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Sampling the stream landscape: improving the applicability of an ecoregion-level capture probability model for stream fishes

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Abstract

Temporal and spatial variability in streams results in heterogeneous gear capture probability (i.e., the proportion of available individuals identified) that confounds interpretation of data used to monitor fish abundance. We modeled tow-barge electrofishing capture probability at multiple spatial scales for nine Ozark Highland stream fishes. In addition to fish size, we identified seven reach-scale environmental characteristics associated with variable capture probability: stream discharge, water depth, conductivity, water clarity, emergent vegetation, wetted width-depth ratio, and proportion of riffle habitat. The magnitude of the relationship between capture probability and both discharge and depth varied among stream fishes. We also identified lithological characteristics among stream segments as a coarse-scale source of variable capture probability. The resulting capture probability model can be used to adjust catch data and derive reach-scale absolute abundance estimates across a wide range of sampling conditions with similar effort as used in more traditional fisheries surveys (i.e., catch-per-unit effort). Adjusting catch data based on variable capture probability improves the comparability of datasets, thus promoting both well-informed conservation and management decisions and advances in stream-fish ecology.

Introduction

Perceived fish distributions across the dynamic stream landscape are largely influenced by the timing and nature of sampling (Jackson et al. 2001; Poff and Zimmerman 2010; Gwinn et al. 2016). Variation in capture probability (i.e., the proportion of available individuals captured) among sampling methods, environmental conditions, and species hinders our ability to effectively detect changes in stream-fish abundance and assemblage structure. The importance of addressing variable capture probability as a basis for sound management and conservation has long been recognized by stream-fish researchers (e.g., Cleary and Greenbank 1954; Larimore 1961). Despite improved analytical approaches to account for variable capture probability (e.g., Williams et al. 2002; MacKenzie et al. 2005; Royle et al. 2013), catch-per-unit-effort (CPUE) remains the most common metric used to evaluate and monitor stream-fish populations (Gwinn et al. 2016). Major limitations of CPUE include calculating only an indirect measure of abundance, relying on a typically untested and often unrealistic assumption of proportional capture probability, and providing no insight about heterogeneity in capture probability among species (see also Gwinn et al. 2016 for a detailed discussion of the inherent limitations of CPUE for stream-fish sampling).

Standardizing sampling conditions (e.g., sampling only at baseflows) to support the use of CPUE may minimize variation in site-specific short-term capture probability. However, maintaining constant capture probability for broad-scale or long-term stream-fish monitoring is challenging because environmental conditions in streams vary extensively across space and time with complex relationships among variables (e.g., interactions at different levels; Jackson et al. 2001; Price and Peterson 2010; Gwinn et al. 2016). Furthermore, identifying relationships between stream fishes and the environment (e.g., flow-ecology relationships), often fundamental

research and management goals, are not possible when limiting sampling to a narrow range of environmental conditions

Sampling gear calibration (Peterson and Rabeni 2001; Peterson and Paukert 2009) is one approach to address the challenges of variable stream-fish capture probability. Gear calibration requires a series of repeat sampling events across a wide range of environmental conditions using either mark-recapture or comparisons with a previously calibrated gear. Data collected during gear calibration can be used to model heterogeneity in capture probability across sampling conditions and among stream fishes. The resulting model estimates capture probability from a single sampling event (i.e., repeat sampling is no longer required) based on site-specific conditions using linear combinations of model coefficients (see Peterson and Paukert 2009). Reduced sampling effort over time is a major long-term benefit of approaches, such as gear calibration, that model capture probability across sites a function of predictor variables (see also Huggins 1991; Pollock 2002; Royle and Dorazio 2006). A reduction in sampling effort over time is not possible with “traditional” methods that account for variable capture probability, but model each site individually without predictor variables (e.g., Zippin 1958; Manly and Seber 1973; Carle and Strub 1978). Analogous to mark-recapture and removal population estimators, the resulting capture probability estimates from the model resulting from gear calibration can be used to adjust raw catch data to an absolute abundance (Huggins 1991; Thompson and Seber 1994; Peterson and Paukert 2009). Thus, effective gear calibration can provide temporally- and spatially-comparable abundance estimates with equivalent sampling effort as CPUE, where standardization of sampling conditions is not required. However, an inherent challenge of effective stream-fish sampling gear calibration is capturing the complexity of capture probability

across environmental conditions while providing an end product that remains practical for implementation into long-term monitoring or research.

Our objective was to develop a practical, flexible, multilevel model to predict capture probability among stream fishes across a wide range of sampling conditions in wadeable warmwater streams using tow-barge electrofishing. We incorporated both fish and multiple instream characteristics into the model. Additionally, we used existing geospatial data to generalize coarse-scale lithological characteristics associated with variable electrofishing capture probability, which was novel to our approach. Previous research addressing stream-fish capture probability has been biased toward salmonids and our study represents a rare effort to model multispecies electrofishing capture probability in wadeable warmwater streams of the southern United States (see also Price and Peterson 2010). We detail an effective, yet straightforward, gear calibration approach that can easily be implemented by stream-fish scientists in other systems or with other sampling methods.

Methods

Study sites. - We sampled stream fishes in 34 stream reaches (each 0.6-1.0 km in length) of the Ozark Highlands ecoregion in northeast Oklahoma and southwest Missouri during summer 2014-2015 (Fig. 1). The Ozark Highlands ecoregion is characterized by oak-hickory forests, with valleys primarily converted to pasture (Woods et. al 2005). The dominant underlying lithology of the Ozark Highlands is cherty limestone; however, there is considerable variation, particularly near the ecotones. Many Ozark Highland streams are classified as groundwater dominated with clear water (but with substantial variation in water clarity; Nigh and Schroeder 2002). All stream reaches were wadeable (i.e., most habitat was < 1 m deep; Rabeni et al. 2009) and comprised

three to five riffle-run-pool sequences to characterize stream habitat. We chose stream reaches haphazardly to represent the study area, with final site selection largely driven by access and landowner permission. Our site selection provided considerable environmental variability in sampling conditions (a key aspect of effective gear calibration; Peterson and Paukert 2009) and included stream reaches near the southern ecotone (Table 1; Fig.1). We sampled stream reaches that were either > 2 stream km apart or we resampled the same site under different environmental conditions > 60 d apart (typically both) to ensure independent surveys (i.e., capture probability at a stream reach was not influenced by sampling at another reach). Any spatial dependence among stream reaches associated with capture probability not explained by predictor variables was accounted for with a random stream reach effect (see capture probability model methods below). We focused on estimating the capture probability of nine common centrarchid species, including popular sportfishes (Table 2). Centrarchids recover quickly from electrofishing with minimal mortality (Bardygula-Nonn et al. 1995; Dolan et al. 2002; Dolan and Miranda 2004).

