American Fisheries Society Symposium 47:409–423, 2005

Fish Assemblage Responses to Urban Intensity Gradients in Contrasting Metropolitan Areas: Birmingham, Alabama and Boston, Massachusetts

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Abstract.—We examined fish assemblage responses to urban intensity gradients in two contrasting metropolitan areas: Birmingham, Alabama (BIR) and Boston, Massachusetts (BOS). Urbanization was quantified by using an urban intensity index (UII) that included multiple stream buffers and basin land uses, human population density, and road density variables. We evaluated fish assemblage responses by using species richness metrics and detrended correspondence analyses (DCA). Fish species richness metrics included total fish species richness, and percentages of endemic species richness, alien species, and fluvial specialist species. Fish species richness decreased significantly with increasing urbanization in BIR ($r = -0.82$, $P = 0.001$) and BOS ($r = -0.48$, $P = 0.008$). Percentages of endemic species richness decreased significantly with increasing urbanization only in BIR ($r = -0.71$, $P = 0.001$), whereas percentages of fluvial specialist species decreased significantly with increasing urbanization only in BOS ($r = -0.56$, $P = 0.002$). Our DCA results for BIR indicate that highly urbanized fish assemblages are composed primarily of largescale stoneroller *Campostoma oligolepis*, largemouth bass *Micropterus salmoides*, and creek chub *Semotilus atromaculatus*, whereas the highly urbanized fish assemblages in BOS are dominated by yellow perch *Perca flavescens*, bluegill *Lepomis macrochirus*, yellow bullhead *Ameiurus natalis*, largemouth bass, pumpkinseed *L. gibbosus*, brown bullhead *A. nebulosus*, and redfin pickerel *Esox americanus*. Differences in fish assemblage responses to urbanization between the two areas appear to be related to differences in nutrient enrichment, habitat alterations, and invasive species. Because species richness can increase or decrease with increasing urbanization, a general response model is not applicable. Instead, response models based on species' life histories, behavior, and autecologies offer greater potential for understanding fish assemblage responses to urbanization.

Introduction

Fish assemblage responses to urbanization have been less studied than those of other stream biota, particularly invertebrates (Paul and Meyer 2001). However, much is known about the negative effects of urbanization on fish assemblages. Urban streams have been reported to support fish assemblages that are functionally less diverse than nonurban streams (Weaver and Garman 1994; May et al. 1997). In addition, stream reaches above or below urban areas are vulnerable to invasion by alien fish species (DeVivo 1996). Urbanization also is associated with increases in tolerant species and the decline of sensitive species (Onorato et al. 2000; Wang et al. 2000; Scott and Helfman 2001).

Despite our understanding of fish assemblage responses to urbanization, a general response model does not exist (Paul and Meyer 2001). Studies of the

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effects of urbanization on stream fish assemblages have included examining multiple sites along single streams (e.g., Matthews and Gelwick 1990; Weaver and Garman 1994; Kemp and Spotila 1997) and analysis of multiple streams in an ecoregion (e.g., Steedman 1988; Wang et al. 2000, 2001; Snyder et al. 2003). Few examinations have been made of fish assemblage responses to urbanization in contrasting ecoregions and zoogeographic areas (Paul and Meyer 2001).

A nationally applicable understanding of fish assemblage responses to urbanization is challenged by the need to simplify the complexity of urban influences on stream biota. Urbanization is a complex environmental gradient that can serve as a framework for assessing effects of urban influences on ecosystems (McDonnell and Pickett 1990). Understanding urbanization effects is complicated by multiple approaches for quantifying ecosystem effects and urbanization (e.g., human population density, urban land use, percentage of impervious surface). Although most studies of the effects of urbanization on stream biota have been based on single measures of urban influences, Yoder et al. (1999) noted that interpretations of ecosystem effects varied with the measures used.

In 2000, the U.S. Geological Survey's National Water-Quality Assessment (NAWQA) Program initiated a series of studies that used a common design to examine the effects of urbanization on aquatic biota in major metropolitan areas (Tate et al. 2005, this volume). The goal of our study was to examine fish assemblage responses to urban gradients in two of these study areas—Birmingham, Alabama (BIR) and Boston, Massachusetts (BOS), which represent different ecoregions, zoogeographic regions, and urban-development histories. Specific objectives were to (1) determine relations between various measures of fish species richness and an urban intensity index (UII, Tate et al. 2005), (2) identify fish assemblages associated with the most and least disturbed sites along a gradient of urbanization, (3) compare fish assemblage responses between the two urban areas, and (4) relate these responses to existing stressor-response models.

Study Areas

To reduce potential sources of natural variation within each study area, the BIR sites were located within the Ridge and Valley ecoregion in Alabama (Omernik 1987). The BOS sites were located within the Northeastern Coastal Zone ecoregion in Maine, New Hampshire, Massachusetts, and Connecticut (Omernik 1987). Surface waters at the BOS sites were classified according to whether they contained predominantly warmwater fish species, coldwater fish species, or a mixture of both (Flanagan et al. 1999). The geographical distinction between cold- and warmwater fisheries closely follows the distinction between the colder-water streams of the Northeastern Highlands and the warmer-water streams of the Northeastern Coastal Zone ecoregions.

In addition to ecoregion differences, the two study areas represent contrasting ichthyogeographic regions. Many factors, including a subtropical climate and freshwater habitat diversity, are combined to make the Mobile River basin, where the BIR study area is located, one of the most diverse natural faunistic regions in North America. Mettee et al. (1996) reported 404 fish species for the state of Alabama and Mobile River basin tributaries in adjacent states. Within Alabama's Ridge and Valley ecoregion alone (the BIR study area), there are about 117 fish species, of which 25 are endemic (Mettee et al. 1996). In contrast, the native fish fauna in the BOS study area is species poor because freshwater habitats were limited during glaciation, and physical barriers precluded colonization following glaciation (Halliwell et al. 1999). Of the 51 fish species reported in the Northeastern Coastal Zone, none are considered endemic (Halliwell et al. 1999)

The BOS study area has more alien fish species compared to the BIR study area, reflecting the longer period of urban development in BOS relative to BIR. Urban development in BIR dates to the late 1800s and is related to industrial development of agricultural land (Lewis 1994). Although urban development in BOS is also related to industrial development of agricultural land, European settlement in BOS dates to the 1600s (Halliwell et al. 1999). Of the 95 fish species introduced into New England (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island; U.S. Geological Survey 2000a), 49 have become established. Many of these introductions occurred prior to 1900, including goldfish *Carassius auratus* in the late 1600s, largemouth bass *Micropterus salmoides* in the mid-1800s, and rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* in the late 1800s (Hartel et al. 2002). The U.S. Geological Survey (2000a) lists 55 fish species introduced into Alabama, and most were introduced after World War II (Mettee et al. 1996). Of these, 18 species are reported to be established (Mettee et al. 1996).

