INFLUENCE OF GEOMORPHOLOGY AND URBAN LAND COVER ON STREAM FISH ASSEMBLAGES IN THE ETOWAH RIVER BASIN, GEORGIA

by

DAVID MATT WALTERS

(Under the Direction of Gene S. Helfman)

ABSTRACT

The Etowah River basin supports a diverse and imperiled fish assemblage increasingly threatened by urbanization. I quantified relationships between fishes, geomorphology, and urbanization in 32 wadeable Piedmont streams in basins of 11-126 km^2. I developed an Index of Biotic Integrity (IBI) using six fish metrics that tracked changes in habitat quality. Low quality sites had more tolerant fishes and higher centrarchid richness, but fewer darter, sculpin, and insectivorous cyprinid species and lower richness and density. IBI scores were positively correlated with basin forested land cover, indicating that biotic integrity was highest in streams draining least-disturbed catchments. A separate multivariate statistical analysis identified strong patterns in species composition that were highly correlated with stream geomorphology. Species composition in these streams shifted from centrarchids and other pool species to darters, cyprinids, and redhorse suckers that are riffle-run, benthic species. Richness and density were correlated with stream size, but species composition was correlated with reach-level variation in stream slope and related benthic habitat variables that were independent of stream size. These findings contrast with a prediction of the River Continuum Concept that species composition varies predictably along stream size gradients. My results support the Process Domain Concept that local geomorphic processes determine stream habitats and disturbance regimes that influence assemblage structure. Urbanization altered the relationships between geomorphology and fishes. After accounting for the effects of stream size and slope, richness, density, darters and sculpin, cyprinids, and endemic species declined with urban land cover, whereas centrarchids persisted and became the dominant species group. Residual analysis indicated that effects were greatest for streams with > 15% urbanization. Most of the development occurred since 1987, suggesting that fishes respond rapidly to urbanization. Urbanization appeared to homogenize fish assemblages by altering stream sediment regimes. Homogenization, quantified as the ratios of Endemic to Cosmopolitan species richness (E_r:C_r) and abundance (E_a:C_a), was associated with high baseflow turbidity and finer beds. Urban land cover positively correlated with baseflow turbidity, and urbanized sites had finer beds and riffles than predicted by stream slope. Baseflow turbidity was the best indicator of urban impacts because it was statistically independent from slope.

INDEX WORDS: Etowah River, Geomorphology, Urbanization, Fish Assemblages, Sedimentation, Homogenization, Turbidity, Stream Ecology, Index of Biotic Integrity, IBI, Indicators

INFLUENCE OF GEOMORPHOLOGY AND URBAN LAND COVER ON STREAM FISH ASSEMBLAGES IN THE ETOWAH RIVER BASIN, GEORGIA

by

DAVID MATT WALTERS

A.B., The University of Georgia, 1991

M.S., The University of Georgia, 1997

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2002

INFLUENCE OF GEOMORPHOLOGY AND URBAN LAND COVER ON STREAM FISH ASSEMBLAGES IN THE ETOWAH RIVER BASIN, GEORGIA

by

DAVID MATT WALTERS

Approved:

Major Professor:	Gene S. Helfman
Committee:	Mary C Freeman David S. Leigh Byron J. Freeman Amy D. Rosemond C. Ronald Caroll

Electronic Version Approved:

Gordhan L. Patel
Dean of the Graduate Scholl
The University of Georgia
August 2002

DEDICATION

For Trish O’Brien

ACKNOWLEDGMENTS

Although the dissertation represents an individual effort, none would be completed without a tremendous amount of assistance. First, it requires money. My research was funded by an Science To Achieve Results grant from the United States Environmental Protection Agency (U.S. EPA STAR grant #R826597-01-0), support from The University of Georgia (UGA) Research Foundation and Museum of Natural History, and a University-Wide scholarship from UGA. I also received travel money from the Graduate School and the Institute of Ecology to present my research at several meetings.

I want to thank my committee (Gene Helfman, David Leigh, Mary Freeman, Bud Freeman, and Amy Rosemond) for their suggestions, support, ideas, and comments. In particular, I want to thank Mary Freeman and David Leigh for challenging me to think about streams and fishes from many perspectives. I never would have sorted through the data without their help and creative input. I owe Bud Freeman a huge debt of gratitude for transforming an archaeologist into an ichthyologist/stream ecologist. I also thank Cathy Pringle for her help in improving several of the chapters in this dissertation.

Most importantly, I had the support of family and an amazing network of friends. My parents offered unflagging support, no matter how long I was a student. My siblings, Gene, Tina, and Mike, made great sport of my student “career”, but also shared their pride with me. My best friend, Brian Gregory, got me interested in the program in the beginning and kept me going along the way. Kevin Barnes helped everyway imaginable. My good friends, Jamie, Jon, Sarah, Jim, Joel, Kathy, Heidi, Wendi, Jon, Sara, Rob,

Wyatt, Dewitt, and Corn provided both support and distraction. Jamie and Jon, having just been through the process, were invaluable. Most of all, I thank my wife Trish for nourishing my body, mind, and spirit. I may have made it without her, but the journey would have been boring at best.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

"...the fluvial system as a whole cannot be ignored, even though only a component of the system is to be studied."

S.A. Schumm

A major goal of stream ecology is to identify environmental gradients structuring lotic communities (Minshall 1988, Power et al. 1988). My dissertation focuses on linkages among stream fish assemblages, geomorphology, and catchment land use. Stream geomorphology forms the habitat template for streams and exerts strong controls on local stream assemblages (sensu Southwood 1977). However, ecologists and geomorphologists recognize that processes operating at larger spatial scales influence local stream conditions (Hynes 1975, Schumm 1985, Frissell et al. 1986). Human disturbance of catchments may affect stream habitats and their associated communities by altering the delivery of sediment and water, organic matter inputs, and chemical compounds from the landscape and by altering stream temperature and light regimes. These environmental changes may profoundly affect stream ecosystems and aquatic biota, and predicting the impact of human disturbance on streams is a critical research agenda (Allan and Flecker 1993, Hunsaker and Levine 1995, Poff 1997).

Over the past century, urbanization has become a pervasive form of environmental disturbance that threatens aquatic systems around the world

(Baer and Pringle 2000). Basin urbanization causes major changes in stream hydrology, geomorphology, water quality, and stream communities (Baer and Pringle 2000 and Paul and Meyer 2001). Degradation of stream ecosystems is detectable at low levels of urban land cover, and the impact of urbanization is more severe than other land uses such as agriculture or forestry (Paul and Meyer 2001). Basin urbanization negatively impacts stream fishes and has been associated with declines in fish richness, diversity, density, and biotic integrity (Paul and Meyer 2001). However, the effects of urbanization on southern Piedmont streams are not well documented except for a few studies that were spatially limited (Lenat and Crawford 1994, Couch et al. 1995, DeVivo et al. 1997). In addition, the mediating effects of geomorphology on lotic community responses to changes in land use are poorly understood.

I conducted this study of tributaries in the Etowah River basin in northern Georgia as part of a team of scientists who also collected much of the data contained herein. This research was funded by a "Science To Achieve Results" grant from the United States Environmental Protection Agency (USEPA STAR grant #R826597-01-0). The Etowah basin is in the Southern Appalachian Highlands, a region with the highest levels of temperate freshwater fish diversity and endemism in the world (Warren and Burr 1994, Lydeard and Mayden 1995). Even compared with neighboring river basins, the Etowah is exceptional in regard to both fish diversity and endemism. Burkhead et al. (1997) estimated that the Etowah originally had 91 native species. Four of these species are endemic to the Etowah basin alone, and 11 species are endemic to highland streams of the larger Alabama River basin. This unique and highly imperiled ichthyofauna is in the midst of decline, and Burkhead et al. (1997) estimate that 9 of 17 imperiled fishes have been extirpated from the Etowah system.

Urbanization poses the greatest current threat to the Etowah fishes. The Etowah is located just north of metropolitan Atlanta, one of the fastest growing regions of the country (U.S. Department of Agriculture 2000). Several of the counties in the study area are currently experiencing exponential population growth that began around 1980 (U.S. Census Office 1930-2000). Consequently, large areas of the basin formerly covered by forests or pastures are currently urbanizing. Mounting development and population pressure led the conservation group American Rivers to list the Etowah and Alabama river systems among the nation's most endangered rivers for 1996 and 1999 (American Rivers 2001). This dissertation should provide timely information for conservation groups and management agencies concerned with protecting the region's unique aquatic fauna.

My dissertation research is guided by two general hypotheses. First, stream geomorphology influences local habitat and fish assemblage structure. Second, catchment urbanization alters relationships between geomorphology and fishes leading to predictable changes in fish assemblage structure. The spread of urban development into relatively rural catchments presents a unique opportunity to test these hypotheses. Forests remain the dominant land cover of many Etowah sub-basins, so I was able to assess urban effects along a gradient of urban land use. Most studies of urbanization effects on fishes have been limited to gradients in single streams or comparisons between urban and reference catchments (Paul and Meyer 2001). Multicatchment investigations of urban gradients and fishes have focused mostly on agricultural-dominated areas of the upper Midwest (e.g., Steedman 1988; Wang et al. 1997, Wang et al. 2000), and comparable studies are lacking for the Piedmont.

Scope of study

In Chapter 2, I develop an Index of Biotic Integrity (IBI) designed to measure general impairment of wadeable Piedmont streams in the Etowah basin. The IBI is a multimetric bioassessment tool designed to detect human impacts to streams based on changes in the structure and function of fish communities (Fausch et al. 1984, Karr et al. 1986). Originally designed to assess fish assemblages in small Midwestern streams of the USA, the IBI has been modified for river systems around the globe. However, fish indices are lacking for the Etowah basin or nearby rivers with similar fish assemblages. In a novel use of the IBI, I modified it to assess past levels of biotic integrity using historic collection records. These records often document thorough collection efforts, but lack the quantitative catch data needed to calculate all IBI metrics (Steedman 1988). Historic data are useful for determining past (e.g., prior to urban development) conditions, and may improve our ability to predict future impacts related to land use change.

In Chapter 3, I investigated the linkages between fishes and geomorphology to identify predictive geomorphic variables and to test conceptual models of fish assemblage structure in small, warmwater streams. Assemblage-level studies commonly use one or a few geomorphic variables selected *a priori* (e.g., Schlosser 1982, Rahel and Hubert 1991, Lyons 1996), but few have modeled fish assemblage properties with a broad spectrum of quantified geomorphic variables. This study uses data from a comprehensive geomorphic survey to identify predictive geomorphic variables without *a priori* assumptions.

Fish assemblage structure in temperate streams frequently is attributed to longitudinal changes in stream geomorphology (e.g., Schlosser 1982, Rahel and Hubert 1991, Paller 1994). Schlosser (1987) developed a conceptual model for fishes in warmwater streams. According to this model, upstream reaches are dominated by small-bodied invertivorous species such as darters and minnows, whereas downstream assemblages tend to be comprised of larger bodied species (e.g., sunfishes and suckers) with more piscivores and generalized carnivores. The model relied heavily on data from annual streams in the Midwest and it is unclear if the model is appropriate for perennial streams in warmer southern climates.

Schlosser's model (Schlosser 1987) generally confirms a prediction of the River Continuum Concept (RCC, Vannote et al. 1980) that stream assemblages vary predictably along a stream-size gradient. Montgomery (1999) challenged this prediction with the publication of the Process Domain Concept (PDC). Montgomery (1999) argued that local-scale (i.e., valley segment and channel reach) geomorphic processes govern stream habitat and disturbance regimes that influence assemblage composition. My results will provide a test of the PDC, which, in contrast to the RCC, appears to lack widespread recognition in the field of lotic community ecology.

In Chapter 4, I investigate effects of urban development on stream fishes while accounting for geomorphic influences identified in Chapter 3. Other urban gradient studies have shown that urbanization leads to declines in fish richness and biotic integrity (Steedman 1988, Wang et al. 1997, Wang et al. 2000), but have not quantified changes in assemblage structure (e.g., species composition). Likewise, urban gradient studies seldom account for the possible confounding influence of local geomorphic variation when reporting direct associations between urbanization and fish variables (e.g., Wang et al. 1997).

Other important aspects of predicting urban effects on stream ecosystems include the relative importance of different types and phases of urban development. Urbanization in the southern Piedmont is a combination of low-density (i.e., residential development) and high-density (i.e., commercial and industrial development) urban land cover, but the relative impacts of these land uses is unknown. Additionally, it is unclear if fish assemblages respond to disturbance during the initial development phase (e.g., increased sediment loading) or to the chronic, long-term effects of increased urban cover (e.g., altered hydrology and poor water quality).

In Chapter 5, I explore the relationships between urbanization, sedimentation, and homogenization of fish assemblages. Homogenization (the replacement of regionally distinctive, often endemic, fauna by widespread invasive species) is a common outcome of habitat degradation (Vitousek et al. 1996, McKinney and Lockwood 1999). Homogenization of stream fishes has received little attention, but Scott and Helfman (2001) showed that human disturbance of riparian zones was related to homogenized assemblages in two Highland basins of the Blue Ridge. To my knowledge, quantitative assessments of the effects of urbanization on fish homogenization are nonexistent.

In this study, I address two questions: 1) Do ratios of endemic to cosmopolitan fishes decline with increasing turbidity and finer stream beds; and 2) Are increasing turbidity and finer stream beds associated with higher levels of urbanization? These questions build on some of the results from Chapters 3 and 4. Most of the Etowah endemics are benthic specialists. In Chapter 3, I found a strong positive correlation between the relative abundance of benthic fishes and bed particle size. In Chapter 4, I found that several measures of endemic abundance declined with urban land cover. The causes of this decline were unidentified, but it is likely that changes in stream sediment regime play a role. Urbanization substantially increases stream sediment inputs through upland erosion and increased bank scour (Wolman 1967). These changes should favor cosmopolitan fishes adapted to lowland river systems that often have higher turbidities and finer stream beds compared to upland streams. I expect cosmopolitans will increase relative to endemics under these habitat conditions, thus homogenizing fish assemblages at the reach scale and reducing regional diversity in the Piedmont portion of the Etowah system.

Together these studies should improve our understanding of factors structuring fish assemblages in highland streams and improve our ability to conserve aquatic biodiversity in the Southern Appalachian Highlands. Drainages of the Highlands have two common characteristics; they have exceptional levels of temperate freshwater fish diversity and endemism, and they have endured over a century of large-scale human disturbance. Prior to the current development boom, the Etowah experienced widespread gold mining, clearing of native forests, and intensive row-crop agriculture (Leigh 1994, Burkhead et al. 1997). Although as many as nine species are extirpated from the system, remnant populations of several imperiled and endemic fishes persist (Burkhead et al. 1997). These fishes have endured intensive human disturbance in the past, but this does not ensure their survival in the face of mounting development pressure. This study is designed in part to predict fish assemblage response to this new threat, a critical step in preserving native fishes in an urbanizing landscape.

REFERENCES

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. Bioscience 42:32-43.

American Rivers. 2001. Nation's Most Endangered Rivers. http://americanrivers.org/mostendangered2001/default.htm

Baer, K. E., and C. M. Pringle. 2000. Special problems of urban river conservation: the encroaching megalopis. Pages 381-398 *in* P. J. Boon, B. R. Davis, and G. E. Potts, editors. Global Perspectives on River Conservation. John Wiley & Sons Ltd., London, U.K.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled Southern Appalachian ecosystem. Pages 375-444 *in* G. W. Benz and D. E. Collins, editors. Aquatic Fauna in Peril, the Southeastern Perspective. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Couch, C. A., J. C. DeVivo, and B. J. Freeman. 1995. What fish live in the streams of Metropolotan Atlanta? Fact Sheet FS-091-95, U.S. Geological Survey. National Water-Quality Assessment Program, Atlanta, Georgia.

Devivo, J. C., C. A. Couch, and B. J. Freeman. 1997. Use of a preliminary index of biotic integrity in urban streams around Atlanta, Georgia. Pages 40-43 *in* K. J. Hatcher, editor. 1997 Georgia Water Resources Conference. Institute of Ecology, University of Georgia, Athens, GA., University of Georgia, Athens, Georgia.

Fausch, K. D., J. R. Karr, and P. R. Yant. 1984. Regional applications of an index of biotic integrity based on stream fish communities. Transactions of the American Fisheries Society 113:39-55.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Hunsaker, C. T., and D. A. Levine. 1995. Hierarchical approaches to the study of water quality in rivers. Bioscience 45:193-203.

Hynes, H. N. B. 1975. The stream and its valley. Internationale Vereinigung fur theoretische und angewandte Limnologie Verhandlungen 19:1-15.

Karr, J. R., K. D. Fausch, P. L. Angermeir, P.R.Yant, and I.J.Schlosser. 1986. Assessing biological integrity in running waters: a method and its rational. Illinois Natural History Survey Special Publications No. 5, Champaign, Ill.

Leigh, D. S. 1994. Gold mining's impact on north Georgia floodplains: mercury contamination and floodplain sedimentation. Pages 215-224 *in* R. A. Marston and V. R. Hasfurther, editors. Effects of human induced change on hydrological systems. Proceedings of AWRA 1994 Summer Symposium.

Lenat, D. R., and J. K. Crawford. 1994. Effects of land-use on water-quality and aquatic biota of 3 North-Carolina Piedmont Streams. Hydrobiologia 294:185-199.

Lydeard, C., and R. L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeast United States. Conservation Biology 9:800-805.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45:329-341.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14:450-453.

Minshall, G. W. 1988. Stream ecosystem theory: a global perspective. Journal of the North American Benthological Society 7:263-288.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association **35**:397-410.

Paller, M. H. 1994. Relationships between Fish Assemblage Structure and Stream Order in South-Carolina Coastal-Plain Streams. Transactions of the American Fisheries Society 123:150-161.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333-365.

Poff, N. L. 1997. Landscape filters and species traits: toward more mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391-409.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Mathews, P. B. Moyle, B. Stazner, and I. R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7:456-479.

Rahel, F. J., and W. A. Hubert. 1991. Fish Assemblages and Habitat Gradients in a Rocky-Mountain Great-Plains Stream - Biotic Zonation and Additive Patterns of Community Change. Transactions of the American Fisheries Society 120:319-332.

Schlosser, I. J. 1982. Fish Community Structure and Function Along 2 Habitat Gradients in a Headwater Stream. Ecological Monographs 52:395-414.

Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Oklahoma.

Schumm, S. A. 1985. Patterns of alluvial rivers. Annual Review of Earth Planet Sciences 13:5-27.

Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26:6-15.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? - Presidential-Address to British-Ecological-Society, 5 January 1977. Journal of Animal Ecology 46:337-365.

Steedman, R. J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. Canadian Journal of Fish and Aquatic Sciences 45:492-501.

U.S. Department of Agriculture. 2000. 1997 National Resource Inventory. Percent Change in Developed Land Area. http://www.nhq.nrcs.usda.gov/land/meta/m5010.html

U.S. Census Office. 1930-2000. Census of the United States. Department of the Interior, Washington, D. C.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468-478.

Wang, L. Z., J. Lyons, P. Kanehl, R. Bannerman, and E. Emmons. 2000. Watershed urbanization and changes in fish communities in southeastern Wisconsin streams. Journal of the American Water Resources Association 36:1173-1189.

Wang, L. Z., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22:6-12.

Warren, M. L., Jr., and B. M. Burr. 1994. Status of freshwater fishes in the United States: overview of an imperiled fauna. Fisheries 19:6-18.

Wolman, M. G. 1967. A cycle of sedimentation and erosion in urban river channels. Geographiska Annaler 49:385-395.

CHAPTER 2

AN INDEX OF BIOTIC INTEGRITY (IBI) TO ASSESS CURRENT AND HISTORICAL FISH ASSEMBLAGES IN A SOUTHERN PIEDMONT RIVER SYSTEM, USA[1]

---

[1] Walters, D.M, M.C. Freeman, B.J. Freeman, D.S. Leigh, M.J. Paul, C.M. Pringle, S. Wenger. To be submitted to *Environmental Monitoring*

Abstract: We developed an IBI to assess recent and historic fish assemblages in a diverse, urbanizing catchment in Southeastern USA. The U.S. EPA Rapid Habitat Assessment Protocol (RHAP) was used to validate metrics and assess the efficacy of the IBI. Low quality sites had more tolerant fishes and higher centrarchid richness, but fewer darter, sculpin, and insectivorous cyprinid species, and lower richness and density. Centrarchid richness is commonly used as a positive indicator in regional IBIs but was negatively correlated ($r = -0.71$) with RHAP in this study. To test the ability of the IBI to assess historical collection data, we calculated a reduced IBI (R-IBI) using those metrics that can be derived using species lists from museum records. IBI and R-IBI covaried strongly ($r = 0.96$) and were highly correlated with RHAP scores ($r = 0.85$ and 0.81, respectively). Catchment forest cover was also significantly correlated with IBI and R-IBI, but was not as predictive as RHAP. The R-IBI detected disturbance at reach and catchment scales, suggesting it will facilitate integration of historic collection data into stream assessments.

INTRODUCTION

The index of biotic integrity (IBI) originally proposed by Karr (1981) has gained widespread use as a tool for assessing the biotic condition of aquatic systems. The IBI is a multimetric assessment protocol designed to detect human impacts based on changes in the structure and function of aquatic communities (Fausch et al. 1984; Karr et al. 1986). Widespread adoption of the IBI in water resource management is largely due to its adaptability. Originally designed to assess fish assemblages in small midwestern streams of the USA, the IBI has since been modified for fish and invertebrate assemblages in a variety of aquatic ecosystems around the globe (Simon and Lyons 1995; Hughes et al. 1998). This paper reports modifications to the IBI to assess stream integrity in a rapidly urbanizing catchment with exceptional fish diversity. We further modify the IBI to test its ability to assess historical collections that lack quantitative catch data.

The Etowah River forms a major arm of the upper Coosa River basin (Mobile River drainage, Figure 2.1). Recent studies (e.g., Burkhead et al. 1997; Warren et al. 2000) have called attention to this region's high level of aquatic diversity and endemism. Burkhead et al. (1997) estimated that the Etowah system originally had 91 native fish species and maintains remnant populations of imperiled fishes that were formerly more widespread in the Mobile River drainage. State and Federal agencies, as well as nongovernmental organizations such as The Nature Conservancy, have prioritized conservation of the Etowah. Portions of the Etowah basin are currently undergoing rapid urbanization associated with the spread of Metropolitan Atlanta. Thus, there is a need for bioassessment tools to evaluate the current condition of regional streams and to monitor the response of fish assemblages to increasing levels of human disturbance.

This study focuses on the portion of the Etowah basin within the Piedmont physiographic province. The Piedmont is a large swath of hilly terrain spanning from southern New York to central Alabama. Generally, the Piedmont extends from the foot of the Appalachian Mountains to the Coastal Plain. Piedmont river systems are biologically significant because they maintain a sizable portion of the notable southeastern fish diversity (Jenkins and Burkhead 1994; Warren et al. 2000). These systems are increasingly threatened by urbanization given that the southern Piedmont is one of the most rapidly developing regions of the United States (USDA 2000). Among Piedmont river systems, the Etowah is exceptional in regard to both fish diversity and rate of urban development and thus is ideally suited to investigate the effects of human disturbance on Piedmont streams.

The primary objective of this paper is to derive an IBI applicable to wadeable streams of the Etowah River basin within the Piedmont physiographic province. The ability of the IBI to reflect human disturbance is directly related to the sensitivity of its component metrics (Smogor and Angermeier 1998b; Karr 1999). In this paper, we use a four-step method modified from Angermeier and Karr (1986), Smogor and Angermeier (1998b), and Karr (1999) to guide metric selection and assess the utility of the final IBI. First, we detail the selection of potential metrics based on the IBI literature and quantitative samples from the study region. Second, we test the validity of metrics by demonstrating empirical relationships between the metrics and stream habitat quality. Third we determine if the metrics contribute useful, interpretable information to the final IBI scores. Finally, we test the utility of the complete IBI as a regional indicator of stream health.

A secondary goal of this paper is to assess the potential of the IBI to evaluate historical fish collection records in the Etowah basin. Historical collections often lack the quantitative catch data needed to calculate all IBI metrics (Steedman 1988). Addition of a long-term temporal component to the analysis of fish assemblage data will enhance our understanding of current stream conditions and potentially improve our ability to predict future outcomes of human disturbance in the Etowah basin. If this method proves effective it could have broad applicability outside of this study region.

METHODS

We employed a stratified random design to select 32 streams in three watershed size groups of approximately 15, 50, and 100 km^2 (+/- 25%) (Figure 2.1). Two sites (Site 3 at 22 km^2 and Site 21 at 126 km^2) slightly exceeded this criterion (Appendix 1). The sites were selected to ensure a wide range of watershed land cover characteristics indicative of different levels of human disturbance (Karr 1999). All sites, except for most heavily urbanized Site 23, fall in the range of 40-95% forest cover, with the remainder primarily as urban and agricultural land (Lo and Yang 2000). Agricultural land cover is primarily pasture for hay production and grazing. Row crop production is a minor component of agricultural land cover in the Piedmont of the Etowah basin, although it was formerly more widespread. All of the stream sites are in the Piedmont, but a few of the catchments have headwaters in the Blue Ridge (Figure 2.1). Site 2 was partially impounded by beavers before we sampled for fishes and was not included in statistical analyses (final $n = 31$).

Fish Collection

We sampled 30 streams in July and August 1999 and two sites (101, 111; Appendix 1) in September 2000. All collections were made at baseflow, and reach length was scaled to approximately 40 times the average baseflow water width within each stream size category (Angermeier and Smogor 1995). Reaches of 200, 300, and 400 meters, were sampled in the 15, 50, and 100 km^2 watersheds, respectively.

We sampled reaches in a single pass (Simon and Lyons 1995) with a crew of four to six persons equipped with a backpack electric shocker, seine, and dipnets. By using a combination of shocking, seine hauling, and dipnetting, all available habitats were thoroughly sampled. Reaches were divided into two sections of equal length. In the first half of the reach, all fishes were anesthetized and preserved except for large fishes > 150 mm standard length and fishes with protected status which were measured and released. The second half of the reach was sampled for additional species. Vouchers for species not observed in the first half were retained. This method allowed us to remove the least number of fishes to assess species abundance while sampling a long enough reach to properly evaluate species richness (Angermeier and Smogor 1995).

Metric Selection and Scoring

We selected metrics for the Etowah fauna based on a study by Miller et al. (1988) (Table 2.1). To assess stream fish communities in the midwestern USA, they used 12 metrics divided into three categories of species richness and composition, trophic composition, and fish abundance and condition. Using this framework, we modified metrics for the Etowah system based on our collections from all 31 sites and expanded or deleted metrics as necessary (Fausch et al. 1984; Karr et al. 1986; Miller et al. 1988). We used ANOVA (Tukey tests, $\propto < 0.05$) to test for the effect of catchment area on potential metrics (Smogor and Angermeier 1998a). Metrics that correlated with catchment area were replaced with similar metrics uncorrelated with stream size or were scored separately within each stream size class (Karr 1981; Karr et al. 1986). From the final set of metrics, we selected a subset of metrics to calculate a reduced IBI (R-IBI). We dropped metrics that required quantitative catch data and only included metrics that could be derived from species lists.

We modified the approach outlined by Minns et al. (1994) for standardizing metric scores. Values were standardized to a scale of 0-10 with the following equations:

$$1)\quad M_S = 10\left(\frac{M_{Observed}}{M_{Max}}\right)$$

$$2)\quad M_S = 10\left(1 - \frac{(M_{Observed} - M_{Min})}{(M_{Max} - M_{Min})}\right)$$

If $M_S < M_{Min}$, then $M_S = M_{Min}$

If $M_S > M_{Max}$, then $M_S = M_{Max}$.

M_S is the standardized metric score and $M_{Observed}$ is the observed metric value. Equation 1 was applied to positive metrics that increase with site quality, and Equation 2 was used on negative metrics that decrease with site quality.

The minimum and maximum thresholds (M_{Min} and M_{Max}) define a floor and ceiling for the standardized metrics. For positive metrics, we set the floor at zero to represent the worst-case scenario (e.g. no fish collected) and the ceiling at the 95th percentile of observed values (Minns et al. 1994). For negative metrics, the floor was the 5th percentile and the ceiling was the 95th percentile (Table 2.1). Metrics with nonnormal distributions were transformed with an arc-sine square root or log transformation to improve normality before setting thresholds. Density and richness were correlated with stream size, so the thresholds were determined separately for each size group. Scores for metrics were summed and scaled to 100 to yield the overall IBI score.

Other researchers have based metric expectations on regional reference sites (Karr 1981; Miller et al. 1988) or historical collection information (Bowen et al. 1996; Hughes et al. 1998). We followed Minns et al. (1994) and used the range of values observed from our collections. We used this technique for two reasons. First, the sites we selected were along a modern disturbance gradient (e.g. urban and agricultural land cover) that included apparent least disturbed catchments with more than 75% forested land cover. Second, historical collections were often qualitative, used different sampling techniques, or varied widely in terms of sampling effort (B.J. Freeman, unpublished data). Given these properties of the historic data, we believe our standardized, quantitative data are better suited for setting metric expectations.

We used the approach of Angermeier and Karr (1986) to analyze the relationships among IBI metrics. First we examined the structure of the metrics' correlation matrix using a principal components analysis (PCA) of the unstandardized metrics. Varimax rotation was used to aid the interpretation of principal components with eigenvalues > 1. Second, we calculated Kendall's *tau*, a nonparametric correlation coefficient, to assess the relationship of standardized metric values to IBI score. This approach was used gauge the relative contribution of each metric to the final IBI score.

Historical Sites

Historical sites were selected from a database of over 700 fish collections maintained by the Georgia Museum of Natural History (B.J. Freeman, unpublished data).

For consistency we selected collection sites on streams draining either 15 or 50 km^2 (+/- 25%) basins in the Piedmont section of the Etowah River basin. All selected sites were sampled between 1989-1999. A total of 55 museum records met these criteria. The final list of sites was trimmed to 23 by eliminating records that represented multiple collections at a single site or records that did not appear to represent a thorough collection effort. We also excluded collections from sites < 1 km from the 31 sites used to calibrate the Etowah IBI. Many of the museum records represent thorough collections and have species lists that document the assemblage at a site but do not include total numbers collected for individual species. We calculated a reduced IBI (R-IBI) for historic samples using four metrics that can be derived using species lists alone.

Stream Quality Assessment

We used the US EPA Rapid Habitat Assessment Protocol (RHAP) to assess stream habitat (Barbour et al. 1999). RHAP uses ten metrics to assess the condition of various stream habitat parameters including benthic habitat quality, channel and bank condition, instream habitat heterogeneity, and riparian vegetation. Each metric is scored on a continuous scale ranging from 0-20 based on a visual assessment of the habitat feature. Metric scores are averaged for an overall RHAP score.

At each site, we assessed habitat metrics over the entire reach sampled for fishes. RHAP was usually calculated the same day as fish sampling and was always evaluated at baseflow to allow comparisons among all sites. Two to four investigators completed RHAP at each site, and final scores were based on the mean of multiple assessments. We used bivariate scatter plots and regression analysis to demonstrate relationships between RHAP and individual metrics, IBI, and R-IBI for sites sampled in this study. We did not calculate RHAP for historical collection sites because current habitat quality at these sites may not reflect habitat quality at the time of the collection.

As a second measure of stream disturbance, we assessed forested land cover within each of the basins. The percentage of land cover was measured for each basin from supervised land cover classifications of Landsat images (Lo and Yang 2000). Forested land cover classes including evergreen, deciduous, and mixed hardwood tree cover categories were combined to make a single variable, % forest. For the 31 sites sampled in 1999 and 2000, we used 1997 land cover data. Watershed land cover for historical collection sites was estimated by averaging forested land cover derived from 1987 and 1997 Landsat images (Lo and Yang 2000) that roughly correspond with the time period for museum records (i.e. 1989-1999). Relationships of % forest to IBI and R-IBI scores were explored using regression analysis.

RESULTS

Sample Collection

We collected 10,628 fishes representing 10 families and 51 species (Appendix 2). One individual *Onchorhynchus mykiss*, an introduced, cold-water species, was collected but was not included in any analyses. Fish abundance ranged from 97-778 individuals per site and density varied from 0.1 – 0.96 fish m^{-2}. Richness ranged from 10 – 30 species per site. Five species, *Campostoma oligolepis, Cyprinella callistia, Hypentelium etowanum, Cottus* sp. cf. *C. carolinae,* and *Percina nigrofasciata,* were the most abundant species and accounted for 53% of the total catch. *C. oligolepis, C. callistia, Semotilus atromaculatus, H. etowanum, Lepomis auritus, L. macrochirus* and *Percina* *nigrofasciata,* were the most frequently collected species and occurred at more than 75% of the sites.

Metric Selection and Properties

The Etowah IBI uses a total of six fish metrics: richness (RIC), percent darter and sculpin species (DAR), percent centrarchid species (CEN), relative abundance of tolerant species (TOL), percent insectivorous cyprinids (INC), and fish density (DEN) (Table 2.1). Five of the metrics included by Miller et al. (1988) were not included in the Etowah IBI. We rarely collected hybrids or fishes that suffered from external anomalies, so neither of these metrics was included. We also removed the number of sucker species because no redhorse suckers, which numerically dominate the Catostomidae in the Etowah catchment, were collected in the smaller streams. The number of intolerant species was not included because objective data regarding intolerance to poor water quality or habitat degradation were lacking for Etowah fishes. Lastly, we removed the relative abundance of top carnivores because all of the fishes in this trophic guild were centrarchids and inclusion of this metric as a positive indicator of stream integrity would have contradicted our interpretation of the centrarchid metric.

Five additional metrics from recent IBI development papers (Hughes et al. 1998; Smogor and Angermeier 1998b; Schleiger 2000) were considered but not used to replace the metrics dropped from Miller et al. (1988). These metrics included the number of benthic species, relative abundance of benthic invertivores, number of introduced species, relative abundance of nonguarding lithophilous spawners, and relative abundance of trophic generalists.

These metrics were not included in the final IBI for a variety of reasons. Both measures of benthic fishes were redundant with DAR. They were highly correlated and most of the species in DAR overlapped with species used to calculate the benthic metrics. The number of introduced species did not apply to the study sites because only one species, rainbow trout (represented by one individual), was definitely introduced into the system. The native status of two other possibly introduced species, *Lepomis auritus* and *Notropis lutipinnis*, is uncertain (Burkhead et al. 1997). The final two metrics were not used because they included species whose observed response to disturbance was the inverse of other species in the guild. For instance, the nonguarding lithophilous spawners typically spawn in coarse gravel, riffle habitat and are presumed to be sensitive to excess sedimentation (Berkman and Rabeni 1987; Hughes et al. 1998). In our samples this guild was numerically dominated by two tolerant taxa, *Hypentelium etowanum* and *Percina nigrofasciata,* that were present and fairly abundant even at highly degraded sites. The trophic generalist metric also mixed species thought to be sensitive to disturbance (i.e. redhorse suckers) with species in our tolerant metric (Appendix 2).

The proportion of *Lepomis cyanellus*, a measure of tolerance, was broadened to include those taxa collected in at least 80% of streams (Appendix 2). Because the study sites reflect a gradient of human disturbance (e.g. urban and agricultural land use), we assumed these ubiquitous species were tolerant to a broad range of human impacts and habitat alteration. *Gambusia affinis*, *G. hobrooki,* and *L. cyanellus* were included in the tolerant category based on other published accounts (Jenkins and Burkhead 1994; Karr et al. 1986; Shields et al. 1995).

Metrics that correlated with stream size (Tukey tests; $\propto = 0.05$) were replaced with similar, uncorrelated metrics or scored to account for the differences (Fausch et al. 1984; Smogor and Angermeier 1998a). The number of sunfish species, number of darter and sculpin species, and relative abundance of insectivorous cyprinids were positively correlated with watershed area and were substituted with proportional metrics (DAR, CEN, and INC; Table 2.1). Species richness, RIC, was positively correlated with watershed area, so metric scores were calculated separately for each catchment size class. The same procedure was followed for fish density, DEN, which was negatively correlated with catchment area.

We followed Smogor and Angermeier (1998b) and Schleiger (2000) in broadening the proportion of darter species to include the one sculpin species, *Cottus* sp. cf. *C. carolinae*, in the system. This species is ecologically similar to most darters in the system and occupies similar habitats. We broadened the sunfish metric to include all members of the family Centrarchidae. Karr et al. (1986) and Miller et al. (1988) included the number of sunfish species in Midwest streams as a positive indicator of quality pool habitat. In contrast, researchers in southeastern stream systems reported that sunfishes tend to increase with declining habitat quality (Jones et al. 1999; Meyer et al. 1999; Walser and Bart 1999). Based on these findings, we reversed the scoring procedure recommended by Karr et al. (1986) for midwestern streams.

Of the six metrics we used, only TOL and DEN required quantitative catch data (Table 2.1). The other four metrics, RIC, DAR, CEN, and INC could be obtained using species lists from historic collections and were used to calculate the R-IBI.

The first two principal components of the correlation matrix accounted for 76% of the variance among the metrics (Table 2.2). The first component (PC I) contrasted sites with high density of fishes and proportion of darter and sculpin species with sites having a higher relative abundance of tolerant fishes and proportion of centrarchid species. PC II was an indicator of species richness and the proportion of insectivorous cyprinid species. A bivariate plot of PC I and PC II (Figure 2.2) illustrated this pattern. Sites with the lowest IBI scores had negative loadings on both axes and plot in the lower left quadrant. Sites with the highest IBI scores occupy the upper right quadrant and had positive scores on both axes.

Tukey tests ($p < 0.05$) indicated that RIC and DEN metrics were related to stream size, and the plot in Figure 2.2 reflected this relationship. Sites in the 15 km^2 group (i.e., numbers 1-10) had higher fish density and lower richness. High-scoring small sites tended to plot near the vector for DEN. Larger sites had greater richness and highest-scoring sites plotted near the vector for RIC. Standardized metrics accounted for the effect of stream size, so final IBI scores were not biased by catchment area.

In the comparison between standardized metrics and overall IBI score, all correlation coefficients were highly significant (Table 2.3). TOL and INC were the most highly correlated with IBI. RIC was the least correlated, indicating that this metric contributed the least amount of information to IBI scores.

Comparisons With Stream Habitat Quality and Forest Cover

Bivariate plots showed that all of the metrics were sensitive to changes in habitat quality (Figure 2.3). RIC and DEN formed distinct right triangles and both increased with RHAP score. Because RIC and DEN are correlated with stream size, the plots showed evidence of stratification. For RIC, the 100 km^2 sites plot along the top with 50 km^2 streams in the middle and 15 km^2 sites form the bottom border. The pattern of stratification was reversed for DEN. Regressions between DEN and RHAP were all significant for individual stream sizes; only the 100 km^2 sites were significant for RIC ($R^2 = 0.69$, $p = 0.003$; Figure 2.3).

The response of the remaining metrics to changes in habitat quality met our assumptions (Figure 2.3). INC and DAR were positively correlated with RHAP. INC were absent from four of the small streams and three of these sites were among the lowest for RHAP scores. CEN and TOL were strongly negatively correlated with RHAP.

Stream RHAP score was a strong predictor of IBI scores ($R^2 = 0.72$, Figure 2.4). Correlation between IBI and R-IBI (Pearson correlation coefficient $r = 0.96$) indicated that the R-IBI retained most of information in the full IBI. R-IBI was positively correlated with RHAP for the 31 sites we sampled for this study, but the amount of variance explained was slightly less than that explained for the full IBI (Figure 2.4). We plotted RHAP by the difference between the two scores ($y = \text{IBI} – \text{R-IBI}$) to determine if the indices scored sites consistently along a habitat quality gradient (Figure 2.5). Most of the values were negative indicating that R-IBI scores were higher than IBI scores. The weak positive trend with RHAP ($R^2 = 0.12$, $p = 0.058$) suggests that R-IBI over prediction was highest at the most degraded sites. This is probably because TOL, which was highest at low quality sites, was not assessed by R-IBI.

Catchment % forest also predicted IBI and R-IBI scores (Figure 2.6) but was not as strong a predictor as RHAP. IBI scores were positively correlated with % forest cover ($R^2 = 0.41$, $p = 0.0007$; Figure 2.6A), and the relationship was nonlinear. R-IBI scores showed a similar trend, but the nonlinearity was more pronounced (Figure 2.6B). This scatter plot indicated that R-IBI scores increased steeply from 40-60% forest cover. IBI scores were highly variable for basins with > 60% forest cover. Separate models for the historic and modern sites (not shown) were similar to the model for all 53 observations. Regressions in Figure 2.6 exclude site 23, the most heavily urbanized and least forested site in the dataset.

DISCUSSION

Characteristics of Metrics

The selection and validation of metrics is a critical but contentious step in IBI development (Minns et al. 1994; Boulton 1999). We followed the procedure of Smogor and Angermeier (1998b) who argued that the validation of metric assumptions requires IBI developers to: 1) assess disturbance in non-IBI terms in their study region; and 2) determine the relationship between each metric and disturbance. This procedure ensures that the resulting IBI is composed of metrics that are both responsive and informative. All of the metrics we used were sensitive to disturbance and responded to disturbance as we predicted. Low quality sites had proportionally fewer darter, sculpin, and insectivorous cyprinid species, lower richness and lower density of fishes. These same sites had higher proportions of centrarchid species and tolerant taxa.

The response of centrarchids to habitat degradation in the Etowah system was contrary to traditional IBI metric scoring assumptions formalized by Smogor and Angermeier (1998b). The number of centrarchids was included in the original IBI by Karr (1981) as a positive indicator of quality pool habitat. The metric is commonly used in regional IBI development (Miller et al. 1988) and was included as a positive indicator for other Piedmont river systems in Georgia (Schleiger 2000).

Our observation that the proportion of centrarchids was inversely related to habitat quality agrees with the results of Jones et al. (1999), Meyer et al. (1999), and Walser and Bart (1999), who showed positive correlations between centrarchids and measures of sediment impairment in five Southeastern river systems. Likewise, Waite and Carpenter (2000) reported a correlation between stream degradation and four introduced centrarchid species in the Willamette River system, Oregon. These findings suggest that centrarchids as a group are tolerant to a broad range of habitat conditions and disturbance regimes and that researchers developing an IBI should carefully consider using measures of centrarchid richness as positive indicators of site quality.

Metrics based on the number of species in certain taxonomic groups are commonly used in IBI development. To account for regional differences in richness and the effects of stream size on candidate metrics, many researchers (e.g. Steedman 1988; Schleiger 2000) use the maximum species richness line technique of Fausch et al. (1984). We used a different approach and substituted proportional richness metrics (DAR, CEN, and INC) for the number of darter and sculpin and sunfish species and the relative abundance of insectivorous cyprinids. Because these metrics were unrelated to stream size, scoring criteria were straightforward, and regression analysis showed that these metrics were sensitive to disturbance.

