A Multi-Scaled Approach to Evaluating the Fish Assemblage Structure Within Southern Appalachian Streams

Joseph E. Kirsch[ac] & James T. Peterson[bd]

[a] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, 30602, USA

[b] U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602, USA

[c] U.S. Fish and Wildlife Service, 850 South Guild Avenue, Suite 105, Lodi, California 95240, USA

[d] U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, 104 Nash Hall, Corvallis, Oregon 97331, USA
Published online: 02 Sep 2014.

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Joseph E. Kirsch[1]

Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, 30602, USA

James T. Peterson[*][2]

U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit,
Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602, USA

Abstract

There is considerable uncertainty about the relative roles of stream habitat and landscape characteristics in structuring stream-fish assemblages. We evaluated the relative importance of environmental characteristics on fish occupancy at the local and landscape scales within the upper Little Tennessee River basin of Georgia and North Carolina. Fishes were sampled using a quadrat sample design at 525 channel units within 48 study reaches during two consecutive years. We evaluated species–habitat relationships (local and landscape factors) by developing hierarchical, multispecies occupancy models. Modeling results suggested that fish occupancy within the Little Tennessee River basin was primarily influenced by stream topology and topography, urban land coverage, and channel unit types. Landscape scale factors (e.g., urban land coverage and elevation) largely controlled the fish assemblage structure at a stream-reach level, and local-scale factors (i.e., channel unit types) influenced fish distribution within stream reaches. Our study demonstrates the utility of a multi-scaled approach and the need to account for hierarchy and the interscale interactions of factors influencing assemblage structure prior to monitoring fish assemblages, developing biological management plans, or allocating management resources throughout a stream system.

North America possesses the richest diversity of temperate freshwater fishes within the world (Jelks et al. 2008). Unfortunately, high fish endemism coupled with environmental degradation has resulted in substantial imperilment among native fishes. Approximately 46% of the 1,187 described freshwater and diadromous fish taxa are now classified as vulnerable, threatened, or endangered, a 92% increase from 1989 (Jelks et al. 2008). Assuming no future catastrophic events, the extinction rate of North American freshwater fishes is projected to increase from 0.4% per decade (Ricciardi and Rasmussen 1999) to 3.2% per decade (Burkhead 2012) due to habitat deterioration associated with anthropogenic land and water development. Sedimentation, nutrient loading, pollution, exotic species introduction, and altered hydrologic regimes are anthropogenic stressors attributed to freshwater fish imperilment in North America (Richter et al. 1997; Ricciardi and Rasmussen 1999; Contreras-Balderas et al. 2003; Dextrase and Mandrak 2006). Effective management strategies need to be developed at the most effective spatial scale to reduce these threats. Before these strategies are developed, it is essential to identify and quantify the primary factors influencing lotic fish assemblage structure to appropriately allocate management resources (Peterson and Dunham 2010).

The structure of a lotic fish assemblage is the result of a combination of biotic interactions and environmental influences (Jackson et al. 2001). Biotic interactions (i.e., predation and competition) reportedly influence fish assemblage composition through species deletions (Gilliam and Fraser 2001) and by altering behavior, such as changing habitat use (Power et al. 1985; Taylor 1996). Instream hydrogeomorphology (e.g., water depth, current velocity) influences fish assemblage composition by providing habitats that allow certain species to persist within species-specific morphological limitations and life history requirements (Schlosser 1982; Moyle and Vondracek 1985; Jackson et al. 2001; Peterson and Rabeni 2001a). Landscape charactersitics, such as topography, terrestrial land use, and stream network topology, can affect the structure of local instream habitat characteristics or disperal processes, which in turn influence fish assemblage structure (Schlosser 1991; Peterson and Kwak 1999; Paul and Meyer 2001; Hitt and Angermeier 2008). Despite the multitude of studies demonstrating the effects of both biotic interactions and environmental characteristics on fish assemblage structure, the percieved importance of mechanisms is not well understood and is typically governed by their association with the scale of study (Jackson et al. 2001; Peterson and Dunham 2010).

Scale is defined by the spatial and temporal resolution of the observational units (i.e., grain) and the dimensions of a study (i.e., extent; Wiens 1989). All mechanisms influencing fish assemblage structure, including biotic interactions and environmental characteristics, potentially operate across multiple spatial and temporal scales (Frissell et al. 1986; Tonn 1990; Poff 1997). The ability to observe or detect the effects of these factors, however, depends on the within-gain and among-grain heterogeneity (Wiens 1989). For example, studies conducted using large sample units in large spatial extents (e.g., stream reaches within watersheds) often conclude that mechanisms operating over broad scales (e.g., topography) are the primary processes affecting lotic fish assemblage structure (e.g., Fausch et al. 1994), whereas studies conducted with smaller sample units and spatial extents (e.g., microhabitat use within a stream reach) probably identify mechanisms operating at smaller scales as primary processes affecting lotic fish assemblage structure (Jackson et al. 2001; Peterson and Dunham 2010). Although the association between spatial scale of a study and the perceived importance of factors influencing fish assemblage structure have been acknowledged (e.g., Crook et al. 2001; Jackson et al. 2001; Fausch et al. 2002; Quist et al. 2005), few studies have elucidated the importance of environmental characteristics in structuring lotic fish assemblages across spatial scales.

In our study we used a multi-scale approach to evaluate the factors influencing fish species occupancy and assemblage structure within a southeastern U.S. river basin. Our objectives were twofold: (1) to develop a multi-scale sampling and modeling framework for evaluating the effects and relative importance of abiotic factors on stream fish occupancy at geomorphic channel-unit and stream-reach spatial scales, and (2) evaluate the scale-specific relations between the most influential factors and fish species presence, habitat use, and assemblage structure.

METHODS

Study area.—We investigated stream fish occupancy and assemblage structure in the Little Tennessee River basin located in western North Carolina and northeast Georgia. The Little Tennessee River is a tributary of the upper Tennessee River and is located in the Blue-Ridge province of the southern Appalachian Mountain range. The basin reportedly contains more than 150 native freshwater fish species (Warren et al. 2000; Etnier and Starnes 2001). The climate is classified as marine humid temperate based on its relatively mild air temperatures and high moisture content (Swift et al. 1988). The Little Tennessee River basin drains an area of approximately 4,117 km^2 and land use is primarily second growth forests due to extensive deforestation in 19th century (Scott et al. 2002). Streams in this region are typically constrained by bedrock; are nutrient-poor in areas uninfluenced by anthropogenic inputs; and generally contain boulder, cobble, and gravel substrates (Scott et al. 2002). Anthropogenic land use within the basin includes both agriculture and urban development (Gragson and Bolstad 2006).