Site Selection

In both study areas, sites were selected from a pool of candidate watersheds representing a gradient from low to high urban intensity. Details about the site-selection process are provided by Tate et al. (2005). Boundaries for the candidate watersheds were delineated using 30-m digital elevation model data in conjunction with geographic information programs (U.S. Geological Survey 2000b), and drainage areas were determined.

Multiple anthropogenic variables describing infrastructure (such as road and housing density), land use, and human population density were normalized by drainage area and used to construct the UII. The UII was formed by standardizing each of the variables so that they ranged from 0 to 1. For each site, a mean of all of the range-standardized variables combined was calculated and then multiplied by 100 to produce an index that ranged from 0 (low urbanization) to 100 (high urbanization). The rationale for, and calculation of, the UII is described in greater detail in McMahon and Cuffney (2000) and Tate et al. (2005).

Candidate sites were visited to assess local stream conditions, such as riparian land use and stream habitat characteristics. This information was used to select sites that represented a gradient from low to high urbanization, while minimizing natural environmental variability and anthropogenic variability that were not directly associated with urbanization, (e.g., agricultural or forestry related activities; Tate et al. 2005). Twenty-one sites were selected in BIR and 30 sites in BOS (Table 1). Sites consisted primarily of 3rd- to 5th-order streams (Short et al. 2005, this volume). In the BIR study area, bed substrates consisted of relatively similar proportions of sand, gravel, and cobble, whereas in the BOS study area, streambed substrate particle size was dominated by cobble-sized particles (Short et al. 2005). The selected sites represented a narrow range in drainage area and elevation and a broad range in population density, percent urban land, and UII (Table 1). Additional information regarding site selection and locations can be found in Tate et al. (2005). Additional information regarding stream habitat characteristics in the study sites can be found in Short et al. (2005).

Methods

We sampled fish in the BIR study area 7–17 May 2001 and in the BOS study area 3 August–5 September 2000. The sampling reach lengths at each site were 20 times the mean wetted channel width, roughly equivalent to one meander wavelength (Fitzpatrick et al. 1998). A sampling distance of at least one meander wavelength is likely to include at least two examples each of two different habitat types (pools, riffles, runs; Leopold et al. 1964). A minimum reach length of 150 m and a maximum reach length of 300 m also were established. Electrofishing a minimum reach length of 150 m in streams less than 4 m wide has been reported to be sufficient to yield accurate and precise estimates of species richness and percentage of abundance (Patton et al. 2000; Reynolds et al. 2003)

We sampled fish with a single backpack electrofisher at 30–60 pulses per second (Meador et al. 1993). Operators of electrofishing equipment received training in the sampling protocol (Meador et al. 1993) and in electrofishing principles, such as power transfer theory, to aid in standardizing the effort and increasing the efficiency of electrofishing operations (Reynolds 1996).

Electrofishing crews usually consisted of four people, all well experienced at electrofishing streams in the respective study areas. All backpack electrofishing was conducted in an upstream direction. Block nets were not used to isolate the sampling area because studies have indicated that using block nets did not improve estimates of species richness or abundance (Vadas and Orth 1993; Simonson and Lyons 1995; Edwards et al. 2003). Fish were removed from the water with dip nets, and upon completion of the first pass, fish that could be identified in the field were counted and transported downstream from the sampling reach. A second pass was then conducted, and the data from each pass were combined. Meador et al. (2003a) indicated that a single backpack electrofishing pass may under represent cyprinids and centrarchids. Fish that could not be identified in the field were

TABLE 1. Site characteristics for streams in the BIR (*N* = 21) and BOS (*N* = 30) study areas.

	BIR			BOS		
	Mean	Range	SD	Mean	Range	SD
Drainage area (km^2)	36.6	6–66	15.2	75.7	46–125	23.2
Elevation (m above mean sea level)	228	163–315	40	115	31–237	59
1999 population density (people/km^2)	340	10–1,543	363	337	25–1,261	359
Developed land (percent)	22.2	0–73.4	19.8	19.5	1.5–66.7	18.9
UII	36.0	1.7–100	26.8	36.4	0–100	30.5

retained for identification and enumeration in the laboratory (Walsh and Meador 1998).

In each study area, we classified fish species as native, endemic, or alien based on Mettee et al. (1996), U.S. Geological Survey (2000a), and Hartel et al. (2002). In addition, we classified all fish species as either fluvial specialists or macrohabitat generalists based on information in Kinsolving and Bain (1993), Mettee et al. (1996), Hartel et al. (2002), and Ipswich River Watershed Association (2002). Fluvial specialists are fish species that generally require flowing-water habitats throughout their lives, though occasionally individuals may be found or stocked in a reservoir or lake. In contrast, macrohabitat generalists are adaptable to a wide variety of habitats and often are found in both lotic and lentic environments.

Data Analysis

Data analysis included a combination of metric and multivariate approaches. The metric approach included total fish species richness, and percentages of richness of endemic species (for BIR only), alien species, and fluvial specialist species. Total fish species richness has been used commonly in bioassessment studies (e.g., Davis and Simon 1995), and alien fish species richness has been shown to be related to increased population density (Meador et al. 2003b). Analysis of fluvial specialist species has been used in both Alabama (Kinsolving and Bain 1993) and New England (e.g., Ipswich River Watershed Association 2002) to assess recovery of fish assemblages along gradients of anthropogenic disturbance. Yoder et al. (1999) suggested that analysis of endemic species richness could lead to improved understanding of fish assemblage responses to urbanization. Percentage calculations were arcsine-square root transformed to improve normality, and we used Pearson correlation analyses to examine relations between species richness metrics and the UII.

