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Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams

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Abstract. Stream biota in urban and suburban settings are thought to be impaired by altered hydrology; however, it is unknown what aspects of the hydrograph alter fish assemblage structure and which fishes are most vulnerable to hydrologic alterations in small streams. We quantified hydrologic variables and fish assemblages in 30 small streams and their subcatchments (area 8–20 km^2) in the Etowah River Catchment (Georgia, USA). We stratified streams and their subcatchments into 3 landcover categories based on imperviousness (<10%, 10–20%, >20% of subcatchment), and then estimated the degree of hydrologic alteration based on synoptic measurements of baseflow yield. We derived hydrologic variables from stage gauges at each study site for 1 y (January 2003–2004). Increased imperviousness was positively correlated with the frequency of storm events and rates of the rising and falling limb of the hydrograph (i.e., storm ''flashiness'') during most seasons. Increased duration of low flows associated with imperviousness only occurred during the autumn low-flow period, and this measure corresponded with increased richness of lentic tolerant species. Altered storm flows in summer and autumn were related to decreased richness of endemic, cosmopolitan, and sensitive fish species, and decreased abundance of lentic tolerant species. Species predicted to be sensitive to urbanization, based on specific life-history or habitat requirements, also were related to stormflow variables and % fine bed sediment in riffles. Overall, hydrologic variables explained 22 to 66% of the variation in fish assemblage richness and abundance. Linkages between hydrologic alteration and fish assemblages were potentially complicated by contrasting effects of elevated flows on sediment delivery and scour, and mediating effects of high stream gradient on sediment delivery from elevated flows. However, stormwater management practices promoting natural hydrologic regimes are likely to reduce the impacts of catchment imperviousness on stream fish assemblages.

Key words: fishes, impervious surface cover, urbanization, hydrology, stormflow, baseflow, sediment, stormwater management.

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Urban development has become an increasingly important disturbance in stream ecosystems worldwide. Approximately 50% of the world's population now lives in cities (vs 12% in 1900), which has increased both the area of land and the number of streams impacted by development (Cohen 2003). A primary mechanism by which urbanization impacts stream ecosystems is through altered hydrology. Urbanization modifies a catchment by clearing of vegetation, compacting of soil, and ditching, draining, piping, and ultimately covering land with impermeable surfaces (Booth and Jackson 1997), which, in turn, may alter instream stormflow and baseflow hydrology (Shaw 1988). Urbanization may 1) increase the proportion of precipitation as surface runoff (Arnold and Gibbons 1996), 2) decrease lag time between precipitation events and elevated stream flows (Graf 1977), 3) increase magnitude of peak discharges by up to 5 times (Hollis 1974), 4) increase frequency of high flow events by ≥ 10 times (Booth 1991), and 5) decrease magnitude of low flows because of reduced groundwater recharge (Ferguson and Suckling 1990).

Changes in stream hydrology from urbanization can affect water quality, geomorphology, and biotic assemblages. Increased surface runoff may accelerate channel erosion (Trimble 1997), alter channel morphology (Doyle et al. 2000, Pizzuto et al. 2000), and increase sediment, nutrient, and contaminant delivery to streams (Wilber and Hunter 1977, Klein 1979, Herlihy et al. 1998, Ometo et al. 2000, Koplin et al. 2002). Fishes and invertebrates respond to urban landcover changes through changes in richness, diversity, density, and biotic integrity (reviewed by Schueler 1994, Paul and Meyer 2001). Studies also have reported changes in fish assemblage composition (Scott and Helfman 2001, Walters et al. 2003a) and feeding ecology (Weaver and Garman 1994, Poff and Allan 1995), with altered assemblages often occurring at relatively low levels of urbanization (e.g., 10–15% imperviousness; Schueler 1994, Wang et al. 2000).

Much of the evidence linking impacts of altered hydrology on fish assemblages is from studies conducted downstream of hydropower dams (Power et al. 1996, Pringle et al. 2000, Freeman et al. 2001). However, theoretical relationships predict that altered hydrology from urbanization also may impact fishes. Increases in storm flow can directly affect assemblages by washing out eggs, larvae, or young-of-year fishes and subsequently disrupting life cycles (Power et al. 1996, Poff et al. 1997, Freeman et al. 2001), and can indirectly affect fishes by increasing suspended sediment, contaminant, and nutrient delivery to streams (Burkhead et al. 1997). Increased storm flows also may impact fishes by increasing channel erosion, which, in turn, may alter pool/riffle sequences, bed texture, and habitat quality (Meade et al. 1990, Waters 1995, Burkhead et al. 1997, Sutherland et al. 2002). Reduced magnitude and increased duration of low flows can reduce habitat availability and quality (e.g., temperature) and subsequently alter foodweb dynamics (Power et al. 1996, Poff et al. 1997). Fish responses to altered hydrology are expected to vary based on the timing of altered flows in relation to their life histories (Power et al. 1996, Poff et al. 1997, Freeman et al. 2001, Bunn and Arthington 2002).

We investigated what aspects of hydrologic alteration accounted for the negative relationships between catchment imperviousness and stream fish assemblages. Although imperviousness may integrate cumulative impacts to water resources (Arnold and Gibbons 1996), various landscape factors (e.g., stormwater connection, impoundments, etc.) can result in variable and nonlinear relations between imperviousness and stream hydrology (Shaw 1988, Walsh et al. 2005a). Thus, we used continuous stream stage data to quantify hydrologic alteration in streams representing an urban gradient and to determine relationships between 1) catchment imperviousness and hydrologic alteration, and 2) measures of hydrologic alteration and fish assemblage integrity.

Methods

Study sites

We studied tributaries of the Etowah River, a 4823-km^2 catchment in north-central Georgia, USA, on the outskirts of metropolitan Atlanta (Fig. 1). The southeastern United States is a hotspot of stream fish diversity and endemism, with 76 extant fish species native to the Etowah River Catchment and 4 endemic species (Burkhead et al. 1997). Seven species are state-protected and 3 species are federally protected under the US Endangered Species Act. For most of the 20th century, land use in the region was

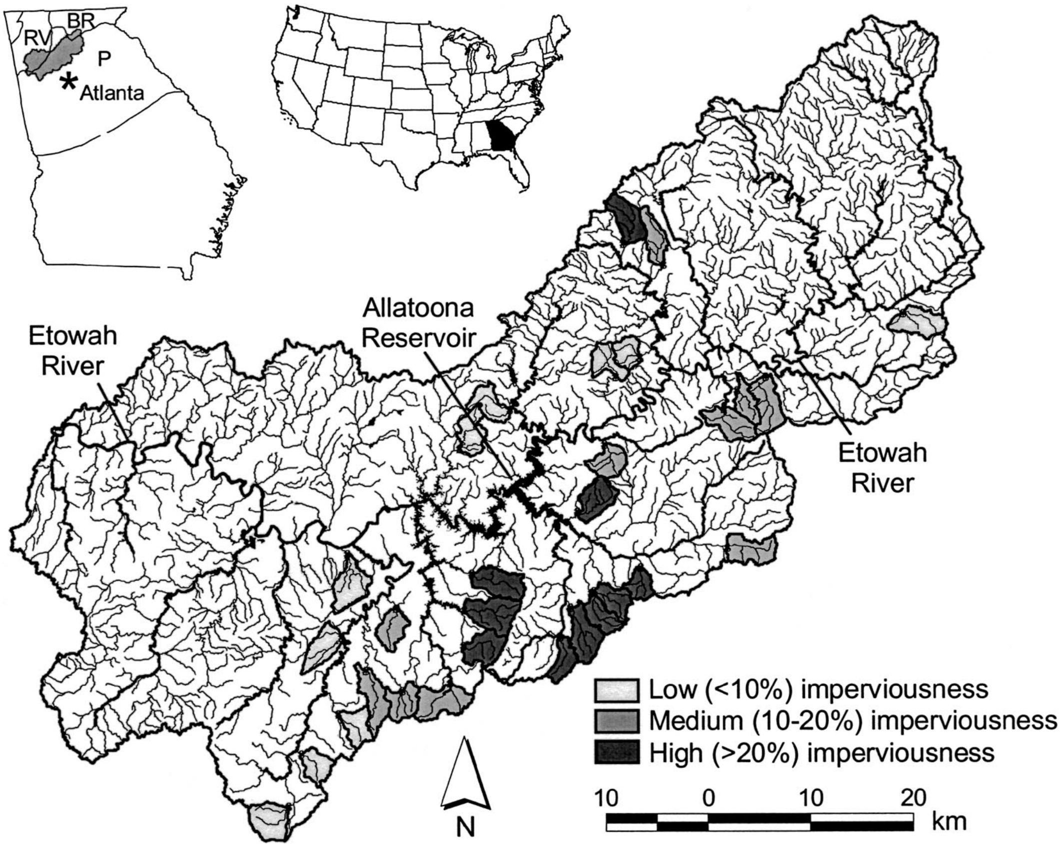

FIG. 1. The 30 study streams and their subcatchments (shaded areas) within the Etowah River Catchment (Georgia, USA). Streams were classified by amount of imperviousness in the subcatchment (<10, 10–20, >20%), based on 1998 landcover data used for site selection. Regions on map of Georgia correspond to physiographic provinces: RV = Ridge and Valley, BR = Blue Ridge, P = Piedmont.

mostly forest (secondary growth) and agriculture (row-crop and pasture); however, land use has undergone rapid changes in the last 20 y. Suburban development spreading north of metropolitan Atlanta (population >4 million) has increased residential and commercial land uses along corridors of population growth. Thus, subcatchments within the Etowah River Catchment show a high range in urban, agricultural, and forest land cover.

