarely exceed bankfull. Sediment loads carried by the creeks are high (98 600 tons/year in Hotopha Creek, Simon & Darby, 1997), resulting in wide, shallow streams with substrates consisting almost entirely of shifting sands (Table 1). Study reaches in both streams lacked canopy cover, and in-stream wood or other cover for fish was rare (Hotopha Creek, Shields et al., 1994, 1998). During the 1980s and 1990s, bank control structures (e.g. stone spurs, Shields et al., 1998) were installed in a segment of Hotopha Creek, and one set of 12-m-long stone spurs (installed in 1991) created the deepest habitats we encountered in that stream.

Buckhorn Creek was less incised (< 3 m bank height) and narrower with a slightly more diverse substrate (Table 1). Sections of the main channel upstream of the study reach, as well as some tributaries, had been straightened. Overbank flows were evidently common in Buckhorn Creek, and sediment and debris transport were apparently high, judging by the large areas of scour and deposition after high flows. Most of the mainstem and major tributaries of Buckhorn Creek, including the study site, were bordered by a nearly-continuous, albeit often narrow (< 25 m wide), riparian forest buffer. In the study site, tree canopy provided extensive shading, and in-stream wood was relatively common, forming debris piles, riffles, scour pools, and undercut banks.

The landscape context and, thus, potential for fish to move among diverse habitats varied among the streams. Hotopha and Buckhorn creeks entered the highly regulated and confined Little

Tallahatchie River downstream of Sardis Reservoir (Fig. 1). In Hotopha Creek, a grade control weir (< 1.8 m high) about 800 m downstream of the study reach likely precluded all upstream fish passage at moderate and low flows, although at high flows, some species, especially large-bodied ones, could evidently pass the weir (Shields et al., 1998). Cypress Creek flows into the Little Tallahatchie Canal (a bypass of the Little Tallahatchie River) upstream of Sardis Reservoir. Although the canal is a highly altered habitat, it retains connectivity to the original Little Tallahatchie River channel and to extensive seasonal wetlands. Moreover, the Cypress Creek floodplain consisted of continuous riparian forest and wetland complexes for 2.5 km upstream of the study site, whereas most adjacent floodplains of Hotopha and Buckhorn creeks were used as pasture or cropland (Shields & Cooper, 1994).

Methods

Data collection

We established a permanent sampling reach (150–200 m each) on each stream and sampled fishes at approximately bi-monthly intervals from May 1993 to October 1994 (Table 2). In each sample reach, we sampled fishes by electrofishing 18–29 discrete plots (36 m^2 each) on each sample date. We sampled each plot by setting a stationary seine (3-m × 2-m, 3.2-mm-mesh) and electrofishing (Smith-Root model 12-A backpack electrofisher) an approximately 12-m-long × 3-m-wide area for an average of 32 s (mean total time = 13 min per reach) in a downstream direction toward the seine; stunned fishes were swept by the current into the seine. In areas of low current, we then pulled the seine through the electrofished area to collect stunned fishes. Sampling plots were chosen haphazardly within the study reach but were distributed roughly proportionally among the few available microhabitat types and allocated similarly among sample dates.

With our sampling method, we overcame four sampling difficulties common to this region: (1) collection of stunned fishes using a seine allowed us to capture fishes regardless of whether we could see them in turbid water conditions, (2) use of the seine eliminated a bias toward capturing larger fishes, because it allowed us to sample age 0 fishes more effectively than possible with dip nets, (3) we captured many more individuals from large schools of minnows than we could have with dip nets even under ideal conditions, and (4) use of discrete sample plots allowed us to more effectively sample large, open expanses of sand substratum where fishes are often ‘pushed’ away from a continuous, moving electrical field. Our sampling efficiency was at least comparable to that obtained by Shields et al. (1998) who sampled about 30 times the stream width in the same segment of Hotopha Creek using a backpack electrofisher and dipnets on eight occasions from 1992 to 1995. Shields et al. (1998) captured more species than we did (31 total species compared to 26), but we caught more total fish (5106 versus 3872) and had higher catch rates (mean number fish per minute sampled = 52 versus 16), largely because our method was more effective at capturing small fishes and schooling cyprinids.

Table 2. Sampling dates and number of ‘plots’ (see text, 1 plot = 1 unit of effort) per date for the three study streams

Cypress Creek		Hotopha Creek		Buckhorn Creek	
25 May 1993	25	24 May 1993	24	24 May 1993	29
14 July 1993	24	13 July 1993	26	13 July 1993	25
21 September 1993	27	22 September 1993	23	22 September 1993	25
1 December 1993	24	30 November 1993	24	30 November 1993	25
7 March 1994	25	15 March 1994	24	3 March 1994	29
6 May 1994	25	5 May 1994	26	5 May 1994	24
8 July 1994	22	7 July 1994	25	6 July 1994	18
18 October 1994	23	18–19 October 94	22	19 October 1994	23
Total plots	195		194		198

We identified all captured fishes and measured their total lengths (TL). We combined two species of topminnows, *Fundulus olivaceus* and *F. notatus*, for analysis due to difficulties in identifying age 0 individuals to species. However, *F. olivaceus* numbers far exceeded those of *F. notatus*.

Within each plot area, we measured current velocity in the center (Marsh-McBirney digital current meter) and depth at three, haphazardly chosen points, and we visually estimated the dominant substrate (clay, silt, sand, gravel) and the area covered by aquatic vegetation, leaves, and large wood (> 10 cm diameter). The latter three variables were each scored as one of five classes (0, 25, 50, 75, 100%), based on percent of area covered. A US Geological Survey stream gauging station (number 07273100) recorded daily discharges for the Hotopha Creek site throughout the study.

