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# Multinomial *N*-Mixture Models Improve the Applicability of Electrofishing for Developing Population Estimates of Stream-Dwelling Smallmouth Bass

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***Abstract***
**Failure to account for variable detection across survey conditions constrains progressive stream ecology and can lead to erroneous stream fish management and conservation decisions. In addition to variable detection's confounding long-term stream fish population trends, reliable abundance estimates across a wide range of survey conditions are fundamental to establishing species–environment relationships. Despite major advancements in accounting for variable detection when surveying animal populations, these approaches remain largely ignored by stream fish scientists, and CPUE remains the most common metric used by researchers and managers. One notable advancement for addressing the challenges of variable detection is the multinomial *N*-mixture model. Multinomial *N*-mixture models use a flexible hierarchical framework to model the detection process across sites as a function of covariates; they also accommodate common fisheries survey methods, such as removal and capture–recapture. Effective monitoring of stream-dwelling Smallmouth Bass *Micropterus dolomieu* populations has long been challenging; therefore, our objective was to examine the use of multinomial *N*-mixture models to improve the applicability of electrofishing for estimating absolute abundance. We sampled Smallmouth Bass populations by using tow-barge electrofishing across a range of environmental conditions in streams of the Ozark Highlands ecoregion. Using an information-theoretic approach, we identified effort, water clarity, wetted channel width, and water depth as covariates that were related to variable Smallmouth Bass electrofishing detection. Smallmouth Bass abundance estimates derived from our top model consistently agreed with baseline estimates obtained via snorkel surveys. Additionally, confidence intervals from the multinomial *N*-mixture models were consistently more precise than those of unbiased Petersen capture–recapture estimates due to the dependency among data sets in the hierarchical framework. We demonstrate the application of this contemporary population estimation method to address a longstanding stream fish management issue. We also detail the advantages and trade-offs of hierarchical population estimation methods relative to CPUE and estimation methods that model each site separately.**

Variability in detection (the proportion of available individuals that are captured) confounds the perceived patterns of fish populations across the landscape (Peterson and Paukert 2009). The failure to account for variable detection can hinder effective sport fish management (Price and Peterson 2010) and rare species conservation (Dorazio et al. 2005). Due to the highly dynamic environments they occupy, stream fish populations present unique challenges for addressing variable detection (Jackson et al. 2001; Poff and Zimmerman 2010). Standardization of environmental conditions (e.g., sampling only at base flows) to maintain constant stream fish detection among surveys is not only challenging but often impractical for meeting management

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and conservation objectives. For example, surveying across a wide range of environmental conditions is essential for establishing stream fish–environment relationships that set the foundation of environmental flow standards (Gwinn et al. 2016).

Examples of how variable detection can influence stream fish management and conservation decisions are pervasive in the fisheries literature. Sammons (2014) showed that seasonal variation in electrofishing detection influenced abundance estimates for lotic centrarchid sport fishes. Suspected decline of the Bridle Shiner *Notropis bifrenatus* in northeastern U.S. streams was attributed to varying detection between sampling gears across environmental conditions rather than to local extirpations (Pregler et al. 2015). An additional challenge to obtaining reliable stream fish survey data is the considerable variability in species traits (e.g., morphology, behavior, and mobility), which results in different trends in detection among stream fishes (Peterson and Paukert 2009; Rabeni et al. 2009). Variable detection among fishes confounds the assessment of instream habitat restoration to improve species diversity (Price and Peterson 2010) and hinders the accurate interpretation of assemblage-level stream fish monitoring efforts (McManamay et al. 2014). In fact, the validity of indices of biotic integrity that use certain stream fishes as surrogates for water quality has come under scrutiny for ignoring variable detection (e.g., Seegert 2000; Price and Peterson 2010). More recently, Gwinn et al. (2016) illustrated how the failure to account for variable detection hinders the establishment of meaningful environmental flow standards for stream fishes. Improved and highly flexible approaches for addressing variable detection are increasingly common in the ecological literature (e.g., Williams et al. 2002; MacKenzie et al. 2005; Royle et al. 2013). Despite the numerous options that are available to the stream fish scientist, the lack of widespread implementation of these contemporary approaches to account for variable detection has impeded progress in both ecology and management (Brewer and Orth 2015; Gwinn et al. 2016).

The Smallmouth Bass *Micropterus dolomieu*, a stream fish of recreational and ecological value (Brewer and Orth 2015), provides an applied example of how the lack of progressive monitoring approaches has prevented improved insight into life history characteristics and demographics and the development of long-term management strategies. Although electrofishing is the most common—and often most practical—stream fish survey method (Rabeni et al. 2009), its use for studying and monitoring local Smallmouth Bass populations is challenging. Longstanding issues with the use of electrofishing to examine trends among Smallmouth Bass populations are prevalent in the gray literature. For example, Lyons and Kanehl (1993) conducted extensive Smallmouth Bass surveys via electrofishing and determined that both removal (known also as depletion; e.g., Zippin 1958; Carle and Strub 1978) and capture–recapture (known also as mark–recapture; e.g., Manly and Seber 1973) methods were generally inappropriate for estimating the abundance of stream-dwelling populations due to the failure to meet assumptions. In particular, Lyons and Kanehl (1993) demonstrated that highly variable detection among removal passes and low Smallmouth Bass capture rates (i.e., low detection) resulted in biased abundance estimates, inflated variance, and wasted resources (i.e., time and money spent on surveying that did not result in usable data). Low detection when conducting electrofishing surveys for Smallmouth Bass in streams is also supported by peer-reviewed studies (e.g., Heimbuch et al. 1997; Dauwalter and Fisher 2007; Hense et al. 2010).

The failure to successfully apply electrofishing to population estimation methods that account for variable detection has led to a reliance on CPUE for ecological information and management decisions pertaining to Smallmouth Bass (Brewer and Orth 2015). For example, in reviewing the biology and ecology of genetically distinct populations of stream-dwelling Smallmouth Bass, Brewer and Long (2015) relied primarily on CPUE data that were collected via electrofishing. In addition to providing only an indirect measure of abundance, the use of CPUE assumes constant detection across time and space, which is often unrealistic in stream environments (Price and Peterson 2010; Gwinn et al. 2016). Thus, the usefulness of CPUE data for long-term data sets or large study areas is limited. An examination of agency reports demonstrates how variable electrofishing detection confounds the results of statewide long-term monitoring efforts that employ CPUEs of lotic Smallmouth Bass populations (e.g., Meneau 2010). Given the importance of Smallmouth Bass, it is surprising that contemporary approaches have rarely been applied to improve the applicability of electrofishing for population estimation methods. Although Dauwalter and Fisher (2007) developed an electrofishing detection model that provided absolute abundance estimates for stream-dwelling Smallmouth Bass populations, those authors surveyed only two streams located in different ecoregions. Additionally, Dauwalter and Fisher (2007) used channel units (e.g., individual pools, backwaters, etc.) to define the 28 "sites," which not only provided a misleading sample size but also was too fine a spatial scale to be practical for obtaining comparable estimates of Smallmouth Bass abundance among distinct populations.

