



Detection of biotic responses to urbanization using fish assemblages from small streams of western Georgia, USA

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Abstract. We examined relationships between stream fish assemblages and land use alteration associated with urbanization in 15 lower Piedmont watersheds along an urbanization gradient north of Columbus, western Georgia. Based on land cover data from 2002 Landsat 7 TM imagery aerial photos, streams drained watersheds that were largely urban, developing (suburban), agricultural (pasture), managed pine forest, and unmanaged mixed-forest. We quantified fish seasonally from 3 run-pool segments in each stream, and used a variety of metrics as response variables in analyses of relationships between fish assemblage structure and land use and natural basin variation. In general, Georgia-Index of Biotic Integrity (GA-IBI) values, Bray-Curtis faunal similarity of streams to mean conditions within reference streams, proportions of fish as lithophilic spawners, and fish lacking eroded fins, lesions, tumors decreased with increasing urbanization. Multiple regression indicated that assemblages were explained by a combination of land use and natural basin variables (basin size, average discharge, nearest distance to a larger downstream tributary [colonization source]), with land use variables being important predictors of summer assemblages and natural basin variables being more important in winter and spring assemblages. Non-metric multidimensional scaling (NMDS) ordinations revealed strong separation between assemblages in urban watersheds and forested watersheds, whereas assemblages in agricultural and developing watersheds were intermediate between those in urban and forested watersheds. Our data suggest that fish are reliable indicators of anthropogenic disturbance at the landscape scale, at least seasonally, and may be used to forecast the magnitude of landscape-level changes in stream structure and function associated with the conversion of forests to urban/suburban land in the Southeast.

Keywords: stream, land use, fish, assemblage structure, urbanization

Introduction

Environmental quality and biotic composition of aquatic systems often are strongly affected by land use (Lenat and Crawford, 1994; Weaver and Garman, 1994; Wang *et al.*, 2001). One of the more pervasive and rapidly growing forms of land use change is the conversion of natural forested or vegetated agricultural land to urban environments (urban sprawl, US Census Bureau, 2001; Wang and Lyons, 2003). Inevitable landscape alteration associated with human population expansion has revealed dramatic effects on water quality and

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aquatic biota (Benke *et al.*, 1981; Hirsch, 1990; Limburg and Schmidt, 1990; Weaver and Garman, 1994). Fish are particularly useful in assessing long-term environmental impacts of urbanization because they integrate multiple trophic levels in aquatic communities, are relatively long-lived, and are easily sampled (Karr, 1987; Barbour *et al.*, 1999). In this context, increasing environmental stress associated with watershed urbanization often may decrease overall fish richness, abundance, and diversity, and cause shifts in assemblages from intolerant to tolerant and/or introduced species (Klein, 1979; Marsh and Minckley, 1982; Onorato *et al.*, 1998; Walters *et al.*, 2003a).

Aquatic system response to urbanization often is linked to increased impervious surfaces within developing watersheds, which can alter stream water quality, quantity, and habitat availability (Hirsch, 1990; Herlihy *et al.*, 1998; Paul and Meyer, 2001; Walsh *et al.*, 2001). Such physicochemical alterations may manifest as increased flood magnitude and frequency (flashiness) and increased delivery of nutrients, metals, pesticides, and organic contaminants to receiving streams, all of which may degrade fish assemblages (Weaver and Garman, 1994; Lenat and Crawford, 1994; Wang *et al.*, 2000, 2003; Paul and Meyer, 2001). A particularly pervasive impact of forest land conversion on fish is through increased sedimentation (Tebo, 1955; Berkman and Rabeni, 1987; Sutherland *et al.*, 2002; Iwata *et al.*, 2003). Sedimentation in streams resulting from agriculture and logging are well known (Tebo, 1953; Cordone and Kelly, 1961; Waters, 1995; Rier and King, 1996), and emerging research suggests sedimentation in urbanized watersheds can reduce habitat quality and cause shifts in fish feeding and reproductive guilds toward generalist species (Berkman and Rabeni, 1987; Schleiger, 2000; Walters *et al.*, 2003a).

In high-gradient upland streams of northern Georgia, USA, a region with naturally high fish diversity and endemism, urbanization has been implicated in increased abundance of cosmopolitan species, or stream 'homogenization' (*sensu* Walters *et al.*, 2003a). Fish assemblages in sandy, low-gradient streams within this same region are naturally less diverse and show comparatively lower endemism (Swift *et al.*, 1986). Urbanization of lowland streams may, therefore, exhibit disparate influences on fishes than in upland systems. We quantified fish assemblage structure in these lowland streams along an urbanization gradient to assess the degree to which assemblages reflected variation in land use from urbanization. Specifically, we examined (1) the relative influence of watershed land use versus natural basin attributes (primarily physical habitat measures) on fish assemblage structure, and (2) if assemblage shifts varied predictably with increasing land use change attributable to urbanization in study watersheds.

Methods

Study area

We studied tributaries of the middle Chattahoochee River, western Georgia, USA, occurring in the Southern Outer Piedmont ecoregion. The Piedmont biogeoclimatic province historically was developed for agriculture, although it now harbors many of the burgeoning metropolitan areas of the Southeast (Richmond, Raleigh/Durham, Greenville/Spartanburg, Atlanta), as well as extensive managed pine plantations. The west Georgia landscape and

the area surrounding the city of Columbus is a notable example of this trend (Lockaby *et al.*, 2005). Present-day development from Columbus is constrained by the Chattahoochee River to the west and a large military installation (Fort Benning) to the southeast, so most land conversion and urban expansion occurs mainly to the northeast.