The proportional species data indicated changes in the fish assemblage that total richness did not detect. Correlation and regression analyses showed that site richness contributed the least amount of information to IBI scores and was only weakly associated with habitat quality. While richness within each stream size group was relatively stable, the species that composed site richness changed along the disturbance gradient. Centrarchids dominated the fish assemblages at low quality sites. At high quality sites, the assemblage shifted to more darter, sculpin, and insectivorous cyprinid species.

IBI properties

The number of metrics needed for an IBI to be a robust predictor of human disturbance is an unresolved issue in IBI development. Our IBI developed for the Etowah basin uses fewer metrics (six) than other published fish IBIs, but showed significant relationships with measures of disturbance. The original IBI (Karr 1981) had twelve metrics, and many regional derivations are comparable (e.g. Steedman 1988; Miller et al. 1988; Hughes et al. 1998). Our six metric Etowah IBI is similar to a seven metric IBI developed by Leonard and Orth (1986) that was capable of discriminating sites impacted by anthropogenic disturbance. Although the final number of metrics was relatively low, the metrics we used met two important criteria. First, they changed predictably along a disturbance gradient. Second, they contributed useful information to the final IBI scores. The end result was a cumulative IBI score that was highly correlated with changes in stream habitat quality.

What are the consequences of using too few metrics in an IBI? Angermeier and Karr (1986) hypothesized that metric sensitivity varies with degradation intensity and the failure to include metrics that respond at the ends of the disturbance spectrum may exclude some biological information. In the hypothetical model of Angermeier and Karr (1986), some metrics have a narrow range of response. For example, the percent of diseased individuals may only be an important factor in streams with relatively high levels of impact (e.g. Leonard and Orth 1986). Similarly, the number of sensitive taxa may decline rapidly at low levels of disturbance.

The range of RHAP scores (i.e. 5.5 – 16.5 out of hypothetical range of 0-20) for these sites indicated that we sampled across a broad disturbance gradient. The metrics that we selected responded across the entire range of habitat quality scores, which is a desirable IBI characteristic (Karr 1999). Based on extensive sampling of streams in the Etowah basin (Walters and B.J. Freeman, unpublished data), we believe that the higher scoring sites have the highest quality habitat available in the system. For this study we did not sample streams that drain high density, long established urban centers, so we may have lost some ability to detect biotic response at the most severely degraded sites. However, the strong correlation between IBI and RHAP suggests that six metrics are adequate to construct a robust measure of biotic integrity that is sensitive to a broad spectrum of habitat decline.

A quality biotic assessment tool should have low variability over time if site condition is stable (Karr et al. 1987). We could not evaluate temporal variability because we developed this IBI using one-time samples; however, several studies have shown that temporal variability of fish assemblages is minor relative to spatial variability. Using multivariate analyses, McCormick et al. (2000) and Waite and Carpenter (2000) documented much higher variability of fish assemblages among sites compared to multiple collections within sites. Temporal variability of IBI scores was also shown to be much lower than spatial variability (Karr et al. 1987; Fore and Karr 1994; Hughes et al. 1998). Hughes et al. (1998) concluded that their IBI was relatively unaffected by short term variability because it was robust to spatial variation, the largest source of variability in their dataset. Likewise, the Etowah IBI tracked spatially variable changes in habitat quality indicating that it is a robust indicator regardless of temporal variation in fish assemblages.

Response of IBI to Disturbance

IBI was highly correlated with disturbance measured at the local and catchment scale. RHAP ($R^2 = 0.72$) was a stronger predictor than basin % forest cover ($R^2 = 0.41$) suggesting that local, reach level variation has greater influence on biotic integrity than landscape level variation. This observation contradicts the findings of Roth et al. (1996) who reported that % forest ($R^2 = 0.479$) was a superior predictor of stream IBI scores compared to a habitat quality index ($R^2 = 0.334$) in the River Raisin basin, Michigan. It is difficult to make direct comparisons with this study because Roth et al. (1996) used a different technique to assess stream habitat, and the upper value in their range of % forest (i.e., 8-27%) corresponded with our lowest value (i.e., 27% forest, site 23).

The correlation between IBI and RHAP was higher than values reported by other studies that linked similar habitat quality measures with biotic assessments. For 27 streams in Mississippi, Shields et al. (1995) did not observe strong relationships between IBI and habitat quality, in part because the sites they sampled were all degraded (i.e., narrow disturbance gradient). Likewise, Whiles et al. (2000) reported no significant relation between RHAP and macroinvertebrate assessment scores for six streams in Nebraska with low slopes and fairly homogenous habitat types. Compared to Shields et al. (1995) and Whiles et al. (2000), we had larger sample size with higher statistical power, and sampled over a broader gradient of habitat and biotic conditions. These differences in sample design may account for the stronger linkages we found between habitat quality and stream biotic integrity.

Our analyses were designed to test the ability of the IBI to detect human disturbance yet several key questions remain unanswered. For instance, is degradation of specific habitats driving the strong relationship between RHAP and IBI? RHAP is a multimetric tool that assesses broad changes in stream habitat quality. We cannot be certain if fishes are responding to specific changes, such as altered flow or increased fine sediments, or if they are responding more to cumulative impacts. Which larger scale processes influence local stream habitat? The relative contribution of catchment disturbance and natural geomorphic variability to stream habitat quality are not quantified for these streams. Exploring these linkages is the focus of ongoing research in this river system.

Performance of R-IBI

The Etowah, and many other river systems, have extensive collection records but comparisons with current collections are often problematic. Species presence-absence data, like those we used to calculate R-IBI, are often interpreted informally because most presence-absence designs suffer from low statistical power (Strayer 1999). In the stream fish literature, historical data have primarily served to assess the temporal stability of fish assemblages (reviewed in Grossman et al. 1990) or to describe the response of fish assemblages to particular types of disturbance (e.g. Weaver and Garman 1994). In most cases, both types of studies use data that are quantitative and represent multiple samples taken at a few sites. In the IBI literature, historical data have been used primarily to help set expectations for species richness (Bowen et al. 1996; Hughes et al. 1998).

To our knowledge this is the first attempt to assess biotic integrity at sites based on historical collections. Our results demonstrated that the R-IBI derived from presence-absence data is a promising tool for evaluating changes in fish assemblages over time. For example, correlation analyses showed that R-IBI is highly correlated ($r = 0.96$) with IBI scores generated from the full compliment of metrics. This result is comparable to those reported by Steedman (1988) and Roth et al. (1996) who showed that a small subset of metrics explained the preponderance of variance in IBI calculated from a broader set of metrics. Regression analysis showed the strong relationship between R-IBI and RHAP. While the R-IBI lost some of the predictive capability of the complete IBI, it was still sensitive to changes in stream habitat quality.

The best test of the R-IBI was in evaluating historic data collections. This analysis demonstrated that R-IBI scores calculated from historic records were correlated with contemporaneous land cover data. Inclusion of the historic records in the analysis served two purposes. First, it increased statistical power cheaply. We added 23 sites to the analysis without incurring the expense of field work and laboratory analysis. Second, we were better able to assess the response of fishes in basins near the end of the disturbance gradient by adding sites in less forested, more heavily impacted catchments. Inclusion of these data did not change the original interpretation that IBI scores show a nonlinear increase with basin % forest cover, but they do suggest biotic integrity declines more steeply in response to basin deforestation than the smaller dataset indicated.

CONCLUSION

Urban development is a global phenomenon that presents a complex challenge to aquatic resource managers. The IBI and R-IBI developed in this study were effective in tracking changes in habitat quality and basin land cover in a rapidly developing Piedmont landscape. These biotic indices hold promise for further evaluation of historic fish collections and assessing changes in biotic integrity over time in the Etowah basin. While the generality of these indices to streams beyond the Etowah basin is not tested here, similar techniques, if not the specific metrics, may be applicable to other southeastern and Piedmont catchments.

ACKNOWLEDGEMENTS

Funding was provided by a grant from the US Environmental Protection Agency (EPA R826597-01-0) with additional support from the University of Georgia Research Foundation and the Georgia Museum of Natural History. We thank T. Burgess, K. Costly, and L. Ormes for help in the field, Dr. C.P. Lo for land cover data, and J. Benstead for commenting on an earlier version of this manuscript.

REFERENCES

Angermeier, P. L., and J. R. Karr. 1986. Applying an index of biotic integrity based on stream-fish communities: considerations in sampling and interpretation. North American Journal of Fisheries Management 6:418-429.

Angermeier, P. L., and R. A. Smogor. 1995. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. Canadian Journal of Fisheries and Aquatic Science 52:936-949.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in wadeable streams and rivers: periphyton, benthic macroinvertebrates, and fish, second edition. Office of Water, Washington, D.C.

Berkman, H. E., and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18:285-294.

Boulton, A. J. 1999. An overview of river health assessment: philosophies, practice, problems, and prognosis. Freshwater Biology 41:469-479.

Bowen, Z. H., M. C. Freeman, and D. L. Watson. 1996. Index of biotic integrity applied to a flow-regulated river system. Proceedings of the Annual Conference of Southeastern Associated Fish and Wildlife Agencies 50:26-37.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled Southern Appalachian ecosystem. Pages 375-444 *in* G. W. Benz and D. E. Collins, editors. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Fausch, K. D., J. R. Karr, and P. R. Yant. 1984. Regional applications of an index of biotic integrity based on stream fish communities. Transactions of the American Fisheries Society 113:39-55.

Fore, L. S., J. R. Karr, and L. L. Conquest. 1994. Statistical properties of an index of biotic integrity used to evaluate water resources. Canadian Journal of Fisheries and Aquatic Sciences 51:1077-1087.

Grossman, G.D., J. F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: a review. Environmental Management. 14:661-671.

Hughes, R. M., P. R. Kaufman, A. T. Herlihy, T. M. Kincaid, L. Reynolds, and D. P. Larson. 1998. A process for developing and evaluating indices of fish assemblage integrity. Canadian Journal of Fisheries and Aquatic Sciences 55:1618-1631.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Jones, E. B. D., III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conservation Biology 13:1454-1465.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Karr, J. R., K. D. Fausch, P. L. Angermeir, P.R.Yant, and I.J.Schlosser. 1986. Assessing biological integrity in running waters: a method and its rational. Illinois Natural History Survey Special Publications No. 5, Champaign, Ill.

Karr, J. R., P. R. Yant, and K. D. Fausch. 1987. Spatial and temporal variability of the index of biotic integrity in three midwestern streams. Transactions of the American Fisheries Society 116:1-11.

Karr, J. R. 1999. Defining and measuring river health. Freshwater Biology 41:221-234.

Leonard, P. M., and D. J. Orth. 1986. Application and testing of an index of biotic integrity in small, coolwater streams. Transactions of the American Fisheries Society 115:401-414.

Lo, C.P., and X. Yang. 2000. Mapping the dynamics of land use and land cover change in the Atlanta metropolitan area using time sequential Landsat images. *ASPRS 2000 Proceedings (in CD form).* Annual meeting held in Washington, DC, May 22-26, American Society of Photogrammetry and Remote Sensing, Bethesda, Maryland.

McCormick, F. H., D. V. Peck, and D. P. Larson. 2000. Comparisons of geographic classification schemes for Mid-Atlantic stream fish assemblages. Journal of the North American Benthological Society 19:385-404.

Meyer, J. L., A. B. Sutherland, K. H. Barnes, D. M. Walters, and B. J. Freeman. 1999. A scientific basis for erosion and sedimentation standards in the Blue Ridge physiographic province. Pages 321-324 *in* K. J. Hatcher, editor. Proceedings of the 1999 Georgia water resources conference. Institute of Ecology, The University of Georgia, Athens, Georgia.

Miller, D. L., P. M. Leonard, R. M. Hughes, J. R. Karr, P. B. Moyle, L. H. Schrader, B. A. Thompson, R. A. Daniels, K. D. Fausch, G. A. Fitzhugh, J. R. Gammon, D. B. Halliwell, P. L. Angermeier, and D. J. Orth. 1988. Regional applications of an index of biotic integrity for use in water resource management. Fisheries 13:1220.

Minns, C. K., V. W. Cairns, R. G. Randall, and J. E. Moore. 1994. An index of biotic integrity (IBI) for fish assemblages in the littoral zone of Great Lakes' Areas of Concern. Canadian Journal of Fisheries and Aquatic Sciences 51:1804-1822.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.

Schleiger, S. L. 2000. Use of an index of biotic integrity to detect effects of land uses on stream fish communities in west-central Georgia. Transactions of the American Fisheries Society 129:1118-1113.

Shields, F. D., Jr., S. S. Knight, and C. M. Cooper. 1995. Use of the index of biotic integrity to assess physical habitat degradation in warmwater streams. Hydrobiologia 312:191-208.

Simon, T. P., and J. Lyons. 1995. Application of the index of biotic integrity to evaluate water resource integrity in freshwater ecosystems. Pages 245-262 *in* W. S. Davis and T. P. Simon, editors. Biological assessment and criteria: tools for water resource planning and decision making. CRC Press, Boca Raton, Florida.

Smogor, R. A., and P. L. Angermeier. 1998a. Effects of drainage basin and anthropogenic disturbance on relations between stream size and IBI metrics in Virginia. Pages 249-272 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, New York, New York.

Smogor, R. A., and P. L. Angermeier. 1998b. Relations between fish metrics and measures of anthropogenic disturbance in three IBI regions in Virginia. Pages 585-610 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, New York, New York.

Steedman, R. J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. Canadian Journal of Fish and Aquatic Sciences 45:492-501.

Strayer, D.L. 1999. Statistical power of presence-absence data to detect population declines. Conservation Biology 13:1034-1038.

U.S. Department of Agriculture. 2000. URL: www.nhq.nrcs.usda.gov/land/meta/m5011.html.

Waite, I. R., and K. D. Carpenter. 2000. Associations among fish assemblage structure and environmental variables in Willamette basin streams, Oregon. Transactions of the American Fisheries Society 129:754-770.

Walser, C. A., and H.L. Bart, Jr. 1999. Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River system. Ecology of Freshwater Fish 8:237-246.

Warren, M. L. Jr., B. M. Burr, S. J. Walsh, H.L. Bart, Jr., R. C. Cashner, D. A. Etnier, B. J. Freeman, B. R. Kuhajda, R. L. Mayden, H. W. Robison, S. T. Ross, and W. C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25:7-31.

Weaver, L.A. and Garman, G.C. 1994. Urbanization of a watershed and historical changes in a stream fish assesmblage. Transactions of the American Fisheries Society 123:162-172.

Whiles, M.R., B.L. Brock, A.C. Franzen, and S.C. Dinsmore, II. 2000. Stream invertebrate communities, water quality, and land-use patterns in an agricultural drainage basin of northeastern Nebraska, USA. Environmental Auditing 26:563-576.

Table 2.1. Metrics and scoring criteria used to compute an IBI for Etowah River tributaries in the Piedmont physiographic province. Five metrics used by Miller et al. (1988), the number of sucker species, number of intolerant species, percent top carnivores, percent hybrids, and percent with disease, tumors, fin damage, and anomalies were dropped from the Etowah IBI.

Miller et al. (1988) IBI Metrics	**Etowah IBI Metrics (Acronym)**	*Raw Values*	
		M_{Min}	M_{max}
Total number of fish species	Richness (RIC) [a]		
	$15\ km^2$	0	17
	$50\ km^2$	0	25
	$100\ km^2$	0	29
Number of darter species	% darter and sculpin species (DAR) [a]	0	0.35
Number of sunfish species	% centrarchid species (CEN) [a]	0.14	0.42
Relative abundance green sunfish	Relative abundance of tolerant taxa (TOL)	0.29	0.89
Relative abundance of insectivorous cyprinids	% insectivorous cyprinid species (INC) [a]	0	0.28
Number of individuals in sample	Density (fish/m^2) (DEN)		
	$15\ km^2$	0	0.9
	$50\ km^2$	0	0.48
	$100\ km^2$	0	0.32

[a] Metrics used to calculate R-IBI

Table 2.2. IBI metric loadings on the first two principal components (PC) following varimax rotation and the percent variance accounted for by each PC.

Metric	**PC I**	**PC II**
RIC	-0.050	0.898
DAR	0.865	0.141
CEN	-0.707	-0.428
TOL	-0.853	-0.277
INC	0.396	0.757
DEN	0.800	-0.386
Variance (%)	51.0	25.3

Table 2.3. Coefficients of concordance (Kendall's tau) between IBI score and standardized metrics. Metric abbreviations are given in Table 1. Significance levels (P < 0.001*, P < 0.0001**).

Metric	**IBI**
TOL	0.675**
INC	0.628**
CEN	0.608**
DAR	0.577**
DEN	0.583**
RIC	0.449*

Appendix 2.1. Catchment characteristics, Rapid Habitat Assessment Protocol (RHAP) and Index of Biotic Integrity (IBI) scores for Etowah River tributary streams.

Site	Name	Drainage Area (km2)	% Urban[a]	% Ag.[a]	% Forest[a]	RHAP	IBI
1	Pumpkinvine Cr.	16.57	10	13	76	12.2	66.1
2	West Fork[b]	13.81	14	30	56	11.4	66.3
3	Avery Cr.	22.32	20	38	40	5.5	32.4
4	Smithwick Cr.	15.63	13	37	49	14.4	63.8
5	McCanless Cr.	13.14	9	23	67	16.9	75.1
6	Bluff Cr.	14.51	8	24	67	13.3	64.7
7	Settingdown Cr.	17.07	16	27	55	6.5	26.0
8	Conn Cr.	14.91	6	7	87	17.1	81.7
9	Polecat Branch	11.34	16	38	43	11.3	75.7
10	Burt Cr.	12.21	16	27	56	14.7	80.0
11	Raccoon Cr.	50.69	11	21	68	15.8	85.1
12	Little Pumpkinvine Cr.	52.00	24	12	63	14.3	80.0
13	Chicken Cr.	59.07	30	22	47	6.3	48.8
14	Little River	52.85	15	26	58	7.7	51.4
15	Mill Cr.	50.68	15	35	49	7.8	56.0
16	Smithwick Cr.	38.61	11	29	60	12.5	84.1
17	Shoal Cr.	53.19	7	15	77	12.7	58.9
18	Settingdown Cr.	53.56	19	32	48	9.6	46.8
19	Darnell Cr.	60.28	5	8	85	12.8	86.7
20	Shoal Cr.	53.77	11	17	71	14.3	93.1
21	Pumpkinvine Cr.	125.67	11	11	77	6.5	47.4
22	Raccoon Cr.	108.47	8	18	74	16.3	69.3
23	Noonday Cr.	85.35	61	11	27	6.1	46.5
24	Settingdown Cr.	96.06	18	32	49	8.8	35.9
25	Little River	122.06	23	24	52	8.4	38.0
26	Mill Cr.	84.63	19	35	46	8.3	45.4
27	Shoal Cr.	101.95	8	16	75	12.8	70.6
28	Sharp Mountain Cr.	103.93	10	27	61	15.0	72.9
29	Long Swamp Cr.	77.36	5	9	85	15.8	89.5
30	Shoal Cr.	90.71	10	13	76	16.5	90.1

Site	Name	Drainage Area (km2)	% Urban[a]	% Ag.[a]	% Forest[a]	RHAP	IBI
101	Little Allatoona Cr.	14.85	37	18	44	7.4	34.9
111	Allatoona Cr.	48.37	33	12	54	12.7	54.7

[a.] Land cover based on 1997 *Landsat* TM scenes for 1997 (Lo and Yang 2000).

[b.] West Fork was dammed by beavers during this study and was excluded from statistical analyses.

Appendix 2.2. Fishes collected in the Etowah River system.

Family Name ***Scientific name***	**Common Name**	**Frequency of occurrence**
Petromyzontidae		
Ichthyomyzon sp.		12
Cyprinidae		
Campostoma oligolepis	largescale stoneroller[a]	29
Cyprinella callistia	Alabama shiner[a,b]	25
C. trichroistia	tricolor shiner[b]	12
C.venusta	blacktail shiner[b]	11
Hybopsis lineapunctata	lined chub[b]	1
Luxilus zonistius	bandfin shiner[b]	3
Nocomis leptocephalus	bluehead chub	11
Notemigonus crysoleucas	golden shiner	3
Notropis chrosomus	rainbow shiner[b]	3
N. longirostris	longnose shiner[b]	1
N. lutipinnis	yellowfin shiner[b]	7
N. stilbius	silverstripe shiner[b]	12
N. xaenocephalus	Coosa shiner[b]	22
Phenacobius catostomus	riffle minnow[b]	9
Pimephales vigilax	bullhead minnow	2
Semotilus atromaculatus	creek chub[a]	25
Catostomidae		
Hypentelium etowanum	Alabama hog sucker[a]	32
Minytrema melanops	spotted sucker	1
Moxostoma duquesnei	black redhorse	13
M. erythrurum	golden redhorse	9
M. poecilurum	blacktail redhorse	8
Ictaluridae		
Ameiurus brunneus	snail bullhead	7

Family Name ***Scientific name***	**Common Name**	**Frequency of occurrence**
A. natalis	yellow bullhead	4
A. nebulosus	brown bullhead	3
Ictalurus punctatus	channel catfish	6
Noturus leptacanthus	speckled madtom	17
Salmonidae		
Onchorhynchus mykiss	rainbow trout	1
Fundulidae		
Fundulus stellifer	southern studfish	20
Poeciliidae		
Gambusia affinis	western mosquitofish[a]	9
G. holbrooki	eastern mosquitofish[a]	6
Cottidae		
Cottus sp. cf. *C. carolinae*	banded sculpin	23
Centrarchidae		
Ambloplites ariommus	shadow bass	6
Lepomis auritus	redbreast sunfish[a]	31
L. cyanellus	green sunfish[a]	16
L. gulosus	warmouth	3
L. macrochirus	bluegill sunfish[a]	28
L. megalotis	longear sunfish	1
L. microlophus	redear sunfish	9
Micropterus coosae	Coosa bass	23
M. punctulatus	spotted bass	12
M. salmoides	largemouth bass	16
Pomoxis nigromaculatus	black crappie	4
Percidae		
Etheostoma etowahae	Etowah darter	4
E. jordani	greenbreast darter	3
E. scotti	Cherokee darter	20

Family Name ***Scientific name***	**Common Name**	**Frequency of occurrence**
E. stigmaeum	speckled darter	11
Percina kathae	Mobile logperch	17
P. nigrofasciata	blackbanded darter[a]	31
P. palmaris	bronze darter	9
P. sp. cf. P. macrocephala	“bridled darter”	2

[a.] tolerant species

[b.] insectivorous cyprinids

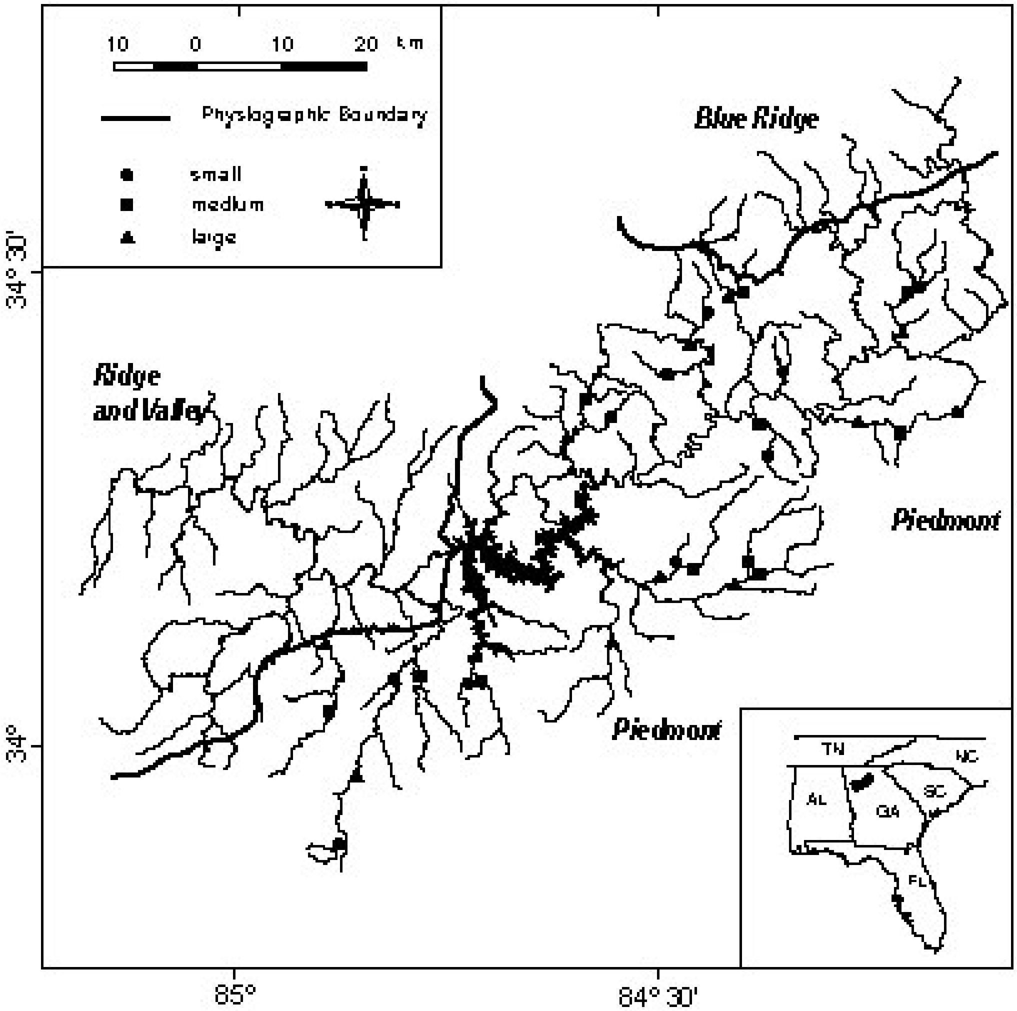

Figure 2.1. Etowah River basin with 32 sampling locations. The large reservoir in the middle of the basin is Lake Allatoona, an impoundment on the Etowah River. Small, medium, and large streams drain catchments of roughly 15, 50, and 100 km^2 (+/- 25%).

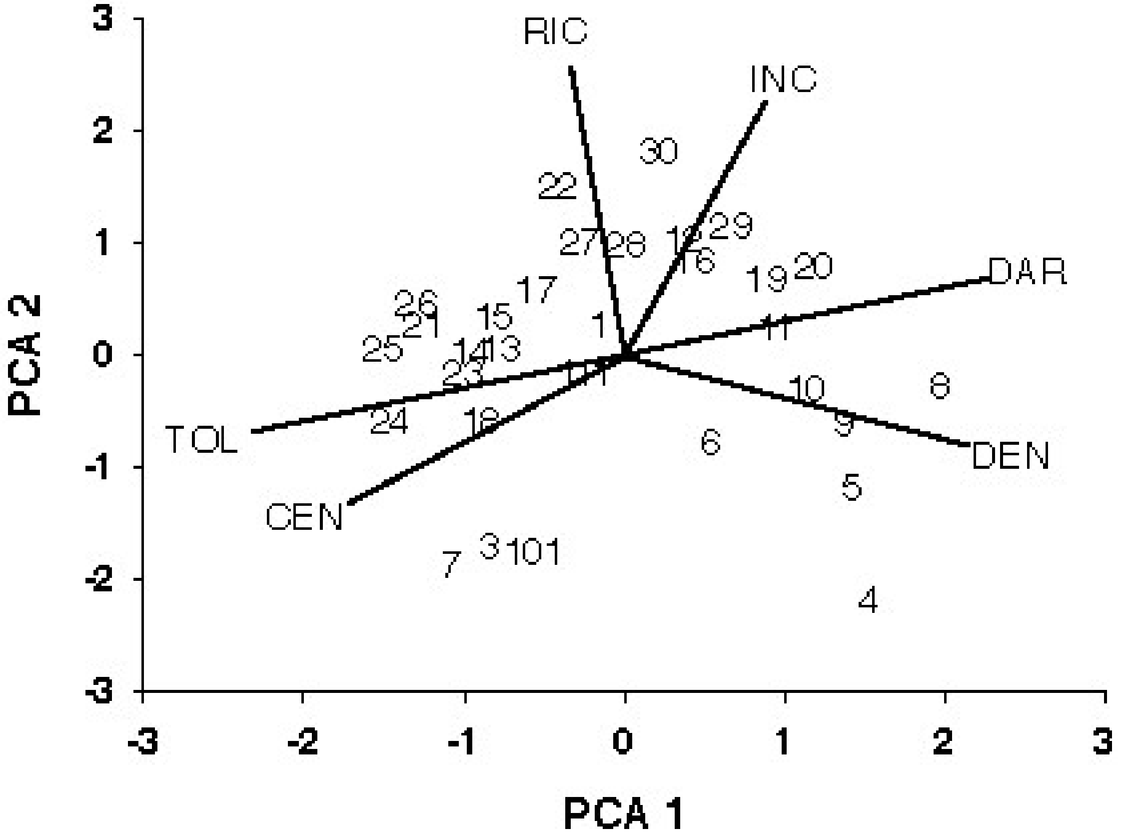

Figure 2.2. Rotated first and second principal component scores from IBI metrics. Sites are shown plotted in metric space. IBI scores are lowest in the lower left quadrant and highest in the upper right quadrant.

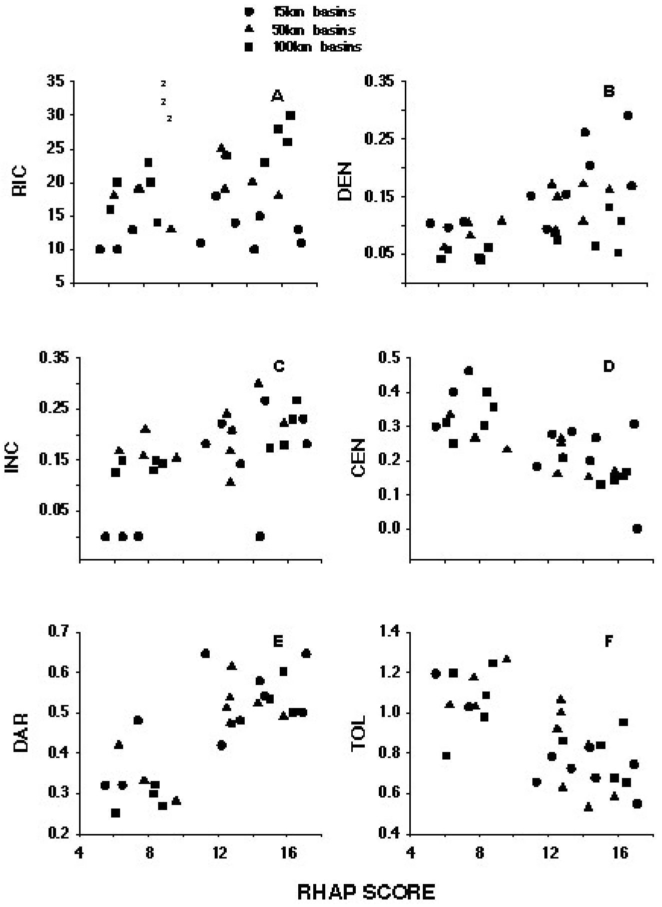

Figure 2.3. Bivariate plots of metrics and RHAP scores. Metric abbreviations are defined in Table 1. Transformations are arc-sine square root for DAR and TOL and log (y+1) for DEN. Significant regressions: **A**) 100 km^2 sites, $R^2 = 0.69$, $p = 0.003$; **B**) 15 km^2 sites, $R^2 = 0.57$, $p = 0.001$; 50 km^2 sites, $R^2 = 0.46$, $p = 0.02$; 100 km^2 sites, $R^2 = 0.45$, $p = 0.035$, all sites, $R^2 = 0.31$, $p = 0.001$; **C**) $R^2 = 0.31$, $p = 0.001$; **D**) $R^2 = 0.48$, $p < 0.0001$; **E**) $R^2 = 0.61$, $p < 0.0001$; **F**) $R^2 = 0.53$, $p < 0.0001$.

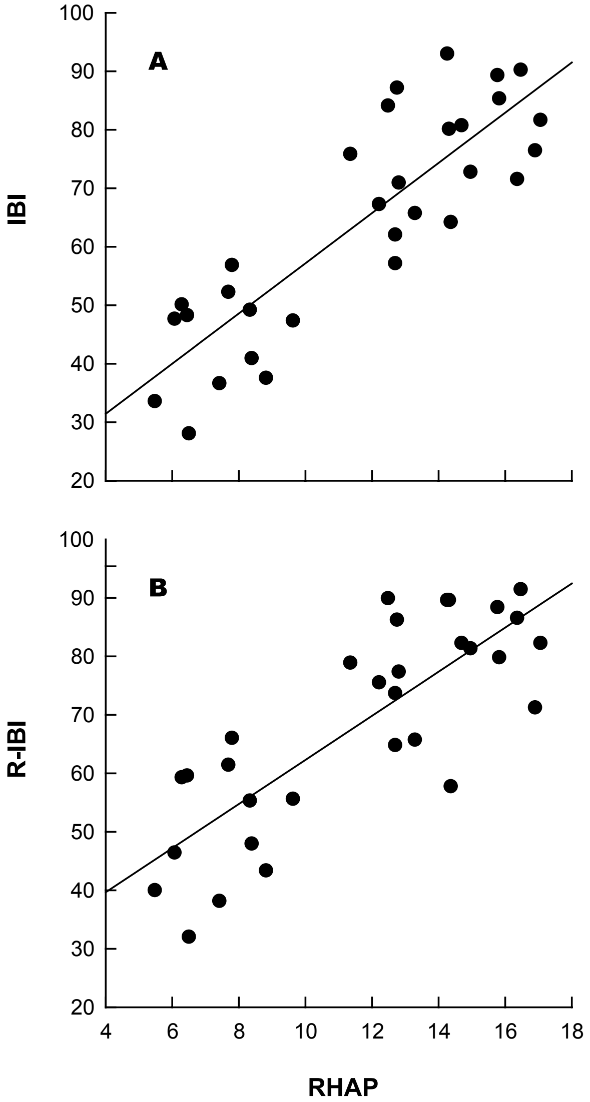

Figure 2.4. Linear regression showing the positive correlation of IBI and R-IBI with habitat assessment scores for 31 sites sampled in 1999 and 2000. **A**) $R^2 = 0.72$, $p < 0.0001$; **B**) $R^2 = 0.65$, $p < 0.0001$.

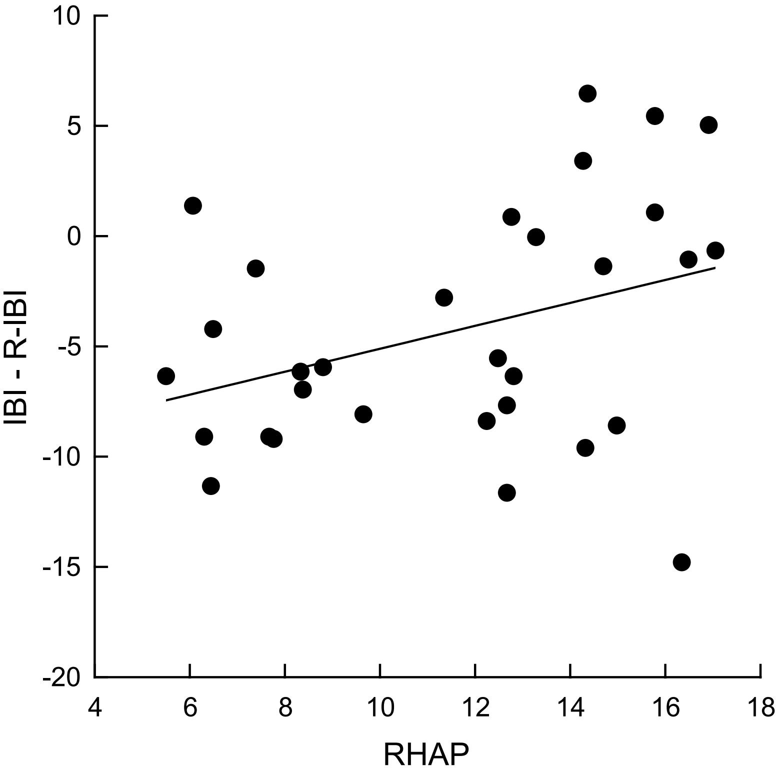

Figure 2.5. Linear regression showing the weak positive correlation between RHAP and the difference of IBI and R-IBI scores ($R^2 = 0.12$, $p = 0.058$).

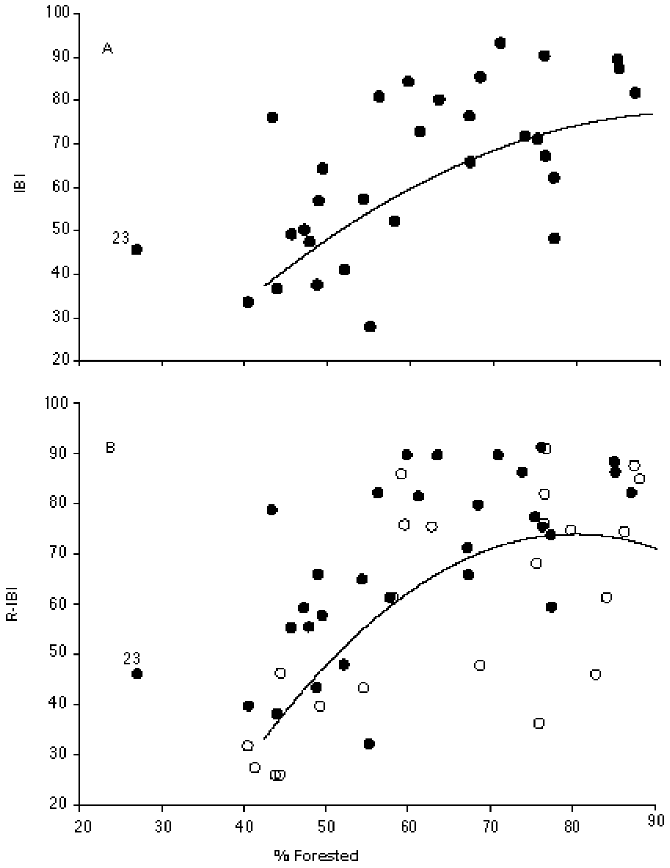

Figure 2.6. Relationship of forested land cover with IBI and R-IBI. Neither regression includes site 23, the least forested and most heavily urbanized site. Forest cover was derived from 1997 Landsat images for sites sampled in 1999 and 2000 and from 1987 images for historic collections. A) Regression of IBI and % forest for sites used to derive the IBI. $\text{IBI} = -46.42 + 2.714(\%\text{forest}) - 0.0145\ (\%\text{forest})^2$; $n=30$, $R^2 = 0.41$, $p = 0.0007$. B) Regression of R-IBI and nonforested land cover. Filled circles represent historic collections, open circles represent sites used to derive the IBI. $\text{IBI} = -93.28 + 4.313\ (\%\text{forest}) - 0.027(\%\text{forest})^2$; $n=53$, $R^2 = 0.46$, $p < 0.0001$.

CHAPTER 3

GEOMORPHIC PROCESSES STRUCTURING FISH ASSEMBLAGES IN A PIEDMONT RIVER BASIN, USA[1]

---

[1] Walters D.M., D.S. Leigh, M.C. Freeman, B.J. Freeman, and C.M. Pringle. To be submitted to *Landscape Ecology*

Abstract: We investigated linkages between fishes and fluvial geomorphology in 31 wadeable streams in the Etowah River basin, Georgia. Streams were stratified into three catchment sizes of approximately 15, 50 and 100 km^2, and fishes and geomorphology were sampled at the reach scale (i.e. 20-40 times baseflow width). Nonmetric multidimensional scaling (NMDS) identified 85% of the among-site variation in fish assemblage structure and identified strong patterns in species composition across sites. Assemblages shifted from domination by centrarchids, and other pool species that spawn in fine sediments and have generalized food preferences, to darter-cyprinid-redhorse sucker complexes that inhabit riffles and runs, feed primarily on invertebrates, and spawn on coarser stream beds. Richness and density were correlated with stream size, but species composition was best predicted (i.e., $|r|$ between 0.60-0.82) by reach-level geomorphic variables (stream slope, bed texture, bed mobility, and tractive force) that were unrelated to stream size. Stream slope was the dominant factor controlling stream habitat. Low slope streams had smaller bed particles, more fines in riffles, lower tractive force, and greater bed mobility compared to high slope streams. Our results contrast with the "River Continuum Concept" which argues that stream assemblages vary predictably along stream size gradients. Our findings support the "Process Domains Concept", which argues that local-scale geomorphic processes determine the stream habitat and disturbance regimes that influence stream communities.

INTRODUCTION

A major goal of stream ecology is to identify environmental gradients structuring lotic communities (Minshall 1988, Power et al. 1988). The River Continuum Concept (RCC Vannote et al 1980), which posits that physical variables present a continuous downstream gradient of habitat conditions controlling community composition, has strongly influenced stream community research. The RCC has been an effective framework for understanding stream attributes within large drainage networks (e.g., headwaters down to large rivers), but within parts of networks, longitudinal relationships maybe obscured by local factors (Bruns et al. 1984, Rice et al. 2001, Poole 2002). Other researchers (Pringle et al. 1988 and Townsend 1989) have promoted the concept of patch dynamics to characterize patterns and processes in heterogeneous stream environments. This approach has been useful for comparing conditions and communities within and between patches (Pringle et al. 1988). However, the ability to predict assemblages across larger portions of stream networks is hampered because processes influencing the spatial and temporal distribution of habitat patches within the network are often unidentified or poorly understood (Montgomery 1999).

Montgomery (1999) argued that neither the RCC or patch dynamics models explicitly address the spatial structure of geomorphic controls on physical stream attributes. As an alternative to the RCC, he proposed the Process Domains Concept (PDC). The main hypothesis of the PDC is that spatial variability in geomorphic processes governs stream habitat and disturbance regimes that influence ecosystem structure and dynamics. Process domains are predictable areas of the landscape within which distinct geomorphic processes operate and thereby impart spatial variability to lotic communities at landscape scales. Montgomery (1999) supported the PDC with published studies of riparian plant, macroinvertebrate, and fish communities but noted that few data existed to directly test the model. The PDC has received little attention from stream ecologists, and to our knowledge has not been objectively evaluated with stream community data. Here we present a comprehensive set of geomorphic variables and their relation to heterogeneity within a stream network of the southern Piedmont. These data provide an empirical test of the PDC.

Patterns in fish assemblage structure are often attributed to longitudinal changes in stream attributes. For example, longitudinal changes in temperature separate cold- from warmwater species (Huet 1959, Rahel and Hubert 1991, Lyons 1996). Downstream increases in pool volume and habitat complexity are also linked to assemblage composition, guild structure, and species richness (Gorman and Karr 1978, Schlosser 1982, Angermeier and Karr 1983, Jones et al. 1999). Schlosser (1987) developed a longitudinal model for fish assemblages in small, warmwater streams. This model linked changes in richness, density, and species composition to downstream declines in disturbance (i.e., more stable flows) and increases in pool depth and habitat diversity. Some exceptions to this longitudinal pattern have been observed. For instance, large woody debris and beaver ponds can strongly influence stream habitat and fish assemblages (Fausch and Northcote 1992, Beechie and Sibley 1997, Snodgrass and Meffee 1998), but these factors generally are unrelated to position along the continuum. Other local geomorphic conditions and processes may contribute to spatial heterogeneity within the stream continuum, but have received less attention in fish assemblage studies.