We selected streams of similar size and with similar potential fish assemblages (Table 1). Study streams and their subcatchments were small (area 8–20 km^2) and were within the Piedmont physiographic province (Fig. 1). Most study sites were >1 km upstream of their junction with a larger river (e.g., mainstem of Etowah River) or reservoir, and were not entirely impounded across upstream tributaries. Our initial criteria limited selection to 54 candidate streams. From this set of candidates, we selected a subset of streams encompassing an expected range of hydrologic alteration, based on subcatchment imperviousness and baseflow yield. First, we grouped streams into 3 classes of subcatchment imperviousness: <10, 10–20, and >20%. We estimated imperviousness using ArcView© Geographic Information System (GIS) by assigning random points within low-density (410 points) and high-density (130 points) urban categories (according to 1998 Landsat TM satellite imagery; 30-m pixels), and classifying each point as pervious or impervious surface using 1999 US Geological Survey color-infrared digital ortho quarter quads (DOQQs, 1-m resolution). We then multiplied impervious

TABLE 1. Environmental characteristics and season of hydrologic data collection for study streams. Streams are listed in order of increasing amount of catchment imperviousness, based on 2001 land cover. Sp1 = early spring (16 Jan.–14 Apr.), Sp2 = late spring (15 Apr.–14 May), Su = summer (15 May–7 Aug.), Au = autumn (15 Aug.–4 Nov.), Wi = winter (11 Nov.–28 Jan.). n = number of streams. Trib. = tributary.

Stream	County	UTM Easting (X)	UTM Northing (Y)	Complete hydrologic data for season					Sub-catchment area (km²)	% imperviousness (2001)	% water (2001)	No. of impoundments/subcatchment area	Stream slope (m/m)	% fine sediment
				Sp1	Sp2	Su	Au	Wi						
Gorman Branch	Cherokee	721372	3794025	X	X	X		X	12.1	1.7	0.0	0.2	0.007	6.9
Boston Creek	Bartow	715143	3789238	X	X	X	X	X	13.5	3.3	0.3	0.3	0.001	54.5
Upper Little Pumpkinvine	Paulding	695481	3749043			X	X	X	11.4	3.5	0.1	0.4	0.001	62.5
Ward Creek	Bartow	701808	3776978						11.2	4.9	0.9	0.8	0.003	12.2
Hickory Log Creek	Cherokee	733291	3797543	X	X	X	X	X	10.7	5.0	0.6	1.1	0.003	1.5
Murphy Creek	Cherokee	736664	3800322			X	X	X	9.5	5.0	0.5	1.2	0.004	7.0
Board Tree Creek	Cherokee	750901	3797621				X	X	17.5	6.5	1.2	1.5	0.003	28.2
West Fork Pumpkinvine	Paulding	701004	3767553				X		10.5	6.7	0.5	1.1	0.002	24.5
Lane Creek	Paulding	696519	3753818	X	X	X	X	X	16.4	7.1	1.7	1.6	0.005	37.9
Buzzard Flapper	Cherokee	747492	3796053	X				X	10.3	7.2	0.9	0.9	0.005	16.3
Black Mill Creek	Dawson	766692	3805091	X	X	X	X	X	16.4	7.2	0.2	0.6	0.003	18.6
Upper Smithwick Creek	Cherokee	745884	3793849	X	X	X	X		15.8	8.0	0.9	1.7	0.003	28.5
Westbrook Creek	Paulding	707590	3770001	X	X		X	X	19.0	8.5	1.1	0.7	0.003	59.5
Scott Mill Creek	Cherokee	732028	3789619	X	X	X	X	X	12.0	9.4	0.6	2.3	0.008	2.4
Possum Creek	Paulding	704003	3763567				X	X	14.6	9.7	1.4	1.2	0.003	29.6
Lawrence Creek	Paulding	701124	3758149		X	X	X	X	12.5	9.8	1.1	0.6	0.002	49.3
Polecat Branch	Pickens	738871	3810736	X	X	X	X		12.1	10.1	1.3	2.0	0.007	5.9
Upper Allatoona Creek	Cobb	713981	3762082						14.5	12.7	0.7	1.4	0.004	4.0
Town Creek	Pickens	734417	3813276		X	X	X	X	15.4	13.0	0.3	0.9	0.009	3.1
Picketts Mill	Paulding	708236	3761223				X	X	19.9	13.4	0.4	1.5	0.004	43.5
Trib. Sweat Mountain	Cherokee	736119	3775362			X	X		8.5	13.7	1.5	2.7	0.005	13.9
Copper Sandy Creek	Fulton	746302	3777695	X		X	X	X	15.6	13.9	2.0	1.2	0.006	30.3
Toonigh Creek	Cherokee	728571	3781614						16.2	15.8	0.4	0.7	0.003	12.7
Clark Creek	Cherokee	717590	3773997						17.0	16.7	0.6	1.3	0.005	26.0
East Fork Rubes Creek	Cobb	730400	3772584	X		X	X	X	11.2	20.5	0.7	2.0	0.002	21.7
West Fork Rubes Creek	Cobb	730386	3772578						11.2	21.8	1.1	0.9	0.002	43.9
Butler Creek	Cobb	715391	3766443	X			X	X	9.8	21.9	0.4	1.2	0.006	3.3
Lower Noonday Creek	Cobb	728024	3770707	X	X	X	X	X	17.0	23.7	0.9	0.6	0.001	16.3
Proctor Creek	Cobb	715642	3770400						19.8	29.8	0.5	0.6	0.003	89.0
Upper Noonday Creek	Cobb	726765	3767250			X	X	X	9.8	31.0	0.5	1.8	0.003	6.9
n				14	12	17	22	20	30	30	30	30	30	30
Minimum									8.5	1.7	0.0	0.2	0.001	1.5
Maximum									19.9	31.0	2.0	2.7	0.009	89.0
Mean									13.7	12.0	0.8	1.2	0.004	25.3

surface proportions by area of that landcover category to estimate total subcatchment imperviousness. We measured baseflow yield (defined as discharge/subcatchment area) one time at the 54 candidate streams on 18 and 19 June 2002 during baseflow conditions >1 wk after a rain event. We randomly selected 5 streams above and 5 streams below the median baseflow yield within each of the 3 imperviousness classes for a total of 30 streams. In the <10% class, stream discharge data revealed a geographic pattern of higher yields in the northeast portion and lower yields in the southwest portion of the Etowah River Catchment (dividing the catchment at the upper end of Allatoona Reservoir, Fig 1). These differences in base flow likely resulted from differences in soils or geology, so we randomly selected 5 northeastern and 5 southwestern streams in the catchment within the <10% imperviousness class to account for this geographic variation. The final set of 30 streams (Table 1) encompassed most of the range of baseflow yield across the catchment (0.0006–0.0062 m^3 s^{-1} km^{-2} for the final 30 streams vs 0.0005–0.0096 m^3 s^{-1} km^{-2} for the 54 candidate streams), but averaged higher mean imperviousness (15.7%; 1998 land cover) compared to a census of all small streams in the catchment (11.6%; AHR, unpublished data).

Landscape assessment

Subsequent to site selection, we re-estimated imperviousness for the Etowah River Catchment using an algorithm created by the Natural Resources Spatial Analysis Laboratory (Institute of Ecology, University of Georgia) based on protocol developed by the US Geological Survey (Yang et al. 2003). A classification and regression tree (CART) model was created to estimate imperviousness using Cubist® software. A training data set was developed using 4 randomly selected 1999 DOQQs (~300 km^2 each, 1-m resolution) in areas of low, medium, and high-density urban land cover north of the metro-Altanta region, and partially overlapping with the study subcatchments. Pixels (1-m) were classified as either impervious or non-impervious surface, and then these data were associated with Landsat ETM+ satellite imagery (30-m pixels, 17 landcover classes) taken in September 2000 (leaf on), March 2001 (spring), and December 2001 (leaf off) to build regressions based on the training data set. Regressions were extrapolated for regions outside the training set to determine imperviousness for the entire region, and assessed accuracy of the CART model by comparing it with a subset of data withheld from the training set (SE = 7.5%, r^2 = 0.89). We assumed the CART model produced more accurate imperviousness estimates than methods used for site selection because it calculated regressions for each of the 17 landcover categories (vs only categories of low- and high-density urban cover and transportation from the original classification).

We quantified the number and area of impoundments in each subcatchment to assess the importance of these hydrologic features in mediating hydrologic alteration effects on fish assemblages. We calculated the % of open water for each subcatchment using 2001 Landsat TM satellite imagery. In addition, we mapped impoundments from 1999 DOQQs and used these data to calculate number of impoundments per subcatchment area.