Site selection.—Our study was conducted in collaboration with the Coweeta Long Term Ecological Research Program's synoptic sampling and assessment project. Study sites were stream reaches chosen to represent the range of land uses, stream sizes, stream network positions, and elevations within the Little Tennessee River basin (Figure 1). Forty-six study reaches, approximately 150 m in length, were sampled during the pilot phase of the project in the summer (July – September) of 2009. Based on the results of the pilot sampling, 8 of the 46 study reaches and 2 additional study reaches were selected to represent common land use within the Little Tennessee River basin. The 10 reaches were sampled during the spring (May) and summer (August) of 2010 and spring 2011 to evaluate potential seasonal influences.

Landscape data.—We obtained riparian buffer condition data for each study reach from Long and Jackson (2014) and recorded whether the study reaches had intact riparian buffers (i.e., was defined as fully forested cover extending 10 m or more on both sides of the channel). All other landscape data for each study reach were estimated using the Coweeta Long Term Ecological Research geographic information system data (CLTER 2011) and ArcGIS software version 9.3. Study reach elevation, gradient, and hydrography data were derived from a U.S. Geological Survey seamless digital elevation model with 9.353-m resolution (USGS 2007). For each study reach, the number of contributing tributaries and watersheds boundaries were delineated using protocol described by Jenson and Domingue (1988). Link magnitude and downstream link
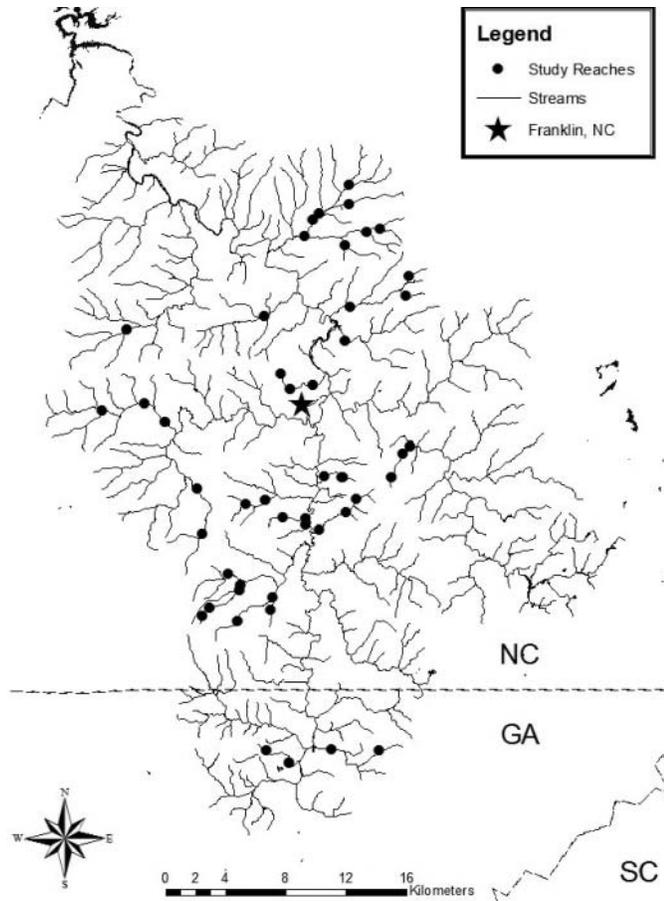
FIGURE 1.   Location of the 48 study-reach sites within the Little Tennessee River basin, Georgia and North Carolina.

less than 3% of land cover among our study reaches and was not included in the analysis.

Sampling design.—We used a multi-scale sample design in which samples were collected from individual geomorphic channel units (henceforth, channel units) nested within study reaches. At each study reach, the stream was stratified into distinct channel unit types (i.e., riffle, run, and pools; Table 1) and sampled using a quadrat sample design (see Williams et al. 2002). Two to four replicates of each of the channel unit types present at a study reach were randomly selected for fish sampling and habitat measurement. During the summer of 2009, the randomly selected channel units were sampled once, whereas each randomly selected sample unit was sampled twice during 2010 and 2011 to facilitate species detection probability estimation. The time between the two sampling occasions was 5–7 d to allow fish to recolonize the previously sampled channel units (Peterson and Bayley 1993).

Fishes were sampled during daylight hours with Smith–Root LR 24 pulsed DC backpack electrofishers operating between 0.2 and 0.3 amperes. At each study reach, fish sampling began at the farthest downstream channel unit with the deployment of a 5-mm-mesh seine across the downstream end for riffles and runs or the upstream end for pools. The seine completely blocked off the end of the channel unit and was secured to the streambed to prevent fishes from leaving. Samples were collected using single-pass electrofishing starting from the opposite end of the channel unit from where the seine was deployed. To minimize the influence of sampling activities and field personnel on fish movement between channel units, samples were not collected from adjacent channel units and field personnel exited the stream after sampling and traveled to the next sample unit away from the shoreline. A single backpack electrofisher was used in streams with average wetted widths ≤4 m; two backpack electrofishers were used in larger streams. At least one additional crewmember accompanied each electrofisher and collected stunned fish with a 5-mm-mesh dip net. All crewmembers involved with electrofishing also disturbed the substrate with their feet during the single electrofishing pass to increase fish capture. Captured fishes were identified to species, measured for total length (TL), and released into the sampled channel unit. Fishes that could not be accurately identified were initially preserved in a 10% formalin solution and brought back to the laboratory. Preserved fishes were later transferred to a 70% ethanol solution, identified to species, and measured (TL).

were calculated to represent study reach size and study reach network positions. Link magnitude was defined as the number of contributing tributary headwater streams upstream of a study reach (Shreve 1966). Downstream link was defined as the link magnitude of the next downstream confluence from a study reach (Osborne and Wiley 1992). Land use data for each study reach were estimated using 2006 land-cover data classified from Landsat Thematic Mapper satellite imagery with 30-m resolution (Hepinstall-Cymerman 2011). Land cover classes were grouped into four land use classes: urban, agriculture, forest, and other (i.e., grassland, shrub, wetland, water, and barren). The "other" land-cover class represented, on average,

TABLE 1.   Physical characteristics used to identify channel-unit types during fish sampling within the Little Tennessee River basin, Georgia and North Carolina (Hawkins et al. 1993; Peterson and Rabeni 2001b).

Channel unit type	Mean water velocity	Surface turbulence	Substrate size	Water depth
Riffle	High	High	High	Low
Run	Moderate	Moderate	Low/moderate/high	Moderate
Pool	Low	Low/moderate	Low/moderate/high	High

Physical habitat measurements.—Water quality and physical instream habitat characteristics expected to influence fish occupancy, or the ability to detect fish, were measured at each study reach and channel unit in conjunction with fish sampling. Prior to fish sampling, water quality characteristics were measured in flowing water using calibrated meters at each study reach for each sampling occasion. Turbidity was measured using an Oakton T-100 meter to the nearest 0.01 nephelometric turbidity unit (NTU). Specific conductance was measured using an Oakton CON 400 Series meter to the nearest 0.01 μs/cm.