Data analyses

We analyzed data at two levels of organization: assemblage and species levels. Methods and results are presented separately for each level. Most analyses were conducted using all fishes captured. In some cases, we conducted additional analyses using only data for fishes > 25 mm TL and again for fishes ≤25 mm TL in order to examine whether results were driven largely by reproduction and whether recruitment was synchronous among streams. Results were usually qualitatively unchanged when using subsets of the fish data, and in most cases, only results for all fish are presented quantitatively.

Assemblage level

We initially characterized and compared assemblages among streams via averages and coefficients of variation (CV) of number of species, species dominance, and CPUE among sites. We tallied the number of species ('total species', hereafter) captured during each site visit and calculated 'total CPUE', the average number of individuals of all species per plot. We calculated species dominance using the Berger–Parker Index (number of individuals of the most abundant species divided by the total number of individuals captured, Magurran, 1988). This index minimizes the influence of rare species on dominance estimates. We calculated species dominance and total CPUE with and without fish ≤25 mm. All CVs were adjusted for small sample-size bias (Sokal & Rohlf, 1995). Comparisons among streams were made using ANOVA.

We assessed relationships of assemblages over time and space and tested hypotheses of assemblage differences to determine whether assemblages were more similar over time or space. We used cluster analysis (UPGMA linkage) with both Sorenson (Bray–Curtis) and relative Sorenson (relativized Manhattan) distances to explore assemblage relationships among all samples and to qualitatively examine whether samples clustered more across space or time. We repeated the analysis using other clustering rules and distance measures to explore the robustness of the observed clustering patterns. Input data were total CPUEs including all fish sizes. We then used multi-response permutation procedures (MRPP, McCune & Mefford, 1999) with relative Sorenson distance on the same total CPUE data to inferentially test hypotheses of (1) no fish assemblage differences among streams (samples grouped by stream across dates) and (2) no assemblage differences among seasons (samples grouped by seasons across streams). We grouped data into three seasons: spring-early summer (March–July), mid summer-fall (July–November), and winter (November–March). We delineated the seasonal groups after sampling based on local stream hydrologic regimes, air temperatures, and expected periods of stream fish spawning and recruitment. We conducted all multivariate procedures using PC-ORD version 4 (McCune & Mefford, 1999).

Using estimates of species turnover and percent dissimilarity (PD), we assessed assemblage persistence and stability over the study period and identified intervals with particularly high or low stability. Species turnover rates accounted only for species composition, whereas PD incorporated the CPUE of each species. We calculated species turnover between pairs of samples as:

$$\text{turnover} = 1 - [C \cdot (T1 + T2)/(2 \cdot T1 \cdot T2)],$$

where C is the number of species common to both samples, and $T1$ and $T2$ are the number of species at time t_1 and t_2, respectively (Cody, 1993). Possible turnover values range from 0, no turnover, to 1, complete turnover. We calculated turnover rates for each pair of consecutive samples as well as for the months that we could compare between years (May and July), and we limited analyses to fish >25 mm TL. We used ANOVA to test for seasonal differences in species turnover rates after grouping data into three seasons. Prior to calculating species turnover rates, we used rarefaction to simulate an equal sampling effort of 21 plots for all but one sample; the July 1994 Buckhorn Creek sample included only 18 plots, but because CPUE and total species were high in the sample, we assumed that the actual fish assemblage was well represented. Using CPUE data for all fish sizes, we calculated percent dissimilarity (PD) (Pielou, 1984) between consecutive samples and between years to compare to species turnover.

We also tested whether assemblage changes were synchronous among streams. We used Spearman's ρ to test for significant among-stream correlations in total species, species dominance, and total CPUE and used Pearson's product–moment correlation for species turnover and PD. Additionally, we tested for correlations in total species and total CPUE using only data for fish ≤25 mm.

We used Mantel tests (McCune & Mefford, 1999) to determine if changes in fish assemblages among dates were related to changes in the measured habitat variables. Tests were conducted separately for each stream. Habitat variables included the mean, standard deviation, and CV of water depth, current velocity, and the amounts of wood, aquatic vegetation, and leaves in sampled areas. We did not include substrate because of the absence of variation. All habitat data were transformed to unit mean and variance. We used Euclidean distance for the habitat matrix and Sorenson distance for the fish assemblage matrix and based significance values on 1000 randomizations.

Species level

For the seven most common species, we examined the percentages of variance in CPUE (by species) attributable to spatial, temporal or interaction effects. We used variance partitioning based on a two-way, random-effects ANOVA model for each species (Matthews, 1990). Following Matthews (1990), we determined (1) the 'fixed spatial variance' due to differences among streams, (2) the 'ephemeral spatial variance' due to interactions between time and space, and (3) the temporal component of variance attributable to CPUE differences between sample dates, regardless of stream. Ratios of the variance components indicated the relative importance of each source of variance for each species (Matthews, 1990). CPUE was transformed by $\log_{10}(x + 0.1)$ prior to analyses. Because we did not quantify sampling error, any error variance was included in the interaction term. The variance partitioning method we used sometimes results in negative variances, which we changed to zeros (Searle et al., 1992)

As a means of assessing temporal stability of individual species and of comparing stability between studies, we examined univariate, temporal fluctuations in species abundances using CV of CPUE values. In each stream, we calculated CVs (adjusted for small sample sizes) across all sample dates for each species that occurred in at least half (4) of the samples for a particular stream and compared results to those for a southern Appalachian Mountain stream (Freeman et al., 1988). We assessed 30 species in 53 species-stream combinations.

Results

Assemblage level

We captured 17 962 fish representing 13 families and 52 species (Fig. 3, Appendix 1). We collected 43, 26, and 24 species from Cypress, Hotopha, and Buckhorn creeks, respectively. The eight most abundant species (>1000 individuals captured) were minnows (family Cyprinidae), but a different species dominated each site (Table 3). *Notropis rafinesquei* and *Cyprinella camura* were the most abundant species overall (3642 and 2998 individuals, respectively) and occurred in all samples. *Lepomis megalotis* was the only other species found in every sample, but its overall abundance was much lower (312 individuals).