Hydrologic monitoring

We gauged streams at the outlet of each subcatchment using 2-m AquaRod® water-level sensors (Advanced Measurements & Controls, Inc., Woodinville, Washington), which use capacitance to measure stage height (distance from water surface to bottom of rod). Sensors were not all the same distance from the bed surface, so we adjusted all hydrologic magnitude variables by the mean recorded stage height at each stream. We set dataloggers (within sensors) to record water level every hour and with every 6-mm change in stage height, and downloaded stage height data seasonally from 16 January 2003 to 28 January 2004.

We used steady flow analysis in HEC-RAS® (version 2.2, Hydrologic Engineering Center, US Army Corps of Engineers) to estimate mean hydraulic depth for the 0.5-y recurrence interval (RI) flood at each site. We did not use mean depth of higher RI floods because very few storms exceeded the mean depth of these magnitude floods in 2003 (mean frequency >1-y RI flood = 2.4 storms/site; AHR, unpublished data). Instead, we used the 0.5-y RI flood and various proportions of this level (100, 75, and 50%) because these levels were inside the bankfull cross-section and were the most appropriate levels for relating to multiple storms throughout the year. We calculated discharges for the 0.5-y RI flood based on subcatchment area at each site using flood-frequency formulas derived for rural streams in the Georgia piedmont (Stamey and Hess 1993). We determined Manning's *n*, stream slope, and bankfull cross-sectional area (Gordon et al. 2004) at the sensor and incorporated these data into the HEC-RAS® model for each stream. We used a Topcon® AT-F6 level and stadia rod to obtain elevations for a channel cross-section at the sensor, and for calculating slope between riffle tops for a 150-m reach. The hydraulic depth (as determined by HEC-RAS®) was adjusted by the minimum annual daily stage at each site to account for differences in sensor locations relative to the stream bed.

We also quantified % fine sediment in riffle habitats; this aspect of habitat quality may be a mechanism by which hydrologic alterations indirectly impact fishes (Walters et al. 2003b). We collected 3 L of bed sediment samples from 3 riffles within each stream reach, transported samples to the laboratory, and dried, sieved, and weighed sediment to determine mean % fine sediment (<2 mm diam).

We calculated 9 baseflow and 18 stormflow variables that were expected to respond to imperviousness and thus could affect fish assemblages (Table 2). We did not have accurate stage–discharge rating curves for each site, so we calculated hydrologic variables based on stage, which is an acceptable measure of hydrologic alteration (McMahon et al. 2003). Baseflow variables included daily low-stage measures, and magnitude and duration of low-stage events <25, 10, and 5% of the median stage. Stormflow variables included frequency (i.e., number of flow excursions above a certain stage), magnitude, duration, and volume (stage height × h) during events above a certain stage, and rate of change (i.e., hydrograph line slope) associated with ascending and descending limbs of storm hydrographs (Table 2). We used percentages (100, 75, and 50%) of the mean stage height of the 0.5-y RI flood to calculate stormflow variables. We divided all magnitude variables by the mean daily stage to adjust for differences in stream size (Table 2).

Fish sampling

We sampled fishes from August to October 2003 during baseflow conditions. Our main objective was to relate among-site differences in resident fish assemblages to hydrologic patterns. Fish assemblages may vary more among locations within a reach than among dates (Peterson and Rabeni 1995), so we sampled a relatively long reach at each site at a single time of the year. We sampled during late summer and early autumn when young-of-year of most fishes were large enough to be captured and low flows optimized our sampling efficiency. We sampled fishes in a 150-m reach at each site, with block nets set every 50 m. We randomly selected 1 of the 3 adjacent 50-m reaches to sample with 3 consecutive passes, and sampled the remaining 2 reaches in a single pass. During each pass, we thoroughly sampled all habitats using a backpack electroshocker (Model 12-B; Smith-Root® Inc, Vancouver, Washington) combined with kicking with a 2.4-m seine held downstream (in areas with sufficient flow), dip netting (in pool habitats), and seine hauling (in sandy, shallow runs). We identified, measured, and released fishes in the field, or euthanized and preserved them with buffered MS-222 and ~8% formalin, respectively, for identification in the laboratory.

We used CAPTURE® (White et al. 1978) to calculate richness estimates using species detectability based on species caught in single-pass samples in 3 consecutive 50-m reaches. We used model M(h), which assumes heterogeneity of capture probabilities among species, to estimate species richness (Williams et al. 2002). We used the removal function in CAPTURE® to calculate capture probabilities for each species that declined in abundance among the 3 passes conducted in one 50-m reach; we then used capture probabilities to estimate species-specific abundance at each site. We were unable to estimate abundance for species that showed no depletion among passes, so instead we used the total number of individuals captured. Our abundance estimates were potentially biased to an unknown extent because, even for taxa exhibiting depletion, we assumed individual capture probabilities remained constant across passes.

We expressed fish assemblage structure based on overall species richness, abundance, and richness and abundance of assemblage subsets, including endemic species, cosmopolitan species, fluvial specialists, lentic tolerants, and sensitive species (Appendix). We defined cosmopolitan species as those fishes native to at least 10 major

TABLE 2. Hydrologic variables (A: Baseflow, B: Stormflow) calculated at each site for each season (see Table 1) from January 2003 to January 2004. Percentiles are based on median stage over the period of record (POR). Mean stage of 100, 75, and 50% of the 0.5-y recurrence interval (RI) flood were calculated using HEC-RAS® based on subcatchment area, stream slope, cross-sectional area, and Manning's *n* (see Methods).

Category	Code	Description
A: Baseflow variables		
Magnitude	MinDaily	Minimum daily stage/mean daily stage
Magnitude	Min7dayMean	Minimum 7-d mean stage/mean daily stage
Magnitude	min7day Max	Minimum 7-d maximum stage/mean daily stage
Magnitude	MeanLow<25	Mean low stage over POR (h); low stage $<25^{\text{th}}$ percentile/mean daily stage
Magnitude	MeanLow<10	Mean low stage over POR (h); low stage $<10^{\text{th}}$ percentile/mean daily stage
Magnitude	MeanLow<5	Mean low stage over POR (h); low stage $<5^{\text{th}}$ percentile/mean daily stage
Duration	DurLow<25	Maximum duration of low stage over POR (h); low stage $<25^{\text{th}}$ percentile
Duration	DurLow<10	Maximum duration of low stage over POR (h); low stage $<10^{\text{th}}$ percentile
Duration	DurLow<5	Maximum duration of low stage over POR (h); low stage $<5^{\text{th}}$ percentile
B: Stormflow variables		
Frequency	Freq>100%Q0.5	Number of excursions >100% mean stage of 0.5-y RI flood
Frequency	Freq>75%Q0.5	Number of excursions >75% mean stage of 0.5-y RI flood
Frequency	Freq>50%Q0.5	Number of excursions >50% mean stage of 0.5-y RI flood
Magnitude	MeanHigh>100%Q0.5	Mean stage height of excursions >100% mean stage of 0.5-y RI flood/mean daily stage
Magnitude	MeanHigh>75%Q0.5	Mean stage height of excursions >75% mean stage of 0.5-y RI flood/mean daily stage
Magnitude	MeanHigh>50%Q0.5	Mean stage height of excursions >50% mean stage of 0.5-y RI flood/mean daily stage
Duration	Dur>100%Q0.5	Number of h of high stage over POR; high stage >100% mean stage of 0.5-y RI flood
Duration	Dur>75%Q0.5	Number of h of high stage over POR; high stage >75% mean stage of 0.5-y RI flood
Duration	Dur>50%Q0.5	Number of h of high stage over POR; high stage >50% mean stage of 0.5-y RI flood
Volume	Vol>100%Q0.5	Area (no. of h × stage height) of stage >100% mean stage of 0.5-y RI flood
Volume	Vol>75%Q0.5	Area (no. of h × stage height) of stage >75% mean stage of 0.5-y RI flood
Volume	Vol>50%Q0.5	Area (no. of h × stage height) of stage >50% mean stage of 0.5-y RI flood
Rate of change	RateRise5	Number of time periods (h) when stage rises by ≥5 cm
Rate of change	RateRise10	Number of time periods (h) when stage rises by ≥10 cm
Rate of change	RateRise20	Number of time periods (h) when stage rises by ≥20 cm
Rate of change	RateFall5	Number of time periods (h) when stage falls by ≥5 cm
Rate of change	RateFall10	Number of time periods (h) when stage falls by ≥10 cm
Rate of change	RateFall20	Number of time periods (h) when stage falls by ≥20 cm

catchments, and those that were expected to increase with urbanization (Walters et al. 2003a). We expected endemics, species primarily limited to the Coosa River Catchment (including the Etowah River), to decrease with urbanization (Walters et al. 2003a). In addition, we examined the ratio of endemics to cosmopolitans, based on species richness and abundance, which should reflect a homogenization of assemblages coincident with loss of endemic species (Scott and Helfman 2001, Walters et al. 2003a). We defined fluvial specialists as those species requiring lotic environments for at least part of their life cycle (Travnichek et al. 1995), determined from Etnier and Starnes (1993) and Mettee et al. (1996). We defined lentic tolerants as those fishes that were habitat generalists and capable of completing their life cycle in lakes or reservoirs (Travnichek et al. 1995). We expected lentic tolerants to increase and fluvial specialists to decrease with increased urbanization. Last, we defined sensitive species as those fishes expected to be sensitive to disturbance because of specific life- history or habitat requirements, and that responded negatively to urbanization at other sites (SJW, unpublished data).

