
Annual Variation in Fish Assemblages of Watersheds with Stable and Changing Land Use
Author(s): Peter E. Schweizer and Glenn R. Matlack
Reviewed work(s):
Source: *American Midland Naturalist*, Vol. 153, No. 2 (Apr., 2005), pp. 293-308
Published by: The University of Notre Dame
Stable URL: http://www.jstor.org/stable/3566669
Accessed: 04/02/2013 15:30

Am. Midl. Nat. 153:293–308

Annual Variation in Fish Assemblages of Watersheds with Stable and Changing Land Use

PETER E. SCHWEIZER AND GLENN R. MATLACK[1]
Department of Environmental and Plant Biology, Porter Hall, Ohio University Athens, Ohio 45701

ABSTRACT.—Freshwater fish assemblages are sensitive to changes in land use, but it is unclear how rapidly assemblages respond to such change or how closely they track physical changes in the stream environment. We monitored fish assemblages at the outflow of three watersheds on the outer coastal plain of Mississippi over a period of 8 y. The watersheds differed in patterns of land use, being predominantly forested, rapidly urbanizing, and long-urbanized, respectively. Watersheds were distinct in fish species composition, differing primarily in abundance of *Etheostoma lynceum, E. stigmaeum, Luxilus chrysocephalus* and *Lythrurus roseipinnis.* Species richness was consistently greatest at the predominantly forested site and least at the urbanized site. Fish assemblages were distinguishable in terms of substrate preference, water-speed, silt tolerance, and trophic habit. The stream draining the urbanizing watershed showed an increase in richness of species of high silt tolerance and a decrease in richness of those preferring a gravel substrate over the sampling period. Contrary to expectation, annual variation in composition was modest relative to differences among sites. Annual variation in richness and numbers was unrelated to measures of streamflow or seasonal precipitation. Changes in stream character related to land use change appear to have impacted the fish assemblages of these streams, but the transition to an urban fish assemblage in the urbanizing stream occurred before the study period, well before the obvious signs of physical degradation appeared at the site.

INTRODUCTION

Human land use strongly influences the quantity and character of rainwater runoff, affecting the hydrology and chemistry of streams draining developed land. Physical effects accompanying land development include increased suspended sediment, deposition of silt, altered flow regime, increased nutrient loading and loss of riparian vegetation (Klein, 1979; Welsch, 1991; Stevens and Cummins, 1999; Sonoda *et al.*, 2001; Sutherland *et al.*, 2002). Such changes in the aquatic environment are easily detected by fish, whether directly through changes in water quality (Reash and Berra, 1987; Aadland, 1993; Schleiger, 2000) or changes in habitat (Angermeier and Schlosser, 1989; Poff and Ward, 1990; Sutherland *et al.*, 2002), or indirectly through the aquatic food web (Power *et al.*, 1985; Power, 1992; Tong, 2001). Streams in urbanized areas frequently have depauperate fish assemblages relative to those of undeveloped landscapes, dominated by species with high silt-tolerance, low demand for dissolved oxygen, and little specificity in their ecological and trophic requirements (Scott *et al.*, 1986; Steedman, 1988; Albanese and Matlack, 1999; Schleiger, 2000).

The contribution of landuse change to loss of aquatic species and degradation of stream quality has been well documented (*e.g.*, Garie and McIntosh, 1986; Booth and Jackson, 1997; Finkenbine *et al.*, 2000; Bledsoe and Watson, 2001). It is unclear, however, what ecological mechanism controls the transition from a natural stream assemblage to an urbanized assemblage. It is reasonable to assume the fish community changes rapidly in response to chemical and physical changes occurring in the impacted stream. Individuals of many species have been shown to respond directly to amount of suspended silt, turbidity, dissolved

---

[1] Corresponding author: Telephone: (740) 593 1131; FAX: (740) 593 1130; e-mail: matlack@ohio.edu

oxygen, and canopy cover (Karr, 1981; Scott and Hall, 1997; Magoulick, 2000; Davis *et al.*, 2003). Alteration in fish assemblages is frequently linked to presence of pollutants such as herbicides and petroleum products (Marsh and Minckley, 1982; Reash and Berra, 1987) presumably acting through their toxic effect on individual fish. Short-term physiological responses may translate into community structure through selective mortality (Tramer, 1977; Ross *et al.*, 1985) or emigration from unsuitable sites (Scott *et al.*, 1986).

In other studies, changes in the fish assemblage do not occur immediately following urbanization, but may take many years with gradual replacement of species (Fitzgerald *et al.*, 1998). In a small warm-water stream in southwest New York, for example, persistence of species and stability in community structure were observed despite progressive stream degradation over a period of 42 y (Hansen and Ramm, 1994). The fish assemblage may change gradually because colonizing species are not available (Helfman *et al.*, 1997), barriers to fish movement delay or preclude colonization (Warren and Pardew, 1998) or because nominally unsuited species continue to colonize a degraded site (*i.e.*, acting as a "sink" population; Pulliam, 1988). Populations of species suited to the degraded site may expand slowly due to limitations on their reproductive rate (Helfman *et al.*, 1997) or because annual variation in the stream environment overrides the effects of progressive watershed alteration (Grossman *et al.*, 1998; Fitzgerald *et al.*, 1998). Furthermore, undisturbed fish assemblages may already consist of species with a wide tolerance for environmental variation so that human-caused stream degradation is easily accommodated (Sheldon, 1968; Tramer and Rogers, 1973).

Small freshwater streams contribute strongly to the biological diversity of terrestrial ecosystems (Vannote *et al.*, 1980; FEMAT, 1993; Forman, 1995). Effective management for diversity requires an understanding of the process of fish community degradation which accompanies watershed development, an increasingly common problem worldwide. To examine the time course of fish assemblage degradation, we censused a freshwater stream site annually for 8 y through a period of upstream watershed urbanization. For comparison, similar data were collected at sites in two nearby streams which drained a rural/forested area and a long-urbanized area, respectively. We began with the expectation that fish assemblages varied among the three sites, reflecting the contrasting land uses in the upstream watersheds (hypothesis 1).

Fish assemblage structure at the urbanizing-watershed site was expected to be more variable among years than the other two streams, which drained watersheds with relatively stable land uses (hypothesis 2). We expected that the fish assemblage in the urbanizing stream would closely track the dramatic physical and hydrological changes observed over the sampling period, reflecting the widely demonstrated sensitivity of individual fish to water quality (hypothesis 3). The fish assemblage of the urbanizing stream at the beginning of the survey was expected to resemble that of the rural/forest stream and progressively shift toward the composition of the urban stream. Finally, we sought to understand the assemblage response in terms of the distinctive life histories and reproductive potentials of species present.

