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PRIMARY RESEARCH PAPER

Longitudinal patterns of fish assemblages in small unregulated subbasins: evaluating reach- and watershed-scale parameters

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Abstract Fish assemblage relationships with environmental parameters were studied in four small unregulated subbasins in the speciose Upper Green River Basin of central Kentucky, USA. One subbasin drains into a tributary of the Green River and produced the lowest species (28) richness. The three other subbasins drain directly into the Green River and supported 41–59 species. Parameters were partitioned into watershed- and reach-scale spatial categories. Watershed area per stream segment and stream-size related environmental parameters at the reach scale produced the highest loadings of a principle components analysis (PCA), and both PCA Axes 1 and 2 for all subbasins were reflective either of watershed area or stream-size parameters. Small loadings were produced by all watershed-scale land-use parameters and all reach-scale water chemistry parameters. Fish richness and diversity were positively correlated with watershed area for the two largest subbasins and for the three Upper Green River subbasins combined. The lack of a linear relationship, however, between the residuals of multiple linear regression models between richness and diversity versus stream width, percent bedrock, percent pool and percent fine substrates indicated that a simple species area relationship was not operating. A detrended correspondence analysis (DCA) performed for each subbasin showed that several fish species were associated mainly either with small, upland segments or conversely the largest, deeper segments, and each subbasin yielded significant correlations between the environmental PCA loadings and fish assemblage DCA site scores. These results indicated that within the regional scale, and in absence of steep disturbance gradients, stream fish assemblages can reflect natural hydrologic and geomorphic gradients.

Keywords Fish · Assemblage · Longitudinal · Watershed · Stream · Land-use

Introduction

Streams are positioned within a hierarchical network of interconnected reaches (Hunsaker & Levine, 1995) and connected longitudinally through an upstream–downstream flow of energy and particles (Vannote et al., 1980). A basic premise of island biogeographic theory is that species richness increases with area (MacArthur & Wilson, 1967), a pattern demonstrated with stream fish assemblages (Angermeier & Schlosser,

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1989). Streams are not islands, however, in that reaches are not spatially discrete ecological units but consist of physical and chemical gradients both longitudinally and laterally. Physical habitat diversity increases as channel morphology becomes more complex with increasing geomorphologic and hydrologic differentiation at the reach scale (Stanford, 1996).

Streams are intrinsically variable across spatial scales (Palmer & Poff, 1997). Streams are linked to their surrounding landscapes (Hynes, 1975), and landscapes vary with respect to land-use patterns (Turner, 1987). Stream fish assemblages are shaped by environmental factors that operate across a variety of spatial and temporal scales. The distribution and diversity of fish within riverine landscapes is influenced by distance from the source (Sheldon, 1968; Horwitz, 1978), habitat availability (Angermeier & Schlosser, 1989; Pearsons et al., 1992), variable rates of migration and extinction (Schlosser, 1987; Power et al., 1988; Taylor & Warren, 2001) and location of the stream reach within the watershed (Osborne & Wiley, 1992). Recently, several authors (e.g. Magalhães et al., 2002) have indicated that an evaluation of local fish assemblages needs to be addressed across spatial scales. Due to the increasing breadth of landscape-level research (Allan, 2004), assessing anthropogenic influence on biotic communities (Meyer, 1997) across scales is critical when natural gradients are steep.

The purpose of this study was to study spatial patterns of fish in four small subbasins of the Upper Green River Basin in central Kentucky, USA. We addressed two sets of interrelated questions. First, does species richness increase accordingly with watershed area? Second, do fish assemblages change in an upstream–downstream fashion due to corresponding changes in reach-scale hydrologic, geomorphic, or physical–chemical attributes? Or, alternatively, do watershed-scale land-use patterns override the reach-scale parameters?

Methods

Study area

All fieldwork was conducted in four small subbasins located in the Interior Plateau Level-III Ecoregion of central Kentucky, USA (Woods et al., 2002). Total drainage area per subbasin ranged from 234 km^2 to 749 km^2. Bacon Creek is a 4th-order subbasin draining into the Nolin River (Fig. 1) and positioned within the Crawford-Mammoth Cave Uplands Level-IV Ecoregion. This karst region is characterized by dissected valleys of Mississipian-age St. Genevieve and St. Louis limestones (McDowell et al., 1988). Springs, sinkholes, and groundwater inputs are common. Big Brush Creek, Little Barren River, and Russell Creek drain into the mainstem of the Green River between the Green River Lake and Mammoth Cave National Park (Fig. 1). These three subbasins are located mainly in the Eastern Highland Rim Level-IV Ecoregion and underlain by limestone, sandstone, and shale.

Field methods

Environmental parameters were partitioned into watershed- and reach-scale spatial categories based on 100-m segments. The number of segments per subbasin varied minimally, with seven segments distributed along Bacon Creek and within the Big Brush Creek subbasin, whereas eight and nine segments were located in the Little Barren River and Russell Creek subbasins, respectively.

