Geomorphology and fish assemblages in a Piedmont river basin, U.S.A.

D. M. WALTERS*, D. S. LEIGH[†], M. C. FREEMAN[‡], B. J. FREEMAN*,[§] AND C.M. PRINGLE*
*Institute of Ecology, The University of Georgia, Athens, GA, U.S.A.
†Department of Geography, The University of Georgia, Athens, GA, U.S.A.
‡USGS Patuxent Wildlife Research Center, Warnell School of Forest Resources, The University of Georgia, Athens, GA, U.S.A.
§Museum of Natural History, The University of Georgia, Athens, GA, U.S.A.

SUMMARY

1. We investigated linkages between fishes and fluvial geomorphology in 31 wadeable streams in the Etowah River basin in northern Georgia, U.S.A. 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 stream width).
2. Non-metric 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 generalised food preferences, to darter-cyprinid-redhorse sucker complexes that inhabit riffles and runs, feed primarily on invertebrates, and spawn on coarser stream beds.
3. Richness and density were correlated with basin area, a measure of 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 with high slope streams.
4. 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.

Keywords: assemblage structure, environmental gradients, Etowah River, Process Domains Concept, stream fishes

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 may be obscured by local factors (Bruns *et al.*, 1984; Rice, Greenwood & Joyce, 2001; Poole, 2002). Other researchers (Pringle *et al.*, 1988; Townsend, 1989) have

Correspondence: David Walters, U.S. EPA, National Exposure Research Laboratory, Ecosystems Research Branch, 26 Martin Luther King, MS-642, Cincinnati, OH 45268, U.S.A.
E-mail: walters.davidm@epa.gov

promoted the concept of patch dynamics to characterise 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. Identification of these processes can provide a mechanistic understanding of the distribution of habitats and stream biota predicted by the river continuum and patch dynamics models. Montgomery (1999) supported the PDC with published studies of riparian plant, macroinvertebrate and fish communities, but he 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 physical and biological 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 & Hubert, 1991; Lyons, 1996). Downstream increases in pool volume and habitat complexity are also linked to assemblage composition, guild structure and species richness (Gorman & Karr, 1978; Schlosser, 1982; Angermeier & 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 & Northcote, 1992; Beechie & Sibley, 1997; Snodgrass & Meffe, 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.

Several studies have linked habitat variables with stream fishes (e.g. Schlosser, 1982; Rahel & Hubert, 1991; Lyons, 1996), but most of these 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 modelled fish assemblage properties with such a broad spectrum of quantified geomorphic variables (but see Dangelo *et al.*, 1997; Peterson & Rabeni, 2001) and datasets of comparable sample size and survey detail are rare even in the geomorphic literature. Our comprehensive 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 in northern Georgia. These streams vary enough in size to assess longitudinal changes in fish assemblages and are comparable with those used by Schlosser (1987) to develop his longitudinal model of fishes in small streams. We have three objectives. First, we describe variation and patterns in fish assemblages among streams. Secondly, 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 River basin lie in the Blue Ridge, Ridge and Valley and Piedmont physiographic provinces (Fig. 1). Our sample reaches were in wade-able streams on the Piedmont, but headwaters of a few catchments drain the Blue Ridge. The Southern Appalachian Highlands, which include the study area, are a hotspot of stream fish diversity and endemism (Warren & Burr, 1994), and 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 31 sample reaches in 23 sub-basins (Fig. 1). The sub-basins were stratified into three size groups of approximately 15, 50 and 100 km^2 ($\pm$25%) (Table 1). These sizes are referred to as small, medium and large streams throughout the text. In four cases, multiple reaches were sampled in the same stream because of the low number of large streams ($n = 11$) in the study

area. None of the sites were influenced by reservoirs or other large hydrologic alterations. Most sites fall in the forest cover range of 40–87%, with the remainder primarily as urban and agricultural land (Lo & 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 29 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 average baseflow water width within each stream size group (Angermeier & Smogor, 1995). Reaches of 200, 300 and 400 m were sampled in small, medium and large streams respectively. All available habitats were thoroughly sampled were sampled in a single pass (Simon & Lyons, 1995) with a crew of four to six persons equipped with a backpack electric shocker, seine and dipnets. Block nets were not used. Reaches were divided into two
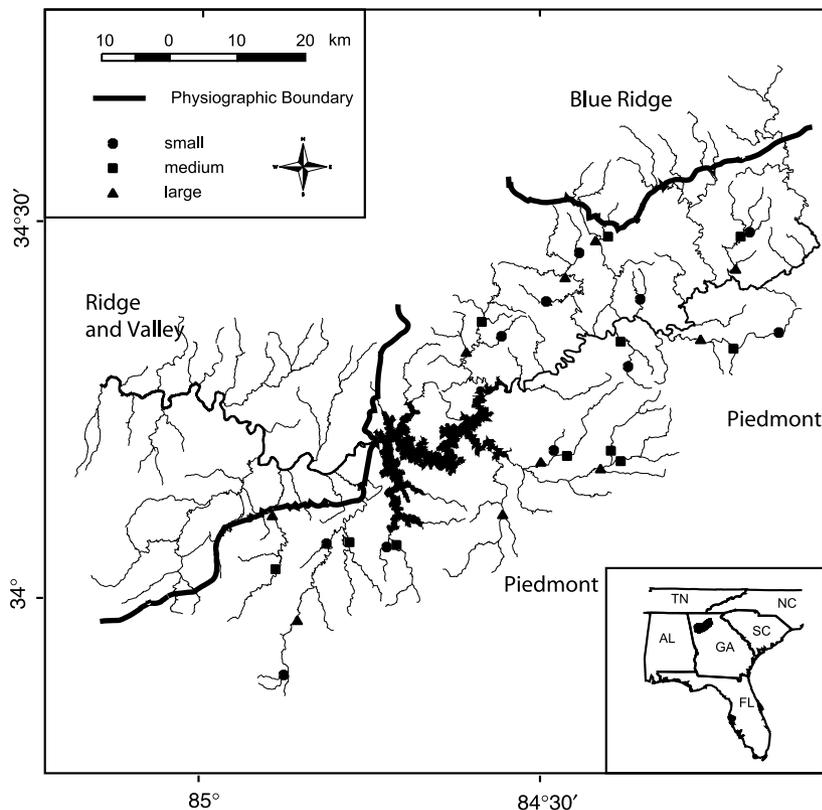

Fig. 1 Etowah River basin with wadeable stream sites. The large reservoir in the centre of the basin is Lake Allatoona, a mainstem impoundment. Small, medium and large streams drain catchments of roughly 15, 50 and 100 km^2 ($\pm$25%).