Physical instream habitat characteristics were estimated within each channel unit at each study reach for each sampling occasion. Mean wetted width, mean water velocity, and mean water depth were estimated by averaging three to five randomly placed measurements within each channel unit (Peterson and Rabeni 2001b). Water depths were measured (cm) using a 2-m top-set wading rod. Water velocities were measured at a depth of 0.6 m, using a Marsh McBirney model 2000 Flo-mate meter. The length and wetted widths of each unit were measured (cm) via a standard measuring tape. The mean cross-sectional area of each channel unit was estimated by multiplying the channel-unit mean width by the channel-unit mean depth. The surface area of each channel unit was estimated by multiplying a channel-unit mean width by length.

Substrate composition within a channel unit was visually estimated by two or more crew and averaged. Substrate composition was categorized based on particle diameter as fine sediment (<5 mm), gravel (5–50 mm), and coarse sediment (≥50 mm; modified from Dunne and Leopold 1978). At least two crew members were trained in determining particle diameter at the beginning of each season using metric rulers, calipers, or sieves. If the substrata were not visible, we randomly collected three to five physical substrate samples using a shovel or similar device for determination. Wood density within the wetted channel unit was estimated by counting the pieces of wood that were at least 50 cm in length and 10 cm in diameter, or aggregates of smaller pieces of wood with comparable volume, and dividing by the channel unit area.

Statistical analysis.—We evaluated the relative importance of in-stream habitat and landscape characteristics, and species specific characteristics on fish occupancy using hierarchical multispecies, multi-scale occupancy models (Royle and Dorazio 2008; Mordecai et al. 2011). This provided a framework for modeling the relation between scale-specific occupancy (i.e., study reach and channel unit within reach) and habitat characteristics for multiple species with different habitat use patterns, while accounting for spatial dependency and incomplete detection. The multi-scale occupancy models were fit using logit linear functions of predictor variables and consisted of three submodels that estimated the probability that a species occupies a study reach (ψ), the probability that the species uses a channel unit within an occupied study reach (θ), and the probability of detecting a species given it occupies a channel

unit (p) in a single modeling framework (Appendix). The primary assumption of the occupancy estimator is that a species cannot colonize or abandon a study reach between sample occasions (MacKenzie et al. 2006). We believe that this assumption was met because sample occasions were 5–7 d apart within a season and did not include periods of seasonal fish migration or seasonal changes in habitat use.

Prior to model-fitting, we estimated Pearson's product moment correlation coefficients between all pairs of potential predictor variables. Forest land cover was strongly and negatively correlated ($r^2 > 0.7$) with urban and agriculture land use and could not be included in the same models due to potential multicollinearity (Dormann et al. 2013). Therefore, the evaluation of the effect of land use on fish occupancy included only urban and agriculture land cover because anthropogenic land conversion was one of the primary management issues in the basin. All continuous instream habitat and landscape data were standardized with a mean = 0 and SD = 1 to facilitate model-fitting. We also created binary indicator variables for species characteristics, channel unit type, summer season, intact riparian buffer, and for instances where two electrofishers were used to sample fish.

We used an information theoretic approach (Burnham and Anderson 2002) to evaluate our primary hypotheses of interest regarding the relative influence of abiotic factors on fish occupancy and detection. We initially developed a global model that contained all predictor variables corresponding to a priori hypotheses about the influence of abiotic factors (Table 2) and species characteristics on fish occupancy at study-reach and channel-unit scales. Based on previous investigations (Freeman et al. 1988; Grossman et al. 1998; Harding et al. 1998; Jones et al. 1999; Scott 2006; Burcher et al. 2008), we hypothesized that species occupancy at the study reach level was influenced by seasonal habitat availability, stream topology and topography, and land cover and that these effects were mediated by species-specific characteristics. Within occupied reaches, we hypothesized that species channel unit use was influenced by channel unit characteristics and varied with species characteristics. The species characteristics evaluated included the size of mature adults (small was ≤100 mm TL and not small was >100 mm TL); common position within the water column (benthic and other), thermal tolerance (warmwater tolerant and warmwater intolerant), and whether or not the species was endemic to the southern Appalachian highlands (Table 3). The global model also contained variables that potentially affected species detection, including the number of backpack electrofishers, surface area and cross sectional area of the channel unit sampled, conductance, turbidity, wood density, mean water velocity, and coarse substrate composition (Peterson and Paukert 2009 and references therein; Price and Peterson 2010).

Before evaluating the support for the candidate models, we determined the best variance structure (i.e., the parameters that needed to vary randomly among species or study reaches)

TABLE 2. Hypotheses and corresponding predictor variables by scale and hypothesis categories used to estimate the study reach and conditional channel unit occupancy and detection probability of common fish species within the Little Tennessee River basin, GA and NC.

Category	Predictor	Hypothesis
Study-reach scale		
Habitat availability	%Riffle [a] +%Pool[a]	The physical habitat availability in a reach affects occupancy.
Stream topology and topography	Link magnitude[a]	The stream size affects fish occupancy by influencing aquatic habitat characteristics, habitat volume, and hydraulic regimes.
	D-Link[a]	The location of a reach within the stream network affects fish occupancy by influencing immigration and colonization rates.
	Elevation[a]	The elevation of a study reach affects fish occupancy by influencing thermal regimes.
	Gradient[a]	The gradient of a study reach affects fish occupancy by influencing hydrodynamic characteristics and colonization rates.
Land cover	Urban[a]	Urban land cover within a watershed negatively affects fish occupancy by altering hydraulic regimes and aquatic habitat characteristics.
	Riparian buffer[a]	Intact riparian buffers positively affect fish occupancy by influencing productivity, thermal regimes, and habitat diversity.
	Agriculture[a]	Agricultural cover within a study reach watershed negatively affects fish occupancy by influencing hydraulic regimes and aquatic habitat characteristics.
Seasonal interactions	Summer × link	Influence of stream size and elevation on fish occupancy differs in the summer by reduced streamflow and increased temperatures.
	Summer × elevation	
Land-cover interactions	Riparian buffer × land cover	The relation between land cover and occupancy is mediated by the presence of riparian buffer.
Species characteristics	Southern Appalachian Highlands endemic × urban	The occupancy of fish species endemic to the southern Appalachian Highlands are more sensitive to the negative effects of urban cover
	Southern Appalachian Highlands endemic × riparian buffer	Intact riparian buffers have a greater, positive effect on the occupancy of fish species endemic to the southern Appalachian Highlands.
	Warmwater intolerant × elevation	The relation between elevation and occupancy differs for fish species intolerant of warmwater.
Channel-unit scale		
Channel-unit type	Pool[a] + riffle[a]	A pool or riffle, relative to a run, affects occupancy by influencing hydrogeomorphic characteristics.
Species characteristics	Pool × body size + riffle × body size	The relation between channel-unit habitat use varies with fish body size and position within the water column.
	Pool × water column + Riffle × water column	
Inter-scale		
Channel-unit and landscape interactions	Gradient × pool + Gradient × riffle	Channel-unit habitat use varies with stream gradient.
	Link × pool + link × riffle	Channel-unit habitat use varies with stream size.
Seasonal channel-unit interactions	Summer × pool + Summer × riffle	Channel-unit habitat use differs during the summer.