Fish sampling. - We installed two sets of block-off nets at both the upstream and downstream end of each stream reach to close the system. Block-off nets were preferentially placed at shallow riffles to further inhibit fish movement (Peterson et al. 2004; Price and Peterson 2010). Either a low-water bridge at low flow ($n = 5$) or a dry riffle located at one end of the reach provided adequate fish barriers in some instances and no block-off nets were installed.

On day one (marking day), we used both a tow-barge electrofisher (Midwest Lake Management, Polo, Missouri) and angling to establish marked populations of centrarchids. Sampling methods were not standardized on marking day because our objective was to capture and mark as many fish as possible. We used angling primarily to increase the number of marked smallmouth bass (*Micropterus dolomieu*) because electrofishing capture probability is often low

for this species (Lyons and Kanehl 1993; Dauwalter and Fisher 2007; Mollenhauer and Brewer 2017), although other captured centrarchids were also included in the marked population. Approximately 300 of the over 17,000 fish were captured via angling. Captured fish were identified to species, measured (1.0-mm TL), and marked with a caudal fin clip. All crew were trained in both fish identification and standardized American Fisheries Society measurement techniques (Neumann et al. 2013). The minimum size of fish included in the marked population was 50-mm TL for *Lepomis* and rock bass (*Ambloplites rupestris*) and 80-mm TL for *Micropterus*. Our size restrictions excluded most age-0 fishes not recruited to electrofishing (McClendon and Rabeni 1986) and was also based on observed mortalities for very small centrarchids (Dolan and Miranda 2004; personal observations). Marked fish were released throughout the stream reach and allowed to recover and redistribute for ≈ 48 h. The time between electrofishing events was double the commonly accepted guideline for system recovery (Peterson and Cederholm 1984; Peterson et. al 2004). We also did not release marked fish until the sampling crew had proceeded a minimum of one riffle-run-pool sequence away to minimize the probability of being recaptured. Fish injured during sampling or that exhibited signs of excessive stress were released outside the blocked-off area.

We used multiple methods to assess delayed fish mortality and determined it was negligible. The blocked-off area was routinely inspected from the surface for dead marked centrarchids, which were removed from the study ($< 0.05\%$ of the marked fish population). As an additional assessment of fish mortality, a snorkel pass was performed at stream reaches with reasonable water clarity ($n = 22$) prior to the recapture event to identify dead centrarchids (none were found).

The recapture event (calibration day) consisted of two standardized removal electrofishing passes per riffle-run-pool sequence. The electrofishing crew comprised three people: one tow-barge operator armed with a hand net and two persons equipped with dip nets, each operating one of the anodes. We used pulsed direct current, 60 Hz, and a 25% duty cycle for electrofishing. Voltage was adjusted to a target power (W) to reduce variation in the electrical field across levels of ambient water conductivity while minimizing electrofishing-induced injuries as described by Miranda (2009). We thoroughly sampled areas ≥ 0.2 -m deep in an upstream direction with a zigzag pattern (i.e., not parallel to the stream channel). Logistic constraints of the tow-barge made very shallow habitats difficult to sample effectively, although use of these habitats is uncommon by centrarchids (Probst et al. 1984; Schlosser 1987; Brewer 2013). Recaptured centrarchids were identified to species and measured (TL). We also identified and measured unmarked fish to provide estimates of relative densities among reaches.

Environmental measurements. - We measured reach-scale instream characteristics hypothesized to influence electrofishing capture probability of stream fishes (Table 2). A conductivity pen (Myron L Company, Carlsbad, California; Model PT1) was used to measure water temperature (0.1 °C) and ambient water conductivity (1.0 $\mu\text{S}/\text{cm}$) at the downstream end of each stream reach. Wetted channel width (1.0 m) and thalweg depth (0.1 m) were measured at 50-m transects. Stream discharge (0.01 $\text{m}^3 \cdot \text{s}^{-1}$) was measured in a homogenous area of a run using the velocity-area method (Gordon et al. 2004). Water clarity (0.5 m) was measured as the horizontal distance an underwater observer could see a fish silhouette. We used both the same observer and fish silhouette at all stream reaches to maintain consistency (Dunham et al. 2009). The fish silhouette was designed to mimic the color, markings, and typical size (≈ 200 mm) of smallmouth bass in our study streams. GPS coordinates were recorded at both the upstream and downstream

end of each stream reach to estimate length (1.0 m). We also measured riffle lengths (1.0 m) to calculate the proportion of riffle habitat relative to the length of each stream reach. Both instream large wood (i.e., instream trees, logs, and rootwads) and emergent vegetation were estimated as the length (1.0 m) and width (1.0 m) of each patch to calculate proportional coverage.

We used geospatial data to classify stream segments (defined as a length of stream between third-order tributaries) by lithology. We based our classifications on both rock fragment type (Miller and White 1998; Pennsylvania State University 2008) and geology type (USGS 2005): cherty limestone, cherty alluvium, stony alluvium, and shale (hereafter referred to “geosol” categories). The geosol categories generalized lithological characteristics among stream reaches and provided surrogates for substrate and streambank characteristics (e.g., streambed complexity and interstitial spaces) that could influence capture probability. We generated a 50-m buffer around each stream segment using ArcMap (version 10.2.1, ESRI, Red Lands, California) and the dominant geosol type was used to characterize each segment.