Detrended correspondence analysis (DCA, Gauch 1982) was used to quantify fish assemblage structure and identify fish assemblages associated with the most and least disturbed sites in both study areas. Species abundances were log transformed ($\log_{10} x + 1$) and rare species (defined as those occurring in less than 20% of the number of collections as the most frequently occurring species) were downweighted in proportion to their frequency.

Ordination techniques, such as DCA, reduce the dimensionality of multivariate data sets while attempting to preserve the structure inherent in the data. The resulting ordination represents the relative differences among sites along derived environmental gradients (DCA axes) where sites with similar compositions are located close together along an axis and sites with very different compositions are located far apart. The primary ordination axis (DCA axis 1) explains the most variation (structure) in the data with each succeeding axis explaining less of the variation. For this study, responses associated with the first two axes of the ordinations (DCA axes 1 and 2) were examined based on the following hypothesis: if urban intensity were an important factor in determining community structure and natural factors had been controlled in the study design, DCA axis 1 should be correlated with measures of urban intensity.

To determine if the primary measure of fish assemblage structure (defined by DCA axis 1) corresponded to urbanization, Pearson correlation analysis was conducted to examine the relation between site scores from DCA axes 1 and 2 and the UII. Assuming that DCA axis-1 site scores represented a gradient of urbanization, whereas DCA axis-2 site scores did not, we wanted to examine the fish assemblages most associated with DCA axis-1 site scores while minimizing associations with nonurban gradients represented by DCA axis-2 site scores. High and low DCA axis-1 site scores were defined by determining the 75th and 25th percentiles of site scores along DCA axis 1, and the mean and standard deviation of DCA axis-2 site scores also were determined. Fish species scores occurring within one standard deviation of DCA axis-2 site scores and greater than the 75th percentile of DCA axis-1 site scores were considered to be high and assumed to represent the fish assemblage most associated with high DCA axis-1 site scores. Similarly, fish species scores occurring within one standard deviation of DCA axis-2 site scores and less than the 25th percentile of DCA axis 1 site scores were considered to be low and assumed to represent the fish assemblage most associated with low DCA axis-1 site scores.

To test that the site-selection process limited natural variation related to drainage area and elevation, Pearson correlation analyses were conducted to examine relations between species richness metrics and log-transformed ($\log_{10} x$) drainage area and elevation. Pearson correlation analysis also was conducted to examine relations between DCA axis-1 and 2 site scores and log-transformed drainage area and elevation. An assessment of relations between fish assemblage measures and urbanization independent of stream-size effects (drainage area and elevation) is desired because fish assemblage composition often is correlated with stream size (Smogor and Angermeier 1999).

To compare linear relations between species richness and urbanization for the two study areas, analysis of covariance (ANCOVA) was conducted by using the model species richness = UII + study area + (UII x study area).

This ANCOVA model fits separate linear regressions of species richness and urbanization for each of the study areas. This linear model assumes that within a study area, species richness varies with urbanization at a constant rate—the slope of the regression line. The inclusion of the interaction term, however, allows the slope to vary between study areas. A significance level of 0.05 was used for all statistical tests.

Locally weighted regression smoothing (LOESS) of data scatter plots was conducted to examine nonlinear patterns in relations between species richness and urbanization. Patterns based on LOESS smoothing were compared to patterns in relations between species richness and stressors based on three response models. Carlisle et al. (2003) provided an example of a dose–response relation, based on a negative, nonlinear response of species richness to a chemical stressor (dose–response model, Figure 1A). Such a response curve illustrates resistance and exhaustion components (Selye 1973). Using data from Ohio, Yoder et al. (1999) suggested a negative, nearly linear fish species richness response to urbanization consisting of three components: (1) loss of endemic species, (2) loss of additional species primarily as a result of habitat degradation, and (3) continued loss of fish species richness as a result of toxicity and organic enrichment (Ohio model, Figure 1B). Scott and Helfman (2001) provided a response model for the southeastern United States, which indicated that habitat destruction associated with anthropogenic activity can result in simultaneous loss of endemic species and an increase in species richness as a result of exploitation of the altered habitat by native and alien invasive species (habitat-disturbance model, Figure 1C).

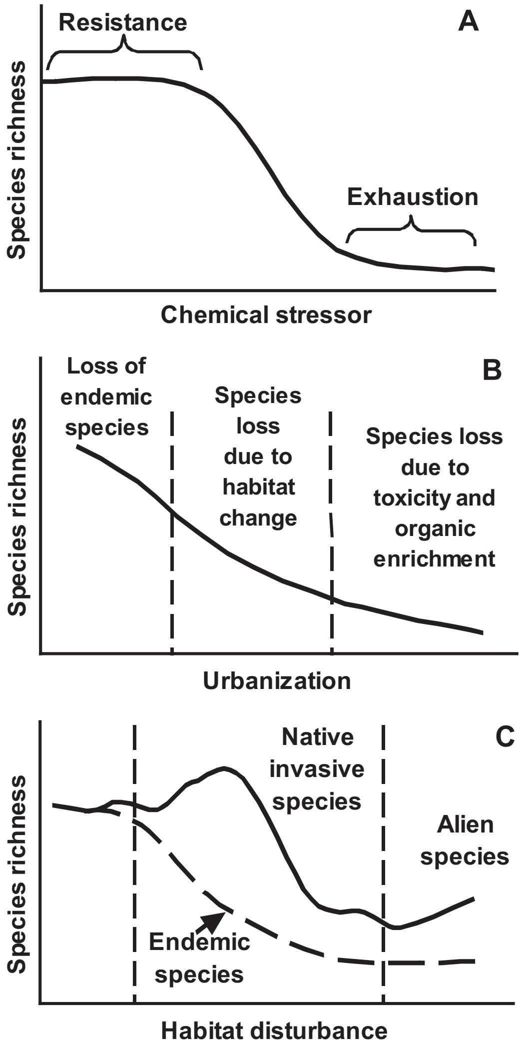

FIGURE 1. Examples of three stressor-response models based on species richness: (A) dose–response model (Carlisle et al. 2003); (B) Ohio model, based on data from Yoder et al. (1999); and (C) habitat-disturbance model (Scott and Helfman 2001).