Data analyses

Many of the water-level sensors (24 of 30) did not function during certain months of the study. To deal with the resulting incomplete data, we divided analyses based on sensor downloading dates. Data for each period of record (POR) included different sets of study sites depending on which had complete data records (Table 1). For simplicity, PORs were denoted as seasons, including early and late spring (16 Jan.–14 Apr., $n = 14$, and 15 Apr.–14 May, $n = 12$), summer (15 May–7 Aug., $n = 17$), autumn (15 Aug.–4 Nov., $n = 22$), and winter (11 Nov.–28 Jan., $n = 20$).

We tested all variables for normality using a Shapiro–Wilk goodness-of-fit test and transformed when necessary. We transformed fish abundance variables using $\log_{10}(x+1)$ and percentage variables (converted to proportions) using arcsin square root. We used correlation analysis (Pearson's r) to relate hydrologic variables to imperviousness ($n = 12$–22), and to relate fish assemblages to imperviousness ($n = 30$) and % fine sediment ($n = 30$). We used principal components analysis (PCA) to reduce baseflow and stormflow variables into a few metrics in each season that described variation in hydrology across sites. We then used multiple linear regression analysis (stepwise regression, forward selection, $\alpha = 0.05$) to predict fish assemblages using % fine sediment and baseflow and stormflow PC axes scores, for summer and autumn. We chose these 2 seasons because they reflected high- (summer) and low- (autumn) flow periods during 2003, had the most complete hydrologic data ($n = 17$ and $n = 22$, respectively), and included time periods most likely to impact fish assemblages (i.e., highest abundances of spawning and young-of-year fishes). We also used correlation to relate baseflow and stormflow PC axes to % fine sediment, % open water in the subcatchment, number of impoundments per subcatchment area, and subcatchment imperviousness. Last, we used multiple linear regression analysis to analyze slope vs mean % fine sediment, imperviousness vs % open water in the subcatchment, and imperviousness vs number of impoundments/subcatchment area. We did analyses using JMP® version 4.0 statistical software (SAS Institute Inc., Cary, North Carolina).

Results

Hydrologic alteration from increased imperviousness

Mean annual daily discharge in the Etowah River was below average (<70% of the 50-y mean discharge) for the 4 y preceding the study (1999–2002). In 2003, mean daily discharge was 20% higher than the 50-y mean and nearly double the discharge of the previous 4 y. Study sites showed a mean of 4.5 storms/y exceeding the 0.5-y RI flood mean stage over the POR (Table 3). Storms primarily occurred during late spring (Apr.–May) and summer (May–Aug.), exceeding the 0.5-y RI flood mean stage at rates equaling 26.4 and 17.4 storms/y, respectively. Storms rarely occurred during autumn (Aug.–Nov.), when sites showed ≤1 storm exceeding the 0.5-y RI flood mean stage (Table 3).

Baseflow stage variables generally showed no relationships with subcatchment imperviousness. For the 9 baseflow variables across 5 seasons, there were only 2 relationships with $r^2 > 0.25$ (Fig. 2). In late spring (Apr.–May), the time of the year with the highest precipitation, minimum daily stage was highest at sites with low

TABLE 3. Frequency of storm events >100, 75, and 50% of mean stage of the 0.5-y recurrence interval (RI) flow for each season during the study. Seasonal storm rates (mean/d) were extrapolated to the number of storms that would occur in the year (mean/y) for comparison. Means over the period of record (16 Jan. 2003–28 Jan. 2004) were calculated by weighting seasonal means by the number of days in each season. N/A = not applicable.

0.5-y RI flood	Mean	Mean/d	Mean/y (at that rate)	Range	SD
Spring (16 Jan.–14 Apr.)					
100%	1.43	0.016	5.9	1–3	0.76
75%	2.00	0.022	8.2	1–4	0.88
50%	2.71	0.030	11.1	1–5	1.33
Spring (15 Apr.–14 May)					
100%	0.92	0.031	11.2	0–1	0.29
75%	1.50	0.050	18.3	1–3	0.80
50%	2.17	0.072	26.4	1–4	1.19
Summer (15 May–7 Aug.)					
100%	0.88	0.010	3.8	0–10	1.02
75%	2.81	0.033	12.1	0–11	2.32
50%	4.06	0.048	17.4	0–13	2.69
Autumn (15 Aug.–4 Nov.)					
100%	0.18	0.002	0.8	0–1	0.39
75%	0.50	0.006	2.2	0–2	0.74
50%	0.91	0.011	4.1	0–3	1.02
Winter (11 Nov.–28 Jan.)					
100%	1.10	0.014	5.1	0–4	1.25
75%	1.50	0.019	6.9	0–5	1.40
50%	2.35	0.030	10.9	0–7	1.75
Mean (Jan. 2003–2004)					
100%	0.91	0.012	4.5	N/A	0.80
75%	1.70	0.023	8.3	N/A	1.29
50%	2.50	0.033	12.2	N/A	1.66

imperviousness, although because of high variation the relationship between the 2 variables was nonsignificant ($p = 0.079$; Fig. 2A). In autumn (Aug.–Nov.), there was a strong positive relationship between the duration of low-flow events <25th percentile flow and imperviousness ($p < 0.001$; Fig. 2B), although duration of lower flows (i.e., <10th and 5th percentiles) was not related to imperviousness. This relationship occurred during the lowest-flow season, a time when measurable reductions in base flows associated with urbanization would be expected.

Stormflow variables were strongly correlated ($r > 0.50$) with imperviousness, primarily during summer, autumn, and winter (Table 4). The frequency of excursions above 50%, 75%, and 100% mean stage of the 0.5-y RI flood and the rate of the rising and falling limbs of the storm hydrograph consistently increased with increasing imperviousness, with the greatest number of high ($r \geq 0.50$) correlations occurring in autumn (Table 4, Fig. 3A–F). Magnitude, duration, and volume of high-flow events were strongly correlated with imperviousness only in autumn (Aug.–Nov., Table 4), and these relationships were driven by a few sites with storms exceeding 100% and 75% of the 0.5-y RI flood. Comparison of 2 sample storm hydrographs with contrasting imperviousness, Lower Noonday Creek (23.7% imperviousness) and Hickory Log Creek (5% imperviousness) revealed that the high-imperviousness site experienced higher frequency and magnitude of storm events relative to the 0.5-y RI flood mean stage than the low-imperviousness site, despite both sites showing similar stage heights during the 6 largest storms (Fig. 4).

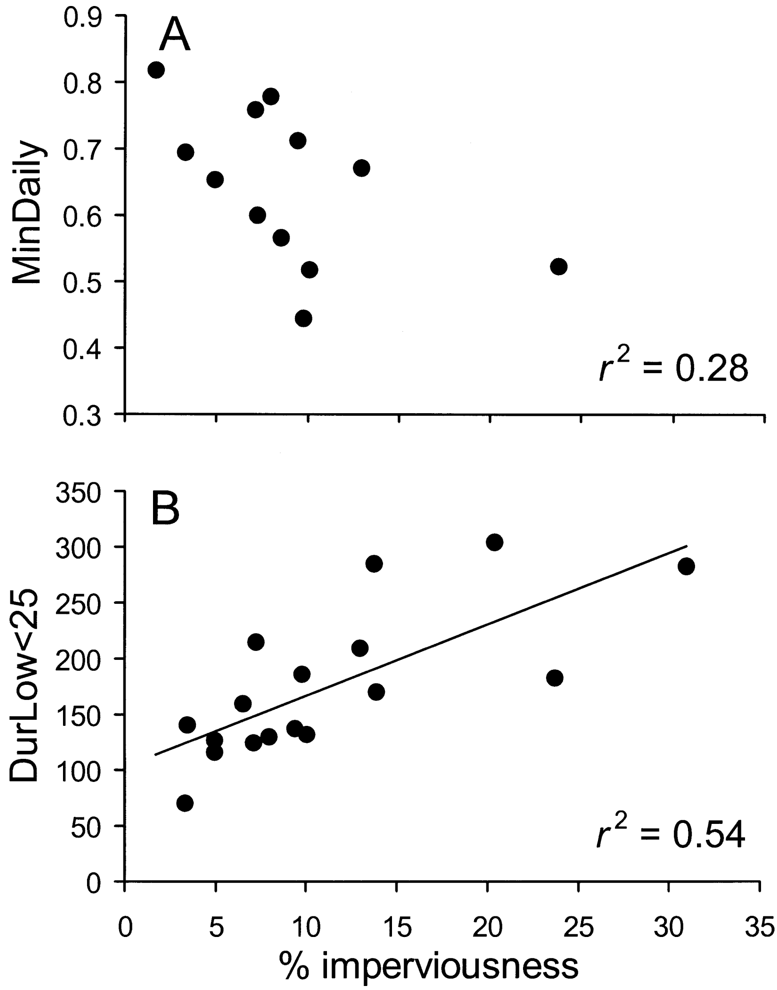

FIG. 2. Linear regression models for the 2 baseflow variables showing the highest correlations with subcatchment imperviousness ($r^2 > 0.25$). A.—Minimum daily stage/mean daily (MinDaily) stage during late spring (Apr.–May). B.—Maximum duration of low stage <25th percentile (DurLow<25) during autumn (Aug.–Nov.).