One notable advancement in addressing the challenges of variable detection when surveying animal populations is a class of models known as multinomial *N*-mixture models (Royle 2004a; Dorazio et al. 2005; Royle and Dorazio 2006). These models use a flexible hierarchical framework to independently estimate both the abundance and the detection probability of spatially distinct subpopulations as a function of covariates, where detection can vary among sites and among surveys. In contrast to similar models that predict species occupancy by reducing counts to binary detection/nondetection data (see MacKenzie et al. 2005), multinomial *N*-mixture models provide inference on species occurrence and species abundance (Royle and Dorazio 2006). Thus, multinomial *N*-mixture models are applicable for common species (i.e., species with counts that are typically > 0 across sites), where the primary focus is typically to estimate variation in local abundance. Multinomial *N*-mixture models also accommodate temporally replicated counts at sites, which makes them applicable to

commonly used fish population estimation methods, such as removal and capture–recapture (Royle 2004a). The hierarchical structure of multinomial *N*-mixture models enables an empirical Bayes approach (Carlin and Louis 2000) to the estimation of abundance across spatially distinct sites. Unlike removal and capture–recapture approaches that calculate abundance at each site separately, the empirical Bayes approach provides site-specific abundance estimates that are a reflection of data collected across all sites (i.e., information for sites can be "borrowed"; Dorazio et al. 2005; Royle and Dorazio 2006). The dependency among data sets in the hierarchical multinomial *N*-mixture model framework not only improves the precision of confidence intervals (CIs) but also reduces bias and improves the estimability of abundance at sites with sparse or insufficient data (e.g., low detection or sample size) given that adequate data are available at some sites; therefore, all data are informative (i.e., there are no wasted resources).

Multiple approaches are available for increasing confidence in the reliability of abundance estimates. One option is to provide a comparison using results from another survey method that is associated with high detection probability. Snorkel counts can provide informative minimum population estimates (i.e., a reliable baseline) to compare with abundance estimates that have been obtained via other methods given adequate water clarity (Mullner et al. 1998; Wildman and Neumann 2003). Visibility is the primary consideration for stream fish detection (Dunham et al. 2009). In fact, snorkel surveys have been shown to generate detection rates as high as 70–90% for noncryptic fishes in clear-water streams (Hillman et al. 1992; Bonneau et al. 1995). Another option for assessing the reliability of abundance estimates is to compare the results with those from an estimation method with known reliability. For example, the traditional Petersen capture–recapture estimator (hereafter, "Petersen capture–recapture") remains a dependable approach for estimating stream fish abundance given that assumptions for unbiased estimates are met (e.g., adequate sample size and recapture rate; Lockwood and Schneider 2000; Rosenberger and Dunham 2005).

Despite the applicability of multinomial *N*-mixture models to common fish estimation methods, reports of their use for stream fishes have been relatively rare in the scientific literature. Coggins et al. (2011), Yard et al. (2011), and Dodrill et al. (2015) used multinomial *N*-mixture models for boat electrofishing surveys in the Colorado River basin. Korman et al. (2016) demonstrated the advantages of multinomial *N*-mixture models for multiple-gear sampling designs. We are not aware of any capture–recapture applications for electrofishing in wadeable warmwater streams (but see Dorazio et al. 2005 for a snorkeling removal example) or for estimating Smallmouth Bass populations. Accordingly, our objective was to use a multinomial *N*-mixture capture–recapture model (hereafter, "multinomial capture–recapture model") to improve the applicability of electrofishing for estimating the abundance of age-1 and older Smallmouth Bass in wadeable streams. We performed tow-barge electrofishing surveys across a range of environmental conditions estimate abundance of and to identify variables that influenced variation in Smallmouth Bass detection. As a basis for comparison with our abundance estimates derived from the multinomial capture–recapture model, we also conducted snorkel surveys at a subset of sites where water clarity was ideal. Snorkeling is an appropriate method for surveying Smallmouth Bass in clear, warmwater streams (Brewer and Ellersieck 2011). Lastly, we compared Smallmouth Bass abundance estimates derived from the multinomial capture–recapture model to estimates derived from Petersen capture–recapture when assumptions were met for unbiased estimates. We used two approaches for comparisons because a wide range of environmental conditions and fish densities across our study area was expected. Example data and code are provided by Chandler (2015).

## METHODS

*Study sites.*—We surveyed age-1 and older Smallmouth Bass in 25 stream reaches that comprised three to five riffle–run–pool sequences to characterize habitat (hereafter, "sites") in the Ozark Highlands ecoregion of northeast Oklahoma and southwest Missouri (Figure 1). The Ozark Highlands are characterized by cherty limestone lithology and oak–hickory forests, with valley primarily converted to pasture (Woods et al. 2005). Streams of the Ozark Highlands are characterized by karst features, substantial groundwater influence, and high fish diversity. All sites were wadeable (the majority of habitat was < 1 m deep; Rabeni et al. 2009). Although there is substantial variation in water clarity among Ozark Highlands streams, our sites are characterized as clear water, with very low suspended sediment at base flow conditions (Nigh and Schroeder 2002). Among our sites, water temperature was 21.5 ± 2.7°C (mean ± SD), and ambient water conductivity was 276 ± 68 μS/cm. The sites represented spatially distinct subpopulations of Smallmouth Bass that were demographically closed during the survey event, with mixing of individuals permitted over longer time periods, which is consistent with assumptions of multinomial *N*-mixture models (Royle 2004a; Dorazio et al. 2005).

*Environmental measurements.*—At each site, we measured environmental variables that were hypothesized to influence electrofishing detection of Smallmouth Bass. Water depth is an important consideration when conducting electrofishing surveys in streams, as it can limit the electrical field and provides areas of fish refuge (Burkhardt and Gutreuter 1995; Peterson and Paukert 2009). Another primary influence on electrofishing detection in streams is ambient water conductivity (Rabeni et al. 2009); however, electrofishing power (W) can be standardized by adjusting voltage, given that ambient conductivity does not vary widely among sites (Burkhardt and Gutreuter 1995; Miranda 2009). Flow also influences electrofishing detection of fishes, although the direction of the

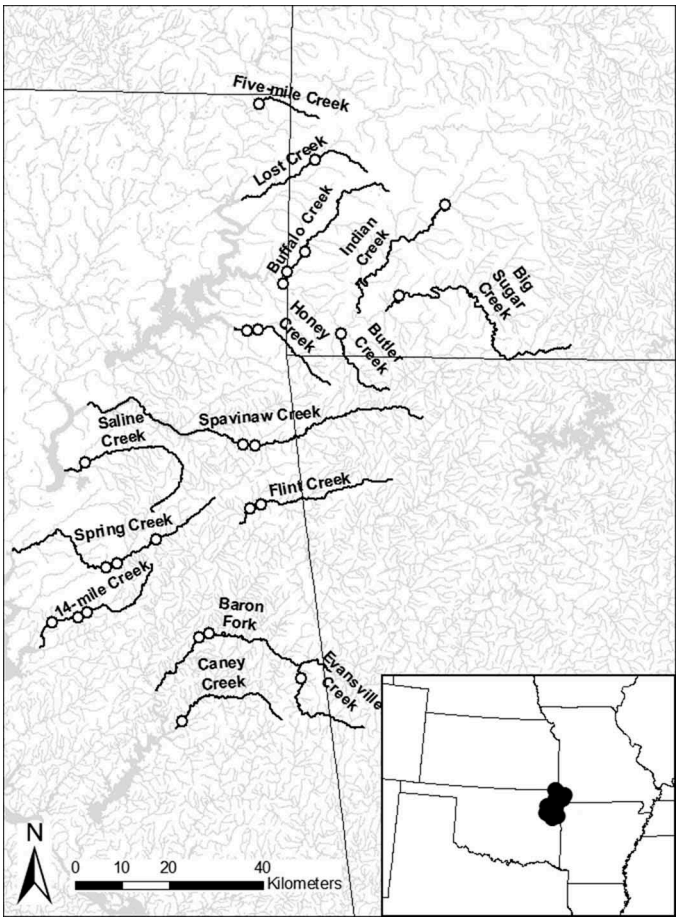


FIGURE 1. Locations of 25 stream reaches within the Ozark Highlands (northeast Oklahoma–southwest Missouri), where spatially distinct Smallmouth Bass subpopulations were surveyed by use of tow-barge electrofishing and snorkeling from July to October 2014–2015.