Table 1 Physical characteristics of streams and catchments sampled in the Etowah basin, summarised 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 'zigzag' 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)

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 euthanised 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 & Smogor, 1995). Voucher specimens of species previously uncollected were retained from this sample.

Assemblage structure was analysed based on species richness, fish density and species composition. Species composition was calculated as the proportion of richness (i.e. the number of species in each group divided by the total number of species) and as relative abundance (i.e. proportion of total catch) of various species groups. These variables measure the relative dominance of groups based on their occurrence and abundance. Poff & Allan (1995) argued that presence/absence and relative abundance data provide coarse- and fine-grained information, respectively, on species tolerance of environmental conditions and that both types of data are useful in identifying environmental determinants of assemblage structure.

Species groups were defined based on taxonomy and ecology of individual species. Selected taxonomic groups included fishes from four of the most species rich families: cyprinids (Cyprinidae), darters (Percidae), redhorse suckers (Catostomidae) and centrarchids (Centrarchidae). 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 widespread, habitat generalist that is locally common in the Etowah system. Species were assigned to guilds in three main categories: habitat use, food preference and spawning behaviour (Appendix 1). Assignments were made based on adult life history information reviewed in Etnier & Starnes (1993); Jenkins & Burkhead (1994) and Mettee, O'Neil & Pierson (1996). In cases where data were lacking (<5% of assignments), guilds were assigned based on the behaviour 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 (Appendix 2) at the reach and basin-wide scales, including the major categories of bankfull channel morphology (nine variables), gradient (six variables), bed texture (26 variables), flow and sediment transport (nine variables), depth (21 variables), width (three variables), basin morphometry (11 variables) and a miscellaneous category (10 variables). These measurements are similar to those specified in widely used stream survey manuals (Harrelson, Rawlins & Potyondy, 1994; Fitzpatrick *et al.* 1998; Lazorchak, Klemm & Peck, 1998). Longitudinal and cross-sectional topography of channels were surveyed with an electronic total station with sub-centimeter accuracy. The length of the surveyed reach was scaled to about 20–25 times the average baseflow width for streams in each size class (i.e. 100, 150 and 200 m lengths for 15, 50 and 100 km^2 basins). These reaches corresponded with

reaches quantitatively sampled for fishes. Topographic features mapped along the reach included three bankfull cross-sections arbitrarily located at 0, 50 and 100% of the defined reach, a continuous string of thalweg points spaced 1–3 m apart and a continuous string of bank and water's edge points spaced at about 5–10 m apart. Survey points on each bankfull cross-section were extended well beyond the channel margin to include floodplains and terraces. The bankfull level of the channel was arbitrarily defined by the height of the first alluvial surface adjacent to the channel at each of the three cross-sections, where the width of the alluvial surface exceeded the height. Bankfull channel dimensions (i.e. width, depth, area, hydraulic radius) were measured from each cross-section and an average value for the reach was calculated from the three cross-sections. Channel slope was measured as the average gradient projected through the tops of riffles in the reach. This measure is a proxy for water surface slope during floods or the energy grade line. Coarse woody debris (CWD) was measured within the bankfull channel of each stream. The length and mean diameter of all wood >10 cm diameter was recorded to calculate the total volume of CWD throughout the reach.

To complement the total station survey, we conducted a 'zigzag' survey to quantify habitat units (riffles, runs, pools), water depths and bed texture (particle size). This method delineated five longitudinal transects (Fig. 2) at approximately 10, 25, 50, 75 and 90% of the wetted width during baseflow conditions, which only includes flow contributed from groundwater sources and excludes runoff events. Seventeen samples were taken on each transect (reach total $n = 85$) that recorded habitat unit, water depth and dominant bed texture. Samples were evenly spaced and systematically staggered to produce an overall zigzag pattern over the entire stream reach (Fig. 2). The dominant bed texture was recorded as whole *phi* intervals ($- \log_2$ of intermediate axis in millimetres) representing the modal particle size observed within a 50 cm diameter patch, where the mode was the *phi* size class occupying the largest area within the patch. 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 is not representative of the fluvial
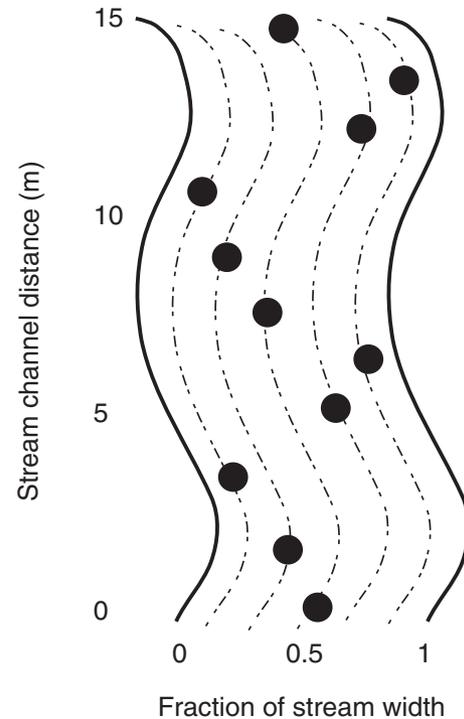

Fig. 2 Schematic of 'zigzag' survey. Dashed lines correspond with longitudinal transects at approximately 10, 25, 50, 75, 90% of the wetted width. Filled circles indicate sample points. Modal sediment size (whole *phi* category), depth and geomorphic unit (pool, riffle and run) were recorded at each point.

sediment and thus skewed the data set with inherently different bed material.

Bed texture was also assessed separately for lateral bars and riffles with Wolman pebble counts (Wolman, 1954) and sieve analysis. Pebble counts were conducted by random walks across a representative lateral bar or riffle ($n = 100$ grains for each riffle or bar). In addition, we collected three sediment samples from the upper 10 cm of the stream bed (about 3.0 L sample volume) from three riffles, pools and bars within each reach (total $n = 9$). These samples were oven dried, sieved and weighed to determine the mean particle size fractionation within each riffle, pool, or bar.