Variation in total species and species dominance was greater among streams than among dates, but total CPUE displayed greater temporal than spatial variation (Table 3 and Fig. 4). The following results are for analyses including all fish sizes, but results were similar when fish ≤25 mm

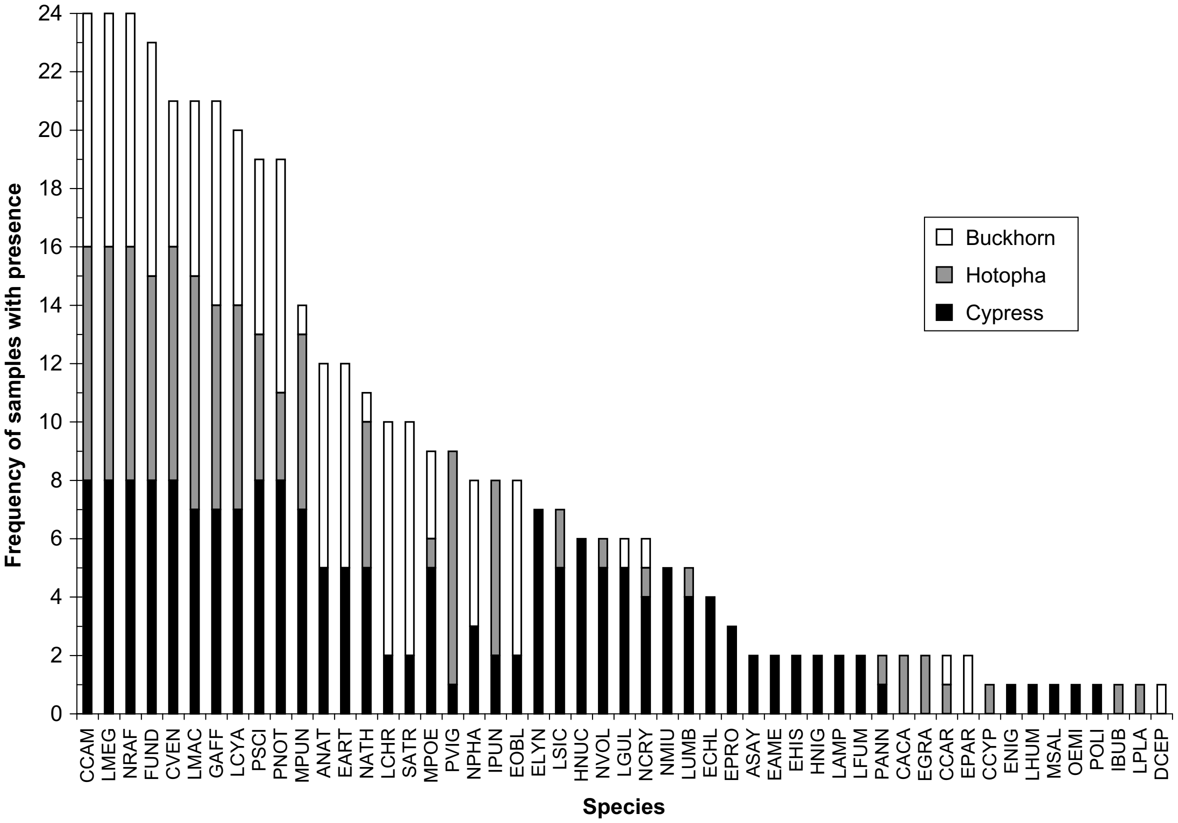

Figure 3. Frequency of samples containing each fish species. Species abbreviations are defined in the Appendix. 'FUND' includes two topminnow species.

were excluded. Total species per sample was significantly higher in Cypress Creek than in Buckhorn and Hotopha creeks (ANOVA, $F = 21.8$, df = 2,21 $p < 0.01$; Fisher LSD pairwise comparisons, $p < 0.05$). Species dominance in Hotopha Creek was significantly higher than in Cypress and Buckhorn creeks (ANOVA, $F = 3.36$, df = 2, 21, $p < 0.05$). Total CPUE did not differ significantly among streams (Kruskal–Wallis, $\chi^2 = 23$, df = 23, $p < 0.46$). Within streams, CVs for total CPUE were high relative to CVs for total species and species dominance (Table 3), indicating that abundance was more variable than species composition over time.

Table 3. Average (and coefficient of variation, %) fish assemblage characteristics for all sample dates with all fish species and sizes included

Stream	Average total species per sample date	Average species dominance	Average catch per unit effort	Numerically dominant species[a]
Cypress Creek	22.8* (19.2)	0.35 (28.2)	25.7 (63.6)	*N. volucellus, N. rafinesquei, C. camura, N. atherinoides*
Hotopha Creek	13.6 (16.1)	0.43* (22.4)	26.7 (64.5)	*C. venusta, N. rafinesquei, C. camura*
Buckhorn Creek	15.3 (9.8)	0.31 (27.6)	37.9 (91.2)	*C. camura, L. chrysocephalus, N. rafinesquei*

Asterisks indicate values that were significantly different ($p < 0.05$) from those for the other two streams (see text).

[a] Includes consideration of number of samples dominated by species, total numbers of individuals, and total numbers of individuals >25 mm. Species are listed in order of dominance.