Capture probability model. - We modeled heterogeneity in electrofishing capture probability among centrarchids across environmental conditions using a generalized linear mixed model (GLMM). GLMMs are a flexible, powerful class of statistical models with a hierarchical (i.e., multilevel) framework that allow for the inclusion of random effects (Gelman and Hill 2007). Random effects broaden the scope of inference, account for a lack of independence among observations (i.e., pseudoreplication), and accommodate both the inherent multiscale structure of stream systems and unequal sample sizes common in ecological data (Wagner et al. 2006; Jamil et al. 2013). We implemented models using the package lme4 (Bates et al. 2014) in the statistical software R (version 3.3.0, R Core Development Team, 2016).

Capture probability was modeled as a Bernoulli process with a binomial error distribution, where recapture was a binary response variable for each marked fish (i.e., 1 = recaptured, 0 = not recaptured). We assigned recaptures by matching each recaptured fish to a marked fish of the same species ± 5.0 -mm TL to incorporate a fish size predictor variable into the model. Individual fish recognition was not required from a modeling perspective (e.g., if two of five smallmouth bass ≈ 200 -mm TL were recaptured, the results of the model would have been identical regardless of which two were assigned as recapture). Accurate species identification and measurements within 5.0-mm TL were essential for reliable results. Given our crew training requirements (see above), we were confident this level of accuracy in our TL measurements was reasonable. Although we accounted for species identity and fish size (both critical for estimating electrofishing capture probability), we made other common mark-recapture assumptions with respect to individual variation (e.g., marked fish behaved similarly to unmarked fish, all fish of a given size and species had equal capture probability, etc.; Williams et al. 2002). We considered multiple reach-level environmental characteristics and the segment-level geosol categories in the model as predictor variables, where shale was the reference geosol category. Random intercepts for both stream reach and stream segment were included in the model. We also treated species as a random effect to develop a multispecies model (i.e., model each species simultaneously). In addition to including a random species intercept, we allowed the reach-level predictor variables to vary by species (i.e., random species slopes) to account for heterogeneity in capture probability among species in relation to instream characteristics. The most complex form of our model can be expressed as

$$(1) \quad \text{logit}(p_i) = \alpha_{j[i]} + \gamma_{k[i]} + \zeta_{m[k]} + \beta_1 x_i + \beta_2 \text{CL}_m + \beta_3 \text{CA}_m + \beta_4 \text{SA}_m + \sum_{z=5}^n (\beta_z v_k - b_{j[k]}),$$

for $i = 1, 2, \dots, n$

$$\begin{pmatrix} \alpha_j \\ b_j \end{pmatrix} \sim N \begin{pmatrix} \sigma_\alpha^2 & \rho\sigma_\alpha\sigma_b \\ \rho\sigma_\alpha\sigma_b & \sigma_b^2 \end{pmatrix}, \text{ for } j = 1, 2, \dots, J$$

$$\gamma_k \sim N(0, \sigma_\gamma^2), \text{ for } k = 1, 2, \dots, K$$

$$\varsigma_m \sim N(0, \sigma_\varsigma^2), \text{ for } m = 1, 2, \dots, M,$$

where p is estimated capture probability for fish i , α is a random intercept indexing species j , γ is a random intercept indexing stream reach k of stream segment m , ς is a random intercept indexing segment m , x is the fish-level continuous variable TL, CL is the cherty-limestone segment-level geosol category, CA is the cherty-alluvium segment-level geosol category, SA is the stony-alluvium segment-level geosol category, v is a reach-level continuous variable, and b is the random slope for species j . All continuous variables were natural-log transformed due to right-skewed distributions and standardized such that each had a mean of zero and a variance of one to improve interpretation of model coefficients and promote model convergence.

We used a selection procedure that both promoted parsimony and resulted in a final model that could be used to predict electrofishing capture probability among centrarchids at the reach scale across a range of sampling conditions. We fitted models using a tiered forward selection process similar to Jamil et al. (2013). The tiered forward selection facilitated the identification of predictor variables related to heterogeneity in capture probability across and among species at different model levels (i.e. fish, stream reach, and stream segment). It was not reasonable to develop a comprehensive competing model set given the number of predictor variables being examined and the interest in species-dependent relationships. Further, use of a backward selection process would have resulted in model convergence issues for the most complex models. Forward selection also allowed correlated predictor variables to be removed as model complexity increased rather than prior to model fitting. Thus, relative model fit can be assessed before removing correlated predictor variables from the analysis. We assessed models

using SigAIC (Broman and Speed 2002; Jamil et al. 2012, 2013). SigAIC is a variant of Akaike information criterion (Burnham and Anderson 2001) that introduces a higher penalty factor (c) for increased model complexity, where we used $\chi^2_{(0.05)} = 3.84$. At each step in the model-fitting process, a predictor variable or interaction term was retained if it decreased SigAIC by ≥ 1 . Our initial (null) model contained only the random intercepts (stream reach, stream segment, and species). For the first tier, we added the fish-level predictor total length as a main effect to account for variation in capture probability due to fish size before examining species-dependent environmental characteristics. We considered 13 reach-level predictor variables during the second tier, where variables were added only as species-dependent random terms (Table 2). The main effects of reach-level variables were not considered during the second tier because the random model components partly accounted for them and it allowed us to better isolate species-dependent relationships (Jamil et al. 2013). We considered both individual reach-level predictor variables and two-way interactions for variables with $|r| < 0.50$, where r is the Pearson's product-moment correlation coefficient. At each step of the second tier, we retained the reach-level variable or interaction term that most decreased SigAIC. Remaining variables with $|r| \geq 0.50$ were eliminated as each reach-level variable or interaction term was added to the model. The second tier concluded by adding the main effects for selected reach-level predictor variables. The objective of the third tier was to identify reach-scale predictor variables related to heterogeneity in capture probability across species, where we examined variables that were not selected or eliminated via correlations during the second tier. Main effects for reach-level variables were added to the model based on aforementioned criteria described for the second tier. For the last tier, we added the segment-level geosol categories to the model as main effects. Because traditional residual plots are uninformative for models with binary response variables, we

examined binned residual plots (Gelman and Hill 2007) to assess the fit of our final model. We bootstrapped 95% confidence intervals for coefficients of main effects in the final model using the “bootMer” function in lme4 ($n = 1,000$) and extracted variance components for random effects. Model coefficients are reported on the logit scale. We used linear combinations of coefficients from our final model to calculate capture probability at varying levels of predictor variables to improve relationship interpretation, where estimates were back transformed from the logit scale.

