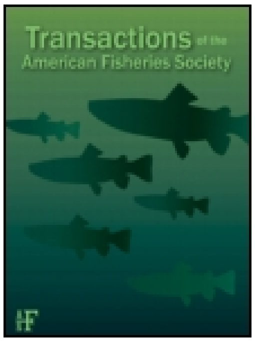

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ARTICLE

Multispecies Occupancy Modeling as a Tool for Evaluating the Status and Distribution of Darters in the Elk River, Tennessee

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Abstract
Sixteen darter species, including the federally endangered Boulder Darter *Etheostoma wapiti*, are known to occur in the Elk River, a large, flow-regulated tributary of the Tennessee River, Tennessee–Alabama. Since the construction of Tims Ford Dam (TFD) in 1970, habitat modification caused by cold, hypolimnetic water releases and peak-demand hydropower generation has contributed to population declines and range reductions for numerous aquatic species in the main-stem Elk River. We developed Bayesian hierarchical multispecies occupancy models to determine the influence of site- and species-level characteristics on darter occurrence by using presence–absence data for 15 species collected from 39 study sites. Modeling results indicated that large-river obligate species, such as the Boulder Darter, were 6.92 times more likely to occur for every 37-km increase in the distance downstream from TFD. In contrast, small-stream species were 2.35 times less likely and cosmopolitan species were 1.88 times less likely to occur for every 37-km increase in distance downstream from TFD. The probability of occurrence for darter species also had a strong negative relationship with the absence of cobble and boulder substrates and the presence of high silt levels, particularly for species that require boulder substrates during spawning. Although total darter species richness was similar across all 39 sample sites, the composition of darter assemblages varied substantially among locations, presumably due in part to species-specific habitat affinities and hydrothermal conditions. The use of multispecies occupancy models allowed us to account for the incomplete detection of species while estimating the influence of physical habitat characteristics and species traits on darter occurrences, including rarely observed species that would have been difficult to model individually.

The southeastern USA harbors one of North America's most diverse fish communities; however, this region also has the second-highest rate of fish imperilment in the United States (Warren et al. 1997). Declines in the region's fish populations have been attributed to a variety of factors, including habitat alteration and fragmentation caused by instream flow alterations and changes in land use practices. Almost all moderate to large river systems in the southeastern United States are impounded, and dam operations have fundamentally affected stream dynamics by altering temperature and flow regimes and increasing downstream bank erosion (Poff et al. 1997; Bednarek and Hart 2005). Altered flow and temperature regimes have been linked with range restriction and fragmentation of warmwater fish species inhabiting tailwaters (Olden

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and Naiman 2010). Benthic warmwater fishes are among the first to be affected by degraded water quality and have the highest proportion of imperiled or extirpated species (Warren et al. 2000).

The Tennessee River basin is one of the most heavily altered river basins in the USA and contains 49 impoundments that are managed by the Tennessee Valley Authority (TVA; C. E. Bohac and M. J. McCall, TVA River Operations, unpublished report). The Elk River, a large tributary of the Tennessee River, is impounded at two locations and supports several imperiled species, including the federally endangered Boulder Darter *Etheostoma wapiti*. The Boulder Darter is restricted to the Elk River basin, where it occupies scattered locations along approximately 100 km of the main channel and the lower reaches of three major tributaries. In 2006, the U.S. Fish and Wildlife Service (USFWS) and TVA reached an agreement to modify operations at Tims Ford Dam (TFD) to improve streamflow and temperature conditions for existing populations of warmwater fish and mussel species. The operational changes also were anticipated to open 50 km of previously unsuitable habitat to possible recolonization by Boulder Darters. Since these changes were implemented in 2007, there has been a substantial amount of monitoring and management activity targeting Boulder Darters. What has been lacking, however, is a comprehensive approach to improve understanding of the current distribution of warmwater fishes, including Boulder Darters, in the main-stem Elk River, as well as quantifying relationships between species occurrence and physical habitat conditions.

Effective monitoring programs ideally provide accurate assessments of status and dynamics for species of management interest. Population-level metrics (e.g., abundance) are commonly used to monitor spatial and temporal changes in fish communities in response to human disturbance, management activities, or environmental variability. However, abundance estimates are often highly variable and imprecise, partly because capture efficiency varies spatially and temporally (Gwinn et al. 2016). Presence–absence, although a coarser measure of population status, can be an efficient and effective alternative for assessing the status and distribution of rare species and for evaluating the influence of biotic and abiotic factors on species occurrence (MacKenzie et al. 2002). A hallmark of occupancy modeling approaches is that they can be used to account for biases associated with the incomplete detection of species. Failure to account for detection biases (i.e., false absences) can lead to bias in probability-of-occurrence estimates (MacKenzie et al. 2002) and can obscure relationships between the probability of occurrence and covariates of interest (Tyre et al. 2003). Where entire communities or assemblages are of management interest, multispecies occupancy modeling approaches (Zipkin et al. 2009, 2010) are especially useful for assessing status (i.e., species richness) and composition (e.g., species richness of particular functional groups). Multispecies approaches also can improve the precision of species-specific estimates of occurrence and covariate effects (Kéry and Royle 2008), which may be of interest to managers working with rare species.

The goal of this research was to (1) assess the current status and distribution of darter species in the Elk River, Tennessee, with particular emphasis on Boulder Darters; and (2) identify the predominant factors influencing darter occurrence and detection. Our specific objectives were to (1) develop a multispecies occupancy model to estimate detection and occupancy probabilities for 15 darter species that are native to the Elk River basin, Tennessee; (2) evaluate the influence of site- and species-level factors on detection and occupancy probabilities; and (3) use the best-approximating multispecies occupancy model to estimate site-specific darter species richness and assemblage composition.