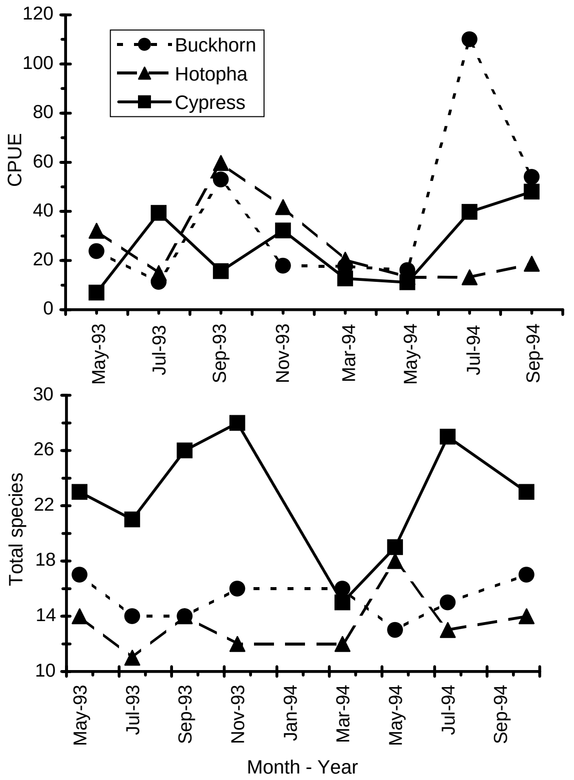

Figure 4. Fish catch per unit effort (CPUE, top) and total species (bottom) values for the three sites across all sample dates.

Phenetic classification of fish assemblages showed more within- than among-stream clustering. Using Sorenson distance, clustering was driven largely by CPUE, but nonetheless, few mixed-stream clusters occurred (Fig. 5). One exception was the November 1993 Buckhorn Creek sample that clustered with Hotopha Creek samples under all clustering rules. Within-stream assemblage similarity was not consistently related to season, although samples often clustered by season. Clustering using relative Sorenson distance resulted in almost complete separation of streams, but clusters still included multiple seasons. Removing data for fish ≤25 mm resulted in slightly more mixed clustering of samples from Cypress and Hotopha creeks but not Buckhorn Creek. The overall clustering pattern was consistent across a variety of clustering rules and distance measures and indicated that assemblages varied more dramatically over space than over time.

Overall and pairwise MRPP tests (with or without small fish) supported the phenetic classification and indicated significant assemblage differences among streams but not among seasons. Tests of assemblages grouped by stream were statistically significant ($A = 0.29$, $p < 0.0001$), indicating that similarities within streams were much greater than expected at random. All

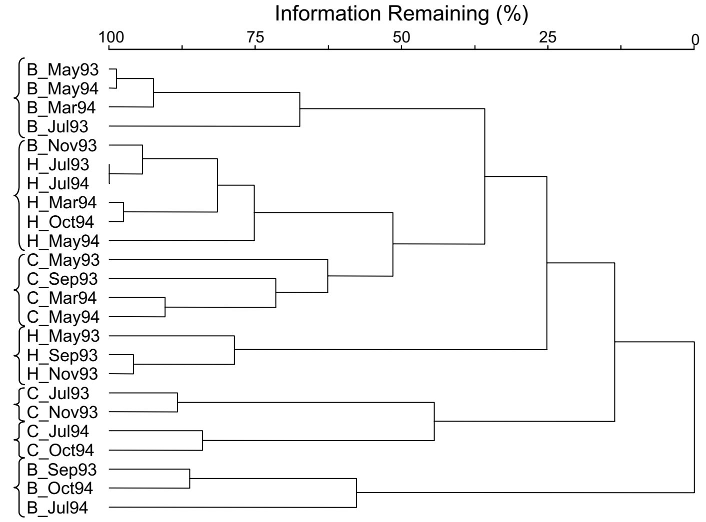

Figure 5. Dendrogram of catch-per-unit-effort data from all samples and fish sizes using Sorenson distance and UPGMA linkage. Distance is interpreted along the horizontal axis. Brackets on left identify clusters. Sample locations are indicated by B – Buckhorn Creek, C – Cypress Creek, and H – Hotopha Creek.

pairwise MRPP tests of assemblages between streams were highly significant ($p < 0.0001$), but effect size was greatest between Buckhorn and Hotopha creeks ($A = 0.34$), the most geographically proximate sites. Assemblages grouped by seasons (across streams) showed no significant differences ($A = 0.002$, $p < 0.40$), indicating that fish assemblages from different streams in the same season were no more similar than expected at random.

Assemblage stability (measured as percent dissimilarity, PD) and persistence (measured as species turnover) typically followed a similar pattern to each other, however, the magnitude of change between samples or years was sometimes much greater for PD (Fig. 6). Species turnover rates and PD were inconsistent among streams, except that the interval May–July 1994 had the highest per-interval species turnover rate in all streams (Fig. 6). Species turnover rates did not differ significantly among seasons (ANOVA, $F = 0.15$, df $= 1, 19$, $p = 0.70$). Annual comparisons of persistence and stability showed mixed patterns. Species turnover and PD on an annual basis were often lower than during intervals of 2–4 months (Fig. 6). However, in Buckhorn Creek, the highest PD was between July 1993 and 1994, reflecting the order of magnitude increase in abundance from July 1993 to 1994 (Fig. 4). This result was consistent when fish ≤25 mm were excluded from analyses. Species turnover rates and PD from May 1993 to 1994 varied among the streams (Fig. 6).

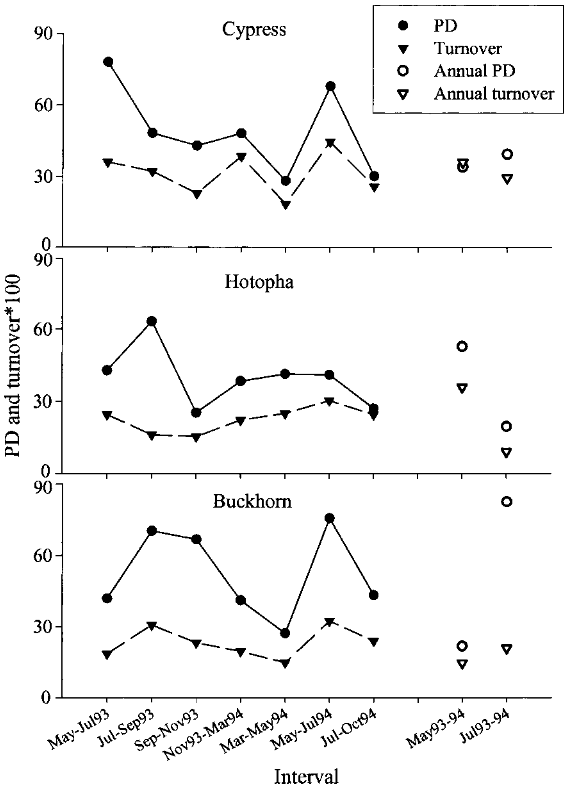

Figure 6. Species turnover rates × 100 and percent dissimilarity (PD) between consecutive samples and annually (between similar dates in 1993 and 1994).