[a] The effect was modeled as varying among species.

TABLE 3. Fish species and sample occupancy data for the Little Tennessee River basin, including the species characteristics—small size (SM), not small size (NS), benthic (B), nonbenthic (NB), intolerant of warm water (IT), tolerant of warm water (T), southern Appalachian Highland endemic (E), and not endemic to the southern Appalachian Highlands (NE)—as determined using Eaton and Scheller (1996), Etnier and Starnes (2001), Scott and Helfman (2001), and Wehrly et al. (2003).

| Species | Number and (%) | | Mean (range) TL (mm) | Species characteristics |
	Sites	Samples		
Mountain Brook Lamprey *Ichthyomyzon greeleyi*	10 (20.8)	40 (7.6)	117.6(52–154)	NS,B,T,NE
Central Stoneroller *Campostoma anomalum*	19 (39.6)	94 (17.9)	94.8(34–237)	SM,B,T,NE
Goldfish *Carassius auratus*	1 (2.1)	1 (0.2)	118.0(117–119)	NS,B,T,NE
Rosyside Dace *Clinostomus funduloides*	18 (37.5)	87 (16.6)	65.5(28–109)	SM,NB,T,E
Whitetail Shiner *Cyprinella galactura*	8 (16.7)	31 (5.9)	80.1(32–169)	SM,NB,T,NE
Warpaint Shiner *Luxilus coccogenis*	12 (25)	65 (12.4)	79.6(30–196)	SM,NB,T,E
River Chub *Nocomis micropogon*	15 (31.2)	73 (13.9)	112.7(33–256)	NS,NB,T,NE
Golden Shiner *Notemigonus crysoleucas*	1 (2.1)	2 (0.4)	82.2(77–88)	SM,NB,T,NE
Tennessee Shiner *Notropis leuciodes*	12 (25)	50 (9.5)	64.2(33–84)	SM,NB,T,E
Yellowfin Shiner *Notropis lutipinnis*	8 (16.7)	41 (7.8)	66.5(30–118)	SM,NB,T,NE
Mirror Shiner *Notropis spectrunculus*	2 (4.2)	3 (0.6)	68.0(64–72)	SM,NB,T,E
Telescope Shiner *Notropis telescopus*	2 (4.2)	8 (1.5)	77.6(66–91)	SM,NB,T,E
Fatlip Minnow *Phenacobius crassilabrum*	5 (10.4)	8 (1.5)	91.3(71–113)	SM,B,IT,E
Fathead Minnow *Pimephales promelas*	1 (2.1)	1 (0.2)	64.0(N/A)	SM,NB,T,NE
Blacknose Dace *Rhinichthys atratulus*	17 (35.4)	85 (16.2)	55.5(23–161)	SM,NB,T,NE
Longnose Dace *Rhinichythys cataractae*	13 (27.1)	50 (9.5)	83.7(31–155)	SM,B,IT,E
Creek Chub *Semotilus atromaculatus*	31 (64.6)	129 (24.6)	69.6(19–193)	SM,NB,T,NE
White Sucker *Catostomus commersonii*	5 (10.4)	11 (2.1)	175.0(86–296)	NS,B,T,NE
Alabama Hog Sucker *Hypentelium etowanum*	15 (31.2)	75 (14.3)	120.0(27–335)	NS,B,T,NE
Black Redhorse *Moxostoma duquesnei*	3 (6.2)	8 (1.5)	400.7(90–506)	NS,B,T,NE
Golden Redhorse *Moxostoma erythrurum*	3 (6.2)	6 (1.1)	153.6(40–432)	NS,B,T,NE
Rainbow Trout *Oncorhynchus mykiss*	20 (41.7)	82 (15.6)	115.1(30–405)	NS,NB,IT,NE
Brown Trout *Salmo trutta*	7 (14.6)	31 (5.9)	138.9(31–505)	NS,NB,IT,NE
Brook Trout *Salvelinus fontinalis*	7 (14.6)	17 (3.2)	143.3(52–362)	NS,NB,IT,E
Western Mosquitofish *Gambusia affinis*	1 (2.1)	1 (0.2)	43.0(N/A)	SM,NB,T,NE
Mottled Sculpin *Cottus bairdii*	38 (79.2)	243 (46.3)	62.5(18–121)	SM,B,T, E
Rock Bass *Ambloplites rupestris*	8 (16.7)	28 (5.3)	124.7(26–262)	NS,NB,T,NE
Redbreast Sunfish *Lepomis auritus*	15 (31.2)	39 (7.4)	98.6(34–183)	SM,NB,T,NE
Green Sunfish *Lepomis cyanellus*	5 (10.4)	13 (2.5)	70.4(34–134)	SM,NB,T,NE
Bluegill Sunfish *Lepomis macrochirus*	8 (16.7)	21 (4)	66.9(38–115)	SM,NB,T,NE
Smallmouth Bass *Micropterus dolomieu*	3 (6.2)	8 (1.5)	226.8(190–253)	NS,NB,T,NE
Spotted Bass *Micropterus punctulatus*	3 (6.2)	4 (0.8)	51.2(42–61)	NS,NB,T,NE
Largemouth Bass *Micropterus salmoides*	2 (4.2)	4 (0.8)	53.9(33–78)	NS,NB,T,NE
Greenside Darter *Etheostoma blennioides*	4 (8.3)	9 (1.7)	98.8(53–121)	SM,B,T,E
Greenfin Darter *Etheostoma chlorobranchium*	1 (2.1)	3 (0.6)	72.6(63–78)	SM,B,T,E
Gilt Darter *Percina evides*	3 (6.2)	19 (3.6)	57.8(44–77)	SM,B,T,E

by evaluating the relative fit of the global model with each parameter systematically treated as a fixed or randomly varying effect. The best approximating variance structure was identified as that with the lowest Akiake Information Criteria (AIC$_c$) with small-sample bias adjustment (Hurvich and Tsai 1989), which included both fixed and random effects. Random effects corresponding to species were estimates of the predictable variability of the effect of a predictor (e.g., elevation) among species and site random effects accounted for spatial autocorrelation. The best approximating variance structure was used during the evaluation of the relative plausibility of the candidate models. Similarly, we used the global reach and channel-unit occupancy submodels and evaluated all possible combinations of parameters in the detection submodel. The detection submodel with the lowest AIC$_c$ also was used to evaluate the relative support for the candidate study reach and channel unit occupancy submodels that represented each possible combination of our occupancy hypotheses.