Variation in fish assemblages

Based on field observations, fish species richness was 7 to 20 species/stream, with total estimated richness ranging from 8 to 25 species/stream (Table 5). We collected a mean of 153 individuals per 50-m stream reach (range 37–435 individuals), and estimated overall total abundance as 37 to 512 individuals in one 50-m stream reach based on the 3-pass removal (Table 5). We report all richness and abundance values henceforth as estimated values based on calculated capture efficiencies.

There were no strong relationships between subcatchment imperviousness and total fish species richness or abundance (r = 0.07–0.49). As expected, richness and abundance of fluvial specialists were low in sites with high imperviousness, and lentic tolerants were high in sites with high imperviousness (Table 5). Abundance of endemic species and ratio of endemic to cosmopolitan abundance also both varied inversely with imperviousness. We also found negative relationships between imperviousness and abundance of fishes that were expected to be sensitive to urbanization. All species groups except cosmopolitan and lentic tolerant species varied inversely with imperviousness (Table 5).

TABLE 4. Pairwise correlations (Pearson's r) between % imperviousness (based on 2001 land cover) and stormflow stage variables for each season from January 2003 to 2004 (n = number of sites). Bold indicates $r \geq 0.50$. Hydrologic variables are defined in Table 2.

Code	Early spring (Jan.–Apr.) ($n = 14$)	Late spring (Apr.–May) ($n = 12$)	Summer (May–Aug.) ($n = 17$)	Autumn (Aug.–Nov.) ($n = 22$)	Winter (Nov.–Jan.) ($n = 20$)
Freq>100%Q0.5	−0.14	−0.26	**0.69**	**0.71**	**0.53**
Freq>75%Q0.5	−0.07	**0.53**	**0.75**	0.48	**0.56**
Freq>50%Q0.5	−0.11	0.14	**0.76**	**0.53**	**0.71**
MeanHigh>100%Q0.5	0.33	−0.29	−0.35	**0.56**	0.21
MeanHigh>75%Q0.5	0.00	−0.32	−0.38	**0.63**	0.18
MeanHigh>50%Q0.5	−0.01	−0.26	−0.40	**0.55**	0.14
Dur>100%Q0.5	0.00	−0.13	0.34	**0.57**	0.47
Dur>75%Q0.5	0.07	−0.03	0.40	0.47	0.39
Dur>50%Q0.5	0.06	−0.15	0.21	0.44	0.07
Vol>100%Q0.5	−0.24	−0.32	0.08	**0.61**	0.34
Vol>75%Q0.5	−0.15	−0.20	0.22	**0.60**	0.38
Vol>50%Q0.5	−0.04	−0.06	0.29	**0.50**	0.16
RateRise5	**0.57**	0.15	**0.69**	**0.57**	**0.65**
RateRise10	0.26	0.37	**0.73**	**0.65**	**0.60**
RateRise20	−0.24	**0.52**	**0.66**	0.47	**0.59**
RateFall5	0.34	0.49	**0.71**	**0.61**	**0.66**
RateFall10	0.14	0.49	**0.63**	**0.57**	**0.61**
RateFall20	0.11	0.31	0.37	0.37	**0.58**

Fish assemblages and hydrology

PCA reduced the set of baseflow and stormflow variables into a smaller, uncorrelated subset of variables for summer (May–Aug.) and autumn (Aug.–Nov.). For the 16 sites with hydrologic data in both seasons, 2 to 3 PCs accounted for most variation in the 9 baseflow variables (≥86% cumulative variance explained for each season; Table 6). For both seasons, PC_1 was related to baseflow magnitude variables and PC_2 was related to duration of low-flow events. PCA reduced the set of 18 stormflow variables to 3 to 4 principal components that explained ≥85% of cumulative variance for each season. PC_1 included equal weightings of the 18 variables in both seasons (except magnitude variables in summer). In summer, PC_2 was highly weighted with stormflow magnitude variables, whereas PC_3 and PC_4 were related to stormflow volume and duration. In autumn, stormflow PC_2 and PC_3 showed mixed variable loadings including magnitude, volume, duration, and measures of storm flashiness (Table 6).

Hydrologic variables (summarized by PC axes) explained up to 67% of the variation in fish richness and abundance measures (Table 7). Endemic richness was predicted by decreased stormflow alteration (frequency, magnitude, duration, volume, and flashiness) in summer months, whereas increased cosmopolitan richness was predicted by longer duration of autumn base flows and lower summer stormflow volume and duration (Table 7). The ratio of endemic to cosmopolitan richness also was predicted by summer stormflow variables. Baseflow duration in autumn explained 67% of the variation in lentic tolerant richness across sites, with longer baseflow durations resulting in more lentic species. Abundance of lentic tolerants was predicted by decreased magnitude of summer storm flows and autumn base flows. Richness and abundance of sensitive species were best explained by stormflow alteration and % fine sediment in riffles. Although stormflow and baseflow PC axes were significantly related to fish assemblages, these hydrologic variables typically explained <½ of the variation in fish assemblages (Table 7).

Correlates of hydrologic alteration and fish assemblages

Mean % fine sediment in riffles was negatively correlated with abundance of endemic spe-

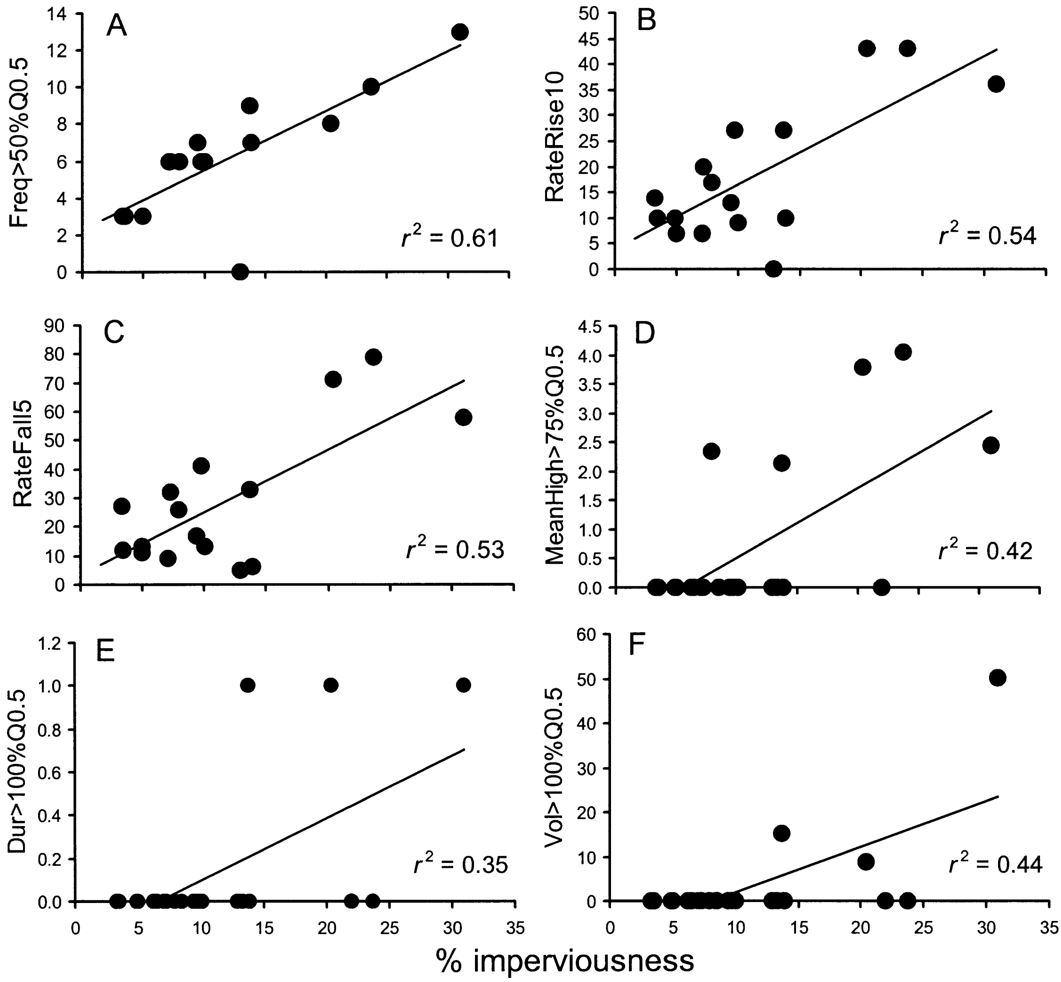

FIG. 3. Linear regression models for stormflow variables and imperviousness in the catchment for variables with the highest r^2 in each category (Table 2) and seasons with the strongest relationships (Table 3). Models for (A) frequency, (B) rate of rising stage, and (C) rate of falling stage are for summer (May–Aug., $n = 17$). Models for (D) magnitude, (E) duration, and (F) volume are for autumn (Aug.–Nov., $n = 22$).

cies, the ratio of endemics to cosmopolitans, and sensitive species ($r > 0.40$; Table 5). In multiple regression analyses, % fine sediment also explained 18 and 46% of the variation in sensitive species richness and abundance, respectively (Table 7). Percent fine sediment was not strongly related to stormflow or baseflow PC axes (all $r < 0.50$; Table 8). However, mean % fine sediment was negatively related to stream slope ($r^2 = 0.24$; $p = 0.006$).