We found no statistically significant evidence of synchrony among the three streams in assemblage metrics. Neither total CPUE, total species, species dominance, species turnover (>25 mm), nor PD values were correlated among streams (at $\alpha = 0.05$ level). Also, neither total species nor total CPUE were significantly correlated among any stream pairs when analyses were restricted to fish ≤25 mm.

Changes in fish assemblages between samples were associated with habitat changes in one of the three streams. Mantel tests indicated a significant association between changes in fish assemblages and stream habitat in Buckhorn Creek (standardized Mantel statistic $r = -0.36$, $p < 0.047$), but not in Cypress and Hotopha creeks (for both streams, $-0.11 < r < 0.02$, $p > 0.32$). Mantel tests using a subset of the standardized habitat variables indicated significant associations between changes in the fish assemblage and changes in the means and standard deviations of depth and water velocity, but not cover, in Buckhorn Creek. During intervals when velocity, and typically depth (except May–July 1994), decreased, percent dissimilarity and species turnover rates were low. Thus, associations between assemblage and water depth and velocity may be simply reflections of seasonal patterns in the fish assemblage.

Species level

CPUE for individual species was generally unstable in the study streams over 17 months. Of the 53 species–stream combinations for which we calculated the CV of CPUE, none were ‘stable’ and 85 % were ‘fluctuating’ according to the classification scheme in Freeman et al. (1988) (Fig. 7). The moderately stable species were all dominant or common cyprinids (*Notropis rafinesquei* and *Pim-*

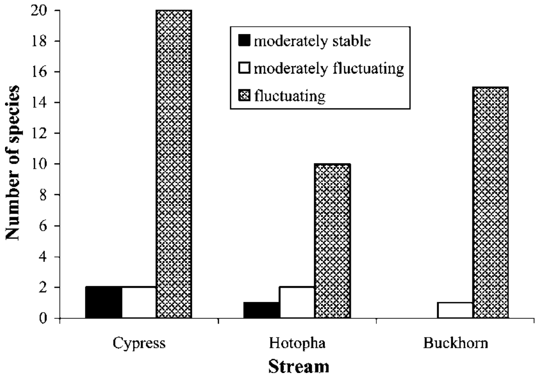

Figure 7. Frequency of species categorized in three stability classes based on coefficients of variation of catch-per-unit-effort data (after Freeman et al., 1988). No species were categorized as 'stable'.

ephales notatus in Cypress Creek and *Cyprinella camura* in Hotopha Creek). Moderately fluctuating species included a dominant cyprinid (*C. camura* in Buckhorn Creek), centrarchids (*Lepomis cyanellus* and *L. megalotis* in Hotopha Creek and *L. macrochirus* in Cypress Creek) and *Fundulus* spp. (in Cypress Creek). *Cyprinella camura,* a dominant at all sites, was the only species with a degree of stability in all three streams, narrowly missing the cutoff for 'moderately fluctuating' in Cypress Creek.

Single-species ANOVA results indicated that the variance in CPUE attributable to spatial versus temporal components varied by species. Three of the seven most common species did not vary significantly in abundance across space or time (*Cyprinella camura, Notropis rafinesquei, and Lepomis megalotis*) (Table 4). Of the four remaining species, two varied more across space (*Cyprinella venusta* and *Fundulus* spp.) and two across time (*Gambusia affinis* and *Lepomis macrochirus*), although for three of the four species, a substantial percentage of the variation in CPUE was accounted for by the space–time interaction, termed 'ephemeral spatial variation' (Matthews, 1990).

The extreme variation in CPUE between July 1993 and 1994 in Buckhorn Creek is an example of the fluctuations possible in these unstable streams, but also indicates that some strong correlations occur in abundances of various species within a stream. The spike in CPUE in July 1994 was due to increases in numerous species, including five minnow species and one species from each of four other families (all increased at least 3-fold). However, CPUE of all sunfishes decreased. Although the same pattern existed in fish ≤25 mm, the increases were also evident in fish >25 mm, sug-

Table 4. *F*-tests of two-way, random effects ANOVA and variance contributions from fixed spatial (stream), fixed temporal (date), and ephemeral spatial (interaction) components for the seven most common species. Variance ratios indicate the importance of each variance source relative to fixed temporal variation

Species	*F*-value		Percent of variance			Variance ratios[a]		
	Stream	Date	Stream	Date	Interaction	$Ss^2:Sd^2$	$Si^2:Sd^2$	$(Ss^2 + Si^2):Sd^2$
Cyprinidae								
C. camura	2.55	0.52	ns	ns	ns			
C. venusta	40.70***	2.79*	76	9	15	8.44	1.67	10.11
N. rafinesquei	0.67	0.10	ns	ns	ns			
Centrarchidae								
L. megalotis	0.05	0.54	ns	ns	ns			
L. macrochirus	2.03	2.80*	7	35	58	0.20	1.66	1.86
Fundulidae								
Fundulus spp.	4.33*	0.86	29	0	71	–	–	–
Poeciliidae								
G. affinis	0.30	3.89**	0	49	51	0.00	1.04	1.04

[a] Ratios of variances due to stream (Ss), interaction (Si), and both relative to variance due to date (Sd).
$^*p < 0.050$; $^{**}p < 0.025$; $^{***}p < 0.001$.

gesting that age 0 recruitment was not solely responsible for the increase.