While several studies have linked habitat variables with stream fishes (e.g., Schlosser 1982, Rahel and Hubert 1991, Lyons 1996), most studies have focused on one or a few variables (e.g., pool volume, bed particle heterogeneity) selected *a priori*. In contrast, our study uses data from a comprehensive geomorphic survey of 31 wadeable streams to identify relationships between stream geomorphology and fish assemblages. Few studies have modeled fish assemblage properties with such a broad spectrum of quantified geomorphic variables (but see Dangelo et al. 1997, Peterson and Rabeni 2001) and comparable datasets in terms of sample size and survey detail are rare even in the geomorphic literature. Our holistic approach allows us to identify critical geomorphic variables structuring fish assemblages without *a priori* assumptions and provides insight into geomorphic process contributing to spatial variation of streams along the continuum.

Our study focuses on reaches of wadeable streams draining 11-126 km^2 Piedmont catchments in the Etowah River basin, Georgia. These streams vary enough in size to assess longitudinal changes in fish assemblages and are comparable to those used by Schlosser (1987) to develop his conceptual model of fishes in small streams. We have three objectives. First, we describe variation and patterns in fish assemblages among streams. Second, we identify the best geomorphic predictors of assemblage structure. Finally, we compare our results with the predictions of existing conceptual models of stream systems and stream fishes.

METHODS

Study Area

Portions of the Etowah basin lie in the Blue Ridge, Ridge and Valley, and Piedmont physiographic provinces (Figure 3.1). Our sample reaches were in wadeable streams on the Piedmont, but headwaters of a few catchments drain the Blue Ridge. The southern Appalachian highland, which includes the study area, is a hotspot of stream fish diversity and endemism (Warren and Burr 1994); Burkhead et al. (1997) estimated that 91 fishes from 18 families are native to the Etowah system. The most diverse families are Cyprinidae (31 species), Percidae (19 species), and Centrarchidae (13 species).

We used a stratified random design to select 32 sample reaches in 23 sub-basins (Figure 3.1). The sub-basins were stratified into three size groups of approximately 15, 50, and 100 km^2 (+/- 25%) (Table 3.1). These sizes are referred to as small, medium, and large streams throughout the text. One small stream was dammed by beavers during the study and was not included in statistical analyses (final $n = 31$). Most sites fall in the forest cover range of 40-87%, with the remainder primarily as urban and agricultural land (Lo and Yang 2000). Agricultural land cover is primarily pasture for hay production and grazing. Row crop production is a minor component of agriculture in the study area, although formerly it was more widespread.

Fish sampling and assemblage variables

We sampled 30 streams in July and August 1999 and two streams in September 2000. All collections were made at baseflow, and reach length was scaled to approximately 40 times the average baseflow water width within each stream size group (Angermeier and Smogor 1995). Reaches of 200, 300, and 400 meters were sampled in small, medium, and large streams respectively. Reaches were sampled in a single pass (Simon and Lyons 1995) with a crew of four to six persons equipped with a backpack electric shocker, seine, and dipnets. All available habitats were thoroughly sampled. Reaches were divided into two sections of equal length. The first half of the reach (i.e., 20 times mean width) was sampled to obtain quantitative catch data. All fishes were euthanized and preserved for identification, except for large fishes (> 20 cm) and fishes with protected status, which were counted and released. The second half of the reach was sampled to improve our estimate of site species richness (Angermeier and Smogor 1995). Voucher specimens of species previously uncollected were retained from this sample.

Assemblage structure was analyzed based on species richness, fish density, and species composition. Species composition had two components, taxonomic groups and ecological guilds. Selected taxonomic groups included fishes from four of the most species rich families: cyprinids (Cyprinidae), darters (Percidae), redhorse suckers (Catostomidae), and centrarchids (Centrarchidae). The contribution of each group was calculated as the proportion of total richness (i.e., the number of species in each group divided by total richness) and as the proportion of total catch (i.e., relative abundance). Cyprinids were further narrowed into insectivorous cyprinids, a group commonly used as an indicator in fish indices of biotic integrity (Miller et al. 1988). Relative abundance of darters was calculated with and without the blackbanded darter, *Percina nigrofasciata*, a species that is widespread and locally common in the Etowah system.

Fishes were classified into ecological guilds based on adult life history attributes. Species were assigned to guilds in three main categories: habitat use, food preference, and spawning behavior (Appendix 3.1). Assignments were made based on life history information reviewed in Etnier and Starnes (1993), Jenkins and Burkhead (1994), and Mettee et al. (1996). Where data were lacking, guilds were assigned based on the behavior of closely related congenerics, body morphology, or personal observations. The contribution of various species guilds was calculated based on relative abundance.

Stream Geomorphology

We measured 95 geomorphic variables at the reach and basin-wide scales (Appendix A). Stream reaches and associated fluvial features were surveyed with an electronic total station. The length of surveyed reach was scaled to approximately 20 times the average baseflow width for streams in each size class (i.e., 100, 150, and 200 m lengths). Features mapped along the reach included bankfull cross-sections, water surface, bank vegetation, thalweg, channel bed, and the extent of riffles, runs, and pools. The bankfull level of the channel was defined by the height of the first prominent bench adjacent to the channel. Stream slope was measured as the average gradient through the tops of riffles. This measure is a proxy for water surface slope during floods. A full cross-section extending onto the floodplain and terraces was surveyed at the ends and the midpoint of each reach. Coarse woody debris (CWD) was measured within the bankfull channel of each stream. The length and mean diameter of all wood >10cm diameter was recorded to calculate the total volume of CWD throughout the reach.

To complement the total station survey, we conducted a “zig-zag” survey to quantify stream depths and bed texture. This method divided the stream into five longitudinal transects at approximately 10, 25, 50, 75, and 90 percent of the wetted width during baseflow conditions (Figure 3.2). Seventeen samples were taken on each transect (n = 85). Samples were evenly spaced along the stream and each one was systematically staggered laterally to produce an overall zig-zag pattern. At each sample point we estimated the modal sediment size within a 50 cm diameter circle. Modal sediment size was recorded in whole *phi* intervals ($-\log_2$ of intermediate axis in mm) and the midpoint of each *phi* interval was used for statistical analyses. *Phi* is calculated using a $-\log_2$

transformation, so smaller particles have larger numbers. Bedrock, which was arbitrarily assigned *phi* = -10.5, was removed from the final analysis because it tended to skew the data and because bedrock is not representative of mobile bed sediment. Depth and geomorphic unit (i.e., riffle, run, and pool) were also recorded at each point.

Bed texture was also assessed with Wolman pebble counts (Wolman 1954) and sieve analysis. Pebble counts were conducted on lateral bars and in riffles (n = 100 grains for each geomorphic unit). For sieve analysis we collected three, 3.0 l sediment samples from pools, riffles, and bars in each stream (total n = 9). These samples were returned to the laboratory, sieved, and weighed to determine the mean percent contribution of different particle sizes within each geomorphic unit.

Bed mobility ratios were calculated to describe the response of the streambed to frequent flood flows. These ratios compare the force exerted on the streambed during the 0.5-year recurrence interval (RI) flood relative to the threshold force (i.e., velocity, shear, and power) needed to initiate motion of average size particles on the whole steam bed or in riffles. The 0.5-year RI flood was estimated by the regional flood frequency equations in Stamey and Hess (1993). These calculations were adjusted by equation 10.6 of Dunne and Leopold (1978) to account for total impervious area within the catchment. Threshold velocity and shear force was estimated by equation 7.14 and 7.18, respectively, in Gordon et al (1992), and threshold unit stream power was estimated by the equation of Bagnold (1980).

ArcInfo® software was used to calculate basin characteristics from 1:24,000 scale digital raster graphics (DRG's) of the latest 7.5 minute USGS quadrangles. Map slope was calculated from DRG's by measuring the distance and elevation changes between the nearest two contour lines crossing upstream and downstream of the reach. Land cover was derived from 1997 Landsat Thematic Mapper scenes with 25 m pixel resolution (Lo and Yang 2000). Total impervious area (TIA) was calculated for each subcatchment by multiplying the percentage of high and low density urban land by 0.9 and 0.65 (Lo and Yang 2000), respectively, and summing the two values.

Statistical Analysis

We quantified among site differences in fish assemblages using nonmetric multidimensional scaling (NMDS) analysis (PC-ORD 4.1 software; MjM Software Design™). NMDS is a distance based ordination method that quantifies the dissimilarity among sites based on biological data (Clarke and Warwick 1994). The resulting ordination is a map of the distance among sites based on the dissimilarity of their biological assemblages. Abundance data from each sample were root-root transformed for the analysis (Field et al. 1982). Rare species, represented in fewer than 10 percent of the samples, were excluded from the analysis (final n = 39 species). Both species of *Gambusia* (Appendix 3.1) and their hybrid progeny were combined into one morphospecies for the analysis. Resulting axes were correlated with fish taxonomic groups and species guilds to identify fishes driving patterns in site dissimilarity.

We used a combination of principal components analysis (PCA) and correlation analysis to screen the set of 95 geomorphic variables. This approach allowed us to eliminate uninformative or redundant variables. Prior to PCA analysis, geomorphic variables were placed into eight categories (Appendix A). Six categories divided local geomorphology into its major components of bankfull morphology, gradient, bed texture, bed transport, depth, and width. Variables that did not fit neatly into these groups were placed into the category “miscellaneous”. Morphometry was the final category and contained variables describing basin-wide geomorphic conditions. All variables were screened for normality with the Kolmogorov-Smirnov test and transformed if necessary.

We ran PCA on each category of variables to identify principal components with eigenvalues > 1. Next, we used correlation analysis to identify variables that correlated at $|r| > 0.8$ with these significant components. If multiple variables correlated with a single component, we screened them for autocorrelation (i.e., among-variable $|r| > 0.8$) and selected one variable to represent each autocorrelated group. Two variables, particle heterogeneity (i.e., the standard deviation of particle sizes in *phi* units) and CWD were not correlated with significant components at $|r| > 0.8$ but were included in the final dataset due to their potential importance as explanatory variables. Particle size heterogeneity was strongly correlated with macroinvertebrate assemblage structure at these sites (Roy et al., in review) and CWD is an important habitat component of small warmwater streams (Angermeier and Karr 1984).

We used a combination of multivariate, linear regression, and multiple regression analysis to link geomorphic variables with fishes. Axes from the NMDS analysis of fish abundances were correlated with geomorphic data to identify physical variables most strongly corresponding to among-site differences in fish assemblages. We used correlation analysis, linear regression, and forward stepwise multiple linear regression to directly link geomorphic variables with fish groups driving among-site differences in fishes. These analyses excluded four sites with >25% urban land cover because urbanization can profoundly alter the relationships between stream communities and habitat (Paul and Meyer 2002). However, these urban sites were retained in plots of the data.

RESULTS

Variation in Fish Assemblages

The NMDS analysis identified three axes that explained 85% of the variance in species abundances among sites. The first axis was significant, but only explained 5% of the variance and was not considered for further analysis. The second and third axes accounted for 81% of the among-site variance and were used to ordinate sites in "species space" (Figure 3.3). Species plotted in the center of the ordination (e.g., *Hypentelium etowanum*) were collected at most sites and were often locally abundant. In general, centrarchids, ictalurids, and *Gambusia* plotted on the left side of the ordination while cyprinids, redhorse suckers, and darters plotted on the right.

Plots of taxonomic groups in species space showed a shift from streams dominated by centrarchids to assemblages composed primarily of darters, cyprinids, and redhorse suckers (Figure 3.4). Cyprinids increased from streams in the upper left to lower right in the ordination. In terms of proportional richness, this trend was clearer for the insectivorous cyprinids (Figure 3.4C, Table 3.2). The proportional richness of darters mirrored the cyprinids, but no trend in relative abundance emerged for the group unless *Percina nigrofasciata* was removed from the analysis (Figure 3.4F, Table 3.2). Redhorse suckers also increased at sites from the upper left to lower right in the ordination. These suckers were absent from small streams, so fewer sites appeared in the plots. The relatively small size of the bubbles showed that redhorse suckers composed a smaller proportion of richness and relative abundance compared with the other taxonomic groups.

In contrast to other species groups, centrarchids decreased from upper left to lower right. The pattern was more apparent for the relative abundance plot (Figure 3.4J) as centrarchids decreased from approximately 60-2% of the total catch along the gradient.

Changes in the relative abundance of some ecological guilds (Figure 3.5A) mirrored the shifts in taxonomic groups. The vectors depicting the most highly correlated guilds were oriented from the upper left to lower right. This gradient contrasted assemblages dominated by pool species with those populated by benthic, riffle-run species. Along this gradient, spawning behavior changed from species that excavate nests in fine sediment to those that rely on larger particles (i.e., crevice spawners and benthic nest builders), but gravel spawners did not correlate with either axis. Feeding behavior shifted from generalized carnivores and trophic generalists to greater specialization in aquatic invertebrates and benthic feeding modes.

Linking Fishes and Geomorphology

Principal Components Analysis explained 83-96% of the variation within geomorphic variable categories. Based on the PCA and subsequent correlation analysis, the original set of 95 variables was trimmed to 26 variables that represented the geomorphic environment (Table 3.3). The plot in Figure 3.5B shows the eight geomorphic variables that were most highly correlated (i.e., $p < 0.001$) with NMDS axes. Seven of these variables (i.e., mean *phi*, % fines in riffles, bed mobility, riffle bed mobility, bankfull tractive force, slope, and map slope) measured stream slope and benthic habitat condition and represented a geomorphic gradient from upper left to lower right in the plot. This gradient contrasted low slope streams having highly mobile, sandy streambeds and fine-textured riffles with steep streams having stable, gravel-cobble beds and high tractive force. Streams with the highest mean *phi* have the finest beds and plot in the upper left of the ordination. Map slope was roughly perpendicular to this gradient and was the only variable highly correlated with Axis 3 (Table 3.4).

The final significant variable, thalweg standard error, describes streambed habitat heterogeneity within the reach. Thalweg slope is calculated with a regression line fitted to bed elevation points surveyed along the sinuous thalweg (Figure 3.6). Large residuals in the plots contribute to high standard error around the regression line. These residuals correspond to prominent riffles (positive residuals) and pools (negative residuals) within the thalweg. These features were related to bed texture. Streams with well developed pools and riffles have rocky beds. In contrast, similar sized sand-textured streams (i.e., streams with high mean *phi*) were dominated by relatively homogenous, shallow run habitat.

Measures of bankfull morphology (with the exception of tractive force), width and depth, pool and riffle habitat, large woody debris, basin morphometry, and floodplain development were not primary predictors of the fish assemblage structure. Local measures of stream geomorphology were more highly correlated with Axis 2 than Axis 3 (Table 3.4). None of the basin-scale morphometry variables correlated with Axis 2. Some of the local-scale variables were correlated with Axis 3, but the highest correlations were with drainage area and map slope.

Variation in geomorphic variables that best predicted fish assemblages did not strongly correspond to differences in basin morphometry and land cover (Table 3.5). However, stream slope was a strong predictor of bed texture and bed mobility. The relationship was strongest for mean *phi*, with slope explaining 85% of the variance. Map slope was weakly correlated with the surveyed slope and was a poor predictor of bed texture and mobility in these sites. Drainage area was significantly correlated with slope, but the relationship was relatively weak (i.e., r = -0.39).

Bed texture, stream slope, bed mobility, and tractive force individually were strong predictors of ecological guilds and taxonomic groups (Table 3.6). Low slope streams with finer beds and riffles, low tractive force, and high bed mobility had larger populations of centrarchids and other pool species. These taxa excavate nests in fine particles and have generalized feeding behaviors. Higher slope streams supported more darters, cyprinids, and redhorse suckers. These taxa tended to be benthic riffle-run species that feed on aquatic invertebrates and spawn on coarse particles. Redhorse suckers were absent from the smallest streams indicating a stream size threshold for their occurrence. However, stream slope and benthic habitat predicted redhorse sucker proportional richness for streams in which they do occur.

Predictive power varied among geomorphic variables. In general, slope and benthic habitat variables poorly predicted richness and density, but strongly predicted species composition. On average, correlations were stronger for ecological guilds than taxonomic groups. Based on the number of significant correlations, the weakest predictor was thalweg standard error. Based on p-values, the strongest predictor was mean *phi*. Stream slope, tractive force, and bed mobility had comparable predictive power, but the percentage of fines in riffles was considerably weaker than mean *phi*.

Linear regression analyses used mean *phi* as a single variable to represent the eight variables in the main geomorphic gradient identified in Figure 3.5B. Regression plots (Figure 3.7) contrasted guilds and taxonomic groups from opposite ends of the biological gradient identified by NMDS analysis. These plots clearly illustrated that pool species, trophic generalist, and centrarchids increase while riffle-run species, benthic invertivores, and darters decline in streams with fine-textured beds. Mean *phi* was not related to richness but showed a weak correlation with density. Urban streams were the largest residuals in some of the regression plots, but no clear trend emerged.

Independent variables for multiple linear regression included mean *phi* and the remaining 19 variables that were not strongly correlated with the NMDS axes. Final models were robust with two or three geomorphic variables explained 55-84% of the variance in assemblage variables (Table 3.7). Mean *phi* was the primary predictor of ecological guilds and taxonomic groups, but was not entered for richness and density models. Secondary predictors included a variety of local (e.g., entrenchment ratio, bankfull area, and CWD), mesoscale (i.e., slope of trunk stream), and basin-wide variables (i.e., compactness). Of the eight secondary predictors selected by the stepwise procedure, only area of the bankfull channel (Abkf) and the 95th percentile of pool depth (95%POOz) were significantly related to basin area. Wetted width and drainage area (i.e., stream size) were the best predictors of richness and density. Sites with steeper trunk streams had higher richness and density, and fish density was positively correlated with drainage density.

DISCUSSION

Species composition in the Etowah streams was strongly linked to patchy, reach-level variation in stream slope, bed texture, bed mobility, and tractive force. Our findings strongly support the Process Domain Concept (PDC), which predicts that geomorphic processes govern the stream habitat and disturbance regimes influencing stream communities (Montgomery 1999). Our results contrast with studies attributing shifts in fish assemblages to longitudinal changes in stream habitat and disturbance regime (Horwitz 1978, Gorman and Karr 1978, Schlosser 1982, Welcomme 1985, Rahel and Hubert 1991, Paller 1994, Poff and Allen 1995). Results from these studies generally confirm the prediction of the River Continuum Concept (RCC) that stream assemblages should vary predictably with stream size (Vannote et al. 1980).

Stream slopes ranging from 0.001- 0.01 represented a continuous environmental gradient that strongly influenced several attributes of benthic habitat and species composition. This result agrees with the observation of Trautman (1981) who argued that stream gradient is the primary factor influencing important elements of stream habitat (e.g., pool and riffle size, bank form, and sediment deposition) and fish assemblages for streams in Ohio. Two multivariate analyses of fishes and stream habitat (Lyons 1996, Maret et al. 1997) found that stream slope was a secondary factor structuring fish assemblages. Compared with our study, these investigations were from more geographically diverse regions drained by cold- and warmwater streams. Not suprisingly, regional differences among streams and thermal regime were the most important predictors of fishes in these studies. Balon and Stewart (1983) and Edds (1993) found that steep cascades and waterfalls influenced fish assemblage structure by limiting dispersal of some species. The stream slopes reported in those studies (e.g., > 0.1) greatly exceed the steepest slope measured in this study (i.e., 0.01). Presumably, stream slopes in the range we observed are not a major impediment to fish dispersal and are instead linked to species composition due to slope-related changes in benthic habitat.

According to textbook scenarios, the longitudinal profile of streams are concave wherein headwaters have steeper slopes than downstream reaches (Knighton 1998). At the scale of our study, reach slope did not follow this pattern. Drainage area only explained 15% of the variance in reach slope. Knighton (1998) reviewed studies of controls on channel slope and reported that slope depends on complex, multivariate relationships with sediment concentration, particle size, discharge, basin relief, width-depth ratio, and lithology. Based on our field observations, stream slope in the Etowah basin is influenced by local topography, geologic structure, and rock type. Thus, relationships between slope and drainage area were weak and local slope varied discontinuously throughout the basin.

Habitat heterogeneity has been linked to longitudinal changes in stream fish assemblages (Gorman and Karr 1978,Schlosser 1982, and Schlosser 1987). We found that depth heterogeneity (i.e., standard error of the thalweg slope regression line) was significantly correlated with one NMDS axis, some elements of species composition, and species richness. However, depth heterogeneity was associated with bed texture rather than stream size. Reaches with large depth variability had coarse-textured beds and were characterized by well-developed riffles and pools. These habitats were less common in low-slope, sand-textured streams because sand particles tend to fill pools and are too mobile to form prominent riffles. These observations concur with the results of Alexander and Hansen (1986) who experimentally increased sand in a Michigan trout stream. They found that excessive sand bedload buried riffles, filled pools, increased run habitat and ultimately lowered habitat diversity.

Floods are a major source of disturbance in streams and may effect recruitment, juvenile abundance, mortality, stability, and structure of fish assemblages (Schlosser 1985, Mathews 1986, Erman et al. 1988, and Freeman et al. 1988). We found that two forms of flood-related disturbance, bed mobility and tractive force, were key predictors of species composition. Bed mobility, which is a function of particle size, and tractive force are strongly influenced by stream slope and entrenchment. Low-slope streams with sand-textured beds experience extensive bed movement during frequently occurring floods (i.e. 0.5-year RI floods). In addition, entrenched streams confine floods and concentrate more energy on the bed. Our results indicate that local geomorphic features determine the disturbance potential of floods and add further support to the process domains model.

Multiple linear regression analysis indicated that both process domain and continuum-like factors influenced assemblage properties. Stream size was the primary predictor of richness and density, a common finding in other fish studies (e.g., Horwitz 1978, Welcomme 1985, Miller et al. 1988, Rahel and Hubert 1991). Two secondary predictors, pool depth and bankfull channel area, were also related to stream size. Pool depth has been linked to downstream increases in large-bodied, pool species such as centrarchids and catostomids (Sheldon 1968, Schlosser 1982). In our streams, pool depth was weakly related to drainage area and only predicted the proportional richness of darters, which are primarily small-bodied, benthic species. These results probably stem from the previously discussed relationship between bed texture and thalweg depth. The deepest streams we sampled had coarse beds dominated by cobble and boulder riffle habitats preferred by most darter species.

The remaining secondary predictors of fishes describe local geomorphic and basin-wide variables that correspond with the Process Domain Concept. For instance, centrarchids were positively correlated with local variation in coarse woody debris, an important component of pool development and habitat diversity in low gradient, sand-bed streams (Shields and Smith 1992). In addition, basin compactness and drainage density were significant predictors of fish variables. Narrow (less compact) catchments are concentrated along the southeastern edge of the Etowah basin. These catchments fall within the Dahlonega Gold belt, a region with folded metamorphic rocks (e.g., gneiss and schist) bounded by extensive fault lines (German 1985). The drainage pattern in these catchments is elongated with truck streams following the long axis of metamorphic folds and faults. As a result, the drainage pattern is more elongated and drainage density is higher. These observations support Montgomery's (1999) argument that geology and topography are important factors that govern channel characteristics, processes, and aquatic communities.

Schlosser (1987) presented compelling evidence for longitudinal patterns in habitat, disturbance, and fishes in small streams of the glaciated Central Lowlands of the midwestern United States. The lack of correspondence between our observations and Schlosser's (1987) conceptual model can be explained by climatic, topographic, and geologic differences between the southern Piedmont and the Central Lowlands. These lowland streams frequently experience intermittent summer flows as well as winter freezing. Deep pools are important refugia for fishes during these harsh conditions. Streams in the Etowah basin never freeze completely and maintain baseflows ranging from 0.01 to 0.7 $m^3 sec^{-1}$ even during a drought. Piedmont topography is fairly steep and variable whereas Central Lowland topography is generally low and uniform. Localized bedrock outcropping also influences the morphology of Piedmont streams, but is less of a factor in Central Lowland streams that flow in thick strata of unconsolidated glacial sediment deposits. Montgomery (1999) stated that relative importance of continuum and process domain factors would depend largely on regional variation in climate, geology, and topography. He predicted that streams with significant relief and complex geology, such as those in the Piedmont, are more likely to exhibit process domain characteristics that those in the Midwest. This prediction was met for Piedmont streams in the Etowah basin.

Studies investigating linkages between the landscape and stream biota are strongly influenced by sample design and the spatial scale of the study (Lammart and Allan 1999). Our streams show considerable longitudinal variation (basin size varies more than one order of magnitude and baseflow discharge varies nearly two orders of magnitude) and are similar in size to those that Schlosser (1987) used to develop his model for fishes in small streams. Across the range of sizes that we sampled, streams attributes and fishes corresponded to process domains, but we expect that longitudinal processes would eventually prevail if we expanded the range of stream sizes. Other studies documenting longitudinal processes in streams have sampled multiple reaches in one or a few streams (e.g., Schlosser 1982, Rahel and Hubert 1991). In contrast, we stratified our samples by stream size and compared reaches from different streams distributed across a relatively large area. With this sampling approach, streams of a given size showed a high degree of geomorphic (e.g., sand versus cobble beds, deeply entrenched channels versus channels with well-developed flood plains) and assemblage variation. Thus, a stratified design allowed us to characterize a broad range of stream physical and biological attributes and may partially explain why our results contrast with other studies that relied on longitudinal sample designs.

Our results have key implications for applied research. First, some watershed and stream classifications systems that incorporate stream slope in their assessments may be too coarse to discriminate among streams. Rosgen (1994) suggests slope categories of < 0.02% or < 0.5% in his stream classification scheme and Barbour et al. (1999) use the categories of “low” and “high” to discriminate sites for habitat assessment. Neither of these categorical approaches would have identified the influence of slope in this study. Our results also indicated that map slope, a variable commonly used in stream studies, only weakly predicted surveyed slope and other slope-related attributes of stream habitat (e.g., bed texture). Thus, we found map slope to be a poor surrogate for surveyed slope in topographically diverse drainages. In addition, researchers developing an index of biotic integrity (IBI) for topographically diverse regions may need to consider stream slope as a primary background variable structuring fish assemblages. The IBI was originally developed for Midwest streams (Karr 1981) where longitudinal processes dominate. Most IBI studies account for the influence of stream size when scoring metrics, but do not consider slope when determining regional expectations for streams. Finally, considerable research has been directed at effects of sediment on stream ecosystems and communities (Waters 1997). Several measures of bed sediment were highly correlated with stream slope in this study. Researchers may need to normalize for influence of stream slope to detect excessive sedimentation related to human activities.

In summary, both process domains and continuum-like processes influence fish assemblages in Etowah basin streams. Richness and density changed along the river continuum but strong patterns in species composition were best explained by local changes in bed texture, bed mobility, tractive force, and depth heterogeneity. Stream slope was the dominant geomorphic factor influencing these benthic habitat and disturbance variables related to fishes. Our results support the main predictions of the Process Domains Concept and suggest that this model provides a useful context for interpreting ecological patterns in streams draining heterogeneous landscapes.

ACKNOWLEDEMENTS

Funding was provided by a grant from the US Environmental Protection Agency (EPA R826597-01-0) with additional support from the University of Georgia Research Foundation and the Georgia Museum of Natural History. We thank A. Bearden, T. Burgess, K. Costly, and L. Ormes for help in the field, Dr. C.P. Lo for land cover data, and W. Cross, G. Helfman and A. Rosemond for commenting on an earlier version of this manuscript.

REFERRENCES

Alexander, G. R., and E. O. Hansen. 1986. Sand bedload in a brook trout stream. North American Journal of Fisheries Management 6:9-23.

Angermeier, P. L., and J. R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Environmental Biology of Fishes 9:117-135.

Angermeier P. L., and J. R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113:716-726.

Angermeier, P. L., and R. A. Smogor. 1995. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. Canadian Journal of Fisheries and Aquatic Science 52:936-949.

Bagnold, R. A. 1980. An empirical correlation of bedload transport rates in flumes and natural rivers. Proceedings of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences 372:453-473.

Balon, E. K., and D. J. Stewart. 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa Zaire System), reflections on river zonation, and description of another new species. Environmental Biology of Fishes 9:225-252.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in wadeable streams and rivers: periphyton, benthic macroinvertebrates, and fish, Second Edition. EPA 841-B-99-002, Office of Water, Washington, D.C.

Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society 126:217-229

Brown, R. H. 2002. The greening of Georgia: the improvement of the environment in the twentieth century. Mercer University Press, Macon, Georgia.

Bruns, D. A., G. W. Minshall, C. E. Cushing, K. W. Cummins, J. T. Brock, and R. L. Vannote. 1984. Tributaries as modifiers of the River Continuum Concept - analysis by polar ordination and regression-models. Archiv Fur Hydrobiologie 99:208-220.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled Southern Appalachian ecosystem. Pages 375-444 *in* G. W. Benz and D. E. Collins, editors. Aquatic fauna in peril, the southeastern perspective. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, UK.

Dangelo, D. J., S. V. Gregory, L. R. Ashkenas, and J. L. Meyer. 1997. Physical and biological linkages within a stream geomorphic hierarchy: a modeling approach. Journal of the North American Benthological Society 16:480-502.

Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. W.H. Freeman, San Francisco, CA.

Edds, D. R. 1993. Fish assemblage structure and environmental correlates in Nepal’s Gandaki River. Copeia: 1993(1):48-60.

Erman, D. C., E. D. Andrews, and M. Yoderwilliams. 1988. Effects of winter floods on fishes in the Sierra-Nevada. Canadian Journal of Fisheries and Aquatic Sciences 45:2195-2200.

Etnier, D. A., and W. C. Starnes. 1993. The fishes of Tennessee. The University of Tennessee Press, Knoxville, Tennessee.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British-Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682-693.

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology - Progress Series 8:37-52.

Freeman, M. C., M. K. Crawford, J. C. Barrett, D. E. Facey, M. G. Flood, J. Hill, D. J. Stouder, and G. D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. Canadian Journal of Fisheries and Aquatic Sciences 45:1949-1958.

German, J. M. 1985. The geology of the northeastern portion of the Dahlonega gold belt. Bulletin 100, Georgia Department of Natural Resources, Atlanta, Georgia.

Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley and Sons, Chichester.

Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59:507-515.

Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs 48:307-321.

Huet, M. 1959. Profiles and biology of Western European streams related to fish management. Transactions of the American Fisheries Society 88:155-163.

Jacobson, R. B. and D. J. Coleman. 1986. Stratigraphy and recent evolution of Maryland Piedmont flood plains. American Journal of Science 286:617-637.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Jones, E. B. D., III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conservation Biology 13:1454-1465.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Knighton, D. 1998. Fluvial forms and processes: a new perspective. Edward Arnold, London.

Lo, C. P., and X. Yang. 2000. Mapping the dynamics of land use and land cover change in the Atlanta Metropolitan Area using the time sequential Landsat images. *in* Annual Meeting of the American Society of Photogrammetry and Remote Sensing, Bethesda, MD.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45:329-341.

Maret, T. R., C. T. Robinson, and G. W. Minshall. 1997. Fish assemblages and environmental correlates in the least-disturbed streams of the upper Snake River basin. Transactions of the American Fisheries Society 126:200-216.

Matthews, W. J. 1986. Fish faunal structure in an Ozark stream - stability, persistence and a catastrophic flood. Copeia:388-397.

Mettee, M. F., P. E. O'Neil, and J. M. Pierson. 1996. Fishes of Alabama and the Mobile Basin. Oxmore House Inc, Birmingham, Alabama.

Miller, D. L., P. M. Leonard, R. M. Hughes, J. R. Karr, P. B. Moyle, L. H. Schrader, B. A. Thompson, R. A. Daniels, K. D. Fausch, G. A. Fitzhugh, J. R. Gammon, D. B. Halliwell, P. L. Angermeier, and D. J. Orth. 1988. Regional applications of an Index of Biotic Integrity for use in water resource management. Fisheries 13:1220.

Minshall, G. W. 1988. Stream ecosystem theory: a global perspective. Journal of the North American Benthological Society 7:263-288.

Montgomery, D. M. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 36:397-410.

Paller, M. H. 1994. Relationships between fish assemblage structure and stream order in South-Carolina Coastal-Plain streams. Transactions of the American Fisheries Society 123:150-161.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333-365.

Peterson, J. T., and C. F. Rabeni. 2001. Evaluating the physical characteristics of channel units in an Ozark stream. Transactions of the American Fisheries Society 130:898-910.

Poff, N. L., and J. D. Allen. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606-627.

Poole, G. C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47:641-660.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Mathews, P. B. Moyle, B. Stazner, and I. R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7:456-479.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme, and M. J. Winterbourn. 1988. Patch Dynamics in Lotic Systems -

the Stream as a Mosaic. Journal of the North American Benthological Society 7:503-524.

Rahel, F. J., and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky-Mountain Great-Plains stream - biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120:319-332.

Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. Canadian Journal of Fisheries and Aquatic Sciences 58:824-840

Rosgen, D. L. 1994. A Classification of Natural Rivers. Catena 22:169-199.

Roy, A. H., A. D. Rosemond, M. J. Paul, D. S. Leigh, and J. B. Wallace. Macroinvertebrate response to urbanization in a Piedmont watershed. *In Review*.

Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52:395-414.

Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66:1484-1490.

Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Oklahoma.

Sheldon, A. L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49:193-198.

Shields, F. D., and R. H. Smith. 1992. Effects of large woody debris removal on physical characteristics of a sand-bed river. Aquatic Conservation-Marine and Freshwater Ecosystems 2:145-163.

Simon, T. P., and J. Lyons. 1995. Application of the index of biotic integrity to evaluate water resource integrity in freshwater ecosystems. Pages 245-262 *in* W. S. Davis and T. P. Simon, editors. Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. CRC Press, Boca Raton, Florida, USA.

Snodgrass, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. Ecology 79:928-942

Stamey, T. C., and G. W. Hess. 1993. Techniques for estimating magnitude and frequency of floods in rural basins of Georgia. Water Resources Investigations Report 93-4016, U.S. Geological Survey, Atlanta, Georgia.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36-50.

Trautman, M. B. 1981. The fishes of Ohio. Ohio University Press. Columbus, Ohio.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Warren, M. L., Jr., , and B. M. Burr. 1994. Status of freshwater fishes in the United States: overview of an imperiled fauna. Fisheries 19:6-18.

Waters, T. F. 1997. Sediment in streams: sources, biological effects, and control. American Fisheries Society, Bethesda, Maryland.

Welcomme, R. L. 1985. River fisheries. FAO Technical Paper 262, Food and Agriculture Organization of the United Nations.

Wolman, M. G. 1954. A method for sampling coarse bed material. American

Geophysical Union, Transactions 35:951-956

Table 3.1. Physical characteristics of streams and catchments sampled in the Etowah basin, summarized separately for small (n = 10), medium (n = 11), and large (n = 10) streams. Stream width was calculated as mean wetted-width from cross-sections, and stream depth was calculated as mean depth from the "zig-zag" survey (see text for methodology). Land cover data are from 1997.

stream size	area (km^2)	slope	width (m)	depth (m)	Q (m^3 sec^{-1}) (baseflow)	urban (%)	agriculture (%)	forest (%)
small								
range	11-22	0.0015-0.0085	3.8-7.7	0.14-0.43	0.01-0.13	6-37	7-38	40-87
mean (se)	15.2 (3)	0.0041 (0.0024)	5.1 (1.1)	0.21 (0.08)	0.06 (0.03)	15 (8.4)	25.6 (10.2)	58.2 (14.7)
medium								
range	39-60	0.0015-0.0100	6.3-10.3	0.12-0.27	0.09-0.43	5-33	8-35	47-85
mean (se)	52.2 (5.6)	0.0041 (0.0026)	8.1 (1.4)	0.21 (0.05)	0.19 (0.1)	16.5 (9.1)	20.8 (8.9)	61.8 (12.4)
large								
range	77-126	0.0010-0.0066	6.8-16.3	0.13-0.50	0.13-0.71	5-61	9-35	27-85
mean (se)	99.6 (16)	0.0026 (0.0018)	11.1 (3.1)	0.24 (0.11)	0.31 (0.17)	17.3 (16.4)	19.6 (9.3)	62.2 (18.3)

Table 3.2. Correlation coefficients (r) between taxonomic groups and NMDS axes of fish abundance.

Assemblage Variable	Axis 2	Axis 3
Proportion of:		
cyprinids	0.43^c	-0.62^a
insectivorous cyprinids	0.81^a	-0.21
darters	0.60^a	-0.26
redhorse suckers[1]	0.74^a	0.20
centrarchids	-0.68^a	0.52^a
Relative abundance of:		
cyprinids[2]	0.67^a	-0.07
insectivorous cyprinids	0.58^a	0.09
darters	0.26	0.07
darters without P. nigrofasciata[2]	0.59^a	-0.17
redhorse suckers[1,2]	0.50^b	0.20
centrarchids[2]	-0.68^a	0.62^a

[1] Excludes small streams

[2] Transformed by arc-sine (square-root (x))

a. $p < 0.001$; b. $p < 0.01$; c. $p < 0.05$

Table 3.3. Summary of PCA analysis for eight categories of geomorphic variables. Only principal components (PC) with eigenvalues > 1 and strong correlations (|r| > 0.8) with geomorphic variables are shown. Amount of variance explained by each PC is given in parentheses.

Category	Final Variables	Definition
Bankfull		
PC I (69.0%)	BKF/UQ2	entrenchment ratio expressed by: bankfull Q / urbanized 2-yr. RI[c] flood Q
Category	Final Variables	Definition
	TRACbkf	tractive force (shear stress) exerted on bed during bankfull flows (N m^{-2})
PC II (15.4%)	Abkf	bankfull channel cross-sectional area (m^2)
PC III (11.0%)	W/DbkfTWEG	width:depth of bankfull channel using thalweg depth
Bed Texture		
PC I (48.4%)	avgPHI(z)	average particle size of subaqueous stream bed (avg. = sum of modal *phi*/n)
	stdvPHI(z)[b]	standard deviation of *phi* sizes used to calculate average *phi*
	avgBARPCphi	Wolman (1954) pebble count on lateral and mid-channel bars of the channel bed.
	%FINESRIFFSV	percent by weight of < 2mm particles in riffles
Depth		
PC I (36.9%)	avgD(z)	average baseflow water depth of entire stream from "zig-zag" survey

Category	Final Variables	Definition
PC II (22.9%)	95%POO-D(z)	95th percentile of baseflow pool depth measurements from "zig-zag" survey
PC III (12.5%)	cvD(z)	coefficient of variation of baseflow water depth from "zig-zag" survey
Bed Transport		
PC I (68.2%)	Vb/Vc0.5	avg. velocity of 0.5-yr RI flood / velocity needed to move avgPHI(z)[d]
	riffsP/sPc0.5	unit stream power (ωm^{-2}) of 0.5 yr. RI flood / ωm^{-2} needed to move avg. riffle particle (mm by Wolman ct.)[d]
Gradient		
PC I (47.3%)	slope	gradient of water surface during floods estimated from elevations of riffle tops.
	twegREGSLOPE	slope of regression line fitted to thalweg elevation vs. sinuous distance along thalweg
PC II (24.3%)	MAPSLOP	slope measured as elevation change between two nearest contours on USGS 7.5' quad.
PC III (19.4%)	twegSTERR	standard error of the estimate for the line fitted on twegREGSLOPE
Morphometry		
PC I (42.3%)	DA	drainage basin area (km^2)
PC II (26.7%)	SLOPTR	relief of trunk stream / distance of trunk stream (basin slope)
PC III (12.9%)	COMP	compactness (basin perimeter squared / basin area)
PC IV (10.1%)	DDEN	drainage density (sum of stream length on 1:24000 scale maps / basin area)

Category	Final Variables	Definition
Width[a]		
	WWbase	water width at baseflow
Miscellaneous		
PC I (33.7%)	%RIFFLEtweg	percentage of riffle habitat along the thalweg
PC II (23.0%)	CWDTOT[b]	coarse woody debris in the bankfull channel
PC III (20.6%)	TERR#of3	# of cross-sections (total n=3) that exhibit terracing (category of 0, 1, 2, 3)
PC IV (13.7%)	%POOL(z)	percentage of pool habitat from "zig-zag" survey

[a] PCA was not run on the three width variables.

[b] Variables included based on published relationships with stream fishes.

[c] Recurrence Interval.

[d] Modeled using HEC-RAS version 2.2.

Table 3.4. Correlation coefficients (r) between geomorphic variables and NMDS axes of fish abundance. Geomorphic variable acronyms are defined in Table 3.3.

Variable	**Axis 2**	**Axis 3**
Bankfull		
TRACbkf	0.74[a]	-0.14
BKF/UQ2	0.49[b]	0.04
Abkf	0.35	0.36[a]
W/DbkfTWEG	0.29	0.06
Bed Texture		
avgPHI(z)	-0.69[a]	0.48[b]
%FINESRIFFSV	-0.65[a]	0.47[b]
avgBARPCphi	-0.55[b]	0.40[a]
stdvPHI(z)	0.47[b]	-0.30
Depth		
avgD(z)	0.36[c]	0.02
95%POO-Dzz5	0.41[c]	0.31
cvD(z)	0.24	0.42[c]
Bed Transport		
Vc0.5/Vb	-0.68[a]	0.42[c]
sPc0.5/riffsP	-0.58[a]	0.44[c]
Gradient		
twegSTERR	0.64[a]	0.18
slope	0.61[a]	-0.38[c]
twegREGSLOPE	0.44[c]	-0.14
MAPSLOP	0.29	-0.70[a]
Morphometry		
DA	0.24	0.50[b]
DDEN	0.20	-0.20
SLOPTR	0.30	-0.37[c]
COMP	0.08	0.17
Width		
WWbase	0.51[b]	0.26

Variable	Axis 2	Axis 3
Miscellaneous		
%riffletweg	0.40[c]	-0.26
TERR#of3	-0.14	-0.25
%POOL(z)	-0.07	0.17
CWDTOT	0.04	-0.14

a. $p < 0.001$; b. $p < 0.01$; c. $p < 0.05$

Table 3.5. Correlations among basin morphometry, land cover, and the best geomorphic predictors of fishes. Geomorphic variable acronyms are defined in Table 3.3.