effect may be species specific (Peterson and Paukert 2009; Price and Peterson 2010; Pregler et al. 2015). Here, we hypothesized that increased discharge would decrease Smallmouth Bass detection probability, which is supported by similar studies involving centrarchids (Price and Peterson 2010). Electrofishing detection of fishes also declines with increased wetted channel width (Peterson and Paukert 2009) and increased water clarity (Price and Peterson 2010). Wetted channel width (1.0 m) and thalweg depth (0.1 m) were measured at 50-m transects to calculate mean wetted channel width and mean depth. Stream discharge (0.01 $m^3/s$) was measured in a homogeneous area of a run by using the velocity–area method (Gordon et al. 2004), and we report the average of three replicates. Water clarity (0.5 m) was measured as the horizontal distance at which an underwater observer could see a fish silhouette. We designed our fish silhouette to mimic the color, markings, and typical size (~200 mm) of Smallmouth Bass in our study streams (Dunham et al. 2009). We also estimated the total sampling area at each site by subtracting the summed length of riffles from the total reach length and multiplying by the mean wetted width.

*Fish sampling.*—To ensure a closed system during the survey period, we installed two sets of block-off nets at the upstream and downstream ends of the site. Block-off nets were preferentially placed at shallow riffles that served as natural barriers to further inhibit fish movement (Peterson et al. 2004; Price and Peterson 2010). Either a low-water bridge at low flows or a dry riffle located at one end of the site provided an adequate fish barrier at a few sites, and in those cases, no block-off nets were installed.

We surveyed the Smallmouth Bass subpopulations over a 3-d period. On day 1 (hereafter, "capture day"), we used a tow-barge electrofisher (Stealth Mini-boat; Midwest Lake Management, Polo, Missouri) to establish marked populations of Smallmouth Bass. All Smallmouth Bass were measured, and fish smaller than 80 mm TL were excluded from the study. Our minimum fish size excluded most age-0 Smallmouth Bass and was also based on both observed mortalities and a lack of recapture via electrofishing of individuals less than 80 mm TL. In addition to size, age-0 Smallmouth Bass were easily recognizable due to their prominent tri-colored tails. We used pulsed DC, 60 Hz, and a 25% duty cycle for electrofishing. Voltage (300–400 V) was adjusted based on ambient water conductivity to maintain a target power as described by Miranda (2009). The electrofishing crew consisted of three people: one tow-barge operator armed with a hand net; and two persons equipped with dip nets, each operating one of the two anodes. We electrofished areas that were at least 0.2 m deep in an upstream direction with a zigzag pattern. The depth limitation of the tow-barge electrofisher excluded most riffle areas, but the use of that habitat by Smallmouth Bass larger than 80 mm TL is very uncommon (Brewer 2013; Oklahoma Department of Wildlife Conservation [ODWC], unpublished snorkel data). Care was taken to thoroughly electrofish areas with structure (e.g., large wood, root wads, and boulders). The crew performed at least two electrofishing passes per riffle–run–pool sequence, although additional passes were conducted at some sites to increase the marked population of Smallmouth Bass for Petersen capture–recapture estimates. Electrofishing time was recorded at each site to estimate variation in effort among sites and between capture and recapture events; electrofishing effort was calculated as the electrofishing time divided by the sampling area. Captured Smallmouth Bass were marked with an upper caudal fin clip. Marked Smallmouth Bass were released throughout the site and were allowed to recover and redistribute for approximately 24 h prior to the snorkel survey and about 48 h prior to the electrofishing recapture event to allow the system to fully recover (Peterson and Cederholm 1984). Smallmouth Bass that were injured during electrofishing or that showed signs of excessive stress were released outside of the blocked-off area. We periodically inspected the block-off nets and the area between them for trapped or dead Smallmouth Bass.

We conducted snorkel counts of Smallmouth Bass subpopulations on day 2 of the survey at 16 sites to provide a coarse estimate of abundance. Three persons were typically used for the snorkel surveys; however, only two snorkelers were used in stream areas where wetted channel width was less than 10 m. Snorkel surveys were only performed at sites where horizontal water clarity was at least 3.0 m. The water clarity criterion is consistent with other stream fish snorkeling studies (e.g., Schill and Griffith 1984) and coincides with the minimum distance the crew members were instructed to achieve before identifying a fish. Prior to the snorkel survey, we inspected the blocked-off area for dead Smallmouth Bass, and mortalities were removed from the marked population. All crew members were trained in snorkeling protocols and had previously participated in "practice" surveys with experienced snorkelers. Areas at least 0.2 m deep were snorkeled slowly in an upstream direction; the snorkelers avoided sudden movements and carefully inspected areas of structure (e.g., searched for fish under logs and between boulders) within reasonable safety constraints. Each snorkeler maintained a designated lane and stayed in line laterally with the other crew members. In general, snorkeling lanes with higher amounts of structure were narrower, and snorkeling lanes with mostly open water were wider. Snorkelers maintained communication with each other to minimize the double counting of individual fish. Smallmouth Bass that were estimated to be at least 80 mm TL and that lacked a prominent tri-colored tail were recorded on an underwater wrist cuff when they either passed the snorkeler or vice versa. Prior to the snorkeling survey, fish silhouettes and rocks of known sizes were used to confirm accuracy among crew members in identifying the 80-mm size cut-off underwater. We also instructed the snorkelers to collect dead Smallmouth Bass for an additional method of estimating delayed mortality.

The electrofishing recapture event for the Smallmouth Bass subpopulations was conducted on day 3 of the survey. The electrofishing procedure on day 3 was identical to the procedure employed on capture day, with the exception that only two passes were performed for each riffle–run–pool sequence at each site. Prior to the recapture event, we again inspected the blocked-off area for dead Smallmouth Bass, and mortalities were removed from the marked population. We recorded both marked and unmarked Smallmouth Bass that were at least 80 mm TL.

*Subpopulation estimates.*—We implemented multinomial capture–recapture models by using the package 'unmarked' (Fiske and Chandler 2011) in R version 3.2.2 (R Development Core Team 2014). Specifically, we used the function 'gmultmix' with a single primary period, which fits a generalized form of the multinomial *N*-mixture model described by Royle (2004a) and assumes a closed system during the capture–recapture event at each site. In the multinomial *N*-mixture model framework, capture–recapture data collected at a set of sites can be used to model variation in both abundance and detection probability, where site-specific abundance $N$ is treated as a latent variable with a discrete distribution (Chandler 2015). Due to evidence of overdispersion in our data set, we specified a negative binomial error distribution, which introduces a dispersion parameter to the model. Overdispersed subpopulations of animals are a common phenomenon because spatial randomness is uncommon in distributions (Dorazio et al. 2005). Following Chandler (2015), the multinomial capture–recapture model is written as

$$\begin{aligned} N_i &\sim \text{Negative binomial}(\theta, \lambda) \\ Y_i|N_i &\sim \text{Multinomial}[N_i, \pi(p)], \end{aligned} \tag{1}$$

where $\theta$ is the overdispersion parameter; $\lambda$ is the estimated number of individuals at each site $i$; $Y_i$ is a vector of counts at each site, representing the three possible capture histories $H \in (11, 10, 01)$; and $\pi(p)$ is a function that converts the detection probability $p$ to multinomial cell probabilities as

$$\pi(p) = \left[p^2, p(1-p), (1-p)p\right], \tag{2}$$

where the probability of not capturing an individual ($H = 00$) is $(1 - p)^2$. This approach differs from Petersen capture–recapture, as information related to detection is considered during both the capture event and the recapture event. Site-specific Smallmouth Bass abundance was modeled using a log-link function as

$$\log_e(\lambda_i) = \beta_0, \tag{3}$$

where $\beta_0$ is the $y$-intercept (here, the mean abundance across sites).