Discussion

Fish assemblages were highly variable over 17 months in the small- to medium-sized, incised, sand-bottom streams of northwestern Mississippi as reflected in dissimilarity measures, species turnover rates, and changes in CPUE. Yet despite substantial temporal variability, fish assemblages maintained characteristics unique to each stream, as evidenced by clustering patterns and differences in dominant species in each stream. Although slightly larger, Hotopha Creek had a significantly lower number of species and higher species dominance than Cypress Creek. Buckhorn Creek had nearly as many species as did nearby Hotopha Creek despite the former being considerably smaller.

All three sites were dominated by cyprinids, and common species were typically small-bodied (median fish size <33 mm TL in all sites), early-maturing, and short-lived. *Notropis rafinesquei*, endemic to the Yazoo River basin, and *Cyprinella camura* were dominant species in all three streams; both are tolerant of shallow, sandy streams and are characteristic of incised channels throughout northern Mississippi (Shields et al., 1995). *Luxilus chrysocephalus* is considered intolerant of degraded conditions (Shields et al., 1995) and was dominant only in Buckhorn Creek, the only unchannelized study stream. *Notropis volucellus* and *N. atherinoides* are common in medium to large rivers and lakes (Ross, 2001), including the Little Tallahatchie River both upstream and downstream of Sardis Reservoir (Warren and Haag, unpublished data); the seasonal prevalence of these species in Cypress Creek is likely due to immigration from downstream populations. In contrast, we attribute their scarcity in Hotopha Creek to the grade control weir downstream of the study reach hindering immigration from the Little Tallahatchie River.

CPUE was highly variable over time, whether or not age 0 fishes were included in analyses. Similarly, fish IBI values varied dramatically over time in streams of the same region (Shields et al., 1995). Also, the coefficient of variation (CV) for total species in Hotopha and Cypress creeks was similar to that for natural or human-modified upstream reaches reported by Schlosser (1987) over a similar length of time, despite draining watersheds about three times as large. The CV of total CPUE in Cypress and Hotopha creeks was similar to the CV of mean fish density for Schlosser's (1987) natural upstream site, but the CV in Buckhorn Creek was more similar to the higher CV value for Schlosser's modified upstream area. Similarly, the CV values for CPUE of individual species reflect unstable abundances. Our results contrast with findings of assemblage stability in warmwater, upland streams (Freeman et al., 1988; Matthews, 1990) but also in Black Creek, Mississippi, a Coastal Plain, blackwater stream (Ross et al., 1987). Differences among studies may be attributable, in part, to analysis methods (Grossman et al., 1990) and spatial and temporal scales examined, however, physical differences among streams undoubtedly contribute to real differences (e.g. Ross et al., 1985).

The degree of spatial versus temporal variation in CPUE of individual species varied, but overall, we found more temporal and less spatial variation than Matthews (1990) found for individual species in the upper Roanoke River, Virginia. However, the spatial and temporal scales of the two studies differed; Matthews studied fishes in individual riffles over 6 months. He predicted that a study encompassing all seasons or multiple years may show an increased temporal relative to spatial component of variation. Thus, the longer duration and multiple habitat types included in our study may explain at least part of the higher contribution of temporal variation. The species with the highest fixed spatial variation, *Cyprinella venusta*, is one that occurs patchily in the area but often at very high densities where present. The high level of ephemeral spatial variation in three of the species indicates that spatial differences varied over time, which is in keeping with an observed lack of synchrony in CPUE of individual species among streams.

The high temporal variability presumably has both natural and anthropogenic causes. Some authors have suggested that high temporal variability is typical of warmwater stream fish assemblages (Grossman et al., 1982; Schlosser, 1987), although some warmwater fish assemblages appear to be quite stable (Ross et al., 1985, 1987). Assemblage stability is typically greater in benign than harsh environments within a region (Ross et al., 1985; Schlosser, 1987). In our study area, channelization and subsequent incision have created harsher conditions in the form of wide, shallow streams with flashy hydrographs in unstable channels that are largely disconnected from their floodplains. Habitat variables at the scale we measured were typically not associated with assemblage changes, suggesting that any habitat influences probably operated at a larger scale.

Fish assemblages characterized by small-bodied, short-lived species able to quickly recolonize stream reaches and by high temporal variability in composition and abundance have been described as 'colonizing' assemblages (Schlosser, 1987). Colonizing assemblages are characteristic of headwater streams, but also of simplified, degraded habitat in larger streams, where assemblages are marked by reduced native species richness and increased species dominance relative to undisturbed streams of similar size (Schlosser, 1987). Changes in large streams that increase seasonal hydrological variability tend to shift assemblages toward greater variability and other characteristics of colonizing assemblages (Poff & Allan, 1995). In light of the watershed and channel degradation in the study streams, colonizing assemblages are expected in the streams. Furthermore, the assemblage in Hotopha Creek contained a more extreme example of a colonizing assemblage than did comparably-sized, but less degraded, Cypress Creek. Compared to Hotopha Creek, the much smaller Buckhorn Creek had a comparable number of species and lower species dominance, presumably due at least in part to more complex, less degraded habitat in the latter.

High temporal variability in the study streams suggests that abiotic control (e.g. environmental variation) may be more important than biotic control (e.g. resource limitation or predation) of assemblage structure (Grossman et al., 1998). However, Ross et al. (1985) observed that high assemblage variability in one stream reach was not necessarily indicative of assemblage instability throughout an entire population. Our sample sites certainly did not encompass entire populations of any of the species examined. However, others studying larger (Shields et al., 1998) or more sites (Shields et al., 1995) within the same region of Mississippi have also found extremely high levels of temporal variability in assemblages, suggesting that it is characteristic of the small, incised, unstable streams in the region. Thus, our results are consistent with Schlosser's colonizing assemblages whose control lies toward the abiotic end of the spectrum.