Geomorphic variable	slope	map slope	drainage area	compactness	drainage density	trunk stream slope	% forest[1]	% agriculture[1]	% urban[1]
avgPHIzz5	-0.92[a]	-0.54[b]	0.26	0.01	-0.19	-0.51[b]	-0.38[c]	0.20	0.37[c]
Vc0.5/Vb	-0.87[a]	-0.46[b]	0.28	-0.07	-0.31	-0.55[b]	-0.45[b]	0.26	0.42[c]
%FINESRIFFSV	-0.80[a]	-0.45[b]	0.26	0.09	-0.29	-0.49[b]	-0.45[b]	0.22	0.42[c]
sPc0.5/riffsP	-0.57[a]	-0.39[b]	0.06	-0.03	-0.23	-0.29	-0.33	0.08	0.38[c]
twegSTERR	0.38[c]	-0.01	0.20	0.07	0.30	0.12	0.43[c]	-0.44[b]	-0.21
TRACbkf	0.85[a]	0.24	0.00	-0.02	0.13	0.23	0.37[c]	-0.40[c]	-0.18
slope	-	0.49[b]	-0.39[c]	-0.08	0.10	0.46[b]	0.31	-0.22	-0.26

[1] 1997 land cover from Lo and Yang (2000).

a. $p < 0.001$; b. $p < 0.01$; c. $p < 0.05$

Table 3.6. Correlation coefficients (r) between relative abundance of species guilds, proportional richness of taxonomic groups, and geomorphic variables. Geomorphic variable acronyms are defined in Table 3.3. Four sites with > 25% urban land cover were excluded from all analyses (n = 27). Small streams were not included for analysis of redhorse suckers (n=17).

assemblage variable	slope	TRACbkf	tweg-STERR	Vc0.5/Vb	sPc0.5/riffsP	avgPHI(z)	%FINES-RIFFSV
Ecological guilds							
pool species	-0.72[a]	-0.78[a]	-0.28	0.76[a]	0.40[c]	0.82[a]	0.62[a]
riffle-run species	0.80[a]	0.69[a]	0.30	-0.83[a]	-0.62[a]	-0.86[a]	-0.65[a]
benthic species	0.52[b]	0.44[b]	0.03	-0.59[b]	-0.44[b]	-0.61[a]	-0.39[c]
nest builders and associates	0.27	0.20	0.06	-0.29	-0.16	-0.25	-0.25
crevice spawners	0.74[a]	0.69[a]	0.19	-0.65[a]	-0.52[b]	-0.75[a]	-0.51[b]
nest excavators	-0.66[a]	-0.66[a]	-0.46[b]	0.79[a]	0.50[b]	0.74[a]	0.62[a]
invertivores	0.59[b]	0.66[a]	0.48[b]	-0.57[b]	-0.46[b]	-0.63[a]	-0.54[b]
trophic generalists	-0.68[a]	-0.74[a]	-0.56[b]	0.67[a]	0.56[b]	0.73[a]	0.60[a]
insectivorous cyprinids	0.29	0.51[a]	0.44[b]	-0.32	-0.27	-0.32	-0.39[c]
benthic invertivores	0.80[a]	0.72[a]	0.36	-0.83[a]	-0.63[a]	-0.84[a]	-0.65[a]
Taxonomic groups							
cyprinids	0.52[b]	0.73[a]	0.53[b]	-0.54[b]	-0.60[a]	-0.52	-0.58[b]
centrarchids	-0.66[a]	-0.62[a]	-0.50[b]	0.63[a]	0.55[b]	0.61[a]	0.51[b]
darters	0.79[a]	0.62[a]	0.44[b]	-0.79[a]	-0.39[a]	-0.80[a]	-0.69[a]
redhorse suckers	0.49[c]	0.47	0.66[b]	-0.54[c]	-0.31	-0.56[c]	-0.14
Richness	0.05	0.42[b]	0.60[a]	-0.16	-0.20	-0.11	-0.15
Density	0.57[b]	-0.06	0.10	-0.56[b]	-0.36	-0.51[b]	-0.57[b]

a. $p < 0.001$; b. $p < 0.01$; c. $p < 0.05$

Table 3.7. Multiple regression models of selected fish assemblage variables (n = 27).

assemblage variable	variables in model	trend	cumulative r^2	*p*	*F*	r^2 of predictor with drainage area[a]
pool species	avgphi(z)	+	0.67	< 0.001	37.53	0.07
	BKF/UQ2	-	0.76	0.006		0.05
riffle-run	avgphi(z)	-	0.73	< 0.001	40.87	0.07
species	avgBARPCphi	-	0.78	0.005		0.04
	COMP	-	0.84	0.007		0.03
trophic	avgphi(z)	+	0.53	< 0.001	25.05	0.07
generalists	Abkf	-	0.68	0.001		**0.58**
benthic	avgphi(z)	-	0.71	< 0.001	34.97	0.07
invertivores	avgBARPCphi	-	0.77	0.005		0.04
	COMP	-	0.82	0.017		0.03
centrarchids	avgphi(z)	+	0.37	< 0.001	14.93	0.07
	CWDTOT	+	0.55	0.004		0.01
darters	avgphi(z)	-	0.64	< 0.001	23.79	0.07
	SLOPTR	+	0.70	0.005		0.14
	95%POO(z)	+	0.76	0.033		**0.23**
richness	WW	+	0.48	< 0.001	18.11	**0.64**
	SLOPTR	+	0.60	0.013		0.14
density	DA	-	0.59	< 0.001	32.65	-
	DDEN	+	0.75	< 0.001		0.01
	SLOPTR	+	0.81	0.048		0.14

[a] Amount of variance explained by drainage area for independent variables selected by the stepwise procedure. Bold values significant at $p < 0.01$.

Appendix 3.1. Fishes collected in the Etowah River catchment. The primary sources for guild designations are Etnier and Starnes (1993), Jenkins and Burkhead (1994), and Mettee et al. (1996).

Habitat guilds are based on preferred habitat of adults: (P) pool, (PR) pool-run, (RR) riffle-run, and (HG) habitat generalist. The HG are species commonly found pools, riffles, and runs. The guilds P, PR, RR, and HG are mutually exclusive. A fifth guild, (B) benthic, describes species that feed, spawn, and shelter on the stream bed.

Feeding guilds are based on preferred foods of adults and are mutually exclusive: (H) herbivores feed on algae, detritus, or plant material; (I) invertivores feed primarily on invertebrates; (TG) trophic generalist commonly feed on multiple food types including detritus, fishes, plant material, and invertebrates; (GC) generalized carnivores are top predators that feed on fish, crayfish, and other invertebrate species. Two other feeding guilds were assigned to indicate a degree of specialization: (BI) benthic invertivores feed on invertebrates on the stream bottom, and (IC) insectivorous cyprinids are members of the family Cyprinidae that feed primarily on aquatic insect larvae.

Spawning guilds are mutually exclusive: (BNB) benthic nest builders construct gravel nests on the stream bottom; (BNA) benthic nest associates spawn over BNB nests but do not aid in their construction; (BNE) benthic nest excavators spawn in nests excavated in fine sediments; (C) crevice spawners deposit eggs in crevices on logs, cobble, or boulders; (CS) cavity spawners deposit eggs in cavities under cobbles or even discarded cans and bottles; (G) gravel spawners spawn directly on or in gravel but do notconstruct a formal nest.; (GB) general broadcasters broadcast eggs over a variety of substrate types; (LB) live bearers do not lay eggs but give birth directly; (RA) rock attachers attach eggs to boulders or cobbles; (U) species whose spawning behavior is unknown.

Family Name *Scientific name*	Common Name	Abbreviation	Habitat Guild	Feeding Guild	Spawning Guild
Petromyzontidae					
Ichthyomyzon sp.		ichspp	P	H	G
Cyprinidae					
Campostoma oligolepis	largescale stoneroller	camoli	HG,B	H	BNB
Cyprinella callistia	Alabama shiner	cypcal	HG	I,IC	C
C. trichroistia	tricolor shiner	cyptri	PR	I,IC	C
C.venusta	blacktail shiner	cypven	PR	I,IC	C
Hybopsis lineapunctata	lined chub	hyblin	P	I,BI,IC	BNA
Luxilus zonistius	bandfin shiner	luxzon	PR	I,IC	BNA
Nocomis leptocephalus	bluehead chub	noclep	HG,B	TG	BNB
Notemigonus crysoleucas	golden shiner	notcry	P	TG	GB
Notropis chrosomus	rainbow shiner	notchr	P	I,IC	BNA
N. longirostris	longnose shiner	notlon	P, B	I,BI,IC	G*
N. lutipinnis	yellowfin shiner	notlut	PR	I,IC	BNA
N. stilbius	silverstripe shiner	notsti	PR	I,IC	U
N. xaenocephalus	Coosa shiner	notxae	PR	I,IC	U
Phenacobius catostomus	riffle minnow	phecat	RR,B	I,BI,IC	BNA
Pimephales vigilax	bullhead minnow	pimvig	HG	TG	CS
Semotilus atromaculatus	creek chub	sematr	HG	TG	BNB
Catostomidae					
Hypentelium etowanum	Alabama hog sucker	hypeto	HG,B	TG	G
Minytrema melanops	spotted sucker	minmel	P,B	TG	G
Moxostoma duquesnei	black redhorse	moxduq	P,B	TG	G

Family Name *Scientific name*	Common Name	Abbreviation	Habitat Guild	Feeding Guild	Spawning Guild
M. erythrurum	golden redhorse	moxery	P,B	TG	G
M. poecilurum	blacktail redhorse	moxpoe	P,B	TG	G
Ictaluridae					
Ameiurus brunneus	snail bullhead	amebru	HG,B	TG	BNE
A. natalis	yellow bullhead	amenat	P,B	TG	BNE
A. nebulosus	brown bullhead	ameneb	P,B	TG	BNE
Ictalurus punctatus	channel catfish	ictpun	P	TG	BNE
Noturus leptacanthus	speckled madtom	notlep	RR,B	I,BI	CS
Salmonidae					
Onchorhynchus mykiss	rainbow trout	oncmyk	HG	GC	BNE
Fundulidae					
Fundulus stellifer	southern studfish	funste	P	TG	G
Poeciliidae					
Gambusia affinis	western mosquitofish	gamspp	P	I	LB
G. holbrooki	eastern mosquitofish	gamspp	P	I	LB
Cottidae					
Cottus sp. cf. *C. carolinae*	"banded sculpin"	cotcar	RR,B	I, BI	CS
Centrarchidae					
Ambloplites ariommus	shadow bass	ambari	P,B	GC	BNE
Lepomis auritus	redbreast sunfish	lepaur	P	TG	BNE
L. cyanellus	green sunfish	lepcya	P	TG	BNE
L. gulosus	warmouth	lepgul	P	TG	BNE
L. macrochirus	bluegill sunfish	lepmac	P	TG	BNE
L. megalotis	longear sunfish	lepmeg	P	I	BNE
L. microlophus	redear sunfish	lepmic	P	I	BNE
Micropterus coosae	Coosa bass	miccoo	PR	GC	BNE

Family Name *Scientific name*	Common Name	Abbreviation	Habitat Guild	Feeding Guild	Spawning Guild
M. punctulatus	spotted bass	micpun	PR	GC	BNE
M. salmoides	largemouth bass	micsal	P	GC	BNE
Pomoxis nigromaculatus	black crappie	pomnig	P	TG	BNE
Percidae					
Etheostoma etowahae	Etowah darter	etheto	RR,B	I,BI	G
E. jordani	greenbreast darter	ethjor	RR,B	I,BI	G
E. scotti	Cherokee darter	ethsco	RR,B	I,BI	RA
E. stigmaeum	speckled darter	ethsti	PR,B	I,BI	G
Percina kathae	Mobile logperch	perkat	PR,B	I,BI	G
P. nigrofasciata	blackbanded darter	pernig	HG	I	G*
P. palmaris	bronze darter	perpal	RR,B	I,BI	G
P. sp. cf. P. macrocephala	“bridled darter”	permac	PR	I	G

* Species observed spawning in sand or sand and gravel.

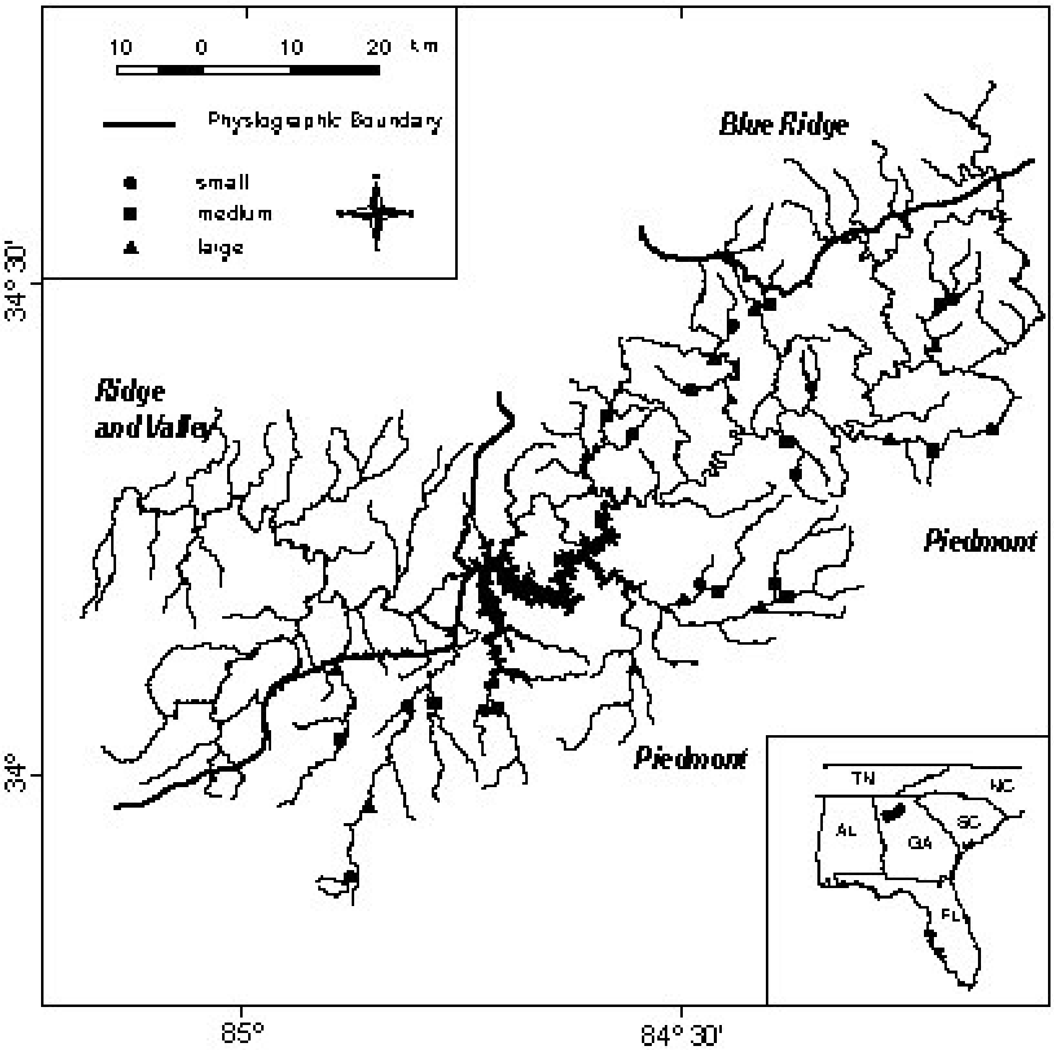

Figure 3.1. Etowah River basin with 32 wadeable stream sites. The large reservoir in the center of the basin is Lake Allatoona, a mainstem impoundment. Small, medium, and large streams drain catchments of roughly 15, 50, and 100 km^2 (+/- 25%).

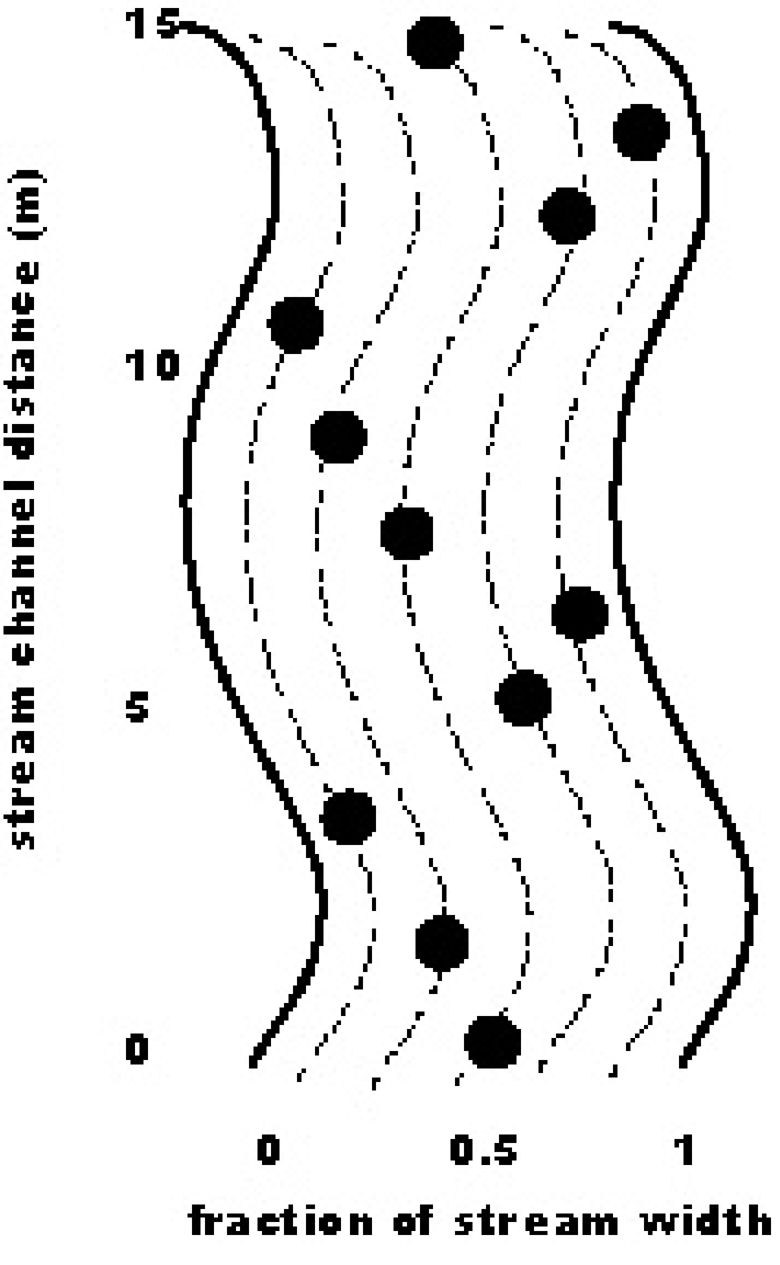

Figure 3.2. Schematic of "zig-zag" survey. Dashed lines correspond with longitudinal transects at approximately 10, 25, 50, 75, and 90 percent of the wetted width. Filled circles indicate sample points. Modal sediment size (whole *phi* category), depth, and geomorphic unit (pool, riffle, and run) were recorded at each point.

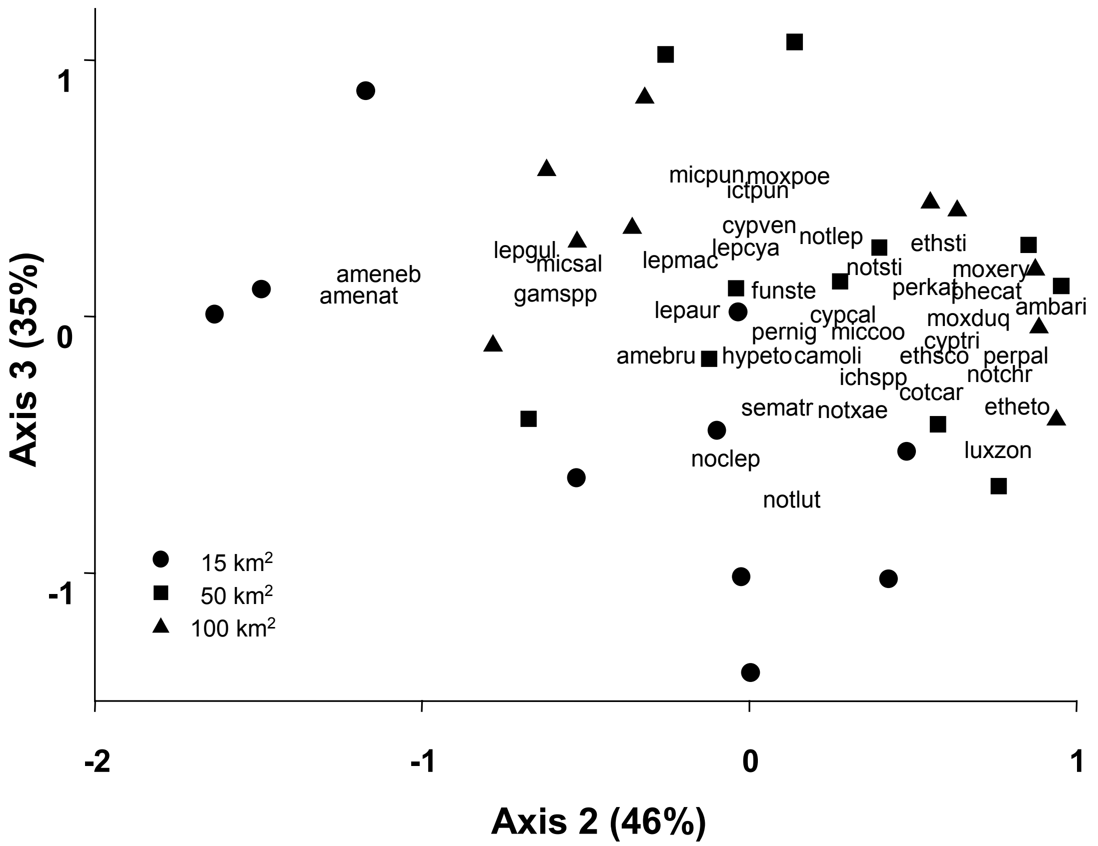

Figure 3.3. NMDS ordination of sites in species space. The amount of variance explained by each axis is shown in parentheses. Species are plotted in species space based on their scores for each axis. Species abbreviations are defined in Appendix 3.1.

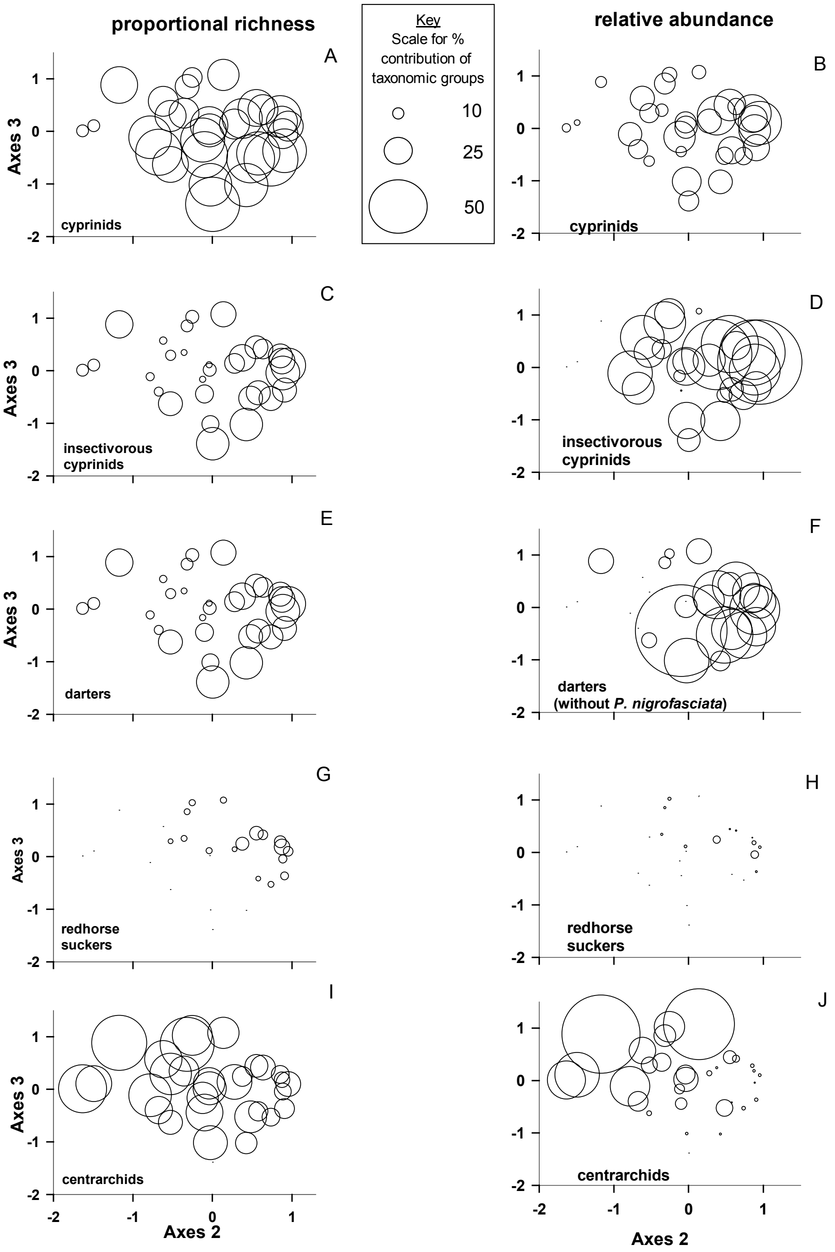

Figure 3.4. Bubble plots of taxonomic groups in species space. Symbols represent the proportional richness and relative abundance of taxonomic groups at each site. Bubbles for the relative abundance of cyprinids are one-half actual size to better illustrate the pattern.

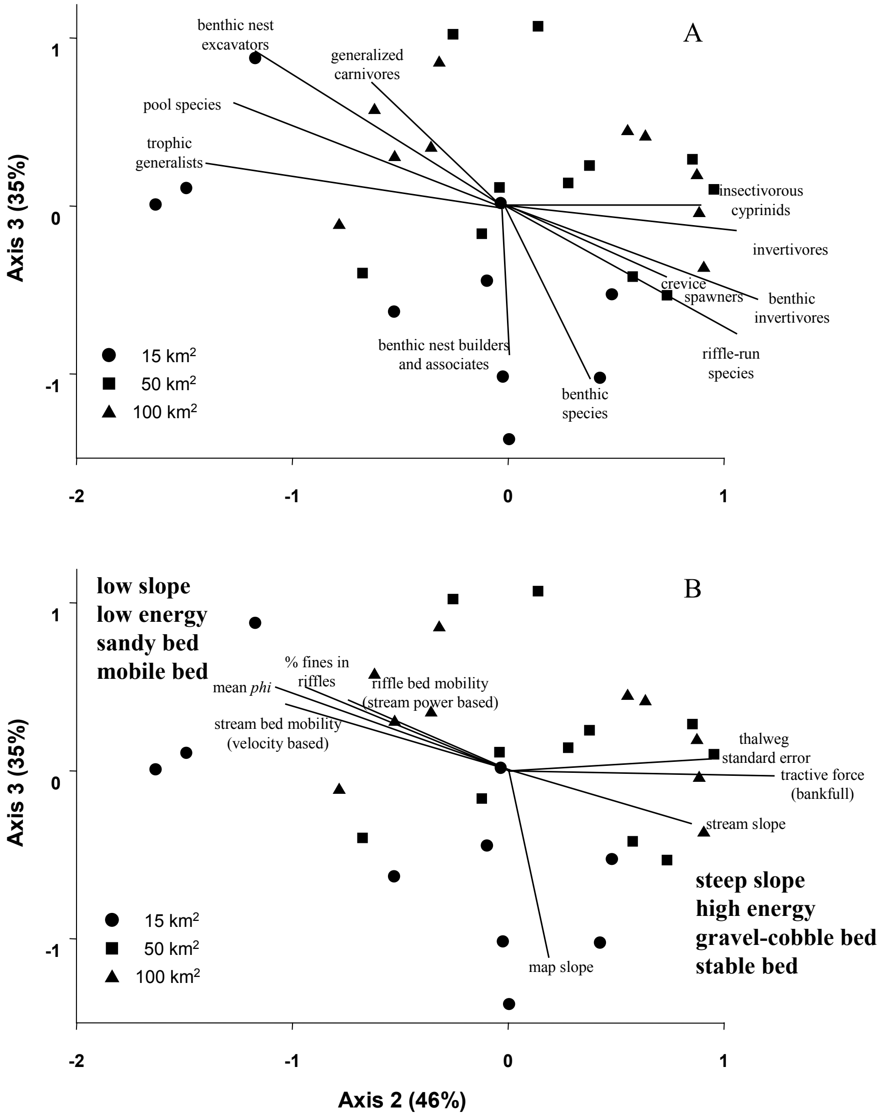

Figure 3.5. Plots of ecological guilds (A) and geomorphic variables (B) most highly correlated with among site differences in fish assemblages. Plotted variables are correlated with either axis at $p < 0.001$. Vectors indicate the direction and magnitude of correlation for each variable and are scaled by 150% for presentation. Primary geomorphic attributes changing along the observed gradient are summarized in the upper left and lower right of panel 5B.

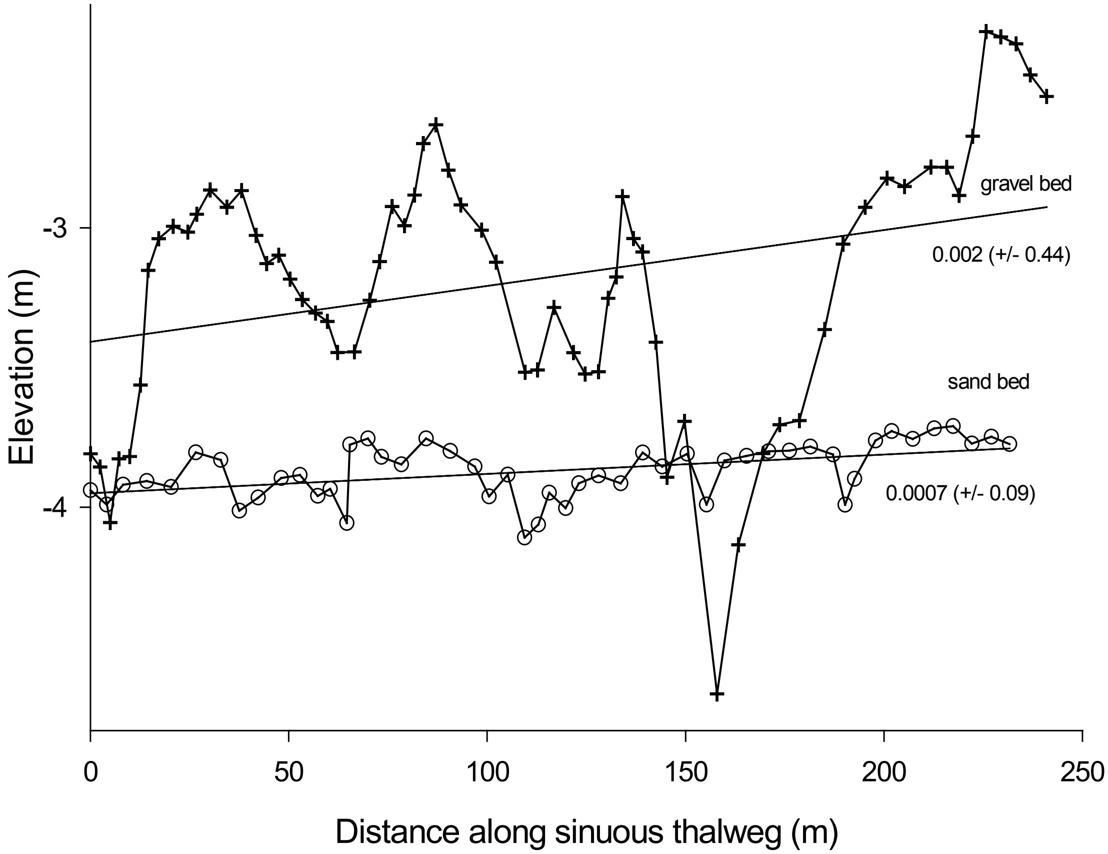

Figure 3.6. Longitudinal plot of thalweg elevation points for sites 21 (open circles, drainage area = 126 km^2) and 30 (plus symbol, drainage area = 102 km^2). Large residuals correspond with prominent riffles and deep pools. Slope (+/- standard error) are given for each regression line. In the plot for site 30, peaks and troughs correspond with prominent riffles and deep pools, respectively.

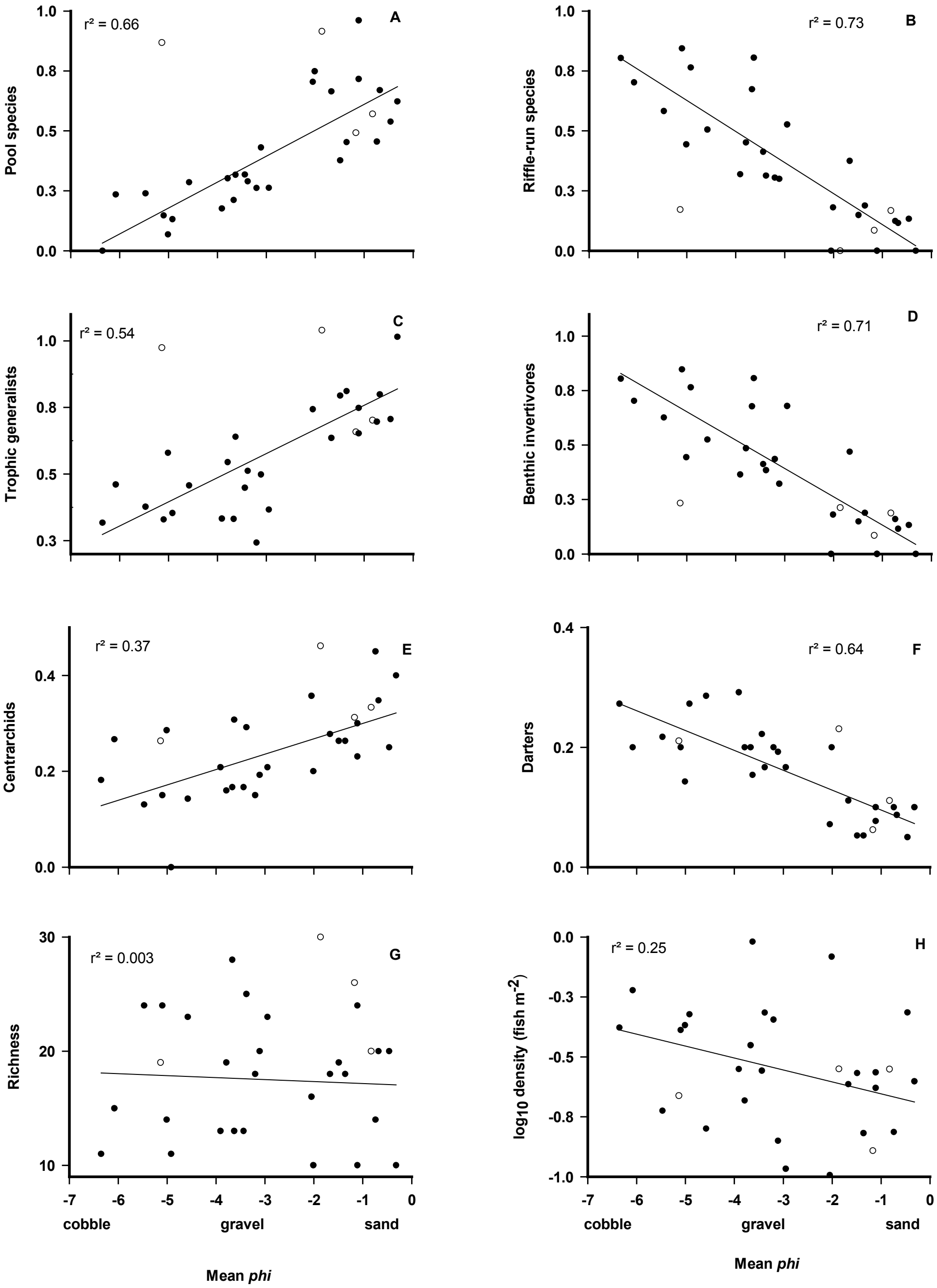

Figure 3.7. Linear regression of mean *phi* and fish assemblage variables. Open circles are sites with > 25% urban land cover and are not included in the analysis.

CHAPTER 4

EFFECT OF URBANIZATION ON FISH ASSEMBLAGES AND HABITAT QUALITY IN A PIEDMONT RIVER BASIN[1]

---

[1] Walters D. M., D.S. Leigh, M.C. Freeman, B.J. Freeman, and C.M. Pringle. To be submitted to *Environmental Monitorin*

Abstract: We quantified the relationships among urban land cover, fishes, and habitat quality to determine how fish assemblages respond to urbanization and if a habitat quality assessment can be used as an indirect measure of urban effects on stream ecosystems. We sampled 30 streams along an urban gradient (5-37% urban land cover) in the Etowah River basin, Georgia. Fish assemblage composition, sampled by electrofishing standardized stream reaches, was assessed as richness and abundance of key taxonomic groups and for endemic species as a group. Habitat quality was scored using a Rapid Habitat Assessment Protocol (RHAP) of the US Environmental Protection Agency. Urban land cover (including total, high-, and low-density urban) was estimated for the basin above each reach. Basins varied in area from 11-126 km^2 and reaches varied in slope from 0.001-0.01. Fish density and richness were correlated with basin area, but species composition was more strongly correlated with slope. Darters and sculpin, cyprinids, and endemics increased with slope whereas centrarchids declined. After accounting for the effects of drainage area and slope, richness and density declined with urban land cover. Darters and sculpin, cyprinids, endemic species also declined whereas centrarchids persisted and became the dominant group. RHAP scores were correlated with observed changes in fish assemblages; however, RHAP was more related to changes in stream slope ($r^2 = 0.66$) than urban land cover ($r^2 = 0.37$). Urban land cover was most strongly related to increases in centrarchids and decline of endemic species ($p < 0.001$). Residual analysis indicated that these effects were greatest for streams with > 15% urban land cover. Most of the development in the study area occurred after 1987, suggesting that fishes respond rapidly to urban development. We predict that the decline of

endemics and other species groups will accelerate and centrarchid-dominated streams will become the norm within the Etowah basin as urban development increases.

INTRODUCTION

Protecting stream resources from human impacts increasingly depends on understanding the linkages between urban land use and stream systems. Relatively low levels of basin urbanization (e.g., 10-20%) cause major changes in stream hydrology, geomorphology, water quality, and stream communities (Baer and Pringle 2000, Paul and Meyer 2001). Urban land cover, or associated variables such as impervious surface area, is linked to declines in fish richness, diversity, density, and biomass as well as changes in population structure of fishes and trophic structure of assemblages (Klein 1979, Scott et al. 1986, Lenat and Crawford 1994, Weaver and Garman 1994, Yoder et al. 1999). Urbanization is also associated with declines in biotic integrity, with increases in tolerant and exotic taxa, and with decline or extirpation of sensitive species (Wang et al. 1997, Boet et al. 1999, Onorato et al. 2000, Wang et al. 2000, Wolter et al. 2000).

In this study, we investigated the effects of urbanization on stream fishes in a southern Piedmont drainage characterized by exceptional species endemism as well as by local variation in assemblage composition. The southern Piedmont is among the most rapidly developing areas of the United States (U.S. Department of Agriculture 2000), and increasing urbanization will likely alter stream communities including fish assemblages. Although biotic integrity is known to decrease with urban sprawl (e.g., Steedman 1988, Wang et al. 1997), it is less clear if specific taxa (such as endemic species) vary predictably with increasing urban land cover. In addition, Walters et al. (*in review*) found that reach-level variation in assemblage structure was strongly linked to stream slope and associated benthic habitat variables in this Piedmont system. This led us to investigate whether an effect of increasing urban land cover on fishes would be detectable given spatial variation in fish assemblages driven by geomorphology. Spatial variation is a common feature of stream communities (Allan 1995); however, most prior studies of urbanization effects on fishes were limited to gradients in single streams or comparisons between urban and reference catchments (Paul and Meyer 2001). Multicatchment investigations of urban gradients and fishes are rare and have mostly focused on agricultural-dominated areas of the upper Midwest (e.g., Steedman 1988, Wang et al. 1997, Wang et al. 2000). Comparable studies are lacking for the Piedmont.

Questions associated with predicting urbanization effects on streams include the relative importance of different forms of urban development and development stage. Urban development in the southern Piedmont is characterized by high-density developments (i.e., commercial and industrial facilities) surrounded by low-density residential areas. Although other studies have shown that urbanization ultimately leads to a loss of biotic integrity and diversity from streams (e.g., Steedman 1988, Lenat and Crawford 1994), the relative impacts of high- and low-density urban development are unknown. In general, temporal effects of land cover change on streams have received less attention than spatial components of land cover change (Allan and Johnson 1997). It is unclear whether fish assemblages respond to disturbance during the initial development phase (e.g., increased sediment loading) or to the chronic, long-term effects of increased urban cover (e.g., altered hydrology and poor water quality). If urban effects accrue rapidly, then fish assemblages in recently urbanized catchments should exhibit changes in structure comparable to those with a longer history of equivalent levels of urbanization.

Another unknown in relation to urbanization effects on stream biota is the relative importance of changes in habitat quality, assessed relative to assumed ideal or reference conditions (sensu Barbour et al. 1999). Linking land use change with stream communities and habitat is a critical step in aquatic resource management (Jacobson et al. 2001). If habitat quality changes predictably with urban land cover and fish assemblages shift in response to habitat quality, then habitat quality assessment can be used as an indirect measure of urban effects on stream biota. However, studies in the Midwest have found that stream habitat quality is more strongly linked to agriculture than to urban development (Roth et al. 1996, Wang et al. 1997, Wang et al. 2001). If urbanization effects on biota precede gross structural changes to streams, then we could expect to find streams in urbanizing catchments with altered biotic assemblages that also appear to have high habitat quality. Conversely, strong correlations among fish assemblage structure, urban land cover, and stream habitat quality would support the use of habitat indices in streams draining urbanizing catchments.

The spread of urban development into relatively rural catchments presents a unique opportunity to examine the complex effects of urbanization on fishes. This study addresses the following questions: (1) How do fish assemblages change along an urban gradient? (2) Which urban land cover categories (i.e., low- and high-density urban) best predict changes in fish assemblages? (3) What is the relative power of past and more recent land cover to predict changes in fish assemblages? and (4) Does a widely-used measure of habitat quality reflect urbanization effects on fish assemblages?

METHODS

Study area and research design

This study was conducted in wadeable tributaries of the Etowah River basin (Figure 4.1), which forms part of the upper Coosa River drainage. Portions of the Etowah basin lie in the Blue Ridge, Ridge and Valley, and Piedmont physiographic provinces of the Southern Appalachian Highlands (Figure 4.1). The Southern Appalachian Highlands are a center of stream fish biodiversity and endemism (Williams et al. 1992, Warren and Burr 1994, Warren et al. 2000), and Burkhead et al. (1997) estimated that 91 species from 18 families are native to the Etowah system. The most diverse families are Cyprinidae (31 spp.), Percidae (19 spp.), and Centrarchidae (13 spp.). Warren et al. (1997) classified 16 species of the Tallapoosa and Coosa River systems as endemic, a level of endemic species richness unsurpassed in Southeastern river systems.