We did not include covariates to explain variation in abundance because our objective was solely to model Smallmouth Bass abundance (i.e., our focus was on how many fish were there rather than why the fish were there); however, the inclusion of covariates is straightforward (see Fiske and Chandler 2011; Chandler 2015). Detection probability was modeled using a logit-link function as

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 v_{ij} + \alpha_2 v_{ij} + \alpha_n v_{ij}, \tag{4}$$

where $v_{ij}$ is a detection covariate corresponding to survey $j$ at site $i$.

We fitted a candidate set of 12 multinomial capture–recapture models with varying levels of complexity (Table 1). An effort detection covariate was included in every model to account for variation in electrofishing intensity among surveys. Mean wetted channel width, mean water depth, discharge, and water clarity were used as detection covariates in the candidate models to characterize environmental variation in survey conditions; discharge was natural log transformed due to a right-skewed distribution. An examination of Pearson's product-moment correlation coefficients ($r$) between detection covariates indicated a moderate level of

TABLE 1. Results from 12 candidate multinomial *N*-mixture capture–recapture models (fitted with a negative binomial error distribution) for estimating site-specific abundance and detection probability of Smallmouth Bass by using tow-barge electrofishing in 25 stream reaches of the Ozark Highlands (northeast Oklahoma–southwest Missouri) from July to October 2014–2015 (λ = latent abundance; *p* = estimated detection probability; effort = electrofishing effort; width = average wetted channel width; *Q* = discharge; depth = average thalweg depth; clarity = horizontal water clarity; θ = overdispersion parameter; *K* = number of parameters in each model; $AIC_c$ = Akaike's information criterion corrected for small sample size; $\Delta AIC_c$ = difference in $AIC_c$ score between the given model and the best-performing model; $w_i$ = Akaike weight, indicating relative support for the given model).

| Model | *K* | Log-likelihood | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| λ, *p*[effort + (width × depth) + clarity], θ | 8 | 3,604.54 | –7,184.09 | 0.00 | 0.95 |
| λ, *p*(effort + width + depth + clarity), θ | 7 | 3,598.67 | –7,176.75 | 7.34 | 0.02 |
| λ, *p*[effort + (width × depth)], θ | 7 | 3,598.34 | –7,176.09 | 8.00 | 0.02 |
| λ, *p*(effort + width + depth), θ | 6 | 3,595.29 | –7,173.91 | 10.18 | 0.01 |
| λ, *p*(effort + depth), θ | 5 | 3,591.39 | –7,169.61 | 14.48 | 0.00 |
| λ, *p*[effort + (width × *Q*) + clarity], θ | 8 | 3,594.18 | –7,163.36 | 20.73 | 0.00 |
| λ, *p*(effort + width + *Q* + clarity), θ | 7 | 3,591.58 | –7,162.58 | 21.51 | 0.00 |
| λ, *p*(effort + width + *Q*), θ | 6 | 3,587.67 | –7,158.68 | 25.41 | 0.00 |
| λ, *p*(effort + width × *Q*), θ | 7 | 3,588.97 | –7,157.35 | 25.41 | 0.00 |
| λ, *p*(effort + *Q*), θ | 5 | 3,883.79 | –7,154.42 | 29.67 | 0.00 |
| λ, *p*(effort + width), θ | 5 | 3,572.88 | –7,132.61 | 51.48 | 0.00 |
| λ, *p*(effort), θ | 4 | 3,562.54 | –7,115.08 | 69.01 | 0.00 |

correlation between discharge and water depth ($r = 0.51$); thus, the two covariates did not co-occur in any candidate models. Water temperature was not included in the candidate models because it did not vary considerably among sites (see Study Area). The candidate models were ranked by using Akaike's information criterion corrected for small sample size ($AIC_c$; Burnham and Anderson 2001), where site was the sample size. The number of sites represents the most conservative estimate of sample size for multinomial *N*-mixture models. The number of residuals in the model corresponds to the number of vector counts across sites (here, $n = 75$) and is a more accurate yet less-conservative estimate of sample size. To confirm that standardization of electrofishing power adequately accounted for any influence of variable ambient water conductivity on Smallmouth Bass electrofishing detection, we used $AIC_c$ to compare our top-ranked model with a model that also included a conductivity detection covariate. Fish size is also an important consideration when estimating electrofishing detection (Peterson and Paukert 2009; Price and Peterson 2010); however, we did not anticipate that it would influence our abundance estimates because the mean Smallmouth Bass TL (mean ± SD = 200 ± 28 mm) did not vary considerably among sites. To evaluate our expectation, we used $AIC_c$ to compare our top-ranked model with a model that also included a fish size detection covariate, with mean Smallmouth Bass TL used to represent each site. Lastly, $AIC_c$ was used to compare our top-ranked model to a model that also included categorical survey event (i.e., capture and recapture) as a detection covariate to confirm that the included covariates adequately accounted for variation in detection between the capture and recapture events. All detection covariates were scaled such that each had a mean of zero and an SD of 1 to promote model convergence and to simplify the interpretation of coefficients.

We assessed the fit of the top model by using both a visual examination of residual versus fitted values and a calculation of $\hat{c}$ (an estimate of overdispersion, where $\hat{c} > 1$ suggests overdispersion). We used a chi-square test as described by MacKenzie and Bailey (2004) with 10,000 bootstrap replications for the calculation of $\hat{c}$. We also calculated 95% CIs for coefficients in the top-ranked model by using a profile likelihood method (see Fiske and Chandler 2011).

Finally, we calculated site-specific detection and abundance estimates for the Smallmouth Bass subpopulations from our estimation methods. We derived cumulative detection probability and abundance at each site by use of the top-ranked multinomial capture–recapture model. Empirical Bayes calculations were used for the multinomial capture–recapture abundance estimates and for the 95% CIs. Petersen capture–recapture estimates were calculated with the Chapman (1954) bias correction by using the library 'Rcapture' (Baillargeon and Rivest 2007) in R software as

$$\hat{N} = [(M+1)(C+1)/(R+1)] - 1, \quad (5)$$

where $\hat{N}$ is the population estimate, *M* is the number of Smallmouth Bass that were marked during the capture event, *C* is the number of Smallmouth Bass that were captured during the recapture event, and *R* is the number of recaptured individuals that were marked. We only calculated Petersen capture–recapture at sites where assumptions were met for unbiased population estimates as outlined by Lyons and Kanehl (1993): (1) at least 20 fish were marked, (2) at least five of the marked fish were recaptured, and (3) at least 15% of the number of fish captured during the recapture event were marked. The 95% CIs for

site-specific Petersen capture–recapture estimates were calculated as $\hat{N} \pm z_{\alpha/2}(\text{SE})$, where we used a bias-corrected SE (Seber 1970). Estimates of Smallmouth Bass abundance derived from empirical Bayes calculations were compared to the snorkel counts and to the Petersen capture–recapture estimates. Environmental measurements and fish counts are reported as mean ± SD.