Results

BIR Study Area

A total of 48 species representing 5,625 fish individuals was collected in the BIR study area (Appendix A; data collected as part of the NAWQA Program can be accessed at http://water.usgs.gov/nawqa/). Species richness per site ranged from 6 to 26 (mean = 15). Overall, the most abundant species was largescale stoneroller *Campostoma oligolepis*, representing 64.5% of the total individuals collected. Two other species represented greater than 5% of the total abundance—longear sunfish *Lepomis megalotis* (11.3%) and western mosquitofish *Gambusia affinis* (5.5%). Two species, largescale stoneroller and bluegill *L. macrochirus*, were collected at all 21 sites. Five additional species were collected at greater than 50% of the 21 sites: green sunfish *L. cyanellus* (95.2%), longear sunfish (95.2%), Alabama hog sucker *Hypentelium etowanum* (90.5%), blackbanded darter *Percina nigrofasciata* (57.1%), and banded sculpin *Cottus carolinae* (52.4%). No alien species were collected. Nine of the species collected are endemic to the BIR study area: Alabama darter *Etheostoma ramseyi*, Alabama shiner *Cyprinella callistia*, burrhead shiner *Notropis asperifrons*, Coosa darter *E. coosae*, Coosa shiner *N. xaenocephalus*, greenbreast darter *E. jordani*, Mobile logperch *P. kathae*, riffle minnow *Phenacobius catostomus*, and tricolor shiner *C. trichroistia* (Appendix A).

The UII was significantly negatively related to species richness ($r = -0.82$, $P = 0.001$) and percentage of endemic species richness ($r = -0.71$, $P = 0.001$). The UII was not significantly related to the percentage of fluvial specialist species richness ($r = -0.41$, $P = 0.064$). Drainage area was not significantly related to species richness ($r = 0.40$, $P = 0.074$), the percentage of endemic species richness ($r = 0.23$, $P = 0.312$), or the percentage of fluvial specialist species richness ($r = 0.41$, $P = 0.066$). Elevation also was not significantly related to species richness ($r = -0.09$, $P = 0.709$), the percentage of endemic species richness ($r = -0.03$, $P = 0.887$), or the percentage of fluvial specialist species richness ($r = 0.32$, $P = 0.162$).

Eigenvalues were 0.26 and 0.14 for the first and second DCA axes, respectively. The UII was significantly related to DCA axis-1 site scores ($r = 0.99$, $P = 0.001$) but not to DCA axis-2 site scores ($r = 0.08$, $P = 0.929$). Three species—largescale stoneroller, largemouth bass, and creek chub *Semotilus atromaculatus*—had high species scores for DCA axis 1 (Figure 2). Seven species—Alabama darter, Alabama shiner, spotted sunfish *L. punctatus*, tricolor shiner, speckled darter *E. stigmaeum*, Mobile logperch, and warmouth *L. gulosus*—had low species scores for DCA axis 1 (Figure 3). Drainage area was not significantly related to DCA axis-1 site scores ($r = -0.28$, $P = 0.220$) or DCA axis-2 site scores ($r = 0.08$, $P = 0.719$). Elevation also was not significantly related to DCA axis-1 site scores ($r = 0.34$, $P = 0.136$) or DCA axis-2 site scores ($r = -0.32$, $P = 0.133$).

BOS Study Area

A total of 29 fish species representing 6,431 individuals was collected in the BOS study area (Appendix B). Overall, six species accounted for greater than 5% of the total abundance—fallfish *S. corporalis* (18.8%), common shiner *Luxilus cornutus* (17.2%), white sucker *Catostomus commersoni* (11.9%), blacknose dace *Rhinichthys atratulus* (10.9%), longnose dace *R. cataractae* (8.6%), and bluegill (6.2%). Seven species were collected at greater than 50% of the 30 sites sampled—white sucker (89.7%), pumpkinseed *L. gibbosus* (86.2%), American eel *Anguilla rostrata* (75.9%), fallfish (72.4%), largemouth bass (58.6%), bluegill (55.2%), and chain pickerel *Esox niger* (55.2%). Nine species are considered alien—black crappie *Pomoxis nigromaculatus*, bluegill, brown trout, green sunfish, largemouth bass, margined madtom *Noturus insignis*, rainbow trout, smallmouth bass *M. dolomieu*, and yellow bullhead *Ameiurus natalis*. Atlantic salmon *Salmo salar*, once native but extirpated, have been reintroduced into New England.

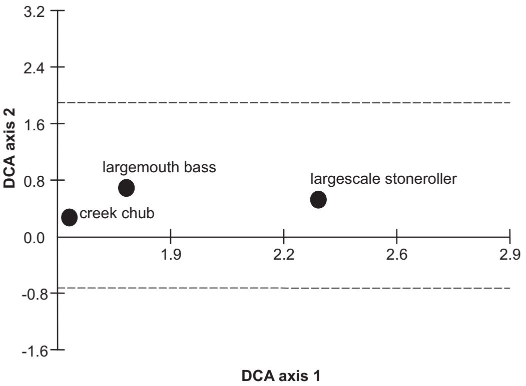

FIGURE 2. Plot of BIR fish species scores greater than the 75th percentile of DCA axis-1 site scores and within one standard deviation of DCA axis-2 site scores. Dashed line represents bounds of one standard deviation of DCA axis-2 site scores. Fish species within these bounds can be considered tolerant of urbanization.

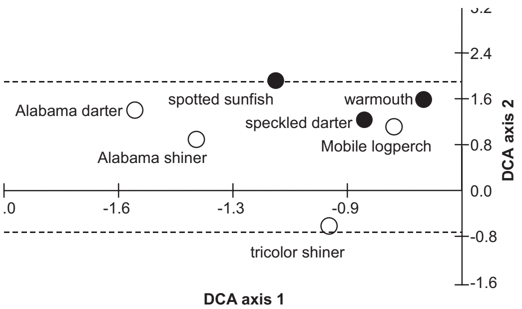

FIGURE 3. Plot of BIR fish species scores less than the 25th percentile of DCA axis-1 site scores and within one standard deviation of DCA axis-2 site scores. Dashed line represents bounds of one standard deviation of DCA axis-2 site scores. Open circles indicate species identified as endemic (Mettee et al. 1996). Fish species within these bounds can be considered intolerant of urbanization.