Bed mobility ratios were calculated to describe the sediment-transport response of the stream bed to frequent flood flows. These ratios compare the velocity, shear, or unit stream power exerted on the streambed during the 0.5-year recurrence interval (RI) flood relative to the threshold values needed to initiate motion of the average particle size on the steam bed or in riffles. The 0.5-year RI flood was

calculated by applying the regional flood frequency equations in Stamey & Hess (1993), which is a standard practice for estimating flood discharges in ungaged streams (Dunne & Leopold, 1978). These calculations were adjusted by equation 10.6 of Dunne & Leopold (1978) to account for total impervious area (TIA) within the catchment, which was measured from 1997 Landsat imagery. The flow velocity, shear and unit stream power values associated with the 0.5-year RI floods were calculated as averages of the three cross-sections, based on flow modelling output from the Hydrologic Engineering Center's River Analysis System (HEC-RAS) version 2.2 program (U.S. Army Corps of Engineers, 1998). Threshold velocity and shear force were estimated by equations 7.14 and 7.18, respectively, in Gordon, McMahon & Finlayson (1992), and threshold unit stream power was estimated by the equation of Bagnold (1980).

ArcView® software was used to calculate basin characteristics from 1 : 24 000 scale digital raster graphics (DRGs) of the latest 7.5 min USGS quadrangles. Map slope of the channel reach was calculated from DRGs 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 & Yang, 2000). TIA was calculated for each subcatchment by multiplying the percentage of high and low density urban land by 0.9 and 0.65 (Lo & Yang, 2000), respectively, and summing the two values.

Statistical analysis

We used a combination of multivariate and regression analysis to quantify the variation in stream fishes and geomorphology and to identify linkages between the two. These exploratory analyses (Hoaglin, Mosteller & Tukey, 1983) are designed to identify the major biological and environmental gradients present in the data. First, we quantified among site variance based on the occurrence and abundance of fishes. Second, we identified key taxonomic groups and ecological guilds driving these among site differences. Third, we screened geomorphic variables to make the dataset statistically manageable and to identify those variables that best differentiate sites. Finally, we linked these elements of stream geomorphology with fish assemblage variables.

We quantified among site differences in fish assemblages using non-metric multidimensional scaling (NMDS) analysis (PC-ORD 4.1 software; MjM Software Design™, Glendale Beach, OR, U.S.A.). NMDS is a procedure for indirect gradient analysis (Jongman, Braak & Tongeren, 1995) shown by Minchin (1987) to be a robust technique for analysing ecological data. NMDS relies on the Bray–Curtis coefficient to quantify the dissimilarity among sites based joint occurrence or abundance of taxa (Clarke & Warwick, 1994). NMDS has been successful at identifying and interpreting patterns in stream and marine benthic community data (e.g. Hawkins *et al.*, 1997; McCormick, Peck & Larsen, 2000; Heino *et al.*, 2002; and Clarke, 1999), and the Bray–Curtis coefficient was recently applied in a series of aquatic community studies from three continents (see references in Hawkins & Norris, 2000).

Abundance data from each sample were root-root transformed for the NMDS analysis (Field, Clarke & Warwick, 1982). Rare species, represented in fewer than 10% of the samples, were excluded from the analysis (final $n = 39$ species). Both species of *Gambusia* (Appendix 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 patterns in species composition among sites (Hawkins *et al.*, 1997).

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 2). Six categories characterise the major components of reach morphology: 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'. The final category, morphometry, 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 course woody debris (CWD) were not correlated with significant components at $|r| > 0.8$ but were included in the final dataset because of their potential importance as explanatory variables. Particle size heterogeneity was strongly correlated with macroinvertebrate assemblage structure at these sites (Roy *et al.*, 2003) and CWD is an important habitat component of small warmwater streams (Angermeier & Karr, 1984; Fausch & Northcote, 1992).

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 (Hawkins *et al.*, 1997). 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 urbanisation can profoundly alter the relationships between stream communities and habitat (Paul & Meyer, 2001). This final analysis was designed to quantify the relationships between key geomorphic and fish variables and to determine if these observed patterns correspond to either the Process Domain or River Continuum models.

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 explained a significant, but small amount of the variance (i.e. 4%) and was not considered for further analysis. Unlike other multivariate techniques like PCA, NMDS does not order axes by the amount of variance explained. The second and third axes accounted for 81% of the among-site variance and were used to ordinate sites in 'species space' (Fig. 3). Species plotted in the centre 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 (represented by axes 2 and 3) confirmed these patterns and showed a shift from streams dominated by centrarchids to assemblages composed primarily of darters, cyprinids and redhorse suckers (Fig. 4). Cyprinids,
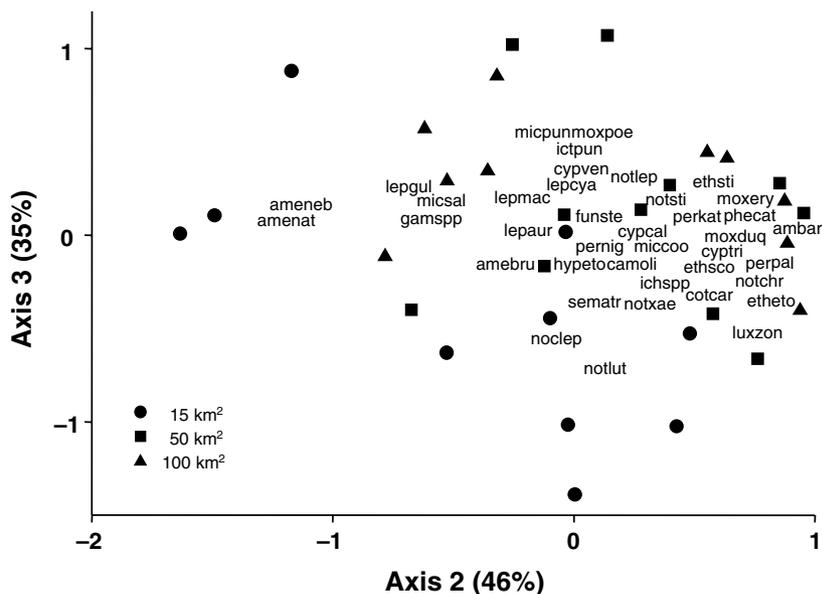