Land cover in the Etowah basin comprises a mixture of forest, agriculture, and urban (Leigh et al. 2001). Agricultural land use is primarily pasture for hay production and grazing, and row crops are a minor component. Recent urban development in the basin is driven by population increases fueled by the spread of metropolitan Atlanta. Several counties have experienced exponential population growth that began in the 1970s and 1980s. The southern most counties near Atlanta show the greatest population increases (Figure 4.1, inset), and Forsyth and Paulding counties were among the 10 fastest growing counties in the United States in 1997 (U.S. Census Bureau 1998).

We randomly selected 32 streams ranging from 0-50% urban land cover based on 1993 land cover (Hermann 1996), the best data available during the site selection process. The streams were stratified into three watershed size groups of approximately 15, 50, and

100 km^2 (+/- 25%) referred to as small, medium, and large streams throughout the text (Figure 4.1). Two sites (Site 3 at 22 km^2 and Site 21 at 126 km^2) slightly exceeded our size criteria after final measurements of basin size were made (Appendix 4.1). All sample reaches are in the Piedmont, but a few of the catchments have headwaters in the Blue Ridge. Two sites were not considered for this analysis (final n = 30 sites). Beavers dammed site 2 before we sampled for fishes, and the most recent available land cover data showed that urban lands upstream of site 23 exceeded our arbitrary limit of 50% (Lo and Yang 2000). None of the land cover variables could be normalized unless this site was removed from the analysis.

Fish sampling and assemblage variables

Fishes were sampled during baseflow conditions in summer and early fall of 1999 and 2000. Reach length was scaled to approximately 40 times the average baseflow water width within each stream size group, a reach slightly longer than the 35 times stream width recommended by Simonson and Lyons (1995) to assess fish assemblages in wadeable streams. Thus, reaches of 200, 300, and 400 meters, were sampled in small, medium, and large streams, respectively. Reaches were sampled in a single pass (Simon and Lyons 1995) using a crew of four to six persons equipped with a backpack electric shocker, seine, and dipnets. Reaches were divided into two sections of equal length. The first half of the reach (i.e., 20 times mean width) was sampled to obtain quantitative catch data for calculating relative abundances (Angermeier and Smogor 1995). Large individuals (> 20 cm) and fishes with protected status were counted and released. All other fishes were euthanized and preserved for laboratory identification. The second half of the reach was sampled to improve our estimate of site species richness, and we retained voucher specimens of species not observed in the first half of the reach.

Assemblage variables used for analyses included richness and density as well as the relative contribution of selected taxonomic groups (Table 4.1). Centrarchids, darters and cyprinids were selected as the primary taxonomic groups because they comprise over 70% of the species we collected, and Walters et al. (*in review*) found that these groups were correlated with among-site differences in species composition in these streams. Sculpin were included with darters because they utilize similar benthic habitats and prey (Etnier and Starnes 1993). We also included insectivorous cyprinids, a subgroup of cyprinids commonly used as a positive indicator in biotic indices (Miller et al. 1988). In addition to these major species groups, we included a category for endemic species (i.e., fishes distributed primarily in the upper Alabama River basin above the Fall Line (Mettee et al. 1996); Appendix 4.2). Several of these species (e.g., *Etheostoma jordani)* also occur at a few scattered locations below the Fall Line on the Coastal Plain of Alabama. All endemics were either darters or cyprinids except for *Cottus carolinae zopherus*, a taxonomically distinct form of banded sculpin endemic to the upper Coosa system (Etnier and Starnes 1993).

Contribution of each species group was calculated as the number of species, the proportion of total richness (i.e., the number of species in each group divided by total richness) and as the proportion of total catch (i.e., relative abundance). Measures of proportional richness are not commonly used in assemblage studies. We used these variables because they can identify groups that persist relative to other species and they can identify patterns in species composition even if overall richness is similar among sites. Numbers of species and proportional richness were derived from species lists compiled from the entire sampled reach (i.e., 40 times stream width). Relative abundance was calculated using catch data from the first half of each reach. Relative abundance of darters was calculated without *Percina nigrofasciata*, a species that is widespread and locally common in the Etowah system (Walters et al., *in review*).

Stream and catchment characteristics

Stream slope was surveyed with an electronic total station over reaches scaled to approximately 20 times the average baseflow width for streams in each size class (i.e., 100, 150, and 200 m reaches). Slope was measured as the average gradient through the tops of riffles. ArcView® software was used to calculate area and percentage of urban land cover for catchments. Catchment boundaries upstream of sample sites were delineated on digital raster graphics of the latest 7.5 minute USGS quadrangles. ArcView® software was used to quantify the percentage of urban land cover within the catchment boundaries.

We used the USEPA Rapid Habitat Assessment Protocol (RHAP) to assess stream habitat quality (Barbour et al. 1999). RHAP uses ten metrics to assess the condition of various stream habitat parameters including benthic habitat quality, channel and bank condition, instream habitat heterogeneity, and riparian vegetation. Each metric is scored on a continuous scale ranging from 0-20 based on a visual assessment of the habitat feature. Metric scores were averaged for an overall RHAP score. We assessed habitat metrics over the entire reach sampled for fishes. RHAP was usually calculated the same day as fish sampling and was always evaluated at baseflow to allow comparisons among all sites. Two to four investigators completed RHAP at each site, and final scores were based on the mean of multiple assessments.

Land cover data were derived from Landsat TM images from June 1987 and July 1997 (Lo and Yang 2000). The images have 25 m resolution and overall classification accuracy of about 90%. Two urban land cover types were classified. High-density urban (HDU) is approximately 80-100% construction material and includes commercial buildings, parking lots, residential development within city cores, and multi-lane highways. Low-density urban (LDU) is roughly 50-80% construction material and is characterized by single or multiple family housing developments and two-lane roads. LDU and HDU were summed to calculate total basin urban land cover (U). Totals from 1987 were subtracted from 1997 totals to calculate the percentage of basin area converted during the decade. A few rural basins had slightly less (e.g. < 2%) urban land cover in 1997 than 1987. We attributed this decline to small error in the accuracy of the data rather than actual loss of urban land. For these catchments, we assigned a value of 0 for 1987-1997 change. We limited our spatial scale to land cover of the entire catchment to assess the total impact of urbanization within a basin (sensu Wang et al. 1997).

Data analysis

Normality of all variables was checked using the Kolmogorov-Smirnov (KS) test using SigmaStat 4.0® and transformations were applied if needed (Table 4.1). Land cover percentages were converted to proportions and transformed using arc-sine (square-root (x)) for correlation analysis. Untransformed land cover data were used in some scatter plots to illustrate trends and identify possible thresholds in the response of dependent variables. Land cover variables covary to some extent because as one element increases, others decline (Cain et al. 1997). The urban variables used in this study suffer from a lack of independence. For instance, all 1987 urban cover is contained in the 1997 urban cover because urbanized land seldom reverts to agricultural or forested cover. We used correlation analysis to quantify autocorrelation among land cover variables.

Relationships among fishes, land cover, geomorphology, and habitat quality were quantified using correlation analysis, linear regression, and nonlinear regression. We report actual probability values for tests, unadjusted for potential inflation of Type I error rate resulting from multiple analyses derived from a single dataset. Relative predictive power of independent variables was assessed based on Pearson's *r* and *p* values. If scatter plots indicated nonlinear relationships between variables, curves were fit to the data using nonlinear equations derived from Sigma Plot 4.0®. We used forward stepwise multiple regression analysis to build models for proportional richness, relative abundance, and RHAP. This procedure allowed us to assess the relative influence of geomorphology and land cover on the dependent variables and to identify the strongest predictors among urban categories. The common $\log_{10}$ transformation is a robust and widely used transformation for nonlinear data (Ott 1988), and we used it as a general transformation for stream slope in multiple linear regression analysis. Other nonlinear equations provided a better fit for some dependent variables, but these transformations (e.g., sigmoidal) were variable specific and complicated comparisons among models. Additionally, geomorphic analysis at these sites indicated that $\log_{10}$ was the most appropriate transformation for linking stream slope with other physical variables (e.g., particle size distribution, Leigh, unpublished data).

RESULTS

Land cover

Low-density urban (LDU) accounted for about 87% of urban (U) land cover (Figure 4.2). Mean U across basins increased 83% from 1987-97. Mean HDU only increased from 1.1 to 1.7% over the decade, so most of the increase in U resulted from changes in LDU. Most 1987 and 1997 variables were autocorrelated (r = 0.70-0.99, Table 4.2). Correlation among land cover variables was highest among categories within a single year (r values 0.85-0.99). Between years, the strongest correlations were within a category (e.g., 1987 U and 1997 U, r = 0.85). Correlations of 1987 and 1997 land cover with the 1987-97 percent urban change were weaker, although all correlations with 1997 land cover were significant (Table 4.2). Basin area and stream slope was unrelated to any urban variables except for a weak correlation between slope and 1987-97 LDU.

Correlations of fishes and RHAP with urban land cover, basin area and slope

Fish assemblage variables showed significant correlations with urban land cover as well as with slope and basin area. Darters and sculpin, cyprinids, insectivorous cyprinids, and endemics generally increased with slope and decreased with urban land cover, whereas these trends were reversed for centrarchids (Table 4.3). Basin area was positively correlated with the number of centrarchids, cyprinid, and insectivorous cyprinid species, as well as overall richness and density and relative abundance of insectivorous cyprinids. Slope, however, was more strongly correlated with species numbers for darters and sculpin, endemics and centrarchids, all proportional richness variables, and the relative abundances of darters and sculpin, and endemics. Urban land cover was most strongly correlated (positively) with relative abundances of centrarchids and (negatively) with all measures of endemic species (Table 4.3). Land cover variables for 1997 and 1987-97 were most frequently correlated with fish variables, and 1997 U had the highest mean Pearson's *r* (Table 4.3).

Plots of untransformed data revealed strongly nonlinear relations between assemblage variables and either slope or land cover. For example, a sigmoidal relation with slope explained 70% of the variance in proportion of endemic species (Figure 4.3A), one of the variables most strongly correlated with urban land cover. Relative abundance of endemics also exhibited strong correlations with slope and land cover, but the data were strongly non-normal (Table 4.1) and so were not analyzed further. The proportion of endemics was 0.1 or less in streams with slopes < 0.002, increased sharply in streams with slopes of 0.002-0.004, and was consistently above 0.2 in streams > 0.004. Slope explains about 90% of the variance in mean particle size in these streams (Walters et al. *in review*), so the increase in proportional richness of endemics corresponded with a predictable coarsening of the stream bed (Figure 4.3A). Proportion of endemics also declined nonlinearly with increasing urban land cover (Figure 4.3B), decreasing sharply as urban approached about 15% of total cover and then mostly scoring low at higher levels of urban cover.

RHAP scores increased with slope and decreased with urban land cover (Table 4.2), similar to the non-centrarchid fish variables. RHAP had a sigmoidal relationship with slope with thresholds similar to those observed for the proportion of endemic species (Figure 4.4A). RHAP also similarly declined with urban land cover, although the most urbanized catchment, site 111, was a large positive outlier (Figure 4.4B). RHAP was also strongly correlated with fish assemblage characteristics (Table 4.3); the relation with proportion of endemics is illustrated in Figure 4.4C. RHAP scores appeared to be bimodal with no streams scoring between 9.6 and 11.4 (Figure 4.4C), but scores did not significantly depart from a normal distribution (KS test, $p=0.09$).

Quantifying urban effects

We used linear regression analysis to test the hypothesis that urban land cover explained variance remaining after accounting for effects of slope and/or basin area on fish assemblage variables and RHAP scores. First, however, we tested whether a $\log_{10}$ transformation of slope was appropriate given the strong sigmoidal relations observed for proportion of endemic species (and RHAP) with slope. Residuals from models of proportion of endemics versus either sigmoidal or $\log_{10}$ transformations of slope were significantly negatively correlated with 1997 U (Figure 4.5). Although the sigmoidal transformation explained more variance in the proportion of endemics (Figure 4.5A), residuals from the $\log_{10}$ model were more strongly correlated with 1997 U (Figure 4.5C). Using either model, as urbanization increased, the proportion of endemics observed was lower than predicted by reach slope. Given the explanatory power of urban land cover for residuals from this $\log_{10}$ slope model, and the significant correlations observed between most fish assemblage variables and $\log_{10}$ slope (Table 4.3), we used this transformation of slope in multiple linear regression models.

Multiple linear regression models of fishes and habitat quality

Drainage area and slope were the primary predictors of RHAP and fish assemblage variables (Table 4.4). Slope was selected first for RHAP and several species composition variables. We treated slope as a background environmental factor and manually entered $\log_{10}$slope into models for centrarchids and proportion of cyprinids based on correlations reported in Table 4.3. After accounting for variation attributable to stream slope and basin area, urban land cover was significantly related to all of the dependent variables except relative abundance of insectivorous cyprinids. Centrarchids increased with basin urbanization whereas RHAP, darters and sculpin, endemics, cyprinids, and insectivorous cyprinids declined. Richness was significantly correlated with urbanization, but basin area and slope explained most of the variance in richness (i.e. 59%). Compared with richness, the effect of urbanization was stronger for density. Models for cyprinids and insectivorous cyprinids were the weakest among species groups, and urban land was unrelated to relative abundance of insectivorous cyprinids. Endemics and centrarchids responded most strongly to urban land cover. In general, models explained more variance in proportional richness than relative abundance.

High-density urban variables were selected in seven of the 11 models that included land cover. The 1997 urban variables were selected most frequently (n = 6 models) compared to 1987 (n = 3) and 1987-1997 (n = 2) variables. A 1987 urban variable was selected for models of richness as well as the proportion of endemics and insectivorous cyprinids. We conducted a second stepwise procedure on these variables that excluded 1987 urban cover. In all three cases, the procedure selected 1997 variables from the same category (e.g., 1997 HDU replaced 1987 HDU for richness) with little loss of explanatory power (i.e., cumulative r^2 reduced by 0.01-0.03).

Urban land cover was most highly correlated with the relative abundance of centrarchids and the proportion of endemics. We regressed residuals from the $\log_{10}$slope models of these variables against 1997 U to illustrate spatial and temporal trends in the response of these species groups (Figure 4.6). Catchments were categorized as having > 10% U in 1987, < 10% U in 1987 but > 10% in 1997, and < 10% U in 1997. Catchments with >10% U in 1987 tended to have the highest urban cover indicating that the most heavily urbanized catchments have also been urbanized for the longest time. The largest residuals in both models were from the most developed basins. At levels > 15% U, the majority of residuals from the centrarchid model were positive and all but three of the residuals from the endemic model were negative. Thus, for basins with > 15% U, observed centrarchid relative abundance is usually higher and the proportion of endemics is consistently lower than predicted by slope.

Urbanization led to higher relative abundance of centrarchids even in the steepest streams. Pie charts (Figure 4.6C) compared the relative abundance of fishes from two sites of similar size and slope but different levels of urban cover. Site 111 had the steepest slope we observed (0.01) and plots as a large positive residual in Figure 4.6B. Slope accurately predicted relative abundance of centrarchids we observed at site 20 (slope = 0.007). Centrarchids were 59.2% of the catch at site 111 in contrast to the general trend for lower centrarchids abundance at high slope streams (Table 4.3). As noted above, RHAP for site 111 also scored higher than predicted from urban land cover.

DISCUSSION

Relationships among fishes, urban land cover, geomorphology, and RHAP

Our results showed that urbanization effects on fishes are detectable even in systems with strong geomorphic control of fish assemblages. Stream size predicted richness and density, and species composition changed along a slope gradient from darter, sculpin, cyprinid complexes characterized by a high degree of endemism to assemblages dominated by centrarchids. As urban land cover increased, richness and density declined, and centrarchids became the dominant group as other species declined or were locally extirpated. By disrupting geomorphic control of among-site differences in fishes, urban development homogenizes (sensu McKinney and Lockwood 2001) fish faunas at the broader scale of the Etowah basin. As catchments urbanize, stream assemblages acquire the characteristics we would expect of assemblages in smaller, low slope streams (i.e., low richness, low endemism, and centrarchid dominance).

Even though we documented stronger relationships between habitat quality and urban land cover than other studies (Roth et al. 1996, Wang et al. 1997, Wang et al. 2001), local slope was the primary predictor and explained two-thirds of the variance in RHAP scores. This strong relationship exists because slope is a primary determinant of benthic habitat at these sites (Walters et al. *in review*) and RHAP includes several metrics to assess benthic habitat quality (e.g., epifaunal substrate, sediment deposition, and embeddedness; Barbour et al. 1999). These results suggest that RHAP may be a poor indicator of human disturbance in steep streams. Alternatively, steep streams may be more resilient to some types of disturbance (e.g., excessive sediment inputs) and maintain higher quality habitats relative to low slope streams. The range of urban land cover in our study was 4.9-37.3% and most of this land was converted within the last 20 years. We predict that more obvious changes in stream habitat (e.g., severe bank erosion and channel incision) will be prevalent as urban land cover increases or as catchments are urbanized for longer time periods.

Our results indicate that including geomorphic variables in models will improve our understanding of land use impacts on stream communities. Several studies have found that fish richness, abundance, and biotic integrity decline with urbanization (e.g., Lenat and Crawford 1994, Onorato et al. 2000, Wang et al. 2000). After accounting for changes in richness associated with geomorphology, urban land cover only explained about 5% of the total variance in richness among sites. These results support the findings of Scott and Helfman (2001) that human disturbance of Southern Appalachian streams may lead to minor changes in species richness but major changes in species composition. Measures of fish assemblage health such as the index of biotic integrity (IBI, Karr 1981) are designed to account for variability associated with stream size. Our results indicate that stream slope may also warrant consideration in fish biotic indices, at least in wadeable Piedmont streams.

Changes in fish assemblages

The number, proportional richness, and relative abundance of darters and sculpin increased with stream slope. Six of these species were included in the endemic group (Appendix 4.2) and the endemics showed a similar increase with slope. All of these species demonstrate a high degree of benthic specialization (Etnier and Starnes 1993, Jenkins and Burkhead 1994, Burkhead et al. 1997). They spawn on or in coarse particles, feed benthically or primarily on benthic macroinvertebrates, and are morphologically adapted (e.g., reduced air bladder, large pectoral fins, and dorso-ventral compression (Helfman et al. 1997)) for high-velocity, riffle-run habitats prevalent in steep streams. Darters as a group are considered to be sensitive to disturbance (Kuehne and Barbour 1984, Jenkins and Burkhead 1994) and endemics suffer a higher degree of imperilment and extinction risk than other taxa (Meffe and Carrol 1994, Angermeier 1995). We found that both groups declined with increasing urban land cover, and similar results were reported for darters in urban streams in Alabama (Onorato et al. 2000) and for the response of endemics to catchment disturbance in Southern Appalachia (Scott and Helfman 2001).

We found that centrarchid relative abundance and proportional richness increased with urban land cover. We analyzed data published by Weaver and Garman (1994, Table 2) for six reaches in a Piedmont stream in Virginia and found the same trend. In their data, centrarchid proportional richness increased from 0.24-0.41 and relative abundance almost doubled from 0.25-0.48 following urban development. As in the Etowah streams, these increases occurred because centrarchids persisted in urban streams whereas other fishes declined or were extirpated. Our findings contribute to a growing body of evidence that centrarchids are more resilient to disturbance than other stream fishes (Detenbeck et al. 1992). Centrarchids increase with turbidity, bed sedimentation, riparian deforestation, and agricultural land cover in other southeastern river systems (Jones et al. 1999, Meyer et al. 1999, Walser and Bart 1999) and Waite and Carpenter (2000) found that introduced populations of centrarchids increased along disturbance gradients in the Willamette River, Oregon. Centrarchid richness was used as a positive indicator of stream integrity in the original IBI and in subsequent regional variations (Karr 1981, Miller et al. 1988, Shaner 1999, Schleiger 2000). Our results, together with the studies reviewed above, suggest that the use of centrarchids as a positive indicator may confound measures of stream health.

Among the species groups we investigated, cyprinids and insectivorous cyprinids were the least correlated with geomorphic and urban land cover gradients (i.e., multiple linear regression models $r^2 = 0.20\text{-}0.34$). Models for these groups may be weak because these fishes respond to variables we did not consider in this analysis (e.g., water chemistry and predation pressure) or because cyprinids exhibit too much ecological variability to model effectively as a group. Based on life history information provided in Jenkins and Burkhead (1994) and Etnier and Starnes (1993), the cyprinids we collected belong to six spawning guilds, three feeding guilds, and prefer habitats ranging from pools to riffles (Walters et al., *in review*). We developed much stronger models for centrarchids, darters and sculpin, and endemics, and these species have greater within group ecological similarity (Etnier and Starnes 1993, Jenkins and Burkhead 1994).

Comparisons among urban land cover categories

It was difficult to identify a single "best" land cover variable because they all covaried and lacked independence to some degree. Percent 1997 U was the best predictor in bivariate analysis and was selected in several multiple linear regression models. This suggests that total urban cover most contemporaneous with stream sampling will be an adequate predictor for associative studies. Because LDU is the dominant form of urban land cover in these catchments, it was virtually indistinguishable from the total U. HDU variables were selected most frequently by the forward stepwise procedure even though HDU accounted for a small fraction of total U. This suggests that HDU may have a disproportionate impact on stream systems compared with LDU. HDU has a higher proportion of impervious surface coverage, a key element of the urban landscape that contributes to stream degradation (Klein 1979, Arnold and Gibbons 1996, Booth and Jackson 1997). High- and low-density urban land cover may affect stream systems differently, but they are both integral parts of the urban landscape. Our results indicate that an aggregate variable, total urban, is a robust predictor of changes in fish species composition.

Future of urbanizing catchments

Fishes responded to low levels of urban development and our results suggest that the response occurred over a relatively short time period. Residual analysis indicated that effects were most pronounced for catchments that 1) had > 10% U for at least ten years, or 2) had > 15 % U. These results are consistent with other urban gradient studies that found that stream ecosystems respond strongly to low levels of urban land cover or impervious surface coverage (Klein 1979, Booth and Jackson 1997, Wang et al. 2001, and studies reviewed by Paul and Meyer 2001). Putting this level of 15% U within the context of land cover change from 1987-1997 provides clues to the time frame over which assemblages changed and to future fish assemblages. In 1987, only three of the study basins had > 15% U. By 1997, 13 catchments exceeded this level, and the mean was 14.8%. Declines of endemics and increases in centrarchids may be recent; however, we cannot test this hypothesis in the absence of historical collection data. The pace of urban development has not slowed since 1997, and most of these basins will surely surpass 15% U within the next decade. Given this scenario, we predict that the decline of endemics and other species groups will become more acute and that centrarchid-dominated streams will become the norm within the Etowah basin.

ACKNOWLEDGEMENTS

Funding was provided by a grant from the US Environmental Protection Agency (EPA R826597-01-0) with additional support from the University of Georgia Research Foundation and the Georgia Museum of Natural History. We thank A. Bearden, T.

Burgess, K. Costly, and L. Ormes for help in the field, Dr. C.P. Lo for land cover data, and G. Helfman and A. Rosemond for commenting on an earlier version of this manuscript.

REFFERENCES

Allan, J. D. 1995. Stream Ecology: Structure and Function of Running Waters. Chapman & Hall, New York, New York.

Allan, J. D., and L. B. Johnson. 1997. Catchment-scale analysis of aquatic ecosystems. Freshwater Biology 37:107-111.

Angermeier, P. L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conservation Biology 9:143-158.

Angermeier, P. L., and R. A. Smogor. 1995. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. Canadian Journal of Fisheries and Aquatic Science 52:936-949.

Arnold, C. L., and C. J. Gibbons. 1996. Impervious surface coverage: the emergence of a key environmental indicator. Journal of the American Planning Association 62:243-258.

Baer, K. E., and C. M. Pringle. 2000. Special problems of urban river conservation: the encroaching megalopis. Pages 381-398 *in* P. J. Boon, B. R. Davis, and G. E. Potts, editors. Global Perspectives on River Conservation. John Wiley & Sons Ltd., London, U.K.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid Bioassessment Protocols for Use in Wadeable Streams and Rivers: Periphyton, Benthic Macroinvertebrates, and Fish, Second Edition. EPA 841-B-99-002, Office of Water, Washington, D.C.

Boet, P., J. Belliard, R. Berrebi-dit-Thomas, and E. Tales. 1999. Multiple human impacts by the City of Paris on fish communities in the Seine river basin, France. Hydrobiologia 410:59-68.

Booth, D. B., and C. R. Jackson. 1997. Urbanization of aquatic systems: degradation thresholds, stormwater detection, and the limits of mitigation. Journal of the American Water Resources Association 33:1077-1090.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled Southern Appalachian ecosystem. Pages 375-444 *in* G. W. Benz and D. E. Collins, editors. Aquatic Fauna in Peril, the Southeastern Perspective. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Cain, D. H., K. Riitters, and K. Orvis. 1997. A multi-scale analysis of landscape statistics. Landscape Ecology 12:199-212.

Detenbeck, N. E., P. W. Devore, G. J. Niemi, and A. Lima. 1992. Recovery of temperate-stream fish communities from disturbance - a review of case-studies and synthesis of theory. Environmental Management 16:33-53.

Etnier, D. A., and W. C. Starnes. 1993. The Fishes of Tennessee. The University of Tennessee Press, Knoxville, Tennessee.

Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. The Diversity of Fishes. Blackwell Science, Malden, Massachusetts.

Hermann, K. A. 1996. The Southern Appalachian Assessment GIS Data Base CD ROM Set. *in*. The Southern Appalachian Man and the Biosphere Program, Norris, TN.

Jacobson, R. B., S. D. Femmer, and R. A. McKenney. 2001. Land Use Changes and the Physical Habitat of Streams - a Review with Emphasis on Studies within the U.S. Geological Survey Federal-State Cooperative Program. Circular 1175, U.S. Geological Survey, Restin, Virginia.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater Fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Jones, E. B. D., III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conservation Biology 13:1454-1465.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Klein, R. D. 1979. Urbanization and stream quality impairment. Water Resources Bulletin 15:948-963.

Kuehne, R. A., and R. W. Barbour. 1984. American Darters. University of Kentucky Press, Lexington, Kentucky.

Leigh, D. S., B. J. Freeman, M. C. Freeman, E. K. Kramer, A. D. Rosemond, M. J. Paul, C. M. Pringle, D. M. Walters, A. Roy, and C. P. Lo. 2001. Overview of land cover and geomorphic indicators of biotic integrity in the Etowah River Basin, Georgia. Pages 225-228 *in* K. J. Hatcher, editor. 2001 Georgia Water Resources Conference. Institute of Ecology, The University of Georgia, Athens, Georgia.

Lenat, D. R., and J. K. Crawford. 1994. Effects of land-use on water-quality and aquatic biota of 3 North-Carolina Piedmont Streams. Hydrobiologia 294:185-199.

Lo, C. P., and X. Yang. 2000. Mapping the dynamics of land use and land cover change in the Atlanta Metropolitan Area using the time sequential Landsat images. *in* Proceedings of the Annual Meeting of the American Society of Photogrammetry and Remote Sensing, Bethesda, MD.

McKinney, M. L., and J. L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. *in* J. L. Lockwood and M. L. McKinney, editors. Biotic Homogenization. Kluwer Academic/Plenum Publishers, New York, New York.

Meffe, G. K., and C. R. Carrol. 1994. Principals of Conservation Biology. Sinauer Associates Inc, Sunderland, Massachusetts.

Mettee, M. F., P. E. O'Neil, and J. M. Pierson. 1996. Fishes of Alabama and the Mobile Basin. Oxmore House Inc, Birmingham, Alabama.

Meyer, J. L., A. B. Sutherland, K. H. Barnes, D. M. Walters, and B. J. Freeman. 1999. A scientific basis for erosion and sedimentation standards in the Blue Ridge physiographic province. Pages 321-324 *in* K. J. Hatcher, editor. 1999 Georgia Water Resources Conference. Institute of Ecology, The University of Georgia, Athens, Georgia.

Miller, D. L., P. M. Leonard, R. M. Hughes, J. R. Karr, P. B. Moyle, L. H. Schrader, B. A. Thompson, R. A. Daniels, K. D. Fausch, G. A. Fitzhugh, J. R. Gammon, D. B. Halliwell, P. L. Angermeier, and D. J. Orth. 1988. Regional applications of an Index of Biotic Integrity for use in water resource management. Fisheries 13:1220.

Onorato, D., R. A. Angus, and K. R. Marion. 2000. Historical changes in the ichthyofaunal assemblages of the upper Cahaba River in Alabama associated with extensive urban development in the watershed. Journal of Freshwater Ecology 15:47-63.

Ott, R. L. 1988. An Introduction to Statistical Methods and Data Analysis, Fourth Edition. Duxbury Press, Belmont, California.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333-365.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.

Schleiger, S. L. 2000. Use of an index of biotic integrity to detect effects of land uses on stream fish communities in west-central Georgia. Transactions of the North American Fisheries Society 129:1118-1113.

Scott, J. B., C. R. Steward, and Q. J. Stober. 1986. Effects of urban-development on fish population-dynamics in Kelsey Creek, Washington. Transactions of the American Fisheries Society 115:555-567.

Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26:6-15.

Shaner, B. L. 1999. Development of a standardized index of biotic integrity for the Piedmont region of Georgia. Pages 287-290 *in* K. J. Hatcher, editor. 1999 Georgia Water Resources Conference. Institute of Ecology, The University of Georgia, Athens, Georgia.

Simon, T. P., and J. Lyons. 1995. Application of the index of biotic integrity to evaluate water resource integrity in freshwater ecosystems. Pages 245-262 *in* W. S. Davis and T. P. Simon, editors. Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. CRC Press, Boca Raton, Florida, USA.

Simonson, T. D., and J. Lyons. 1995. Comparison of catch per effort and removal procedures for sampling stream fish assemblages. North American Journal of Fisheries Management 15:419-427.

Steedman, R. J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. Canadian Journal of Fish and Aquatic Sciences 45:492-501.

U.S. Census Bureau. 1998. U.S. Department of Commerce News. CB98-41, Washington D.C.

U.S. Census Office. 1930-2000. Census of the United States. Department of the Interior, Washington, D. C.

U.S. Department of Agriculture. 2000. 1997 National Resource Inventory. Percent Change in Developed Land Area. http://www.nhq.nrcs.usda.gov/land/meta/m5010.html.

Waite, I. R., and K. D. Carpenter. 2000. Associations among fish assemblage structure and environmental variables in Willamette Basin streams, Oregon. Transactions of the American Fisheries Society 129:754-770.

Walser, C. A., and H. L. Bart Jr.. 1999. Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River system. Ecology of Freshwater Fish 8:237-246.

Walters, D.M., D. S Leigh, M. C. Freeman, B. J. Freeman, and C. M. Pringle. Geomorphic influence on fishes in a southern Piedmont river system. *In review.*

Wang, L. Z., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28:255-266.

Wang, L. Z., J. Lyons, P. Kanehl, R. Bannerman, and E. Emmons. 2000. Watershed urbanization and changes in fish communities in southeastern Wisconsin streams. Journal of the American Water Resources Association 36:1173-1189.

Wang, L. Z., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22:6-12.

Warren, M. L., Jr., B. M. Burr, S. J. Walsh, J. H.L. Bart, R. C. Cashner, D. A. Etnier, B. J. Freeman, B. R. Kuhajda, R. L. Mayden, H. W. Robison, S. T. Ross, and W. C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25:7-31.

Warren, M. L., Jr., P. L. Angermeier, B. M. Burr, and W. R. Haag. 1997. Decline of a diverse fish fauna: patterns of imperilement and protection in the southeastern United States. Pages 105-164 *in* G. W. Benz and D. E. Collins, editors. Aquatic Fauna in Peril, the Southeastern Perspective. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Warren, M. L., Jr., and B. M. Burr. 1994. Status of freshwater fishes in the United States: overview of an imperiled fauna. Fisheries 19:6-18.

Weaver, L. A., and G. C. Garman. 1994. Urbanization of a watershed and historical changes in a stream fish assemblage. Transactions of the American Fisheries Society 123:162-172.

Williams, J. D., J. M. L. Warren, K. S. Cummings, J. L. Harris, and R. J. Neves. 1992. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18:6-22.

Wolter, C., J. Minow, A. Vilcinskas, and U. A. Grosch. 2000. Long-term effects of human influence on fish community structure and fisheries in Berlin waters: an urban water system. Fisheries Management and Ecology 7:97-104.

Yoder, C. O., R. J. Miltner, and D. White. 1999. Assessing the status of aquatic life designated uses in urban and suburban watersheds. EPA/625/R-99/002.

Table 4.1. Fish assemblage variables used in correlation and regression analysis.

Fish assemblage variable	Description	Transformation
Richness[a]	total species	$\log_{10}(x)$
Density[b]	fishes m^{-2}	$x^{0.25}$
Number of species[a]		
darters and sculpin		none
centrarchids		none
cyprinids		none
insectivorous cyprinids		none
endemic species		none
Proportion of species[a]		
darters and sculpin	# (darters and sculpin)/richness	none
centrarchids	# centrarchids/richness	none
cyprinids	# cyprinids/richness	none
insectivorous cyprinids	# insectivorous cyprinids/richness	none
endemic species	# endemics/richness	none
Relative abundance[b]		
darters and sculpin	abundance/total catch	none
centrarchids	abundance/total catch	arc-sine(square-root (x))
cyprinids	abundance/total catch	none
insectivorous cyprinids	abundance/total catch	none
endemic species	abundance/total catch	none (unable to normalize)

[a] Calculated from total reach (40 X stream width)

[b] Calculated from first half of reach (20 X stream width). See Methods for details.

Table 4.2. Correlation matrix (Pearson's *r*) of independent variables. Land cover abbreviations: U = Urban; HDU = High Density Urban; LDU = Low Density Urban. All land cover variables are transformed percentages: arc-sine (square-root (x)). Correlations significant at $p < 0.05$ are in bold; $p < 0.01$ are in bold and italics; $p < 0.001$ are in bold, italics, and underlined.

	basin area (km^2)	$\log_{10}$ slope	1987 % U	1987 % HDU	1987 % LDU	1997 % U	1997 % HDU	1997 % LDU	1987-97 % U	1987-97 % HDU	1987-97 % LDU
basin area	1										
$\log_{10}$ slope	**-0.37**	1									
1987 U	-0.10	0	1								
1987 HDU	-0.18	0.10	***0.90***	1							
1987 LDU	-0.07	-0.02	***0.99***	***0.86***	1						
1997 U	-0.11	-0.17	***0.85***	***0.75***	***0.85***	1					
1997 HDU	-0.22	0.04	***0.82***	***0.86***	***0.78***	***0.84***	1				
1997 LDU	-0.08	-0.20	***0.83***	***0.70***	***0.83***	***0.99***	***0.78***	1			
1987-97 U	-0.04	-0.35	**0.36**	0.28	**0.38**	***0.79***	***0.50***	***0.82***	1		
1987-97 HDU	-0.11	-0.03	0.35	0.31	0.34	***0.58***	***0.74***	***0.53***	***0.56***	1	
1987-97 LDU	-0.04	**-0.37**	0.35	0.26	**0.36**	***0.77***	**0.43**	***0.81***	***0.99***	**0.46**	1
RHAP	-0.08	***0.66***	***-0.47***	**-0.42**	***-0.47***	***-0.56***	***-0.48***	***-0.56***	***-0.47***	-0.31	**-0.46**

Table 4.3. Correlations of physical characteristics and basin urban land cover with fish assemblage variables (n = 30 sites). All correlations are Pearson's *r* except for relative abundance of endemics (Spearman's *r*) which could not be normalized. Land cover abbreviations: U = Urban; HDU = High Density Urban; LDU = Low Density Urban. All land cover variables are transformed percentages: arc-sine (square-root (x)). Fish assemblage variables and transformations are defined in Table 4.1. Correlations significant at $p < 0.05$ are in bold; $p < 0.01$ are in bold and italics; $p < 0.001$ are in bold, italics, and underlined.

	basin	$\log_{10}$		1987 %			1997 %			1987-97 % converted		
assemblage variable	area (km^2)	slope	RHAP	U	HDU	LDU	U	HDU	LDU	U	HDU	LDU
richness	***0.67***	0.05	0.27	-0.33	**-0.39**	-0.31	-0.30	**-0.43**	-0.27	-0.13	-0.24	-0.12
density	***-0.71***	***0.50***	***0.52***	-0.25	-0.17	-0.26	-0.30	-0.18	-0.32	-0.26	-0.18	-0.25
# of species												
darters and sculpin	0.19	***0.60***	***0.69***	**-0.37**	-0.32	**-0.38**	***-0.47***	**-0.40**	***-0.47***	**-0.42**	-0.26	**-0.41**
centrarchids	***0.48***	***-0.51***	**-0.43**	0.10	-0.06	0.14	0.27	0.05	0.31	**0.39**	0.21	**0.39**
cyprinids	**0.36**	0.35	***0.55***	**-0.36**	-0.31	**-0.36**	**-0.39**	**-0.45**	**-0.36**	-0.25	**-0.40**	-0.21
insectivorous cyprinids	**0.44**	0.27	***0.52***	**-0.45**	**-0.45**	**-0.44**	**-0.44**	***-0.49***	**-0.41**	-0.25	-0.30	-0.22
endemics	0.11	***0.54***	***0.74***	***-0.60***	***-0.52***	***-0.61***	***-0.64***	***-0.54***	***-0.64***	***-0.47***	-0.31	***-0.46***
proportion of species												
darters and sculpin	-0.31	***0.79***	***0.74***	-0.17	-0.10	-0.18	-0.35	-0.20	**-0.37**	***-0.48***	-0.22	***-0.47***
centrarchids	0.00	***-0.56***	***-0.69***	**0.40**	0.28	**0.41**	***0.57***	***0.46***	***0.57***	***0.56***	***0.49***	***0.54***
cyprinids	-0.20	***0.49***	***0.56***	-0.13	-0.03	-0.15	-0.22	-0.21	-0.21	-0.24	-0.35	-0.20
insectivorous cyprinids	0.22	**0.38**	***0.56***	**-0.39**	**-0.40**	**-0.38**	**-0.39**	**-0.41**	**-0.38**	-0.27	-0.23	-0.25
endemics	-0.21	***0.68***	***0.84***	***-0.53***	***-0.47***	***-0.54***	***-0.62***	***-0.48***	***-0.63***	***-0.53***	-0.29	***-0.52***

	basin	$\log_{10}$			1987 %			1997 %			1987-97 % converted	
assemblage variable	area (km^2)	slope	RHAP	U	HDU	LDU	U	HDU	LDU	U	HDU	LDU
relative abundance												
darters and sculpin	-0.10	***0.55***	***0.73***	-0.24	-0.22	-0.24	**-0.41**	-0.22	**-0.43**	***-0.49***	-0.08	***-0.50***
centrarchids	-0.06	-0.29	***-0.63***	***0.54***	**0.44**	***0.54***	***0.77***	***0.66***	***0.77***	***0.75***	***0.66***	***0.72***
cyprinids	0.24	0.25	**0.42**	-0.31	-0.28	-0.31	**-0.42**	**-0.45**	**-0.40**	**-0.38**	**-0.45**	-0.35
insectivorous cyprinids	**0.41**	0.15	0.34	-0.32	-0.31	-0.31	**-0.37**	**-0.38**	-0.35	-0.31	-0.24	-0.30
endemics	-0.25	***0.72***	***0.74***	***-0.58***	***-0.49***	***-0.58***	***-0.64***	**-0.43**	***-0.65***	***-0.58***	-0.27	***-0.61***
# significant correlations	6	12	15	9	7	9	12	12	12	10	4	9
mean |r|	0.25	0.38	0.51	0.31	0.27	0.31	0.39	0.33	0.38	0.34	0.27	0.33

Table 4.4. Multiple linear regression models of RHAP score and fish assemblage variables. Transformations for dependent variables are given in Table 4.1. All land cover variables were transformed by arc-sine (square-root(x)). Values in parentheses are statistics for 1997 variables substituted for the 1987 variables selected by the forward stepwise procedure after 1987 variables were removed from consideration. The relative abundance of endemics could not be normalized and is not included in this analysis.

independent variable	variables in model	trend	cumulative r^2	*p*	*F*
RHAP	$\log_{10}$ slope	+	0.43	< 0.001	28.55
	97 HDU	-	0.68	< 0.001	
richness	basin area	+	0.45	< 0.001	15.58
	$\log_{10}$ slope 87	+	0.59	0.02	
	HDU	-	0.64	0.02	
	(97 HDU)	(-)	(0.63)	(0.03)	(14.96)
density	basin area	-	0.50	< 0.001	25.29
	97 U	-	0.65	0.002	
proportion of species					
darters and sculpin	$\log_{10}$ slope	+	0.63	0.001	28.80
	97 HDU	-	0.68	0.02	
centrarchids	$\log_{10}$ slope^a	-	0.31	0.001	16.48
	97 U	+	0.54	< 0.001	
cyprinids	$\log_{10}$ slope	+	0.24	0.006	7.73
	87-97 HDU	-	.035	0.04	
insectivorous cyprinids	$\log_{10}$ slope^a	+	0.15	0.04	7.04
	87 HDU	-	0.34	0.009	
	basin area	+	0.44	0.03	
	(97 HDU)	-	(0.32)	0.01	(6.29)
endemics	$\log_{10}$ slope 87	+	0.46	< 0.001	41.78
	HDU	-	0.76	< 0.001	
	(97 HDU)	(-)	(0.73)	(< 0.001)	(36.09)

independent variable	variables in model	trend	cumulative r^2	*p*	*F*
relative abundance					
darters and sculpin	$\log_{10}$ slope	+	0.30	0.002	9.35
	97 LDU	-	0.41	0.04	
centrarchids	$\log_{10}$ slope[a] 97	-	0.08	0.12	20.00
	U	+	0.63	< 0.001	
	87-97 HDU	+	0.70	0.02	
cyprinids	87-97 HDU	-	0.20	0.01	7.05
insectivorous cyprinids	basin area	+	.017	0.26	5.56

[a] $\log_{10}$ slope manually entered into models as the primary predictor.

Appendix 4.1. Characteristics of study streams and catchments in the Etowah River Basin. Attributes shown include scores for Rapid Habitat Assessment Protocol (RHAP) and percent urban land cover in total urban (U), high-density urban (HDU), and low-density urban (LDU) in 1987, 1997, and % change in basin area from 1987-97.