Land-use was quantified at the watershed scale using 8-, 11-, and 14-digit Hydrologic Unit Code (HUC) watersheds produced by the US Geological Survey (U.S.G.S.). Karst inferred drainages and karst basins were obtained as GIS layers through the Kentucky Division of Water. Surface drainages upstream of particular sites were selected using the National Hydrography Dataset (NHD) and NHD Toolkit published by the U.S. Environmental Protection Agency (E.P.A.). Selections of partial HUC watersheds (e.g., upstream from a particular sampling site) were made using 30-m USGS Digital Elevation Models (DEMs) and combining those partial sections with appropriate HUC watersheds. Where necessary, sections of contributing karst drainage basins were added to surface flow watersheds for accuracy in evaluating contributing area and runoff sources. Buffer polygons were created using ArcGIS with the

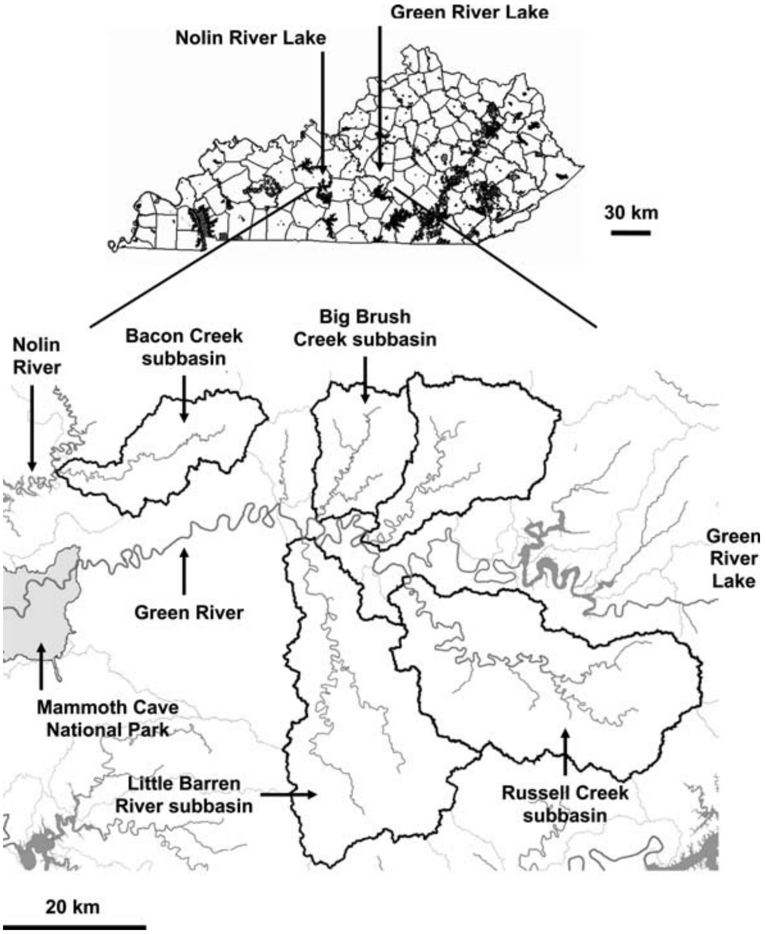

Fig. 1 Map showing the location the study subbasins within the Upper Green River Basin, central Kentucky, USA

NHD as the stream layer. The Kentucky Land Cover Data Set used for the land-use data source was published by the USGS in 1999, a joint project of the U.S.G.S. and E.P.A., and was derived from Landsat Thematic Mapper (TM) data obtained ca. 1992 with a spatial resolution of 30 m. Land-use classes assigned were those of the National Land Cover Dataset (NLCD) Land Cover Classification System (Rev. 07/99). To derive land-use summaries, polygon features were converted to raster format using Spatial Analyst, and land-use and polygon (watershed or buffer) rasters were combined, adding an area calculation to the derived attribute table, and summing areas for each land-use class. GIS work was performed using ArcGIS 8.1, with NHD work using ArcView 3.2.

Total watershed area above each sampling point was determined using an online tool to obtain drainage area for Kentucky streams (U.S.G.S., 2004). In-stream parameters were quantified from May to October 2002 and 2003 by a two-tiered approach. Tier one parameters were measured monthly with a Hydrolab Series 4a multiprobe sonde (Loveland, CO, USA) (2002) and Hydrolab Quanta (Loveland, CO, USA) (2003) as temperature (°C), pH (S.U.), turbidity (NTU), dissolved oxygen (mg/l), total dissolved solids (mg/l), and conductivity (μs/cm). Tier two parameters were analyzed bimonthly according to Standard Methods (APHA, 1998) as nitrate (mg/l), ammonia (mg/l), orthophosphate (mg/l), total phosphorous (mg/l), sulfate (mg/l), chloride (mg/l), and total suspended solids (mg/l).

Environmental parameters that fell below detection limits (DL) were treated as DL/2 prior to statistical analyses (Helsel, 1990; EPA, 1998).

Segment width (m), depth (cm), and current velocity (m/s) were quantified during baseflow conditions, the latter with a Marsh–McBirney Flo-Mate Model 2000 Portable Flowmeter (Frederick, MD, USA). The proportion of riffle, run, and pool were estimated visually, and proportions of individual substrates (e.g., cobble) were estimated visually according to the Wentworth Scale (Cummins, 1962).

Sampling for fish assemblages followed a two-step protocol. Each segment was sampled twice between 2001 and 2003. First, each segment was subjected to seining with a 3.05 × 1.83 m seine with 0.48 cm mesh. Seining proceeded for a period of 30 (minimum) to 60 min (maximum). Second, visible habitats were sampled with a Smith-Root back-pack electroshocker (Vancouver, WA, USA) for 900 shocking seconds. Habitats subject to electroshocking included, but were not limited to, riffles, runs, wadable pools, root masses, undercut banks, and accumulations of coarse woody debris. Fish were field-identified to species or preserved in 10% formalin and returned to the laboratory and subsequently identified following comparison to a reference collection**.** All fish species were identified by the same personnel and subsequently rinsed and stored in 75% ethyl alcohol.