All models were fit using Markov Chain Monte Carlo (MCMC) implemented in WinBUGS version 1.4 (Lunn et al. 2000) with diffuse priors for each parameter (Kéry and Royle 2008), 700,000 iterations and a burn-in of 200,000 iterations. The number of required iterations was estimated using the global model and testing for convergence with the Gelman and Rubin diagnostic test (Gelman and Rubin 1992). Because MCMC methods produce a distribution of deviance, we used the mean deviance from MCMC iterations to calculate AIC_c for inference (Fonnesbeck and Conroy 2004). The relative fit of candidate models were determined by calculating Akaike weights (w), and the strength of evidence was calculated using the ratios of Akaike weights (Burnham and Anderson 2002). Candidate models with Akaike weights within 12% of the best-approximating candidate model's Akaike weight were considered plausible (Royall 1997), included within the confidence set of occupancy models, and used for inferences.

The precision of fixed-effect parameter estimates was assessed by calculating 95% credible intervals that are analogous to 95% confidence intervals (Congdon 2001). Credible intervals that contained zero were considered imprecise and represented a weak or inconclusive relationship. We also estimated fish species assemblage metrics using the best-approximating model and the approach described by Royle and Dorazio (2008). For each study reach and channel unit type within each reach, we estimated the total number of species present and the number of species present that possessed each species characteristic (Table 3). We also calculated the proportion of the total number of species present that possessed each species characteristic at both reach and channel-unit scales.

RESULTS

A total of 525 channel units were sampled in the 48 (pilot and in-depth) study reaches, and 183 (35%) channel units were classified as pools, 200 (38%) as riffles, and 142 (27%) as runs. Half of the study reaches (24) contained all three channel-unit types and 7 reaches consisted of a single habitat type. The latter group was primarily small headwater streams with link magnitudes of <10 or high gradient streams. The study reaches represented a wide range of stream sizes, physical characteristics, and land uses typical of the region (Table 4).

We captured 36 species during the study (Table 3). The most commonly detected species were Mottled Sculpin and Creek Chub, which were collected at more than half of the study reaches. In general, few large-bodied piscivorous fishes (e.g., Smallmouth Bass) were collected. No species were collected at all of the study reaches, and no fish species were collected in five study reaches.

Detection Modeling

The best approximating species-detection model contained the number of backpack electrofishers, channel-unit current

TABLE 4. Mean (SD) and range of environmental conditions in sampled study reaches and channel units within the Little Tennessee River basin during the summer of 2009, spring and summer of 2010, and spring of 2011.

Variable	Mean (SD)	Range
Study reach characteristics		
Elevation (m)	691.8 (88.21)	611–1060
Gradient (%)	4.6 (5.09)	0.5–23.7
Link magnitude	25.1 (28.31)	1–116
Downstream link magnitude	68.4 (174.86)	2–1112
Watershed area (km^2)	7.3 (8.44)	0–36
Riparian buffer intact (%)	46.05 (50.04)	0–100
Urban cover (% watershed)	6.9 (11.26)	0–48
Agricultural cover (% watershed)	6.5 (6.89)	0–31
Forest cover (% watershed)	83.9 (17.94)	30–100
Pool (% study reach area)	37.2 (23.54)	0–100
Riffle (% study reach area)	39.6 (19.39)	0–100
Run (% study reach area)	23.2 (24.04)	0–100
Channel unit characteristics		
Conductivity (μs/cm)	26.5 (10.67)	8–56
Turbidity (NTU)	8.0 (4.93)	1–35
Surface area (m^2)	39.8 (26.898)	1–196
Mean cross sectional area (m^2)	0.94 (0.751)	0.02–4.9
Mean depth (m)	0.24 (0.120)	0.02–0.7
Mean velocity (m/s)	0.32 (0.173)	0.02–1.0
Coarse sediment (%)	33.72 (20.768)	0–90
Fine sediment (%)	38.65 (26.075)	5–95
Woody debris (number/m^2)	0.03 (0.052)	0–0.4

velocity, surface area, and a species-specific random effect (Table 5). The Akaike weights indicated that the model was better by >33 times the next best-approximating detection model that contained only current velocity, surface area, and a species-specific random effect. The probability of detecting a species was positively related to increases in channel-unit surface area and negatively related to increases in current velocity and the use of two backpack electrofishers. The species-specific random effect also indicated that detection varied among fish species and was, on average, greatest for commonly collected species including Mottled Sculpin, Creek Chub, and Blacknose Dace (Figure 2). This best-fitting detection model was used during model fit and evaluation of occupancy.

Occupancy analysis.—The best-approximating occupancy model for predicting study-reach occupancy contained season; stream size and spatial context parameters (i.e., elevation, gradient, link magnitude, and downstream link magnitude); land-cover parameters (i.e., urban cover and riparian buffer); and species–trait interactions (i.e., elevation × warmwater intolerant species and urban land cover × southern Appalachian highland endemic species). The best model also included channel unit occupancy modeled as a function of channel unit type, channel unit type and season interaction, and channel unit type and small benthic species interaction (Table 5). The

TABLE 5. Parameter estimates (SD), upper and lower 95% credible intervals for the best approximating multiscale, multispecies occupancy model for wadeable streams in the Little Tennessee River basin. Random effects are expressed as standard deviations.