We sampled fifteen 2nd - to 3rd-order streams in 15 watersheds (4–25 km²) along an urbanization gradient stretching from the geologic fall line in the city of Columbus to an area 80 km northeast (figure 1, Table 1). Study streams were typical of those in the lower Piedmont, consisting of sandy-bottom channels and a run-pool morphology with infrequent riffles (Mulholland and Lenat, 1992). Average pool depth was ~0.25 m and channel width ~10 m. Watersheds ranged in land use/cover from intense urbanization (up to 50% urban cover) and active suburban development to heavily forested (up to 95% forest cover). This relatively large range in landscape character allowed us to compare across geomorphically similar streams that differed primarily in watershed-level land use and associated variation in streamwater physicochemical conditions (Schoonover *et al.*, 2005).

Landscape classification

Initially, we quantified land use/cover in study watersheds using 2002 Landsat 7 TM imagery (30-m resolution) and ArcView© software (Version 3.2a, Environmental Systems Research Institute, Inc., Redlands, California). We derived 4 primary land use categories (showing >30% of a given category) from this classification: % of the watershed occurring as urban (= % **Urban**), % of the watershed as coniferous forest (= % **Conifer**), % of the watershed as mixed coniferous-deciduous forest (= % **Mixed**), and % of the watershed as pasture (= % **Pasture**). We also classified certain forested watersheds with active or recent development into a separate category (**Developing**). In addition to quantifying % Conifer and % Mixed we also combined these 2 classifications into a single forest category (= % **Total Forest**) for each watershed.

Following analysis of Landsat data, we quantified amount of impervious surface in study watersheds by manually digitizing 1-m resolution, 3-band aerial photographs (taken March 2003). We determined watershed boundaries, size, average slope, and nearest distance to a larger downstream tributary (used as a conservative measure of potential source habitat for fishes) from USGS 30-m resolution digital elevation models (DEMs) and ArcView.

Field sampling

We quantified fish seasonally (summer/fall, winter, spring) from July 2002 to September 2003 from 3 run and pool habitats per stream along a representative 100-m reach. We sampled fish in most habitats to depletion with block nets and backpack electroshocker (Smith-Root LR-24), and supplemented larger habitats with additional seining when necessary. We excluded juvenile fish (<20 mm total length, TL) from analyses because of inefficiency in their capture. We identified fish to species, measured TL, and then examined them for eroded fins, lesions, tumors and overall health (% DELT, Schleiger, 2000). Except for voucher specimens, we returned all fish to the stream near the point of capture. Three streams (SB2, MU3, HC) could not be sampled in Summer 2002 because of stream drying,

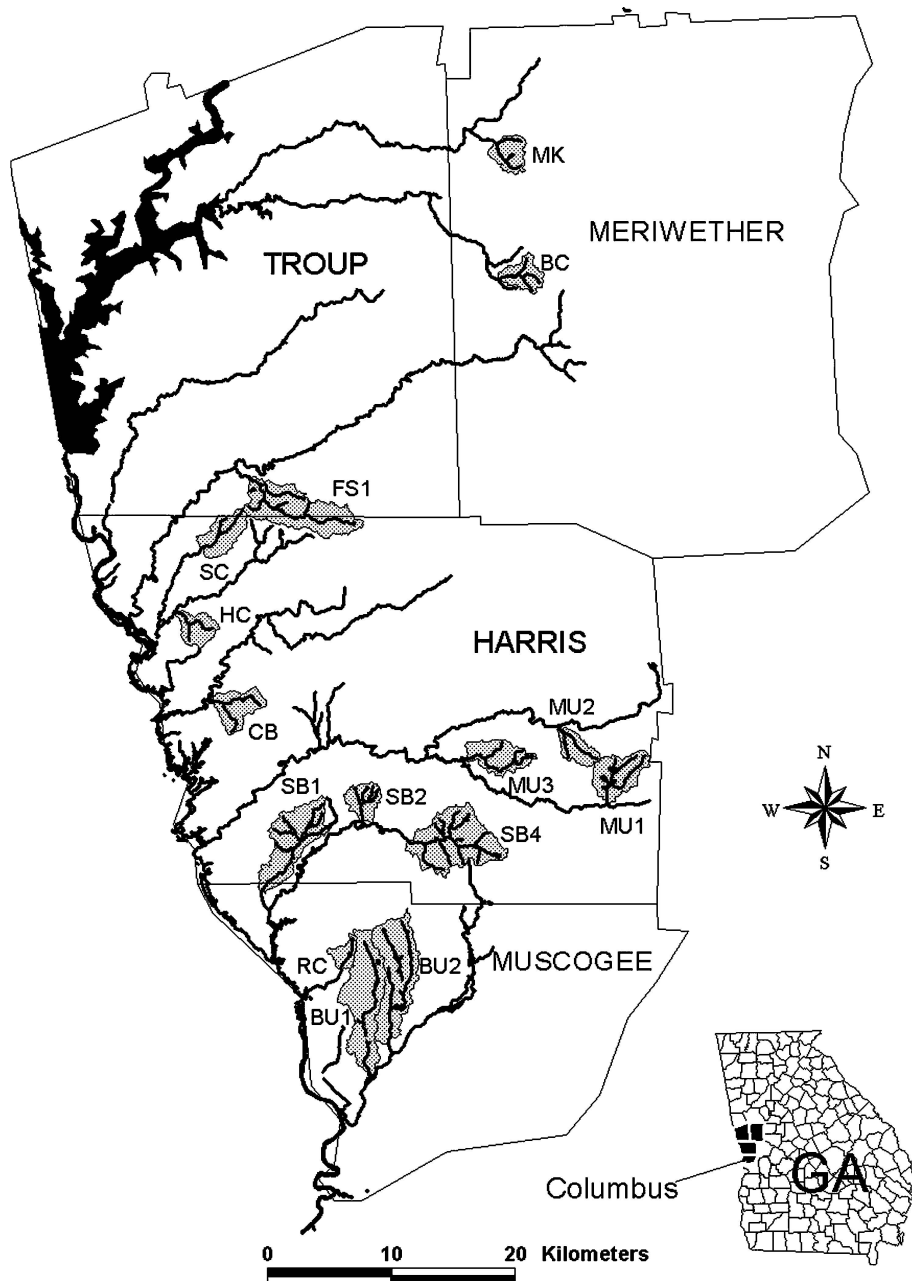


Figure 1. Map of the 15 study watersheds (shaded regions) in the middle Chattahoochee River Basin in Muscogee, Harris, Meriwether, and Troup counties, west Georgia.

and 1 stream (MU1) contained no fish in Winter 2002, so we excluded these streams from multiple regression analyses.