METHODS

Study area.—The Elk River is a large tributary of the Tennessee River that drains an area of 5,824 km^2 and flows 320 km through south-central Tennessee into north-central Alabama (Jandebeur 1972; Shepard et al. 2005). From its headwaters in Grundy County, Tennessee, the Elk River flows through the Central Basin of the Tennessee Valley district into the Highland Rim physiographic region (Isom et al. 1973). Streams in the Highland Rim, which are characterized by moderate gradients with substrates of gravel, sand, and bedrock, contain one of the most diverse fish faunas of any comparably sized area in North America (Etnier and Starnes 1993). Land use in the Elk River basin primarily consists of cultivated crops and pastureland. The Elk River is impounded three times: first by Woods Dam (river kilometer [rkm] 250), next by TFD (rkm 214), and finally by Wheeler Lake, a main-stem Tennessee River reservoir that inundates the lowermost 45 km of the main-stem Elk River (Shepard et al. 2005). Tims Ford Dam, located near Tullahoma, Tennessee, was constructed in 1970 by the TVA for purposes of hydropower generation and flood control for the city of Fayetteville, Tennessee (TVA 2008). The facility has one large operational generating unit (45 MW), a smaller but inoperable secondary turbine, a spillway with three bays, and a sluiceway with vertical slots (TVA 2008). During full power generation, discharge from the turbine averages approximately 100 m^3/s (TVA 2008) of clear, hypolimnetic water that creates coldwater habitat extending for approximately 20 km downstream of TFD.

Prior to changes in TFD operations (implemented in 2007), year-round hydropeaking caused depths downstream to vary by up to 1.5 m during full power generation (Shepard et al. 2005), and discharged water was hypoxic during periods of stratification in the reservoir. During full generation, hydropeaking lowered the water temperatures throughout the main-stem Elk River to its confluence with the Tennessee River—a distance of approximately 200 km (TVA 2008). Since the mid-1990s, the TVA has pumped liquid O_2 through hoses anchored in the forebay to improve downstream water quality (TVA 2008). Due to the hypolimnetic water releases, the tailwater below TFD harbors a popular, hatchery-supported fishery for Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta*, managed by the Tennessee Wildlife Resources Agency. Although temperature conditions in the upper tailwater are suitable for trout (Bettoli and Besler 1996), they are generally unsuitable for native warmwater fish and mussel species (USFWS 2011).

Site selection.—We selected sites in the Elk River main stem between TFD and Wheeler Reservoir and in three large tributaries (Beans, Richland, and Mulberry creeks; Figure 1). Thirty-nine sites were selected based on the presence of suitable darter habitat (i.e., riffle–run–pool complexes). Each site contained varying amounts of the following mesohabitat types: edgewaters, riffles, runs, and eddies or wadeable pools, following Bain and Stevenson (1999). All sites were generally representative of the physical habitat that is typical of wadeable riffle–run–pool complexes in the main-stem Elk River.

Fish collection.—From spring 2011 through spring 2013, we surveyed the 39 study sites via backpack electrofishing (pulsed DC) and seining protocols that were developed by the TVA. All sampling was conducted during daylight hours between April and November. Multiple samples (hereafter, "quadrats") were collected at each site (mean = 25.5 quadrats; range = 15–55 quadrats), with study sites varying in length (80–150 m) depending upon habitat heterogeneity and wadeability. Fishes were collected by using a Smith–Root Model LR-24 backpack electrofishing unit and a seine (3 × 2 m; 0.5-cm delta knotless mesh). Sampling began at the lower end of each site, and downstream block-netted quadrats were placed in a zigzag pattern moving upstream through representative mesohabitats. Each quadrat was approximately 9 m^2 and was bounded on the downstream side by the seine, which acted as the block net. Backpack electrofishing commenced at the upstream side of the quadrat and proceeded downstream throughout the entire 9-m^2

FIGURE 1. Surveyed sites in the Elk River, Tennessee, and its tributaries, where darters were sampled from 2011 to 2013.

area, and all stunned fish were collected in the seine. In addition to electrofishing, kick sets (i.e., disturbing the substrate with kicks upstream of a seine) and seine hauls were conducted in eddies and stream margins. After fish sampling, the lower-left corner (looking upstream) of each quadrat sample was marked with a metal washer equipped with orange flagging tape to facilitate relocation during collection of habitat data (see below). All collected fish were identified to species and enumerated. All Boulder Darters were measured for TL (mm) and photographed; they were allowed to fully recover in a floating minnow bucket and then were released.

Quadrat-level physical habitat measurements.—After fish collection, individual 9- × 9-m quadrats were relocated by using the flagged washers and were visually divided into four quadrants. The following habitat characteristics were measured in each quadrant: depth, velocity at the stream bottom, velocity at 0.60 × stream depth, dominant and subdominant substrates, degree of siltation, amount of vegetation, presence of woody structure, habitat type, and fish sampling method. Depth (m) and velocity (m/s) were measured by using a Marsh-McBirney Flo-Mate Model 201 portable velocity meter that was equipped with a top-setting wading rod. Dominant and subdominant substrate types were visually estimated by using the modified Wentworth scale (Grossman and Ratajczak 1998). Siltation was visually estimated as silt free, normal, moderate, or high based on Ohio Environmental Protection Agency metrics (OHEPA 2006). Vegetation density was visually estimated as high, moderate, low, or none based upon the proportion of the quadrat that was covered by vegetation (OHEPA 2006). The presence of woody structure—defined as a root wad or submerged log that was at least 10 cm in diameter and that substantially affected flow patterns in the quadrat—was recorded as a binary variable (present = 1; absent = 0).

Site-level physical habitat measurements.—We assessed the average or dominant conditions for several quadrat-level physical habitat variables to quantify their average site-level conditions. The presence of bedrock, boulder, or cobble was coded as a binary variable; if that substrate type was dominant in at least one quadrat at a site, then the variable was coded as 1; otherwise, it was coded as 0. If sites had moderate or high amounts of vegetation in the majority of quadrat samples, they were coded as 1; otherwise, they were coded as 0. Lastly, we also summarized three spatial covariates for each site: distance (km) downstream from TFD and whether the site was in a tributary (coded as 1; 0 otherwise) *or* within 1 km of a major tributary (coded as 1; 0 otherwise; Table 1). We assessed the spatial covariates by using ArcGIS version 10.0 (Environmental Systems Research Institute, Redlands, California).