STUDY SITES

The three streams used in this study drain gently undulating landscapes on the outer coastal plain of Mississippi (USA) 100–120 km north of the Gulf of Mexico. The streams cut through Pleistocene deposits of sand, gravel, and clay which form layers of varying hardness apparent in the stream beds (USDA, 1979). All streams drain into the Bouie or Leaf rivers in the Pascagoula drainage. All connect near the city of Hattiesburg, Mississippi, and are likely to share the same species pool.

Mixons Creek (MC) is a medium-sized stream draining ca. 25 km^2 on the western edge of the city (sampled at 31°21′15″N, 89°20′45″W). The watershed above the sample point was predominantly forest and pastureland (>95%) until ca. 1970. Aerial photos show corridors of forest flanking most of the main stem at that time. Around 1970, suburban development began in the eastern portion of the watershed, accelerating in the 1980s and culminating in the 1990s with several major development projects straddling the main stem (<20% pasture and forest in October 2000). At the beginning of the observation period (April 1996), Mixons Creek was ca. 4 m wide at the sample reach with a sand/gravel substrate and low vegetated banks ≤50 cm from the water. The tree canopy was intermittently open above the stream, with tree crowns closing across the stream at many points. Occasional sand bars ≤30 cm high were observed (G.R. Matlack, pers. obs.).

Through the period of observation bank scouring became evident along the sample reach, increasing dramatically in 1999. By 2001 bank erosion had undercut many trees, broadly opening the canopy above the reach and a considerable distance up- and downstream. By 2001 sand bars increased to 80–120 cm height and the stream widened to 5–6 m. At the time of writing (summer 2003), the stream is 6–10 m wide with severe bank cutting (bank heights of 4 m in some places). At one location, 100 cm of bank retreat was recorded in a nine-month period (Schweizer and Matlack, unpubl.). A railway bridge 100 m downstream was destroyed by undercutting of abutments in 2003. Limestone riprap has recently been applied to control bank cutting in a section of the sample reach.

Two additional streams were sampled to provide baselines for an undeveloped rural watershed and a long-urbanized watershed. Clear Run (CR; sampled at 31°28′45″N; 89°34′00″W) flows through forest and pasture (>95%) in a watershed of ca. 23 km^2. Clear Run is situated 20 km NW of Mixons Creek. Aerial photos show forest along most of the main stem upstream of the sample site. Forest canopy was closed over the sample reach with the exception of ca. 10 m next to the bridge that provided access. Vegetated banks came to within 30 cm of the water. Substrate consisted of a series of hard clay ledges interspersed with patches of gravel. Tangles of woody debris collected on fallen logs and bridge supports. The stream was 3–4 m wide, and did not change during the sample period. Invertebrates at the site included stoneflies (order Plecoptera), mayflies (Ephemeroptera), damselfly larvae (Zygoptera), caddisflies (Trichoptera), and hellgrammites (*Corydalus* sp.; Bobbie Meyer, pers. comm.) suggesting low concentrations of dissolved nutrients and relatively high levels of dissolved oxygen. Hydrological and vegetation conditions did not change noticeably during the sampling period (G.R. Matlack, pers. obs.).

In contrast to the little-disturbed Clear Run, Gordons Creek (GC; sampled at 31°19′30″N, 89°18′45″W) flowed through the urban center of the City of Hattiesburg draining an area of ca. 22 km^2. Most of the drainage is occupied by commercial and residential neighborhoods built between 1880–1960 (1–2% forest and pasture). Although small-scale development continues in some parts of the watershed, none occurred along the main stem during the sampling period. Long sections have been channelized, constrained within limestone-filled gabions and concrete walls. The sample reach was 6–8 m wide defined by high graded banks covered by limestone riprap. Substrate was predominantly sand and silt. Low sand bars (<50 cm) were common and were frequently redistributed during floods. There was no natural vegetation near the sample area. Tubifex worms (*Tubifex tubifex*) and rattail maggots (Syrphidae) were observed in the sample reach, suggesting eutrophication. Floating mats of algae were common. These conditions did not change noticeably during the sample period (G.R. Matlack, pers. obs.).

METHODS

In each stream, a single 50 m section was sampled for fish in late spring 1996–2003. Each sample section included the range of mesohabitats typical of lower reaches of the respective stream such as overhanging banks, woody debris, riffles, pools, and sand bars. Hydrological conditions were qualitatively different among the sample sections and consistent with the general character of each stream (as described above).

Data were collected in late April/early May (except 2001 and 2003 in which censuses were conducted in mid-June). Sampling efforts on each date consisted of 60 minutes active fish capture during daylight. Fish were collected using 1.5 m × 4 m nylon seines with a 0.32 cm mesh. Dip nets were used to probe woody debris and bank recesses which might shelter fish. An effort was made to sample all potential microhabitats within the reach. Sampling method was standardized in an effort to assure equal capture efficiency in all sites and all years.

Sampling was completed in 1–2 d in most years. In 2001 a large algal mat clogged almost the entire reach of Gordons Creek seriously interfering with sampling (many individuals were seen to escape the seine around the mat edges). To improve sampling effectiveness, the site was revisited several days later after a shower had washed the mat downstream.

Fish were fixed in 10% formalin, transported to our laboratory at the University of Southern Mississippi (Hattiesburg), and identified using keys in Ross (2001). All fish were then preserved in 70% ethyl alcohol and archived in the University of Southern Mississippi Museum of Ichthyology.

ANALYSIS

Variation among sites and years was assessed visually by plotting total numbers of adult fish, species richness, and Shannon's H′, a measure of species diversity incorporating relative abundance (Magurren, 1988). This approach assumes a high level of species detectibility with detectibility equal in all species, assumptions hardly ever met in real fish communities. To control this source of bias, true species richness was estimated nonparametrically based on observed distributions of species abundance at each site and sampling date (Burnham and Overton, 1979; Williams *et al.*, 2001). An appropriate-order jackknife estimator was selected with a limiting value as species frequency is assumed to be infinite (SPECRICH; Hines *et al.*, 1999). Estimated richness and standard error were plotted against sampling date. Although this approach reduces bias in the measure of species richness, it should be noted that heterogeneity of detectibility and underestimation of species presence still affects all results reported here (as in most studies; Williams *et al.*, 2001).

Variation in species composition was considered by ordinating sample sites/dates using Nonmetric Multidimensional Scaling, an ordination technique based on ranking species-hyperspace distances (*i.e.*, multivariate dissimilarity) among sample sites and dates (McCune and Grace, 2002). Sorenson's measure was used as the estimate of distance. From comparison of 40 trials from random starting points, a likely model was selected on the basis of good conformity of model distance to distance in the original hyperspace (low "stress") and dependable stability of stress through many iterations of the model. The reported stress value is standardized by the sum of interpoint distances in ordination space (Mather, 1976) and rescaled to give a value between 0–100 (McCune and Grace, 2002). A Monte Carlo test for the usefulness of the model was performed by comparison with stress levels based on randomized data. Ordination scores were tested for correlations with individual species' abundance to discover which species contributed most strongly to differences in composition.