Fig. 3 Non-metric multidimensional scaling ordination of sites in species space. The amount of variance explained by each axis is shown in parentheses. Species are plotted in species space based on their scores for each axis. Species abbreviations are defined in Appendix 1.
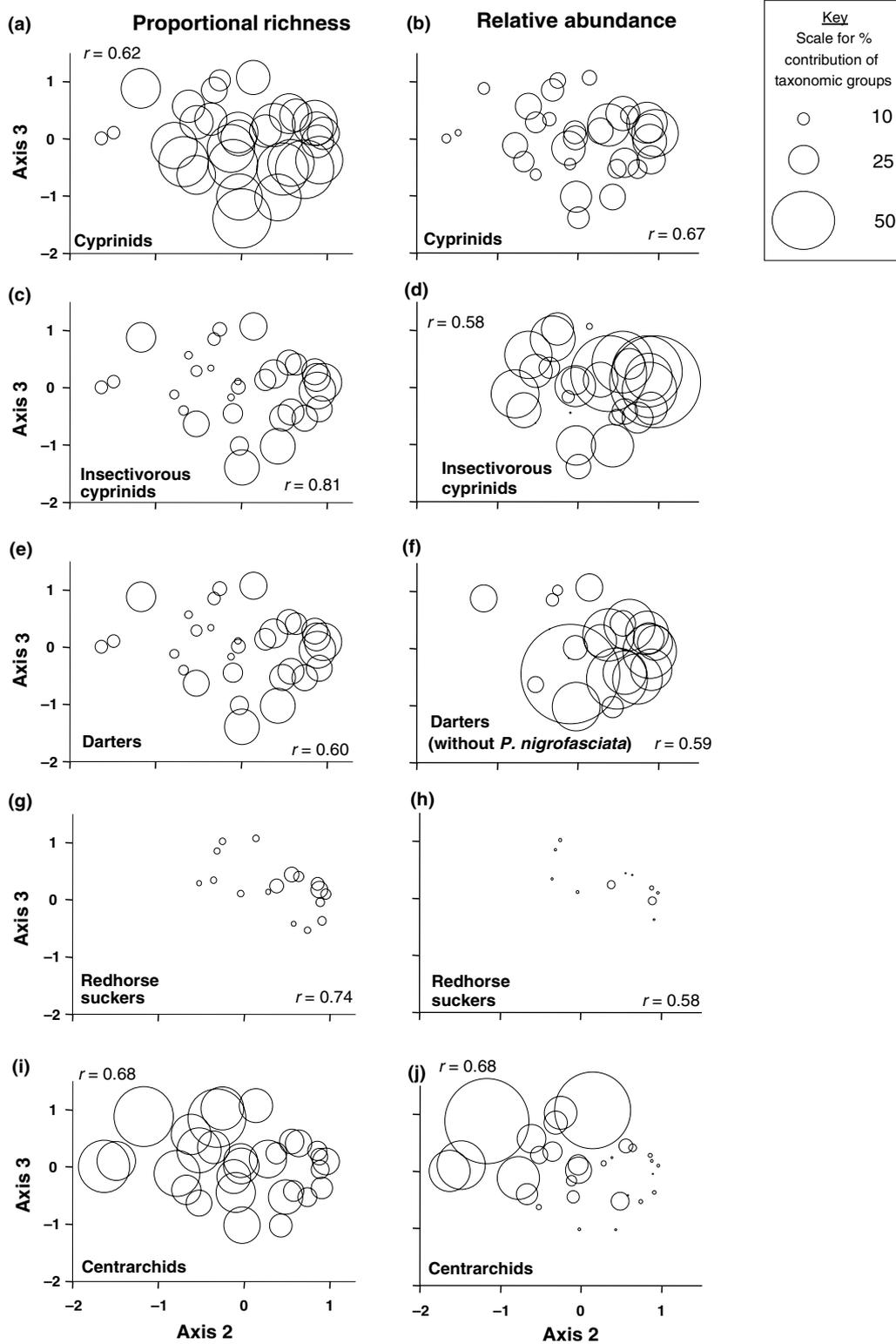
Fig. 4 Bubble plots of taxonomic groups in species space. Symbols represent the proportional richness and relative abundance of taxonomic groups at each site. Bubbles for the relative abundance of cyprinids are one-half actual size to better illustrate the pattern. Correlation coefficients (Pearson's r) are shown for the dominant axis in each plot.

darters and redhorse suckers all increased from upper left to lower right in these plots. Redhorse suckers were absent from small streams, so fewer sites appeared in the plots. In contrast to other species groups, centrarchids decreased from upper left to lower right.

Changes in the relative abundance of some ecological guilds (Fig. 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 behaviour changed from species that excavate nests in fine sediment to those that rely on larger particles (i.e. crevice spawners and benthic nest

builders). Feeding behaviour shifted from generalised carnivores and trophic generalists to greater specialisation 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 2). The plot in Fig. 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*, percentage fines in riffles, bed
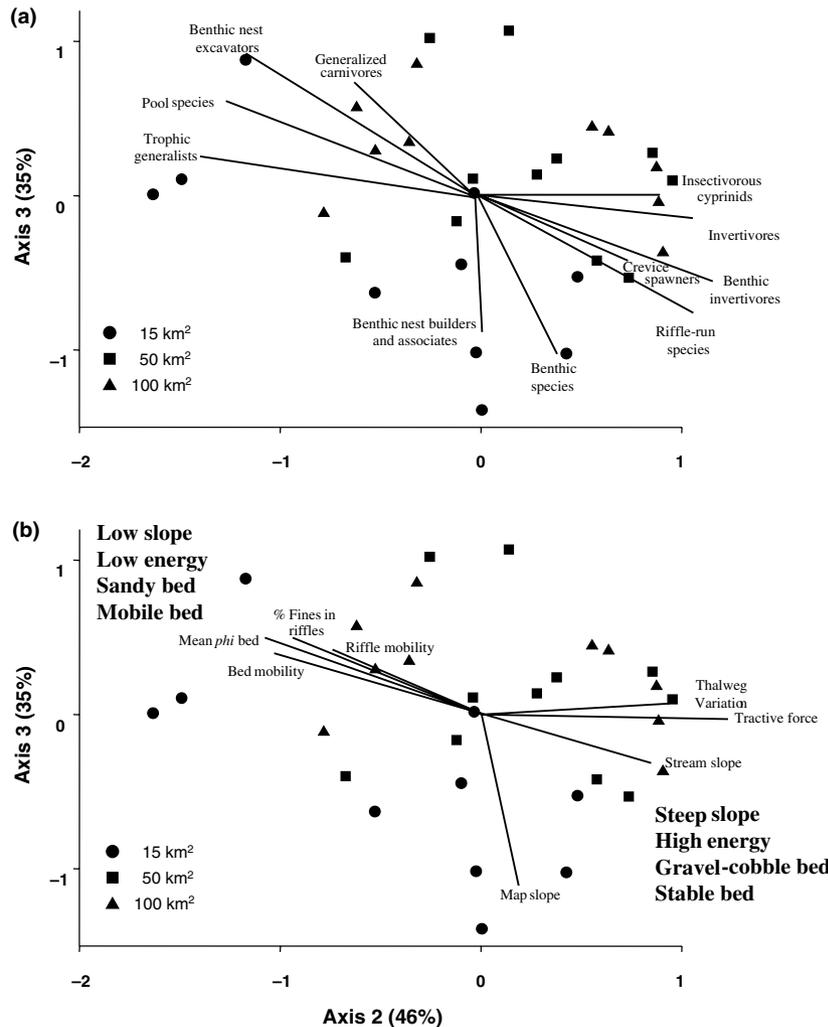
Fig. 5 Plots of ecological guilds (a) and geomorphic variables (b) most highly correlated with among site differences in fish assemblages. Plotted variables are correlated with either axis at $P < 0.001$. Vectors indicate the direction and magnitude of correlation for each variable and are scaled by 150% for presentation. Primary geomorphic attributes changing along the observed gradient are summarised in the upper left and lower right of panel 5b.