Species traits.—A suite of life history traits that we suspected might explain occupancy patterns of Elk River darters was assigned to each of the 15 darter species based on published species accounts (Page 1983; Etnier and Starnes 1993; Boschung and Mayden 2004). Each trait was categorized into one of two themes: reproductive strategy and stream size preference (Table 2). The reproductive strategy trait included whether or not a species used boulder substrates during spawning (i.e., for egg deposition or as a velocity shelter). A binary variable representing the stream size preference (i.e., the stream size that generally supports the highest density) of each darter species was assigned: small-stream species, large-river obligate species, or cosmopolitan species. Small-stream species were defined as those that tend to be more common in small streams (i.e., first- to third-order streams) but occasionally inhabit moderate to large rivers (i.e., greater than third-order streams). Darters that only occur in moderate to large rivers were considered large-river obligate species. Lastly, species that could inhabit a wide variety of stream sizes and in high abundance were placed into the cosmopolitan group.

Multispecies occupancy modeling.—We developed single-season, Bayesian hierarchical multispecies occupancy models (MacKenzie et al. 2002; Royle and Dorazio 2008) to estimate the relationship between site- and species-level characteristics and the probability of occupancy and detection for 15 darter species native to the Elk River. We note that although the 39 sites were surveyed in 2011–2013, each site was surveyed only once during that time period (i.e., during only one of those years); hence, we deemed it reasonable to combine collections across all locations and over the entire time period and to model the system as a single-

TABLE 1. Scale of measurement, number of observations (*N*), mean, SD, range, and range of continuous and categorical predictor variables used in the hierarchical multispecies occupancy model (TFD = Tims Ford Dam).

Variable	Scale	*N*	Mean	SD	Range
Bottom velocity (m/s)	Quadrat	1,037	0.19	0.17	0.01–1.52
Depth (m)	Quadrat	1,037	1.21	0.68	0.03–1.13
Distance downstream from TFD (km)	Site	39	71.10	37.80	21.00–159.00
Number of sites with high silt	Site	5			
Number of sites with no cobble present	Site	9			
Number of sites with boulders present	Site	24			
Number of tributary samples	Site	3			
Number of sites within 1 km of major tributary	Site	4			

TABLE 2. Traits of the 15 darter species included in candidate occupancy and detection models relating stream size preference and reproductive strategy to the probability of occurrence (binary coding for each trait: 0 = absent; 1 = present).

Species	Small-stream species	Cosmopolitan species	Large-river species	Use of boulders
Greenside Darter *Etheostoma blennioides*	0	1	0	1
Blenny Darter *E. blennius*	1	0	0	0
Rainbow Darter *E. caeruleum*	1	0	0	0
Bluebreast Darter *E. camurum*	0	0	1	1
Ashy Darter *E. cinereum*	0	0	1	0
Blackside Snubnose Darter *E. duryi*	0	1	0	1
Fantail Darter *E. flabellare*	1	0	0	1
Blueside Darter *E. jessiae*	0	1	0	0
Blackfin Darter *E. nigripinne*	1	0	0	1
Redline Darter *E. rufilineatum*	0	1	0	1
Snubnose Darter *E. simoterum*	0	1	0	1
Boulder Darter *E. wapiti*	0	0	1	1
Banded Darter *E. zonale*	0	1	0	0
Logperch *Percina caprodes*	0	1	0	0
Gilt Darter *P. evides*	0	0	1	0

season occupancy model. Occupancy models produce estimates of two probability-based parameters: detection (p), which is defined as the probability of detecting a species given that it is present at a site and available for capture; and occurrence (Ψ), which is the probability that a species is present at a site during sampling (MacKenzie et al. 2002). We used a zero-inflated binomial likelihood to model the partially observed state process (i.e., true occupancy) as a Bernoulli random variable denoted by $z_{ij} \sim$ Bernoulli(Ψ_{ij}), where Ψ_{ij} represents the probability that species j occurred at site i ($z_{ij} = 1$). Similarly, we modeled the observation process (i.e., detection of a species during sampling) as a Bernoulli random variable denoted by $y_{ijk} \sim$ Bernoulli($p_{ijk} \times z_{ij}$), where y_{ijk} represents the detection ($y_{ijk} = 1$) or nondetection ($y_{ijk} = 0$) of species j during quadrat sample k at site i; and p_{ijk} is the probability of detecting species j in quadrat k at site i given that species j was present at site i ($z_{ij} = 1$; i.e., if $z_{ij} = 0$, then $p_{ijk} = 0$).

Conventional occupancy studies are usually conducted by repeatedly sampling the same area. Given the logistical constraints associated with revisiting most of our study sites, however, we used a space-for-time approach to generate the repeat sample data that were required for estimation of species detection probabilities. Here, each quadrat sample was considered a separate visit, and detection was defined as the probability of detecting a species in a quadrat given that the species was present at a site. As such, species detection probabilities in our study likely represented the product of two conditional probabilities: (1) the probability that a species was present in a quadrat given that it was present at the site; and (2) the probability of detecting a species in a quadrat given that it was available for detection (Cam et al. 2002; Kendall and White 2009). Therefore, species detection probabilities in our study may have varied among repeat surveys (i.e., a new set of quadrat samples at the same site) due to differences in these two conditional probabilities. We made every attempt to conduct quadrat surveys in *all* available habitats at each study site, and we assumed that doing so resulted in a cumulative detection probability (i.e., detection probabilities combined across all quadrat samples) that represented a good measure of our ability to detect each of the 15 darter species at each site by using our survey methods. Unfortunately, we were unable to adequately assess the extent to which cumulative species detection probability varied among repeat surveys because only 3 of the 39 sites were revisited with an additional set of quadrats. However, other studies have used a similar approach to estimate species detection probabilities for stream-dwelling fishes, including darters (Albanese et al. 2007; Hagler et al. 2011; Anderson et al. 2012). Lastly, although there is some evidence that the use of a space-for-time approach to estimate species detection probability results in minimal or no bias of occupancy-related parameters (Kéry and Royle 2016), this aspect of occupancy and detection modeling is an area of research that requires further treatment.

We suspected that the probability of detection and occupancy varied among species as a function of unknown, unmeasured species-level covariates (i.e., species-level dependence). For example, detection may have varied among species because of differences in abundance or behavior. Similarly, we suspected that the darters' probability of detection and occupancy could vary among sites as a function of unknown, site-level covariates (i.e., spatial dependence). Hence, we used the global model (all parameters) to assess the relative support for seven different error structures representing different combinations of random effects: (1) no random effects, (2) species-level random effects associated with the occupancy and detection intercepts, (3) a species-level random effect associated with the occupancy intercept only, (4) a species-level random effect associated with the detection intercept only, (5) site-level random effects associated with the detection and occupancy intercepts, (6) a site-level random effect associated with the occupancy intercept only, and (7) a site-level random effect associated with the detection intercept only. All random components were assumed to be normally distributed with a grand mean intercept and random-effect-specific variance.