The UII was significantly negatively related to species richness ($r = -0.48$, $P = 0.008$) and percentage of fluvial specialist species richness ($r = -0.56$, $P = 0.002$), but was not significantly related to the percentage of alien species richness ($r = 0.07$, $P = 0.446$). Drainage area was not significantly related to species richness ($r = -0.06$, $P = 0.772$), the percentage of alien species richness ($r = 0.19$, $P = 0.306$), or the percentage of fluvial specialist species richness ($r = 0.32$, $P = 0.089$). Elevation was not significantly related to species richness ($r = 0.33$, $P = 0.079$), the percentage of alien species richness ($r = 0.24$, $P = 0.214$), or the percentage of fluvial specialist species richness ($r = 0.31$, $P = 0.096$).

Eigenvalues were 0.43 and 0.17 for the first and second DCA axes, respectively. The UII was significantly related to DCA axis-1 site scores ($r = 0.73$, $P = 0.001$), but was not significantly related to DCA axis-2 site scores ($r = 0.23$, $P = 0.237$). Seven species—yellow perch *Perca flavescens*, bluegill, yellow bullhead, largemouth bass, pumpkinseed, brown bullhead *A. nebulosus*, and redfin pickerel *Esox americanus*—had high DCA axis-1 species scores (Figure 4). Nine species—common shiner, blacknose dace, longnose dace, sea lamprey *Petromyzon marinus*, brook trout *Salvelinus fontinalis*, white sucker, swamp darter *E. fusiforme,* fallfish, and creek chubsucker *Erimyzon oblongus*—had low DCA axis-1 species scores (Figure 5). Drainage area was not significantly related to DCA axis-1 site scores ($r = 0.27$, $P = 0.157$) or DCA axis-2 site scores ($r = -0.11$, $P = 0.575$). Elevation was also not significantly related to DCA axis-1 site scores ($r = -0.32$, $P = 0.080$) or DCA axis-2 site scores ($r = -0.01$, $P = 0.976$).

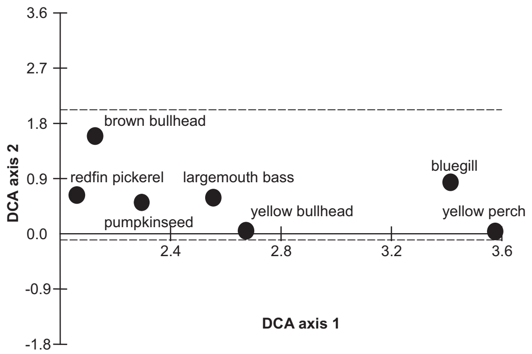

FIGURE 4. Plot of BOS fish species scores greater than the 75th percentile of DCA axis-1 site scores and within one standard deviation of DCA axis-2 site scores. Dashed line represents bounds of one standard deviation of DCA axis-2 site scores. Fish species within these bounds can be considered tolerant of urbanization.

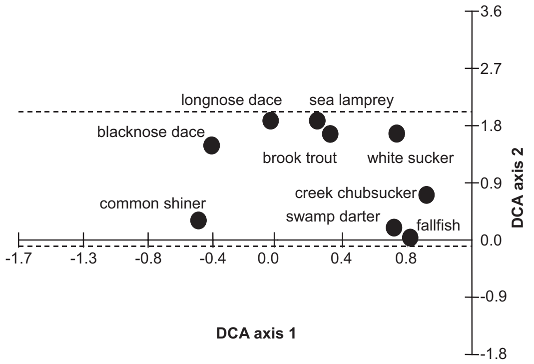

FIGURE 5. Plot of BOS fish species scores less than the 25th percentile of DCA axis-1 site scores and within one standard deviation of DCA axis-2 site scores. Dashed line represents bounds of one standard deviation of DCA axis-2 site scores. Fish species within these bounds can be considered intolerant of urbanization. All species except swamp darter are considered fluvial specialists.

Combined Analyses

The full ANCOVA model of fish species richness, UII values, and study area was significant ($P = 0.001$), and the UII by study area interaction term in the model also was significant ($P = 0.004$, Table 2). The scatter plot of the relations between fish species richness and the UII for both study areas indicates possible variation in relations between species richness and UII scores less than 50 compared to scores greater than 50 (Figure 6). In addition, of the 19 BOS sites with UII values less than 50, 9 sites had relatively low species richness values (BOS1<50), whereas 10 sites had relatively high species richness values for the same UII scores (BOS2<50).

A total of 18 species were collected from all sites in the BOS1<50 group. Overall, six species accounted for greater than 5% of the total abundance for this group (3,450) and included common shiner (23.8%), fallfish (23.5%), blacknose dace (15.3%), longnose dace (12.9%), white sucker (11.7%), and margined madtom (6.4%). A total of 25 species were collected from all sites in the BOS2<50 group. Overall, eight species accounted for greater than 5% of the total abundance for this group (1,650) and included common shiner (17.5%), fallfish (17.2%), blacknose dace (9.7%), white sucker (8.9%), Atlantic salmon (8.5%), bluegill (8.1%), longnose dace (6.5%), and redbreast sunfish *L. auritus* (6.2%). Eight species were collected in the BOS2 < 50 that were not collected in the BOS1<50, including black crappie, green sunfish, rainbow trout, redfin pickerel, sea lamprey, smallmouth

TABLE 2. Analysis of covariance models of fish species richness with the urban intensity index (UII), study area, and the interaction of the UII and study area. The BIR and BOS study areas were divided into five groups—BIR UII values < 50 (BIR<50), BOS with relatively low species richness and UII values < 50 (BOS1<50), BOS with relatively high species richness and UII values < 50 (BOS2<50), BIR UII values > 50 (BIR>50), and BOS UII values > 50 (BOS>50).

Model	Model *P*-value	UII *P*-value	Study area *P*-value	UII × study area *P*-value
BIR, BOS	0.001	0.001	0.001	0.004
BIR < 50, BOS1 < 50, BOS2 < 50	0.001	0.001	0.001	0.099
BIR > 50, BOS > 50	0.607	0.307	0.595	0.620

bass, swamp darter, and tessellated darter *E. olmstedi*. Of these, black crappie, green sunfish, and smallmouth bass are alien species and macrohabitat generalists; rainbow trout is an alien species and fluvial specialist, whereas swamp darter is a native macrohabitat generalist.

An ANCOVA was conducted on species richness data for sites with UII values less than 50 for three groups—BIR<50, BOS1<50, and BOS2<50. The full ANCOVA model was significant (P = 0.001) and the UII by study area (group) interaction term in the model was not significant (P = 0.099, Table 2). An ANCOVA was also conducted for UII values greater than 50 on species richness data for the BIR>50 and BOS>50. For these sites, the full ANCOVA model was not significant (P = 0.607, Table 2).