Table 2 Summary of principal components analysis and correlation analyses for eight categories of geomorphic variables. Only principal components (PC) with eigenvalues >1 and strong correlations ($|r| > 0.8$) with geomorphic variables are shown

Category (number of variables)	Final variables	Definition
Bankfull (9)		
PC I (69.0%)	Entrenchment	Entrenchment ratio expressed by bankfull discharge/urbanised 2 year. RI* flood discharge
	Tractive force	Tractive force (shear stress) exerted on bed during bankfull flows (N m^{-2})
PC II (15.4%)	Channel area	Bankfull channel cross-sectional area (m^2)
PC III (11.0%)	Width/Depth (*t*)	Width : depth of bankfull channel using bankfull width and thalweg depth
Bed texture (26)		
PC I (48.4%)	Mean *phi*	Average particle size of subaqueous stream bed (average = sum of *phi/n*)
	Stdv *Phi* Bed†	Standard deviation of *phi* sizes used to calculate average *phi*
	Mean *Phi* Bar	Average *phi* value of Wolman (1954) pebble count (*n* = 100) on lateral and mid-channel bars of the channel bed
	Riffle % Fines	Percentage (by dry weight) of <2 mm particles in riffles
Depth (21)		
PC I (36.9%)	Mean depth	Average baseflow water depth of entire stream from 'zigzag' survey (m)
PC II (22.9%)	95% Pool depth	95th percentile of baseflow pool depth measurements from 'zigzag' survey (m)
PC III (12.5%)	Depth CV	Coefficient of variation of baseflow water depth from 'zigzag' survey
Flow and sediment transport (9)		
PC I (68.2%)	Bed mobility (v)	Average velocity of 0.5-year RI* flood/velocity needed to move average particle size (mm) on stream bed, modelled from HEC-RAS program
	Riffle mobility (p)	Unit stream power (ω m^{-2}) of 0.5-year. RI* flood/ω m^{-2} needed to move average riffle particle (mm), modelled from HEC-RAS program
Gradient (6)		
PC I (47.3%)	Reach slope	Gradient of water surface during floods estimated from elevations of riffle tops
	Thalweg slope	Slope of regression line fitted to thalweg elevation versus sinuous distance along thalweg
PC II (24.3%)	Map Slope	Slope measured as elevation change between two nearest contours on USGS 7.5 min quadrangle
PC III (19.4%)	Thalweg variation	Standard error of the estimate for the line fitted to thalweg elevation versus sinuous distance along thalweg
Morphometry (11)		
PC I (42.3%)	Basin area	Drainage basin area (km^2)
PC II (26.7%)	Trunk stream slope	Relief of trunk stream/length of trunk stream
PC III (12.9%)	Basin compactness	Compactness (basin perimeter squared/basin area)
PC IV (10.1%)	Drainage density	Drainage density (sum of total stream length in the blue-line network on 1 : 24 000 scale maps/basin area) (km)
Width‡ (3)	Baseflow width	Water width at baseflow (m)
Miscellaneous (10)		
PC I (33.7%)	Riffle % of thalweg	Percentage of riffle habitat along the thalweg
PC II (23.0%)	Course woody debris†	Total coarse woody debris in the bankfull channel (m^3/100 m^2)
PC III (20.6%)	Terraces	Number of cross-sections (out of *n* = 3) that exhibit terracing (categorical values of 0, 1, 2, 3)
PC IV (13.7%)	Pool % of stream	Percentage of pool habitat from the 'zigzag' survey

Amount of variance explained by each PC is given in parentheses.
*Recurrence interval (derived from USGS regional flood frequency equations).
†Variables included based on published relationships with stream fishes.
‡PCA was not run on the three width variables.

mobility, riffle bed mobility, bankfull tractive force, slope and map slope) are measures of 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
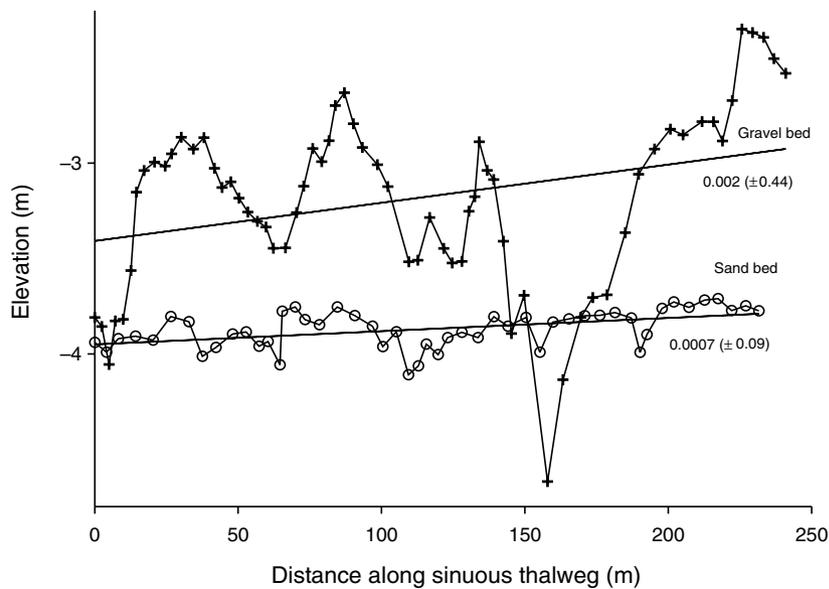
Fig. 6 Longitudinal plot of thalweg elevation points for sites 21 (open circles, drainage area = 126 km^2) and 30 (plus symbol, drainage area = 102 km^2). Slope (±SE) are given for each regression line. In the plot for site 30, peaks and troughs correspond with prominent riffles and deep pools, respectively.