We performed a leave-one-out cross validation to assess “on the ground” performance of our final model at the reach scale. For each cross-validation test ($n = 34$), we removed one stream reach from the dataset and modeled the remaining data using predictor variables included in our final model. Thus, the cross-validation allowed us to test the predictive ability of our final model at 34 “new” stream reaches (i.e., we tested the model, with less information, against data it had never seen 34 times). We used values of TL and reach-scale environmental characteristics and the segment-scale geosol classification for the left-out stream reach to derive back transformed species capture probabilities for each stream reach based on linear combinations of model coefficients. Capture probability for each species was calculated using the median TL of 25-mm size classes and the weighted average was used to represent overall species capture probability. We compared model-predicted capture probabilities at the left-out stream reach to observed recapture proportions for species with both ≥ 1 recapture and ≥ 20 marked individuals. We assessed the bias and relative accuracy of our final model. Model bias was calculated as

$$(2) \quad \text{Bias} = \frac{1}{n} \sum_{i=1}^n (\hat{y}_i - y_i),$$

where n is the number of species capture probabilities examined across all cross-validation tests, $\hat{y}_i$ is the model-predicted capture probability, and y_i is the observed recapture proportion.

We used root-mean-square deviation (RMSD) to assess relative accuracy. RMSD is a more conservative measure of model accuracy than mean absolute error because error in model-predicted estimates are inflated as they deviate further from the observed value (Freund et al. 2010). RMSD was calculated as

$$(3) \quad \text{RMSD} = \sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{y}_i - y_i)^2}.$$

Although the observed recapture proportions of species at stream reaches provided an informative reference to compare model estimates of capture probability, there of course was inherent uncertainty with respect to representing “true” capture probability. Thus, we also calculated 95% binomial probability confidence intervals for observed recapture proportions at left-out stream reaches using the exact Clopper-Pearson method (Freund et al. 2010), which provided a plausible range of “true” capture probabilities. We calculated a single binomial probability confidence interval for each species (not size bin) both for simplicity and to construct more restrictive intervals to test model predictions (i.e., confidence intervals would have been wider for each size bin due to smaller sample size). We evaluated how often model-predicted species capture probabilities were contained in the intervals. Because there was also uncertainty in the model estimates, we also assessed how often 95% confidence intervals around model-predicted capture probability overlapped with the binomial probability confidence intervals. The delta method (Oehlert 1992) was used to estimate standard error for model coefficients prior to back transforming to the probability scale, where we used the package msm (Jackson 2011) in the statistical software R.

Results

312 *Fish sampling and environmental measurements.* - We marked 17,123 centrarchids across the 34
313 stream reaches (mean $\pm$ SD: 504 $\pm$ 302 fish; Table 2; see also online Supplementary Material
314 Table S1¹). As expected, *Micropterus* size was greater and more variable than other centrarchids,
315 rock bass tended to be larger than *Lepomis*, and longear sunfish (*Lepomis megalotis*) was the
316 most abundant species. Reach-scale environmental characteristics varied considerably, with the
317 exception of instream large wood and water temperature (Table 1). In particular, discharge was
318 highly variable among stream reaches and we sampled under both low- and high-flow
319 conditions. Stream reaches were distributed among 20 stream segments and approximately half
320 the segments were classified as cherty limestone.

321 *Capture probability model.* - The predictor variables in our final model resulting from the
322 selection process comprised fish TL, seven reach-level environmental characteristics, and the
323 geosol categories (Table 1 and Table 3). The reach-level main effects provided a comprehensive
324 characterization of stream sampling conditions, which included a percent riffle-discharge
325 interaction term. The final model also included random species slopes for water depth and
326 discharge (Table 3 and Table 4). Remaining variation in capture probability was lower among
327 stream segments (variance $\pm$ SD: 0.01 $\pm$ 0.08) than stream reaches (0.04 $\pm$ 0.21; see online
328 Supplementary Material Fig. S1¹). The binned residual plot indicated adequate model fit (see
329 online Supplementary Material Fig. S2¹). Approximately 95% of the binned residuals were
330 contained in theoretical error bounds and the plot did not reveal any concerning trends (Gelman
331 and Hill 2007). None of the bootstrapped 95% confidence intervals overlapped with zero for
332 coefficients of main effects that could be interpreted in that sense (i.e., significance; Table 3).
333 The coefficient for the percent riffle main effect was interpreted with respect to the percent riffle-
334 discharge interaction term (i.e., the relationship with capture probability was dependent on

different levels of both predictor variables). Because water depth was modeled among species (i.e., varying slopes), it was interpreted only with respect to the species-dependent terms (Table 4; i.e., the coefficient for the main effect represents the average relationship among species). The coefficient for the discharge main effect was interpreted in context of both the percent riffle-discharge interaction term and the species-dependent terms.

The relationship between predictor variables in the final model and estimated electrofishing capture probability was heterogeneous both among and across centrarchids. As expected, there was a strong positive relationship between capture probability and fish size (Table 3). Capture probability was higher for all geosol categories relative to shale, but there was a stronger positive relationship with stony alluvium. Capture probability decreased across species with increasing emergent vegetation, water clarity, and wetted channel width-depth ratio. Although we adjusted electrofishing power across stream reaches, there was a moderate increase in capture probability with increasing ambient water conductivity across species. There was no capture probability-riffle habitat relationship under higher flow conditions (Fig. 2A). However, capture probability increased with increasing riffle habitat under low-flow conditions due to the discharge-percent riffle interaction (Fig. 2B). Thus, the percent riffle-discharge interaction resulted in a sharp increase in estimated capture probability at low flows, even with a moderate amount of riffle habitat (Fig. 2C). Although the increase in estimated capture probability under low flows (i.e., the interaction term) was similar across species, the nature of the relationship with stream discharge varied among species (Table 3 and Table 4). For example, there was no relationship between green sunfish (*Lepomis cyanellus*) capture probability across higher flow conditions, with an increase under low flows similar to other species (Fig. 3). The relationship between capture probability and water depth also varied among stream fishes (Table 4). For

example, there was no water depth-capture probability relationship for longear sunfish, but capture probability decreased with deeper conditions for other species (Table 4; Fig. 4). The negative relationship with water depth was most pronounced for smallmouth bass, where capture probability was much higher in shallower stream reaches compared to deeper reaches (Fig 4).