Seeking an ecological interpretation for variation in species composition, we categorized species in each of four aspects of life history based on Ross (2001), and plotted fish abundance and species richness within life history type by years and sites. Species were classified by reported tolerance of suspended silt (high, medium, low), preferred substrate in the stream bed (rock/gravel, silt, generalist), preferred water speed (fast/moderate, slow/none), and food source (omnivore, surface/water-column invertivore, benthic invertivore). The numbers of individuals and species in each class is expressed as a proportion to reduce the effect of systematic variation among years.

Proportional abundance in each life history group was compared among sites. Treating annual samples as replicates within sites, differences among sites were tested by the Kruskal-Wallis test, and if significant, individual sites were compared by pairwise Wilcoxon tests. To consider causes of variation among years, fish assemblage metrics were compared by correlation and visual assessment with five measures of recent weather which might affect stream flow or water quality. We tested precipitation in the month before sampling, precipitation in the previous 3 mo, precipitation 3–6 mo previous, mean monthly river flow in the nearby Bouie River (USGS, 2003; Bouie River gauging station, Hydrologic Unit Code 02472500), and mean monthly temperature (NOAA, 2003).

Long-term trends were difficult to discern due to considerable variation observed among years. To avoid false positives in recognizing long-term effects, an intentionally conservative definition was adopted: a study-length trend was recognized when all values of a fish assemblage metric in the first three years of observation were > (indicating a declining trend) or < (an increasing trend) all values of the metric in the last 3 y.

RESULTS

In the whole study 4112 adult fish were caught, representing 47 species (Appendix). Most abundant were *Lythrurus roseipinnis*, *Cyprinella venusta* and *Gambusia affinis* representing 26, 23, and 13% of adult fish, respectively. The Cyprinidae were well represented with 14 species including five members of the genus *Notropis*. The Centrarchidae were also particularly abundant; the genus *Lepomis* was represented by seven species with *L. macrochirus* (Bluegill) being the most abundant. Less-numerous taxa of interest include members of the Percidae: *Etheostoma stigmaeum* (Speckled Darter), *E. lynceum* (Brighteye Darter), *E. swaini* (Gulf Darter) and *Percina nigrofasciata* (Blackbanded Darter), and the petromyzontid *Ichthyomyzon gagei* (Southern Brook Lamprey). The last five species were collected only at Clear Run, the least developed watershed in our study.

Large numbers of young fish occurred in some samples. These were mainly Cyprinids <30 mm including 473 individuals at Mixons Creek in 2001; 29 at Clear Run in 2003; and 600 at Gordons Creek in 2003. Unidentifiable juveniles were listed as "young of the year" and placed in a separate category. Although noted, they were not used in most analyses. Presumably, many of the small juveniles died soon after the sample date. Survivors would appear in adult fish data in the subsequent year, however, so our inability to identify juveniles does not cause the study to miss their contribution to community structure.

Total number of adult fish (a measure of the general suitability of a site) showed a declining trend through the observation period at Clear Run, an increasing trend at Gordons Creek, and varied inconclusively at Mixons Creek (Fig. 1). As a result, Gordons Creek eventually replaced Clear Run as the most densely populated sampling site.

Species richness ranged from 27 and 22 species at Clear Run in 1997 and 2000, respectively, to 2 and 4 species at Gordons Creek in 1998, 1999, and 2000. Richness formed a consistent ranking in 7 of the 8 years: CR $\geq$ MC $\geq$ GC (Kruskal Wallis $X^2 = 15.24$, 2df, $P = 0.0005$; Wilcoxon $P = 0.021–0.0005$) although there was considerable within-site variation among years (Fig. 2). Mixons Creek declined in species richness through the sampling period, dropping from 18 species in 1997 to 10 in 2003. Similar trends were observed in the jackknife estimate of species richness (Fig. 3). Thus, differences in richness among years and sites do not appear to be due to differences in detectibility and variation in detectibility has

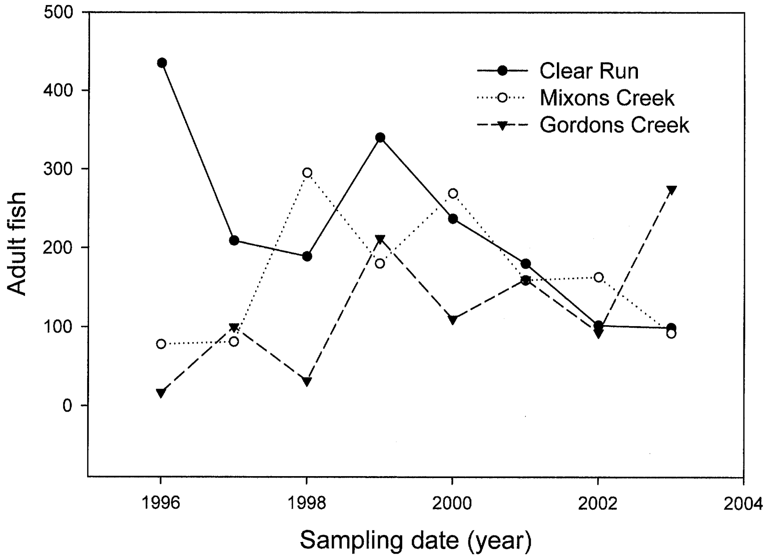

FIG. 1.—Total numbers of fish collected in three streams on the outer coastal plain of Mississippi, USA, 1996–2003. Unidentifiable juveniles are excluded

not masked trends in species richness. We will continue to use numbers directly observed as the most convenient measure of species richness. Diversity (Shannon's H′) showed no simple trend with time at any site (Fig. 4), but maintained a clear ranking: CR ≃ MC > GC (Kruskal Wallis $X^2 = 6.78$, 2df, $P = 0.0338$; Wilcoxon $P = 0.014$–0.016).