We also assessed whether imperviousness, % open water in subcatchment, and number of impoundments/subcatchment area were strongly related (i.e., $r > 0.50$) to hydrologic variables summarized by PC axes. Imperviousness was positively correlated with stormflow alteration (PC_1) in summer and autumn, negatively correlated with summer stormflow magnitude (PC_2), and positively correlated with autumn baseflow duration (PC_2, Table 8). The % open water in the subcatchment was positively correlated with summer baseflow duration (PC_2) and negatively correlated with summer stormflow magnitude (PC_2, Table 8). The number of impoundments also was negatively correlated with summer stormflow magnitude (PC_2), but positively correlated with increased autumn stormflow alteration (PC_1) and summer base-

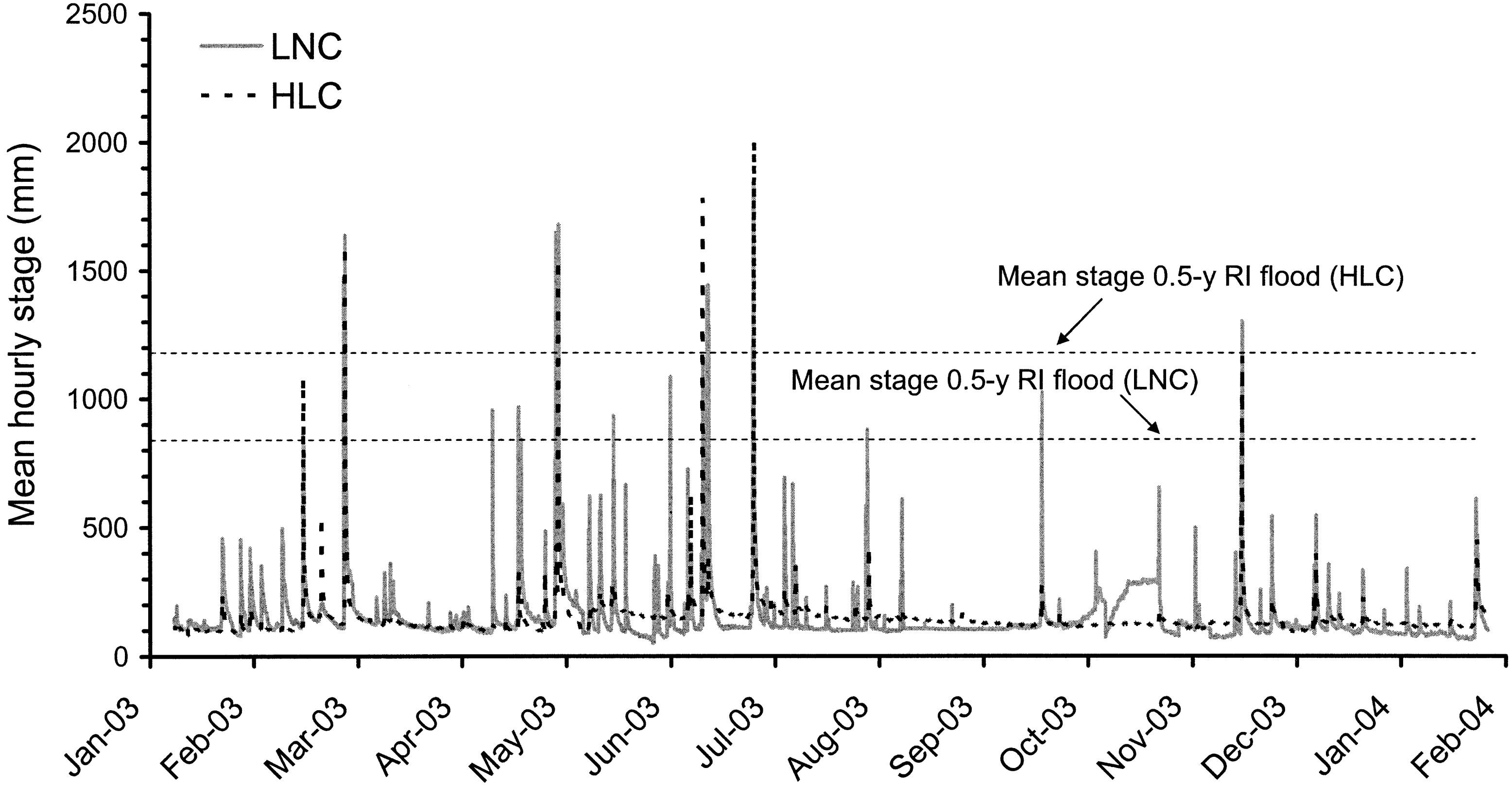

FIG. 4. Comparison of mean hourly stage data for one study stream with high subcatchment imperviousness (Lower Noonday Creek [LNC], 23.7%) vs a second stream with low imperviousness (Hickory Log Creek [HLC], 5.0%). Horizontal dashed lines show mean stage of the 0.5-y recurrence interval (RI) flood (as calculated using HEC-RAS®) for each stream (see Methods).

TABLE 5. Means (±1 SD) and ranges for fish assemblage metrics and pairwise correlations (Pearson's r) between assemblage variables and catchment imperviousness (2001 data) and % fine sediment in riffles.

Metric	Mean (SD)	Range	Imperviousness[a]	% fine sediment[a]
Fish richness				
Total	17.4 (4.1)	8–25	−0.27	−0.14
Endemic	2.4 (1.6)	0–6	−0.29	−0.28
Cosmopolitan	10.1 (3.0)	5–17	−0.11	−0.11
Endemic/cosmopolitan[b]	0.3 (0.2)	0–0.8	−0.23	−0.13
Fluvial specialist	12.3 (4.2)	5–21	−0.49	−0.15
Lentic tolerant	5.4 (2.0)	3–11	0.44	0.06
Fluvial/lentic	2.6 (1.2)	0.5–5.7	−0.47	−0.01
Sensitive	2.7 (1.9)	0–7	−0.48	−0.33
Fish abundance (no. of individuals)				
Total[b]	184.9 (123.8)	37–512	−0.07	−0.15
Endemic[b]	46.6 (70.4)	0–335	−0.38	−0.44
Cosmopolitan[b]	88.5 (80.1)	12–431	0.28	0.19
Endemic/cosmopolitan[b]	1.10 (2.5)	0–13.1	−0.43	−0.42
Fluvial specialist[b]	128.5 (108.7)	10–469	−0.42	−0.34
Lentic tolerant[b]	56.9 (76.4)	2–412	0.45	0.08
Fluvial/lentic[b]	7.0 (15.7)	0.5–87.5	−0.47	−0.23
Sensitive[b]	16.7 (21.6)	0–103	−0.39	−0.46

[a] Transformed for analysis using arcsin square root
[b] Transformed for analysis using $\log_{10}(x + 1)$

flow magnitude (PC_1, Table 8). In separate analyses (data not in tables), subcatchment imperviousness was not strongly correlated with % open water ($r = 0.21$) or the number of impoundments/subcatchment area ($r = 0.26$).

Discussion

Impacts of catchment imperviousness on small streams

Although previous studies have documented predictable alterations to stormflow and baseflow hydrology with increasing urbanization, many of these results are based on data from large streams and rivers with long-term gauge records (Ferguson and Suckling 1990, Rose and Peters 2001) or data extrapolated from other gauged streams (Booth and Jackson 1997, but see Utah sites in McMahon et al. 2003). For the small streams in our study, our exploratory analyses demonstrated a positive relationship between subcatchment imperviousness and the frequency of high storm flows across multiple seasons (Table 4). There was also an indication of increased flashiness in more urbanized streams, as demonstrated by higher rates of the rising and falling limbs of storm hydrographs in streams with high (vs low) imperviousness (Fig. 3). These results are consistent with studies of urban effects on stream storm hydrology (Hollis 1974, Shaw 1988, Booth 1991).

Interestingly, we did not find strong evidence that increased urbanization resulted in reduced base flows at our sites. Hydrologists have suggested a decrease in magnitude of low flows associated with urbanization because of reduced groundwater recharge (Shaw 1988, Ferguson and Suckling 1990). One explanation for the lack of response in our sites is that the groundwater table remained high during 2003, a year with higher than average precipitation. Further, there is a high density of septic systems in the Etowah River Catchment (74–94% of households have on-site treatment systems; Evans et al. 1999), which may provide sufficient enough groundwater recharge in urban areas to offset losses from reduced infiltration associated with high imperviousness. However, we did observe in autumn (during the lowest flow months) that duration of low flows was positively correlated with imperviousness (Fig. 2). The abnormally high flows in 2003 (20% higher than the 50-y

TABLE 6. Principal components analysis (PCA) axes for baseflow and stormflow stage variables for summer and autumn. Cumulative % variance explained by selected axes is in parentheses. Eigenvalues, % variance explained, axis interpretation (in text, based on variable loadings), and highest variable loadings (+/− indicates direction of loading) on each axis are listed. Hydrologic variables are defined in Table 2.