Analytical methods

Data were placed into subbasin-specific species abundance and environmental matrices. Rare species, defined as occurring in one segment or less, were eliminated. Species richness and Shannon's diversity index were calculated based on the reduced biological data. The abundance matrix was based on mean values across the two sampling events. Abundance data were $\log_{10}$ $(1 + x)$-transformed, where x = number of individuals per species, prior to analyses. Environmental parameters were likewise transformed prior to statistical analyses. Proportion parameters (e.g., riffle, land-use) were transformed by arcsine $[(x/100)^{1/2}]$ and all remaining environmental parameters were $\log_{10}$-transformed.

Indirect gradient analyses and Pearson correlation analyses were used to assess the relationship between fish abundance and environmental parameters. Detrended correspondence analysis (DCA) was applied to the fish matrices and principle components analysis (PCA) was performed on the environmental matrix. Both ordination procedures reduce complexity into linear axes that describe similarity of biological or environmental data. Sites scores from DCA indicate relative abundance patterns of fish species while the PCA site scores depict environmental characteristics. Pearson correlation analyses tested the relationship between site scores of the first two DCA axes of each matrix and the first three PCA axes. A Pearson product–moment correlation analysis initially assessed the linear relationship between watershed area and both fish species richness and the Shannon's diversity index. Richness values and diversity indices were regressed independently on parameters that produced the highest PCA loadings in a multiple linear regression. The resulting residuals were then regressed against watershed area to test for an area effect on species richness and diversity independent of the other variables that loaded strongly on the PCA. The same suite of parameters was used in each regression and all four subbasins were addressed separately. The ordination analyses and the Shannon diversity index calculation were performed with PC-ORD Version 4 for Windows (MJM Software Design, 1999) and the Pearson correlations and regression analyses using SPSS 12.0 (SPSS Inc., 2003).

Results

Environmental parameters

Forest, pasture-hay, and row-cropping were the main land-uses along Bacon Creek (Table 1), while only the former two dominated in the Upper Green River subbasins. With few exceptions, nutrient levels were generally <1.0 mg/l per segment. Dissolved oxygen levels were high and stream temperatures were cooler in the upland tributary segments. All reaches had alkaline pH

Table 1 Range and mean of watershed- and reach-scale environmental parameters from Bacon Creek (BC) and combined data from the three Upper Green River (UGR) subbasins

Parameter	Description	BC		UGR	
		Range	Mean	Range	Mean
Watershed					
WSAREA	Watershed area (km^2)	55.9–234.1	152.5	11.0–748.8	230.9
URBAN	% urban land-use	0.4–2.1	1.2	<0.1–1.6	0.9
FOREST	% forest land-use	41.2–60.2	51.9	48.5–94.9	74.1
AGRPH	% pasture-hay land-use	24.6–39.3	31.1	4.5–33.4	17.0
AGRRC	% row-cropping land-use	12.4–16.3	14.3	0.2–16.4	7.7
WETL	% wetland land-use	0–2.9	1.5	0–0.9	0.3
Reach					
NIT	Nitrate (mg/l)	0.9–2.1	1.4	0.1–1.6	0.8
AMM	Ammonia (mg/l)	0.3–0.4	0.3	0.1–5.7	0.8
OPHOS	Orthophosphate (mg/l)	0.5–1.2	0.8	0.1–0.7	0.3
TPHOS	Total phosphorous (mg/l)	0.4–0.8	0.6	0.1–0.5	1.3
SULF	Sulfate (mg/l)	4.2–7.7	5.7	2.0–49.7	24.1
CHL	Chloride (mg/l)	3.9–7.1	5.3	4.0–21.0	10.1
DO	Dissolved oxygen (mg/l)	6.4–7.2	6.9	6.1–8.9	7.7
TEMP	Temperature (°C)	16.8–18.5	17.9	15.9–20.0	18.0
PH	PH	7.6–7.9	7.8	7.5–8.1	7.8
COND	Conductivity (μs/cm)	328.2–374.4	358.9	233.6–506.0	349.1
TURB	Turbidity (NTU)	13.1–41.3	26.1	6.6–42.8	17.2
TSS	Total suspended solids (mg/l)	16.4–38.0	23.9	0.8–42.8	8.6
TDS	Total dissolved solids (mg/l)	0.20–0.24	0.2	n.d.	n.d.
WIDTH	Bankfull width (m)	4.6–13.4	8.4	2.0–26.1	9.5
DEPTH	Riffle depth (cm)	15–51	27.6	1.7–21.3	10.5
BFVEL	Bankfull velocity (cm/s)	0.5–1.2	0.8	<0.1–0.6	0.3
%RIF	% riffle habitat	5–50	21.4	5–75	25.0
%RUN	% run habitat	10–65	31.4	5–95	56.7
%POL	% pool habitat	10–80	47.1	0–7	18.3
%BED	% substrate as bedrock	0–5	0.7	0–95	39.6
%BLD	% substrate as boulder	0–20	8.0	0–15	1.9
%COB	% substrate as cobble	0–30	14.9	2–50	16.9
%GRV	% substrate as gravel	5–25	17.1	3–60	21.0
%FIN	% substrate as silt, sand, and clay	30–90	59.3	0–70	20.6

levels and naturally high conductivity due mainly to the parent calcareous lithology of all subbasins.

The first three PCA axes contributed 90–93% of the variation in the environmental data. However, because the first two axes comprised most of the variation (80–83%) the third axis was eliminated from subsequent analyses (Table 2). High PCA loadings were evident for watershed area for 6 of 8 Axes 1 and 2 combined. All high loadings were associated with reach-scale parameters that represented a stream-size gradient, namely stream width, percent pool, percent bedrock, and percent fine substrates (Table 3). These four parameters were placed into the multiple linear regression models against both richness and diversity. Loadings were low for watershed-scale land-use parameters. Loadings were also low for all nutrients, ions, and temperature.