We classified species into breeding and feeding guilds, and assigned them to intolerant, moderately intolerant, tolerant, or pioneer tolerance classes (S. L. Schleiger, Georgia Department of Natural Resources, personal communication, Table 2). We defined pioneers as those species that quickly reinvade a previously disturbed habitat (Smith, 1979). We assigned fish to 5 breeding guilds (see Muncy *et al.*, 1979; Berkeman and Rabeni, 1987). Fish were first classified into complex or simple breeders, based on the degree to which species prepare spawning sites, defend nests, and show pre-spawning social behavior (Pflieger, 1975; Trautman, 1981). We further divided complex breeders into those species showing parental care (=P/C) and those that do not (= No P/C). We divided simple breeders into spawners requiring clean, gravel substrate (lithophilous spawners, = Lithophils) and those capable of spawning on sand, silt, or vegetation (generalist spawners, = Simple Spawners). We also calculated several community variables (Table 2) including density, species richness, diversity (Shannon's H'), and relative abundance for each stream and season.

We used Bray-Curtis similarity index (Krebs, 1999) to determine the pairwise similarity of fish assemblages at each stream based upon mean conditions from 4 reference watersheds (MK, CB, BC, MU3, Table 1). We considered these sites to be close to or at the reference condition, based on (1) a high proportion of their watersheds in forest and correspondingly

Table 1. Characteristics of the 15 study watersheds. LU/LC refers to the dominant land use/land cover in the watershed based on GIS

Site	Stream	Watershed size (km ²)	LU/LC	UTM North	UTM East
SB 1	Schley Creek	20.09	Developing	0685312	3608722
SB 2	Standing Boy Creek Trib.	6.34	Developing	0693082	3614122
SB 4	Standing Boy Creek	26.59	Developing	0696898	3612214
HC	House Creek Trib.	6.55	Coniferous	0678280	3630695
MU 2	Mulberry Creek Trib.	6.06	Coniferous	0709195	3621084
SC	Sand Creek	8.96	Coniferous	0680325	3635890
BC	Beech Creek	6.47	Mixed	0704322	3657675
MK	Flat Creek Trib.	6.63	Mixed	0703887	3668333
CB	Cline's Branch	8.97	Mixed	0681196	3623522
MU 3	Turntime Branch	10.44	Mixed	0701795	3619093
FS 1	Wildcat Creek	24.20	Pasture	0684280	3641319
MU1	Ossahatchie Creek Trib.	11.95	Pasture	0712764	3615524
BU 1	Lindsey Creek	25.47	Urban	0693619	3593874
BU 2	Cooper Creek	24.69	Urban	0695357	3596969
RC	Roaring Branch Creek	3.67	Urban	0691329	3602142

A watershed was classified only if it contained >30% of a given land use category, except for Developing, which showed <30% urban cover but contained active residential development. UTM coordinates were taken at the sampling site furthest downstream. Trib. = tributary.

Table 2. Fish metrics quantified by stream and season in the 15 study watersheds

Diversity/similarity	Feeding guild	Breeding guild	Tolerance value
Shannon's H'	Filter-feeder	Complex	Pioneer
Bray-Curtis similarity	Insectivore	Complex P/C	Tolerant
	Piscivore	Complex No P/C	Moderate
	Herbivore	Simple Spawners	Intolerant
	Omnivore	Simple Lithophils	
	Generalist		

Complex breeders that lack parental care were simply classified "Complex". P/C = complex breeders showing parental care, No P/C = complex breeders showing no parental care. See text for definitions of breeding guilds and tolerance values.

low silviculture, agriculture, or urbanization, and (2) their generally high apparent stream biotic integrity and physical condition. We used tolerance values and breeding and feeding guilds in an Index of Biotic Integrity (IBI) developed for streams fishes in west-central Georgia (Schleiger, 2000).

We also measured stream discharge monthly over the sampling period using the velocity-area method (Gore, 1996) with a Marsh-McBirney flow meter (Schoonover *et al.*, 2005). We used mean discharge along with basin size, average slope, and downstream distance to the next largest stream as measures of variation in hydrologic and geomorphologic conditions among study watersheds, and as a suite of natural basin variables to contrast with land use variables in statistical analyses.

Data analyses

First, we used simple Pearson correlations (Zar, 1999) to examine general relationships between fish variables and land use/natural basin variables. This procedure allowed us to assess general trends and identify potential multicollinearity among variables. Second, we used stepwise multiple regressions to develop season-specific models of relationships among fish and land use/natural basin variables (30-m resolution classification, Table 3) to assess the relative strength of land use vs. natural basin variables on fish variables. We used variance inflation factors (VIF) to reduce the number of environmental variables in multiple regressions and avoid multicollinearity (variable removed if $VIF > 10$, Myers, 1990). Model selection was based on Mallows's $C(p)$, R_{adj}^2 , and parsimony (Myers, 1990). Third, in addition to multiple regressions applied to 30-m spatial data, we used simple linear regressions between % impervious surface in the watershed, quantified from the 1-m resolution spatial data, against fish variables. Impervious surface is considered a useful landscape metric in studies characterizing urbanization impacts on streams (McMahon and Cuffney, 2000; Walsh *et al.*, 2004), so we considered this analysis potentially useful in describing additional variation between fish and land use variables. Finally, we used non-metric multidimensional scaling (NMDS) to describe overall variation in fish assemblages

Table 3. Initial land use and natural basin variables quantified in the 15 study watersheds

Variable	Mean	Range
<i>Land use</i>		
Urban (%)*	11.1	0.1–48.9
Impervious surface (%)*	8.66	1.22–37.11
Pasture (%)*	24.6	4.0–52.7
Mixed Forest (%)	37.2	22.5–55.2
Conifer (%)	26.0	8.4–69.6
Total Forest (%)	63.2	30.9–94.8
<i>Natural basin</i>		
Average discharge (m ³ /s)*	0.282	0.003–0.910
Basin size (ha)*	1352	366–2659
Average basin slope (%)	13.6	5.3–146.1
Average channel slope (%)	0.05	0.02–0.08
Distance to downstream source (km)*	2.9	0.2–10.0
Link magnitude (count)	4.3	1.0–12.0

Asterisks indicate those variables used in final analyses.