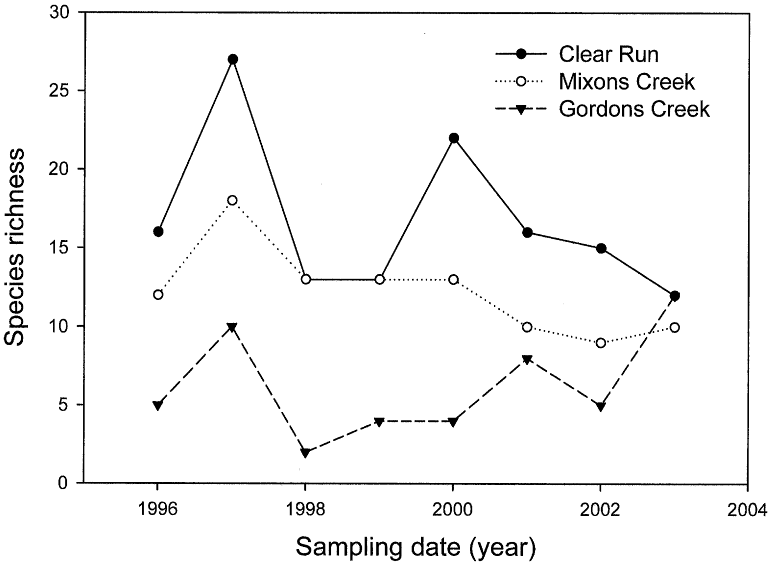

FIG. 2.—Number of species of fish collected in three streams on the outer coastal plain of Mississippi, USA, 1996–2003. Unidentifiable juveniles are excluded

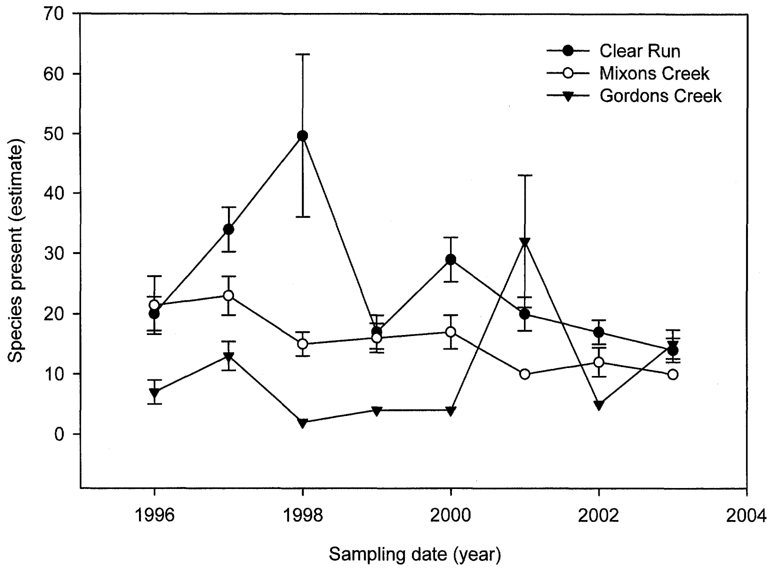

FIG. 3.—Species richness at three streams estimated by the jackknife procedure of Burnham and Overton (1979) to correct for variation in detectibility between sites and seasons. Error bars are ± one standard error

SPECIES COMPOSITION

In community ordination, the first two dimensions described 60.9 and 23.4% of variation in composition, respectively, with a final stress of 12.4. Subsequent dimensions each reduced stress less than five points and were within the 95% confidence limits of the randomly calculated models (Monte Carlo test), so were not judged to be useful.

Compositions of the three sites were clearly distinguishable on the first NMS axis (Fig. 5) confirming our first hypothesis. Mixons Creek samples lay close to those from Gordons Creek, but the sites didn't overlap; Clear Run consisted entirely of high values on the first axis, well separated from Mixons and Gordons creeks. Sites were not distinguishable on the second axis which is dominated by annual variation within sites. Scores on the first axis were most strongly correlated with abundance of *Etheostoma lynceum* (Pearson r = 0.640), *E. stigmaeum* (r = 0.627), *Luxilus chrysocephalus* (r = 0.629), and *Lythrurus roseipinnis* (r = 0.664). Scores on the second axis were strongly correlated with abundance of *Gambusia affinis* (r = 0.735).

The ordination (Fig. 5) revealed two exceptional data points. Gordons Creek in 2001 had a markedly lower score on axis 2 than other Gordons Creek samples. It is possible that the large algal mat observed on this date, which delayed sampling, influenced the composition data making comparison problematic. We regard this point as an outlier. The second exceptional point, MC 2003, was sampled without incident according to the standard protocol and cannot be dismissed so easily. At the time of data collection the streambed was scoured down to a hard clay substrate not previously observed at this site. The position of the MC, 2003 point can perhaps be explained in terms of a fish assemblage response to the novel substrate. Setting aside these points, Mixons Creek occupies an ordination space similar in area to those of Gordons Creek and Clear Run. Thus, contrary to our second

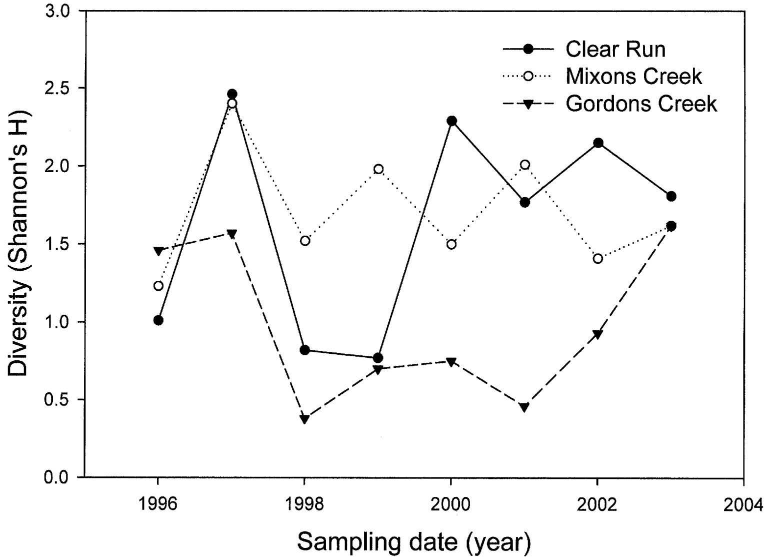

FIG. 4.—Diversity of fish collected in three streams on the outer coastal plain of Mississippi, USA, 1996–2003. Diversity is described as Shannon's H. Unidentifiable juveniles are excluded

hypothesis, the fish assemblage of the urbanizing-watershed site was no more compositionally variable than those of the two stable watersheds.

LIFE HISTORIES

Trophic and habitat preference allow easy discrimination among fish assemblages at the three sites (Table 1). In substrate preference, individuals of species preferring gravel were proportionately more numerous at the urbanized Gordons Creek than at other sites. More individuals preferring a silt substrate were observed at the undeveloped Clear Run than other sites. In terms of species richness, significantly more substrate-generalists were observed at Gordons and Mixons creeks than at Clear Run.

Individuals of species preferring moderate-fast stream flow were proportionately less numerous at the undisturbed Clear Run than in the streams draining more-developed watersheds (Table 1). Individuals preferring slow-no flow were more numerous at Clear Run than other sites. In contrast to numbers of individuals, species richness favored moderate-fast flow species at the undeveloped Clear Run relative to the other sites. Conversely, Clear Run had significantly fewer slow-flow preferring species than the other sites.