	Eigenvalue	% variance explained	Axis interpretation	Variables loadings
Summer (15 May–7 Aug.)				
Baseflow (86.9%)				
PC_1[a]	4.8	53.4	Magnitude	(+) Min7dayMean, (+) Min7dayMax, (+) MeanLow<25, 10, 5
PC_2	2.0	22.3	Duration	(+) MinDaily, (+) DurLow<25, 10, 5
PC_3	1.0	11.2	Duration	(+) MinDaily, (+ DurLow<25
Stormflow (92.3%)				
PC_1	8.5	47.3	All	(+) All variables except MeanHigh 100, 75, 50%Q0.5
PC_2	3.9	21.7	Magnitude	(+) MeanHigh100, 75, 50%Q0.5
PC_3	2.6	14.6	Volume/duration	(+) Vol>50%Q0.5, (+) Dur>75, 50%Q0.5
PC_4	1.6	9.0	Volume/duration	(−) Vol>100, 75%Q0.5, (−) Dur>100%Q0.5, (+) Dur>50%Q0.5
Autumn (15 Aug.–4 Nov.)				
Baseflow (89.2%)				
PC_1[a]	6.8	75.6	Magnitude	(+) All variables except DurLow<25
PC_2[a]	1.2	13.6	Duration	(+) DurLow<25, 10, 5
Stormflow (85.4%)				
PC_1[a]	11.5	64.0	All	(+) All variables
PC_2	2.5	14.1	Mix	(−) MeanHigh>100%Q0.5, (+) MeanHigh>50%Q0.5, (−) Vol>100%Q0.5, (−) Dur>100%Q0.5
PC_3[a]	1.3	7.3	Mix	(+) RateFall20, (+) Freq100%>Q0.5, (+) MeanHigh75%Q0.5

[a] Not normally distributed

TABLE 7. Significant multiple linear regression models for fish assemblage metrics using stepwise regression ($n = 16$ sites, forward selection, $p < 0.05$). Predictor variables included in model for selection were % fine sediment and baseflow and stormflow principal components analysis (PCA) axes for summer (su) and autumn (au). Baseflow PC_1 for summer was excluded in models because of autocorrelation with baseflow PC_1 for autumn ($r = 0.85$). +/− indicates direction of relationship between response and predictor variables.

	Adjusted R^2	Partial R^2	p	Predictor variables
Fish richness				
Endemic	0.31	0.35	0.015	(−) Stormflow PC_1 (su)
Cosmopolitan	0.50	0.38	0.008	(+) Baseflow PC_2 (au)
		0.19	0.037	(−) Stormflow PC_4 (su)
Endemic/cosmopolitan	0.44	0.27	0.019	(−) Stormflow PC_1 (su)
		0.25	0.022	(+) Stormflow PC_2 (su)
Lentic tolerant	0.67	0.69	<0.001	(+) Baseflow PC_2 (au)
Sensitive	0.63	0.39	0.007	(−) Stormflow PC_1 (su)
		0.18	0.005	(−) % fine sediment
		0.14	0.033	(+) Stormflow PC_3 (au)
Fish abundance (no. of individuals)				
Cosmopolitan	0.35	0.39	0.010	(+) Baseflow PC_3 (su)
Lentic tolerant	0.62	0.43	<0.001	(−) Stormflow PC_2 (su)
		0.24	0.008	(−) Baseflow PC_1 (au)
Fluvial/lentic	0.22	0.27	0.005	(+) Stormflow PC_2 (su)
Sensitive	0.74	0.46	<0.001	(−) % fine sediment
		0.25	0.003	(−) Stormflow PC_1 (au)
		0.12	0.048	(+) Stormflow PC_2 (au)

mean) may have masked the response of base flows to urbanization during other seasons. It is also possible that reduced base flows may not be a predictable result of altered hydrology from urbanization, especially in geographic regions with relatively high precipitation. McMahon et al. (2003) also hypothesized that urban streams would show reduced duration of low

TABLE 8. Pairwise correlations (Pearson's r) between summer and autumn hydrologic alteration variables (principal component [PC] axes) and environmental variables. Bold indicates $r \geq 0.50$.

Hydrology	% fine sediment[a]	Imperviousness[a]	% open water in subcatchment[a]	No. impoundments/ subcatchment area
Summer				
Baseflow PC_1	−0.46	0.04	0.01	**0.52**
Baseflow PC_2	−0.02	−0.02	**0.55**	0.01
Baseflow PC_3	0.37	0.44	0.01	0.04
Stormflow PC_1	0.16	**0.64**	0.01	0.03
Stormflow PC_2	0.25	**−0.52**	**−0.56**	**−0.56**
Stormflow PC_3	0.39	−0.41	0.02	−0.41
Stormflow PC_4	0.24	0.00	0.32	−0.13
Autumn				
Baseflow PC_1	−0.41	−0.08	−0.03	0.26
Baseflow PC_2	−0.41	**0.70**	0.14	0.49
Stormflow PC_1	−0.06	**0.70**	0.14	**0.50**
Stormflow PC_2	0.07	−0.22	0.07	−0.27
Stormflow PC_3	0.00	0.31	0.05	−0.37

[a] Transformed for analysis using arcsin square root

flows; however, McMahon et al. (2003) were unable to confirm this prediction from Alabama, Massachusetts, or Utah streams. Low flows are not only influenced by groundwater, but also depend on topography, evapotranspiration, and instream hyporheic processes (Nilsson et al. 2003). Further, groundwater recharge from leaky pipes (Yang et al. 1999) and increased lawn irrigation (Al-Rashed and Sherif 2001) may offset any reductions in infiltration in urban areas. Cumulatively, these factors suggest that reduced base flows in urban settings of the southeastern US may not be a typical symptom of the ''urban stream syndrome'' characterized by Meyer et al. (2005, see also Walsh et al. 2005b).

Low correspondence between stormflow hydrology and catchment imperviousness in spring may have been related to seasonal variation in runoff patterns in relatively forested catchments. During this season, flows often are high, soils are saturated, and evapotranspiration is low; hence, precipitation events in forested catchments may behave similarly to catchments with high imperviousness (Hollis 1974). In contrast, precipitation occurring during the relatively drier summer and autumn seasons often may infiltrate soils in forested catchments, thus minimizing surface runoff and maximizing differences in runoff between low- vs high- imperviousness catchments. Moreover, the high frequency of large storms during 2003 likely limited relationships between imperviousness and storm magnitude, volume, and duration. The positive correlations between hydrology and imperviousness observed in autumn were driven only by a few storms, and thus did not demonstrate a strong response to imperviousness (Table 4, Fig. 3).

We recorded very few storms that exceeded the mean depth of the 1-y RI flood (2.4 over ~1 y) and higher-stage thresholds, which forced us to calculate stormflow variables using lower thresholds (i.e., mean depth of the 0.5-y RI flood and percentages thereof). Our data indicated that these small, frequent storm events can impact fish assemblages, explaining up to 43% of the variation in assemblage structure. However, larger storms may also be important, especially because they are likely to affect stream geomorphology (e.g., 1- to 2.3-y RI flood determines bankfull conditions, Williams 1978). A longer data set encompassing both low- and high-flow years and several large storm events (i.e., ≥ 2-y RI floods) is necessary to determine the relations between imperviousness and larger storm events, and also the importance of interannual variation in storm hydrology, both of which may be important influences on stream ecosystems.

Natural and anthropogenic drivers of fish assemblages

Increasing urbanization across our study sites was associated with an apparent shift toward fish assemblages dominated by habitat generalist species (tolerant of lentic conditions) and a loss of stream-dependent species (i.e., fluvial specialists). The putative shift toward lentic tolerant species, in turn, was associated with lower and more prolonged low-flow conditions in high-imperviousness streams during autumn. We expect that low flows favor lentic tolerant species because of 1) increased pool and backwater habitats during low flows (e.g., preferred by lentic tolerant species, Travnicek et al. 1995), or 2) decreased competition from stream-dependent species (Power et al. 1988). Conversely, we observed low abundances of lentic tolerant species in streams with higher summer stormflow magnitude and autumn baseflow magnitude. Elevated storm flows can depress juvenile survival of many fishes (Freeman et al. 2001); however, storm flows may have particularly strong effects on species residing and/or spawning in scour-prone habitats such as pools, the habitat of lentic tolerant species.

We also observed that abundance of endemic species and the ratio of endemic to cosmopolitan species were low in urban streams (Table 5), supporting geographic patterns described by Burkhead et al. (1997) and results of Walters et al. (2003a) in the region. Richness of endemic species and richness and abundance of sensitive species were predicted by altered storm flow (Table 7); however, these variables also were predicted by % fine sediment in riffles (Table 5). Changes in streambed coarseness could be a consequence of altered stormflow hydrology in urban streams, but we did not find strong correlations between % fines and stormflow variables (e.g., highest $r = 0.39$ with summer stormflow PC_3). Depending on the time since urbanization and the stability of the channel, storm flows could have variable effects on sedimentation (Henshaw and Booth 2000) and, subsequently, fish assemblages. For example, in unstable urbanizing streams, high-flow events may increase bank erosion and sediment inputs to channels, or may mobilize historic bed sediment within the stream (Trimble 1997). In contrast, streams draining urban catchments for several decades may experience bed coarsening and scouring during high-flow events (Finkenbine et al. 2000). We believe that both scenarios likely occur within the study streams, and potentially hamper the ability to predict fish assemblages based on stormflow variables.