(using species abundance data) among sites and seasons. NMDS is an ordination technique that uses pairwise similarity or dissimilarity matrices to determine positions of sites in terms of species space (Hawkins *et al.*, 1997; McCune and Grace, 2002). Sites nearest to or furthest from each other on the ordination are those displaying highest and lowest faunal similarity, respectively. We transformed proportional relative abundance data using arcsin-square root to satisfy assumptions of normality and homoscedasticity, and we excluded rare species (those in <10% of sites) for each season to reduce the influence of rare taxa on ordinations. This step resulted in a 42 × 20 site by species matrix on which we based ordinations using a Sorenson distance measure. We used SAS (version 8.2, SAS Institute Inc., Cary, North Carolina) for all correlation and regression analyses and PC-ORD (version 4, MjM Software Design, Glenden Beach, Oregon) for NMDS.

Results

We collected 33 fish species (3772 individuals) from 7 families (Catastomidae, Centrarchidae, Cyprinidae, Ictaluridae, Percidae, Petromyzontidae, Poeciliidae) during the study. Centrarchidae and Cyprinidae were the most common families, composing 24 and 55% of total fish collected, respectively. Bandfin shiners (*Luxilus zonistius*), bluegill (*Lepomis macrochirus*), redbreast sunfish (*L. auritus*) and mosquitofish (*Gambusia affinis*) were the most abundant species. *Lepomis auritus* was the most frequently collected species, occurring in 90% of samples, *L. macrochirus* was the 2nd-most frequent (74% of samples), and the silverjaw minnow (*Ericymba buccata*) the 3rd-most frequent fish in collections (62%).

Table 4. Summary fish data for the 15 study watersheds. Values are cumulative for the sites (seasons combined)

	Mean	Range
<i>Assemblage variable</i>		
Number collected	91.9	2–284
H'	1.47	0.17–2.24
Species richness	8.4	2.0–16.0
Bray-Curtis similarity	31.05	3–68
IBI	41.37	24–52
Tolerant species (%)	16.34	0–98.47
Pioneer species (%)	28.56	0–82.76
% DELT	6.61	0–85.7
<i>Feeding guild variable</i>		
Piscivore (%)	1.99	0–14
Herbivore (%)	5.53	0–50
Omnivore (%)	4.2	0–28
Insectivore (%)	81.85	49–100
Filter feeder (%)	2.71	0–44
Generalist feeder (%)	3.64	0–23
<i>Breeding guild variable</i>		
No P/C (%)	25.15	0–5.26
P/C (%)	34.11	0–96.95
Simple spawner (%)	17.02	0–100
Lithophilic spawner (%)	23.49	0–78.57

IBI = GA Index of Biotic Integrity (see Schleiger, 2000).
 % DELT = proportion of fish in the sample with eroded fins, lesions, or tumors. P/C = proportion of complex breeders showing parental care, No P/C = proportion of complex breeders showing no parental care. See text for further explanation of variables.

The number of fish collected ranged from 2 to 284 per stream, richness from 2 to 16, H' from 0 to 2.24, and IBI score from 24 to 52 (Table 4). Insectivores (~82% of total assemblage) and complex breeders with parental care (P/C, ~34%) were the most abundant feeding and breeding guilds, respectively (Table 4). In general, IBI, Bray-Curtis similarity to mean reference condition, and % of the assemblage as lithophilic spawners were negatively correlated with % Urban, whereas % DELT and % of the assemblage as herbivores (primarily *Campostoma pauciradii*) were positively correlated with % Urban, and in turn negatively correlated with % Total Forest (Table 5). In particular, abundance of *E. buccata*, *L. zonistius*, *Nocomis leptcephalus*, *N. longirostris*, and *Semotilus atromaculatus*

Table 5. Pearson product-moment correlation coefficients between selected fish variables and land use variables (based on 30-m resolution Landsat data, see text)

Fish variable	% Urban	% Pasture	% Conifer	% Mixed	% Total forest
% Herbivore	0.4804***	ns	ns	ns	-0.3136*
% Simple spawner	ns	ns	ns	ns	ns
% Lithophilic spawner	-0.4454**	ns	0.453**	ns	0.4829***
% Tolerant	ns	0.4238**	ns	ns	ns
% DELT	0.7222***	-0.3075*	-0.371*	-0.3405*	-0.5244***
Taxa richness	ns	ns	ns	ns	ns
H'	ns	ns	ns	ns	ns
Bray-Curtis similarity	-0.3795*	ns	0.3117*	0.3001*	0.4486**
IBI	-0.6012***	ns	0.4714**	0.3803**	0.6365***

% Herbivore = proportion of herbivorous species in the sample, % Simple spawner = proportion of species in the sample showing no complex spawning behavior, % Lithophils = proportion of species in the sample requiring clean, gravel substrate for spawning, %Tolerant = proportion of tolerant species in the sample, % DELT = proportion of fish in sample with eroded fins, lesions, or tumors in the sample, Bray-Curtis = stream faunal similarity to average reference condition, IBI= Georgia Index of Biotic Integrity (see Schleiger, 2000).