Parameter	Fixed effects			Random effects		
	Estimate	Lower	Upper	Estimate	Lower	Upper
Study reach occupancy (ψ)						
Intercept	−3.345 (0.461)	−4.212	−2.481	4.798 (0.603)	3.633	5.879
Link magnitude	2.379 (0.665)	1.201	3.818	2.421 (0.478)	1.670	3.543
D-link	−0.817 (0.436)	−1.718	−0.014	1.344 (0.431)	0.668	2.329
Elevation	−2.314 (1.122)	−4.680	−0.282	4.970 (0.646)	3.641	5.951
Gradient	−5.749 (1.053)	−7.812	−3.704	5.140 (0.581)	3.825	5.960
Riparian buffer	−2.513 (1.046)	−4.620	−0.500	5.528 (0.381)	4.597	5.982
Urban	−0.924 (0.855)	−2.595	0.803	3.085 (0.595)	2.091	4.406
Summer	0.261 (0.161)	−0.044	0.592			
Elevation × warmwater intolerant	0.879 (0.416)	0.035	1.523			
Urban × endemic	−0.914 (0.490)	−1.986	−0.027			
Site[a]				3.612 (0.570)	2.659	4.895
Conditional channel-unit occupancy ($\theta\,\vert\,\psi$)						
Intercept	1.494 (0.161)	1.202	1.851			
Pool	3.134 (0.696)	1.835	4.584	1.803 (0.582)	0.953	3.202
Riffle	−1.624 (0.495)	−2.550	−0.585	1.931 (0.561)	1.103	3.281
Summer × pool	−0.682 (0.415)	−1.491	0.117			
Summer × riffle	−0.008 (0.232)	−0.447	0.459			
Small benthic × pool	−3.079 (0.877)	−4.749	−1.119			
Small benthic × riffle	4.129 (1.037)	2.139	6.197			
Conditional detection probability ($p\,\vert\,\psi\theta$)						
Intercept	−0.011 (0.281)	−0.570	0.532	1.502 (0.234)	1.106	2.022
Velocity	−0.138 (0.053)	−0.243	−0.034			
Surface area	0.121 (0.053)	0.018	0.225			
Two shockers	−0.269 (0.117)	−0.497	−0.039			

[a]Site fixed effect was set at zero.

best-fitting model ($w = 0.588$) was only slightly better supported than the next best-approximating candidate model ($w = 0.355$) that was identical to the best model and also contained a riparian buffer and southern Appalachian highland endemic interaction. The parameter estimate for this interaction, however, was fairly imprecise, and the confidence limits contained zero. These also were the only models in the confidence set. As a result, we based all of our inferences on the best-approximating model.

The best-approximating model indicated that study reach occupancy was generally greatest in larger, low-elevation, lower-gradient streams that were connected to smaller streams at the next downstream confluence (Table 5). However, the relation between study-reach occupancy and these characteristics varied considerably among species as indicated by the relatively large random effects. For example, the link magnitude parameter estimate varied, on average, by 102% (2.421/2.379) among species. Similarly, the downstream link magnitude parameter estimate varied, on average, by 165% (1.344/0.817) among species. Fish species occupancy also was negatively related in urban land cover, and urban land cover had a greater effect on highland endemic species relative to other species. Model estimates indicated that the proportion of all species present at study reaches that consisted of highland endemic species decreased with increased urban land cover (Figure 3). Fish species occupancy was generally negatively related to elevation, but the effect of elevation was smaller on species intolerant of warm water (Table 5). The estimated proportion of species at a reach that were warmwater intolerant increased with increasing elevation, and these species predominated the species pool in study reaches at the highest elevations (Figure 4). Parameter estimates suggested that, on average, fish species were more likely to use pool channel types and less likely to use riffle channel types than run channel types (Table 5). However, small, benthic species tended to use riffle channel types more than the other species. The number of species using each channel unit
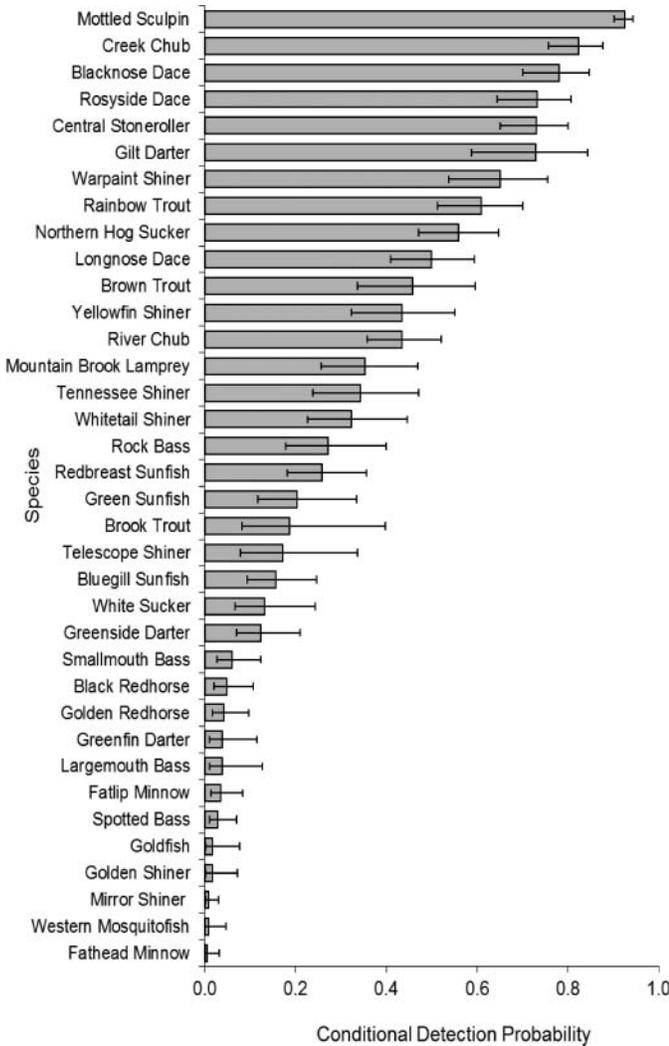
FIGURE 2. Estimated mean conditional detection probabilities $(p \mid \psi\theta)$ per sample and their 95% credible intervals for observed fish species sampled using a single shocker under average channel unit conditions (current velocity = 0.32 m/s, surface area = 39.8 m²). Species are listed in descending order of mean conditional detection probabilities.

increased with increased stream size for all channel unit types, the greatest increases being in pools and runs (Figure 5).

DISCUSSION

We found that stream topology and topography, urban land cover, and channel-unit types were the most important factors affecting fish occupancy within the Little Tennessee River basin. However, the relative importance of these factors varied among species and spatial scale. We surmise that environmental stability, habitat quality, and the thermal regime largely controlled the occupancy and assemblage structure of fish among stream reaches, but the hydrogeomorphological characteristics of channel unit types affected occupancy within
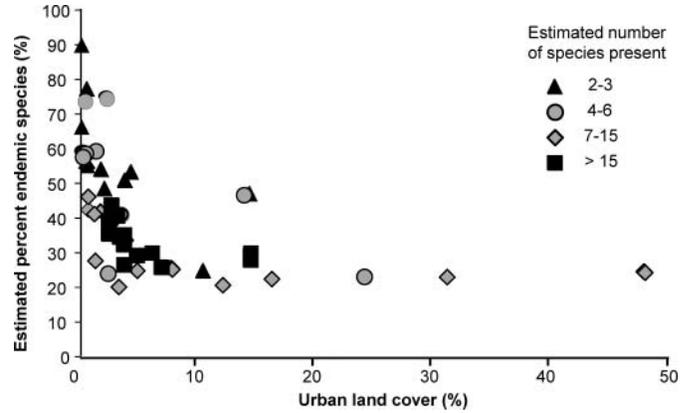

FIGURE 3. Average proportion of all species in a study reach that were endemic to the southern Appalachian highlands versus urban cover in wadeable streams the Little Tennessee River basin. The proportion of species was estimated using the best approximating multispecies, multiscale occupancy model and assuming summer season.

stream reaches. These results suggest that identifying the primary mechanisms controlling a lotic fish assemblage requires an understanding of the local and landscape-scale processes and the recognition that the relative importance of these processes may vary with scale.