with the highest mean *phi* have the finest beds and plot in the upper left of the ordination.

The final significant variable, thalweg variation, 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 (Fig. 6). Large residuals in the plots contribute to high standard error, (i.e. variation) around the regression line. These residuals correspond to prominent riffles (positive residuals) and pools (negative residuals) along the thalweg. These features were related to bed texture. Streams with well-developed pools and riffles have coarse textured beds. In contrast, similarly sized sand-textured streams were dominated by relatively homogenous, shallow run habitat and exhibited low thalweg variation.

Measures of bankfull morphology (with the exception of tractive force), width and depth, large woody debris, basin morphometry and floodplain development were poor predictors of assemblage structure. Direct, continuous measures of pool and riffle area were poor predictors as well, although elements of pool and riffle development influence thalweg variability as discussed above.

Variation in geomorphic variables that best predicted fish assemblages did not strongly correspond to differences in basin morphometry or land cover (Table 3). 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

Table 3 Correlation coefficients (Pearson's *r*) among basin morphometry, land cover (Lo & Yang, 2000) and the best geomorphic predictors of fishes. Geomorphic variables are defined in Table 2

Geomorphic variable	Reach slope	Map slope	Drainage area	Compactness	Drainage density	Trunk stream slope	% Forest	% Agriculture	% Urban
Mean *phi*	**−0.92**	−0.54	0.26	0.01	−0.19	−0.51	−0.38	0.20	0.37
Bed mobility	**−0.87**	−0.46	0.28	−0.07	−0.31	−0.55	−0.45	0.26	0.42
Riffle % fines	**−0.80**	−0.45	0.26	0.09	−0.29	−0.49	−0.45	0.22	0.42
Riffle mobility	**−0.57**	−0.39	0.06	−0.03	−0.23	−0.29	−0.33	0.08	0.38
Thalweg variation	0.38	−0.01	0.20	0.07	0.30	0.12	0.43	−0.44	−0.21
Tractive force	**0.85**	0.24	0.00	−0.02	0.13	0.23	0.37	−0.40	−0.18
Reach slope	–	0.49	−0.39	−0.08	0.10	0.46	0.31	−0.22	−0.26

Values in bold have *P*-values <0.001. Values are uncorrected for sequential test and are meant only to serve as a rough guide to correlation strength.

Table 4 Correlation coefficients (Pearson's *r*) between relative abundance of species guilds, proportional richness of taxonomic groups and geomorphic variables. Four sites with >25% urban land cover were excluded from all analyses (*n* = 27). Small streams were not included for analysis of redhorse suckers and mean *phi* (*n* = 17)

Assemblage variable	Mean *phi*	Basin area	Mean depth	Baseflow width
Ecological guilds				
Pool species	**0.82**	−0.07	−0.27	−0.12
Riffle-run species	**−0.86**	−0.25	0.16	−0.01
Benthic species	**−0.61**	−0.33	−0.05	−0.15
Nest builders and associates	−0.25	−0.48	−0.08	−0.22
Crevice spawners	−0.09	**0.60**	0.14	**0.64**
Nest excavators	**0.74**	0.13	−0.15	−0.08
Invertivores	**−0.63**	0.21	0.39	0.39
Trophic generalists	**0.73**	−0.13	−0.37	−0.39
Insectivorous cyprinids	−0.32	0.43	0.23	0.54
Benthic invertivores	**−0.84**	−0.21	0.22	0.06
Generalised carnivores	0.41	0.08	−0.07	−0.03
Taxonomic groups				
Cyprinids	−0.54	0.21	−0.11	0.04
Centrarchids	**0.61**	−0.10	−0.17	−0.20
Darters	**−0.80**	−0.19	0.29	0.03
Redhorse suckers	−0.56	**0.63**	0.43	**0.79**
Richness	−0.10	**0.66**	0.31	**0.70**
Density	−0.52	**−0.77**	−0.11	−0.59

Values in bold have *P* < 0.001. *P*-values are uncorrected for sequential test but are shown as a rough guide to correlation strength.

bed texture and mobility in these sites. Drainage area was significantly correlated with slope, but the relationship was weak (i.e. *r* = −0.39, *P* = 0.05).

Taken together, the proceeding statistical analyses indicated that a synthetic measure of assemblage structure (i.e. NMDS axes) was more strongly related to stream slope, bed texture and associated variables than to longitudinal changes in stream size. We used correlation analysis to compare the power of mean *phi* and longitudinal variables (basin area, mean depth and baseflow width) to predict key taxonomic and ecological groups. We chose mean *phi* to represent the main geomorphic gradient because it was most highly correlated with the NMDS axes and it is the simplest of the eight variables to measure in the field. Mean *phi* was a much stronger predictor of species composition than measures of stream size (Table 4) and was highly correlated with nine of the 15 fish variables. Baseflow width and basin area were better predictors of richness and density as well as redhorse suckers and crevice spawners, which were absent from all or most of the small streams. Regression plots of selected taxa and mean *phi* clearly illustrated that species composition changes predictably along a gradient from cobble to sand bed streams (Fig. 7).

We used multiple linear regression analysis to determine if longitudinal variation was a secondary predictor of richness, density and species composi-

tion. Final models used two or three geomorphic variables and explained 55–84% of the variance in assemblage variables (Table 5). As expected, mean *phi* was the primary predictor of species composition, but was not entered for richness and density models. Only two secondary predictors, channel area and 95% pool depth, were significantly related to basin area.