The cross-validation test comparisons ($n=124$) indicated that the final model performed well with respect to predicting electrofishing capture probability among centrarchids at the reach scale across a range of sampling conditions. Capture probability estimates did not tend to either overpredict or underpredict when compared to observed recapture proportions (overall bias was 0.00; Table 5). Capture probability estimates tended to be lower than the observed recapture proportion for both redear sunfish (*Lepomis microlophus*) and warmouth (*Lepomis gulosus*). However, we were only able to make a small number of comparisons due to the relatively small size for these less-common centrarchids in our study area (Table 1). Overall RMSD across the cross-validation tests was 0.10 (Table 5). RMSD was lowest for smallmouth bass (0.13), which was not surprising due to the degree of heterogeneity in capture probability across levels of both discharge and water depth (Table 4). Model-estimated capture probability compared favorably to the observed recapture proportions when accounting for inherent uncertainty. Capture probability estimates were contained in 95% binomial probability confidence intervals 90% of the time, with similar trends among species (Table 5). Only one 95% confidence interval around model-estimated capture probability did not overlap with the binomial probability confidence intervals (Table 5).

Discussion

We detailed an effective, yet straightforward, approach to model capture probability among stream fishes at multiple spatial scales with practical applications for research and management. We sampled across a wide range of conditions and identified multiple environmental characteristics associated with heterogeneous electrofishing capture probability. A novel aspect of our study was using geospatial data to generalize lithological characteristics among stream reaches, which allowed us to account for coarse-scale factors associated with variation in capture probability. The inclusion of the geosol groups not only reduced field effort, but also increased the spatial extent of the model's applicability. For example, stream reaches across a broad spatial area may sometimes share temporally-variable instream characteristics, but differ in underlying lithology that contribute to variation in stream-fish capture probability. Our study supports well-informed stream-fish management and conservation decisions and promotes the establishment of species-environment relationships. Although we chose to model capture probability of stream-dwelling centrarchids using tow-barge electrofishing, the gear calibration approach described here is easily adaptable to other fish species and sampling gears.

Our findings highlight the complexity of capture probability across the dynamic stream landscape. Low flows resulted in very shallow (sometimes dry) riffles and sharp increases in capture probability, particularly with higher proportions of riffle habitat. The disconnected riffle-run-pool sequences not only eliminated potential fish movement across deeper riffle areas, but may also have altered centrarchid habitat use. For example, Hafs et al. (2010) found that smallmouth bass tended to congregate in shallow areas at low flows, presumably due to altered foraging strategies. The combination of less available run and pool habitat and the occupancy of shallow areas at low flows potentially explains the sharp increase in capture probability at sites

with high proportions of riffle. Fish became highly susceptible to electrofishing by being concentrated in shallow-water areas.

We identified species-dependent capture probability relationships among taxonomically- and morphologically-similar stream fishes that could be related to differences in habitat use and behavior. For example, the weak relationship between green sunfish capture probability and discharge could be explained by their feeding strategy. Green sunfish are sit-and-wait predators, which results in an affinity for structure in calmer stream areas (Werner and Hall 1977; Stuber et al. 1982). Thus, green sunfish would be expected to have similar capture probability across flow conditions. Conversely, capture probability would be expected to decrease with increasing discharge for species occupying areas of higher flow due to the increased difficulty of netting shocked fish. Smallmouth bass capture probability was likely reduced at higher flows relative to other centrarchids due to their tendency to move downstream when approached by the electrofishing crew, which made capture difficult at stream reaches with elevated discharge. Decreasing smallmouth bass capture probability with increasing depth was also not surprising given that this species is associated with deep pools in Ozark streams (Brewer 2013); however, the magnitude of the relationship was an interesting finding. Our findings indicate that longear sunfish capture probability did not vary with changes in depth. Longear sunfish typically occupy shallow pools and runs (Laughlin and Werner 1980; Bietz 1981); therefore, increased availability of deep water habitats would not be expected to influence capture probability.

The flexible hierarchical framework of GLMMs promoted robustness in our capture probability estimates, accommodated the multilevel structure of our dataset and the unequal sample sizes, and allowed us to model species simultaneously. Our capture probability estimates reflected data collected across all stream reaches and species because each coefficient for a

random effect shares information (i.e., borrowing strength) and is pulled towards a common value (shrinkage; Pinheiro and Bates 2000). For example, treating stream reach as a random effect (i.e., modeling the variance) resulted in reach-specific intercepts that represented a compromise (i.e., partial pooling) between estimates obtained from separate reach-specific analyses (no-pooling) and an analysis that assumed all reaches had the same intercept (complete pooling). Partial pooling and shrinkage reduce bias in coefficients for main effects and increase reliability in model estimates (Wagner et al. 2006; Gelman and Hill 2007). The hierarchical model framework and shrinkage also increased the reliability of estimates at sites where basic mark-recapture assumptions would not have been met (e.g., too few marked or recaptured fish)-, which is impossible when modeling each site individually (Dorazio et al. 2005). Additionally, treating species as a random effect and allowing the slopes to vary with instream characteristics resulted in a single multispecies model. The multispecies GLMM was both a superior and more statistically-appropriate approach than fitting separate generalized linear models (GLMs) because it promoted better species-specific fit and valid comparisons could be made among species (Jamil et al. 2013). Also, the ability to borrow strength from the entire ensemble of data allowed us to provide capture probability estimates that had a degree of robustness for data-poor species, which would have been impossible with a single-species GLM. A multispecies GLM that treated species as a fixed categorical effect would have been unlikely to converge if all species were included due to the additional parameters and unequal sample sizes. The inclusion of additional species, even those with small sample size, was beneficial in the hierarchical modeling framework because it promoted robustness in the random effect variance components. Additional species can seamlessly be added to the model, where initially capture probability

estimates would be strongly pulled towards the grand mean, but over time (i.e., as sample size increased) also reflect species-specific fit.