Our primary objective was to determine the relative influence of site- and species-level characteristics on darter species occupancy and detection in the Elk River. Covariates that could affect occupancy and detection were selected based on the literature and represented a series of a priori hypotheses (Table 3). Detection models were constructed to estimate species-specific detection probabilities as a function of multiple habitat-level covariates (i.e., sampling method, column velocity, depth, substrate type, and amount of vegetation) that varied among quadrats. Similarly, the probability of occurrence for species j at site i was modeled as a function of (1) site-level covariates (i.e., distance from TFD, amount of silt, substrate type, and whether the site was in a tributary or within 1 km of a major tributary) and (2) species-level covariates (i.e., whether individual species were large-river obligates, small-stream species, or cosmopolitan species; and whether boulders were used during spawning). A binary variable for silt was created: if a site had moderate to high levels of silt, it was assigned a 1; otherwise, it was assigned a 0. Binary variables were used to designate whether two types of substrate (i.e., cobble and boulder) were dominant in at least one quadrat at a site (coded as 1 if present; otherwise coded as 0). A binary variable was used to classify sites that were in tributaries (coded as 1) or the main-stem Elk River (coded as 0).

Model fitting and selection.—There is currently no consensus regarding the appropriate methods for conducting model selection (e.g., use of model selection criteria such as Akaike's information criterion or the deviance information criterion) with Bayesian hierarchical models (Hooten and Hobbs 2015). As such, we followed methods described by King et al. (2016) to identify the best-approximating multispecies occupancy model. We first constructed a global model that contained all detection and occupancy predictor variables. We then fitted the global model by using each of the seven different error structures described above, and we assessed each model's goodness of fit by calculating Bayesian discrepancy statistics, which range from 0 to 1; Bayesian discrepancy statistics close to 0.5 indicate that a model adequately fits the data (Zipkin et al. 2009). We considered the model with the simplest error structure (i.e., the fewest random effects) and an acceptable Bayesian discrepancy statistic (i.e., close

TABLE 3. A priori hypotheses associated with site- and species-level predictor variables used in multispecies occupancy models (TFD = Tims Ford Dam).

Variable	Interpretation or hypothesis
Distance downstream from TFD (km)	Sites farther away from TFD are larger, have higher temperatures, and have the potential for more habitat diversity and more primary productivity.
High silt	Silt may clog interstitial spaces, disrupt fish behavior, and impair the ability of fish to rely on visual cues for reproduction and feeding.
Boulder present; cobble absent	Many darter species use coarse substrates (i.e., boulder or cobble) for the completion of life history processes (e.g., reproduction or feeding).
Tributary sample; within 1 km of a major tributary	Darter assemblages likely differ in tributaries based on species-specific traits. Areas within 1 km of a tributary could be influenced by nutrient or sediment loading.
Small-stream specialist; cosmopolitan species; large-river obligate species	Small-stream species are more likely to be in tributary samples and closer to TFD, where operations create conditions similar to those in headwater streams. Cosmopolitan species inhabit a variety of habitats and are not limited by location within the system. Large-river obligates are likely to be more common farther away from TFD.
Use of boulders during spawning	Many darters require boulder substrates to fulfill life history processes.
Seine haul; kick-set	Detection of a species is likely affected by the sampling method (i.e., electrofishing, seine hauls, and kick-sets may target certain species).
Bottom velocity; depth	Certain darter species have habitat preferences that can be described by stream bottom velocity and depth (e.g., riffle, run, and eddy).
Cobble; slab rock; and vegetation	The type of substrate and amount of vegetation could affect the ability to detect species (e.g., fish that are captured in areas dominated by slab rock are less likely to get stuck behind substrates).

to 0.5) to be the best-approximating model. In this way, we attempted to balance model fit with model complexity. We then based all inferences on parameter estimates from the best-approximating model, and we considered occupancy and detection covariates to be important if their 90% credible interval (CI) did not include zero. To avoid multicollinearity, covariates with Pearson's product-moment correlation coefficients greater than |0.50| were not used in the same detection or occupancy models. To facilitate model fitting, we standardized all continuous covariates with a mean of 0 and an SD of 1. We used Markov chain–Monte Carlo (MCMC) simulations implemented in OpenBugs version 3.2.2 to fit the candidate multispecies occupancy models (Lunn et al. 2009). All models were fitted by using 1,000,000 iterations with a burn-in of 250,000 iterations (i.e., the first 250,000 iterations were discarded). To evaluate MCMC convergence, we used the Gelman–Rubin diagnostic, which calculates the ratio of variance within and between chains across all iterations (Gelman et al. 2004).

Species assemblage assessment.—An additional objective was to estimate site-level species richness and evaluate the composition of darter assemblages at each of the 39 sites. We used the best-approximating multispecies occupancy model to determine species richness by summing the known (i.e., observed) and predicted (i.e., latent) occupancy states (z_{ij} values) across species for each study site. Although 16 darter species are known to occur in the Elk River basin, we failed to collect one of the species, the Dusky Darter *Percina sciera*, during this study. Hence, our study focused on estimating darter species richness under a known maximum species richness of 15 species; we acknowledge, however, that some locations could have supported Dusky Darter populations. Our known maximum species richness of 15 darter species precluded the use of data augmentation techniques that are useful for estimating community-level parameters, such as species richness, when maximum species richness is unknown (Royle and Dorazio 2008). In addition to total species richness, we also estimated species richness for the three designated darter assemblage types (small-stream species, large-river obligate species, and cosmopolitan species), which allowed for an assessment of spatial (among-site) differences in darter assemblage composition.