Site	Name	basin area (km^2)	Reach slope	RHAP	1987 %			1997 %			1987-97 %		
					U	HDU	LDU	U	HDU	LDU	U	HDU	LDU
1	Pumpkinvine Cr.	16.6	0.0029	12.2	2.9	0.3	2.6	10.5	1.0	9.5	7.6	0.7	6.8
2	West Fork	13.8	0.0045	11.4	8.9	1.2	7.7	13.7	1.2	12.5	4.8	0.0	4.8
3	Avery Cr.	22.3	0.0015	5.5	7.5	1.3	6.2	19.8	4.0	15.9	12.4	2.7	9.7
4	Smithwick Cr.	15.6	0.0023	14.4	8.2	1.3	6.9	13.3	1.1	12.1	5.1	0.0	5.3
5	McCanless Cr.	13.1	0.0031	16.9	5.8	0.2	5.6	9.4	0.9	8.5	3.6	0.7	2.9
6	Bluff Cr.	14.5	0.0035	13.3	6.6	0.6	6.0	7.7	1.1	6.6	1.1	0.4	0.6
7	Settingdown Cr.	17.1	0.0020	6.5	9.9	1.5	8.4	16.1	2.0	14.1	6.2	0.5	5.7
8	Conns Cr.	14.9	0.0058	17.1	3.7	0.5	3.2	6.4	0.3	6.1	2.7	0.0	2.9
9	Polecat Branch	11.3	0.0085	11.3	17.9	3.3	14.6	16.0	3.7	12.3	0.0	0.4	0.0
10	Burt Cr.	12.2	0.0080	14.7	5.9	1.2	4.7	15.9	3.2	12.7	10.0	2.0	8.0
11	Raccoon Cr.	50.7	0.0034	15.8	4.1	0.2	3.9	10.6	0.6	9.9	6.5	0.5	6.1
12	Little Pumpkinvine Cr.	52.0	0.0045	14.3	13.6	2.0	11.5	24.2	2.4	21.8	10.6	0.4	10.3
13	Chicken Cr.	59.1	0.0015	6.3	12.7	1.3	11.5	29.9	3.0	26.9	17.2	1.7	15.5
14	Little River	52.8	0.0025	7.7	7.6	0.8	6.8	14.6	0.7	13.9	7.0	0.0	7.1
15	Mill Cr.	50.7	0.0015	7.8	9.4	1.3	8.1	15.4	1.3	14.2	6.0	0.0	6.1
16	Smithwick Cr.	38.6	0.0052	12.5	7.7	1.1	6.6	11.0	0.8	10.2	3.3	0.0	3.5

Site	Name	basin area (km^2)	Reach slope	RHAP	1987 %			1997 %			1987-97 %		
					U	HDU	LDU	U	HDU	LDU	U	HDU	LDU
17	Shoal Cr. (Cherokee Co.)	53.2	0.0029	12.7	3.7	0.3	3.4	7.0	0.5	6.5	3.3	0.2	3.1
18	Settingdown Cr.	53.6	0.0019	9.6	10.1	2.0	8.1	18.7	2.6	16.2	8.7	0.6	8.1
19	Darnell Cr.	60.3	0.0044	12.8	2.7	0.2	2.5	4.9	0.3	4.6	2.2	0.2	2.1
20	Shoal Cr. (Dawson Co.)	53.8	0.0074	14.3	4.7	0.7	4.0	11.2	1.2	10.0	6.5	0.6	6.0
21	Pumpkinvine Cr.	125.7	0.0010	6.5	6.4	0.4	5.9	10.8	1.0	9.9	4.5	0.5	3.9
22	Raccoon Cr.	108.5	0.0028	16.3	4.1	0.2	3.9	8.1	0.4	7.7	4.0	0.2	3.8
23	Noonday Cr.	85.3	0.0015	6.1	46.1	17.2	28.9	60.7	25.5	35.2	14.7	8.3	6.4
24	Settingdown Cr.	96.1	0.0021	8.8	10.4	1.9	8.6	18.4	2.3	16.1	8.0	0.5	7.5
25	Little River	122.1	0.0010	8.4	10.5	1.2	9.4	22.6	1.8	20.7	12.0	0.7	11.4
26	Mill Cr.	84.6	0.0013	8.3	10.3	1.4	8.9	18.8	2.0	16.8	8.4	0.6	7.9
27	Shoal Cr. (Cherokee Co.)	101.9	0.0025	12.8	5.4	0.4	5.0	8.5	0.6	7.9	3.1	0.2	2.9
28	Sharp Mountain Cr.	103.9	0.0066	15.0	9.7	2.0	7.7	10.0	2.6	7.4	0.3	0.6	0.0
29	Long Swamp Cr.	77.4	0.0043	15.8	3.5	0.5	2.9	5.0	0.6	4.4	1.5	0.1	1.4
30	Shoal Cr., (Dawson Co.)	90.7	0.0033	16.5	4.7	0.7	4.1	10.1	1.1	9.0	5.4	0.4	5.0
101	Little Allatoona Cr.	14.8	0.0029	7.4	17.0	3.4	13.6	37.3	5.2	32.2	20.4	1.8	18.6
111	Allatoona Cr.	48.4	0.0100	12.7	18.6	2.0	16.6	33.2	3.6	29.5	14.5	1.6	12.9

Appendix 4.2. Fishes collected in the Etowah River basin.

Family Name ***Scientific name***	**Common Name**
Petromyzontidae	
Ichthyomyzon sp.	
Cyprinidae	
Campostoma oligolepis	largescale stoneroller
Cyprinella callistia	Alabama shiner[, 1]
C. trichroistia	tricolor shiner[1, 2]
C.venusta	blacktail shiner[1]
Hybopsis lineapunctata	lined chub[1, 2]
Luxilus zonistius	bandfin shiner[1]
Nocomis leptocephalus	bluehead chub
Notemigonus crysoleucas	golden shiner
Notropis chrosomus	rainbow shiner[1, 2]
N. longirostris	longnose shiner[1]
N. lutipinnis	yellowfin shiner[1]
N. stilbius	silverstripe shiner[1]
N. xaenocephalus	Coosa shiner[1, 2]
Phenacobius catostomus	riffle minnow[1, 2]
Pimephales vigilax	bullhead minnow
Semotilus atromaculatus	creek chub
Catostomidae	
Hypentelium etowanum	Alabama hog sucker
Minytrema melanops	spotted sucker
Moxostoma duquesnei	black redhorse
M. erythrurum	golden redhorse
M. poecilurum	blacktail redhorse
Ictaluridae	
Ameiurus brunneus	snail bullhead

Family Name ***Scientific name***	**Common Name**
A. natalis	yellow bullhead
A. nebulosus	brown bullhead
Ictalurus punctatus	channel catfish
Noturus leptacanthus	speckled madtom
Salmonidae	
Onchorhynchus mykiss	rainbow trout
Fundulidae	
Fundulus stellifer	southern studfish
Poeciliidae	
Gambusia affinis	western mosquitofish
G. holbrooki	eastern mosquitofish
Cottidae	
Cottus carolinae zopherus	Coosa banded sculpin[2]
Centrarchidae	
Ambloplites ariommus	shadow bass
Lepomis auritus	redbreast sunfish
L. cyanellus	green sunfish
L. gulosus	warmouth
L. macrochirus	bluegill sunfish
L. megalotis	longear sunfish
L. microlophus	redear sunfish
Micropterus coosae	Coosa bass
M. punctulatus	spotted bass
M. salmoides	largemouth bass
Pomoxis nigromaculatus	black crappie
Percidae	
Etheostoma etowahae	Etowah darter[2]
E. jordani	greenbreast darter[2]
E. scotti	Cherokee darter[2]

Family Name ***Scientific name***	**Common Name**
E. stigmaeum	speckled darter
Percina kathae	Mobile logperch
P. nigrofasciata	blackbanded darter
P. palmaris	bronze darter[2]
P. sp. cf. P. macrocephala	"bridled darter" [2]

[1] insectivorous cyprinid

[2] endemic species

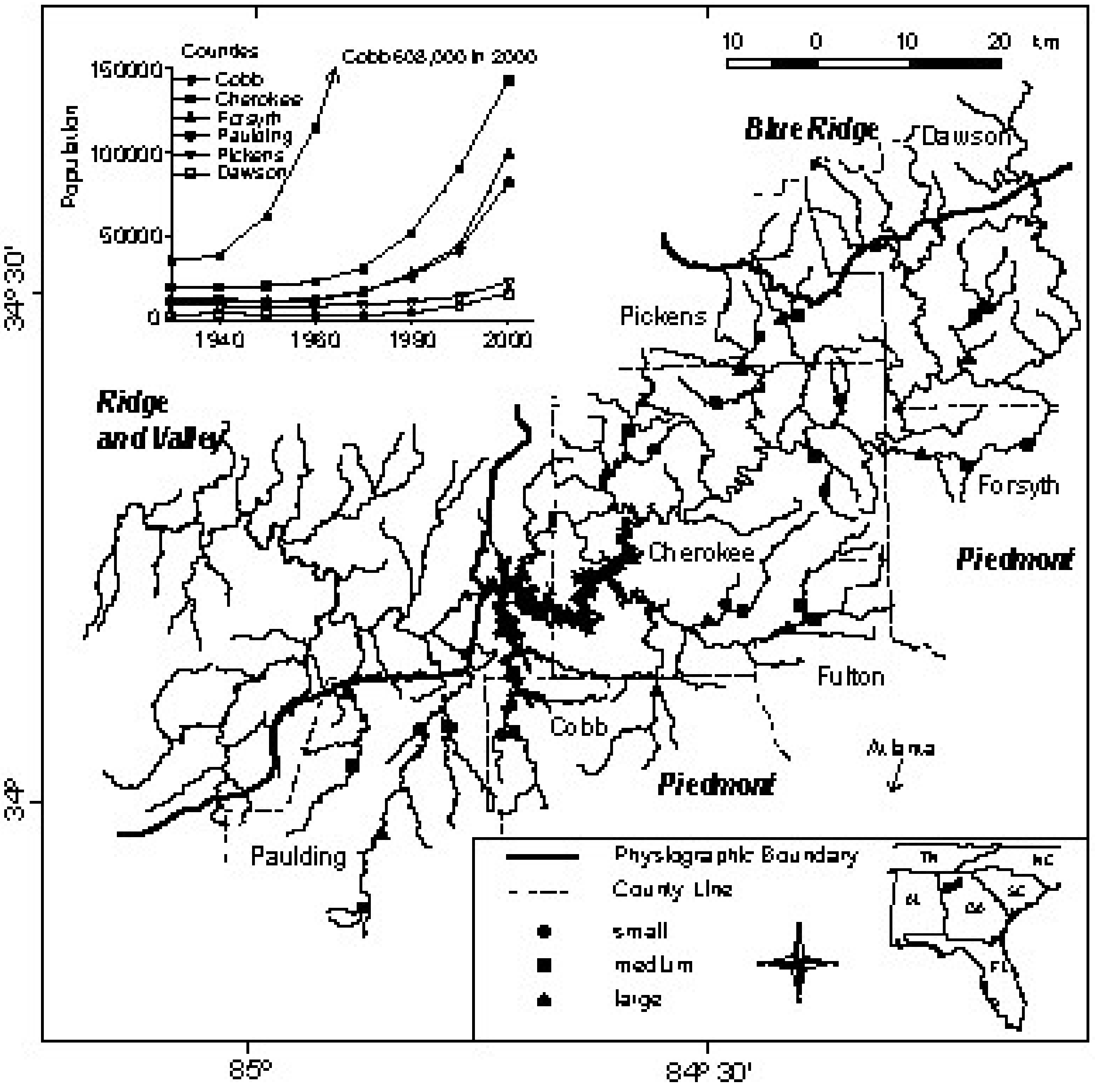

Figure 4.1. Map of sample sites in the Etowah River basin. The inset graph shows population growth 1930-2000 (U.S. Census Office 1930-2000) for counties in the study area except for Fulton County, which was strongly influenced by the population of Atlanta. Population growth in Fulton County basins in this study is similar to the trend observed for neighboring Cherokee Co.

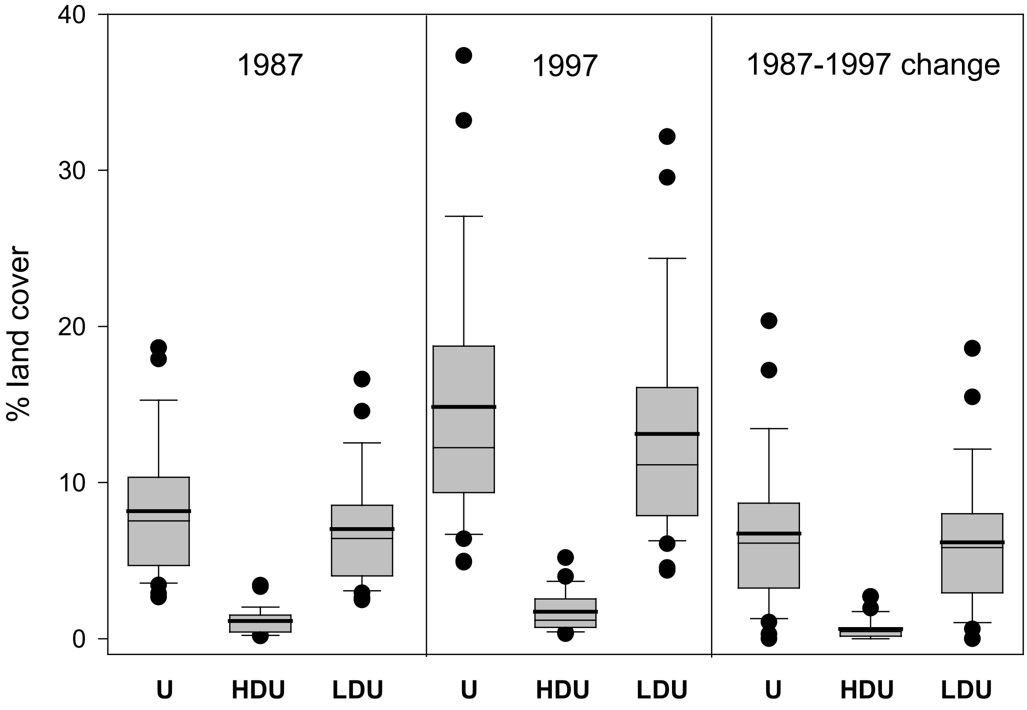

Figure 4.2. Box and whisker plots of total urban (U), high-density urban (HDU), and low-density urban (LDU) for basins upstream of 30 sample reaches in Etowah River tributaries. Top and bottom boundaries of the box indicate 75th and 25th percentiles, respectively. Within the boxes, thin lines indicate the median and thick lines indicate the mean. Whiskers above and below the box indicate the 90th and 10th percentiles.

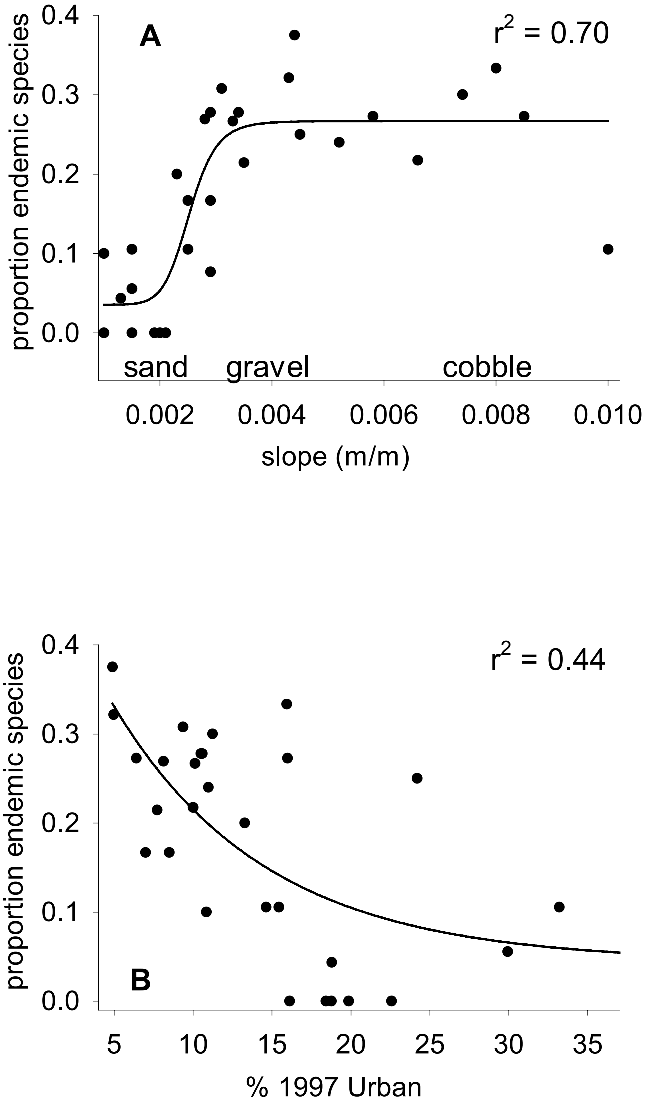

Figure 4.3. Plots showing the relationship between the proportion of endemic species, slope, 1997 % urban land cover. Solid line in **A** represents a four parameter sigmoidal model of proportional richness of endemics change fit to the data. Average texture classes corresponding to slope are labeled on the x-axis and are based on data in Walters et al. (*in review*). A negative exponential model was fit to the data in **B**.

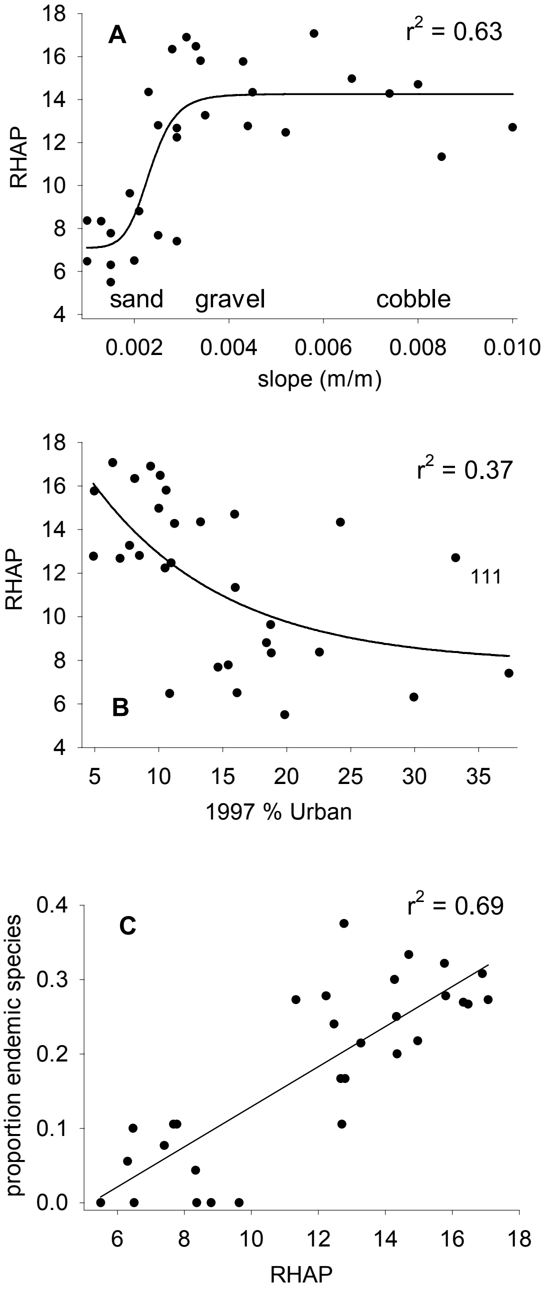

Figure 4.4. Plots showing the relationship of RHAP with slope, 1997 % urban land cover and proportion of endemic species. Solid line in **A** represents a four parameter sigmoidal model of RHAP change fit to the data. Average texture classes corresponding to slope are labeled on the x-axis and are based on data in Walters et al. (*in review*). A negative exponential model was fit to the data in **B** and a linear model was fit to the data in **C**.

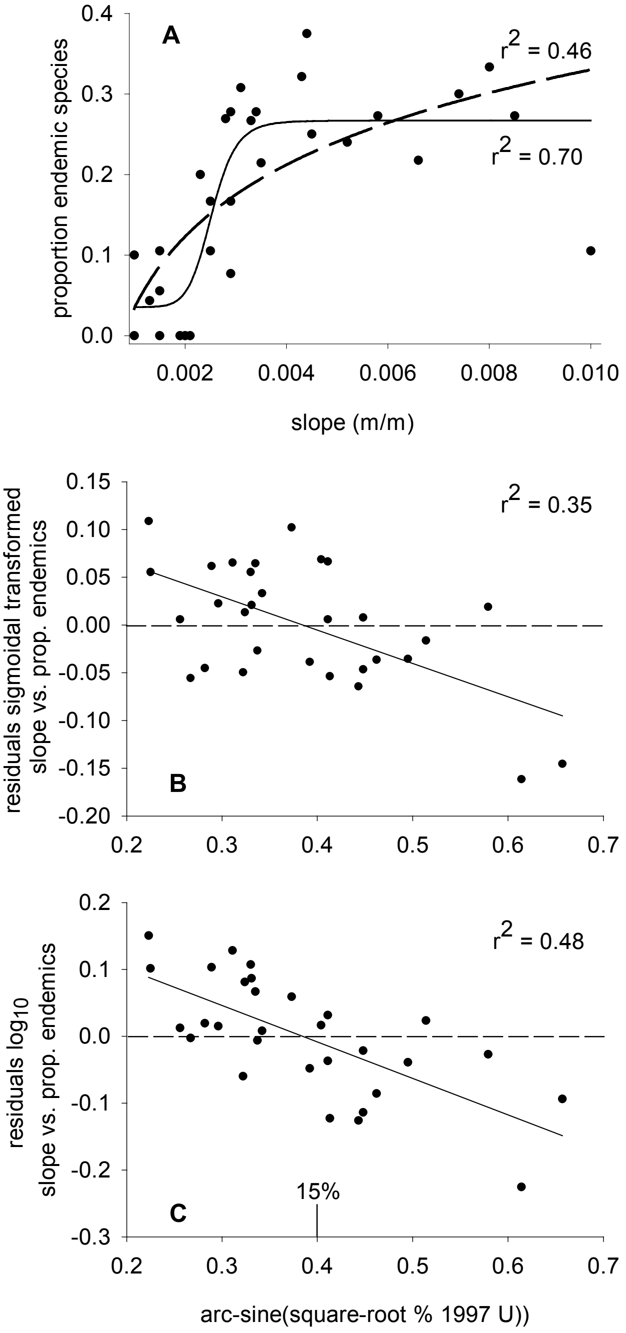

Figure 4.5. Comparison of sigmoidal (solid line) and $\log_{10}$ transformation (dashed line) of stream slope versus the proportion of endemic species (**A**). Plots **B** and **C** show the residuals from these models plotted against transformed (arc-sine square root) 1997 % U. The level of 15% U is indicated on the x-axis.

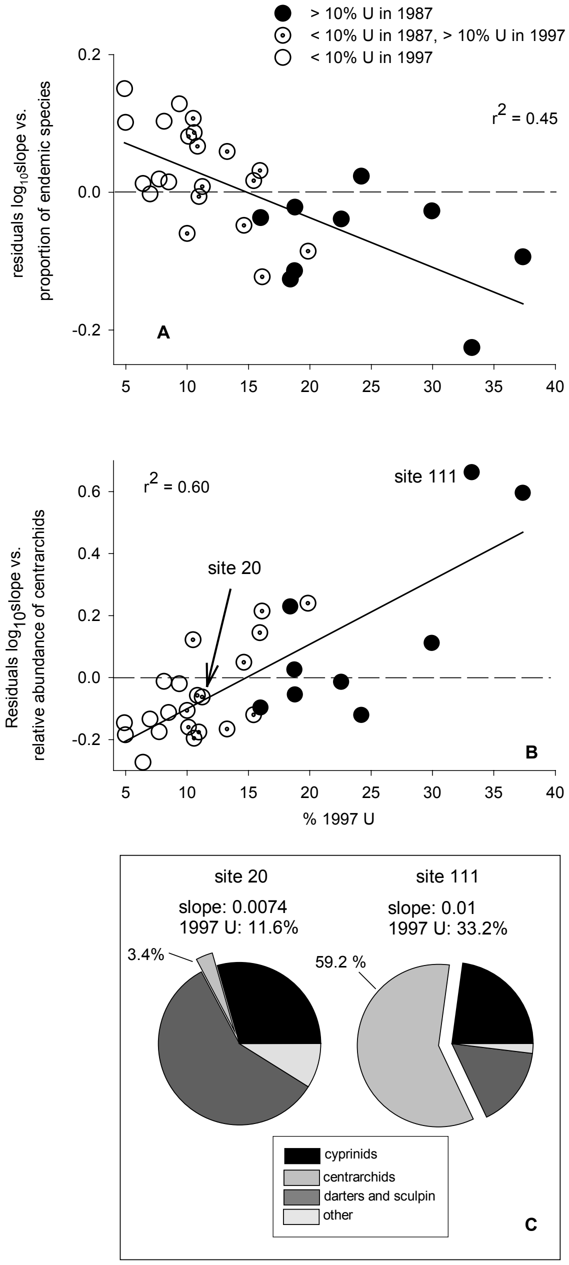

Figure 4.6. Linear regression of % 1997 U versus residuals from slope models of the proportional richness of endemics (**A**) and the relative abundance of centrarchids (**B**). Basins are coded based on 1987 and 1997 urban land cover data. Panel **C** compares the relative abundance of major taxonomic groups from two sites identified in (**B**)

CHAPTER 5

URBANIZATION, SEDIMENTATION, AND HOMOGENIZATION OF FISHES IN THE ETOWAH RIVER BASIN, GEORGIA PIEDMONT, USA[1]

---

[1] Walters, D. M., D. S. Leigh, and A. B. Bearden. Submitted to *Hydrobiologia*

Abstract: Human alteration of landscapes contributes to the homogenization of regional faunas. We tested the hypothesis that basin urbanization alters stream sediment regimes and homogenizes fish assemblages in 30 tributary basins of the Etowah River. Sediment variables included average particle size (mean *phi*) of the streambed from visual counts, percent fines in riffles by sieve weight, and baseflow turbidity (NTU). Homogenization was quantified as the ratios of endemic to cosmopolitan species richness (E_r:C_r) and abundance (E_a:C_a). High baseflow turbidity and finer bed particles were associated with more homogenized assemblages (i.e., lower E:C). Mean *phi* and NTU were significantly correlated with E:C ratios ($r = -0.74$ to -0.76) and, when combined using multiple linear regression, accounted for around 73% of the variance in the ratios. Stream slope strongly covaried with mean *phi* ($r = -0.92$) and percent fines in riffles ($r = -0.79$). Multiple linear regression models indicated that urban land cover was significantly related to stream bed texture; urbanized sites had finer beds and riffles than predicted by stream slope. Urban land cover was the primary predictor of baseflow NTU ($r^2 = 0.42$) and, combined with slope in multiple regression, explained 51% of the variance in turbidity. Our results indicate that (1) stream slope is a background variable predicting the distribution of bed particle sizes and E:C ratios in these streams; and (2) urbanization disrupts these relationships by transforming clear streams with coarse beds into turbid streams with finer beds. These conditions lead to predictable declines in endemic richness and abundance and ultimately homogenize fish assemblages. Bed texture was linked to urbanization and homogenization; however, baseflow NTU was the best indicator of urban impacts because it was statistically independent from slope.

Key Words: erosion, assemblage structure, endemism, stream gradient, land use, suspended sediment

INTRODUCTION

Urban development is a pervasive form of environmental disturbance that globally threatens stream systems. Urbanization causes major changes in stream hydrology, geomorphology, water quality, and stream communities (Baer and Pringle 2000). Degradation of stream ecosystems occurs at low levels of urban land cover, and a growing body of evidence suggests that the impact of urbanization is more severe than other land uses such as agriculture or forestry (Paul and Meyer 2001). Urbanization has been associated with declines in fish richness, diversity, density, and biotic integrity (Paul and Meyer 2001), but its role in homogenizing fish assemblages is unstudied.

Homogenization generally refers to the replacement of regionally distinct faunas with a few invasive species tolerant of human disturbance (McKinney and Lockwood 1999). These invasive species are usually characterized as widespread, generalist, cosmopolitan or “weedy” species that gain access to degraded habitats either through range expansion or human introduction. They replace narrowly distributed, often specialized, endemic taxa that are sensitive to habitat alteration (McKinney and Lockwood 1999). This process is well documented for terrestrial systems and organisms such as birds and plants (McKinney and Lockwood 1999), but is relatively understudied for aquatic systems and fishes. Recently, Rahel (2000) found that extensive homogenization of fishes in the conterminous United States was due largely to introductions of fishes for angling and aquaculture. Scott and Helfman (2001) attributed homogenization of assemblages in Southern Appalachian streams to range expansion of native cosmopolitans and riparian disturbance, and they hypothesized that differential tolerance of endemic and cosmopolitan species to excessive sedimentation contributed to the process.

In this study, we quantified relationships between urbanization and homogenization in the Etowah River basin, a system with exceptional endemicity and a long history of land disturbing activities (e.g., mining and agriculture) (Burkhead et al. 1997). In an earlier study of these streams, Walters (2002) found that endemics were benthic specialists positively associated with steep gradients and coarse stream beds, but that endemics declined with increasing urban land cover. The mechanism of decline was not identified, but altered sediment regime was implicated. Urbanization substantially increases stream sediment inputs through upland erosion or increased bank scour (Wolman 1967), and we predict that changes in sediment regime contribute to the decline of endemics fishes. We predict that cosmopolitans will increase because they are adapted to lowland river systems that often have higher turbidities and finer stream beds than upland streams and that, as upland streams become more sediment-laden, they become more hospitable to cosmopolitan species. Specifically, we address the questions: 1) Do ratios of endemic to cosmopolitan fishes decline with increasing turbidity and finer stream beds; and 2) Are increasing turbidity and finer stream beds associated with urbanization in a basin with a history of soil disturbing activities?

STUDY AREA

We sampled 30 Piedmont streams draining basins of 11-126 km^2 in the Etowah River basin north of Atlanta in north Georgia, USA. Large-scale human disturbance of the region began around 1830 and included gold mining, deforestation, and row crop agriculture (Burkhead et al. 1997). Much of the area was reforested after around 1930. Extensive urbanization of the area began around 1980 and the Atlanta metropolitan area is currently one of the most rapidly developing regions in the United States (U.S. Department of Agriculture 2000). The Etowah drains part of the Southern Appalachian Highlands, a region widely recognized as a global hotspot of temperate freshwater fish diversity and endemism (Warren et al. 2000). The Etowah has 91 native fishes in 18 families including 11 species endemic to the larger Alabama River drainage, which includes the Etowah basin (Burkhead et al. 1997).

MATERIALS AND METHODS

Fishes were sampled by electrofishing within standardized stream reaches in summer 1999 and 2000. Detailed sampling methodology is available in Walters (2002). Homogenization was calculated as the ratios of endemic to cosmopolitan species richness (E_r:C_r) and abundance (E_a:C_a). Low values indicate dominance by cosmopolitan species and a high degree of homogenization. We defined cosmopolitan species as fishes native to at least 10 major drainages (Warren et al. 2000) and endemics as species whose distributions are limited primarily to the highland region of the Alabama River drainage (Mettee et al. 1996) (Appendix 5.1).

Stream slope and bed sediment variables were measured in reaches scaled to 20 times average baseflow stream width. Slope was calculated as the average gradient of the water surface between the tops of riffles and was surveyed with an electronic total station. Mean *phi* of the stream bed was determined from visual counts conducted systematically along 5 longitudinal transects within the wetted channel (Walters 2002). Mean percentage of fines in riffles (by sieved weight) was calculated from three-liter soil samples taken from three riffles in each reach. Geometric mean turbidity (nephelometric turbidity units, NTU) was calculated from six baseflow samples collected throughout the year.

Land cover data were derived from Landsat TM images from June 1987 and July 1997 (Lo and Yang 2000). Two urban land cover types were classified. High-density urban (HDU) was 80-100% construction material and included commercial developments and multi-lane highways. Low-density urban (LDU) is 50-80% construction material and is characterized by single or multiple family housing developments and smaller roads. The percentage of LDU and HDU were summed to calculate total basin urban land cover (U). Totals from 1987 were subtracted from 1997 totals to calculate the percentage of basin area converted to each urban category. These urban conversion variables indicated the intensity of urbanization for each basin over the decade.

We used correlation analysis to assess the relationship of sediment and urban variables to endemic cosmopolitan richness and abundance as well as homogenization. Appropriate transformations were applied to achieve normality of independent and dependent variables prior to statistical analysis. Endemic abundances could not be normalized, so Spearman's r was calculated for this variable. Stream slope and basin area was included in these analyses because they were predictive of some elements of fish assemblage structure and because slope covaried with some bed texture variables (Walters 2002). We used forward stepwise regression to develop three sets of models linking homogenization to independent variables. First, we developed models of sediment and E:C ratios. Second, we modeled sediment variables using stream size, slope, and urban land cover. Finally, we modeled E:C ratios combining urban, geomorphic, and sediment variables. The latter hierarchical models assessed the relative predictive power of variables measured at basin, reach, and microhabitat (i.e., fines in riffles) scales to explain variation in E:C ratios.

RESULTS

Species richness ranged from 10 to 30 species across sites with a range of 0 to 38% endemic species and 0 to 65% endemic abundances. Reach slope varied from

0.001 to 0.01, mean *phi* ranged from –6.4 (cobble) to 0.4 (sand), and baseflow turbidity varied from 2.7 to 17.8 NTU. Urban land cover (U) varied from 5-37% and mean U across sites nearly doubled from 8 to 15% from 1987-97. Low-density urban (LDU) was the dominant type of development and accounted for about 87% of total U.

Endemic richness and abundance were negatively correlated with NTU, mean *phi*, % fines in riffles, and urban land cover but were positively correlated with slope. Cosmopolitan richness was most strongly related (positive) to drainage area, but was also positively correlated with mean *phi* and % fines in riffles. Abundance of cosmopolitan species was not significantly correlated with any of the predictors. The E:C ratios were highly autocorrelated ($r = 0.94$) and showed a similar response to sediment and urban variables. Homogenization ratios were negatively correlated with NTU, fines in riffles, and mean *phi* indicating that endemic species decline and cosmopolitan species increase in turbid streams with fine-textured beds (Table 5.1). The E:C ratios increased with stream slope and were negatively correlated with urban land cover. Urban land cover was a poor predictor of bed texture, but was positively correlated with baseflow NTU. In contrast, stream slope was a strong predictor of both bed texture variables and was negatively correlated with NTU.

Mean *phi* and baseflow NTU explained nearly 75% of the variance in E:C ratios (Table 5.2). In the *phi* scale, smaller particles have lower larger values, so the negative correlations indicated that E:C ratios increased as the size of bed sediment increased. Much of the variation in local bed texture and NTU was explained by a combination of reach slope and urban land cover. Slope was the primary predictor of bed texture, but urban land cover was associated with finer stream beds and riffles than predicted by slope alone. Finer stream beds were associated with LDU development from 1987-97, and fines in riffles increased significantly with HDU. Urban land cover was the primary predictor of NTU, but lower baseflow NTU was also associated with steeper streams.

We could not include both mean *phi* and slope in the stepwise procedure because they covaried too strongly. Compared with bed sediment, slope is essentially invariant to changes in catchment land use in the context of our study. Thus, we treated slope as a background variable controlling bed texture and used it for the stepwise analysis. Even though NTU and 1997 U were also related, correlation strength ($r = 0.65$) was low enough to include both variables in the analysis. The stepwise procedure indicated that baseflow NTU was the strongest predictor of homogenization ratios followed by slope, and 1997 U. Hierarchical models explained 81% and 77% of the variance in E_r:C_r and E_a:C_a, respectively. Percent 1997 U entered into the models along with NTU suggesting that additional urban influences (other than elevated turbidity) contribute to homogenization of the fish assemblages.

DISCUSSION

Our results agree with the general hypothesis that large-scale human disturbance homogenizes regional faunas (McKinney and Lockwood 1999). Urbanization alters stream habitats and led to predictable declines in endemic richness and abundance, increased cosmopolitan richness, and lower E:C ratios. Reach-level variation in stream slope controlled bed texture, which is the primary predictor of E:C ratios. We used multiple linear regression to account for the nonanthropogenic influence of slope and to isolate the urban effect. This analysis indicated that urban development disrupted the relationships between fishes, bed sediment, and slope in at least two ways. Urbanization was associated with smaller bed-particle sizes and increased baseflow NTU. Thus, urbanization transforms clear streams with coarse beds into turbid streams with finer beds, favoring cosmopolitan species over endemic taxa.

Baseflow NTU was a better indicator of urban effects on fishes than measures of bed sediment. Although urban land cover explained significant variance in bed texture, the changes were subtle compared to the overriding influence of stream slope. Prior to intense human disturbance, the study area was forested and streams reportedly were clear during low flows (Burkhead et al. 1997). Thus, high baseflow NTU indicates a departure from the natural condition and may identify streams that suffer from chronic sediment disturbance. The sources of fines contributing to baseflow NTU were not identified. Likely sources include baseflow transport of fine bed material introduced during flood flows and persistent near-stream disturbances such as road and housing construction.

Our study reports correlations and thus does not isolate causal mechanisms driving the response of fishes to changes in bed and suspended sediment. However, differences in life history traits among the two fish groups provide some clues about why cosmopolitan species appear to thrive under these conditions. The endemic species are, for the most part, benthic habitat specialists that inhabit riffles and runs, spawn in coarse gravel, and are specialist feeders on benthic macroinvertebrates (Etnier and Starnes 1993). Bed sedimentation can negatively affect these species by burying riffle habitat, reducing egg and fry survivorship, and lowering prey densities through habitat destruction or increased drift (Waters 1997). Cosmopolitan species exhibit a number of traits that make them more resilient to bed sedimentation. For example, centrarchids and ictalurids spawn in nests constructed in fine sediments. Many cosmopolitans are habitat generalists that frequent pools and runs and have less dependence on riffle habitat. In addition, these species are often omnivores or trophic generalists that rely less on production of benthic macroinvertebrates.

Elevated baseflow turbidity may impact trophic pathways and spawning success of endemic species. Turbidity induces drift of invertebrates and depletes local populations (Waters 1997). In addition, turbidity reduces the capture success and reactive distance of drift feeding fishes (Waters 1997, Sweka and Hartman 2001). Turbidity can affect spawning behavior by disrupting spawning cues or curtailing spawning activity for species that exhibit striking nuptual coloration (Seehausen et al. 1997, Burkhead and Jelks 2001), a common trait among Etowah endemics. Burkhead and Jelks (2001) showed that suspended sediment delayed spawning and reduced egg laying in *Cyprinella trichroistia*, one of the endemics in our study. Their experiment mimicked turbidities associated with high stream flows (e.g., a spike in suspended sediment concentration followed by a gradual attenuation as fines settled out of suspension). Our results were based on *baseflow* turbidity. High baseflow NTU indicates chronic turbidity problems that could inhibit spawning activity of some fishes indefinitely.

In summary, local variation in bed texture and baseflow turbidity predicted patterns in species composition. High endemic richness and abundance characterized assemblages in clearer streams with coarse beds, whereas cosmopolitan species dominated turbid streams with finer beds. As these basins urbanized, stream assemblages were homogenized as endemics declined in richness and abundance and cosmopolitan richness increased. These changes were apparently related to fine-textured beds and increased suspended sediment. We detected changes in sediment regime related to urbanization even though the Etowah basin had a prior history of large-scale mining and agricultural disturbance. Because of the confounding influence of stream slope on bed texture, baseflow turbidity was a better indicator of sediment-related urban impacts. Our results indicate that baseflow NTU is a suitable measure of chronic sedimentation problems in these highland streams.

ACKNOWLEDGEMENTS

Funding was provided by a “Science to Achieve Results” grant from the US Environmental Protection Agency (EPA R826597-01-0) with additional support from the University of Georgia Research Foundation and the Georgia Museum of Natural History. We thank C.P. Lo for land cover data, and M. Freeman, G. Helfman, and A. Rosemond for commenting an earlier version of this manuscript.

REFERENCES

Baer, K. E., and C. M. Pringle. 2000. Special problems of urban river conservation: the encroaching megalopis. In Boon, P. J., B. R. Davis, and G. E. Potts (eds), Global Perspectives on River Conservation. John Wiley & Sons Ltd., London, U.K.: 381-398.

Burkhead, N. M., and H. L. Jelks. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. Trans. Am. Fish. Soc. 130:959-968.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled Southern Appalachian ecosystem. In Benz, G. W. and D. E. Collins, (eds), Aquatic Fauna in Peril, the Southeastern Perspective. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia: 375-444.

Etnier, D. A., and W. C. Starnes. 1993. The Fishes of Tennessee. The University of Tennessee Press, Knoxville, Tennessee.

Lo, C. P., and X. Yang. 2000. Mapping the dynamics of land use and land cover change in the Atlanta Metropolitan Area using the time sequential Landsat images. Annual Meeting of the American Society of Photogrammetry and Remote Sensing (CD), Bethesda, MD.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14:450-453.

Mettee, M. F., P. E. O'Neil, and J. M. Pierson. 1996. Fishes of Alabama and the Mobile Basin. Oxmore House Inc, Birmingham, Alabama.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Ann. Rev. Ecol. Syst. 32:333-365.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854-856.

Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26:6-15.

Seehausen, O., J. J. M. vanAlphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808-1811.

Sweka, J. A., and K. J. Hartman. 2001. Influence of turbidity on brook trout reactive distance and foraging success. Trans. Am. Fish. Soc. 130:138-146.

U.S. Department of Agriculture. 2000. 1997 National Resource Inventory. Percent Change in Developed Land Area. http://www.nhq.nrcs.usda.gov/land/meta/m5010.html.

Warren, M. L., Jr., and 13 others. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25:7-31.

Walters D. M. 2002. Influence of geomorphology and urban land cover on fish assemblages in the Etowah River basin, Georgia. Doctoral Dissertation. The University of Georgia, Athens, Georgia.

Waters, T. F. 1997. Sediment in Streams: Sources, Biological Effects, and Control. American Fisheries Society, Bethesda, Maryland.

Wolman, M. G. 1967. A cycle of sedimentation and erosion in urban river channels. Geographiska Annaler 49:385-395.

Table 1. Correlation coefficients of fish variables with stream sediment variables, basin area and reach slope, and basin urban land cover (n = 30 sites). Values are Pearson's *r* except for "endemic abundance" which could not be normalized. Values for endemic abundance are expressed as Spearman's *r*. E_r:C_r, Endemic to Cosmopolitan richness; E_a:C_a; Endemic to Cosmopolitan abundance. Land cover (U = Urban; HDU = High Density Urban; LDU = Low Density Urban) is the % of each category in 1997. Only 1997 urban variables are shown because the 1987 and 1987-97 land cover variables showed similar trends. Correlations significant at $p < 0.05$ are in bold; $p < 0.01$ are in bold and italics; $p < 0.001$ are in bold, italics, and underlined.