Warmwater stream fish assemblage structure is strongly dependent on downstream processes and connectivity (Osborne & Wiley, 1992; Porto et al., 1999). Variations among the study streams in connectivity to diverse habitats downstream may help explain some differences in assemblage characteristics. The low species richness in Hotopha Creek relative to similarly-sized Cypress Creek is likely due, in part, to the presence of the grade control weir on lower Hotopha Creek that restricts migration from the Little Tallahatchie River. Further, at the point where Hotopha enters it, the Little Tallahatchie River is highly regulated by Sardis Dam, and thus, may support a reduced species source pool for Hotopha Creek. In contrast, Cypress Creek flows unobstructed into a segment of the Little Tallahatchie River that contains a variety of habitats which are expected to support a large species pool.

The occasional high species turnover rates and the changes in total CPUE that were not attributable to age 0 recruitment indicate that fish movement is considerable in the streams and that immigration and emigration are extremely important to the assemblage structure at a given time. Our data do not allow us to ascertain the distance of movements, only that fish must have moved in and out of the study sites. Longer study sites may have minimized the effects of movements. However, the relative uniformity of the channels leads us to believe that many of the movements may have been over distances of hundreds of meters to several kilometers, indicating that hydraulic connectivity is integral to maintenance of these fish assemblages (Winston et al., 1991). Linfield (1985) suggested that cyprinids in English streams are extremely mobile, aggregating in winter and dispersing widely in summer.

The order of magnitude increase in total CPUE in the Buckhorn Creek site from July 1993 to 1994 was the most extreme example of variation in abundance, reflecting dramatic increases in densities of nearly all common fish species in the creek during the second summer of study. Because the increase was not due solely to reproduction, it further illustrates the importance of immigration to assemblage dynamics. Concomitant habitat changes were not evident, although differences in flow between years may have contributed to the spike in total CPUE. Average depth, current velocity, and stream discharge were nearly identical between the two July samples, but the CV of current velocity was higher in July 1994. Compared to 1993, flows in 1994 were much higher throughout the winter, and some higher flows occurred in early summer in nearby Hotopha Creek (Fig. 2) and presumably in Buckhorn Creek as well (see also Shields et al., 1998, p. 74, Fig. 5). All sunfishes in Buckhorn Creek declined from July 1993 to 1994, which supports previous findings that centrarchids thrive during periods of stable, low flows (Ross et al., 1985; Schlosser, 1985; Grossman et al., 1998; but see Shields et al., 1998). CPUE of all cyprinids increased in 1994 in Buckhorn Creek; however, in Hotopha and Cypress creeks, some cyprinid numbers decreased from July 1993 to 1994, whereas others increased.

Identifying seasons of relative stability and instability is helpful both for understanding assemblage dynamics and for developing research or monitoring plans. Several patterns in species turnover rates indicate that spring to early summer is the period of greatest change in assemblage composition in the study streams. First, many of the highest single-interval turnover rates occurred in the May–July intervals. Second, average values for species turnover between consecutive samples in spring-early summer (i.e. March–May and May–July) tended to be higher than values calculated from March to July, suggesting that after March the assemblages undergo a period of change, but by early July return to a composition more similar to that in March. Finally, annual species turnover rates between July samples were lower than or similar to annual rates between May samples and were often lower than turnover rates between consecutive samples. Although species composition appears to be more stable in summer than spring, abundances can vary radically from one summer to the next, as occurred in Buckhorn Creek. The higher variability of PD compared to species turnover was evidently due to a combination of fish movements and age 0 recruitment. High species turnover rates in spring may reflect seasonal migrations and movements to and from spawning locations, which tend to peak in spring and early summer in warmwater streams (Funk, 1957; Hall, 1972; Whitehurst, 1981; Porto et al., 1999). Although the duration of the study prevented comparisons from one winter to the next, winter may be a period of relative stability in both assemblage composition and structure; in winter, stream metabolism and age 0 recruitment are low, and movements are probably more limited (Hall, 1972; Whitehurst, 1981). However, highly unpredictable winter stream discharges in the region could confound attempts to conduct annual winter sampling. Some caution should be exercised in interpreting the rates because sampling intervals were not constant. In particular, the November 1993 to March 1994 interval was about twice as long as most others.

Processes in fish assemblages were not synchronized even in neighboring streams, as revealed by the lack of correlation among assemblage metrics (e.g. total species, dominance, abundance). The substantial difference in stream size may be responsible, in part, for the lack of synchrony between Buckhorn and Hotopha creeks, despite their proximity. Between Cypress and Hotopha creeks, differences in hydrology both at the sites and in more distant parts of the stream network may have contributed to the lack of correlation.

The seasonal and annual variation in the fish assemblages within sites, in the absence of obvious changes in habitat conditions, suggests that the statistical power of many fish-based monitoring designs in degraded, Coastal Plain streams will be extremely limited. Fish-based indices (e.g. the index of biotic integrity) tend to have wide confidence intervals in stream segments that contain colonizing assemblages, such as the ones we studied (Schlosser, 1990; Shields et al., 1995). A fish monitoring program focused on population trends may be overwhelmed by the observed background variation, even if a long time series of observations prior to the action of interest were available, which is rarely the case (Grossman et al., 1990). Only extreme trends in population levels would be detectable given the high variability we observed (Maxell, 1999). The claim is often made that at least large changes in abundance and species composition will be detectable by monitoring programs with minimal sampling prior to the action of interest. However, an order of magnitude change in fish abundance over 1 year in the absence of measurable habitat change at our Buckhorn Creek site suggests otherwise. Even if assemblages are more stable when viewed at the whole-stream scale, as Ross et al. (1985) observed, most monitoring programs are not able to cover such large areas.