RESULTS

Thirty-nine sites were sampled from 2011 to 2013 (Figure 1). Among all sites and years, 1,037 quadrats were sampled (mean = 25 quadrats/site; range = 15–55 quadrats/site). Approximately 12,000 fish were collected, representing 12 families, 27 genera, and 56 species, including 15 darter species. The most commonly collected darter species were the Snubnose Darter (all 39 sites), Redline Darter (38 sites), Greenside Darter (37 sites), and Banded Darter (33 sites). The least commonly collected species were the Ashy Darter (1 site), Bluebreast Darter (2 sites), Gilt Darter (9 sites), and Boulder Darter (10 sites).

Multispecies Occupancy Modeling

The assessment of alternative error structures indicated support for species-level dependence in the occupancy and detection models, but we found little evidence for spatial dependence; thus, only species-level random effects associated with intercepts were included in the candidate occupancy and detection models. A Bayesian discrepancy statistic of 0.61 indicated that the model provided an adequate description of the data. Visual assessment of MCMC convergence using the Gelman–Rubin diagnostic provided no evidence for a lack of MCMC convergence.

The global species detection model included nine covariates: seine haul, kick-set, column velocity, presence of bedrock, presence of boulders, presence of cobble, high vegetation coverage, column velocity, and depth (Table 4). Eight of the nine covariates had 90% CIs that did not include zero. Parameter estimates indicated that darter species detection was negatively related to stream depth and the use of seining and kick-set sampling (relative to backpack electrofishing) and was positively related to column velocity; the presence of bedrock, boulder, and cobble; and high vegetation coverage. The estimate of the species-level random effect indicated substantial among-species variability in detection probability (Table 4; Figure 2).

The global occupancy model included 12 predictor variables: distance (km) downstream from TFD (hereafter, "distance from TFD"), absence of cobble, high silt, large-river obligate species, and three interactions (large-river obligate species × distance from TFD; small-stream species × distance from TFD; and boulder use × presence of boulder; Table 4). Seven of the 12 variables had 90% CIs that did not overlap zero. Parameter estimates indicated substantial differences in the probability of occurrence depending upon species-specific stream size preferences. Odds ratios indicated that large-river obligate species were 20.80 times and small-stream species were 2.36 times less likely to be present than cosmopolitan species (Table 4). Parameter estimates for two interaction terms—large-river obligate species × distance from TFD and small-stream species × distance from TFD—indicated that the presence of large-river obligates had a strong positive relationship with distance from TFD, whereas the presence of small-stream species was negatively related to distance from TFD. Odds ratios indicated that large-river obligate species were 6.92 times more likely to occur for every 37-km (1 SD) increase in distance from TFD. In contrast, small-stream species were 2.13 times less likely to occur for every 37-km increase in distance from TFD (Table 4). Odds ratios also indicated that cosmopolitan darter species were, on average, 1.88 times less likely to be present for every 37-km increase in distance from TFD. Darter species presence was negatively related to high silt levels and the absence of cobble substrates (Figure 3). Lastly, darter species that required boulder substrates for reproduction were 2.80 times more likely to occur at sites where boulders were the dominant substrate in at least one quadrat.

TABLE 4. Parameter estimates, SDs, upper and lower 90% credible limits (UCL and LCL), and odds ratios (OR) for the best-approximating multispecies occupancy (Ψ) and detection (p) models.

Parameter	Mean	SD	LCL	UCL	OR
Occupancy (Ψ)					
Fixed effects					
Intercept	1.68	0.74	0.38	2.82	
Distance (km) downstream from TFD	–0.63	0.22	–0.99	–0.28	0.53
Small-stream specialist	–0.86	0.93	–2.28	0.79	0.42
Large-river obligate species	–3.04	0.96	–4.49	–1.33	0.05
Small-stream species × distance downstream from TFD	–0.76	0.42	–1.48	–0.12	0.47
Large-river obligate species × distance downstream from TFD	1.93	0.47	1.27	2.70	6.92
Cobble absent	–0.74	0.41	–1.43	–0.07	0.48
High silt	–0.82	0.46	–1.57	–0.05	0.44
Boulder present	–0.49	0.45	–1.23	0.25	0.61
Boulder-dependent species	0.38	0.77	–0.82	1.73	1.47
Boulder present × boulder-dependent species	1.03	0.58	0.08	1.99	2.80
Tributary site	–0.60	0.59	–1.55	0.38	0.55
Main-stem site within 1 km of tributary	–0.14	0.53	–0.99	0.73	0.87
Random effect					
Intercept (species)	1.68	0.74	0.38	2.82	
Detection (p)					
Fixed effects					
Intercept	–2.26	0.38	–2.88	–1.63	
Seine haul	–1.56	0.18	–1.86	–1.27	0.21
Kick-set (no electrofishing)	–0.98	0.19	–1.29	–0.68	0.38
Bedrock substrate	0.44	0.15	0.19	0.69	1.56
Boulder substrate	0.24	0.10	0.08	0.41	1.28
Cobble substrate	0.36	0.13	0.14	0.58	1.44
Woody debris present	–0.02	0.16	–0.28	0.23	0.98
High vegetation	0.17	0.10	0.00	0.34	1.18
Column velocity	0.24	0.04	0.18	0.30	1.27
Depth	–0.38	0.04	–0.44	–0.32	0.68
Random effect					
Intercept (species)	1.44	0.33	1.00	2.05	

Total darter species richness was relatively constant across the 39 sample sites, averaging 9.10 and ranging from 5.70 to 12.30. Assemblage richness of cosmopolitan species generally declined with distance from TFD, although the relationship was weak (Figure 4). In contrast, assemblage richness of large-river obligates increased strongly with distance from TFD, whereas assemblage richness of small-stream species declined strongly with distance from TFD (Figure 4).

DISCUSSION

Similar to other rivers in the southeastern United States, the Elk River hosts exceptional biological diversity, with environmental conditions (temperature, flow, and physical habitat) that are strongly influenced by the operation of an upstream dam. Although several decades of flow regulation have influenced aquatic species in the river, ongoing management and conservation activities by state and federal agencies should continue to improve conditions for warmwater species in the Elk River. We found that the present-day distribution of darters in the Elk River was strongly influenced by biotic and abiotic factors, including substrate conditions, distance from TFD, and species-specific life history characteristics. We believe that our approach can aid managers and biologists who are charged with conserving aquatic resources in the Elk River and other flow-regulated systems by (1) providing a standardized monitoring approach that also accounts for incomplete detection of species during sampling; (2) establishing baseline patterns of species distribution and improving the understanding of biotic and abiotic factors' relative influences on darter occurrence; and (3) providing a useful monitoring framework for estimating species responses (i.e., occupancy dynamics) to changing environmental conditions that follow operational changes at hydropower facilities.