Stream slope also is an important factor driving streambed coarseness and, consequently, fish assemblages in the Etowah River Catchment (Walters et al. 2003a, b). Specifically, Walters et al. (2003a) found that low-slope streams had finer bed sediments and fishes dominated by cosmopolitan species (relative to endemic species) than higher-slope streams ($r = 0.70$ and 0.67 for correlation between slope and endemic to cosmopolitan ratios of richness and abundance, respectively). In our study, although slope was negatively correlated with % fine sediment in riffles ($r = 0.51$), this relationship was slightly weaker than that reported by Walters et al. (2003a, $r = 0.62$), and there were also weaker relationships between slope and fish assemblage variables than found by Walters et al. (2003a) (e.g., in our study, highest correlations with sensitive abundance, $r = 0.56$, and sensitive richness, $r = 0.46$; all other fish variables $r < 0.24$). Streams in Walters et al. (2003a) were selected randomly within the Etowah River Catchment, so they had lower mean % urban land cover (15.0%) compared to our streams (25.2%), and higher ratios of endemic to cosmopolitan richness (0.40) and abundance (1.27) compared to our streams (0.26 and 1.11, respectively). In urban streams, effects of altered hydrology on bed texture and fish assemblages may mask the strong geomorphic control of stream slope on fish assemblages.

There were two critical seasons when we expected altered hydrology to have the largest influence on fish assemblages: 1) in late spring and summer during spawning, and 2) in autumn during low-flow periods with limited habitat availability. During spring spawning events, high storm flows may increase mortality of eggs and young-of-year fishes (Power et al. 1996, Poff et al. 1997, Freeman et al. 2001, Bunn and Arthington 2002). We did not have a sufficiently complete spring data set to test these hypotheses, but we did observe low richness of 3 assemblage groups in streams with high stormflow alteration during summer (May–Aug., Table 7). The extent and magnitude of the effects of storms during 2003 may be best reflected by the relative abundance of fishes in future years. We also saw evidence that prolonged, low base flows in autumn were related to high richness of cosmopolitan and lentic tolerant species. The lack of relationships with other fishes, however, suggests that reduced base flows are not a dominant driver of fish assemblage alteration. The few autumn storms that occurred, consequently raising water levels in the urban streams, may have been sufficient to offset effects of catchment imperviousness on reduced base flows.

Studies have suggested that total imperviousness is not a useful measure of urban impacts on streams because it does not account for connections between impervious surfaces and the stream network (Brabec et al. 2002, Walsh et al. 2005a). For example, precipitation falling on roads in forested catchments (i.e., disconnected from storm pipes) may infiltrate into bare ground next to roads and not alter stream hydrology (e.g., noneffective impervious area; Alley and Veenhuis 1983). By quantifying instream hydrology, however, we directly measured the effectiveness of catchment imperviousness (or catchment connection) at linking surface runoff to streams. For the 16 sites with hydrologic data across 2 seasons, variance explained by hydrologic alteration variables was 2 to 36% (mean = 21%) higher than that explained by imperviousness alone. Effective imperviousness may be a good surrogate for altered hydrology in catchments that are unaffected by small impoundments and other water detention ponds. However, instream hydrologic measurements will provide the best picture of direct physical impacts to stream ecosystems.

Management implications

Historically, stormwater management has involved moving the water off streets and paved parking lots as efficiently as possible to ensure maximum public safety and convenience (Arnold and Gibbons 1996), but has failed to account for maintenance of ecological function in aquatic systems (Postel et al. 1996). Stormwater management for instream needs requires a shift in the way policymakers and public safety officers think about precipitation. To minimize fish assemblage alteration in urban streams, we believe that ordinances should be adopted to avoid exacerbating the frequency and magnitude of high-storm events, and to reduce stream flashiness during storm events. This strategy is especially important during seasons with medium and low precipitation. Impervious cover also may reduce groundwater recharge, so stormwater detention/retention catchments might not be the best tool for managing stormwater for instream needs (Heitz et al. 2000, Booth et al. 2002). Alternative management tools include increasing perviousness in urban areas through porous road and parking lot materials, raingardens, and/or drainage swales (Konrad and Burges 2001, Booth et al. 2002). Increasing the amount of infiltration within the catchment and decreasing the connectedness of stormwater pipes (Walsh et al. 2005a) in urban areas should work best at mimicking natural landscapes and minimizing alteration to stream ecosystems. Hydrologic alteration is an important pathway by which urban development may affect fishes, but other urban stressors also must be addressed to evaluate the relative effectiveness of hydrologic management at protecting fish integrity.

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APPENDIX Fished collected and frequency (freq.) of occurrence within the 30 study streams. Habitat preference is either fluvial specialist (FLU) or lentic tolerant (LEN). Highland endemic species (END) and cosmopolitan, widespread species (COS) are indicated (after Walters et al. 2003a). Determination of sensitive fishes (SEN) was based on life-history traits (i.e., expected sensitivity) and negative relationships with % urban land cover from previous fish collection data (SJW, unpublished data). N/A = not applicable.

Taxon	Common name	Composition categories	Freq. of occurrence
Petromyzontidae			
Ichthyomyzon sp. cf. *gagei*	Southern brook lamprey	FLU	12
Cyprinidae			
Campostoma oligolepis	Largescale stoneroller	FLU, COS	29
Cyprinella callistia	Alabama shiner	FLU, SEN	12
Cyprinella trichroistia	Tricolor shiner	FLU, END, SEN	3
Cyprinella venusta	Blacktail shiner	FLU	5
Hybopsis lineapunctata	Lined chub	FLU, END	1
Hybopsis sp. cf. *winchelli*	Clear chub	FLU, END	2
Luxilus zonistius	Banfin shiner	FLU	2
Nocomis leptocephalus	Bluehead chub	FLU	5
Notemigonus crysoleucas	Golden shiner	LEN, COS	1
Notropis chrosomus	Rainbow shiner	FLU, END, SEN	2
Notropis longirostris	Longnose shiner	FLU, COS	3
Notropis lutipinnis	Yellowfin shiner	FLU	3
Notropis stilbius	Silverstripe shiner	FLU, SEN	4
Notropis xaenocephalus	Coosa shiner	FLU, END	15
Phenacobius catostomus	Riffle minnow	FLU, END	1
Semotilus atromaculatus	Creek chub	FLU, COS	23
Catastomidae			
Hypenteluim etowanum	Alabama hog sucker	FLU	30
Minytrema melanops	Spotted sucker	FLU, COS	3
Moxostoma duquesnei	Black redhorse	FLU, COS, SEN	10
Moxostoma erythrurum	Golden redhorse	FLU, COS, SEN	8
Moxostoma poecilurum	Blacktail redhorse	FLU, COS	3
Ictaluridae			
Ameiurus brunneus	Snail bullhead	FLU, COS, SEN	7
Ameiurus natalis	Yellow bullhead	LEN, COS	5
Ameiurus nebulosus	Brown bullhead	LEN, COS	2
Ictalurus punctatus	Channel catfish	LEN, COS	3
Noturus leptacanthus	Speckled madtom	FLU, COS, SEN	5
Salmonidae			
Oncorhynchus mykiss	Rainbow trout	N/A	1
Fundulidae			
Fundulus stellifer	Southern studfish	FLU	24
Poeciliidae			
Gambusia affinis	Eastern mosquitofish	LEN, COS	6
Gambusia holbrooki	Western mosquitofish	LEN, COS	2
Gambusia holbrooki × *affinis*	Hybrid mosquitofish	LEN, COS	4
Cottidae			
Cottus carolinae zopherus	Coosa banded sculpin	FLU, END	23
Centrarchidae			
Ambloplites ariommus	Shadow bass	FLU, COS	1
Lepomis auritus	Redbreast sunfish	LEN, COS	30

APPENDIX Continued.

Taxon	Common name	Composition categories	Freq. of occurrence
Lepomis cyanellus	Green sunfish	LEN, COS	22
Lepomis gulosus	Warmouth	LEN, COS	6
Lepomis macrochirus	Bluegill	LEN, COS	29
Lepomis microlophus	Redear sunfish	LEN, COS	5
Lepomis punctatus	Spotted sunfish	LEN, COS	9
Lepomis macrochirus × *auritus*	Hybrid sunfish	LEN, COS	1
Micropterus coosae	Coosa bass	FLU	23
Micropterus punctulatus	Spotted bass	FLU, COS	4
Micropterus salmoides	Largemouth bass	LEN, COS	22
Pomoxis annularis	White crappie	LEN, COS	1
Pomoxis nigromaculatus	Black crappie	LEN, COS	2
Percidae			
Etheostoma scotti	Cherokee darter	FLU, END, SEN	18
Etheostoma stigmaeum	Speckled darter	FLU, COS, SEN	10
Perca flavescens	Yellow perch	LEN, COS	2
Percina kathae	Mobile logperch	FLU	14
Percina nigrofasciata	Blackbanded darter	FLU, COS	27
Percina palmaris	Bronze darter	FLU, END, SEN	1