* $p = 0.05$, ** $p = 0.01$, *** $p < 0.001$. ns = nonsignificant.

decreased with increasing % Urban. Proportion of the assemblage as tolerant species was positively correlated with % Pasture but was uncorrelated with % Urban (Table 5). The % of the assemblage as lithophilic spawners, IBI, and Bray-Curtis similarity to reference condition all were significantly correlated with % Conifer, % Mixed, and/or % Total Forest in study watersheds (Table 5).

As a result of multicollinearity determined by inspection of high VIF scores, we used only 5 independent variables in multiple regressions, including 2 land use variables (% Urban, % Pasture) and 3 natural basin variables (basin size, average discharge, nearest distance to a downstream source). We observed significant relationships between the above independent variables and 10 fish variables, although the strength of relationships varied seasonally (Table 6). Percent DELT and IBI were the only fish variables that were consistently explained by land use (vs natural basin) variables. The % DELT was explained by % Urban in all 3 seasons (summer: $R_{adj}^2 = 0.755$, $p = 0.0002$; winter: $R_{adj}^2 = 0.591$, $p = 0.0008$; spring: $R_{adj}^2 = 0.582$, $p = 0.0006$), whereas IBI were explained by % Urban and % Pasture, but only in summer ($R_{adj}^2 = 0.495$, $p = 0.0187$, Table 6).

In contrast, several fish variables were best explained by natural basin variables. H' was explained by basin size and average discharge ($R_{adj}^2 = 0.342$, $p = 0.0321$), but only in winter. Proportion of the assemblage as cyprinid insectivores was explained by basin size and distance to a larger downstream source in summer ($R_{adj}^2 = 0.433$, $p = 0.0314$), and by basin size and discharge in winter ($R_{adj}^2 = 0.406$, $p = 0.0027$). Proportion of the assemblage as pioneer species and omnivores both were explained by the distance to a downstream source in some (but not all) seasons (Table 6). However, variation in most fish metrics was explained by a mixture of land use and natural basin variables. For example, richness and

Table 6. Seasonal multiple regression models for select fish metrics using two 30-m resolution land use variables (% Urban, % Pasture, see text) and three natural basin variables (basin size, discharge, distance to source), and simple linear regressions of fish metrics with 1-m resolution % impervious surface

		Variables in multiple regression model		Impervious surface	
		R^2 adj	p	R^2	p
Summer					
H'	–	–	–	–	–
Species richness	urban, pasture, basin size	0.4760	0.0432	–	–
Tolerant species	urban, pasture, basin size	0.672	0.0071	–	–
% Herbivore	pasture, source distance	0.461	0.0252	0.456 (+)	0.0160
% Omnivore	–	–	–	–	–
% Cyprinid insectivore	basin size, source distance	0.433	0.0314	–	–
% Pioneer	source distance	0.340	0.0274	–	–
% DELT	urban	0.755	0.0002	0.871 (+)	<0.0001
Bray-Curtis similarity	–	–	–	–	–
IBI	urban, pasture	0.495	0.0187	0.376 (–)	0.0341
Winter					
H'	basin size, discharge	0.342	0.0321	–	–
Species richness	–	–	–	–	–
Tolerant species	–	–	–	–	–
% Herbivore	urban, discharge	0.681	0.0007	0.636 (+)	0.0006
% Omnivore	–	–	–	–	–
% Cyprinid insectivore	basin size, discharge	0.4060	0.0027	–	–
% Pioneer	–	–	–	–	–
% DELT	urban	0.591	0.0008	0.733 (+)	<0.0001
Bray-Curtis similarity	–	–	–	–	–
IBI	urban, discharge	0.529	0.0064	0.414 (–)	0.0130
Spring					
H'	–	–	–	–	–
Species richness	–	–	–	–	–
Tolerant species	pasture, discharge	0.341	0.0324	–	–
% Herbivore	–	–	–	–	–
% Omnivore	source distance	0.8183	<0.0001	–	–
% Cyprinid insectivore	–	–	–	–	–
% Pioneer	source distance	–	–	–	–
% DELT	urban	0.582	0.0006	0.720 (+)	<0.0001
Bray-Curtis similarity	pasture, discharge	0.398	0.0190	–	–
IBI	urban, pasture, basin size	0.6381	0.0024	0.369 (–)	0.0163

% Herbivore = proportion of herbivorous species in the sample, % Omnivore = proportion of omnivorous species in the sample, % Cyprinid insectivore = proportion of insectivorous species in the family Cyprinidae, % Pioneer = proportion of pioneer species in the sample, % DELT = proportion of fish in sample with eroded fins, lesions, or tumors in the sample, Bray-Curtis = stream faunal similarity to reference stream, and IBI = Georgia Index of Biotic Integrity (see Schleiger, 2000). Direction of relationships for simple regressions are denoted by (+) and (–) in the R^2 column when appropriate.

% tolerant species were explained by a combination of % Urban, % Pasture, and basin size ($R_{\text{adj}}^2 = 0.510$, $p = 0.0335$; $R_{\text{adj}}^2 = 0.660$, $p = 0.0082$, respectively) in summer. In winter, IBI and proportion of the assemblage as herbivores were explained by % Urban and basin size ($R_{\text{adj}}^2 = 0.529$, $p = 0.0064$; $R_{\text{adj}}^2 = 0.681$, $p = 0.0007$, respectively). In spring, % Urban, % Pasture, and basin size best explained IBI ($R_{\text{adj}}^2 = 0.638$, $p = 0.0024$) and % Pasture and average discharge explained proportion of the assemblage as tolerant species ($R_{\text{adj}}^2 = 0.341$, $p = 0.0324$, Table 6).

Use of finer scale (1-m resolution) % impervious surface data in simple regressions did little to improve relationships between land use and fish assemblages (Table 6). We found significant relationships for only 3 fish variables: % DELT increased with increasing impervious surface, and IBI decreased with increasing impervious surface (all seasons), whereas % herbivores increased with increasing impervious surface (summer and winter, Table 6).