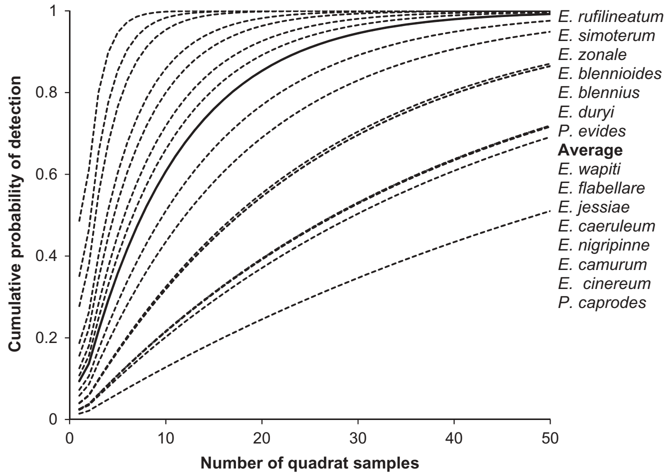

FIGURE 2. Species-specific detection probabilities for 15 darter species that were collected in the Elk River system, Tennessee, during 2011–2013. The vertical order of probability curves corresponds to the order of species listed to the right. Common names are defined in Table 2.

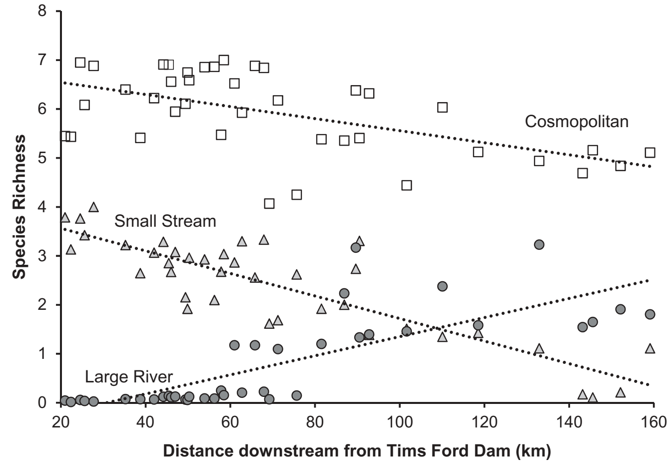

FIGURE 4. Estimated mean species richness for three darter assemblages (small-stream species, cosmopolitan species, and large-river obligate species) at each of the 39 sites sampled in the Elk River during 2011–2013. Dashed lines represent trendlines for darter assemblage richness in relation to distance downstream from Tims Ford Dam.

Species-specific habitat affinities appear to strongly influence the distribution of darters in the Elk River. Although darter species share morphological characteristics, many species exhibit specific habitat requirements and are likely to respond differently to changes in environmental conditions. Distance from TFD served as a proxy for other environmental variables with which it is often highly correlated (especially in regulated river systems), including stream size, water temperature, primary production, and flow stability. As such, it is difficult to tease apart the independent roles of these variables in a system like the Elk River. It is widely understood, however, that stream size strongly influences the distribution of stream fishes, with larger-order streams generally supporting greater species richness (Poff et al. 1997; Taylor et al. 2006). This is of particular interest in regulated rivers, where dam operations fundamentally shape river dynamics and change instream characteristics. Fish species that are adapted for life in headwater streams may tolerate sites closer to dams because those reaches mimic the conditions in headwater streams, where shallow-water habitats are often eliminated during periods of high flows (Bain et al. 1988). Conversely, large-river obligate species require more environmental stability and typically reside farther away from the dam, where the effects of flood pulsing and temperature changes can be attenuated across the downstream gradient. We hypothesize that the patterns of darter stream-size assemblage groups observed in the Elk River partially reflect the downstream hydrothermal gradient imposed by the operation of TFD.

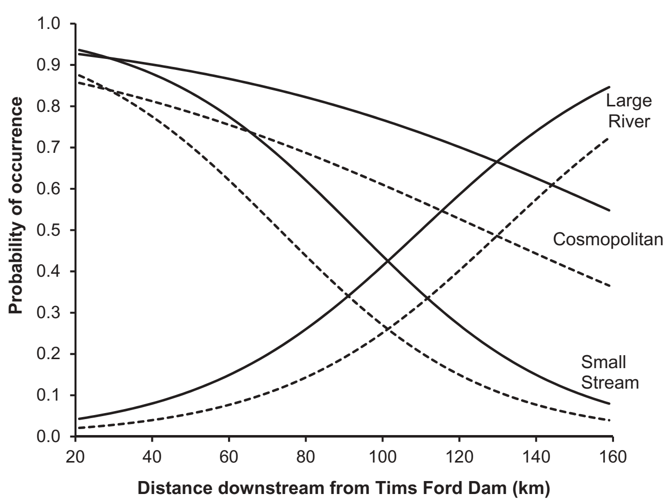

FIGURE 3. Predicted average probability of occurrence with respect to distance downstream of Tims Ford Dam for three Elk River darter assemblages (small-stream species, cosmopolitan species, and large-river obligate species) at sites with (solid line) and without (dashed line) cobble as the dominant substrate.