## RESULTS

### Environmental Measurements

We surveyed Smallmouth Bass subpopulations across a range of environmental conditions. Mean wetted channel width varied from 9 to 18 m (14 ± 3 m) among sites, and mean water depth varied from 0.5 to 1.1 m (0.8 ± 0.1 m) among sites. Discharge and water clarity displayed the greatest among-site variation: discharge ranged from 0.091 to 5.81 $m^3/s$ (1.50 ± 1.43 $m^3/s$), and water clarity ranged from 1.5 to 7.0 m (3.5 ± 1.3 m). Electrofishing effort varied among surveys (0.013–0.053 $min/m^2$; 0.033 ± 0.011 $min/m^2$) and between capture and recapture events (mean = 0.036 and 0.030 $min/m^2$, respectively).

### Fish Sampling

Monitoring of the study area provided evidence that we maintained a closed system during the surveys and that delayed mortality of Smallmouth Bass due to capture and handling was trivial. No Smallmouth Bass (living or dead) were found in the block-off nets or in the area between them. Only three dead marked Smallmouth Bass were found during routine inspections of a site (one fish was found at Buffalo Creek site 2; two fish were found at 14-Mile Creek site 2).

The number of marked Smallmouth Bass, the proportion of fish recaptured, and the number of fish encountered during snorkeling were highly variable among sites. The number of Smallmouth Bass marked at a site ranged from 8 fish at Caney Creek to 120 fish at 14-Mile Creek site 2 (39 ± 30 fish; Table 2). The proportion of Smallmouth Bass recaptured at a site ranged from 0.00 at Flint Creek site 1 to 0.57 at 14-Mile Creek site 2 (0.24 ± 0.15). Baseline population estimates obtained via snorkel counts ranged from 18 fish at Caney Creek to 247 fish at Spring Creek site 1 (127 ± 75 fish; Table 2).

### Subpopulation Estimates

A top-ranked multinomial capture–recapture model was evident and included the following detection covariates: electrofishing effort, water clarity, and the mean wetted channel width × mean water depth interaction ($AIC_c$ = –7,184.09; Tables 1, 3). There was no evidence that either water conductivity or mean fish size influenced Smallmouth Bass detection among sites when they were added as covariates to the top-ranked model ($AIC_c$ = –7,179.95 and –7,179.35, respectively). Comparison between the top-ranked model and a model that also included categorical survey event as a detection covariate provided evidence that the detection covariates adequately explained variation in detection probability between capture and recapture events ($AIC_c$ = –7,180.41). Site-specific cumulative detection of Smallmouth Bass varied considerably—from 0.23 at Big Sugar Creek to 0.84 at 14-Mile Creek site 3 (0.45 ± 0.15; Table 2). Estimated detection probability at mean levels of covariates for a single survey was 0.25 ± 0.02 (Table 3). Smallmouth Bass detection probability increased with increases in electrofishing effort and water clarity (Table 3; Figure 2). The interaction term in the model indicated that the relationship between Smallmouth Bass detection and both wetted channel width and water depth varied at different levels of these covariates. To interpret the interaction term, we predicted detection probability at various levels of mean wetted channel width and mean depth by using linear combinations of model coefficients. Detection probability decreased sharply as mean depth increased in narrower surveying conditions; however, the magnitude of the relationship diminished at higher levels of mean depth (Figure 3a). Conversely, there was only a slight negative trend in detection probability with increasing mean depth in wider surveying conditions (Figure 3b). Similarly, detection probability increased with mean wetted width in shallower surveying conditions (Figure 3c), whereas there was virtually no trend in detection probability as mean wetted width increased in deeper surveying conditions (Figure 3d). The interaction effect of mean depth × mean wetted width on Smallmouth Bass detection probability indicated that (1) the influence of each covariate was more pronounced at lower levels of the alternate covariate, (2) there was no influence of wetted width in deep conditions, and (3) detection probability (although low) no longer decreased considerably at high levels of wetted width and depth (i.e., very wide and very deep). The $\hat{c}$ estimate from the chi-square test ($\hat{c} < 1$) did not indicate overdispersion in the model. A plot of predicted versus fitted residuals ($n$ = 75) also suggested adequate model fit (i.e., there was no evidence of heteroscedasticity).

A comparison of the empirical Bayes calculations derived from the multinomial capture–recapture model to secondary methods increased confidence in the reliability of the estimates. Although we only met the assumptions for unbiased Petersen capture–recapture estimates at 11 of 25 sites, the estimates were in general agreement with the empirical Bayes estimates, and the 95% CIs overlapped at every site (Table 2). However, the range of the CIs for the empirical Bayes estimates was more precise at every site than the Petersen capture–recapture CIs. The width of CIs was 48 ± 16 fish for empirical Bayes and 109 ± 83 fish for Petersen capture–recapture at sites where both estimates were available. There was a similar level of precision for empirical Bayes CIs that were calculated across all sites, where the CI width ranged from 14 to 87 fish (49 ± 20 fish). The empirical Bayes CIs contained the snorkel count at 8 of 13 sites. We did not consider the snorkel counts at three sites

TABLE 2. Summary of snorkel surveys and capture–recapture estimates for 25 Smallmouth Bass subpopulations in Ozark Highlands streams; *M* is the total number of fish captured during the capture event, *C* is the total number of fish captured (both marked and unmarked) during the recapture event, "recap" is the proportion of marked fish that were recaptured, and cumulative detection is the estimated proportion of Smallmouth Bass that were captured across both capture and recapture events. Cumulative detection, multinomial abundance estimates, and multinomial 95% confidence intervals (CIs) were derived from a multinomial *N*-mixture capture–recapture model with a negative binomial error distribution. Petersen abundance estimates were calculated by use of the Petersen capture–recapture method with the Chapman (1954) bias correction. Petersen 95% CIs were calculated with a bias-corrected SE (Seber 1970) as $\hat{N} \pm z_{\alpha/2}(\mathrm{SE})$. For snorkel count, "NA" indicates that the site was not surveyed due to insufficient water clarity. For Petersen abundance estimates and Petersen 95% CIs, "NA" indicates sites at which the assumptions for unbiased estimates were not met, as described by Lyons and Kanehl (1993).

| Site | *M* | *C* | Recap | Snorkel count | Cumulative detection | Multinomial abundance estimate | Multinomial 95% CI | Petersen abundance estimate | Petersen 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| Baron Fork site 1 | 71 | 37 | 0.13 | NA | 0.46 | 214 | 185–246 | 299 | 147–451 |
| Baron Fork site 2 | 16 | 11 | 0.38 | NA | 0.54 | 41 | 30–53 | NA | NA |
| Big Sugar Creek | 24 | 11 | 0.08 | 138 | 0.23 | 144 | 105–188 | NA | NA |
| Buffalo Creek site 1 | 79 | 96 | 0.47 | 153 | 0.75 | 183 | 169–199 | 204 | 167–241 |
| Buffalo Creek site 2 | 11 | 17 | 0.09 | 85 | 0.32 | 86 | 62–114 | NA | NA |
| Buffalo Creek site 3 | 15 | 17 | 0.07 | 59 | 0.35 | 91 | 68–118 | NA | NA |
| Butler Creek | 64 | 60 | 0.36 | 244 | 0.43 | 232 | 200–267 | 164 | 123–204 |
| Caney Creek | 8 | 6 | 0.13 | 18 | 0.45 | 31 | 21–45 | NA | NA |
| Evansville Creek | 70 | 44 | 0.36 | 66 | 0.52 | 170 | 147–195 | 128 | 101–155 |
| Five-Mile Creek | 15 | 13 | 0.20 | 61 | 0.50 | 52 | 39–67 | NA | NA |
| Flint Creek site 1 | 14 | 21 | 0.00 | NA | 0.33 | 107 | 81–137 | NA | NA |
| Flint Creek site 2 | 28 | 45 | 0.18 | 208 | 0.30 | 224 | 183–270 | NA | NA |
| 14-Mile Creek site 1 | 32 | 40 | 0.25 | 59 | 0.40 | 159 | 131–190 | 150 | 75–224 |
| 14-Mile Creek site 2 | 36 | 25 | 0.14 | NA | 0.51 | 109 | 91–130 | 162 | 57–268 |
| 14-Mile Creek site 3 | 120 | 97 | 0.57 | 66 | 0.84 | 176 | 166–188 | 173 | 157–188 |
| Honey Creek site 1 | 59 | 50 | 0.42 | NA | 0.62 | 135 | 118–153 | 117 | 93–141 |
| Honey Creek site 2 | 12 | 12 | 0.17 | NA | 0.30 | 75 | 52–103 | NA | NA |
| Indian Creek | 14 | 19 | 0.21 | NA | 0.31 | 97 | 72–128 | NA | NA |
| Lost Creek | 9 | 4 | 0.22 | NA | 0.62 | 19 | 13–27 | NA | NA |
| Saline Creek | 48 | 29 | 0.04 | 156 | 0.40 | 186 | 156–220 | NA | NA |
| Spavinaw Creek site 1 | 63 | 59 | 0.13 | 167 | 0.40 | 282 | 244–323 | NA | NA |
| Spavinaw Creek site 2 | 41 | 32 | 0.34 | NA | 0.44 | 133 | 110–160 | 92 | 64–120 |
| Spring Creek site 1 | 29 | 39 | 0.31 | 247 | 0.33 | 176 | 142–214 | 120 | 66–174 |
| Spring Creek site 2 | 85 | 84 | 0.40 | 225 | 0.62 | 215 | 194–238 | 207 | 167–248 |
| Spring Creek site 3 | 17 | 18 | 0.47 | 84 | 0.40 | 69 | 51–90 | NA | NA |