Fish assemblage composition and relationship to environmental variables

Bacon Creek

Total richness per segment ranged between 12 and 20 species. Watershed area was positively correlated with fish diversity and not correlated with fish richness (Table 4), yet the residuals resulting from both multiple linear regressions were not related to watershed area. Nine species, *Lythrurus fasciolaris* (Gilbert), *Pimephales nota-*

Table 2 Summary of fish species collected specific to Bacon Creek and each Upper Green River subbasin

Species	Common name	BC		BBC		LBR		RC	
		#	%	#	%	#	%	#	%
Ambloplites rupestris (Rafinesque)	Rock bass	8	1.7	8	1.7	7	1.2	7	0.5
Ameiurus natalis (Lesueur)	Yellow bullhead	1	<0.1	1	<0.1	5	0.1	4	0.2
Aplodinotus grunniens Rafinesque	Freshwater drum	–	–	–	–	1	<0.1	2	<0.1
Campostoma oligolepis Hubbs & Greene	Largescale stoneroller	8	11.7	7	15.0	8	21.0	9	15.7
Catostomus commersoni (Lacepede)	White sucker	1	<0.1	5	0.6	3	<0.1	–	–
Cottus carolinae (Gill)	Banded sculpin	8	9.9	7	3.5	8	1.3	6	0.3
Cyprinella spiloptera (Cope)	Spotfin shiner	2	0.1	2	1.7	8	3.0	7	1.0
Cyprinella whipplei Girard	Steelcolor shiner	–	–	1	0.1	6	1.1	5	1.4
Cyprinus carpio Linnaeus	Common carp	–	–	–	–	1	<0.1	3	0.1
Dorosoma cepedianum (Lesueur)	Gizzard shad	–	–	–	–	2	<0.1	–	–
Erimystax dissimilis (Kirtland)	Streamline chub	–	–	–	–	4	0.3	5	0.4
Esox americanus Gmelin	Grass pickerel	3	0.2	–	–	–	–	–	–
Etheostoma barbouri Kuehne & Small	Teardrop darter	–	–	–	–	1	0.6	1	<0.1
Etheostoma bellum Zorach	Orangefin darter	–	–	4	1.4	8	2.5	8	1.0
Etheostoma blennioides Rafinesque	Greenside Darter	8	7.1	7	3.0	8	5.4	9	3.2
Etheostoma caeruleum Storer	Rainbow darter	6	2.2	7	4.5	8	5.6	9	4.2
Etheostoma flabellare Rafinesque	Fantail darter	4	0.6	6	0.8	4	0.4	5	2.1
Etheostoma lawrencei Ceas & Burr	Headwater darter	–	–	3	0.1	4	0.2	5	4.8
Etheostoma maculatum Kirtland	Spotted darter	–	–	–	–	4	0.2	1	<0.1
Etheostoma nigrum Rafinesque	Johnny darter	3	0.1	3	0.2	6	0.2	1	<0.1
Etheostoma rafinesquei Burr & Page	Kentucky darter	8	10.6	7	6.9	8	1.6	7	1.4
Etheostoma squamiceps Jordan	Spottail darter	1	0.1	1	<0.1	1	<0.1	2	0.1
Etheostoma stigmaeum (Jordan)	Speckled darter	–	–	2	0.1	3	0.2	4	0.3
Etheostoma zonale (Cope)	Banded darter	–	–	4	0.8	7	1.5	6	0.5
Fundulus catenatus (Storer)	Northern studfish	–	–	6	2.9	8	4.3	9	3.5
Gambusia affinus (Baird & Girard)	Western mosquitofish	4	0.9	2	<0.1	–	–	5	0.2
Hybopsis amblops (Rafinesque)	Bigeye chub	–	–	5	1.2	8	0.5	7	1.3
Hypentelium nigricans (Lesueur)	Northern hog sucker	6	1.0	7	3.3	7	2.1	8	2.8
Ictalurus punctatus (Rafinesque)	Channel catfish	–	–	–	–	2	<0.1	3	<0.1
Ictiobus bubalus (Rafinesque)	Smallmouth buffalo	–	–	–	–	–	–	1	<0.1
Labidesthes sicculus (Cope)	Brook silverside	–	–	–	–	6	0.4	5	0.4
Lampetra aepyptera Abbott	Least brook lamprey	–	–	2	0.1	–	–	1	<0.1
Lepisosteus osseus (Linnaeus)	Longnose gar	–	–	–	–	3	0.1	2	<0.1
Lepomis cyanellus Rafinesque	Green sunfish	4	0.8	5	0.2	8	0.5	8	0.5
Lepomis humilis (Girard)	Orangespotted sunfish	–	–	–	–	1	0.1	1	<0.1
Lepomis macrochirus Rafinesque	Bluegill	8	1.2	2	0.4	6	0.5	9	0.8
Lepomis megalotis (Rafinesque)	Longear sunfish	8	2.7	6	2.6	8	9.5	9	8.1
Lepomis miniatus Jordan	Redspotted sunfish	–	–	–	–	–	–	1	<0.1
Luxilus chrysocephalus Rafinesque	Striped shiner	4	0.3	7	4.9	8	3.5	8	7.1
Lythrurus fasciolaris (Gilbert)	Rosefin shiner	8	25.9	7	18.5	8	8.6	9	3.3
Micropterus dolomieu Lacepede	Smallmouth bass	–	–	7	0.8	7	1.1	3	0.1
Micropterus punctulatus (Rafinesque)	Spotted bass	3	0.3	2	0.2	8	1.2	7	0.8
Micropterus salmoides (Lacepede)	Largemouth bass	2	0.1	–	–	–	–	2	<0.1
Minytrema melanops (Rafinesque)	Spotted sucker	–	–	2	0.1	2	<0.1	4	0.1
Moxostoma duquesnei (Lesueur)	Black redhorse	–	–	1	<0.1	2	<0.1	4	0.4
Moxostoma erythrurum (Rafinesque)	Golden redhorse	1	0.1	6	2.0	7	2.1	7	2.3
Moxostoma macrolepidotum (Lesueur)	Shorthead redhorse	–	–	1	<0.1	–	–	5	0.6
Notropis ariommus (Cope)	Popeye shiner	–	–	–	–	2	<0.1	–	–
Notropis boops Gilbert	Bigeye shiner	–	–	1	0.1	4	0.4	5	0.3
Notropis photogenis (Cope)	Sinver shiner	7	2.0	4	2.7	7	1.1	6	2.9
Notropis rubellus (Agassiz)	Rosyface shiner	–	–	1	0.9	4	0.8	2	0.1
Notropis volucellus (Cope)	Mimic shiner	–	–	1	0.1	3	0.1	–	–
Noturus elegans Taylor	Elegant madtom	–	–	–	–	2	<0.1	1	<0.1
Noturus eleutherus Jordan	Mountain madtom	–	–	–	–	2	<0.1	–	–
Percina caprodes (Rafinesque)	Logperch	3	0.8	1	0.1	5	0.1	5	0.3