Darters were less likely to occur at sites where cobble substrates were absent, and darter species requiring boulders for reproduction were less likely to occur at sites that lacked boulders as the dominant substrate. Many darter species use coarse substrates for reproduction and foraging and as refuge during high flows (Hlohowskyj and Wissing 1986; Burkhead and Williams 1992; Harding et al. 1998; Tiemann 2008). For crevice-spawning species such as the Boulder Darter, the interstitial spaces created by coarse substrate are required for egg deposition (Burkhead and Williams 1992). Similarly, Tiemann (2008) found that the abundance of the Bluebreast Darter, a gravel-spawning species, was positively correlated with the amount of cobble and boulder substrates and that they were seldom collected in habitats lacking those substrates. Coarse substrates are essential foraging habitat for most benthic insectivores, as benthic invertebrates are generally associated with larger substrates (Quinn and Hickey 1990). Additionally, crevices between large substrates provide important refuge habitat for benthic fish species during high flows. For instance, Harding et al. (1998) found that Rainbow Darters used large substrates as velocity shelters during all seasons. The types of substrate used by darters denote their habitat preferences, and knowledge of such preferences can guide the assessment and management of critical habitats. However, conservation efforts could benefit from future studies that assess the role of competition and territoriality on microhabitat selection or resource partitioning among darter species. Hlohowskyj and Wissing (1986) found that Greenside Darters and Fantail Darters preferred large substrates; however, in the presence of Greenside Darters and Rainbow Darters, the Fantail Darters selected smaller substrates. In addition to substrate, current velocity and water depth also play important roles in habitat partitioning among different darter species (Fullenkamp 2010).

The occurrence of darter species in the Elk River was negatively affected by high silt levels. Siltation in the form of suspended sediment can reduce the ability of stream fishes to rely on visual cues for reproduction, feeding, and predator avoidance (Ryan 1991; Sutherland 2007; Hazelton and Grossman 2009; Becker 2012). Becker (2012) found that high turbidity degraded the anti-predator responses of Fountain Darters *E. fonticola* by impeding the chemical stimuli necessary for initiation of those responses. The Becker (2012) study also revealed that even low turbidity levels increased the amount of time needed by Fountain Darters to initiate foraging, thereby resulting in decreased prey consumption. Collectively, these findings suggest that in turbid environments, darters expend more energy in foraging, thus reducing the amount of energy available for other essential behaviors. High silt loads can also reduce the reproductive success of crevice-spawning species. For instance, high levels of suspended sediment reduced the spawning success of Whitetail Shiner *Cyprinella galactura*, which are crevice spawners (Sutherland 2007).

In a laboratory setting, Boulder Darters abandoned interstitial spaces that were clogged by silt (Burkhead and Williams 1992). Silt loads may therefore have significant conservation implications for endangered species, particularly crevice-spawning species like the Boulder Darter. We found no evidence suggesting that the amount of silt at a site was related to the distance from TFD; thus, the level of siltation at a site may represent a local effect, such as adjacent land use practices or sediment transport from nearby tributaries.

Estimating the community- and species-level relationships among the 39 sample sites in the present study provided estimates of darter assemblage richness in wadeable riffle–run complexes in the Elk River. Overall, total darter assemblage richness in the Elk River was relatively constant in relation to distance from TFD, but darter assemblage composition changed substantially with increasing distance downstream from the dam. From a management perspective, the knowledge of total darter species richness may not be a particularly useful metric. However, a multispecies occupancy model framework allows for two things that we believe are useful to managers: (1) an improved ability to estimate occupancy for rare species and (2) the ability to assess not only species richness but also assemblage richness based on subsets of the community at large. With respect to the management and conservation of Elk River darter species, our modeling framework enabled a specific focus on large-river obligate species (i.e., the Boulder Darter, Gilt Darter, Ashy Darter, and Bluebreast Darter), all of which are species of high conservation concern in the Elk River system.

Accurate information on the occupancy patterns of target species is critical when management actions can have a direct impact on species distributions. Results from this study provide a snapshot of the current distribution of darter species within the Elk River system as well as an assessment of the effects of biotic and abiotic factors on darter detection and occupancy. Operational modifications that aim to stabilize conditions in the TFD tailwater could create more desirable environmental conditions for large-river obligate species, thereby facilitating upstream movement into and subsequent recolonization of previously unsuitable stream reaches. Knowledge of current species distributions and habitat–occupancy relationships is important for (1) maintaining the existing populations through habitat conservation activities and (2) identifying sites where new populations could become established via natural recolonization or reintroductions.

Unfortunately, rare and less-mobile species appear to recover more slowly after local extinction events (Albanese et al. 2009), and Boulder Darters are very unlikely to exhibit substantial migration in the event that habitat conditions are improved by altered dam operations (Shea et al. 2015). As such, future efforts to conserve the species may benefit not only from ensuring that physical habitat conforms to the conditions necessary for the persistence of populations but also from reintroduction via propagation or translocations to promote the species' range expansion in the Elk River.

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REFERENCES

Albanese, B., P. L. Angermeier, and J. T. Peterson. 2009. Does mobility explain variation in colonization and population recovery among stream fishes? Freshwater Biology 54:1444–1460.

Albanese, B., J. T. Peterson, B. J. Freeman, and D. A. Weiler. 2007. Accounting for incomplete detection when estimating site occupancy of Bluenose Shiner (*Pteronotropis welaka*) in southwest Georgia. Southeastern Naturalist 6:657–668.

Anderson, G. B., M. C. Freeman, M. M. Hagler, and B. J. Freeman. 2012. Occupancy modeling and estimation of the Holiday Darter species complex within the Etowah River system. Transactions of the American Fisheries Society 141:34–45.

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology 69:382–392.

Bain, M. B., and N. J. Stevenson, editors. 1999. Aquatic habitat assessment: common methods. American Fisheries Society, Bethesda, Maryland.

Becker, L. S. 2012. Effects of turbidity on anti-predator response and foraging behavior in the Fountain Darter, *Etheostoma fonticola*. Master's thesis. Texas State University, San Marcos.

Bednarek, A. T., and D. D. Hart. 2005. Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. Ecological Applications 15:997–1008.

Bettoli, P. W., and D. A. Besler. 1996. An investigation of the trout fishery in the Elk River below Tims Ford Dam. Tennessee Wildlife Resources Agency, Fisheries Report 96-22, Nashville.

Boschung, H. T. Jr., and R. L. Mayden. 2004. Fishes of Alabama. Smithsonian Books, Washington, D.C.

Burkhead, N. M., and J. D. Williams. 1992. The Boulder Darter: a conservation challenge. Endangered Species Technical Bulletin XVII(3-8):4–6.

Cam, E., J. D. Nichols, J. E. Hines, J. R. Sauer, R. Alpizar-Jara, and C. H. Flather. 2002. Disentangling sampling and ecological explanations underlying species–area relationships. Ecology 83:1118–1130.

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

Fullenkamp, A. E. 2010. Microhabitat selection among five congeneric darter species in two Indiana watersheds. Master's thesis. Ball State University, Muncie, Indiana.