Locally weighted regression smoothing plots for the BIR UII scores illustrate a negative, nearly linear pattern with total species richness and with endemic species richness, particularly for UII values less than 75 (Figure 7A). In contrast, LOESS plots for the BOS UII suggested a nonlinear pattern with total species richness, indicating periodic increases and decreases in species richness (Figure 7B). The corresponding LOESS plot of BOS UII values and fluvial specialist richness indicates that, following an initial decline, the

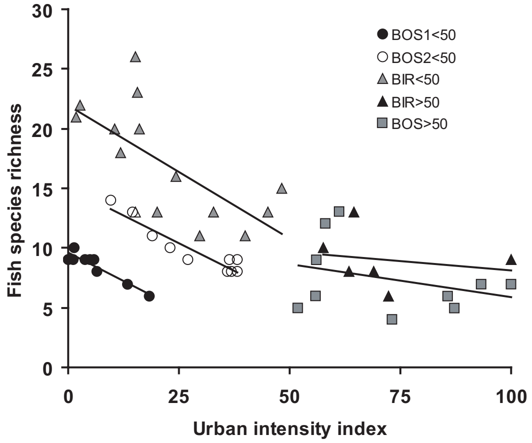

FIGURE 6. Scatter plot showing relations between fish species richness and UII values for five groups: BIR < 50, BOS1<50, BOS2<50, BIR>50, and BOS>50. See Table 2 for group definitions. Lines represent linear trends.

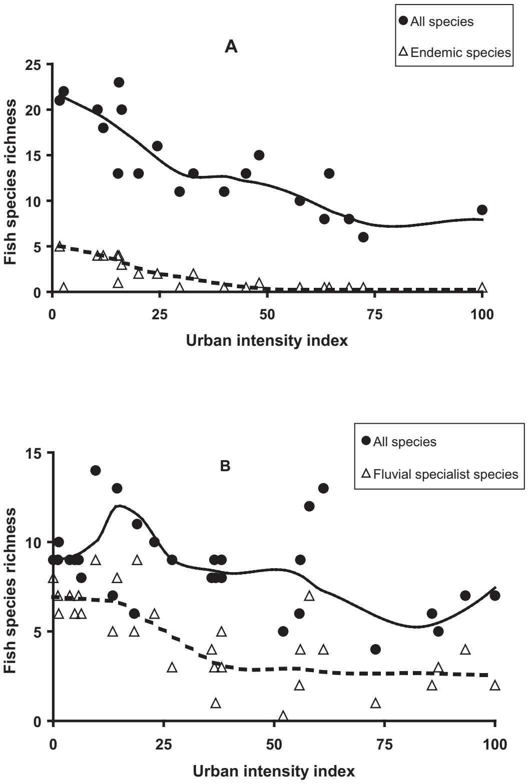

FIGURE 7. LOESS plots of relations between fish species richness, endemic species richness, and richness of fluvial specialist species, and the UII for the BIR (A) and the BOS (B) study areas.

number of fluvial specialist species remained relatively stable for UII scores greater than 40.

Discussion

Species richness decreases with increasing urbanization in the BIR and BOS study areas, similar to results reported elsewhere (Onorato et al. 2000; Wang et al. 2000; Paul and Meyer 2001). In our study, species richness measures are not related to drainage area or elevation, suggesting that variability related to these factors is limited along the gradients of urbanization.

In BIR, the decline in species richness related to increasing urbanization appears to result from a decline in endemic species richness. Similar findings were reported by Walters et al. (2005, this volume) in the Etowah River basin, Georgia. Endemic species tend to be prone to extinction because of their small geographic ranges and specific habitat requirements (Meffe and Carroll 1997). In a study of the upper Cahaba River system in Alabama, Onorato et al. (2000) reported that the decline of Alabama shiner and tricolor shiner, endemic species that require silt-free substrates for crevice spawning, may be attributed to siltation associated with urban development.

In the BOS study area, which lacks endemic species, the decline in species richness appears to be a function of the loss of fluvial specialists. Similar results have been reported for the Ipswich River, Massachusetts (Armstrong et al. 2001). As noted by Halliwell et al. (1999), many coldwater, flowing habitats in the northeastern United States were degraded by the mid-1800s by the construction of small mill dams and canals, many of which still exist. Thus, historical alterations to hydrology and habitat combined with present-day alterations of flow (Armstrong et al. 2001), which are related to increased urbanization, may explain the decline in fluvial specialists in the BOS study area.

Assessment of the relations between fish assemblages and urbanization based on DCA reveals that eigenvalues for the first DCA axes are relatively low, particularly for the BIR study area. An eigenvalue represents a relative measure of the strength of an axis, the amount of variation along an axis, and ideally, the importance of an ecological gradient. In general, higher eigenvalues for DCA axes are related to higher beta diversities or species turnover along environmental gradients (McCune et al. 2002). Thus, an axis or gradient with relatively low eigenvalues may suggest that some species will be common to both ends of an environmental gradient or that relatively few species are being added along the gradient. Cuffney et al. (2005, this volume) conducted ordination analyses of invertebrate assemblage data for the BIR and BOS study areas and also reported relatively low eigenvalues for DCA. Cuffney et al. (2005) noted that the relatively low eigenvalues may reflect a continual loss of species richness along the urban gradient with little replacement by more adaptable taxa. Similarly, we noted a continual loss of fish species richness along the urban gradient in our study.

Though increasing urbanization is related to changes in fish assemblages in both BIR and BOS, differences occurred in the fish assemblages most strongly associated with urbanization. In the BIR study area, the urban fish assemblage is characterized by three species and dominated by a single species, the largescale stoneroller. Largescale stonerollers tend to congregate in large schools during spawning, typically in April in Alabama (Mettee et al. 1996), a factor that may have contributed to the collection of largescale stonerollers at all 21 sites in the BIR study area. Walters et al. (2005) reported that centrarchids were associated with increasing urbanization in the Etowah River and suggested that centrarchids, classified as macrohabitat generalists, are more resilient to disturbance than other stream fishes. Walters et al. (2005) also suggested that the presence of centrarchids with increasing urbanization in the Etowah River was primarily related to changes in hydrology. One centrarchid species in the BIR study area, the macrohabitat generalist largemouth bass, is associated with increasing urbanization. However, the largescale stoneroller, classified as a fluvial specialist, is an herbivore that can persist in streams chronically stressed both chemically and physically (Mettee et al. 1996).