NMDS revealed 2 axes that together accounted for 65.9% of the total variation in the fish assemblage among sites and seasons (figure 2). Axes 1 and 2 accounted for 21.1 and 44.8% of the total variation, respectively (number of dimensions = 3, number of iterations = 162, final stress = 14.21%). The distance from the study site to a larger downstream source was negatively related to Axis 1 ($R^2 = 0.20$, $p = 0.0033$, Table 7), whereas percent impervious surface was negatively related to Axis 2 ($R^2 = 0.34$, $p < 0.0001$, Table 7). Further, % Conifer ($R^2 = 0.43$, $p < 0.0001$) and % Total Forest ($R^2 = 0.40$, $p < 0.0001$) were positively related to Axis 2 (Table 7). Streams in urban and developing watersheds

Table 7. Watershed and fish variables regressed against Axes 1 and 2 in non-metric multidimensional scaling (NMDS) space based on abundance of 20 most common fish species in the 15 study watersheds

	NMDS Axis 1	NMDS Axis 2
<i>Watershed variables</i>		
% Impervious surface		0.3375
% Pasture		
% Conifer		0.4305
% Total Forest		0.3975
Basin size		0.0963
Distance from source	0.2004	
<i>Fish variables</i>		
% Pioneer	0.4504	0.2288
% Omnivore	0.3218	
% Lithophilic Spawner		0.4956
% DELT		0.2145
Bray-Curtis similarity		0.3561
IBI		0.3829

Values are R^2 that were significant ($p < 0.05$).

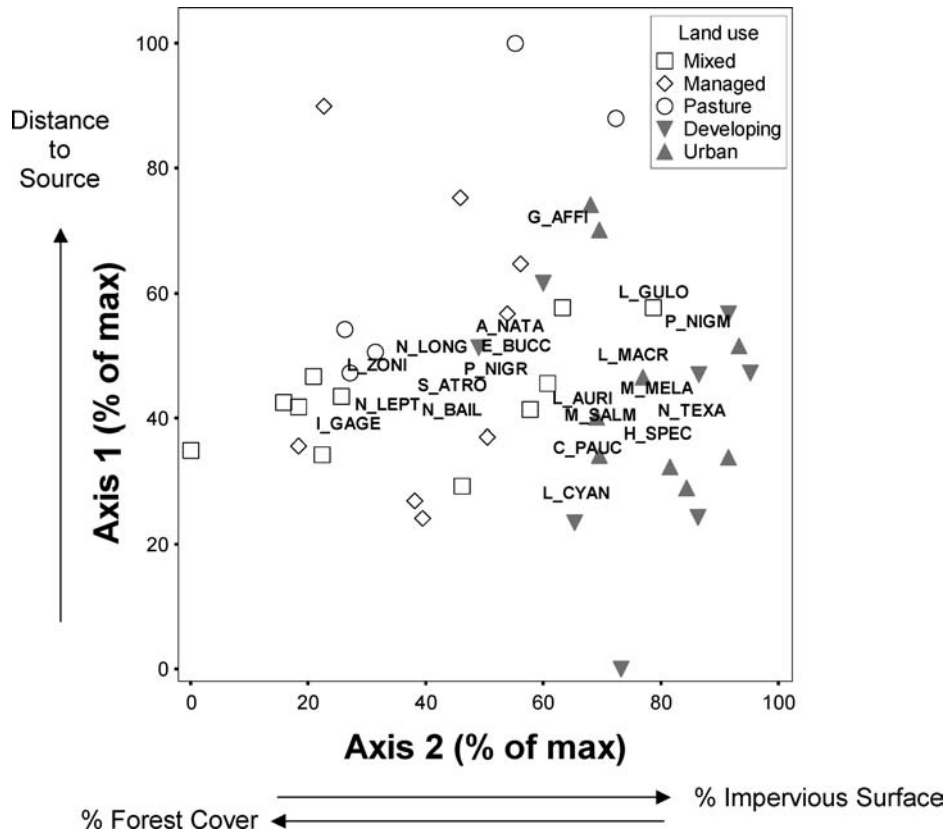


Figure 2. Non-metric multidimensional scaling (NMDS) ordination of study sites in fish species space. Axes are scaled proportionate to the longest axis (% of Max). Symbols are the 15 study streams in different seasons, and fish species are labeled according to abbreviations defined in Table 8. Land use classifications were based on the predominant land use in the watershed (>30% of a given land use category), except for “Developing” sites, which showed <30% urban cover but contained active residential development. Land use and natural basin variables significantly correlated with NMDS axes were the proportions of watershed impervious surface (= % Impervious Surface) and total forest cover (= % Forest Cover) on Axis 1, and nearest distance from the study site to a larger downstream tributary (= Distance to Source) on Axis 2. Arrows on x and y axes show direction of increasing values. Axes 1 and 2 explain 21.1 and 44.8% of the total variation, respectively.

tended to group to the right of the ordination, whereas streams draining watersheds with less urbanization, including managed (high % Conifer) and unmanaged (high % Mixed) streams, grouped to the left (figure 2). Streams within agricultural watersheds (high % Pasture) showed no clear grouping with respect to Axes 1 and 2 (figure 2).