Fish assemblage structure in a stream reach is influenced partly by thermal regimes (Jackson et al. 2001; Wehrly et al. 2003; Quist et al. 2005), which often varies with elevation, longitudinal position, and riparian cover within a stream network (Scott et al. 2002; Martin and Petty 2009). The reach-level occupancy of warmwater tolerant fish species in the Little Tennessee River basin was negatively related to elevation, but the effect of elevation was much weaker for warmwater intolerant fishes. Scott et al. (2002) demonstrated that high-elevation stream reaches within the Little Tennessee River basin were generally cooler during the summer, and this was
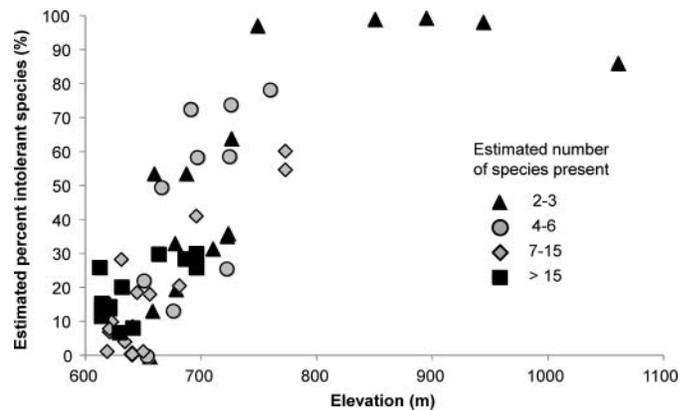

FIGURE 4. Average proportion of all species at a study reach that were warmwater intolerant versus study reach elevation in wadeable streams the Little Tennessee River basin. The proportion of species was estimated using the best approximating multispecies, multiscale occupancy model and assuming summer season.
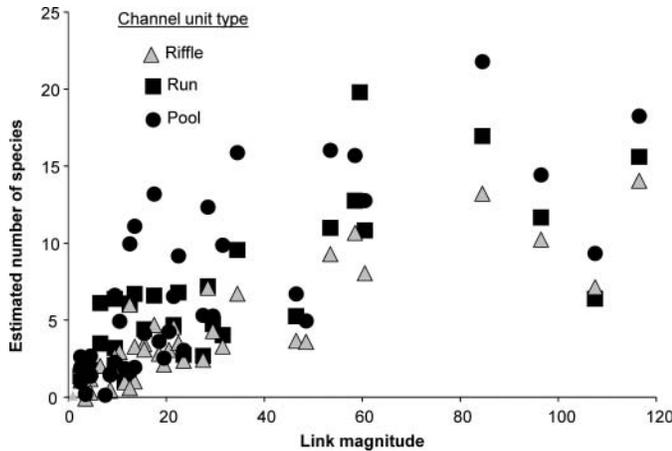
FIGURE 5. Average total number of species present in channel units within study reaches versus link magnitude and channel-unit types among study reach sites in the Little Tennessee River basin. Total number of species was estimated using the best approximating multispecies, multiscale occupancy model and assuming summer season.

consistent with our observations. Previous studies also reported that the distribution of warmwater intolerant fishes (e.g., Brook Trout) is often restricted to cooler reaches at higher elevations (Swift and Messer 1971; Vannote et al. 1980; Rahel and Hubert 1991; Jackson et al. 2001; Wehrly et al. 2003; Martin and Petty 2009). Similarly, we found that fish assemblages at higher-elevation reaches were predominated by warmwater intolerant fishes, but that many of the warmwater intolerant species still occurred at lower-elevation reaches. Warmer streams generally are more productive than cooler streams of similar size, and fishes have greater metabolic rates and growth potential in warmer-water habitats (Vannote et al. 1980; Schlosser 1982; Huryn and Wallace 1987). As a result, fishes that can physiologically tolerate warm water occur in streams at lower elevations to presumably exploit the available resources (Rahel and Hubert 1991; Wehrly et al. 2003). Based on these studies, we hypothesize that fish distribution and assemblage structure in Little Tennessee River basin stream reaches were influenced by the thermal tolerances of fishes.

We observed that fish occupancy was positively related to link magnitude and negatively related to gradient within the Little Tennessee River basin. We also found that the total number of species occupying stream reaches increased with link magnitude, which was consistent with other fish assemblage investigations (Gorman and Karr 1978; Grenouillet et al. 2004). Headwater reaches typically possess relatively shallow and smaller habitats with less structural diversity (e.g., substrate, depth, and current) and greater hydrologic variability than did lower-gradient reaches farther downstream (Whiteside and McNatt 1972; Gorman and Karr 1978; Vannote et al. 1980; Schlosser 1982; Resh et al. 1988; Reice et al. 1990; Osborne and Wiley 1992). We observed that headwater reaches in the Little Tennessee River basin were less

structurally diverse and primarily composed of a single channel-unit type, whereas larger stream reaches were more diverse and typically contained all channel-unit types. Furthermore, we observed that high-gradient reaches were predominated by riffle habitats with faster current velocities. These results provide additional evidence that larger stream reaches with more structural diversity and habitat stability support more diverse fish assemblages.

Fish species occupancy within a stream reach also was related to the size of the nearest downstream reach. Similar patterns have been reported for fishes in variety of stream systems ranging from low-gradient, warmwater streams in the Midwest (Osborne and Wiley 1992) and Southeast Coastal Plain (McCargo and Peterson 2010) to higher-gradient cool-water and warmwater streams in the Appalachian Plateau (Hitt and Angermeier 2008; Martin and Petty 2009). Presumably, the influence of the size of downstream reaches on reach-level occupancy reflects the species pool and dispersal dynamics of fishes inhabiting the downstream reaches. The relation between reach occupancy and downstream link magnitude, however, varied substantially among species. We believe that this high variability probably reflects the variation in dispersal ability or behavior among species.