Table 2 continued

Species	Common name	BC		BBC		LBR		RC	
		#	%	#	%	#	%	#	%
Percina evides (Jordan & Copeland)	Gilt darter	–	–	–	–	–	–	2	<0.1
Percina maculata (Girard)	Blackside darter	1	<0.1	–	–	–	–	1	<0.1
Percina sciera (Swain)	Dusky darter	–	–	–	–	–	–	1	<0.1
Percina stictogaster Burr & Page	Frecklebelly darter	–	–	–	–	–	–	1	0.1
Phoxinus erthrogaster (Rafinesque)	Southern redbelly dace	–	–	2	0.9	–	–	2	0.3
Pimephales notatus (Rafinesque)	Bluntnose minnow	8	16.9	7	13.5	7	15.7	9	26.0
Pimephales promelas Rafinesque	Fathead minnow	–	–	–	–	–	–	1	<0.1
Pimephales vigilax (Baird & Girard)	Bullhead minnow	–	–	–	–	1	<0.1	–	–
Pomoxis annularis (Rafinesque)	White crappie	–	–	–	–	1	<0.1	1	<0.1
Pylodictis olivaris (Rafinesque)	Flathead catfish	–	–	–	–	–	–	3	<0.1
Semotilus atromaculatus (Mitchill)	Creek chub	7	2.7	7	3.6	7	0.4	5	0.5
	Total # species	28		41		52		59	
	# species per segment	12–20		21–28		17–37		25–39	

BC = Bacon Creek, BBC = Big Brush Creek, LBR = Little Barren River, RC = Russell Creek. # = number segments collected, % = percent of all individuals collected. Species collected from only one segment were removed from data analyses

tus (Rafinesque), *Campostoma oligolepis* Hubbs & Greene, *Etheostoma rafinesquei* Burr & Page, *Cottus carolinae* (Gill), *E. blennioides* Rafinesque, *Lepomis megalotis* (Rafinesque), *Ambloplites ruprestris* (Rafinesque), and *Lepomis macrochirus* Rafinesque, were recorded from each segment (Table 3). The first six species comprised 82% of the total number of individuals. *Micropterus salmoides* (Lacepede), *E. nigrum* Rafinesque, and *Percina caprodes* (Rafinesque) produced the highest positive species scores for Bacon Creek DCA Axis 1 (Table 5), indicative of increasing abundance in the downstream reaches. The only species with a significant negative species score for Axis 1 was *Esox americanus* Gmelin.

The relative abundance of fish species for DCA Axis 1 was positively correlated with PCA Axis 1, and DCA Axis 2 was negatively correlated with PCA Axis 2 (Table 6). The positive correlation indicated that the increasing abundance of *M. salmoides*, *E. nigrum*, and *P. caprodes* occurred with increasing watershed area, increasing proportion of boulder and cobble substrates, and decreasing proportions of fine substrates. The negative correlation was derived from the increasing abundance of *M. punctulatus* (Rafinesque) and *E. americanus* with decreasing proportion of run habitat and increasing proportion of pool habitat.

Upper Green River Basin

Total richness per subbasin ranged between 41 (Big Brush Creek) and 59 (Russell Creek) species. Fish richness and diversity were positively correlated with watershed area individually for the Little Barren River and Russell Creek subbasins and for the three subbasins combined (Table 4). However, all linear multiple regressions residuals were unrelated to watershed area (Table 4). Four species, *C. oligolepis*, *P. notatus*, *E. blennioides*, and *E. caeruleum* Storer, were obtained from all 24 segments. These species comprised 45% of the total individuals collected from these three subbasins. Several species in the Upper Green River Basin had high species scores for Axis 1 (Table 5). *Ameiurus natalis* (Lesueur), *E. lawrencei* Ceas & Burr, and *Phoxinus erythrogaster* (Rafinesque) produced high positive Axis 1 scores in the Big Brush Creek and Russell Creek subbasins, with each species collected mainly from upland tributary segments. *Etheostoma flabellare* Rafinesque produced high positive and negative Axis 1 scores in the Russell Creek and Little Barren River subbasins, respectively. In both subbasins *E. flabellare* were also more abundant in the smaller upland segments. *Minytrema melanops* (Rafinesque) was the only other species with high axes scores in multiple subbasins,