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 local 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 (Gorman & Karr, 1978; Horwitz, 1978; Schlosser, 1982; Welcomme, 1985; Rahel & Hubert, 1991; Paller, 1994; Poff & Allan, 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
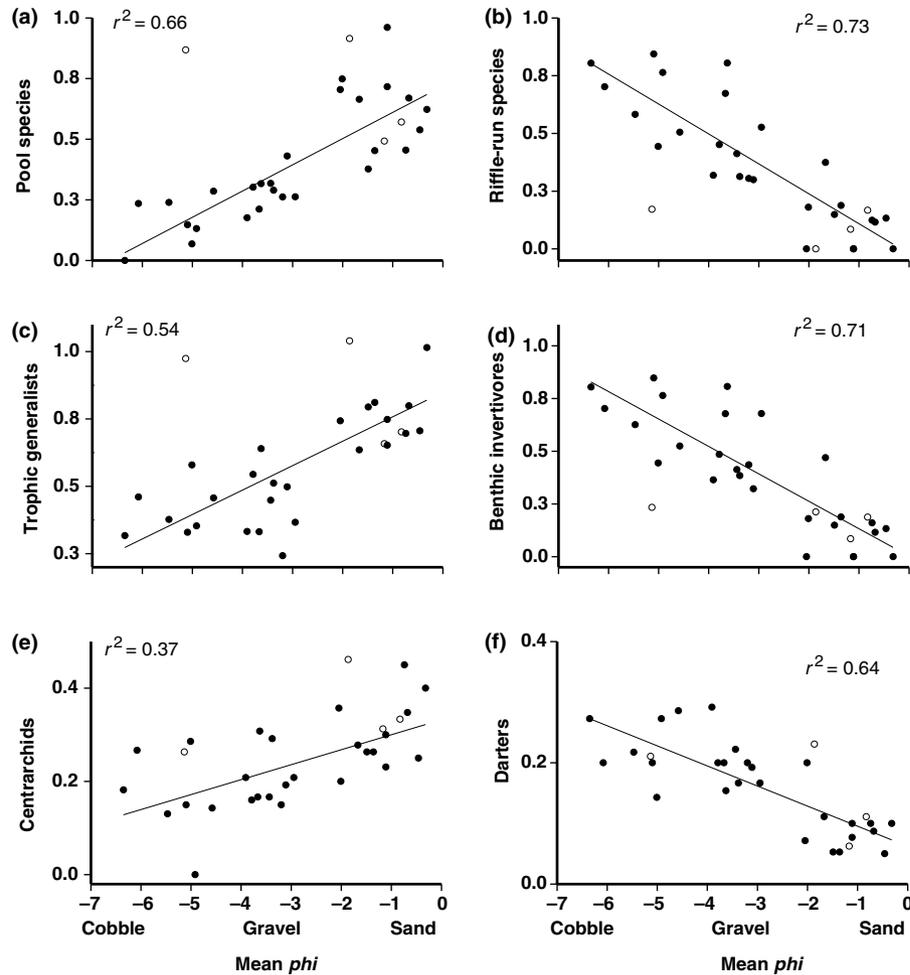
Fig. 7 Linear regression of mean *phi* and fish assemblage variables. Open circles are sites with >25% urban land cover and are not included in the analysis. Selected species composition variables represent opposite ends of the biological gradient identified in Fig. 5a.

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, Robinson & Minshall, 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 & 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). Stream slopes in the range we observed apparently are not a major impediment to fish dispersal and are instead linked to species composition because of 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

Table 5 Multiple regression models of selected fish assemblage variables ($n = 27$). Independent variables included mean *phi*, which was used to represent the eight variables identified in Figure 5b. The remaining 18 variables were those identified by principal components analysis as explaining significant geomorphic variation among sites (Table 2)

Assemblage variable	Variables in model	Trend	Cumulative r^2	P	F	r^2 of predictor with drainage area*
Pool species	Mean *phi*	+	0.67	<0.001	37.53	0.07
	Entrenchment	−	0.76	0.006		0.05
Riffle-run	Mean *phi*	−	0.73	<0.001	40.87	0.07
Species	Mean *phi* bar	−	0.78	0.005		0.04
	Basin compactness	−	0.84	0.007		0.03
Trophic generalists	Mean *phi*	+	0.53	<0.001		0.07
	Channel area	−	0.68	0.001	25.05	**0.58**
Benthic invertivores	Mean *phi*	−	0.71	<0.001	34.97	0.07
	Mean *phi* bar	−	0.77	0.005		0.04
	Basin compactness	−	0.82	0.017		0.03
Centrarchids	Mean *phi*	+	0.37	<0.001	14.93	0.07
	Wood in bankfull	+	0.55	0.004		0.01
Darters	Mean *phi*	−	0.64	<0.001	23.79	0.07
	Trunk stream slope	+	0.70	0.005		0.14
	95% pool depth	+	0.76	0.033		**0.23**
Richness	Baseflow width	+	0.48	<0.001	18.11	**0.64**
	Trunk stream slope	+	0.60	0.013		0.14
Density	Basin area	−	0.59	<0.001	32.65	–
	Drainage density	+	0.75	<0.001		0.01
	Trunk stream slope	+	0.81	0.048		0.14

P-values are uncorrected for sequential test but are shown as a rough guide to correlation strength.
*Amount of variance explained by drainage area for independent variables selected by the stepwise procedure.
Bold values significant at $P < 0.01$.

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 & Karr, 1978; Schlosser, 1982; and Schlosser, 1987), and we found that thalweg variation (i.e. depth heterogeneity) was significantly correlated with one NMDS axis. However, depth heterogeneity was associated with bed texture rather than stream size. Reaches with large depth variability had coarse-textured beds and were characterised 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 & 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 heterogeneity.