(Evansville Creek, 14-Mile Creek site 1, and 14-Mile Creek site 2) due to evidence of low detection, although Petersen capture–recapture estimates were available for each of these sites. The empirical Bayes CIs exceeded the Smallmouth Bass snorkel count at four sites; however, the snorkel count was within 9 fish of the lower confidence limit (LCL) at two sites (Buffalo Creek site 3 and Caney Creek) and within 16 fish of the LCL at Buffalo Creek site 1. The Smallmouth Bass snorkel count exceeded the empirical Bayes CI only at Spring Creek site 1. The three approaches compared favorably at the sites for which the empirical Bayes abundance estimate could be compared to both snorkel counts and Petersen capture–recapture estimates (Buffalo Creek site 1, Butler Creek, Spring Creek site 1, and Spring Creek site 2). Only for five sites were we unable to compare Smallmouth Bass abundance estimates derived from the multinomial capture–recapture model with estimates from secondary methods.

## DISCUSSION

We used a highly flexible hierarchical population estimation model to address a longstanding stream fish management issue. Dynamic stream environments present a widespread challenge for both effective stream fish monitoring and quality research due to variable detection among surveys. The application of electrofishing—the most common stream fish survey method—to population estimation methods has been challenging, particularly with Smallmouth Bass, because of highly variable and low detection. The modeling approach we have presented here effectively addresses concerns raised by Lyons

TABLE 3. Coefficients from a multinomial *N*-mixture capture–recapture model (with a negative binomial error distribution) for estimating the abundance of 25 Smallmouth Bass subpopulations in Ozark Highlands streams that were surveyed via tow-barge electrofishing. Using Akaike's information criterion corrected for small sample size, the model was chosen from a set of 12 candidate models that incorporated the following detection covariates: discharge, mean wetted width, mean depth, water clarity, and electrofishing effort. The model had a high level of support (Akaike weight = 0.95; Table 1). Estimates of abundance and dispersion are reported on a natural-log scale. Detection covariates are reported on a logit scale and are standardized such that the intercept estimates the detection at mean values and the coefficients represent a unit change of 1 SD. The 95% confidence limits (CLs) were calculated by using a profile likelihood method (see Fiske and Chandler 2011).

| Parameter | Estimate ± SE | Lower 95% CL | Upper 95% CL |
|---|---|---|---|
| Latent abundance | 4.91 ± 0.13 | 4.66 | 5.18 |
| Detection: intercept | −1.08 ± 0.08 | −1.24 | −0.92 |
| Detection: water clarity | 0.24 ± 0.07 | 0.11 | 0.36 |
| Detection: electrofishing effort | 0.28 ± 0.06 | 0.17 | 0.39 |
| Detection: mean wetted width | −0.13 ± 0.09 | −0.30 | 0.04 |
| Detection: mean depth | −0.39 ± 0.07 | −0.52 | −0.25 |
| Detection: mean wetted width × depth | 0.21 ± 0.06 | 0.09 | 0.33 |
| Dispersion | 1.10 ± 0.29 | 0.49 | 1.65 |

and Kanehl (1993) regarding the use of capture–recapture electrofishing to estimate Smallmouth Bass abundance in streams. The inclusion of covariates in our multinomial capture–recapture model effectively accounted for variable Smallmouth Bass detection across a range of electrofishing effort levels, environmental conditions, and fish densities. Abundance estimates derived from our model for spatially distinct Smallmouth Bass populations compared favorably to both the baseline estimates obtained via snorkel counts and the unbiased Petersen capture–recapture estimates. Additionally, the CIs derived using an empirical Bayes estimator were much more precise than the Petersen capture–recapture CIs. The increased precision of the empirical Bayes CIs was due to the hierarchical framework of multinomial *N*-mixture models, which introduces a dependency among data sets (i.e., sites are modeled simultaneously by using data collected across all

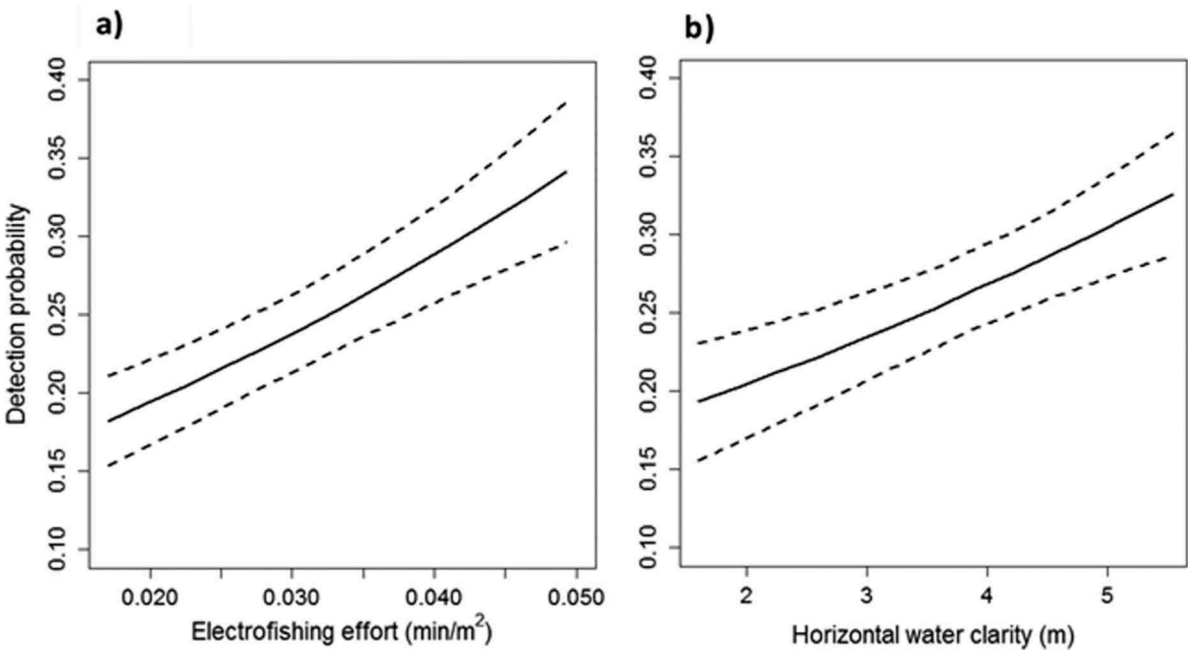


FIGURE 2. Trends in Smallmouth Bass detection probability with increasing **(a)** electrofishing effort and **(b)** water clarity in 25 stream reaches of the Ozark Highlands that were surveyed via tow-barge electrofishing from July to October 2014–2015. Estimates of detection probability were derived from a multinomial *N*-mixture capture–recapture model with a negative binomial error distribution; mean wetted channel width and mean depth were held at mean survey levels (Table 2). Dashed lines indicate 95% confidence intervals.