The choice of approaches to model capture probability represents tradeoffs between complexity and practicality. Hierarchical capture probability models are increasingly common in the fisheries literature and the statistical advantages are well described here and elsewhere (e.g., Wyatt 2002; Rivot et al. 2008; Ruiz and Laplanche 2010). Nevertheless, improved statistical techniques to account for variable capture probability have rarely been applied by stream-fish researchers and managers (Gwinn et al. 2016). We argue that the increased complexity of improved analytical methods has contributed to the minimal implementation by stream-fish scientists and authors describing these techniques have tended to focus more on statistical nuances than practical applications (but see Mäntyniemi and Romakkaniemi 2002; Dorazio et al. 2005; Gwinn et al. 2011). For example, Bayesian hierarchical approaches to model stream-fish capture probability (e.g., Rivot et al. 2008; Webster et al. 2008; Price and Peterson 2010) offer even more flexibility and potentially more precise estimates than the maximum likelihood framework we describe here. However, the statistical complexity and challenging software (e.g., WinBUGS) that comes with Bayesian approaches may not be a desirable trade-off for many stream-fish scientists. The modeling framework that we present here is by no means simple. However, the gear calibration approach can be easily replicated by anyone with a reasonable understanding of hierarchical models and R coding (described elsewhere for these models; Jamil et al. 2013; Bates et al. 2014) and could certainly be done in a Bayesian framework if desired (e.g., Price and Peterson 2010). In conjunction with necessary statistical jargon, we provided systematic details from the data-collection process through the selection of predictor variables. We also highlighted “real-world” applications of our approach, which includes reliable reach-

scale capture probability estimates and the reduction of sampling effort over time when incorporated into long-term stream-fish monitoring.

Our model allowed a fish-level predictor variable (TL) to be included without the need for individual recognition. Both Ford et al. (2012) and Breton et al. (2013) detail effective mark-recapture methods to account for heterogeneity in capture probability among individuals; however, neither model is practical if inherent individual recognition is difficult (most fish species) or a very large number of fish will be marked. Although accurate measures of fish size were critical for our method to be effective, this assumption would be essential to any model that accounted for size variation among individuals. Price and Peterson (2010) used a method to ours using size bins. We chose to model total length at the individual level before generating size bins that were more practical for the reach-scale species capture probability estimates. Our method could easily be extended to other fish-level characteristics that may influence capture probability (e.g. sex) and is not limited by sample size.

The cross-validation procedure provided a means to assess the “on the ground” performance of our final model. From a practical perspective, the model performed well with respect to providing reliable capture probability estimates. Capture probability estimates that differed considerably from observed recapture proportions at stream reaches could sometimes be explained by atypical sampling conditions. Evansville Creek, the stream reach where we encountered extreme low-flow conditions ($0.09 \text{ m}^3 \cdot \text{s}^{-1}$), had the highest number of capture probability estimates not contained in the binomial probability confidence intervals (3 of 5). The model tended to overestimate capture probability at Evansville Creek; however, this was not surprising due to the higher level of uncertainty at very low flow (Figure 2). Furthermore, we were extrapolating when predicting capture probability at Evansville Creek because these data

were removed from the cross-validation test. Therefore, our final model based on all available data would presumably perform better at another site sampled under extreme low flows. We could relate other instances where the model-estimated capture probabilities differed considerably from observed recapture proportions to unusual observations. For example, recapture proportion was curiously low for longear sunfish at Lost Creek (0.03) and uncommonly high for rock bass at Fivemile Creek (0.55). It is reasonable to assume that our model-derived estimates, which were a reflection of data collected across all sites, better represented expected capture probability under the given sampling conditions on occasions where recapture proportions were unusual.

Gear calibration is not without its limitations. A considerable amount of effort is required before sampling intensity can be reduced to a single event. Although here we report favorable results with only two intensive field seasons, remaining “noise” in the model would be expected to continue to decrease over time with additional repeat sampling. We also experienced periodic rainfall throughout both our field seasons, which increased the environment variability encountered during sampling. As we demonstrated with the cross-validation test at Evansville Creek, the model would not be expected to predict well outside of environmental conditions measured during the gear calibration process. Thus, additional repeat sampling would be required if new conditions were encountered and additional geospatial data may need to be compiled if the spatial extent of sampling increased. Similarly, additional repeat sampling would be required if fish size varied considerably from year-to-year to effectively model its relationship with capture probability or if new species were being considered. The amount of sampling necessary for effective gear calibration depends on system dynamics, the species of interest, and the level of model precision desired to meet research or management objectives. Although gear

calibration leads to reduced sampling effort over time, additional effort is required for all sites to compile data for predictor variables. However, we required < 2 h at each site to measure the physicochemical parameters and the spatial data used for the geosol categories were easily obtained.

The relationships that we identified between stream-fish capture probability and environmental variables may not be analogous to other systems, species, or sampling gears. For example, instream large wood has been associated with stream-fish capture probability (Kruse et al. 1998; Rosenberger and Dunham 2005; Price and Peterson 2010), but this variable was not included in our final model. Instream large wood likely did not vary enough among our stream reaches to contribute to variation in capture probability. Also, seining has been shown to have different capture probability relationships with environmental variables than electrofishing (Price and Peterson 2010; Pregler et al. 2015). Stream-fish researchers and managers performing gear calibration might benefit from measuring a comprehensive suite of environmental variables they hypothesize will influence capture probability rather than solely relying on results of other studies, particularly those involving dissimilar species, different gears, or conducted in different ecoregions.