Long-term monitoring to determine ranges of temporal variation in assemblage structure in the absence of anthropogenic alterations will facilitate both planning and interpretation in stream fish monitoring programs (Schlosser, 1990). Nonetheless, the overwhelming importance of hydrologic regime to structuring the fish community (Grossman et al., 1998) may mask the effects of more subtle habitat changes on fish assemblages in these incised streams. Metrics other than abundance, such as species composition-based metrics (Shields et al., 2000), functional group composition, and assemblage size/age structure (Schlosser, 1982; Shields & Knight, 2004) may be more appropriate for assessing assemblage changes resulting from changes in stream conditions. If long enough time series before and after a change are available, then the degree of variability in abundance, itself, may be a useful indicator of a shift along the continuum of 'colonizing' to 'stable' assemblages as habitat shifts along the harsh to benign continuum (Schlosser, 1982, 1987).

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Appendix 1. Families, scientific names, abbreviations, and common names of fish species collected in Cypress, Hotopha, and Buckhorn creeks, Mississippi, USA, from May 1993 to October 1994. Arranged in alphabetical order by family and scientific name

Family	Scientific name	Abbreviation	Common name	Number captured
Aphredoderidae	*Aphredoderus sayanus*	ASAY	Pirate perch	3
Atherinidae	*Labidesthes sicculus*	LSIC	Brook silverside	27
Catostomidae	*Erimyzon oblongus*	EOBL	Creek chubsucker	54
Catostomidae	*Hypentelium nigricans*	HNIG	Northern hogsucker	5
Catostomidae	*Ictiobus bubalus*	IBUB	Smallmouth buffalo	1
Catostomidae	*Moxostoma poecilurum*	MPOE	Blacktail redhorse	23
Catostomidae	*Carpiodes carpio*	CACA	River carpsucker	7
Catostomidae	*Carpiodes cyprinus*	CCYP	Quillback	4
Centrarchidae	*Lepomis cyanellus*	LCYA	Green sunfish	74
Centrarchidae	*Lepomis gulosus*	LGUL	Warmouth	8
Centrarchidae	*Lepomis humilis*	LHUM	Orangespotted sunfish	1
Centrarchidae	*Lepomis macrochirus*	LMAC	Bluegill	183
Centrarchidae	*Lepomis megalotis*	LMEG	Longear sunfish	312
Centrarchidae	*Micropterus punctulatus*	MPUN	Spotted bass	68
Centrarchidae	*Micropterus salmoides*	MSAL	Largemouth bass	1

Continued on p. 61

Appendix 1. (Continued)

Family	Scientific name	Abbreviation	Common name	Number captured
Centrarchidae	*Pomoxis annularis*	PANN	White crappie	3
Clupeidae	*Dorosoma cepedianum*	DCEP	Gizzard shad	1
Cyprinidae	*Cyprinella camura*	CCAM	Bluntnose shiner	2998
Cyprinidae	*Cyprinella venusta*	CVEN	Blacktail shiner	2323
Cyprinidae	*Cyprinus carpio*	CCAR	Common carp	3
Cyprinidae	*Hybognathus nuchalis*	HNUC	Mississippi silvery minnow	370
Cyprinidae	*Luxilus chrysocephalus*	LCHR	Striped shiner	1790
Cyprinidae	*Lythrurus fumeus*	LFUM	Ribbon shiner	9
Cyprinidae	*Lythrurus umbratilis*	LUMB	Redfin shiner	15
Cyprinidae	*Notropis atherinoides*	NATH	Emerald shiner	664
Cyprinidae	*Notemigonus crysoleucas*	NCRY	Golden shiner	10
Cyprinidae	*Notropis rafinesquei*	NRAF	Yazoo shiner	3642
Cyprinidae	*Notropis volucellus*	NVOL	Mimic shiner	1198
Cyprinidae	*Opsopoeodus emiliae*	OEMI	Pugnose minnow	3
Cyprinidae	*Pimephales notatus*	PNOT	Bluntnose minnow	787
Cyprinidae	*Pimephales vigilax*	PVIG	Bullhead minnow	172
Cyprinidae	*Semotilus atromaculatus*	SATR	Creek chub	647
Esocidae	*Esox americanus*	EAME	Grass pickerel	2
Fundulidae	*Fundulus notatus* and *F. olivaceus*[a]	FUND	Blackstripe topminnow Blackspotted topminnow	485
Ictaluridae	*Ameiurus natalis*	ANAT	Yellow bullhead	50
Ictaluridae	*Ictalurus punctatus*	IPUN	Channel catfish	21
Ictaluridae	*Noturus miurus*	NMIU	Brindled madtom	13
Ictaluridae	*Noturus phaeus*	NPHA	Brown madtom	22
Ictaluridae	*Pylodictis olivaris*	POLI	Flathead catfish	1
Lepisosteidae	*Lepisosteus platostomus*	LPLA	Shortnose gar	1
Percidae	*Etheostoma chlorosomum*	ECHL	Bluntnose darter	6
Percidae	*Etheostoma gracile*	EGRA	Slough darter	2
Percidae	*Etheostoma histrio*	EHIS	Harlequin darter	4
Percidae	*Etheostoma lynceum*	ELYN	Brighteye darter	37
Percidae	*Etheostoma nigrum*	ENIG	Johnny darter	1
Percidae	*Etheostoma parvipinne*	EPAR	Goldstripe darter	5
Percidae	*Etheostoma proeliare*	EPRO	Cypress darter	4
Percidae	*Etheostoma artesiae*	EART	Redspot darter	115
Percidae	*Percina sciera*	PSCI	Dusky darter	75
Petromyzontidae	*Ichthyomyzon sp.*	LAMP	Lamprey ammocoete	4
Poeciliidae	*Gambusia affinis*	GAFF	Western mosquitofish	585

[a] Species were combined because age 0 individuals could not be distinguished consistently, however, *F. olivaceus* numerically greatly exceeded *F. notatus*.