Gelman, A. J., H. S. Carlin, D. B. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Chapman and Hall/CRC Press, New York.

Grossman, G. D., and R. E. Ratajczak. 1998. Long-term patterns of microhabitat use by fish in a southern Appalachian stream from 1983 to 1992: effects of hydrologic period, season and fish length. Ecology of Freshwater Fish 7:108–131.

Gwinn, D. C., L. S. Beesley, P. Close, B. Gawne, and P. M. Davies. 2016. Imperfect detection and the determination of environmental flows for fish: challenges, implications and solutions. Freshwater Biology 61:172–180.

Hagler, M. M., M. C. Freeman, S. J. Wenger, B. J. Freeman, P. L. Rakes, and J. R. Shute. 2011. Use of recent and historical records to estimate status and trends of a rare and imperiled stream fish, *Percina jenkinsi* (Percidae). Canadian Journal of Fisheries and Aquatic Sciences 68:739–748.

Harding, J. M., A. J. Burry, and C. M. Way. 1998. Habitat preference of the Rainbow Darter, *Etheostoma caeruleum*, with regard to microhabitat velocity shelters. Copeia 1998:988–997.

Hazelton, P. D., and G. D. Grossman. 2009. The effects of turbidity and an invasive species on foraging success of Rosyside Dace (*Clinostomus funduloides*). Freshwater Biology 54:1977–1989.

Hlohowskyj, I., and T. E. Wissing. 1986. Substrate selection by Fantail (*Etheostoma flabellare)*, Greenside (*E. blennioides)*, and Rainbow (*E. caeruleum*) darters. Ohio Journal of Science 86:124–129.

Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.

Isom, B., P. Yokley, and C. Gooch. 1973. Mussels of the Elk River basin in Alabama and Tennessee, 1964–1967. American Midland Naturalist 89:437–442.

Jandebeur, T. S. 1972. A study of the fishes of the Elk River drainage in Tennessee and Alabama. Master's thesis. University of Alabama, Tuscaloosa.

Kendall, W. L., and G. C. White. 2009. A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. Journal of Applied Ecology 46:1182–1188.

Kéry, M., and J. A. Royle. 2008. Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. Journal of Applied Ecology 45:589–598.

Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Elsevier, New York.

King, A. J., D. C. Gwinn, Z. Tonkin, J. Mahoney, S. Raymon, and L. Beesley. 2016. Using abiotic drivers of fish spawning to inform environmental flow management. Journal of Applied Ecology 53:34–43.

Lunn, D., D. Spiegelhalter, A. Thomas, and N. Best. 2009. The BUGS project: evolution, critique and future directions. Statistics in Medicine 28:3049–3067.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

OHEPA (Ohio Environmental Protection Agency). 2006. Methods for assessing habitat in flowing waters: using the qualitative habitat evaluation index (QHEI). OHEPA, Division of Surface Water, Technical Bulletin EAS/2006-0601, Columbus.

Olden, J. D., and R. J. Naiman. 2010. Incorporating thermal regimes into environmental flow assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55:86–107.

Page, L. M. 1983. Handbook of darters. T.F.H. Publications, Neptune, New Jersey.

Poff, N. L., D. Allan, B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.

Quinn, J. M., and C. W. Hickey. 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in New Zealand rivers. New Zealand Journal of Marine and Freshwater Research 24:411–427.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Elsevier, San Diego, California.

Ryan, P. A. 1991. Environmental effects of sediment on New Zealand streams: a review. New Zealand Journal of Marine and Freshwater Research 25:207–221.

Shea, C. P., P. W. Bettoli, K. M. Potoka, C. F. Saylor, and P. W. Shute. 2015. Use of dynamic occupancy models to assess the response of darters (Teleostei: Percidae) to varying hydrothermal conditions in a southeastern United States tailwater. River Research and Applications 31:676–691.

Shepard, T. E., P. E. O'Neil, S. W. McGregor, and M. F. Mettee. 2005. Survey of the Elk River system in Alabama for fish species of moderate to highest conservation concern: report of results for 2004–2005. Geological Survey of Alabama, Open-File Report 0525, Tuscaloosa.

Sutherland, A. B. 2007. Effects of increased suspended sediment on the reproductive success of an upland minnow. Transactions of the American Fisheries Society 136:416–422.

Taylor, C. M., T. L. Holder, R. A. Fiorillo, L. R. Williams, R. B. Thomas, and M. L. Warren. 2006. Distribution, abundance, and diversity of stream fishes under variable environmental conditions. Canadian Journal of Fisheries and Aquatic Sciences 63:43–54.

Tiemann, J. S. 2008. Distribution and life history characteristics of the state-endangered Bluebreast Darter *Etheostoma camurum* (Cope) in Illinois. Transactions of the Illinois State Academy of Science 101:235–246.

TVA (Tennessee Valley Authority). 2008. Tims Ford Dam flow modification for habitat quality improvements. TVA, Final Environmental Assessment, Project 2007-44, Knoxville.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.

USFWS (U.S. Fish and Wildlife Service). 2011. Biological opinion: permit application for U.S. Geological Survey for sampling Boulder Darter populations in the Elk River, Tennessee. USFWS, Cookeville Ecological Services Field Office, Report 2011-F-0225, Cookeville, Tennessee.

Warren, M. L., P. L. Angermeier, B. M. Burr, and W. R. Haag. 1997. Decline of a diverse fish fauna: patterns of imperilment and protection in the southeastern United States. Pages 105–164 *in* G. W. Benz and D. E. Collins, editors. Aquatic fauna in peril: the southeastern perspective. Lenz Design and Communications, Southeast Aquatic Research Institute, Special Publication 1, Decatur, Georgia.

Warren, M. L., B. M. Burr, S. J. Walsh, H. L. Bart Jr., R. C. Cashner, D. A. Etnier, B. J. Freeman, B. R. Kuhajda, R. L. Mayden, H. W. Robinson, S. T. Ross, and W. C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25(10):7–29.

Zipkin, E. F., A. DeWan, and J. A. Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modeling. Journal of Applied Ecology 46:815–822.

Zipkin, E. F., J. A. Royle, D. K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biological Conservation 143:479–484.