Individuals of high suspended-silt tolerance were significantly less common at Clear Run than at other sites (Table 1). Individuals of low-tolerance species showed a clear ranking of proportionate abundance: CR > MC > GC. Species richness showed a similar ranking as high-tolerance species were more proportionately common at more disturbed sites: GC > MC > CR. Species of low tolerance showed the reverse trend: CR > MC > GC. Species of moderate tolerance dominated the degrading Mixons Creek site: MC > CR ~ GC.

Finally, sites were distinguishable in abundance and richness of trophic groups. Omnivores were significantly less numerous at the undeveloped Clear Run than at other sites. Surface/water column invertivores showed lower species richness at Clear Run.

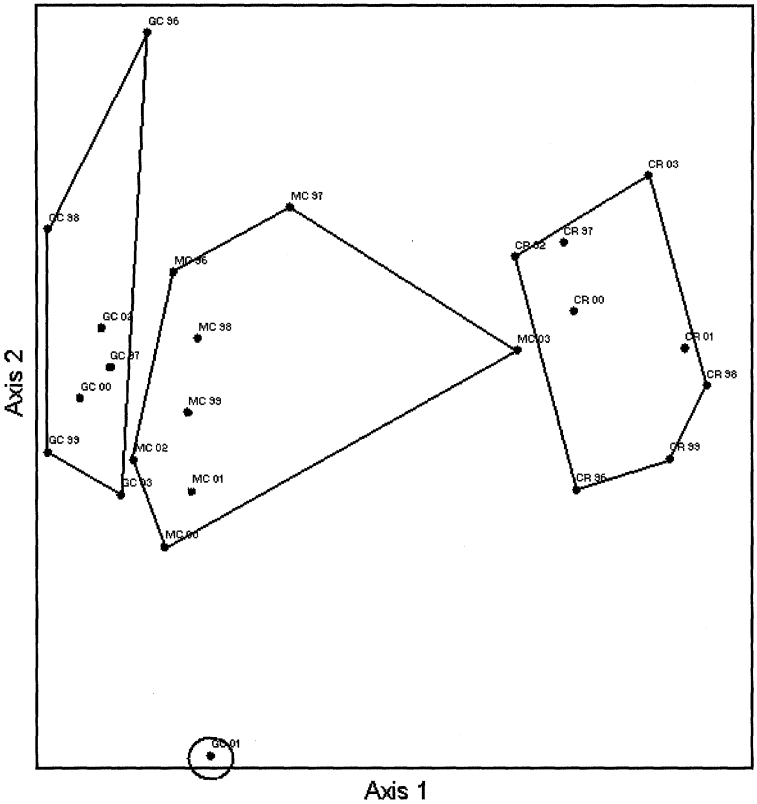

FIG. 5.—Composition of the fish assemblage at three sample sites between, 1996–2003. Sites and dates are ordinated according to scores on the first and second NMS axes

Benthic feeders were more common at Clear Run than other sites, both in terms of number of individuals and species richness.

TEMPORAL VARIATION

Considerable temporal variation was observed in fish assemblage metrics, with much apparently unsystematic variation among years. At Clear Run individuals of moderate suspended silt tolerance showed a declining trend over the sample period, while those of low tolerance increased. Species preferring moderate-fast current and gravel substrates increased over the sampling period at the Clear Run site. At the long-channelized Gordons Creek there was much annual variation on the scale of the other sites, but it did not meet the criterion for a systematic trend. Mixons Creek, the evolving site, showed an increase in richness of species of high silt tolerance over the sampling period and a decrease in omnivores as a proportion of the total number of individuals.

Annual variation within sites could not be linked to regional weather or stream flow. Neither precipitation, stream flow data in the Bouie River, nor air temperature were significantly correlated with any aspect of the fish assemblage ($P > 0.05$), nor were patterns apparent in plots of the data.

TABLE 1.—Rankings of streams according to numbers of species and individual fish in eleven life history classes. Kruskal Wallis X^2 statistic and probability are shown. If significant differences are detected within a group, sites are ranked by pairwise Wilcoxon tests. Streams: Clear Run, CR; Mixons Creek, MC; Gordons Creek, GC. "ns" indicates nonsignificance

	Fish numbers		Species richness	
Life history group	X^2	P	X^2	P
Substrate preference				
Gravel	6.29	0.410	ns	
	GC > MC ~ CR			
Silt	9.47	0.0088	ns	
	CR > GC ~ MC			
General	ns		13.29	0.0013
			GC ~ MC > CR	
Rate of flow				
Moderate-fast	38.21	0.0165	9.91	0.0070
	MC ~ GC > CR		CR > GC ~ MC	
Slow-none	7.87	0.0196	10.37	0.0056
	CR > MC ~ GC		GC ~ MC > CR	
Silt tolerance				
High	11.38	0.0034	17.97	<0.0001
	GC ~ MC > CR		GC > MC > CR	
Moderate	ns		7.23	0.027
			MC > CR ~ GC	
Low	19.11	<0.0001	19.01	<0.0001
	CR > MC > GC		CR > MC > GC	
Trophic preference				
Omnivore	6.12	0.0470	ns	
	GC ~ MC > CR			
Surface/column invertivores	ns		10.27	0.0059
			MC ~ GC > CR	
Benthic invertivores	18.50	<0.0001	19.06	<0.0001
	CR > GC ~ MC		CR > GC > MC	

DISCUSSION

The three streams were easily distinguishable in terms of species richness and community composition, consistent with their strongly contrasting watershed conditions. The relatively undisturbed Clear Run was the most species-rich site but only marginally greater than the other sites in species diversity, indicating that high richness was caused by a few individuals of uncommon species. At the other disturbance extreme, Gordons Creek was least species-rich and least diverse. As predicted, the evolving hydrology of Mixons Creek placed it between Gordons Creek and Clear Run in all assemblage metrics. Assemblage composition reflected the pattern observed in fish numbers and species richness: Clear Run was distinct from other sites throughout the sampling period, having greater abundance of several habitat and trophic specialist species. Composition at Mixons Creek was distinct from Gordons Creek, but the two sites remained close in ordination space.

Mixons Creek is typical of urbanizing systems described in the literature. It was characterized by low diversity throughout the sampling period (Weaver and Garman, 1994;

Scott and Hall, 1997; Wang *et al.*, 2000; Schleiger, 2000) and a fish assemblage which trended toward habitat and trophic generalists (Reash and Berra, 1987; Lenat and Crawford, 1994; Kemp and Spotila, 1997; Schleiger, 2000). Such community responses show great generality, manifested as clearly on the outer coastal plain of Mississippi as they are in urban streams as widespread as central North Carolina (Lennat and Crawford, 1994), southeastern Wisconsin (Wang *et al.*, 2000), suburban Philadelphia (Kemp and Spotila, 1997) and elsewhere.