Axis 1 of the NMDS ordination was defined largely by abundance of pioneer species, primarily *G. affinis* and *C. pauciradii*, and 2 *Lepomis* species (Table 8, figure 2). In contrast, Axis 2 was defined mostly by abundance of lithophilic spawners, particularly *N. leptcephalus* and *L. zonistius* (Table 8, figure 2). IBI and Bray-Curtis similarity values were

Table 8. Pearson product-moment correlation coefficients and associated p values of fish species associations with Axes 1 and 2 of a non-metric multidimensional scaling (NMDS) ordination based on abundance of 20 most common fish species in the 15 study watersheds

Species	Species code	NMDS Axis 1	p	NMDS Axis 2	p
<i>Ameirus natalis</i>	A_NATA	0.211	0.1858	-0.175	0.2733
<i>Campostoma pauciradii</i>	C_PAUC	-0.599	<0.0001	0.196	0.2202
<i>Ericymba buccata</i>	E_BUCC	0.196	0.2190	-0.241	0.1283
<i>Gambusia affinis</i>	G_AFFI	0.836	<0.0001	0.093	0.5640
<i>Hybopsis sp.</i>	H_SPEC	-0.262	0.0979	0.293	0.0628
<i>Ichthyomyzon gagei</i>	I_GAGE	-0.180	0.2588	-0.542	0.0003
<i>Lepomis auritus</i>	L_AURI	-0.470	0.0002	0.430	0.0052
<i>Lepomis cyanellus</i>	L_CYAN	-0.416	0.0069	0.059	0.7157
<i>Lepomis gulosus</i>	L_GULO	0.153	0.3385	0.294	0.0624
<i>Lepomis macrochirus</i>	L_MACR	0.024	0.8785	0.659	<0.0001
<i>Luxilus zonistius</i>	L_ZONI	0.016	0.9187	-0.820	<0.0001
<i>Micropterus salmoides</i>	M_SALM	-0.200	0.2089	0.210	0.1886
<i>Minytrema melanops</i>	M_MELA	-0.100	0.5345	0.195	0.2228
<i>Nocomis leptocephalus</i>	N_LEPT	-0.227	0.1530	-0.700	<0.0001
<i>Notropis baileyi</i>	N_BAIL	-0.184	0.2482	-0.319	0.0418
<i>Notropis longirostris</i>	N_LONG	0.099	0.5389	-0.508	0.0007
<i>Notropis texanus</i>	N_TEXA	-0.203	0.2023	0.390	0.0160
<i>Percina nigrofasciata</i>	P_NIGF	-0.036	0.8216	-0.271	0.0865
<i>Pomoxis nigromaculatus</i>	P_NIGM	0.098	0.5425	0.371	0.1710
<i>Semotilus atromaculatus</i>	S_ATRO	-0.098	0.5404	-0.543	0.0002

Significant correlations and associated p values are shown in bold.

negatively associated with Axis 2 ($R^2 = 0.38$, $p < 0.001$; $R^2 = 0.36$, $p < 0.0001$, respectively, Table 7), whereas % DELT was positively associated with this axis ($R^2 = 0.22$, $p = 0.0023$).

Discussion

Our results provide correlative evidence that watershed urbanization and the concomitant reduction in forest cover may exert strong negative impacts on stream fish assemblages. These data corroborate earlier findings of stream fish studies in other urbanizing areas of the United States (e.g., Weaver and Garman, 1994; Wang *et al.*, 2000; Walters *et al.*, 2003a). In other studies, impacts of urbanization often manifest as decreased richness, diversity, sensitive species, and fish health as well as increased tolerant and introduced species (Roth *et al.*, 1996; Wang *et al.* 2000). We observed many of these same patterns in west Georgia streams. Fish health (as indicated by the % DELT), the proportion of fish in environmentally sensitive breeding guilds (% lithophilic spawners), and measures

of fish biotic integrity (IBI values, Bray-Curtis similarity scores) all generally signaled a decline in fish assemblages with increasing watershed urbanization (Table 5). Proportions of tolerant fish species increased with increasing watershed pastureland, however, somewhat surprisingly, this variable was unassociated with watershed urbanization.

Seasonality of fish response

The purported mechanisms of declines in fish health and assemblage structure in urbanized streams often stem from altered physicochemical and hydrologic conditions (Booth and Jackson, 1997; Sutherland *et al.*, 2002; Schoonover *et al.*, 2005). We suspect alterations of the hydrograph (i.e., increased flashiness and attendant increases in bed shear stress) in urbanized and developing watersheds, and increased sedimentation in the pasture-dominated watersheds, are important drivers of fish assemblage structure in west Georgia streams. Several anticipated relationships were not observed, however, such as decreasing species richness and diversity with increasing urbanization. Although difficult to reconcile, it is tempting to suggest that this disparity results from relatively high abundance of cosmopolitan fish species in our study streams, possibly resulting from a combination of biogeography and an extended history of human landscape alteration in the region (Smith, 1981; Hilliard, 1984; Swift *et al.*, 1986; Feminella, 2000).

We observed considerable seasonal variation in the importance of watershed land use versus natural basin variables on fish assemblages. Whereas 2 fish variables (% DELT, IBI) showed consistent relationships with land use in every season (Table 6), relationships between land use/natural basin attributes and virtually all other fish variables were inconsistent across seasons. Perhaps most indicative of urban impact was the strong, seasonally invariant relationship between % Urban and the % of fish with eroded fins, lesions, and tumors. Moreover, land use both as high % urban cover and % pasture was particularly important in terms of low IBI values in summer, a time when streams are at baseflow, and dissolved nutrients, pathogenic bacteria, and other contaminants may reach highest annual concentrations (Schoonover *et al.* 2005).

In contrast, the higher relative importance of natural basin variables on fish assemblages in winter and spring may result from a combination of a decreased influence of factors linked with urbanization (e.g., reduced chemical toxicity during times when discharge is high and streamwater concentrations are low and fish are metabolically less active), and an attendant increase in importance of hydrological or geomorphological factors that structure fish assemblages by physical means (e.g., high shear stress during peak discharge, availability of refugia). Precipitation and discharge is typically highest during winter and spring in our streams (B. Helms, unpublished data). Hence naturally larger basins or those with altered hydrographs from substantial landscape change, such as in high urban watersheds, may show higher peak discharges and greater physical disturbance to fish and other biota (Shaw, 1988; Booth *et al.*, 2002). Taken together, our data suggest that in addition to quantifying remote landscape features it is necessary to consider the importance of local geomorphic factors that may influence the degree to which changes in landscape conditions can exert strong effects on stream biota (Process Domain Concept, *sensu* Montgomery, 1999; see also Walters *et al.*, 2003b).