Fish Variables	NTU[1]	mean *phi*	% fines[2]	basin area (km^2)	slope	% U	% HDU	% LDU
# endemic species	***-0.79***	***-0.59***	***-0.61***	0.11	***0.54***	***-0.64***	***-0.54***	***-0.64***
# cosmopolitan species	0.05	**0.39**	**0.40**	***0.72***	**-0.41**	0.19	-0.01	0.22
endemic abundance	***-0.81***	***-0.74***	***-0.63***	-0.08	***0.70***	***-0.63***	**-0.43**	***-0.64***
cosmopolitan abundance	0.02	0.12	-0.11	0.36	-0.06	0.13	0.02	0.15
E_r:C_r	***-0.75***	***-0.75***	***-0.69***	-0.25	***0.70***	***-0.62***	***-0.48***	***-0.63***
E_a:C_a	***-0.74***	***-0.76***	***-0.62***	-0.17	***0.67***	***-0.62***	**-0.45**	***-0.64***

[1] Geometric mean turbidity at baseflow

[2] Percent fines < 2 mm (by weight) in riffles

Table 5.2. Multiple linear regression models of endemic to cosmopolitan richness and abundance (E_r:C_r and E_a:C_a) and sediment variables. Land cover abbreviations are for low-density urban (LDU), high-density urban (HDU), and total urban (U).

independent variable	variables in model	trend	cumulative r^2	*p*	*F*
sediment models of homogenization					
E_r:C_r	mean *phi*	-	0.57	< 0.001	38.84
	NTU	-	0.74	< 0.001	
E_a:C_a	mean *phi*	-	0.58	< 0.001	37.88
	NTU	-	0.73	< 0.001	
slope and land cover models of sediment variables					
mean *phi*	slope	-	0.84	< 0.001	120.10
	1987-97 LDU	-	0.90	< 0.001	
% fines in riffles	slope	-	0.62	< 0.001	28.37
	1997 HDU	+	0.68	0.04	
NTU	1997 U	+	0.42	< 0.001	14.00
	slope	-	0.51	0.04	
hierarchical models of homogenization					
E_r:C_r	NTU	-	0.57	< 0.001	37.00
	slope	+	0.76	< 0.001	
	1997 U	-	0.81	0.01	
E_a:C_a	NTU	-	0.54	< 0.001	28.81
	slope	+	0.71	0.005	
	1997 U	-	0.77	0.01	

Appendix 5.1. Endemic and cosmopolitan fishes collected in the Etowah River system. Value in parentheses is the number of southern U.S. drainages in which widespread species are native (Warren et al. 2000). Endemics have ranges that are primarily limited to highlands in the Alabama River drainage.

Family Name ***Scientific name***	**Common Name**
Endemic Highland Species	
Cyprinidae	
Cyprinella trichroistia	tricolor shiner
Hybopsis lineapunctata	lined chub
Notropis chrosomus	rainbow shiner
N. xaenocephalus	Coosa shiner
Phenacobius catostomus	riffle minnow
Cottidae	
Cottus carolinae zopherus	Coosa banded sculpin
Percidae	
Etheostoma etowahae	Etowah darter
E. jordani	greenbreast darter
E. scotti	Cherokee darter
Percina palmaris	bronze darter
P. sp. cf. P. macrocephala	“bridled darter”
Cosmopolitan Species	
Cyprinidae	
Campostoma oligolepis	largescale stoneroller (15)
Notemigonus crysoleucas	golden shiner (51)
Notropis longirostris	longnose shiner (10)
Pimephales vigilax	bullhead minnow (32)
Semotilus atromaculatus	creek chub (41)
Catostomidae	
Minytrema melanops	spotted sucker (40)
Moxostoma duquesnei	black redhorse (21)
M. erythrurum	golden redhorse (26)
M. poecilurum	blacktail redhorse (12)

Family Name ***Scientific name***	**Common Name**
Ictaluridae	
Ameiurus brunneus	snail bullhead (10)
A. natalis	yellow bullhead (40)
A. nebulosus	brown bullhead (30)
Ictalurus punctatus	channel catfish (40)
Noturus leptacanthus	speckled madtom (14)
Poeciliidae	
Gambusia affinis	western mosquitofish (24)
G. holbrooki	eastern mosquitofish (15)
Centrarchidae	
Ambloplites ariommus	shadow bass (15)
Lepomis auritus	redbreast sunfish (16)
L. cyanellus	green sunfish (36)
L. gulosus	warmouth (47)
L. macrochirus	bluegill sunfish (35)
L. megalotis	longear sunfish (37)
L. microlophus	redear sunfish (35)
Micropterus punctulatus	spotted bass (30)
M. salmoides	largemouth bass (47)
Pomoxis nigromaculatus	black crappie (44)
Percidae	
Etheostoma stigmaeum	speckled darter (17)
Percina nigrofasciata	blackbanded darter (15)

CHAPTER 6

CONCLUSIONS

In Chapter 2, I developed an index of biotic integrity (IBI) for wadeable Piedmont streams of the Etowah basin. This IBI fills a key resource management need because fish-based biomonitoring tools are generally lacking for the Etowah or the upper Piedmont of Georgia, a region experiencing exponential population growth and subsequent degradation of stream ecosystems (Couch et al. 1995, Devivo et al. 1997). The Etowah IBI used six metrics that tracked changes in stream habitat quality. Low quality sites had more tolerant fishes and higher centrarchid richness, but fewer darter, sculpin, and insectivorous cyprinid species as well as lower richness and density. Centrarchid richness is often used as a positive indicator in regional IBIs (Karr 1981, Shaner 1999, Schleiger 2000) but was negatively correlated with habitat quality in this study. The percentage of basin forest cover was positively correlated with IBI scores, suggesting that the IBI was sensitive to human impacts at the landscape level. Less forested basins have higher levels of disturbance (e.g., urban and agricultural land use), and catchment deforestation has been associated with impaired biotic communities in other basins (e.g., Richards and Host 1994, Roth et al. 1996, Wang et al. 1997).

I constructed a reduced IBI (R-IBI) by excluding the two metrics (density and relative abundance of tolerant taxa) that required quantitative abundance data for scoring. The R-IBI was designed as a tool for evaluating past levels of biotic integrity from historic fish collections that lack quantitative catch data. R-IBI was highly correlated with IBI scores for the 32 streams I sampled for this study, and R-IBI scores calculated from species lists for 23 streams sampled in the 1980s showed a similar increase with basin forested land cover. R-IBI is a promising tool for integrating historical collection data into watershed studies and for improving our ability to assess changes in stream biotic integrity over time. Historical data on species occurrence are typically underutilized because presence-absence designs suffer from low statistical power (Strayer 1999). The use of R-IBI improved two key aspects of my study. First, I was able to increase sample size cheaply by adding 23 sites to the analysis without incurring the expense of fieldwork and laboratory analysis. Second, I was able to extend the disturbance gradient by adding sites in less forested, more heavily impacted catchments than I sampled for my dissertation study.

In Chapter 3, I documented strong correlations between fish assemblages and stream geomorphology. Species composition in these streams shifted from centrarchids and other pool species to darters, cyprinids, and redhorse suckers that are riffle-run, benthic species. Changes in species composition were highly correlated with patchy, reach-level variation in stream slope, the dominant factor influencing benthic habitat. Lower gradient streams had smaller bed particles, more fines in riffles, less tractive force, and greater bed mobility compared to higher gradient streams. Variables related to stream size were only weakly related to species composition, but were the best predictors of species richness and fish density.

My results contrast with findings of other studies that attributed shifts in fish assemblages to longitudinal changes in stream size (Guillory 1982, Fausch et al. 1984, Welcomme 1985, Rahel and Hubert 1991, Paller 1994). Thus, my results contradict a general prediction of the River Continuum Concept (RCC; (Vannote et al. 1980) that species composition should vary predictably along a stream-size gradient. My findings were more in agreement with a prediction of the Process Domain Concept (Montgomery 1999) that local-scale (i.e., valley segment and channel reach) geomorphic processes govern the stream habitats and disturbance regimes that influence species composition. Most studies documenting strong longitudinal controls on local fish assemblages have sampled multiple reaches along the continuum in a single stream (e.g., Schlosser 1982, Rahel and Hubert 1991). My study used an alternative scale of analysis that focused on multiple reaches in streams of three size classes. Within a given size class, stream reaches were characterized by a high degree of geomorphic variation (e.g., local slope 0.01 to 0.001). This variation among streams proved to be more predictive of fish assemblage structure than longitudinal changes related to stream size.

Regional differences in climate and topography may also explain why my results conflict with those of other studies. For instance, Piedmont streams in the Etowah do not exhibit major discontinuities in stream temperature (i.e., cold vs. warmwater streams) or major geomorphic barriers (e.g., waterfalls) that control longitudinal distributions of fishes in other river systems (Schlosser 1982, Balon and Stewart 1983, Rahel and Hubert 1991, Lyons 1996, Waite and Carpenter 2000). Additionally, the type of disturbance regime influencing local assemblages may vary across regions. Schlosser's (Schlosser 1987) model was developed primarily for fishes in Midwestern, USA prairie streams that frequently experience intermittent summer flows and winter freezing. Deep pools, which occur in larger streams, are important refugia for fishes during these harsh conditions.

Streams in the Etowah do not experience this type of environmental perturbation. They never freeze completely and maintain some flow even during severe droughts. My results indicate that bed movement, a key component of disturbance in lotic systems (Hildrew and Giller 1992), may be an important environmental factor driving species composition in the Etowah streams.

Basin urbanization disrupts the relationships between stream geomorphology and fish assemblages. In Chapter 4, I found that richness and density declined with urban land cover regardless of stream size. Darters and sculpin, cyprinids, and endemic species also declined whereas centrarchids persisted and became the dominant group. Several other studies have shown that centrarchids are resilient to various forms of stream habitat degradation (Detenbeck et al. 1992, Jones et al. 1999, Walser and Bart 1999, Waite and Carpenter 2000) suggesting that their use as positive indicators of stream integrity (Karr 1981) is questionable. I analyzed the relative power of low-density (LDU), high-density (HDU), and total urban (U) land cover to predict changes in fish assemblages, but no clear "best" variable emerged. LDU, HDU, and U each appeared to more strongly influence different elements of fish assemblage structure. Because urban variables covary strongly, it was difficult to tease apart separate effects. Total urban land cover was a suitable variable for broadly assessing urbanization impacts on stream fishes in this study.

My results show that fishes respond to low levels of urban development and that the response time is brief. The effects were most pronounced for catchments that 1) had been > 10% U for at least ten years, or 2) catchments with > 15 % U. These results support the findings of other urban gradient studies that stream ecosystems respond strongly to low levels of urbanization (Klein 1979, Booth and Jackson 1997, Wang et al. 2001). Considering the level of 15% U within the context of land cover change 1987-1997 provides clues to the time frame over which assemblages changed and to the future structure of fish assemblages. The majority of urban development in the study basins occurred between 1987 and 1997. In 1987, only three of the study basins had > 15% U. By 1997, 13 catchments exceeded this level, and the mean was 14.8%. As urbanization progresses, I predict that endemics and other species groups will experience further declines and that centrarchid-dominated streams will become the norm within the Etowah basin.

In Chapter 5, I questioned if ratios of endemic to cosmopolitan fishes declined with increasing turbidity and finer stream beds, and if increasing turbidity and finer stream beds were associated with urbanization in a basin with a history of land disturbing activities. Local variation in bed texture and baseflow turbidity predicted patterns in species composition. Endemic richness and abundance was higher in clearer streams with coarse beds, whereas cosmopolitan species dominated turbid streams with finer beds. Urbanization was correlated with increasing bed and suspended sediment. After accounting for the influence of slope on bed texture, I found that basin urbanization lowered average particle size and increased fines in riffles. Baseflow turbidity was directly related to urban land cover. Thus, urbanization transformed clear streams with rocky beds into turbid streams with finer beds. These conditions favored cosmopolitan species and ultimately homogenized stream fish assemblages.

Baseflow turbidity was a strong predictor of homogenized fish assemblages. Prior to intense human disturbance, the study area was forested and streams presumably ran clear during low flows (Burkhead et al. 1997). Thus, high baseflow NTU indicates a departure from the natural sediment regime and may identify streams that suffer from chronic (i.e., "press") disturbance. High baseflow turbidity can negatively impact fishes by reducing foraging efficiency of drift feeding taxa (Waters 1997, Sweka and Hartman 2001) and disrupting spawning cues of fishes with vibrant nuptial coloration (Seehausen et al. 1997, Burkhead and Jelks 2001). Even though most sediment transport occurs during floods (Meade et al. 1990), storm flows are episodic and difficult to monitor (Meyer et al. 1999). In contrast, baseflow NTU is simple and cheap to monitor and was a strong indicator of urban effects in this study.

Protecting fishes of the Etowah River basin is a conservation priority for preserving the diversity of Southeastern fishes. The Etowah has a long history of human disturbance and has lost as many as nine species; however, the Etowah still maintains remnant populations of imperiled species that were formerly more widespread (Burkhead et al. 1997). Many of the unique fishes in Etowah streams are adapted to high-gradient, rocky reaches that have a patchy distribution across the landscape. As urban development increases, endemic species and other benthic fishes are lost and replaced by cosmopolitan species commonly found in low-gradient, sandy streams. These changes are evident at low levels of urban land cover, and given the current pace of urbanization in the region, the future of imperiled Etowah fishes is bleak.

REFERENCES

Balon, E. K., and D. J. Stewart. 1983. Fish Assemblages in a River with Unusual Gradient (Luongo, Africa Zaire System), Reflections on River Zonation, and

Description of Another New Species. Environmental Biology of Fishes 9:225-252.

Booth, D. B., and C. R. Jackson. 1997. Urbanization of aquatic systems: degradation thresholds, stormwater detection, and the limits of mitigation. Journal of the American Water Resources Association 33:1077-1090.

Burkhead, N. M., and H. L. Jelks. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. Transactions of the American Fisheries Society 130:959-968.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled Southern Appalachian ecosystem. Pages 375-444 *in* G. W. Benz and D. E. Collins, editors. Aquatic Fauna in Peril, the Southeastern Perspective. Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Couch, C. A., J. C. DeVivo, and B. J. Freeman. 1995. What fish live in the streams of Metropolotan Atlanta? Fact Sheet FS-091-95, U.S. Geological Survey. National Water-Quality Assessment Program, Atlanta, Georgia.

Detenbeck, N. E., P. W. Devore, G. J. Niemi, and A. Lima. 1992. Recovery of temperate-stream fish communities from disturbance - a review of case-studies and synthesis of theory. Environmental Management 16:33-53.

Devivo, J. C., C. A. Couch, and B. J. Freeman. 1997. Use of a preliminary index of biotic integrity in urban streams around Atlanta, Georgia. Pages 40-43 *in* K. J. Hatcher, editor. 1997 Georgia Water Resources Conference. Institute of Ecology, University of Georgia, Athens, GA., University of Georgia, Athens, Georgia.

Fausch, K. D., J. R. Karr, and P. R. Yant. 1984. Regional applications of an index of biotic integrity based on stream fish communities. Transactions of the American Fisheries Society 113:39-55.

Guillory, V. 1982. Longitudinal Gradients of Fishes in Thompson Creek, Louisiana. Southwestern Naturalist 27:107-115.

Hildrew, A. G., and P. S. Giller. 1992. Patchiness, species interactions and disturbance in the stream benthos. *in* P. S. Giller, A. G. Hildrew, and D. G. Raffaelli, editors. Aquatic ecology : scale, pattern and process : the 34th Symposium of the British Ecological Society with the American Society of Limnology and Oceanography,. Blackwell Scientific Publications, Oxford, UK.

Jones, E. B. D., III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conservation Biology 13:1454-1465.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Klein, R. D. 1979. Urbanization and stream quality impairment. Water Resources Bulletin 15:948-963.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45:329-341.

Meade, R. H., T. R. Yuzyk, and T. J. Day. 1990. Movement and storage of sediment in rivers of the United States and Canada. Pages 255-280 *in* M. G. Wolman and H. C. Riggs, editors. Surface water hydrology: Boulder, Colorado. Geological Society of America. The Geology of North America 0-1.

Meyer, J. L., A. B. Sutherland, K. H. Barnes, D. M. Walters, and B. J. Freeman. 1999. A scientific basis for erosion and sedimentation standards in the Blue Ridge physiographic province. Pages 321-324 *in* K. J. Hatcher, editor. 1999 Georgia Water Resources Conference. Institute of Ecology, The University of Georgia, Athens, Georgia.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 35:397-410.

Paller, M. H. 1994. Relationships between Fish Assemblage Structure and Stream Order in South-Carolina Coastal-Plain Streams. Transactions of the American Fisheries Society 123:150-161.

Rahel, F. J., and W. A. Hubert. 1991. Fish Assemblages and Habitat Gradients in a Rocky-Mountain Great-Plains Stream - Biotic Zonation and Additive Patterns of Community Change. Transactions of the American Fisheries Society 120:319-332.

Richards, C., and G. E. Host. 1994. Examining land use influences on stream habitats and macroinvertebrates: a GIS approach. Water Resources Bulletin 30:729-738.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.

Schleiger, S. L. 2000. Use of an index of biotic integrity to detect effects of land uses on stream fish communities in west-central Georgia. Transactions of the North American Fisheries Society 129:1118-1113.

Schlosser, I. J. 1982. Fish Community Structure and Function Along 2 Habitat Gradients in a Headwater Stream. Ecological Monographs 52:395-414.

Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Oklahoma.

Seehausen, O., J. J. M. vanAlphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808-1811.

Shaner, B. L. 1999. Development of a standardized index of biotic integrity for the Piedmont region of Georgia. Pages 287-290 *in* K. J. Hatcher, editor. 1999 Georgia Water Resources Conference. Institute of Ecology, The University of Georgia, Athens, Georgia.

Strayer, D. L. 1999. Statisitical power of presence-absence data to detect population declines. Conservation Biology 13:1034:1038.

Sweka, J. A., and K. J. Hartman. 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. Canadian Journal of Fisheries and Aquatic Sciences 58:386-393.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Waite, I. R., and K. D. Carpenter. 2000. Associations among fish assemblage structure and environmental variables in Willamette Basin streams, Oregon. Transactions of the American Fisheries Society 129:754-770.

Walser, C. A., and J. H.L. Bart. 1999. Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River system. Ecology of Freshwater Fish 8:237-246.

Wang, L. Z., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28:255-266.

Wang, L. Z., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22:6-12.

Waters, T. F. 1997. Sediment in Streams: Sources, Biological Effects, and Control. American Fisheries Society, Bethesda, Maryland.

Welcomme, R. L. 1985. River fisheries. FAO Technical Paper 262, Food and Agriculture Organization of the United Nations.

APPENDICES

A. GEOMORPHIC VARIABLE DEFINITIONS

Variable	Tranform used	Definition	Units	Observations used to calculate variable
Bankfull		***Bankfull stage is defined by the height of the first prominent bench, where the bench width exceeds the bench height.***		
Rbkf	none	bankfull hydraulic radius, which is bankfull area divided by wetted perimeter	m	3 cross-sections
Abkf	none	bankfull channel cross-sectional area	m^2	3 cross-sections
W/DbkfTWEG	log(10)	ratio of bankfull width divided by bankfull depth using top width and thalweg depth	dimensionless	3 cross-sections
BKF/UQ2	log(10)	entrenchment ratio expressed by ratio of bankfull flood discharge to the urbanized 2 yr RI flood discharge	dimensionless	3 cross-sections
BKF/RQ2	log(10)	entrenchment ratio expressed by ratio of bankfull flood discharge to the rural 2 yr RI flood discharge	dimensionless	3 cross-sections
VELbkf	none	average bankfull flow velocity calculated with the Manning Eqn.	m/sec	3 cross-sections
TRACbkf	log(10)	tractive force (shear stress) exerted on stream bed during bankfull flows	N/m^2	3 cross-sections
POWERbkf	log(10)	total stream power exerted by the average bankfull flood	watts	3 cross-sections
UPOWERBKF	log(10)	unit stream power of the average bankfull flood	watts/m^2	3 cross-sections
Bed Texture		***Bed texture variables pertain to the composition of sediment on the stream bed, including point count and sieve methods.***		
MANNN	none	Mannings roughness coefficient (n) for the bankfull channel as defined by Arcement and Schneider (1989)	dimensionless	based on the entire reach appearance
%BEDROCK(z)	Asin(Sqrt (x/100))	percent of observations on the subaqueous stream bed that were bedrock, rather than sediment	%	85 spots on zig-zag survey
avgPHI(z)	none	average particle size of the subaqueous stream bed from observations of the modal phi interval, not including bedrock	dimensionless	85 spots on zig-zag survey
stdvPHI(z)	none	standard deviation of modal phi size observations used to calculate average phi size (avgPHI(z)), not including bedrock	dimensionless	85 spots on zig-zag survey

Variable	Tranform used	Definition	Units	Observations used to calculate variable
avgRIFFPCphi	none	average intermediate diameter of sediment particles on a representative riffle from subaqueous pebble counts	phi	100 particles on a subaqueous riffle
stdvRIFFPCphi	none	standard deviation of sediment particles used to calculate average particle size (avgRIFFPCphi) on a representative riffle	phi	100 particles on a subaqueous riffle
avgBARPCphi	none	average intermediate diameter of particles on a representative emergent bar (lateral or mid-channel) from pebble counts	phi	100 particles on an emergent bar
stdvBARPCphi	none	standard deviation of particles used to calculate average particle size (avgBARPCphi) on a representative emergent bar	phi	101 particles on an emergent bar
avgRIFFSVphi	none	average phi size (by dry weight of all whole phi intervals retained on sieves) of samples from representative riffles	phi	100 particles on a subaqueous riffle
%MVCG-RIFFSV	Asin(Sqrt (x/100))	average percent (by dry weight of <63 mm whole phi intervals) of 8-63 mm gravel in samples from representative riffles	%	3 grab samples of riffle sediment
%COBBRIFFSV	Asin(Sqrt (x/100))	average percent (by dry weight of all whole phi intervals) of cobbles (63-256 mm) in samples from representative riffles	%	3 grab samples of riffle sediment
%GRAVRIFFSV	Asin(Sqrt (x/100))	average percent (by dry weight of all whole phi intervals) of gravel (2-63 mm) in samples from representative riffles	%	3 grab samples of riffle sediment
%FINESRIFFSV	Asin(Sqrt (x/100))	average percent (by dry weight relative to the whole sample) of all fines (<2 mm) in samples from representative riffles	%	3 grab samples of riffle sediment
%SICF-RIFFSV	Asin(Sqrt (x/100))	average percent (by dry weight of <2 mm fraction) of silt plus clay (<0.063 mm) in samples from representative riffles	%	3 grab samples of riffle sediment
avgBARSVphi	none	average phi size (by dry weight of all whole phi intervals retained on sieves) of samples from representative emergent bars	phi	3 grab samples of bar sediment
%MVCG-BARSV	Asin(Sqrt (x/100))	average percent (by dry weight of <63 mm whole phi intervals) of 8-63 mm gravel in samples from representative emergent bars	%	3 grab samples of bar sediment
%COBBBARSV	Asin(Sqrt (x/100))	average percent (by dry weight of all whole phi intervals) of cobbles (63-256 mm) in samples from representative emergent bars	%	3 grab samples of bar sediment
%GRAVBARSV	Asin(Sqrt (x/100))	average percent (by dry weight of all whole phi intervals) of gravel (2-63 mm) in samples from representative emergent bars	%	3 grab samples of bar sediment
%FINESBARSV	Asin(Sqrt (x/100))	average percent (by dry weight relative to the whole sample) of all fines (<2 mm) in samples from representative emergent bars	%	3 grab samples of bar sediment
%SICF-BARSV	Asin(Sqrt (x/100))	average percent (by dry weight of <2 mm fraction) of silt plus clay (<0.063 mm) in samples from representative emergent bars	%	3 grab samples of bar sediment

Variable	Tranform used	Definition	Units	Observations used to calculate variable
avgPOOLSVphi	Asin(Sqrt (x/100))	average phi size (by dry weight of all whole phi intervals retained on sieves) of samples from representative pools	phi	3 grab samples of pool sediment
%MVCG-POOLSV	Asin(Sqrt (x/100))	average percent (by dry weight of <63 mm whole phi intervals) of 8-63 mm gravel in samples from representative pools	%	3 grab samples of pool sediment
%COBBPOOLSV	Asin(Sqrt (x/100))	average percent (by dry weight of all whole phi intervals) of cobbles (63-256 mm) in samples from representative pools	%	3 grab samples of pool sediment
%GRAVPOOLSV	Asin(Sqrt (x/100))	average percent (by dry weight of all whole phi intervals) of gravel (2-63 mm) in samples from representative pools	%	3 grab samples of pool sediment
%FINESPOOLSV	Asin(Sqrt (x/100))	average percent (by dry weight relative to the whole sample) of all fines (<2 mm) in samples from representative pools	%	3 grab samples of pool sediment
%SICF-POOLSV	Asin(Sqrt (x/100))	average percent (by dry weight of <2 mm fraction) of silt plus clay (<0.063 mm) in samples from representative pools	%	3 grab samples of pool sediment
Depth		***Depth-related variables pertain to water depths during either baseflow or bankfull flow conditions.***		
Dbkf	none	bankfull cross-sectional depth computed as area divided by width	m	3 cross-sections
W/Dbkf	log(10)	bankfull water surface width (WWbkf) divided by average bankfull depth (Dbkf)	m	3 cross-sections
DTWEG	none	water depth of the thalweg (deepest part of the channel) at bankfull stage	m	3 cross-sections
DEPTHbase	log(10)	water depth during baseflow conditions computed from 5 cross-sections spaced at equal intervals throughout the reach	m	5 cross-sections at quarter-reach
avgD(z)	log(10)	average of baseflow water depth observations from the zig-zag survey	m	85 spots on zig-zag survey
StdvD(z)	log(10)	standard deviation of baseflow water depth observations from the zig-zag survey	m	85 spots on zig-zag survey
cvD(z)	log(10)	coefficient of variation of baseflow water depth observations from the zig-zag survey	m	
95%D(z)	log(10)	95th percentile value of baseflow water depth observations from the zig-zag survey	m	85 spots on zig-zag survey
avgPOO-D(z)	log(10)	average of baseflow pool depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey

Variable	Tranform used	Definition	Units	Observations used to calculate variable
stdPOO-D(z)	none	standard deviation of baseflow pool depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
cvPOO-D(z)	none	coefficient of variation of baseflow pool depth observations from the zig-zag survey	dimensionless	<85 spots on the zig-zag survey
95%POO-D(z)	none	95th percentile value of baseflow pool depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
avgGLID-D(z)	log(10)	average of basefow glide depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
stdGLID-D(z)	none	standard deviation of baseflow glide depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
95%GLID-D(z)	none	95th percentile value of baseflow glide depth observations from the zig-zag survey	dimensionless	<85 spots on the zig-zag survey
avgRIFF-D(z)	none	average of basefow riffle depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
stdRIFF-D(z)	none	standard deviation of baseflow riffle depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
cvRIFF-D(z)	log(10)	coefficient of variation of baseflow riffle depth observations from the zig-zag survey	dimensionless	<85 spots on the zig-zag survey
95%RIFF-D(z)	none	95th percentile value of baseflow riffle depth observations from the zig-zag survey	m	<85 spots on the zig-zag survey
DepVarAllCV	none	Coefficient of variation of serial depth (n-1) for all observations from the zig-zag survey	dimensionless	85 spots on zig-zag survey
DepVar0.5CV[?]	log(10)	Coefficient of variation of serial depth (n-1) for observations in the middle of the stream from the centerline of the zigzag survey	dimensionless	85 spots on zig-zag survey
Discharge		***Discharge-related variables include bankfull discharge and sediment transport variables related to the 0.5 yr RI urbanized flood.***		
Qbkf	log(10)	average bankfull discharge (m3/s) computed by multiplying the average velocity obtained by the Manning Equation by cross-sectional area	m^3/sec	3 cross-sections
Vb/Vc0.5	none	ratio of stream bed velocity divided by the threshold of velocity needed to move the average bed particle in the 0.5 yr RI flood	dimensionless	3 cross-sections used in HEC-RAS flow
riffVb/Vc0.5	log(10)	ratio of riffle bed velocity divided by the threshold of velocity needed to move the average riffle bed particle during the 0.5 yr RI flood	dimensionless	3 cross-sections used in HEC-RAS flow

Variable	Tranform used	Definition	Units	Observations used to calculate variable
sP/sPc0.5	log(10)	ratio of unit stream power to the threshold of stream power needed to move the average bed particle during the 0.5 yr RI flood	dimensionless	uses surveyed bank polygon
riffsP/sPc0.5	log(10)	ratio of unit stream power on riffles to threshold of stream power on riffles needed to move the average riffle bed particle during the 0.5 yr RI flood	dimensionless	uses surveyed bank polygon
P/Pc0.5	log(10)	ratio of unit stream power to the critical stream power needed to move the average stream bed particle during the 0.5 yr RI flood	dimensionless	3 cross-sections used in HEC-RAS flow
P/Pc0.5yrR	log(10)	ratio of unit stream power on riffles to the critical stream power on riffles needed to move the average riffle bed particle during the 0.5 yr RI flood	dimensionless	3 cross-sections used in HEC-RAS flow
TR0.5/TRc	log(10)	ratio of tractive force to critical tractive force needed to move the average stream bed particle during the 0.5 yr RI flood	dimensionless	3 cross-sections used in HEC-RAS flow
riffTR0.5/TRc	log(10)	ratio of tractive force on riffles to critical tractive force on riffles needed to move the average riffle bed particle during the 0.5 yr RI flood	dimensionless	3 cross-sections used in HEC-RAS flow
Gradient		***Gradient-related variables characterize attributes of the slope of the stream channel***		
mapslope	log(10)	map slope computed as the measured height/distance of the two contours nearest the surveyed reach from 1:24000 USGS topographic maps	dimensionless	2 map contours
slope	log(10)	slope of the surveyed reach computed from the best-fit line across the tops of riffles in the surveyed length of stream	dimensionless	>1 riffle survey points
slope/mapslope	log(10)	ratio of surveyed slope / map slope	dimensionless	not applicable
twegRcoeff	none	Pearson correlation coefficient relating curvilinear thalweg distance upstream for the bottom of the surveyed reach to the thalweg elevation	dimensionless	all thalweg survey points
twegSTERR	log(10)	standard error about the predicted relationship between curvilinear thalweg distance upstream and thalweg elevation	dimensionless	all thalweg survey points
twegREGSLOPE	log(10)	slope of the linear regression between curvilinear thalweg distance upstream and thalweg elevation in the surveyed reach	dimensionless	all thalweg survey points

Variable	Tranform used	Definition	Units	Observations used to calculate variable
Morphometry		***Morphometry variables describe various aspects of the drainage basin upstream of the surveyed reach***		
DA	none	drainage area of the catchment upstream of the surveyed reach	km^2	measured on maps in ArcView 3.2
PERIM	none	perimeter of the catchment upstream of the surveyed reach	km	measured on maps in ArcView 3.2
COMP	none	compactness - a measure of the departure of basin shape from a perfect circle, which has a minimal compactness value of 1.0	dimensionless	measured on maps in ArcView 3.2
AXSH	none	axial Shape - ratio of the perimeter of a circle of similar area to basin perimeter	dimensionless	measured on maps in ArcView 3.2
LENSTR	none	total stream length of the stream network upstream from the sampled reach as measured on 1:24,000 scale USGS topographic maps	km	measured on maps in ArcView 3.2
LENTR	log(10)	length of the trunk stream measured from the basin divide down to the outlet of the surveyed reach	km	measured on maps in ArcView 3.2
DDEN	none	drainage density or the total stream length within the basin divided by the area of the basin above the downstream point of the surveyed reach	km/km^2	measured on maps in ArcView 3.2
TOTREL	log(10)	total basin relief, which is the elevation difference between the surveyed reach and the maximum height of the interstream divide of the basin	m	measured on maps in ArcView 3.2
LOCREL	log(10)	local relief - elevation difference between the ridge tops and stream bottom along a transect perpendicular to the stream in the surveyed reach	m	measured on maps in ArcView 3.2
RELTR	log(10)	relief of the trunk stream, which is the elevation difference between surveyed reach and the drainage divide at the head of the trunk stream	m	measured on maps in ArcView 3.2
SLOPTR	none	slope of the trunk stream, which is the gradient of the trunk stream measured from its interstream divide down to the surveyed reach	dimensionless	measured on maps in ArcView 3.2
Width				
WWbkf	none	wetted width at bankfull, measured as the water surface of the bankfull cross-section	m	3 cross-sections
WIDTHlow	none	channel width during low flow (0.5-1.0 yr RI) floods approximately waist deep, measured as the polygon area divided by length from survey data	m	uses surveyed bank polygon
WWbase	none	average water width during baseflow conditions computed from 5 cross-sections spaced at equal intervals throughout the reach	m	5 cross-sections at quarter-reach

Variable	Tranform used	Definition	Units	Observations used to calculate variable
Miscellaneous				
TERR#of3	none	number of cross sections that exhibit terraces on either side	dimensionless	3 cross-sections
TBANK#of6	log(10)	number of stream banks that exhibit terraces above the top level of the bankfull channel or floodplain	dimensionless	3 cross-sections
CWDTOT	log(10)	total large woody debris (LWD) - the total LWD within the low-flood polygon, which correlates to about a 1 yr RI event	m^3/100m^2	variable
CWDWET	log(10)	total wetted large woody debris (LWD) - total LWD that is in contact with the water at baseflow	m^3/100m^2	variable
CWDFXN	log(10)	total functional large woody debris (LWD) - total LWD producing functional geomorphic habitat such as flow diversions and pools	m^3/100m^2	variable
%RIFFLEtweg	Asin(Sqrt (x/100))	percent of the linear thalweg that is classified as a riffle under a binary riffle-pool system	%	<85 spots on the zig-zag survey
%POOLtweg	Asin(Sqrt (x/100))	percent of the linear thalweg that is classified as pool under a binary riffle-pool system	%	<85 spots on the zig-zag survey
%POOL(z)	Asin(Sqrt (x/100))	percent pool space from point counts along a zig-zag survey	%	<85 spots on the zig-zag survey
%GLIDE(z)	Asin(Sqrt (x/100))	percent glide space from point counts along a zig-zag survey	%	<85 spots on the zig-zag survey
%RIFFLE(z)	Asin(Sqrt (x/100))	percent riffle space from point counts along a zig-zag survey	%	<85 spots on the zig-zag survey

B. GEOMORPHIC DATA (RAW) USED FOR PCA ANALYSIS.

Site	Rbkf	Abkf	W/DbkfT WEG[1]	BKF/ UQ2[1]	BKF/ RQ2[1]	VEL-bkf	TRAC-bkf[1]	POWER-bkf[1]	UPOWER-BKF[1]
1	1.27	17.4	5.15	1.22	1.32	1.47	36.16	742.01	65.32
2	1.16	18.2	5.95	2.02	2.23	1.91	51.37	1727.48	139.63
3	0.48	3.6	8.56	0.08	0.09	0.58	7.05	33.18	4.94
4	0.82	9.0	7.01	0.38	0.42	0.87	18.51	178.01	18.31
5	0.92	10.1	6.26	0.66	0.71	1.09	28.09	363.81	41.92
6	1.16	12.7	3.87	0.85	0.90	1.27	39.97	559.23	69.15
7	1.54	23.3	3.69	1.59	1.80	1.55	30.14	711.03	60.69
8	0.96	9.7	5.42	0.75	0.78	1.44	54.81	820.20	97.38
9	0.88	7.4	5.07	0.60	0.68	1.41	73.45	879.19	130.18
10	0.99	12.6	6.61	1.17	1.33	1.63	78.07	1682.60	157.97
11	1.38	26.4	8.21	0.91	0.98	1.52	46.02	1345.30	80.02
12	2.06	55.6	6.62	2.63	3.13	2.31	90.43	5717.76	243.42
13	1.58	23.5	4.57	0.56	0.69	1.31	22.70	449.56	38.08
14	1.45	23.1	5.55	0.78	0.87	1.57	35.94	905.94	68.48
15	2.36	53.6	4.59	1.96	2.20	1.68	35.55	1354.20	72.46
16	1.63	30.0	5.75	1.67	1.81	2.06	83.18	3175.01	203.11
17	1.25	19.7	6.19	0.58	0.61	1.31	35.08	726.92	55.85
18	1.61	27.5	5.40	0.84	0.97	1.47	29.49	754.75	54.14
19	1.37	21.4	5.72	0.78	0.81	1.68	59.30	1603.02	131.81
20	1.67	31.9	5.93	1.28	1.39	1.86	121.47	4304.31	263.95
21	2.29	55.9	5.41	0.99	1.07	1.42	22.45	780.54	37.96
22	1.43	38.3	11.73	0.77	0.82	1.44	39.24	1511.88	60.02
23	2.01	45.8	5.69	0.76	1.19	1.49	28.55	977.16	52.06
24	1.77	36.7	6.31	0.79	0.91	1.51	35.55	1134.97	64.40
25	1.82	34.6	5.35	0.49	0.58	1.22	18.67	434.70	27.75
26	1.41	32.6	10.49	0.57	0.66	1.14	17.68	475.26	22.58
27	2.68	80.2	6.02	2.42	2.59	2.09	65.67	4104.64	160.75
28	1.87	53.3	8.91	1.86	2.02	2.33	121.21	8569.39	355.30
29	1.76	41.0	7.66	1.38	1.44	1.88	73.38	3236.39	161.45
30	2.25	59.8	5.99	1.91	2.06	2.04	71.87	3946.97	179.08
101	1.40	19.0	4.04	1.26	1.64	1.56	39.97	854.63	79.38
111	1.6	26.2	4.55	1.39	1.76	2.66	158.93	6877.09	527.22

Recommended transformations: [1]$\log_{10}$; [2]Asin(Sqrt(x/100))

Site	MANNN	%Bed-rock(z)^2	avg-PHI(z)	stdv-PHI(z)	avgRIFF-PCphi	stdvRIFF-PCphi	avgBARPCphi	stdvBARPCphi	avgRIFFSVphi
1	0.043	21	-1.7	2.1	-3.5	1.8	-2.5	2.2	-3.13
2	0.038	0	0.4	3.8	-5.4	0.6	-3.3	2.4	-4.77
3	0.040	0	-1.1	1.6	-2.8	1.6	0	0	-0.58
4	0.048	2	-2	2	-4	1.6	-3.4	1.8	-2.56
5	0.048	7	-3.6	3.7	-5.2	1.7	-4	1.9	-3.59
6	0.052	19	-5	2.2	-4.5	1.3	-2.9	1.9	-4.01
7	0.038	0	-0.3	0.9	-0.6	1.1	-0.3	1	-1.09
8	0.051	2	-4.9	2.8	-5.4	1.9	-3.3	1.8	-3.61
9	0.060	26	-6.4	2.4	-5.2	1.6	-4.3	2.5	-3.96
10	0.054	27	-6.1	1.9	-5.2	2.3	-5.4	2	-4.38
11	0.047	8	-3.4	2	-4.3	1.2	-4.5	1.3	-2.95
12	0.047	4	-3.2	3.6	-5.9	1.9	-4.5	1.8	-4.06
13	0.040	2	-0.8	1.6	-0.6	1	0	0	-1.61
14	0.041	0	-1.4	2	-5.5	1.5	-1.7	1.6	-1.83
15	0.041	0	-1.5	1.7	-3.3	1.2	-3.1	1.4	-1.54
16	0.048	9	-3.8	2.6	-4.9	1.1	-4.8	2.4	-4.06
17	0.047	1	-3.4	1.9	-3.2	1.2	-3	1.7	-1.85
18	0.040	4	-1.1	1.9	-3.8	2.3	-2.5	2.4	-3.86
19	0.049	6	-3.9	2.4	-4.8	1.7	0	0	-4.08
20	0.065	52	-5.1	2.6	-6.8	1.8	-5.9	2.1	-4.92
21	0.039	0	-0.5	1	-2.3	1.2	-0.4	0.9	-0.27
22	0.047	6	-3.1	2.1	-4.2	1.3	-4.3	1.3	-2.91
23	0.041	0	-1.2	1.5	-2.5	1.5	-0.9	1.4	-0.58
24	0.044	1	-2.1	3	-3.8	2.2	-0.5	1.1	-3.98
25	0.039	4	-0.7	1.3	-2.8	1.5	-1.7	2.1	-1.74
26	0.039	0	-0.7	1.1	-3	1.4	-1.6	1.6	-0.60
27	0.046	26	-3	1.9	-4.9	2.1	-5	1	-2.38
28	0.053	26	-5.5	2.5	-5.8	2.1	0	0	-2.27
29	0.050	1	-4.6	2.1	-5.3	0.9	-4.8	1.3	-4.96
30	0.048	1	-3.7	2.8	-6.2	0.6	-4.4	1.9	-4.82
101	0.043	0	-1.9	2.3	-2.9	2	-2.8	1.9	-1.11
111	0.052	67	-5.1	2.8	-6.7	0.9	-2.1	2.2	-4.94

Recommended transformations: ^{1}log$_{10}$; ^{2}Asin(Sqrt(x/100))

Site	%MVCG-RIFFSV^2	%COBBRIFFSV^2	%GRAVRIFFSV^2	%FINESRIFFSV^2	%SICF-RIFFSV^2	avgBARSV phi	%MVCG-BARSV^2
1	49.30	14.38	59.44	26.18	3.22	-1.27	19.78
2	90.35	0.00	96.11	3.89	4.61	-1.66	22.83
3	5.10	0.00	25.38	74.62	4.01	-0.29	2.08
4	46.94	0.00	70.65	29.35	2.46	-2.40	45.82
5	65.18	3.03	75.28	21.69	10.10	-3.23	46.09
6	76.64	0.00	86.63	13.37	3.71	-2.66	49.54
7	12.42	0.00	41.55	58.45	4.10	-1.06	14.01
8	65.17	4.62	81.49	13.89	5.56	-4.08	74.50
9	77.89	0.00	87.38	12.62	7.99	-2.59	41.62
10	82.40	6.89	85.86	7.25	8.88	-3.68	62.61
11	57.39	0.00	76.16	23.84	3.33	-2.67	48.79
12	74.06	5.59	78.11	16.30	1.88	-3.07	61.76
13	14.67	12.20	26.50	61.30	2.71	-1.13	14.19
14	24.73	6.29	43.85	49.87	2.74	-0.44	2.28
15	24.89	0.00	51.16	48.84	2.65	-1.45	23.08
16	64.92	20.11	66.54	13.36	1.88	-3.96	55.69
17	25.90	0.00	68.11	31.89	5.03	-2.22	37.12
18	66.09	11.57	68.86	19.57	4.10	-3.34	57.00
19	72.94	8.12	78.98	12.89	7.05	-1.08	19.06
20	76.86	36.32	57.40	6.27	2.83	-4.16	71.81
21	1.08	0.00	13.13	86.87	3.01	-0.25	0.48
22	56.01	0.00	73.21	26.79	3.56	-3.49	66.78
23	4.65	0.00	26.15	73.85	4.21	-0.64	6.62
24	66.99	15.97	63.23	20.81	3.38	-0.19	0.39
25	31.44	0.00	52.68	47.32	3.92	-1.03	18.06
26	5.67	0.00	26.19	73.81	2.36	-0.22	1.23
27	41.13	0.00	64.08	35.92	6.98	-2.49	45.43
28	39.97	0.00	63.26	36.74	4.47	-0.02	0.10
29	85.37	24.22	70.65	5.13	3.92	-4.55	68.15
30	79.14	26.36	67.22	6.42	3.37	-2.94	54.85
101	15.36	0.00	41.93	58.07	9.09	-1.98	33.72
111	83.98	26.57	68.83	4.59	5.10	-0.98	15.65