Deforestation and urbanization affect fish assemblages through several mechanisms, including the introduction of contaminants and nutrients (Wiley et al. 1990; Webster et al. 1992; Paul and Meyer 2001; Pusey and Arthington 2003; Miltner et al. 2004), increased sedimentation (Webster et al. 1992; Harding et al. 1998; Jones et al. 1999; Paul and Meyer 2001; Sutherland et al. 2002), and altered hydrothermal regimes (Webster et al. 1992; Paul and Meyer 2001; Allan 2004; Alberti et al. 2007). These anthropogenic stream modifications can result in the loss and degradation of aquatic habitats, thereby facilitating the loss of endemic fish species and the homogenization of stream fish assemblages (Jones et al. 1999; Rahel 2000; Scott and Helfman 2001; Sutherland et al. 2002; Miltner et al. 2004; Scott 2006). Our modeling results demonstrated that all fish species, particularly those endemic to the southern Appalachian highlands, were less likely to occur in watersheds with greater urbanization. We also found that the proportion of highland endemic species within the species pool decreased as urban land use increased. Therefore, we surmise that urbanization is affecting fish assemblage structure within the Little Tennessee River basin by modifying the processes that create and maintain diverse physical and chemical stream characteristics within a stream reach.

Geomorphic channel-unit types represented unique, predictable combinations of water depth, current velocity, and substrate composition. We found channel unit types influenced the distribution and fish assemblage structure within but not among study reaches. Previous studies suggest that high current velocity habitats, such as riffles, contain relatively high densities of macroinvertebrate prey (Huryn and Wallace 1987) but can be energetically demanding for large or pelagic fishes

that do not possess the hydrodynamic adaptations that reduce the energetic costs of occupying high-current habitats (Facey and Grossman 1990; Facey and Grossman 1992; Etnier and Starnes 2001). Indeed, we found that small benthic fish species had affinities for riffle and run channel unit types, whereas all other fish species had strong affinities for pool channel types. Fish vulnerability to predation can be low for fishes occurring in deeper habitats (e.g., pools) devoid of aquatic predators (Werner et al. 1983; Harvey and Stewart 1991). We observed few large bodied piscivorous fishes during the study, so the risk of aquatic predation was likely small within pool-channel types. Thus, we hypothesize that the differences in fish occupancy and assemblage structure within a stream reach was largely mediated by local hydrogeomorphological characteristics and species traits.

MANAGEMENT IMPLICATIONS

The allocation of fishery management resources is generally based on the availability of resources and the perceived importance of biotic and abiotic processes on fishes of concern. Fish resource managers typically identify the relative importance of environmental variables and processes by using data to relate the differences within a fish assemblage to environmental factors. However, the spatial scale of fish surveys used to collect fish data can vary considerably. Within lotic systems, surveys are often conducted on stream-reach or channel-unit scales. If natural resource managers do not incorporate hierarchy (Frissell et al. 1986; Poff 1997) and interscale interactions of factors within their sample design and subsequent analyses, the prioritization of environmental variables and their processes influencing fish assemblages can be inaccurate, which can have both biological and economic consequences (Crook et al. 2001; Peterson and Dunham 2010). In our study, a multiscaled framework permitted us to account for the incomplete detection of fishes, the hierarchical nature of lotic fish assemblages, the effect of scale, and identify the relative importance of abiotic processes on fish occupancy and assemblage structure at the stream-reach and channel-unit scales.

Our data indicate that the fish assemblage within the Little Tennessee River basin is hierarchically structured and primarily influenced by stream topology and topography, watershed land cover, and channel unit types. We found that landscape scale processes, such as thermal regime, largely constrained fish distribution throughout much of the stream network and that local scale processes, such as habitat use, influenced fish distribution when suitable landscape conditions existed for each species. These results demonstrate the utility of a multiscaled approach and the importance of accounting for interscale interactions prior to monitoring fish assemblages, developing biological management plans, or allocating management resources throughout a stream system (Frissell et al. 1986; Tonn 1990; Fausch et al. 1994; Poff 1997; Scheurer et al. 2003; Quist et al. 2005).

As the need for more accurate, efficient, and economical management approaches continues to rise, studies that are able to robustly assess the relative importance of variables that operate at multiple spatial and temporal scales across larger extents will become essential. Currently, there are over seven species of concern that inhabit the Little Tennessee River basin, e.g., Brook Trout and Rosyside Dace (Warren et al. 2000; Etnier and Starnes 2001; NCWRC 2005). Given that management resources are finite, we suggest that the management of fishes within the Little Tennessee River basin and other similar southern Appalachian watersheds should initially focus on the landscape-scale or watershed-scale processes for treatment or research to identify the optimal spatial extents or conditions to implement effective local-scale treatments (e.g., channel unit restoration) if larger scale treatments are not feasible. The use of our multiscaled framework can provide fish managers with a more holistic approach to the prioritization of environmental processes affecting lotic fish assemblages and, thus, natural resource management. Future studies should consider expanding on both the resolution and extent of the multiscaled approach used here.

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Appendix: the Structure of Occupancy Models

The hierarchical models used to estimate study reach occupancy (ψ), the probability that the species uses a channel unit within an occupied study reach ($\theta \mid \psi$), and the probability of detecting a species given it occupies a channel unit (p) are

$$\text{Logit}(\psi_{ij}) = \alpha_{0j} + \alpha_{0i} + \alpha_{1i}W_1 + \ldots + \alpha_{ri}W_r,$$

$$\text{Logit}(\theta_{ij} \mid \psi_{ij}) = \gamma_0 + \gamma_{1i}X_1 + \gamma_{2i}X_2 + \ldots + \gamma_{ri}X_r,$$

and

$$\text{Logit}(p_{ijh} \mid \psi_{ij}, \theta_{ij}) = \beta_{0i} + \beta_1 Y_1 + \ldots + \beta_r Y_r,$$

where i indexes species, j indexes study reaches, h indexes replicated samples, W_r represents a study reach-specific predictor variable (e.g., terrestrial landscape characteristic), α_{0j} represents a randomly varying intercept that varied among study reaches, α_{0i} represents a randomly varying intercept that varied among species, α_{ri} represents the effect of W_r on reach occupancy that varied among species, X_r represents a channel-unit-specific predictor variable (e.g., physical instream habitat characteristic), γ_0 represents a fixed intercept, γ_{ri} represents the effect of X_r on channel unit occupancy that varied among species, Y_r represents an in-stream habitat predictor variable (e.g., water quality or physical instream habitat characteristic), β_{0i} represents a randomly varying intercept that varied among species, and β_r represents the effect of Y_r on detection. Random effects (i.e., randomly varying intercepts and slopes) were assumed to be normally distributed with a mean of zero and random effect-specific variance (Royle and Dorazio 2008).

APPENDIX REFERENCES

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, London.