A recent trend in freshwater fisheries is advocating standardized sampling to promote comparability of datasets both within and among regions (e.g., Bonar et al. 2009; Bonar et al. 2015; Bonar et al. 2017). Standardizing methods (e.g., gear type, procedures, and effort) and, when feasible, environmental conditions are important foundations of stream-fish research and monitoring protocols. For example, standardization can minimize human-induced influences on capture probability and reduce model data dimensionality. However, we demonstrated that standardization does not alleviate the inferential issues associated with heterogeneous stream-fish

capture probability (see also Peterson et al. 2004; Price and Peterson 2010; Mollenhauer and Brewer 2017). We used standardized two-pass electrofishing at all sites, yet capture probability varied considerably in relation to instream dynamics. Clearly, standardizing multiple instream characteristics across space and time to minimize variability in capture probability is unrealistic. We also attempted to standardize electrofishing power using accepted guidelines (Miranda 2009); however, capture probability still increased with increasing ambient water conductivity. Electrofishing capture probability also varied among both stream reaches due to differences in lithology and centrarchids. Thus, our findings highlight the challenges and limitations of using a standardized stream-fish sampling approach, particularly across regions and species, for comparable datasets. Relying blindly on standardization (i.e., not considering the multifaceted factors that can influence capture probability) can result in gross misrepresentations of stream-fish population size and assemblage structure. More importantly, inaccurate population assessments can lead to inappropriate conservation and management decisions and impede progress in stream-fish ecology.

The gear calibration approach we detail here requires an acceptable level of effort relative to the long-term benefits and balances complexity with practicality. Approaches that focus on applicability in conjunction with statistical intricacies promote increased implementation of stream-fish studies and monitoring efforts that both account for variable capture probability and sample across a broader range of conditions to establish species-environment relationships. We believe applications similar or complementary to the approach presented here will both maximize available resources and promote advances in stream-fish ecology and management.

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Table 1. Reach-scale characteristics for 34 stream reaches in the Ozark Highlands ecoregion of northeast Oklahoma and southwest Missouri during summer 2014-2015.

Variable	Definition	Mean $\pm$ SD	Range
Cross-sectional area (m ²)	Mean wetted width times thalweg depth measured at 50 m transects	13.5 $\pm$ 6.5	4.9 - 39.4
*Discharge (m ³ • s ⁻¹)	Mean of three replicates in a homogenous area of a run	1.9 $\pm$ 2.1	0.09 - 8.52
Percent cover	Percent emergent vegetation plus percent instream large wood	5.8 $\pm$ 5.9	1 - 28
*Percent emergent vegetation	Total area divided by sampling area times 100	2.8 $\pm$ 5.6	1 - 25
Percent instream large wood	Total area divided by sampling area times 100	3.0 $\pm$ 2.3	1 - 10
*Percent riffle	Total length divided by reach length times 100	22.0 $\pm$ 8.8	0.07 - 0.42
Pool depth (m)	Mean maximum pool depth	1.4 $\pm$ 0.3	1.1 - 4.0
*Water clarity (m)	Horizontal distance underwater observer could see a fish silhouette	3.3 $\pm$ 1.5	1.0 - 7.0
*Water conductivity (μ S/cm)	Ambient conductivity measured at the downstream end of reach	284.2 $\pm$ 80.4	160 - 500
*Water depth (m)	Mean thalweg depth measured at 50 m transects	0.8 $\pm$ 0.2	0.5 - 1.3
Water temperature (°C)	Measured at downstream end of the reach	21.6 $\pm$ 2.6	16.1 - 25.7
Wetted channel width (m)	Mean wetted width measured at 50 m transects	15.1 $\pm$ 4.7	9 - 32
*Width-depth ratio	Mean wetted width of reach divided by mean thalweg depth of reach	18.7 $\pm$ 5.1	9.9 - 33.9

785 **Note:** * indicates reach-scale variables included in the capture probability model using the model-selection process described in the
786 text.

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Table 2. Summary of fish species marked in 34 stream reaches in the Ozark Highlands ecoregion of northeast Oklahoma and southwest Missouri during summer 2014-2015.

Common name	Scientific name	Number	Mean TL $\pm$	
		marked	SD (mm)	TL range (mm)
Bluegill	<i>Lepomis macrochirus</i>	1,904	94 $\pm$ 25	50 - 215
Green sunfish	<i>Lepomis cyanellus</i>	2,503	106 $\pm$ 29	50 - 207
Largemouth bass	<i>Micropterus salmoides</i>	513	175 $\pm$ 73	50 - 196
Longear sunfish	<i>Lepomis megalotis</i>	8,595	94 $\pm$ 21	50 - 186
Redear sunfish	<i>Lepomis microlophus</i>	158	85 $\pm$ 24	50 - 286
Rock bass	<i>Ambloplites rupestris</i>	2,032	128 $\pm$ 37	52 - 182
Smallmouth bass	<i>Micropterus dolomieu</i>	1,150	200 $\pm$ 61	80 - 460
Spotted bass	<i>Micropterus punctulatus</i>	28	165 $\pm$ 67	80 - 404
Warmouth	<i>Lepomis gulosus</i>	240	113 $\pm$ 23	90 - 360

Table 3. Coefficients and bootstrapped 95% confidence intervals (CI) for main effects from a generalized linear mixed model developed to examine heterogeneity in electrofishing capture probability among stream fishes of the Ozark Highlands ecoregion.

Parameter	Coefficient ± SE	95% CI
Intercept	-1.71 ± 0.19	(-2.09, -1.35)
TL	0.31 ± 0.02	(0.25, 0.36)
*Discharge	-0.25 ± 0.09	(-0.42, -0.07)
Percent emergent vegetation	-0.24 ± 0.06	(-0.37, -0.12)
Percent riffle	0.08 ± 0.06	(-0.04, 0.20)
Water conductivity	0.18 ± 0.07	(0.05, 0.31)
Water clarity	-0.19 ± 0.06	(-0.31, -0.09)
*Water depth	-0.10 ± 0.09	(-0.27, 0.06)
Width-depth ratio	-0.13 ± 0.06	(-0.25, -0.01)
Discharge x percent riffle	-0.16 ± 0.05	(-0.26, -0.05)
Geosoil (Cherty alluvium)	0.54 ± 0.19	(0.16, 0.95)
Geosoil (Stony alluvium)	1.22 ± 0.24	(0.75, 1.71)
Geosoil (Cherty limestone)	0.38 ± 0.19	(0.03, 0.76)

Note: Coefficients are reported on a logit scale. All continuous variables were standardized such that each had a mean of zero and a standard deviation of one, where the model intercept estimates capture probability at mean conditions and coefficients for continuous variables represent a unit change of one standard deviation. Geosoil was defined as a categorical variable

800 with shale as the reference category. Asterisks indicate site-level variables that were also
801 modeled as species-dependent random terms (Table 4).