Table 3 Loadings for PCA axes 1 and 2 of environmental parameters from Bacon Creek and each Upper Green River subbasin

Parameter	BC		BBC		LBR		RC	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Watershed								
WSAREA	**0.434**	0.081	**–0.429**	**–0.559**	–0.278	**0.511**	**–0.604**	**–0.376**
URBAN	0.055	0.010	0.039	0.042	–0.010	–0.006	–0.007	–0.042
FOREST	0.125	0.048	0.145	0.084	0.050	0.031	0.027	0.155
AGRPH	–0.105	–0.036	–0.099	–0.059	–0.038	–0.023	–0.011	–0.124
AGRRC	–0.039	–0.008	–0.104	–0.068	–0.022	–0.021	–0.022	–0.063
Reach								
NIT	–0.124	–0.033	–0.102	–0.086	–0.049	0.075	–0.012	–0.042
AMM	–0.007	0.002	–0.036	0.007	–0.006	0.036	–0.120	0.134
OPHOS	–0.020	–0.041	–0.008	0.006	–0.019	0.040	–0.017	–0.056
TPHOS	–0.082	–0.035	–0.024	0.004	–0.025	–0.007	–0.003	0.004
SULF	–0.018	–0.051	0.094	0.021	–0.026	0.011	0.175	–0.018
CHL	–0.134	0.113	–0.087	–0.002	–0.048	–0.028	0.059	–0.047
DO	–0.010	–0.033	–0.003	–0.019	0.016	0.026	0.014	0.015
TEMP	0.023	0.021	–0.004	–0.015	–0.015	0.015	–0.008	–0.017
PH	0.010	–0.002	–0.014	0.001	0.006	0.005	–0.003	–0.001
COND	0.039	0.013	–0.027	–0.003	–0.007	0.008	0.079	0.032
TURB	–0.159	–0.131	0.022	–0.069	–0.170	0.176	0.013	–0.240
TSS	–0.101	–0.184	–0.275	–0.075	–0.183	0.104	–0.160	**–0.517**
WIDTH	0.157	**0.284**	–0.128	–0.289	–0.241	**0.435**	**–0.296**	–0.073
DEPTH	0.152	**–0.219**	–0.128	–0.216	**–0.302**	0.296	–0.153	–0.162
BFVEL	–0.045	–0.020	–0.022	–0.045	–0.029	0.054	–0.060	–0.040
%RIF	0.268	–0.181	0.222	0.129	0.022	0.163	–0.117	–0.101
%RUN	–0.151	**–0.509**	**–0.406**	–0.008	0.209	0.214	0.264	–0.005
%POL	0.071	**0.688**	**0.309**	**–0.270**	**–0.345**	**–0.472**	–0.189	0.197
%BED	0.071	0.052	**–0.492**	**0.469**	**0.562**	0.105	**0.441**	**–0.510**
%BLD	**0.374**	–0.069	–0.034	–0.002	n.a.	n.a.	0.029	–0.055
%COB	**0.371**	0.032	0.219	–0.039	–0.118	0.014	–0.059	0.034
%GRV	0.121	–0.024	0.111	–0.042	–0.123	0.094	–0.135	**0.301**
%FIN	**–0.503**	0.110	0.146	**–0.455**	**–0.436**	**–0.300**	**–0.318**	0.157
% variance explained	53.9	26.8	60.4	19.1	62.3	21.1	60.3	22.9

Scores in bold type form the basis of interpretation per axis. See Table 2 for abbreviations

Table 4 Pearson correlation analyses between fish richness and watershed area

BC	BBC	LBR	RC	UGR
$n = 7$	$n = 7$	$n = 8$	n = 9	$n = 24$
0.498	0.402	***0.915**	***0.855**	****0.836**

* $P < 0.01$, ** $P < 0.001$. See Table 2 for abbreviations

as Axis 2 for both the Big Brush Creek and Little Barren River subbasins.

In the Big Brush Creek subbasin DCA Axis 1 was positively correlated with PCA Axis 2 and DCA Axis 2 was negative correlated with PCA Axis 1 (Table 6). The positive correlation was driven by the presence of *P. erythrgaster* and *Lampetra aepyptera* Abbott found solely in the upland reaches with a small watershed area, low proportion of pool habitat and fine substrates, and high proportion of boulder substrates. The negative correlation was mainly due to increasing abundance of *L. macrochirus*, *M. melanops*, and *A. natalis* with decreasing watershed size, proportion of bedrock substrates, and run habitat. There was a single significant positive correlation each for the Little Barren River and Russell Creek subbasins. Little Barren River DCA Axis 1 was positive correlated with PCA Axis 2 (Table 6), indicating that increasing abundance of *Dorosoma cepedianum* (Lesueur), *Noturus eleutherus* Jordan, and *Lepisosteus osseus* (Linneaus) were associated with increasing watershed size and stream width. The highest positive correlation was exhibited

Table 5 Detrended correspondence analysis species scores for axes 1 and 2 of fish species abundance specific to Bacon Creek and each Upper Green River subbasin