Impervious surface and fish response

Somewhat surprisingly, use of % impervious surface at a finer scale of resolution (i.e., 1-m, cf 30-m spatial data) did not improve relationships between urbanization and fish assemblage structure, as several variables were unassociated with this measure (Table 6). Watershed imperviousness has been considered a good indicator of urbanization and has been implicated as a main driver in urban stream degradation (Schueler, 1994; McMahon and Cuffney, 2000; Walsh, 2000; Paul and Meyer, 2001; Walsh *et al.*, 2004). Degradation typically occurs at low watershed imperviousness (10–15%, Schueler, 1994; Wang *et al.*, 2000), a level close to average imperviousness in our watersheds (~8%, Table 3). At least 2 explanations for this equivocal pattern exist. First, whereas we selected sites that spanned a wide range of imperviousness overall (0 to 37%), impervious surface in all but 3 watersheds (BU1, BU2, RC, Table 1) was <10%, including our 3 developing sites (SB1, SB2, SB4, Table 1). Thus it is possible that generally low correspondence between fish variables and impervious surface in simple regression models may have resulted, at least in part, from a lack of intermediate levels of impervious surface watersheds in our data set. Developing watersheds were primarily selected based on active development, rather than proportion of impervious surface. Thus, from a spatial perspective and in terms of impervious surface and forest cover, developing watersheds appeared more like forested than urban watersheds. Second, recent studies suggest that total impervious surface may not reflect an accurate hydrologic connection between watershed imperviousness and actual runoff delivered to streams (Brabec *et al.*, 2002; Walsh *et al.*, in press). If true for our watersheds, then imperviousness, while relatively simple to quantify from remotely sensed imagery, may be a less useful measure of the linkage between landscape alteration and stream structure and function. However, fish assemblages in developing watersheds, in general, were more similar to urban watersheds than forested watersheds (figure 2). Taken together, these data suggest that impervious surface, while a reliably persistent component of the urban environment, is not the sole force governing fish assemblages in these watersheds. Our multiple regression models suggested that fishes in these watersheds are responding not to a single landscape factor or driver, but rather a complex suite of anthropogenic, basin, stream, and seasonality influences.

Urbanization and fish assemblage structure

There was a strong shift in fish assemblage structure along our urbanization gradient, a result reported from other systems (Weaver and Garman, 1994; Walters *et al.*, 2003a). Clear separation existed between assemblages in urban/developing streams and those from forested watersheds, which was largely evident by differences in proportions of centrarchid species (figure 2). Centrarchids in our streams, primarily including *Lepomis auritus*, *L. macrochirus*, *L. cyanellus*, and *Micropterus salmoides*, are generally tolerant species that often are numerical dominants in disturbed habitats (Karr, 1981; Weaver and Garman, 1994). Also locally abundant in our urban sites and curiously scarce in other streams was the weed shiner, *N. texanus*. This coastal plains minnow was rarely found outside of the urban streams, yet its low abundance in streams from forested watersheds likely resulted

more from these watersheds being at the periphery of this species' range (Boschung and Mayden, 2004). The bluefin stoneroller (*C. pauciradii*) also was abundant in urban streams. Species in *Campostoma* are herbivores as adults and can readily consume large turfs of filamentous algae (Power and Matthews, 1983). Thus, the predominance of *C. pauciradii* in urban sites may be a combination of its tolerance of physicochemical extremes and this species' capacity to consume abundant algae resulting from high $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ levels in these streams (Schoonover *et al.*, 2005, B. Helms, unpublished data).

Abundance of lithophilic spawners was clearly related to urbanization, being prevalent in forested watersheds and comparatively scarce in urban watersheds. This pattern was largely driven by abundances of the bluehead chub (*N. leptocephalus*), bandfin shiner (*L. zonistius*), and the longnose minnow (*N. longirostris*). Other fish associated with the less-urbanized sites were the rough shiner (*N. baileyi*), creek chub (*S. atromaculatus*), and the filter-feeding Southern brook lamprey (*Ichthyomyzon gagei*). Some of these species patterns may reflect interspecific associations as well as differential environment tolerance. For example, during spawning male bluehead chubs create, maintain, and guard gravel-mound nests where females deposit eggs, and males tolerate nest associates such as bandfin shiners and rough shiners (Johnston and Birkhead, 1988). Bluehead chub and bandfin shiner abundances were highly correlated in our study ($r = 0.684$, $p < 0.0001$). It is unknown if nest association between bluehead chubs and bandfin shiners is obligatory or facultative (Johnston and Birkhead, 1988). If the association is facultative, then each species may respond to stresses of urbanization independently. However, if nest association between species is obligatory, then absence of bluehead chubs from urbanized streams will likely govern bandfin shiner abundance. Further, subtle changes in stream abiotic conditions (e.g. initial changes associated with urbanization) could alter the reproductive behavior of these fishes and increase the currently benign impact of introduced nest associates like *N. baileyi* on *L. zonistius* (Herrington and Popp, 2004). Such indirect effects of urbanization on the dynamics of fish assemblages are largely unknown but may be potentially far-reaching.

In summary, our results suggest urban land use in general, but not solely in terms of the proportion of impervious surface, was a strong determinant of fish assemblage structure. Moreover, fish assemblages showing clear signs of deteriorating health were consistently observed in urban and developing streams, so urban land use appears to exert a stronger influence on fish assemblages than watersheds predominantly in agricultural or silvicultural land use. Our results also demonstrate that streams with relatively low levels of species endemism also can display dramatic shifts in assemblages in response to urbanization similar to systems with high endemism (Walters *et al.*, 2003a). However, increases in the magnitude of urbanization are likely to increase dramatically in the future (Cohen, 2003), so to understand the responses of fish assemblages it may be necessary to investigate the complex interplay among several environmental factors including land use, seasonality, stream geomorphology and hydrology, and biotic interactions.

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