LIFE HISTORIES

Habitat and trophic preferences of the dominant fish species were consistent with the hydrology of the respective streams. The relatively undisturbed Clear Run site was dominated by species preferring gravel/rock substrates, moderate-fast current, and low levels of suspended silt, for example, *Etheostoma lynceum* and *E. stigmaeum* (Ross, 2001). The heavy sediment loads found in Mixons and Gordons Creeks probably excluded these species by laying down a fine-textured substrate and clouding the water. Although *Luxilus chrysocephalus* and *Lythrurus roseipinnis* typically tolerate a degree of suspended silt, they may have been uncommon in the urban streams due to a scarcity of invertebrates such as stoneflies, mayflies, and caddisflies in eutrophied waters. In addition, larvae of *L. roseipinnis* tend to be associated with eddies in deep pools with large woody debris (Ross, 2001). The lack of debris microhabitat may have contributed to the noticeable absence of these species in Mixons and Gordons Creeks. It is also possible that the two species were excluded by poor access to the flood plain imposed by the high banks. *Lythrurus roseipinnis* has been shown to use terrestrial food resources by moving onto the floodplain during seasonal flood events (O'Connell, 2003).

Clear Run was distinctive in the prominence of species feeding on benthic invertebrates; the other sites were dominated by omnivores and/or surface invertivores. Richness of benthic-feeding species may indirectly reflect stream flow. Hard or gravelly bottoms (such as Clear Run) tend to have higher current velocities than those with silty/sandy bottoms such as we observed at the other sites (Pratt *et al.*, 1981; Garie and McIntosh, 1986; Kennen, 1999). Mixons Creek was similar to Gordons Creek in fish life histories, both including more substrate generalist species, more species preferring slow current and more species tolerant of suspended silt than Clear Run. Similarity to the urbanized stream suggests that Mixons Creek is well advanced in the transition to the urban condition.

An interesting exception to the site contrasts described above is the pollution-resistant Western Mosquitofish (*Gambusia affinis*). *Gambusia affinis* can survive in oxygen-poor water by skimming the thin film of oxygenated surface water with its supra-terminal mouth (Helfman *et al.*, 1997; Ross, 2001). Consistent with its disturbance-tolerant behavior, abundance of *G. affinis* did not vary among sites (*i.e.*, weak correlations with NMS axis 1) although it accounted for much of the background variation in all sites (axis 2). A high degree of environmental tolerance appears to have decoupled it from the disturbance dynamic of these streams, and may be the reason for its wide regional distribution.

Patterns of fish number often contrasted with species richness. Stream flow preference, for example, showed opposite site rankings in number and richness. Total number of fish is related to reproductive capacity of individual species, and may be expected to track changes in the environment relatively quickly. Reproductive potential doubtless accounts for the prominence of *Gambusia affinis* in annual variation at these sites. *Gambusia*'s life span rarely exceeds 12 mo and the species may produce broods with 14–218 young from February to August (Ross, 2001). In contrast to fish numbers, species richness is dependent on the metapopulation dynamic of species loss and replacement—a process which may be relatively slow in some species (Albanese, 2001). We may expect species richness to be an index of the average condition over a period of several years, and thus, a better indicator of watershed condition than fish number.

TRENDS THROUGH TIME

Long-term changes in assemblage structure probably occurred at these sites, but are difficult to recognize against a background of strong annual variation. Applying the trend-definition criterion, changes were observed at two sites. The Mixons Creek site gained species of moderate silt tolerance—a change understandable in terms of increased sediment loading and siltation in the urbanizing watershed—and lost individuals of omnivore species. If a single marginal value is excused (2003 again), Mixons Creek may be decreasing in the number of species preferring a gravel substrate. Mixons Creek may be moving towards the silt-oriented fauna of Gordons Creek, and losing the gravel/rock preferring species typical of Clear Run.

The significance of these changes is less clear, however, when compared with changes at the Clear Run site, which had relatively stable land use through the sampling period. The fish assemblage at Clear Run shifted to low silt tolerance, fast current preference, and gravel substrate (opposite to the general trend at Mixons Creek). The long-urbanized Gordons Creek site showed variation in silt tolerance and substrate preference on the same scale as the other sites but failed to meet the trend criterion. Thus, streams draining stable watersheds may show as much variation in the fish assemblage as urbanizing streams. It is possible that the observed "trends" are not long-term changes linked to land use at all, but only a form of natural cyclic variation. Cyclic variation is consistent with the relative position of sites in ordination space. All sites showed considerable variation in composition among years, but such variation did not result in systematic change over the sampling period.

Assemblage composition appeared to be decoupled from the rapid physical changes observed in Mixons Creek. Gradual faunal changes in response to rapid urbanization have also been reported in small warm-water streams of southwest New York (sampling over 42 y; Hansen and Ramm, 1994) and cold-water streams of southeast Ontario (10 y; Fitzgerald *et al.*, 1998). Our data do not allow us to suggest a mechanism accounting for the lack of an obvious fish assemblage change, but several observations are suggestive. First, the generalist species hypothesis (Sheldon, 1968, Tramer and Rogers, 1973) can be rejected. Habitat-specialists were the basis for distinguishing these sites. The response to urbanization does not appear to have been obscured by the wide environmental tolerance of generalist species.

Second, the assemblage response to stream condition does not appear to be limited by reproductive capacity. The species distinguishing sites in assemblage ordination show relatively high reproductive capacity due to high fecundity (*Etheostoma stigmaeum, Notropis texanus*), short pre-reproductive period (*Etheostoma* spp), and high frequency of spawning (*Etheostoma lynceum, Notropis* spp) (Helfman *et al.*, 1997; Ross, 2001); it is reasonable to expect that their populations could respond quickly to changes in the physical or hydrological environment.

Rejecting demographic-limitation hypotheses, we infer that annual variation in fish assemblages reflects annual variation in habitat quality. Indeed, natural streams in the region show appreciable change in species abundances corresponding to annual flow levels (Ross and Baker, 1983). Large annual variation due to natural causes may override the more modest variation due to urbanization, thereby delaying fish community responses to land use (Grossman *et al.*, 1998; Fitzgerald *et al.*, 1998). Annual fluctuation in composition may reflect the sporadic bursts of reproduction which we classified as unidentifiable juveniles. It appears that there is strong background variation on several time scales irrespective of stability in land use and stream habitat quality. Such variation confounds the use of Gordons Creek and Clear Run as controls for watershed disturbance.

Assuming Mixons Creek once had a fish assemblage similar to Clear Run, one can infer the Mixons Creek assemblage has gradually changed towards that of Gordons Creek, which it now resembles. The observed distribution of life histories is consistent with a transition from trophic and habitat specialists to silt-tolerant generalists as urbanization progresses. The intermediate stages of this transition are not evident, however, contrary to the initial hypothesis. Although incremental changes may be inferred in a few life history groups, in most respects the Mixons Creek fish assemblage changed very little over the 8-y observation period. The critical shift from the undisturbed condition to heavily impacted must have occurred before our window of observation. In that case, shifts in composition would correspond to the initial period of land development rather than to later, development-induced hydrological changes in the stream.