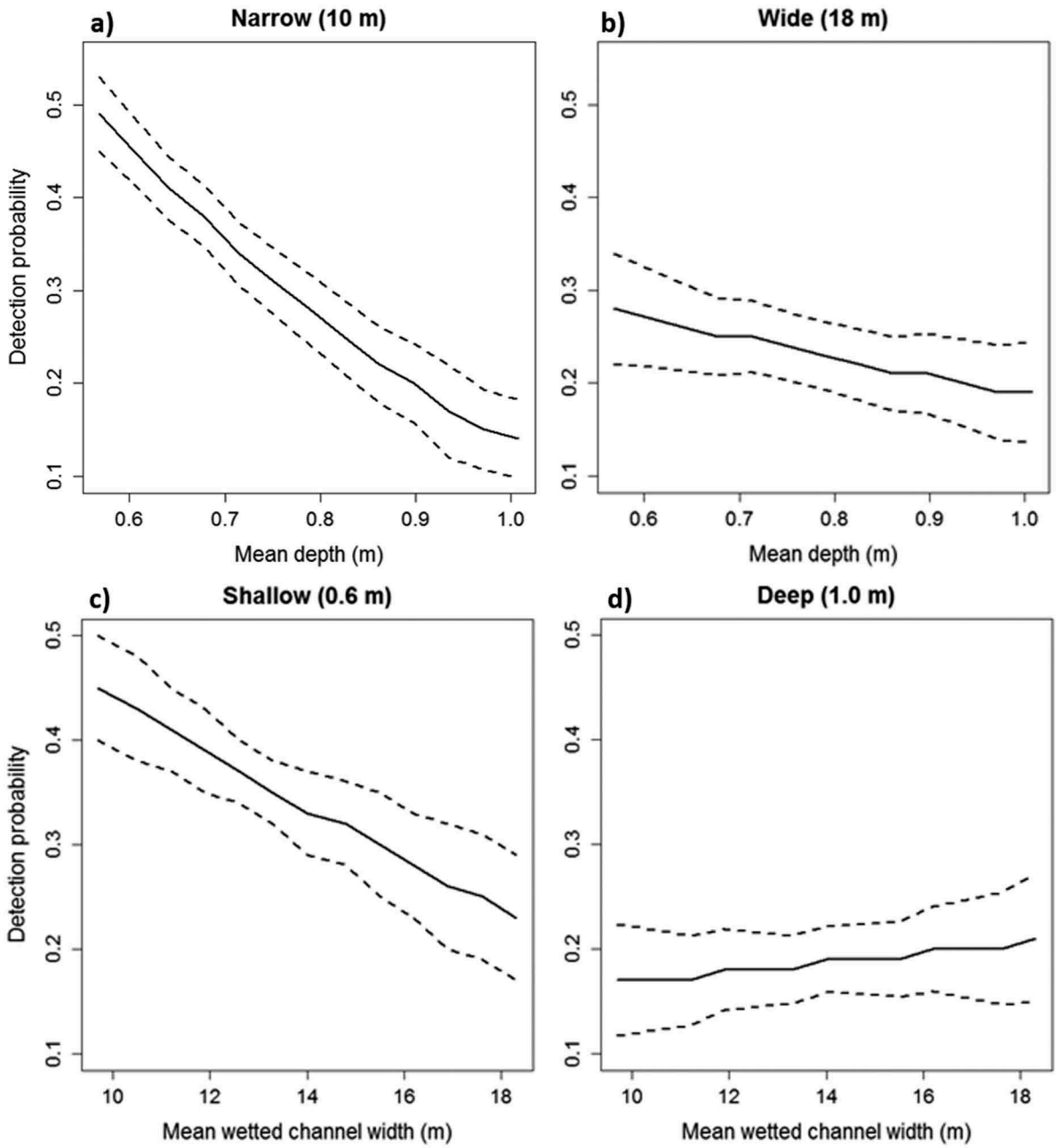


FIGURE 3. Relationship between the mean wetted width × mean depth interaction and Smallmouth Bass detection probability in 25 stream reaches of the Ozark Highlands, which were surveyed by use of tow-barge electrofishing from July to October 2014–2015. Estimates of detection probability were derived from a multinomial *N*-mixture capture–recapture model with a negative binomial error distribution; electrofishing effort and water clarity were held at mean survey levels (Table 2). "Narrow" and "wide" represent mean wetted width values that were –1 SD and +1 SD, respectively, from mean survey conditions. "Shallow" and "deep" represent mean depth values that were –1 SD and +1 SD, respectively, from mean survey conditions. Dashed lines indicate 95% confidence intervals.

sites), thereby improving the reliability of abundance estimates for sites with deficient data (Dorazio et al. 2005; Royle and Dorazio 2006). Dorazio et al. (2005) presented similar results using multinomial *N*-mixture models for surveying Okaloosa Darter *Etheostoma okaloosae* populations by use of a removal estimation method, which yielded CIs that were consistently more precise than those derived from an approach in which each site was modeled individually. Although Dauwalter and Fisher (2007) proposed a model to address the challenges of Smallmouth Bass electrofishing detection, those authors failed to provide an approach that would be usable by stream managers, as the number of streams was extremely limited ($n$ = 2; each in a different ecoregion) and the modeling of detection occurred at a spatial

scale that was far too fine to be practical for comparing local abundance estimates across a study area (i.e., managers typically do not sample individual channel units for comparison across sites). Conversely, we modeled the abundance of Smallmouth Bass subpopulations in reaches of 15 streams across a large study area with similar geologic and climate constraints (i.e., a single ecoregion). Thus, we demonstrated a broadly applicable approach for monitoring stream fish populations at an ecologically meaningful scale (i.e., representative habitat directly related to variation in local abundance). Although we focused on electrofishing of stream-dwelling Smallmouth Bass, the approach detailed here is easily adaptable to other gear types and other stream fishes.

Multiple environmental covariates explained the variation in Smallmouth Bass detection probability. We observed a positive trend in detection with increasing water clarity, which contradicts the findings of studies that have examined backpack electrofishing detection of stream fishes (e.g., Price and Peterson 2010). A common behavioral response of Smallmouth Bass during our surveys was to evade capture by moving in a downstream direction around sampling crews, even if initially pushed upstream. The reduced detection with decreasing water clarity was presumably due to Smallmouth Bass shocked behind the anode operators going unseen by the tow-barge operator, thus suggesting that detection increased when operators were netting fish under clear conditions. We also identified wetted channel width and depth, which together characterize the cross-sectional survey area in a stream, as factors contributing to variable electrofishing detection of Smallmouth Bass. The observed interaction of wetted channel width and depth highlights both the complexity of factors that contribute to variable electrofishing detection in streams and the need to survey across a wide range of environmental conditions to identify trends. Although we identified specific environmental covariates that explained Smallmouth Bass electrofishing detection probability among our study sites, many environmental factors affect stream fish detection, and the magnitude of influence varies considerably among systems and among species (Peterson et al. 2004; Hense et al. 2010; Price and Peterson 2010). Thus, stream fish managers might benefit from measuring a comprehensive suite of environmental covariates that they hypothesize will influence detection rather than solely relying on the results of other studies, particularly those involving dissimilar species or that have been conducted in different ecoregions.