Species	BC		BBC		LBR		RC	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Ambloplites rupestris	17	–18	51	–18	174	61	–44	92
Ameiurus natalis	–	–	**305**	**355**	–89	**296**	**276**	3
Aplodinotus grunniens	–	–	–	–	–	–	–212	85
Campostoma oligolepis	95	107	65	57	75	34	106	33
Catostomus commersoni	–	–	221	210	118	–72	–	–
Cottus carolinae	9	35	63	113	145	72	–17	–75
Cyprinella spiloptera	–	–	–204	49	50	75	41	–200
Cyprinella whipplei	–	–	–	–	–18	201	–75	**294**
Cyprinus carpio	–	–	–	–	–	–	–179	**–262**
Dorosoma cepedianum	–	–	–	–	**357**	–58	–	–
Erimystax dissimilis	–	–	–	–	268	139	–93	188
Esox americanus	**–373**	**488**	–	–	–	–	–	–
Etheostoma bellum	–	–	–127	20	143	–141	–44	–94
Etheostoma blennioides	101	77	2	162	102	58	110	56
Etheostoma caeruleum	166	–67	146	–64	–16	13	127	–15
Etheostoma flabellare	247	–50	197	–99	**–312**	–99	**247**	56
Etheostoma lawrencei	–	–	**294**	**–295**	–211	–79	**316**	57
Etheostoma maculatum	–	–	–	–	271	242	–	–
Etheostoma nigrum	**336**	–23	–171	91	185	–222	–	–
Etheostoma rafinesquei	–21	44	103	33	108	–20	158	95
Etheostoma squamiceps	–	–	–	–	–	–	137	–53
Etheostoma stigmaeum	–	–	–109	141	–182	–33	–64	**372**
Etheostoma zonale	–	–	–162	78	202	110	–109	–84
Fundulus catenatus	–	–	22	–43	37	–25	135	–6
Gambusia affinus	49	148	–	–	–	–	5	–124
Hybopsis amblops	–	–	45	–181	–17	–22	126	0
Hypentelium nigricans	186	114	48	111	161	22	5	85
Ictalurus punctatus	–	–	–	–	–	–	–102	–21
Labidesthes sicculus	–	–	–	–	122	–149	–95	–191
Lampetra aepyptera	–	–	**418**	–187	–	–	–	–
Lepisosteus osseus	–	–	–	–	**315**	–152	–164	124
Lepomis cyanellus	–198	**–355**	135	233	90	68	148	104
Lepomis macrochirus	101	54	267	**421**	–134	–17	58	60
Lepomis megalotus	56	–52	–5	131	78	3	81	30
Luxilus chrysocephalus	15	190	126	33	10	78	19	80
Lythrurus fasciolaris	–27	17	49	84	0	49	97	114
Micropterus dolomieu	–	–	145	44	217	101	–181	100
Micropterus punctulatus	224	**371**	–239	49	–3	21	–56	55
Micropterus salmoides	**338**	–149	–	–	–	–	–50	**–408**
Minytrema melanops	–	–	163	**360**	188	**619**	–41	–225
Moxostoma duquesnei	–	–	–	–	20	**549**	–1	185
Moxostoma erythrurum	–	–	–25	158	50	132	–78	65
Moxostoma macrolepidotum	–	–	–	–	–	–	–138	130
Notropis ariommus	–	–	–	–	292	–268	–	–
Notropis boops	–	–	–	–	88	–289	–122	–41
Notropis photogenis	154	–93	–98	104	196	105	–75	97
Notropis rubellus	–	–	–	–	259	–187	26	**452**
Notropis volucellus	–	–	–	–	245	**–298**	–	–
Noturus elegans	–	–	–	–	8	**–344**	–	–
Noturus eleutherus	–	–	–	–	**344**	–70	–	–
Percina caprodes	**295**	–16	–	–	203	154	–132	–18
Percina evides	–	–	–	–	–	–	–118	230
Phoxinus erthrogaster	–	–	**432**	–112	–	–	**404**	39
Pimephales notatus	47	64	102	104	1	37	115	48

Table 5 continued

Species	BC		BBC		LBR		RC	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Pylodictis olivaris	–	–	–	–	–	–	–99	**–275**
Semotilus atromaculatus	–171	76	207	–75	65	–81	**241**	85

Scores in bold type form the basis of interpretation per axis. See Table 2 for abbreviations

Table 6 Pearson correlation analyses (*r*) relating DCA sites scores for fish abundance with PCA site scores for enviromental parameters specific to Bacon Creek and each Upper Green River subbasin

		PCA Axis 1	PCA Axis 2
BC	DCA Axis 1	***0.807**	–0.203
	DCA Axis 2	0.279	***–0.794**
BBC	DCA Axis 1	0.503	***0.777**
	DCA Axis 2	***–0.742**	–0.055
LBR	DCA Axis 1	–0.491	***0.719**
	DCA Axis 2	0.212	0.437
RC	DCA Axis 1	****0.846**	0.232
	DCA Axis 2	0.049	0.098

* $P < 0.05$, ** $P < 0.01$. See Table 2 for abbreviations

between Russell Creek's DCA Axis 1 with PCA Axis 1 (Table 6). The prevalence of uplands species (e.g. *P. erythrogaster*, *E. lawrencei*) was associated with segments with small watershed area, high proportion of bedrock and low proportion of fine substrates.

Discussion

Environmental relationships with fish assemblages vary spatially from localized in-stream habitat structure (Gorman & Karr, 1978), landscape-level parameters (Wang et al., 2003), to broad-scale regional factors (Brazner et al., 2005). The indirect gradient and subsequent site score correlation analyses generated in this study showed that within all four subbasins that natural environmental gradients at the reach scale were more influential than watershed-scale land-use features on fish assemblages. Wang et al. (2003) also demonstrated that reach-scale variables explained a greater amount of variation than either riparian- or watershed-scale variables on local fish assemblages in northern U.S. streams.