Extensive urban development in BIR has increased water use and point-source discharges in the upper Cahaba River system (Shepard et al. 1997). During low flow periods, nearly 100% of the flow in the upper Cahaba River is removed for municipal water supply (Onorato et al. 1998). Twenty-six municipal wastewater-treatment plants each discharge secondarily treated water into the upper Cahaba River system (Shepard et al. 1997). Whereas secondarily treated wastewater removes particulate matter and oxygen-consuming wastes, it generally contains elevated nutrient concentrations that contribute to eutrophication. El-Kaddah and Carey (2004) suggest that such point-source discharges may account for significant nitrogen input into the Cahaba River, greater than the input from nonpoint sources. Shepard et al. (1997) reported that biodiversity has decreased in the upper Cahaba River system and that eutrophication may be a contributing factor. Onorato et al. (2000) reported that the largescale stoneroller was collected in a larger percentage of samples from the upper Cahaba River system in 1997 compared to historical records and attributed the increase in this disturbance-tolerant species to the fact that it can persist in streams disturbed by wastewater. Eutrophication provides an abundant source of nutrients to sustain the production of algae consumed by these herbivores.

In contrast to BIR, the urban fish assemblage in BOS consisted of seven macrohabitat generalists. Alterations in hydrology and associated increased water temperature have been suggested as causative factors related to a reduction in the ranges of coldwater fluvial specialists, such as brook trout, and the expansion of ranges of warmer-water macrohabitat generalists, such as redfin pickerel, in the Ipswich River basin (Armstrong et al. 2001). Increased urbanization and concomitant increased water withdrawals for public water supply have increased the severity and duration of low flows in streams in the Ipswich River basin (Armstrong et al. 2001). These authors determined that groundwater withdrawals, wastewater transfers, and land-use alterations that increase impervious areas combined to result in flow reductions of more than 90% in the upper Ipswich River. These hydrological alterations result in lower base flows, which support streamflow between precipitation events. Diminished base flows during the summer will likely result in warmer water temperatures because when cool inflow is reduced, the reduced volume of water in the river heats more rapidly. In addition to increases in stream temperature caused by direct heating of reduced volumes of streamflow, groundwater withdrawals can cause the loss of coldwater springs that provide important areas of refuge during low-flow periods.

Analysis of covariance of fish species richness indicates that the linear rate of species-richness decrease with increasing urbanization varied between the relatively species-rich BIR and the comparatively species-poor BOS. Further examination of the data reveals two distinct patterns in the relation between species richness and urbanization in the BOS study area for UII values less than 50. The greater number of species in the BOS2<50 compared with the BOS1<50 resulted from the addition of alien species and native macrohabitat generalists, such as black crappie, green sunfish, and smallmouth bass. Thus, even at relatively low levels of urbanization, increases in species richness were noted in the BOS study area.

When the data were divided into groups based on urban intensity, ANCOVA indicates that linear patterns in responses of fish species richness to urbanization are similar between the BIR and BOS study areas. ANCOVA indicates that for relatively low UII values, slopes of relations between fish species richness and UII values do not vary significantly among the BIR study area and the two groups of BOS sites. These results indicate that despite the addition of species at some BOS sites at relatively low levels of urbanization, the linear rate of species loss is similar. Results of the ANCOVA also indicate that at UII values greater than 50, there is insignificant loss of species richness with increased urbanization for BIR and BOS.

Examination of patterns in LOESS plots indicates differences in relations between species richness and urbanization for BIR and BOS compared to species-richness stressor models. In the BIR study area, the response appeared to be nearly linear, similar to the response using the Ohio model. Although there was no evidence to suggest a resistance response, as suggested by the dose–response model, there appeared to be an exhaustion response.

In contrast, patterns in LOESS plots suggest a nonlinear response in relations between species richness and urbanization in BOS. This nonlinear response suggests periodic decreases and increases in species richness. This pattern is similar to that of the habitat-disturbance model, a model developed for the species-rich southeastern United States. Patterns in responses of total species richness and the number of fluvial specialist species indicate resistance. An exhaustion response is evident in the relation between fluvial specialist richness and urbanization. An exhaustion response in the relation between total species richness and urbanization is not as clear and follows the proposed slight increase in species richness as indicated by the habitat-disturbance model.

Despite contrasts in ecoregions and ichthyogeographic regions, similarities exist in the responses of fish assemblages to urbanization in BIR and BOS. In both study areas, species richness declined, and the rate of species decline was similar regardless of large-scale differences (BIR and BOS) or smaller-scale differences (groups within the BOS study area) in relations between species richness and urbanization. In both study areas, declines in total species richness were associated with declines of species expected to be sensitive to urbanization—endemic species in BIR and fluvial specialists in BOS.

Although increased urbanization in both study areas may be related to changes associated with altered hydrology, increased urbanization results in different fish assemblage structures in the BIR and BOS. These differences appear to be the result of differences in native invasive and alien species between the two study areas, resulting in periodic increased species richness with increasing urbanization. Increased species richness can result from the addition of alien species and because of tolerant, generalist, native species that can invade from downstream areas (Scott and Helfman 2001). This increase in species richness is likely a function predominantly of physical habitat changes that provide more suitable conditions for new species. An absence of habitat changes or the presence of increased chemical toxicity and organic enrichment at high levels of urbanization may prohibit the addition of new species.

Differences noted in fish assemblage responses may be the result of differences in urban-development histories between the two study areas. Understanding the effects of urban influences on ecosystems can often be complicated by factors including antecedent land use (e.g., urbanization of agricultural areas as opposed to urbanization of forested land). Harding et al. (1998) noted the importance of antecedent land use as a determinant for understanding the effects of human influences on stream fishes. Whereas a multimetric UII may provide a better understanding of the effects of urbanization on stream biota compared to single-dimension measures of spatial variation in urban influences, a better understanding of temporal aspects of urban influences is needed.