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Table 4. Species-dependent coefficients (i.e., random intercepts and slopes) with SD from a generalized linear mixed model developed to examine heterogeneity in electrofishing capture probability among stream fishes of the Ozark Highlands ecoregion.

Species	Intercept ± SD	Discharge ± SD	Water depth ± SD
Bluegill	-1.53 ± 0.06	-0.25 ± 0.07	-0.06 ± 0.06
Green sunfish	-1.48 ± 0.06	-0.07 ± 0.06	-0.10 ± 0.05
Largemouth bass	-1.91 ± 0.10	-0.32 ± 0.09	-0.13 ± 0.08
Longear sunfish	-1.61 ± 0.05	-0.30 ± 0.04	0.02 ± 0.04
Redear sunfish	-1.54 ± 0.15	-0.31 ± 0.11	0.01 ± 0.11
Rock bass	-1.91 ± 0.07	-0.14 ± 0.07	-0.15 ± 0.06
Smallmouth bass	-2.20 ± 0.08	-0.32 ± 0.07	-0.42 ± 0.06
Spotted bass	-1.80 ± 0.21	-0.28 ± 0.11	-0.12 ± 0.13
Warmouth	-1.37 ± 0.12	-0.25 ± 0.10	0.06 ± 0.09

Note: Standard deviation was calculated as the square root of the variance for each random term.

Table 5. Results of a leave-one-out cross validation that evaluated the performance of a generalized linear mixed model for estimating tow-barge electrofishing capture probability among fishes in 34 stream reaches of the Ozark Highlands: bias and relative accuracy (RMSD), the number of estimates contained in the 95% binomial probability CI (contained), and the number of times predicted 95% CI overlapped with the binomial probability 95% CI (overlap).

Species	Bias	RMSD	Contained 95% CI	Overlapped 95% CI
All	0.00	0.10	90% (112 of 124)	99% (123 of 124)
Bluegill	-0.01	0.10	95% (18 of 19)	100% (19 of 19)
Green sunfish	0.01	0.09	91% (20 of 22)	100% (22 of 22)
Largemouth bass	0.00	0.07	100% (10 of 10)	100% (10 of 10)
Longear sunfish	0.02	0.08	87% (26 of 30)	97% (29 of 30)
Redear sunfish	-0.04	0.07	100% (2 of 2)	100% (2 of 2)
Rock bass	0.01	0.11	90% (18 of 20)	100% (20 of 20)
Smallmouth bass	0.00	0.13	88% (15 of 17)	100% (17 of 17)
Warmouth	-0.05	0.11	75% (3 of 4)	100% (4 of 4)

Note: RMSD is root-mean-square error and CI is confidence interval (see Methods for a full description of calculations).

Fig 1. Thirty-four stream reaches of the Ozark Highland ecoregion in northeast Oklahoma and southwest Missouri (black dots). Reaches (0.6-1 km) were sampled during summer 2014-2015 to develop a capture probability model for tow-barge electrofishing.

Fig. 2. Electrofishing capture probability across levels of discharge and percent riffle habitat using estimates from a generalized linear mixed model that included an interaction term between the two predictor variables (Table 3). Panel A shows the relationship between capture probability and riffle habitat at higher flows (discharge held at 1 SD). Panel B shows the relationship between capture probability and riffle habitat at low flows (discharge held at -1.5 SD). Panel C shows the relationship between capture probability and discharge with percent riffle held at 1 SD, where capture probability increases sharply at lower flow due to the interaction. The x-axes represent levels of either percent riffle or discharge from -2 to 2 SD. Capture probability was calculated for the average-sized longear sunfish (*Lepomis megalotis*), although the general relationships were similar among species and across fish size (see also Fig. 3). In all of the panels, other reach-level predictor variables included in the model were held at mean values and the geosol category was cherty limestone (see Table 3). Dashed lines are 95% confidence intervals.

Fig. 3. Relationship between electrofishing capture probability and discharge among stream fishes of the Ozark Highlands using species-dependent random terms derived from a generalized linear mixed model (Table 4). The left panel represents the average-size bluegill (*Lepomis macrochirus*) and the right panel represents the average-size green sunfish (*Lepomis cyanellus*). The x-axis represents levels of discharge from -2 to 2 SD. Other reach-level variables included in

the model were held at mean values and the geosol category was cherty limestone (see Table 3).

Dashed line are 95% confidence intervals.

Fig. 4. Relationship between electrofishing capture probability and water depth among stream fishes of the Ozark Highlands using species-dependent random terms derived from a generalized linear mixed model (Table 4). The left panel represents average-size smallmouth bass (*Micropterus dolomieu*) and right panel represents the average-size longear sunfish (*Lepomis megalotis*). The x-axis represents levels of mean water depth from -2 to 2 SD. Other reach-level variables included in the model were held at mean values and the geosol category was cherty limestone (see Table 3). Dashed line are 95% confidence intervals.

Fig 1. Thirty-four stream reaches of the Ozark Highland ecoregion in northeast Oklahoma and southwest Missouri (black dots). Reaches (0.6-1 km) were sampled during summer 2014-2015 to develop a capture probability model for tow-barge electrofishing.

144x187mm (150 x 150 DPI)

Fig. 2. Electrofishing capture probability across levels of discharge and percent riffle habitat using estimates from a generalized linear mixed model that included an interaction term between the two predictor variables (Table 3). Panel A shows the relationship between capture probability and riffle habitat at higher flows (discharge held at 1 SD). Panel B shows the relationship between capture probability and riffle habitat at low flows (discharge held at -1.5 SD). Panel C shows the relationship between capture probability and discharge with percent riffle held at 1 SD, where capture probability increases sharply at lower flow due to the interaction. The x-axes represent levels of either percent riffle or discharge from -2 to 2 SD. Capture probability was calculated for the average-sized longear sunfish (*Lepomis megalotis*), although the general relationships were similar among species and across fish size (see also Fig. 3). In all of the panels, other reach-level predictor variables included in the model were held at mean values and the geosol category was cherty limestone (see Table 3). Dashed lines are 95% confidence intervals.

254x190mm (96 x 96 DPI)

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254x190mm (96 x 96 DPI)

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254x190mm (96 x 96 DPI)