Floods are a major source of disturbance in streams and may effect recruitment, juvenile abundance, mortality, stability, and structure of fish assemblages (Schlosser, 1985; Matthews, 1986; Erman, Andrews & Yoderwilliams, 1988; and Freeman *et al.*, 1988). We found that two forms of flood-related disturbance, bed mobility and bankfull tractive force, were key predictors of species composition. Bed mobility, which is a function of particle size and bankfull 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 & Hubert, 1991). Two secondary predictors, 95th percentile of pool depth and 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 only predicted the proportional richness of darters, small-bodied, riffle 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 PDC. 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 & 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 trunk 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 ('lithotopo units') 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. Central 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 maintained baseflows ranging from 0.01 to 0.7 $m^3 sec^{-1}$ even during a severe summer drought of 2001. Piedmont topography is fairly steep and variable, whereas Central Lowland topography is generally low and uniform. Localised bedrock outcropping also influences the morphology of Piedmont streams, but is less of a factor in Central Lowland streams that flow over thick strata of unconsolidated glacial sediments. 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 than 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). Other studies documenting longitudinal processes in streams have sampled multiple reaches in one or a few streams (e.g. Schlosser, 1982; Rahel & Hubert, 1991). In contrast, we compared reaches from different streams distributed across a large area, a design that is increasingly used in stream studies (Hawkins & Norris, 2000). Using this sample design, we observed that streams of a given size had a high degree of geomorphic variation (e.g. sand versus cobble beds, deeply entrenched channels versus channels with well-developed flood plains) that corresponded with patterns in species composition. As a result, the distribution of stream habitats and associated fish assemblages in our streams are best characterised as a mosaic (sensu Pringle *et al.*, 1988) rather than a continuum when viewed at the basin scale.

Our results have key implications for applied research. First, stream classifications systems that use categorical measures of stream slope in their assessments may be too coarse to discriminate among streams. For example, Rosgen (1994) suggests a low slope category of <2% 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 major changes in stream physical and biological characteristics that we observed as slope increased from 0.1–1.0%. We found 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) and may be a poor surrogate for surveyed slope in topographically diverse basins. In addition, researchers developing an index of biotic integrity (IBI) for streams draining heterogeneous landscapes should 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 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). We found that bed sediment characteristics were highly correlated with stream slope suggesting that researchers should normalise for the influence of stream slope in order to detect excessive sedimentation related to human activities.

In summary, both process domains and continuum-like processes influence fish assemblages in streams of the Etowah basin. Richness and density changed along the river continuum but distinct 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 PDC and suggest that this model provides a useful context for interpreting ecological patterns in streams draining heterogeneous landscapes.

Acknowledgments

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Appendix 1

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

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

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

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

Family Name *Scientific name*	Common name	Abbreviation	Habitat guild	Feeding guild	Spawning guild
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
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
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
Percina sp. cf. *P. macrocephala*	'bridled darter'	permac	PR	I	G

*Species observed spawning in sand or sand and gravel.

Appendix 2

Geomorphic variables (95) used in this study. Total number of variables for each category is given in parentheses

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Bankfull channel characteristics (9). 'Bankfull' defined here is the first alluvial surface along the channel, which could be a terrace or flood plain. Variables are derived from three cross-sections at 0, 50 and 100% of reach length, using the HEC-RAS flow model or direct measures from plots of the bankfull cross-sections, including hydraulic radius (m), cross-sectional area (m^2), average flow velocity (m sec^{-1}), tractive force (N m^{-2}), unit power (watts m^{-2}), total power (watts), width/depth ratio, entrenchment ratio expressed by bankfull discharge/2-year recurrence interval discharge and an entrenchment ratio expressed by bankfull discharge/urbanised 2-year recurrence interval discharge

Bed Texture (26). These variables describe the particle size composition of the stream bed and they include average values derived from dominant *phi* size classes from the zigzag survey, pebble counts of riffles and bars and sieved fractions from bars, riffles and pools, including percentage of bedrock (by count) from points on zigzag survey, average (avg) and standard deviation (stdv) of *phi* size from points on zigzag survey of entire stream bed (*phi*), avg and stdv of emergent bars from Wolman pebble counts (*phi*), avg & stdv of riffle sediment from Wolman pebble counts (*phi*), sieved percentages (by dry weight) of five different size categories (<0.063, <2, 2–64, 16–64 and 64–128 mm, and mean *phi* of 2–64 mm) for each of three geomorphic units (pool, riffle, emergent bars), making 15 different observations and Manning's Roughness Coefficient (n), which is highly correlated with bed texture

Depth (21). These variables include water depths observed at baseflow as well as average water depths derived from plots of the three bankfull cross-sections, including bankfull depth (m), bankfull width/depth ratio, bankfull thalweg depth (m), average baseflow depth from five cross-sections (m), average (avg) baseflow depth from zigzag survey (m), standard deviation (stdv) of baseflow depth (m) from zigzag survey, coefficient of variation (CV) of baseflow depth from zigzag survey, the 95th percentile of baseflow depth (m) from zigzag survey, cv of serial baseflow depth ($n-1$) for the entire stream from zigzag survey, CV of serial baseflow depth ($n-1$) for the stream centreline transect, avg and stdv, and 95th percentile measurements for riffles, pools, and glides from zigzag survey

Flow and Sediment Transport (9). Bankfull discharge (m^3 sec^{-1}) and six iterations of stream bed mobility during the urbanised 0.5 year recurrence-interval flood event. These iterations used estimates of bed velocity, unit stream power and bed shear stress modelled from the HEC-RAS program (v. 2.2) for both riffles as well as the entire stream bed. Two additional mobility ratios were based on unit stream power estimated from overall average stream width, rather than cross-sections

Gradient (6). Map slope, surveyed slope, ratio of surveyed slope/map slope, Pearson correlation coefficient (*r*) of thalweg distance versus elevation, standard error of the correlation between thalweg distance and elevation and constant (slope value) for the linear regression between surveyed thalweg distance and elevation

Morphometry (11). Drainage area (km^2), perimeter (km), compactness, axial shape, total stream length (km), trunk stream length (km), drainage density (km), total relief (m), local relief of the valley (m), trunk stream relief (m) and trunk stream slope

Width (3). Average bankfull water surface width (m), avg. 0.5 year RI* water surface width and average baseflow water width

Miscellaneous (10). Number of cross-sections with terraces (of three), number of stream banks with terraces (of six), total coarse woody debris (m^3 100m^{-2}), coarse woody debirs in contact with the baseflow (m^3 100m^{-2}), functional coarse woody debris creating habitat (m^3 100m^{-2}), % riffle habitat along the thalweg, % pool habitat along the thalweg and reach totals for % pool, % riffle and % glide habitat estimated from the zigzag survey

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*Recurrence interval (derived from USGS regional flood frequency equations).