Recommended transformations: $^1\log_{10}$; ^{2}Asin(Sqrt(x/100))

Site	%COBBB ARSV^2	%GRAVB ARSV^2	%FINESB ARSV^2	%SICF-BARSV^2	avgPOOLSV phi^2	%MVCG-POOLSV^2	%COBB-POOLSV^2
1	0.00	44.10	55.90	8.44	-0.49	6.64	0.00
2	3.96	46.47	49.57	10.87	-0.77	8.94	0.00
3	0.00	13.11	86.89	5.14	-0.45	3.12	0.00
4	0.00	70.10	29.90	4.46	-2.44	45.87	0.00
5	16.28	57.19	26.53	13.60	-0.17	0.81	0.00
6	0.00	70.89	29.11	6.07	-4.07	73.91	4.94
7	0.00	38.97	61.03	4.44	-0.13	0.03	0.00
8	6.05	81.72	12.23	4.63	-1.60	28.50	0.00
9	4.65	65.18	30.17	11.30	-3.00	55.66	3.25
10	11.82	66.88	21.31	11.30	-2.48	48.23	0.00
11	3.00	65.86	31.14	5.12	-3.72	72.56	0.00
12	0.00	75.28	24.72	4.11	-1.39	10.19	11.71
13	6.00	14.08	79.92	22.21	-0.18	1.49	0.00
14	0.00	20.47	79.53	6.95	-0.48	5.71	0.00
15	0.00	50.16	49.84	3.97	-1.23	15.51	0.00
16	25.30	54.60	20.10	7.33	-1.71	23.65	5.64
17	0.00	75.43	24.57	5.80	-1.41	15.86	0.00
18	9.74	63.81	26.45	9.61	-0.24	1.54	0.00
19	0.00	24.94	75.06	23.25	-1.19	22.95	0.00
20	13.96	71.53	14.51	7.06	-2.72	44.84	3.77
21	0.00	13.39	86.61	3.83	-0.28	1.89	0.00
22	0.00	81.22	18.78	5.57	-1.43	26.47	0.00
23	0.00	27.37	72.63	4.09	-0.56	9.61	0.00
24	0.00	9.98	90.02	3.54	-0.22	1.46	0.00
25	0.00	32.39	67.61	5.02	-0.30	4.09	0.00
26	0.00	10.50	89.50	2.77	-0.19	1.91	0.00
27	0.00	65.51	34.49	9.09	-1.54	20.40	0.00
28	0.00	0.32	99.68	7.62	-0.43	2.39	0.00
29	31.87	54.69	13.44	9.91	-3.43	61.65	8.24
30	0.00	69.71	30.29	7.77	-2.21	34.24	0.00
101	0.00	64.62	35.38	6.61	-0.28	0.93	0.00
111	0.00	33.34	66.66	4.25	-0.95	11.62	0.00

Recommended transformations: $^1\log_{10}$; ^{2}Asin(Sqrt(x/100))

Site	%GRAV-POOLSV[2]	%FINES-POOLSV[2]	%SICF-POOLSV[2]	Dbkf	W/Dbkf[1]	DTWEG	DEPTH base[1]
1	19.26	80.74	3.45	1.54	7.40	2.20	0.16
2	31.18	68.82	12.69	1.47	8.39	2.08	0.43
3	20.85	79.15	3.43	0.53	12.58	0.78	0.17
4	69.44	30.56	4.55	0.92	10.53	1.39	0.20
5	8.28	91.72	28.77	1.16	7.47	1.39	0.15
6	80.90	14.15	8.71	1.57	5.15	2.09	0.23
7	7.26	92.74	3.33	1.99	5.89	3.18	0.25
8	35.87	64.13	4.75	1.16	7.28	1.55	0.17
9	70.15	26.60	9.53	1.10	6.15	1.33	0.21
10	69.53	30.47	14.41	1.19	8.97	1.61	0.14
11	86.78	13.22	4.07	1.57	10.69	2.05	0.17
12	17.16	71.14	1.19	2.37	9.92	3.55	0.27
13	7.84	92.16	1.93	1.99	5.94	2.58	0.22
14	18.88	81.12	3.92	1.75	7.58	2.38	0.17
15	48.44	51.56	2.91	2.87	6.52	4.07	0.12
16	35.65	58.71	3.70	1.92	8.14	2.72	0.18
17	56.65	43.35	5.97	1.51	8.59	2.10	0.24
18	11.24	88.76	1.45	1.97	7.08	2.58	0.16
19	28.25	71.75	9.85	1.76	6.92	2.13	0.26
20	67.04	29.19	2.57	1.95	8.34	2.75	0.26
21	12.88	87.12	3.82	2.72	7.57	3.80	0.13
22	38.43	61.57	3.07	1.52	16.56	2.15	0.23
23	18.60	81.40	3.61	2.44	7.70	3.30	0.21
24	10.41	89.59	3.36	2.08	8.47	2.79	0.22
25	11.31	88.69	2.74	2.21	7.09	2.93	0.16
26	8.13	91.87	2.27	1.55	13.58	2.01	0.15
27	49.36	50.64	18.29	3.14	8.13	4.24	0.33
28	21.47	78.53	5.89	2.21	10.92	2.71	0.27
29	67.08	24.68	4.33	2.05	9.80	2.62	0.18
30	61.75	38.25	3.07	2.72	8.12	3.68	0.50
101	15.42	84.58	5.32	1.76	6.11	2.67	0.19
111	38.57	61.43	4.73	2.01	6.50	2.87	0.22

Recommended transformations: [1] $\log_{10}$; [2] Asin(Sqrt(x/100))

Site	avgD(z)[1]	StdvD(z)[1]	cvD(z)[1]	95%D(z)[1]	avgPOO-D(z)[1]	stdPOO-D(z)	cvPOO-D(z)
1	19.90	14.60	0.70	48.50	23.49	15.93	0.68
2	52.70	28.60	0.50	106.50	57.45	25.59	0.45
3	22.10	12.10	0.50	46.50	26.26	13.49	0.51
4	24.40	13.40	0.60	52.00	29.66	13.04	0.44
5	19.60	12.50	0.60	40.50	25.74	11.95	0.46
6	29.60	11.10	0.40	47.25	31.67	9.1	0.29
7	32.10	12.00	0.40	57.00	31.96	10.82	0.34
8	19.20	11.60	0.60	42.75	25.75	13.94	0.54
9	25.90	7.60	0.30	40.25	24.33	11.68	0.48
10	16.60	13.00	0.80	44.50	22.5	18.07	0.8
11	21.40	18.80	0.90	63.75	28.91	25.84	0.89
12	33.90	22.30	0.70	83.25	43.09	25.54	0.59
13	26.80	16.80	0.60	60.25	34.89	22.95	0.66
14	22.20	13.70	0.60	51.25	32.55	20.12	0.62
15	16.30	8.70	0.50	33.75	15.08	9.03	0.6
16	22.00	14.90	0.70	50.00	30.89	16.73	0.54
17	28.90	17.70	0.60	60.25	40.26	18.14	0.45
18	21.10	11.80	0.60	41.75	16	8.49	0.53
19	31.90	22.00	0.70	70.50	41.5	27.37	0.66
20	28.10	14.10	0.50	53.50	28.32	14.99	0.53
21	17.10	8.30	0.50	35.25	30.88	13.2	0.43
22	27.30	25.60	0.90	88.50	44.82	28.75	0.64
23	26.40	18.20	0.70	66.25	43	24.2	0.56
24	29.50	17.20	0.60	61.25	39.02	18.91	0.48
25	20.20	11.90	0.60	45.75	36.64	13.88	0.38
26	20.70	20.80	1.00	43.00	44.07	41.3	0.94
27	42.70	22.30	0.50	81.50	53.77	17.69	0.33
28	35.40	23.30	0.70	84.50	50.69	26.84	0.53
29	22.00	13.00	0.60	48.75	32.32	14.68	0.45
30	58.40	44.70	0.80	161.25	76.55	44.91	0.59
101	18.20	11.60	0.60	46.60	20.9	13.1	0.63
111	23.10	18.20	0.80	53.00	29.8	24.4	0.82

Recommended transformations: [1]$\log_{10}$; [2]Asin(Sqrt(x/100))

Site	95%POO-D(z)	avgGLID-D(z)[1]	stdGLID-D(z)	95%GLID-D(z)	avgRIFF-D(z)	stdRIFF-D(z)	cvRIFF-D(z)[1]
1	56.3	12.8	5.16	20	10.81	5.54	0.51
2	107.3	0	0	0	6.63	6.59	0.99
3	48	16.95	7.4	31.8	0	0	0
4	52	19.86	11.46	48.5	7.75	2.5	0.32
5	44	15.17	7.65	28.3	8.52	4.44	0.52
6	44.9	33.29	10.72	49	21.17	8.9	0.42
7	52.75	35.08	15.16	60.4	1	0	0
8	53.6	24.72	8.66	43	11.03	4.73	0.43
9	37	35.91	5.41	42.95	24.46	6.57	0.27
10	56.2	19.38	10.55	44	10.29	5.27	0.51
11	79.75	20.76	8.09	32.3	9.9	4.54	0.46
12	107.4	27.65	7.69	40.5	16.89	6.99	0.41
13	78.1	22.96	11.46	43	21.17	7.11	0.34
14	70	19.59	9.02	39.6	14.43	7.79	0.54
15	31.85	19.24	9.07	36.8	11.54	5.05	0.44
16	64.65	20.47	7.36	36.25	12.82	7.79	0.61
17	65.55	26.81	8.18	45.3	15.17	8.4	0.55
18	22	20.78	12.22	39.4	23.82	9.2	0.39
19	101.2	31.92	15.46	56.2	19.89	11.23	0.56
20	57.2	37.69	15.64	61.1	24.79	11.7	0.47
21	50	15.66	6.12	26.65	0	0	0
22	112.15	14.5	5.36	23.3	10	4.91	0.49
23	87.9	20.88	10	41.3	12.2	6.65	0.55
24	78.35	19.28	6.01	30.25	20.62	7.96	0.39
25	55.7	18.05	9.74	40.35	15.91	8.29	0.52
26	132.4	16.63	8.16	32	7	7.66	1.09
27	84.3	26.3	11.73	52	16.5	6.89	0.42
28	99.75	32.09	11.73	62.1	18.44	8.38	0.45
29	59.5	20.78	10.16	36	14.21	7.39	0.52
30	168.75	38.1	14.72	57	18.55	11.92	0.64
101	49.5	17.7	8.6	32	11.7	5.4	0.46
111	85	26.2	10.2	46.7	14.7	9	0.61

Recommended transformations: [1]log$_{10}$; [2]Asin(Sqrt(x/100))

Site	95%RIFF-D(z)	DepVarAllCV	DepVar0.5CV	Qbkf^1	Vb/Vc0.5	riffVb/Vc0.5^1	sP/sPc0.5^1	riffsP/sPc0.5^1
1	19.4	99.69	105.88	26	1.86	0.73	66.51	5.22
2	19	91.04	109.66	39	5.24	0.67	686.78	2.73
3	0	89.71	93.23	2	2.97	1.16	97.97	7.48
4	11	87.55	93.46	8	1.52	0.62	50.43	4.5
5	15.35	87.65	101.8	12	0.8	0.39	11.66	1.74
6	37.35	90.17	84.79	16	0.6	0.61	4.93	5.11
7	1	93.81	93.96	36	3.23	2.41	308.64	137.48
8	19.7	77.81	96.78	14	0.76	0.48	8.93	2.76
9	36	86.21	81.42	11	0.46	0.52	3.03	4.11
10	19	93.26	98.34	21	0.55	0.49	2.61	2
11	17.25	111.22	104.13	40	1.14	0.74	21.71	6.97
12	26.6	120.05	83.85	130	1.47	0.46	36.76	1.74
13	35	91.74	102.2	31	3.07	2.81	180.32	140.34
14	26	100	89.95	36	2.85	0.59	148.9	2.18
15	20.4	85.41	101.82	90	2.11	0.99	74.06	9.27
16	25.95	98.97	97.06	62	1.21	0.72	21.32	5.34
17	32	101.77	128.7	26	1.08	1.01	18.39	15.57
18	46.1	101.69	166.14	41	2.68	0.72	148.83	4.18
19	42	93.16	93.91	37	1.18	0.71	22.89	5.91
20	49.15	66.75	68.21	59	0.78	0.36	12.71	1.74
21	0	89.41	85.88	80	2.89	1.35	195.53	23.76
22	21.8	122.74	94.03	55	1.19	0.7	19.69	4.82
23	22	114.88	97.04	69	2.78	1.44	145.95	23.98
24	35.95	87.41	90.87	56	2.02	0.73	75.2	4.81
25	27.95	85.73	94.22	42	3.16	1.28	146.94	12.26
26	17	115.15	159.71	38	2.69	1.02	117.26	8.29
27	30.6	104.12	96.24	167	1.4	0.53	30.12	2.21
28	32.6	90.5	86	132	0.74	0.49	7.47	2.5
29	29.2	64.75	66.62	78	0.81	0.57	8.78	3.48
30	39	95.54	109.25	124	1.4	0.56	17.8	1.59
101	23	102.93	92.9	30	1.77	0.84	80.68	10.64
111	34.5	95.54	89.5	70	0.21	0.11	20.77	4.07

Recommended transformations: ^{1}log$_{10}$; ^{2}Asin(Sqrt(x/100))

Site	P/Pc0.5[1]	P/Pc0.5yrR[1]	TR0.5/TRc[1]	riffTR0.5/TRc[1]	map slope[1]	slope[1]	slope/mapslope[1]
1	51.86	4.07	3.9	0.59	0.0043	0.0029	0.680
2	892.5	3.55	27.32	0.45	0.0042	0.0045	1.080
3	175.86	13.43	8.58	1.3	0.0028	0.0015	0.545
4	35.39	3.16	3.22	0.54	0.0034	0.0023	0.675
5	6.39	0.95	0.9	0.21	0.0051	0.0031	0.603
6	3.38	3.51	0.57	0.59	0.0039	0.0035	0.905
7	180.68	80.48	8.96	4.99	0.0038	0.0020	0.526
8	7.62	2.36	0.98	0.39	0.0063	0.0058	0.925
9	2.76	3.74	0.48	0.61	0.0084	0.0085	1.010
10	4.76	3.64	0.63	0.51	0.0064	0.0080	1.259
11	16.12	5.18	1.7	0.73	0.0029	0.0034	1.169
12	35.21	1.67	2.86	0.28	0.0052	0.0045	0.854
13	140.31	109.2	7.49	6.25	0.0017	0.0015	0.875
14	147.02	2.15	7.72	0.33	0.0015	0.0025	1.688
15	56.41	7.07	4.06	0.89	0.0023	0.0015	0.659
16	22.55	5.65	2.1	0.74	0.0025	0.0052	2.078
17	12.24	10.37	1.43	1.27	0.0021	0.0029	1.383
18	105.56	2.96	6.2	0.45	0.0014	0.0019	1.295
19	18.74	4.84	1.87	0.67	0.0019	0.0044	2.341
20	12.36	1.7	1.52	0.32	0.0048	0.0074	1.530
21	104.78	12.73	6.03	1.31	0.0009	0.0010	1.122
22	16.31	3.99	1.72	0.6	0.0019	0.0028	1.456
23	111.37	18.3	6.25	1.68	0.0015	0.0015	0.940
24	54.93	3.51	3.99	0.52	0.0017	0.0021	1.228
25	139.06	11.61	7.4	1.22	0.0021	0.0010	0.510
26	99.22	7.02	5.95	0.86	0.0019	0.0013	0.678
27	24.11	1.77	2.27	0.32	0.0026	0.0025	0.944
28	7.69	2.58	0.94	0.4	0.0034	0.0066	1.943
29	7.49	2.97	0.97	0.48	0.0025	0.0043	1.707
30	42.49	3.8	3.03	0.49	0.0034	0.0033	0.967
101	45.67	6.02	3.53	0.79	0.0013	0.0029	2.200
111	23.69	4.65	2.01	0.57	0.0009	0.0100	11.123

Recommended transformations: [1]log$_{10}$; [2]Asin(Sqrt(x/100))

Site	twegRcoeff	tweg STERR[1]	tweg REGSLOPE[1]	DA	PERIM	COMP	AXSH
1	0.18	0.15	0.0001	16.6	17.2	17.92	1.16
2	0.68	0.24	0.0059	13.8	18.1	23.63	2.27
3	0.08	0.12	0.0003	22.3	23.2	24.02	1.12
4	0.51	0.16	0.0022	15.6	19.0	23.05	2.08
5	0.05	0.14	0.0002	13.1	16.9	21.75	1.37
6	0.46	0.11	0.0016	14.5	19.5	26.20	2.13
7	0.66	0.06	0.0018	17.1	19.8	22.91	1.39
8	0.81	0.13	0.0053	14.9	17.8	21.13	1.44
9	0.97	0.07	0.0091	11.3	17.1	25.87	2.66
10	0.88	0.15	0.0079	12.2	19.1	29.86	2.34
11	0.7	0.26	0.0044	50.7	37.7	28.07	1.70
12	0.07	0.35	0.0003	52.0	39.7	30.36	1.86
13	0.25	0.14	0.0007	59.1	36.1	22.07	1.58
14	0.57	0.15	0.0019	52.8	38.6	28.15	2.42
15	0.76	0.08	0.0018	50.7	43.1	36.65	3.17
16	0.84	0.2	0.0051	38.6	30.6	24.31	1.35
17	0.48	0.25	0.0028	53.2	43.3	35.22	1.28
18	0.58	0.13	0.0001	53.6	36.4	24.74	1.59
19	0.64	0.23	0.0038	60.3	37.4	23.20	1.10
20	0.92	0.16	0.0068	53.8	30.8	17.68	1.26
21	0.48	0.09	0.0007	125.7	52.3	21.78	1.19
22	0.43	0.29	-0.0017	108.5	60.3	33.50	1.90
23	0.37	0.12	0.0007	85.3	43.3	21.97	1.62
24	0.34	0.11	0.0007	96.1	51.5	27.64	1.86
25	0.48	0.09	0.0007	122.1	52.0	22.14	1.15
26	0.59	0.1	0.0011	84.6	56.1	37.19	1.99
27	0.61	0.25	0.0028	101.9	54.8	29.45	1.27
28	0.84	0.23	0.005	103.9	50.0	24.09	1.13
29	0.89	0.14	0.0036	77.4	44.5	25.58	1.29
30	0.31	0.44	0.002	90.7	42.2	19.66	1.48
101	0.22	0.15	0.0023	14.8	19.1	24.68	2.07
111	0.87	0.22	0.0117	48.4	36.8	28.06	1.19

Recommended transformations: [1]$\log_{10}$; [2]Asin(Sqrt(x/100))

Site	LENSTR	LENSTR	DDEN	TOT-REL[1]	LOC-REL[1]	REL-TR[1]	SLOPTR	WWbkf	WIDTHlow
1	35.37	36.37	2.13	118	46	98	0.0134	11.36	8.12
2	32.07	33.07	2.32	111	67	76	0.0104	12.37	8.22
3	49.67	50.67	2.23	88	70	73	0.0116	6.71	6.40
4	38.23	39.23	2.45	77	70	55	0.0087	9.72	6.07
5	32.92	33.92	2.50	110	113	79	0.0128	8.68	6.55
6	33.55	34.55	2.31	105	64	79	0.0123	8.09	5.09
7	38.42	39.42	2.25	149	44	52	0.0085	11.72	4.59
8	35.55	36.55	2.38	141	70	73	0.0134	8.42	5.37
9	25.28	26.28	2.23	102	46	70	0.0090	6.75	5.81
10	27.34	28.34	2.24	121	54	101	0.0123	10.65	8.91
11	117.48	118.48	2.32	182	76	149	0.0089	16.81	11.70
12	115.98	116.98	2.23	131	76	116	0.0060	23.49	13.16
13	137.71	138.71	2.33	107	46	55	0.0030	11.80	8.93
14	119.56	120.56	2.26	109	52	61	0.0042	13.23	9.57
15	116.83	117.83	2.31	121	46	79	0.0045	18.69	9.85
16	94.02	95.02	2.44	103	82	79	0.0059	15.63	11.21
17	125.42	126.42	2.36	303	64	180	0.0122	13.01	12.00
18	127.19	128.19	2.37	162	52	64	0.0044	13.94	9.20
19	139.89	140.89	2.32	689	152	165	0.0168	12.16	9.82
20	125.44	126.44	2.33	193	64	143	0.0110	16.31	9.87
21	284.07	285.07	2.26	168	55	119	0.0053	20.56	11.33
22	254.25	255.25	2.34	210	58	180	0.0059	25.19	23.65
23	196.37	197.37	2.30	315	37	34	0.0019	18.77	13.00
24	226.53	227.53	2.36	256	62	76	0.0036	17.62	11.97
25	278.83	279.83	2.28	116	46	67	0.0035	15.67	13.07
26	193.03	194.03	2.28	131	75	91	0.0040	21.05	16.70
27	244.68	245.68	2.40	323	70	198	0.0081	25.53	15.21
28	244.34	245.34	2.35	395	61	131	0.0068	24.12	16.98
29	177.01	178.01	2.29	698	102	433	0.0233	20.05	16.01
30	214.60	215.60	2.37	238	101	189	0.0083	22.04	16.38
101	33.26	34.26	2.24	84	27	76	0.0098	10.77	6.28
111	114.12	115.12	2.36	200	27	107	0.0075	13.04	8.73

Recommended transformations: [1]log$_{10}$; [2]Asin(Sqrt(x/100))

Site	WWbase	TERR#of3	TBANK#of6^1	CWDTOT^1	CWDWET^1	CWDFXN^1	%RIFFLE tweg^2	%POOL tweg^2
1	5.84	1	1	0.108	0.042	0.061	30.2	69.8
2	7.74	1	1	0.019	0.011	0.000	14.2	85.8
3	4.92	3	5	0.058	0.021	0.039	32.1	67.9
4	3.76	3	4	0.784	0.620	1.167	22.8	77.2
5	5.40	2	3	0.031	0.018	0.011	39.3	60.7
6	5.06	0	0	0.090	0.047	0.056	37.2	62.8
7	3.88	0	0	0.080	0.039	0.077	41.3	58.7
8	4.92	2	2	0.599	0.085	0.277	52.8	47.2
9	5.16	0	0	0.084	0.018	0.034	58.2	41.8
10	5.24	2	3	0.022	0.011	0.012	39.7	60.3
11	9.82	2	3	0.060	0.020	0.048	60.9	39.1
12	10.27	1	1	0.151	0.043	0.126	25.8	74.2
13	6.32	1	1	0.951	0.150	1.174	28.4	71.6
14	7.74	1	2	0.655	0.242	0.743	39	61
15	8.76	0	0	0.082	0.033	0.043	31.8	68.2
16	8.12	1	1	1.343	0.190	1.736	55.7	44.3
17	6.28	0	0	0.196	0.129	0.262	56.2	43.8
18	9.12	1	1	0.198	0.094	0.130	19.6	80.4
19	7.97	1	1	0.179	0.057	0.140	40.4	59.6
20	8.94	2	2	0.123	0.006	0.042	60.3	39.7
21	8.08	0	0	0.063	0.016	0.033	18.1	81.9
22	15.19	1	1	0.111	0.068	0.107	28.6	71.4
23	6.83	0	0	0.478	0.156	0.729	27.4	72.6
24	10.31	1	1	0.184	0.181	0.176	13.2	86.8
25	9.88	0	0	0.069	0.017	0.047	14.9	85.1
26	10.47	3	3	0.038	0.018	0.021	27.3	72.7
27	12.60	0	0	0.225	0.140	0.193	32.2	67.8
28	16.26	1	1	0.039	0.008	0.014	47.4	52.6
29	8.57	0	0	0.203	0.055	0.244	47.3	52.7
30	12.92	1	1	0.255	0.087	0.214	23.8	76.2
101	4.08	1	1	0.114	0.027	0.062	31	69
111	6.31	0	0	0.017	0.0004	0.004	60	40

Recommended transformations: $^1\log_{10}$; ^{2}Asin(Sqrt(x/100))

Site	%POOL $(z)^2$	%GLIDE $(z)^2$	%RIFFLE $(z)^2$
1	69.4	11.8	18.8
2	90.6	0	9.4
3	55.3	44.7	0
4	51.8	43.5	4.7
5	58.8	14.1	27.1
6	24.7	48.2	27.1
7	83.5	15.3	1.2
8	28.2	29.4	42.4
9	3.5	12.9	83.5
10	30.6	28.2	41.2
11	41.2	34.1	24.7
12	55.3	23.5	21.2
13	32.9	60	7.1
14	23.5	68.2	8.2
15	15.3	54.1	30.6
16	43.5	17.6	38.8
17	45.9	18.8	35.3
18	2.4	84.7	12.9
19	40	28.2	31.8
20	25.9	18.8	55.3
21	9.4	90.6	0
22	45.9	28.2	25.9
23	27.1	67.1	5.9
24	50.6	34.1	15.3
25	12.9	74.1	12.9
26	16.5	78.8	4.7
27	67.1	11.8	21.2
28	41.2	27.1	31.8
29	29.4	37.6	32.9
30	64.7	11.8	23.5
101	58.8	20.6	20.6
111	40.2	20.6	39.2

Recommended transformations: $^1\log_{10}$; ^{2}Asin(Sqrt(x/100))

C. FISH ASSEMBLAGE VARIABLES USED IN ANALYSES

			Proportional Richness						
Site #	rich ness	density	cyprinids	insectivorous cyprinids	redhorse suckers	darters	centrarchids	darters & sculpin	endemics
1	18	0.24	0.28	0.22	0.00	0.11	0.28	0.17	0.28
2	23	0.59	0.39	0.13	0.13	0.13	0.26	0.17	0.17
3	10	0.27	0.10	0.00	0.00	0.10	0.30	0.10	0.00
4	10	0.83	0.30	0.00	0.00	0.20	0.20	0.30	0.20
5	13	0.96	0.38	0.23	0.00	0.15	0.31	0.23	0.31
6	14	0.43	0.36	0.14	0.00	0.14	0.29	0.21	0.21
7	10	0.25	0.10	0.00	0.00	0.10	0.40	0.10	0.00
8	11	0.48	0.45	0.18	0.00	0.27	0.00	0.36	0.27
9	11	0.42	0.36	0.18	0.00	0.27	0.18	0.36	0.27
10	15	0.60	0.40	0.27	0.00	0.20	0.27	0.27	0.33
11	18	0.45	0.33	0.22	0.11	0.22	0.17	0.22	0.28
12	20	0.28	0.35	0.30	0.10	0.20	0.15	0.25	0.25
13	18	0.15	0.17	0.17	0.06	0.11	0.33	0.17	0.06
14	19	0.27	0.32	0.16	0.05	0.05	0.26	0.11	0.11
15	19	0.21	0.37	0.21	0.00	0.05	0.26	0.11	0.11
16	25	0.48	0.36	0.24	0.04	0.20	0.16	0.24	0.24
17	24	0.23	0.25	0.17	0.04	0.17	0.29	0.21	0.17
18	13	0.28	0.38	0.15	0.00	0.08	0.23	0.08	0.00
19	24	0.41	0.25	0.21	0.08	0.29	0.21	0.33	0.38
20	20	0.48	0.45	0.30	0.05	0.20	0.15	0.25	0.30
21	20	0.14	0.25	0.15	0.05	0.05	0.25	0.10	0.10
22	26	0.13	0.31	0.23	0.12	0.19	0.19	0.23	0.27
23	16	0.10	0.25	0.13	0.00	0.06	0.31	0.06	0.06
24	14	0.15	0.36	0.14	0.00	0.07	0.36	0.07	0.00
25	20	0.10	0.20	0.15	0.05	0.10	0.45	0.10	0.00
26	23	0.11	0.26	0.13	0.04	0.09	0.35	0.09	0.04
27	24	0.19	0.25	0.21	0.08	0.17	0.21	0.21	0.17
28	23	0.16	0.26	0.17	0.13	0.22	0.13	0.26	0.22
29	28	0.35	0.25	0.18	0.07	0.29	0.14	0.32	0.32
30	30	0.28	0.37	0.27	0.07	0.20	0.17	0.23	0.27
101	13	0.28	0.31	0.00	0.00	0.23	0.46	0.21	0.08
111	19	0.22	0.26	0.11	0.05	0.21	0.26	0.26	0.11

	Relative Abundance											
Site #	cyprinids	insectivorous cyprinids	darters	darters*	redhorse suckers	centrarchids	darters & sculpin	endemics	habitat generalists	pool spp.	pool-run spp.	riffle-run spp.	benthc spp.
1	0.37	0.32	0.11	0.04	0.00	0.20	0.20	0.38	0.29	0.38	0.20	0.13	0.28
2	0.14	0.06	0.22	0.19	0.09	0.22	0.25	0.10	0.11	0.60	0.25	0.04	0.39
3	0.10	0.00	0.07	0.00	0.00	0.37	0.07	0.00	0.33	0.67	0.00	0.00	0.28
4	0.18	0.00	0.07	0.02	0.00	0.04	0.09	0.03	0.50	0.46	0.00	0.03	0.41
5	0.18	0.01	0.48	0.48	0.00	0.10	0.52	0.53	0.37	0.10	0.01	0.52	0.82
6	0.48	0.30	0.24	0.13	0.00	0.02	0.29	0.43	0.44	0.00	0.32	0.18	0.52
7	0.14	0.00	0.23	0.00	0.00	0.32	0.23	0.00	0.66	0.34	0.00	0.00	0.31
8	0.34	0.19	0.09	0.00	0.00	0.00	0.57	0.53	0.27	0.02	0.19	0.48	0.69
9	0.40	0.33	0.06	0.03	0.00	0.02	0.55	0.61	0.38	0.00	0.11	0.52	0.56
10	0.29	0.13	0.23	0.21	0.00	0.14	0.44	0.49	0.34	0.05	0.11	0.42	0.70
11	0.65	0.59	0.18	0.15	0.06	0.02	0.18	0.61	0.29	0.10	0.45	0.16	0.33
12	0.63	0.55	0.25	0.11	0.01	0.03	0.30	0.30	0.53	0.07	0.31	0.09	0.27
13	0.25	0.25	0.24	0.01	0.03	0.26	0.25	0.01	0.56	0.29	0.14	0.03	0.22
14	0.36	0.21	0.14	0.00	0.03	0.16	0.16	0.03	0.73	0.19	0.05	0.04	0.39
15	0.53	0.10	0.04	0.00	0.00	0.08	0.06	0.05	0.68	0.14	0.07	0.02	0.66
16	0.46	0.20	0.20	0.11	0.00	0.01	0.31	0.19	0.63	0.09	0.09	0.19	0.59
17	0.40	0.27	0.30	0.06	0.00	0.05	0.35	0.09	0.75	0.08	0.10	0.10	0.38
18	0.33	0.27	0.09	0.00	0.00	0.17	0.09	0.00	0.52	0.43	0.02	0.00	0.18
19	0.72	0.71	0.11	0.07	0.02	0.02	0.15	0.56	0.34	0.03	0.53	0.10	0.24
20	0.29	0.24	0.16	0.14	0.00	0.03	0.58	0.65	0.24	0.02	0.16	0.56	0.69
21	0.21	0.16	0.28	0.00	0.02	0.15	0.28	0.02	0.70	0.26	0.04	0.02	0.32
22	0.53	0.48	0.18	0.04	0.02	0.11	0.19	0.13	0.61	0.17	0.14	0.09	0.24
23	0.41	0.37	0.06	0.00	0.00	0.22	0.06	0.32	0.32	0.22	0.45	0.01	0.25
24	0.39	0.37	0.05	0.00	0.00	0.33	0.05	0.00	0.55	0.42	0.02	0.00	0.15
25	0.36	0.35	0.16	0.01	0.02	0.18	0.16	0.00	0.69	0.19	0.12	0.02	0.29
26	0.33	0.26	0.04	0.00	0.00	0.14	0.04	0.03	0.51	0.38	0.08	0.01	0.29
27	0.28	0.24	0.34	0.15	0.01	0.06	0.57	0.24	0.54	0.07	0.15	0.25	0.52
28	0.45	0.36	0.16	0.06	0.03	0.02	0.40	0.30	0.58	0.06	0.07	0.30	0.55
29	0.53	0.43	0.19	0.17	0.06	0.01	0.27	0.49	0.40	0.08	0.29	0.23	0.51
30	0.44	0.25	0.16	0.10	0.02	0.03	0.45	0.48	0.36	0.04	0.19	0.39	0.65
101	0.19	0.00	0.12	0.04	0.00	0.65	0.12	0.00	0.30	0.63	0.07	0.00	0.15
111	0.23	0.05	0.16	0.04	0.00	0.59	0.16	0.02	0.33	0.58	0.06	0.03	0.13

*(excluding *P. nigrofasciata*)

	Relative Abundance												
Site #	nets builders & associates	nest excavators	rock attachers	crevice spawner	cavity spawner	gravel spawner	gravel spawner*	live bearer	generalized carnivore	herbivore	insect-ivore	trophic generalist	benthic invertivore
1	0.13	0.20	0.04	0.12	0.10	0.25	0.08	0.04	0.02	0.06	0.56	0.35	0.20
2	0.07	0.22	0.02	0.01	0.02	0.33	0.28	0.27	0.03	0.05	0.55	0.37	0.19
3	0.10	0.40	0.00	0.00	0.00	0.24	0.01	0.27	0.10	0.10	0.34	0.46	0.00
4	0.18	0.04	0.02	0.00	0.02	0.75	0.42	0.00	0.00	0.10	0.09	0.81	0.03
5	0.16	0.10	0.48	0.01	0.04	0.20	0.00	0.00	0.01	0.10	0.53	0.36	0.52
6	0.24	0.02	0.13	0.00	0.05	0.31	0.00	0.00	0.02	0.08	0.60	0.30	0.18
7	0.14	0.39	0.00	0.00	0.00	0.46	0.00	0.00	0.05	0.00	0.23	0.72	0.00
8	0.29	0.00	0.00	0.00	0.48	0.18	0.02	0.00	0.00	0.12	0.76	0.12	0.48
9	0.07	0.02	0.03	0.24	0.49	0.06	0.00	0.00	0.02	0.01	0.88	0.10	0.52
10	0.19	0.07	0.12	0.08	0.21	0.24	0.09	0.00	0.01	0.15	0.57	0.20	0.42
11	0.07	0.02	0.13	0.58	0.00	0.20	0.11	0.00	0.01	0.04	0.77	0.19	0.16
12	0.09	0.03	0.04	0.32	0.05	0.27	0.12	0.00	0.01	0.09	0.84	0.06	0.18
13	0.00	0.28	0.00	0.16	0.03	0.43	0.04	0.01	0.06	0.00	0.53	0.42	0.03
14	0.14	0.16	0.00	0.18	0.04	0.45	0.05	0.00	0.02	0.06	0.40	0.53	0.04
15	0.43	0.09	0.00	0.05	0.02	0.36	0.07	0.00	0.03	0.30	0.17	0.51	0.02
16	0.30	0.02	0.06	0.14	0.11	0.36	0.13	0.00	0.01	0.22	0.50	0.27	0.22
17	0.14	0.05	0.02	0.22	0.07	0.46	0.08	0.00	0.00	0.11	0.65	0.24	0.14
18	0.08	0.21	0.00	0.25	0.00	0.20	0.00	0.27	0.00	0.00	0.63	0.37	0.00
19	0.03	0.02	0.02	0.49	0.04	0.19	0.07	0.00	0.02	0.02	0.86	0.11	0.13
20	0.12	0.02	0.01	0.15	0.42	0.24	0.13	0.00	0.01	0.05	0.83	0.10	0.56
21	0.05	0.16	0.00	0.15	0.02	0.57	0.06	0.05	0.02	0.06	0.50	0.42	0.02
22	0.10	0.11	0.01	0.43	0.02	0.33	0.11	0.00	0.03	0.05	0.70	0.23	0.10
23	0.04	0.22	0.00	0.05	0.01	0.31	0.04	0.05	0.09	0.05	0.49	0.37	0.01
24	0.04	0.39	0.00	0.36	0.00	0.12	0.00	0.09	0.01	0.01	0.52	0.46	0.00
25	0.01	0.20	0.00	0.30	0.02	0.42	0.03	0.01	0.04	0.00	0.55	0.41	0.03
26	0.07	0.14	0.00	0.23	0.01	0.43	0.18	0.09	0.04	0.05	0.40	0.51	0.01
27	0.04	0.06	0.01	0.24	0.25	0.41	0.15	0.00	0.01	0.04	0.82	0.13	0.39
28	0.13	0.05	0.01	0.30	0.24	0.24	0.09	0.00	0.01	0.09	0.77	0.14	0.34
29	0.11	0.02	0.00	0.37	0.09	0.36	0.24	0.00	0.01	0.09	0.70	0.19	0.25
30	0.30	0.02	0.01	0.08	0.29	0.23	0.12	0.00	0.01	0.18	0.70	0.11	0.39
101	0.11	0.65	0.00	0.00	0.08	0.16	0.04	0.00	0.07	0.06	0.12	0.74	0.04
111	0.06	0.59	0.02	0.03	0.13	0.15	0.03	0.00	0.02	0.06	0.23	0.68	0.05

* excludes *H. etowanum and P. nigrofasciata*

	Number Species									
Site #	darters & sculpin	centrarchids	cyprinids	insectivorous cyprinids	endemics	cosmopolitans	cosmopolitan abundance	endemic abundance	endemic spp./ cosmpolitan spp.	endemic abun./ cosmpolitan abun.
1	3	5	5	4	5	8	51	54	0.63	1.06
2	4	6	9	3	3	15	396	45	0.20	0.11
3	1	3	1	0	0	8	111	0	0.00	0.00
4	3	2	3	0	2	5	84	10	0.40	0.12
5	3	4	5	3	4	5	135	273	0.80	2.02
6	3	4	5	2	3	7	53	94	0.43	1.77
7	1	4	1	0	0	9	74	0	0.00	0.00
8	4	0	5	2	3	3	47	123	1.00	2.62
9	4	2	4	2	3	4	21	131	0.75	6.24
10	4	4	6	4	5	6	75	153	0.83	2.04
11	4	3	6	4	5	9	113	405	0.56	3.58
12	5	3	7	6	5	9	150	129	0.56	0.86
13	3	6	3	3	1	11	81	2	0.09	0.02
14	2	5	6	3	2	11	151	9	0.18	0.06
15	2	5	7	4	2	10	123	14	0.20	0.11
16	6	4	9	6	6	10	226	112	0.60	0.50
17	5	7	6	4	4	13	99	20	0.31	0.20
18	1	3	5	2	0	8	229	0	0.00	0.00
19	8	5	6	5	9	9	44	273	1.00	6.20
20	5	3	9	6	6	6	56	421	1.00	7.52
21	2	5	5	3	2	12	129	4	0.17	0.03
22	6	5	8	6	7	13	125	49	0.54	0.39
23	1	5	4	2	1	10	48	44	0.10	0.92
24	1	5	5	2	0	9	174	0	0.00	0.00
25	2	9	4	3	0	14	77	0	0.00	0.00
26	2	8	6	3	1	15	73	6	0.07	0.08
27	5	5	6	5	4	12	173	116	0.33	0.67
28	6	3	6	4	5	12	146	156	0.42	1.07
29	9	4	7	5	9	12	130	294	0.75	2.26
30	7	5	11	8	8	12	206	349	0.67	1.69
101	3	6	4	0	1	12	108	0	0.08	0.00
111	5	5	5	2	2	12	187	5	0.17	0.03

	NMDS axes		
Site #	Axis 1	Axis 2	Axis 3
1	-0.3772	-0.0349	0.0176
2	-	-	-
3	-0.2354	-1.4913	0.1068
4	-0.3572	-0.5282	-0.6289
5	-0.8919	-0.0992	-0.4445
6	-0.0516	-0.0244	-1.0156
7	0.4565	-1.6339	0.0083
8	0.3607	0.0035	-1.3884
9	-0.1501	0.4254	-1.0236
10	-0.5675	0.4805	-0.5258
11	-0.9802	0.3765	0.2416
12	-0.4045	0.8540	0.2788
13	0.4697	-0.2550	1.0230
14	0.4251	-0.0405	0.1108
15	0.2121	-0.1220	-0.1646
16	0.4148	0.5767	-0.4204
17	0.1132	0.2778	0.1372
18	0.7169	-0.6744	-0.3994
19	-0.2197	0.9532	0.0985
20	-0.2747	0.7357	-0.5315
21	-0.1122	-0.3569	0.3447
22	-0.2398	0.5535	0.4441
23	-0.3421	-0.6186	0.5702
24	0.8212	-0.7824	-0.1143
25	0.6508	-0.3189	0.8521
26	0.0215	-0.5255	0.2905
27	0.2692	0.6361	0.4126
28	0.2875	0.8749	0.1821
29	-0.0261	0.8850	-0.0439
30	0.0132	0.9068	-0.3695
101	-0.1316	-1.1721	0.8810
111	0.1294	0.1385	1.0708

D. SITE NAMES AND COORDINATES*

Site #	Name	East	North
1	Pumpkinvine Cr.	695083	3747693
2	West Fork	701380	3767325
3	Avery Cr.	734950	3781237
4	Smithwick Cr.	745877	3793789
5	McCanless Cr.	727204	3798328
6	Bluff Cr.	733795	3803526
7	Settingdown Cr.	768141	3798846
8	Conns Cr.	747712	3803838
9	Polecat Branch	738694	3810792
10	Burt Cr.	763873	3813837
11	Raccoon Cr.	694183	3763833
12	Little Pumpkinvine Cr.	704335	3768023
13	Chicken Cr.	744746	3779690
14	Little River	743375	3780570
15	Mill Cr.	736685	3780568
16	Smithwick Cr.	745327	3797553
17	Shoal Cr.	724391	3801008
18	Settingdown Cr.	761820	3796386
19	Darnell Cr.	742069	3812785
20	Shoal Cr.	763014	3813453
21	Pumpkinvine Cr.	696800	3756265
22	Raccoon Cr.	693655	3771511
23	Noonday Cr.	727429	3772031
24	Settingdown Cr.	756802	3797630
25	Little River	742477	3778845
26	Mill Cr.	732865	3779307
27	Shoal Cr.	722377	3796036
28	Sharp Mountain Cr.	736655	3807345
29	Long Swamp Cr.	741812	3812930
30	Shoal Cr.	761864	3808253
101	Allatoona Cr.	711265	3766819
111	Little Allatoona Cr.	711620	3766814

*Universal Transmercador (UTM) projections of site benchmark. North American Datum 1983, UTM gridzone 16.