This finding is disturbing because fish composition flux did not match the strong qualitative changes in hydrology, channel morphology, and vegetation observed at the Mixons Creek site. At the beginning of the study (April 1996) the site was dominated by intact forest and a natural stream channel. Nevertheless, the major faunal impact had already occurred at that date, perhaps indicated by the small sand bars. Two conclusions emerge: (1) Stream flow integrates watersheds; human impacts upstream appear to have been transmitted a considerable distance to the sample sites; (2) Local hydrology and vegetation may be a poor predictor of a stream's fish assemblage in dynamic landscapes. Thus, conservation efforts must encompass watersheds, not stream reaches, and must begin early in the process of hydrological alteration. When obvious signs of degradation (*e.g.*, bank cutting, siltation) appear, intervention may be too late.

Acknowledgments.—We are grateful to Martin O'Connell, Brett Albanese, Tanya Peterson Darden, and Richard Darden for identification of fishes. Stephen Ross graciously made the resources of the Museum of Ichthyology, University of Southern Mississippi, available to us. Brett Albanese, Martin O'Connell, Stephen Ross, and two anonymous reviewers made helpful comments on the manuscript.

LITERATURE CITED

AADLAND, L. P. 1993. Stream habitat types: their fish assemblages and relationships in flow. *North American Journal of Fisheries Management,* **13**:790–806.

ALBANESE, B. 2001. Movement of fishes in a network of streams and implications for persistence. Dissertation, Virginia Polytechnic University, Blacksburg, Virginia.

——— AND G. R. MATLACK. 1999. Utilization of parking lots in Hattiesburg, Mississippi and impacts on local streams. *Environmental Management,* **24**:265–271.

ANGERMEIER, P. L. AND I. J. SCHLOSSER. 1989. Species-area relationship for stream fishes. *Ecology,* **70**: 1450–1462.

BLEDSOE, B. P. AND C. C. WATSON. 2001. Effects of urbanization on channel instability. *Journal of the American Water Resources Association.* Vol. 37. no. 2. p. 255–270.

BOOTH, D. B. AND C. R. JACKSON. 1997. Urbanization of aquatic systems: degradation thresholds, stormwater detection and the limits of mitigation. *Journal of the American Water Resources Association,* **33**:1077–1090.

BURNHAM AND OVERTON. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology,* **60**:927–936.

DAVIS, N. M., V. WEAVER, K. PARKS AND M. J. LYDY. 2003. An assessment of water quality, physical habitat, and biological integrity of an urban stream in Wichita, Kansas prior to restoration improvements (phase I). *Archives of Environmental Contamination and Toxicology,* **44**:351–359.

FEMAT. 1993. Forest ecosystems management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team, July, 1993. US Government Printing Office: 794–478, Washington, D.C.

FINKENBINE, J. K., J. W. ATWATER AND D. S. MAVINIC. 2000. Stream health after urbanization. *Journal of the American Water Resources Association,* **36**:1149–1160.

FITZGERALD, D. G., E. KOTT, R. P. LANNO AND D. G. DIXON. 1998. A quarter century of change in the fish assemblages of three small streams modified by anthropogenic activities. *Journal of Aquatic Ecosystem Stress and Recovery,* **6**:111–127.

FORMAN, R. T. 1995. Landscape mosaics: the ecology of landscapes and regions. Cambridge University Press, New York. pp. 632.

GARIE, H. L. AND A. MCINTOSH. 1986. Distribution of benthic macroinvertebrates in a stream exposed to urban runoff. *Water resources Bulletin American Water Resource Association,* **22**:447–455.

GROSSMAN, G. D., R. E. RATAJCZAK, M. CRAWFORD AND M. C. FREEMAN. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs,* **68**:395–420.

HANSEN, M. J. AND C. W. RAMM. 1994. Persistence and stability of fish assemblage structure in a southwest New York stream. *American Midland Naturalist,* **132**:52–67.

HELFMAN, G. S., B. B. COLLETTE AND D. E. FACEY. 1997. The diversity of fishes. Blackwell Science Inc., Oxford, England. pp. 528.

HINES, J. E., T. BOULINIER, J. D. NICHOLS, J. R. SAUER AND K. H. POLLOCK. 1999. COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* **46**(Suppl.):S209–S217.

KARR, J. R. 1981. Assessment of biotic integrity using fish assemblages. *Fisheries,* **6**:21–27.

KEMP, S. J. AND J. R. SPOTILA. 1997. Effects of urbanization on brown trout *Salmo trutta,* other fishes and macroinvertebrates in Valley Creek, Valley Forge, Pennsylvania. *American Midland Naturalist,* **138**:554–68.

KENNEN, J. G. 1999. Relation of macroinvertebrate assemblage impairment to catchment characteristics in New Jersey streams. *Journal of the American Water Resources Association,* **4**:939–955.

KLEIN, R. D. 1979. Urbanization and stream quality impairment. *Water Resources Bulletin,* **15**:948–963.

LENAT, D. R. AND J. K. CRAWFORD. 1994. Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. *Hydrobiologia,* **294**:185–194.

MAGOULICK, D. D. 2000. Spatial and temporal variation in fish assemblages of drying stream pools: the role of abiotic and biotic factors. *Aquatic Ecology,* **34**:29–41.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, New Jersey. p. 192.

MARSH, P. C. AND W. L. MINKLEY. 1982. Fishes of the Phoenix metropolitan area in central Arizona. *North American Journal of Fisheries Management,* **4**:395–402.

MATHER, P. M. 1976. Computational methods of multivariate analysis in physical geography. *J. Wiley and Sons,* London. 532 p.

MCCUNE, B. AND J. GRACE. 2002. Analysis of ecological assemblages. MJM Software Design, Gleneden Beach, Oregon.

NOAA. 2003. Annual Climatologic Summary for Station: 223887/99999; Hattiesburg 5 SW, Mississippi. National Oceanic and Atmospheric Administration United States Department of Commerce. National Climatic Data Center. URL : http://cdo.ncdc.noaa.gov/ancsum/ACS.

O'CONNELL, M. T. 2003. Direct exploitation of prey on an inundated floodplain by cherryfin shiners (Lythrurus roseipinnis) in a low order, blackwater stream. *Copeia,* **2003**:635–645.

POFF, N. L. AND J. V. WARD. 1989. Implications of streamflow variability and predictability for lotic assemblage structure: a regional analysis of streamflow patterns. *Canadian Journal of Fish and Aquatic Science,* **46**:1805–1817.

POWER, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology,* **73**:1675–1688.