Because species richness can increase or decrease with increasing urbanization, depending on factors such as physical and chemical alterations associated with urbanization, the presence of alien species, and the ability of tolerant native species to invade altered habitats, a single general-response model of fish species richness to urbanization may not be broadly applicable. Whereas the Ohio model may describe species richness responses to urbanization in the BIR study area, the habitat-disturbance model appears to be more applicable in the BOS study area. However, response models based on total species richness may be misleading because aquatic ecosystem integrity can degrade despite increases in species richness (Scott and Helfman 2001). Thus, developing response models based on life history and behavioral and ecological requirements may provide a better understanding of fish assemblage responses to urbanization than approaches using total species richness.

Acknowledgments

We thank the biologists, hydrologists, and technicians, too numerous to name individually, who collected data as part of the NAWQA Program. This study was conducted as part of ecological synthesis through the NAWQA Program.

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APPENDIX A. Scientific and common names of fish collected in the BIR study area. (^{E} indicates species identified as endemic [Mettee et al. 1996]; ^{FS} indicates species identified as fluvial specialists; ^{MG} indicates species identified as macrohabitat generalists [Kinsolving and Bain 1993; Mettee et al. 1996]. Scientific names follow Robins et al. [1991]).

Family	Scientific name	Common name
Petromyzontidae	*Ichthyomyzon gagei*	southern brook lamprey^{FS}
Cyprinidae	*Campostoma oligolepis*	largescale stoneroller^{FS}
	Cyprinella callistia	Alabama shiner$^{E, FS}$
	C. trichroistia	tricolor shiner$^{E, FS}$
	C. venusta	blacktail shiner^{MG}
	Luxilus chrysocephalus	striped shiner^{FS}
	Lythrurus bellus	pretty shiner^{FS}
	Notropis asperifrons	burrhead shiner$^{E, FS}$
	N. chrosomus	rainbow shiner^{FS}
	N. stilbius	silverstripe shiner^{FS}
	N. xaenocephalus	Coosa shiner$^{E, FS}$
	Phenacobius catostomus	riffle minnow$^{E, FS}$
	Semotilus atromaculatus	creek chub^{MG}
Catostomidae	*Hypentelium etowanum*	Alabama hog sucker^{FS}
	Minytrema melanops	spotted sucker^{MG}
	Moxostoma duquesnei	black redhorse^{MG}
	M. erythrurum	golden redhorse^{MG}
	M. poecilurum	blacktail redhorse^{MG}
Ictaluridae	*Ameiurus natalis*	yellow bullhead^{MG}
	Ictalurus punctatus	channel catfish^{MG}
	Noturus leptacanthus	speckled madtom^{FS}
Esocidae	*Esox niger*	chain pickerel^{MG}
Fundulidae	*Fundulus olivaceus*	blackspotted topminnow^{MG}
	F. stellifer	southern studfish^{FS}
Poeciliidae	*Gambusia affinis*	western mosquitofish^{MG}
Cottidae	*Cottus carolinae*	banded sculpin^{FS}
Centrarchidae	*Ambloplites ariommus*	shadow bass^{FS}
	Lepomis auritus	redbreast sunfish^{MG}
	L. cyanellus	green sunfish^{MG}
	L. gulosus	warmouth^{MG}
	L. macrochirus	bluegill^{MG}
	L. megalotis	longear sunfish^{MG}
	L. microlophus	redear sunfish^{MG}
	L. miniatus	redspotted sunfish^{MG}
	L. punctatus	spotted sunfish^{MG}
	Micropterus coosae	redeye bass^{FS}
	M. punctulatus	spotted bass^{MG}
	M. salmoides	largemouth bass^{MG}
	Pomoxis nigromaculatus	black crappie^{MG}
Percidae	*Etheostoma coosae*	Coosa darter$^{E, FS}$
	E. jordani	greenbreast darter$^{E, FS}$
	E. ramseyi	Alabama darter$^{E, FS}$
	E. stigmaeum	speckled darter^{FS}
	E. swaini	Gulf darter^{FS}
	E. whipplei	redfin darter^{FS}
	Percina caprodes	logperch^{FS}
	P. kathae	Mobile logperch$^{E, FS}$
	P. nigrofasciata	blackbanded darter^{FS}

APPENDIX B. Scientific and common names of fish collected in the BOS study area. (^{A} indicates fish species identified as alien [Hartel et al. 2002]; ^{FS} indicates species identified as fluvial specialists; ^{MG} indicates species identified as macrohabitat generalists [Hartel et al. 2002; Ipswich River Watershed Association 2002]. Atlantic salmon, once native but extirpated, have been reintroduced into New England. Scientific names follow Robins et al. [1991]).

Family	Scientific name	Common name
Petromyzontidae	*Petromyzon marinus*	sea lamprey^{FS}
Anguillidae	*Anguilla rostrata*	American eel^{FS}
Cyprinidae	*Luxilus cornutus*	common shiner^{FS}
	Notemigonus crysoleucas	golden shiner^{MG}
	Notropis hudsonius	spottail shiner^{MG}
	Rhinichthys atratulus	eastern blacknose dace^{FS}
	R. cataractae	longnose dace^{FS}
	Semotilus corporalis	fallfish^{FS}
Catostomidae	*Catostomus commersonii*	white sucker^{FS}
	Erimyzon oblongus	creek chubsucker^{FS}
Ictaluridae	*Ameiurus natalis*	yellow bullhead$^{A, MG}$
	A. nebulosus	brown bullhead^{MG}
	Noturus insignis	margined madtom$^{A, FS}$
Esocidae	*Esox americanus*	redfin pickerel^{MG}
	E. niger	chain pickerel^{MG}
Salmonidae	*Oncorhynchus mykiss*	rainbow trout$^{A, FS}$
	Salmo salar	Atlantic salmon^{FS}
	S. trutta	brown trout$^{A, FS}$
	Salvelinus fontinalis	brook trout^{FS}
Centrarchidae	*Lepomis auritus*	redbreast sunfish^{MG}
	L. cyanellus	green sunfish$^{A, MG}$
	L. gibbosus	pumpkinseed^{MG}
	L. macrochirus	bluegill$^{A, MG}$
	Micropterus dolomieu	smallmouth bass$^{A, MG}$
	M. salmoides	largemouth bass$^{A, MG}$
	Pomoxis nigromaculatus	black crappie$^{A, MG}$
Percidae	*Etheostoma fusiforme*	swamp darter^{MG}
	E. olmstedi	tessellated darter^{FS}
	Perca flavescens	yellow perch^{MG}