The only watershed-scale parameter that appeared initially to impart influence in this study was watershed area. The lack of a positive correlation between fish richness or diversity and watershed area for both Bacon Creek and the Big Brush Creek subbasin could be attributed to the shallower area gradient seen here than in either the Little Barren River or Russell Creek subbasins. Watershed size for Bacon Creek and the Big Brush Creek subbasins ranged from 56 km^2 to 234 km^2 and 11 km^2 to 199 km^2, respectively. In contrast, the latter two subbasins ranged from 47 km^2 to 649 km^2 and 13 km^2 to 749 km^2, respectively. The lack of the linear relationship, however, between the residuals of the multiple linear regression models between richness or diversity and the combination of stream width, percent bedrock, percent pool, and percent fine substrates eliminated the simplistic species-area relationship. Several workers have shown relationships between fish assemblages and physical variation (e.g., Meffe & Sheldon, 1988; Edds, 1993; Smiley et al., 2005). Schlosser (1982) revealed that fish community change longitudinally in a small Illinois stream was associated with increases in both habitat diversity and volume. Gelwick (1990) depicted a similar trend in headwater Ouachita Mountain stream pool habitats. Longitudinal patterns of species replacements and additions in relation to decreasing hydrologic variability was proposed initially by Schlosser (1987) for warmwater fish assemblages and was subsequently supported by Taylor and Warren (2001). Larger stream sites with lower hydrologic variability allowed individual species to maintain higher abundances and lower local-scale extinction rates.

The Green River is one of the top four rivers in the U.S. according to fish (151 species) and mussel (71 species) diversity (The Nature

Conservancy, 2005) and has been characterized as possessing a highly diverse and unusual fish fauna (Burr & Page, 1986). Within the three Upper Green River subbasins, total fish richness per segment ranged from 17 to 39 species. The Upper Green River Basin is encompassed within the ancestral Ohio River Basin (Burr & Page, 1986), suggesting that the study area once supported a holistic species pool prior to land-use alteration and subsequent habitat fragmentation. The mainstem upper Green River, in a simple sense, represents an open conduit allowing for active dispersal between these three proximate subbasins. Bacon Creek was less speciose than each of the three Upper Green River subbasins. Of the several *Etheostoma* species that are endemic to the Upper Green River Basin (i.e., *E. barbouri* Kuehne & Small, *E. bellum* Zorach, *E. lawrencei, E. rafinesquei*), only the latter occurred in Bacon Creek. Although all four subbasins are hierarchically located in the Green River Basin, Bacon Creek is a tributary of the Nolin River and drains into the mainstem Green River 110 river km downstream of the nearest Upper Green River subbasin (i.e., Little Barren River). In contrast, each Upper Green River subbasin empties into the mainstem Green River within a 42 river km section.

In Bacon Creek the environmental PCA depicted a longitudinal gradient associated with increasing stream size, with increasing proportion of boulder substrates and with a corresponding decrease in the proportion of fine substrates. Several species of stream fishes, *M. salmoides*, *M. punctatulatus*, *E. flabellare*, *E. nigrum*, and *P. caprodes* were obtained mainly from the downstream segments of Bacon Creek. Local-scale species pools are regulated by the availability of taxa within a broader, regional pool (Poff, 1997). The location of the most downstream Bacon Creek segment was only 3 km from the Nolin River, providing a likely colonization source for these larger stream species. In lotic habitats both *Micropterus* species are typically associated in larger streams (Etnier & Starnes, 1993). Similarly, *P. caprodes* inhabits larger streams and small rivers (Page, 1983; Burr & Warren, 1986). *Etheostoma flabellare* occurs in riffles with coarse substrates (Burr & Warren, 1986; Etnier & Starnes, 1993), a habitat characteristic in the downstream reaches of Bacon Creek. There were no fish species obtained solely from the upstream segments. In contrast, several fish species typically associated with small streams were obtained mainly in the upland segments of the Upper Green River Basin. Prominent upland species included *P. erythrogaster* (Burr & Warren, 1986; Etnier & Starnes, 1993), *L. aepyptera* (Burr & Warren, 1986; Etnier & Starnes, 1993), and *E. lawrencei* (Ceas & Burr, 2002).

We attribute the lack of an urban influence on fish assemblages in this study to the rural nature of the watershed. Urban land-use has been shown to negatively influence fish integrity in Wisconsin streams (Wang et al., 2001) where urban-forest gradients were considerably steeper. The sole town (Bonnieville) located along Bacon Creek has a population of only 354 residents (U. S. Census Bureau, 2000) and the highest urban land-use was 2.1%. A similar lack of an urban influence was exhibited in the three Upper Green River subbasins, where the highest urban land-use was only 1.6%.

There was a broad range of agricultural land-use activities in the Bacon Creek watershed categorized as pasture/hay (25–47%) and row-cropping (11–20%), yet even the former had only the 7th- and 11th-highest loadings for PCA Axis 1 and 2, respectively. Similarly, although the upstream segments had the highest levels of many agricultural-related parameters, including nitrate, total phosphorous, turbidity, and total suspended solids, these also resulted in small loading values for both PCA axes. The agricultural influence in the Upper Green River Basin was likely limited by the low mean of row-cropping (7.7%) and pasture-hay (17.0%) activities across the three subbasins. Despite the high proportion of forest (mean = 74.1%), the shallow gradient exhibited for this land-use category across the three subbasins resulted in low PCA loading scores. With the exception of one segment with a percent forest land-use = 48.5%, all segments had percent forest values >60%.

The speciose Upper Green River Basin of central Kentucky provides an excellent backdrop for investigating distribution patterns of stream fish assemblages. Our data indicated that fish abundance patterns shifted longitudinally from the small, uplands stream segments to the deeper, larger segments at the downstream end of each subbasin, with a near lack of an overriding influence of land-use patterns. These results indicated that at the regional scale, and in absence of steep agricultural or urban disturbance gradients, stream fish assemblages can be reflective of natural reach-scale hydrologic and geomorphic gradients.

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