Hierarchical population estimation approaches, such as multinomial *N*-mixture models, offer many advantages to stream fish managers relative to both CPUE and population estimation methods that model each site separately; however, there are trade-offs that should be considered. The primary advantages of all population estimation methods over CPUE include the ability to calculate a direct measure of abundance and the ability to account for variable detection across environmental conditions. Accounting for variable detection across time and space is particularly important for dynamic stream systems because standardization of environmental conditions is often unrealistic. Adjusting for variable detection allows stream fish abundance estimates to be comparable over long time periods across broad study areas. For example, long-term state-wide stream fish monitoring is a common agency objective, and reliance on CPUE data can hinder the identification of trends in populations and the refinement of management strategies (see Introduction). The ability to estimate abundance across variable conditions at greater temporal scales also promotes the establishment of stream fish–environment relationships, which are essential to both ecology and management. As we have demonstrated, hierarchical population estimation methods offer additional advantages. In addition to decreased uncertainty in Smallmouth Bass abundance estimates (i.e., narrower CIs) relative to Petersen capture–recapture, the use of a multinomial capture–recapture model allowed us to obtain reliable population estimates at sites with deficient data. Using Petersen capture–recapture, calculation of unbiased Smallmouth Bass abundance estimates was possible at less than half of our sites. For long-term stream fish monitoring, the failure to obtain usable data at all sites results in both lost information and wasted resources. However, adequate data at some sites (e.g., reasonable sample size and detection) are required for hierarchical population estimation methods to be effective (Dorazio et al. 2005). Multinomial *N*-mixture models have the additional flexibility to incorporate covariates that explain variation in abundance independent of detection. Requirements of multinomial *N*-mixture models do include collecting environmental covariate information at each site and conducting repeat surveys (i.e., both capture and recapture events or additional removal passes), which necessitate extra time and labor. However, both the hierarchical framework and the use of covariates to explicitly model detection for each survey event enable an optional application of multinomial capture–recapture models that is not possible with capture–recapture methods that model each site separately and only implicitly account for variable detection. Once covariates that influence detection are well established, a site-specific detection probability from a single survey (i.e., survey effort identical to CPUE) can be derived from the multinomial *N*-mixture model to adjust catch data to an absolute abundance estimate (see Thompson and Seber 1994; Peterson and Paukert 2009). We identified trends between Smallmouth Bass electrofishing detection and environmental covariates with a reasonable number of sites. The increased statistical complexity of multinomial *N*-mixture models is another important consideration. However, the necessary R code is well described in the manual for the 'unmarked' package (Fiske et al. 2015) and in related literature (e.g., Fiske and Chandler 2015; Chandler 2015). There is also a dedicated website available to users of 'unmarked' (//groups.google.com/forum/#!forum/unmarked) for troubleshooting and advice. Hierarchical population estimation models are also applicable to nonwadeable systems where closure is not feasible. Chandler et al. (2011) detailed a version

of multinomial *N*-mixture models that relaxes the closed-system assumption (see also Gwinn et al. 2011). We also refer readers to Royle (2004b) for a discussion of hierarchical population estimation models that accommodate spatially replicated point counts, which also have applications to stream fish surveys (see also Flowers and Hightower 2015 for a fisheries example).

Our findings also highlight the advantage of using secondary methods to increase confidence in the reliability of abundance estimates (see also Rosenberger and Dunham 2005). Baseline snorkel counts and unbiased Petersen capture–recapture estimates, both independently and in conjunction, supported the Smallmouth Bass abundance estimates that were derived from the multinomial capture–recapture model. Petersen capture–recapture CIs were consistently in general agreement with the empirical Bayes estimates, thus supporting our Smallmouth Bass abundance estimates at sites for which such comparisons were possible. The snorkel surveys provided a coarse comparison for the empirical Bayes estimates at sites where unbiased Petersen capture–recapture estimates were not obtainable. For example, the Smallmouth Bass snorkel count at Caney Creek supported a low abundance rather than suggesting a detection probability lower than what was estimated by the multinomial capture–recapture model. Conversely, at Big Sugar Creek, the Smallmouth Bass snorkel count supported the low detection estimated by the multinomial capture–recapture model rather than low abundance. All three approaches were in general agreement at sites where comparison was possible, which provided weighted evidence for the reliability of the empirical Bayes estimates. To assess the usefulness of our secondary methods to support our multinomial capture–recapture estimates, we also compared snorkel counts and Petersen capture–recapture estimates to multinomial two-pass removal electrofishing estimates. We anticipated that the removal model would overestimate Smallmouth Bass electrofishing detection due to a failure to meet removal assumptions across sites (e.g., increasing capture among passes). As expected, both snorkel counts and Petersen capture–recapture abundance estimates were consistently much higher than the empirical Bayes estimates (our unpublished data). The three sites with low snorkeling detection were not surprising. Both 14-Mile Creek and Evansville Creek are located near the southern ecoregion boundary of the Ozark Highlands and resemble streams of the Boston Mountains ecoregion, with different underlying lithology (Woods et al. 2005). During the Smallmouth Bass snorkel surveys in these streams, we observed increased countershading and high amounts of interstitial spaces, which likely greatly reduced detection.

One limitation of multinomial *N*-mixture models (common to most population estimation methods; but see Ford et al. 2012) is the inability to account for variation in detection among individuals (Chandler 2015). Veech et al. (2016) showed that when detection probability is less than 0.50, nonrandom individual variation (e.g., behavior) may result in erroneous abundance estimates when using *N*-mixture models. Two primary sources of individual variation in detection for single-species electrofishing are fish size and a "trap response" (i.e., differences in detection between marked and unmarked individuals during the recapture event). Our results indicated that neither fish size nor a trap response influenced the estimated Smallmouth Bass detection. Mean Smallmouth Bass TL did not vary considerably among sites, and the inclusion of a fish size covariate did not improve model fit. Additionally, the mean and variation of Smallmouth Bass TL at our sites were consistent with findings from other studies in the Ozark Highlands ecoregion (e.g., Brewer and Long 2015), suggesting that our results are applicable to unsurveyed sites within the study area. We also found no evidence of considerable remaining variation in detection between capture and recapture events, which precludes a trap response. If a trap response is suspected, the influence on detection can be addressed by modifying the capture–recapture function in the 'unmarked' package by introducing a behavioral covariate to the capture histories (see Chandler 2015).

We demonstrated how a contemporary population estimation method can be a viable alternative to CPUE but while using similar survey methods. We argue that the long-term benefits of hierarchical population estimation methods greatly outweigh the additional effort and learning curve. Although standardized survey methods are an important aspect of sound fisheries research and management (Bonar et al. 2009), attempting to maintain equal stream fish detection across space and time by replicating environmental conditions is often an unrealistic expectation that constrains progressive ecology and management. Additionally, we concur with Gwinn et al. (2016) that examination of relationships between stream fishes and the environment (e.g., seasonal changes in populations and flow–ecology relationships) is fundamental to advancing science and requires surveying across a broad range of conditions. Multinomial *N*-mixture models and other flexible contemporary approaches that account for variable detection and promote both strategic and flexible monitoring protocols are readily available.

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