———, W. J. MATTHEWS AND A. J. STEWART. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology,* **66**:1448–1456.

PRATT, J. M., R. A. COLER AND P. J. GODFREY. 1981. Ecological effects of urban stormwater runoff on benthic macroinvertebrates inhabiting the Green River, Massachusetts. *Hydrobiologia,* **83**:29–42.

PULLIAM, H. R., 1988. Sources, sinks, and population regulation. *American Naturalist,* **132**:652–661.

REASH, R. J. AND T. M. BERRA. 1987. Comparison of fish assemblages in a clean-water stream and an adjacent polluted stream. *American Midland Naturalist,* **118**:301–322.

ROSS, S. T., W. J. MATTHEWS AND A. A. ECHELLE. 1985. Persistence of stream fish assemblages: effects of environmental change. *American Naturalist,* **126**:24–40.

———. 2001. Inland fishes of Mississippi. University Press of Mississippi, Jackson. 624 p.

———. AND J. A. BAKER. 1983. The response of fishes to periodic spring floods in a southeastern stream. *American Midland Naturalist* **109**:1–14.

SCHLEIGER, S. L. 2000. Use of an index of biotic integrity to detect effects of land uses on stream fish assemblages in west-central Georgia. *Transactions of the American Fisheries Society,* **129**:1118–1133.

SCOTT, J. B., C. R. STEWARD AND Q. J. STOBER. 1986. Effects of urban development on fish population dynamics in Kelsey Creek, Washington. *Transactions of the American Fisheries Society,* **115**:555–567.

SCOTT, M. C. AND L. W. HALL, JR. 1997. Fish assemblages as indicators of environmental degradation in Maryland coastal plain streams. *Transactions of the American Fisheries Society,* **126**:349–360.

SHELDON, A. L. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology,* **49**:193–198.

SONADA, K., J. A. YEAKLEY AND C. E. WALKER. 2001. Near-stream landuse effects on streamwater nutrient distribution in an urbanizing watershed. *Journal of the American Water Resource Association,* **37**:1517–1532.

STEEDMAN, R. J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. *Canadian Journal of Fisheries and Aquatic Science,* **45**:492–501.

STEVENS, H. M. AND K. W. CUMMINS. 1999. Effects of long-term disturbance on riparian vegetation and in-stream characteristics. *Journal of Freshwater Ecology,* **14**:1–17.

SUTHERLAND, A. B., J. L. MEYER AND E. P. GARDINER. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology,* **47**: 1791–1805.

TONG, S. T. 2001. An integrated exploratory approach to examining the relationships of environmental stressors and fish responses. *Journal of Aquatic Ecosystem Stress and Recovery,* **9**:1–19.

TRAMER, E. J. 1977. Catastrophic mortality of steam fishes trapped in shrinking pools. *American Midland Naturalist,* **97**:469–478.

———. AND P. M. ROGERS. 1973. Diversity and longitudinal zonation in fish populations of two streams entering a metropolitan area. *American Midland Naturalist,* **90**:366–374.

USDA. 1979. Soil survey of Lamar County, Mississippi. Soil Conservation Service. US Government Printing Office, Washington, D.C.

U.S. GEOLOGICAL SURVEY (USGS). 2003. USGS Water Resources of Mississippi, Real time data for USGS 02472500 Bouie Creek near Hattiesburg, MS. URL: http://ms.waterdata.usgs.gov/nwis/uv?02472500

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL AND C. E. CUSHING. 1983. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science,* **37**:130–137.

WANG, L., J. LYONS, P. KANEHL, R. BANNERMAN AND E. EMMONS. 2000. Watershed urbanization and changes in fish assemblages in southeastern Wisconsin streams. *Journal of the American Water Resources Association,* **36**:1173–1189.

WARREN, M. L. AND M. G. PARDEW. 1998. Road crossing as barriers to small-stream fish movement. *Transactions of the American Fisheries Society,* **127**:637–644.

WEAVER, A. L. AND G. C. GARMAN. 1994. Urbanization of a watershed and historical changes in stream fish assemblage. *Transactions of the American Fisheries Society,* **123**:162–172.

WELSCH, D. J. 1991. Riparian forest buffers, function and design for protection and enhancement of water resources. United States Department of Agriculture, Forest Service, Radnor, Pennsylvania.

WILLIAMS, B. K., J. D. NICHOLS AND M. J. CONROY. 2001. Analysis and management of animal populations. Academic Press, New York.

SUBMITTED 17 FEBRUARY 2004 ACCEPTED 16 AUGUST 2004

APPENDIX.—Fish species collected in three Mississippi streams

		Total number observed		
		CR	MC	GC
Petromyzontidae	*Ichthyomyzon gagei*	6	0	0
Cyprinidae	*Cyprinella venusta*	60	400	489
	Ericymba bucrata	9	18	0
	Luxilus chrysocephalus	161	24	0
	Lythrurus roseipinnis	1021	59	0
	Nocomis leptocephalus	33	0	0
	Notemigonus crysoleucas	0	67	13
	Notropis baileyi	124	1	0
	Notropis longirostris	4	123	3
	Notropis texanus	23	178	109
	Notropis volucellus	1	0	0
	Notropis winchelli	11	3	0
	Opsopoeodus emiliae	5	0	0
	Pimephales vigilax	0	32	0
	Semotilus atromaculatus	2	2	0
Catostomidae	*Hypentilium nigricans*	28	0	0
	Minytrema melanops	1	2	0
	Moxostoma poecilurum	1	4	0
Ictaluridae	*Ameiurus natalis*	0	0	1
	Ictalurus punctatus	0	2	0
	Noturus leptacanthus	8	0	0
	Noturus nocturnus	1	0	0
Esocidae	*Esox americanus*	1	0	0
	Esox niger	1	0	0
Fundulidae	*Fundulus olivaceus*	25	13	8
Poeciliidae	*Gambusia affinis*	6	241	303
	Gambusia holbrooki	1	0	7
Atherinidae	*Labidesthes sicrulus*	30	0	0
Centrarchidae	*Ambloplites ariommus*	1	0	0
	Lepomis cyanellus	2	8	11
	Lepomis gulosus	0	1	1
	Lepomis macrochirus	42	71	22
	Lepomis marginatus	0	0	6
	Lepomis megalotis	35	26	3
	Lepomis microlophis	0	5	1
	Lepomis miniatus	2	0	1
	Micropterus punculatus	34	18	17
	Micropterus salmoides	2	15	1
Percidae	*Ammocrypta vivax*	2	0	0
	Etheostoma lynceum	27	0	0
	Etheostoma parvipinne	2	2	0
	Etheostoma stigmaeum	47	1	0
	Etheostoma swaini	10	1	0
	Percina nigrofasciata	16	0	0
	Percina sciera	6	0	0