Using Hierarchical Bayesian Multispecies Mixture Models to Estimate Tandem Hoop-net-Based Habitat Associations and Detection Probabilities of Fishes in Reservoirs

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Using Hierarchical Bayesian Multispecies Mixture Models to Estimate Tandem Hoop-net-Based Habitat Associations and Detection Probabilities of Fishes in Reservoirs

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Abstract
Species distribution models are useful tools to evaluate habitat relationships of fishes. We used hierarchical Bayesian multispecies mixture models to evaluate the relationships of both detection and abundance with habitat of reservoir fishes caught using tandem hoop nets. A total of 7,212 fish from 12 species were captured, and the majority of the catch was composed of Channel Catfish *Ictalurus punctatus* (46%), Bluegill *Lepomis macrochirus* (25%), and White Crappie *Pomoxis annularis* (14%). Detection estimates ranged from 8% to 69%, and modeling results suggested that fishes were primarily influenced by reservoir size and context, water clarity and temperature, and land-use types. Species were differentially abundant within and among habitat types, and some fishes were found to be more abundant in turbid, less impacted (e.g., by urbanization and agriculture) reservoirs with longer shoreline lengths; whereas, other species were found more often in clear, nutrient-rich impoundments that had generally shorter shoreline length and were surrounded by a higher percentage of agricultural land. Our results demonstrated that habitat and reservoir characteristics may differentially benefit species and assemblage structure. This study provides a useful framework for evaluating capture efficiency for not only hoop nets but other gear types used to sample fishes in reservoirs.

Species distribution models have become an important tool for fisheries scientists and managers. Models are developed using sampling data that relates the number of individuals captured to locations that consists of different habitat characteristics (Olden and Jackson 2001; Wenger et al. 2008; Webster et al. 2008). Abiotic and biotic factors influence distribution of aquatic organisms differently across the landscape (Olden and Jackson 2001) and may influence detection probability. However, many of these models fail to account for error in detection, and variation in detection can result in variation in observed counts that might not be dependent on a change in true abundance (Royle 2004; Royle et al. 2005). Because perfect detection is nonexistent, it is important to account for detection when estimating relationships with abundance to reduce misleading inference when comparing both spatial and temporal replicated counts (Webster et al. 2008).

It is well known that the influence of habitat on population dynamics can operate at both fine and coarse scales (Frissell et al. 1986; Dunham and Vinyard 1997; Harig and Fausch 2002). Ecosystems are structured hierarchically where factors at coarse scales (e.g., lake or reservoir) should influence factors at fine scales (e.g., site-level habitat) (Frissell et al. 1986; Lanka et al. 1987; Poff 1997; Harig and Fausch 2002). For instance, in reservoirs, the riparian buffer and surrounding landscape...
influences site-level sediment dynamics (Berkman and Rabeni 1987), habitat composition (Sass et al. 2006), and food availability (Fischer et al. 2010). Therefore, reservoir characteristics at the basin scale are an extension of landscape interactions (Frissell et al. 1986; Brewer et al. 2007), confounding fine-scale assessments due to correlation with higher-level factors that govern abiotic and biotic dynamics (Dunham and Vinyard 1997). Because landscape–riparian interactions likely affect local fish dynamics, it is important to consider land use when determining species–habitat relationships (Bodie 2001; Olden and Jackson 2001; Sass et al. 2006), something often examined by stream ecologists but rarely studied in lake and reservoir studies. Failure to account for these multiscale relationships may reduce the predictive power of species distribution models that use variables measured at a single scale (Leftwich et al. 1997; Rich et al. 2003; Pont et al. 2005; Sindt et al. 2012).

Capture efficiency of sampling gears used in fisheries has received considerable attention (Kirsch and Peterson 2014). Hoop nets are commonly used to sample fish in lentic and lotic environments (Yeh 1977; Muoneke et al. 1992; Pugh and Schramm 1998), though mostly for Channel Catfish Ictalurus punctatus (Michaletz and Sullivan 2002; Stewart and Long 2012), sunfishes (Centrarchidae) (Colotelo et al. 2013), larval fishes (Wu et al. 2013), and Northern Pike Esox lucius (Ziliukiené and Žiliukas 2012). Only one study that we are aware of has evaluated the capture efficiency of hoop nets (Buckmeier and Schlechte 2009), but this study focused solely on a single species. In our experience, multiple species are often captured in hoop nets (i.e., bycatch) and sometimes in high abundance. Thus, it would be of interest to determine capture efficiencies of the most commonly encountered species.

Most modeling exercises use a single-species approach that can be very inefficient when the number of species and candidate models is high. Unlike single-species models, a multispecies approach is more efficient because it uses species-specific parameters to attain estimates for each species simultaneously, essentially improving the precision of the estimators because information is shared among species due to the hierarchical structure of the models (Sauer and Link 2002; Russell et al. 2009). Secondarily, it would be useful to determine factors influencing the spatial aggregation of these species.

Developing a hierarchical framework that accounts for both probability of detection (i.e., capture efficiency) and nested effects while simultaneously estimating parameter estimates for multiple species can be conveniently analyzed using Bayesian methods (Kirsch and Peterson 2014). The benefit of a Bayesian framework is that the model accounts for uncertainty for all parameters (fixed and random effects) while easily describing latent random variables associated with parameters that are functions of other parameters and environmental factors (Snijders and Bosker 1999; Latimer et al. 2006; Stewart et al. 2016), but using a multispecies approach increases the complexity of the latent random variable model. Classical maximum likelihood estimation methods may not work well when the number of latent random variables increases within a model (Royle and Dorazio 2008). Therefore, constructing hierarchical Bayesian models to account for both latent random variables and random effects would allow us to more accurately evaluate factors driving species distributions, given that we are constructing a model that accounts for factors affecting our ability to effectively sample the species assemblage (Royle and Dorazio 2008).

There are relatively few studies describing patterns of fish distributions in lentic systems using empirical models that estimate detectability (Haynes et al. 2014). To improve our understanding of factors influencing fish assemblages in lentic systems, we sought to determine species–habitat relationships using hierarchical Bayesian multispecies models that evaluate factors associated with abundance in tandem hoop nets and detection probabilities of fishes in reservoirs. Because hoop nets capture many species that vary in life history and habitat specificity (Samuel 1976; Dauble 1986; Cartabiano et al. 2015), the results from this study will illustrate species-specific responses to landscape controls affecting lake-specific variation in detectability.

METHODS

Study area.—To study the detection of fish caught using hoop nets, we selected six impoundments, located in north-central and eastern Oklahoma (Figure 1), which vary in productivity, land use, and water chemistry characteristics (Table 1). Lakes McMurtry (465 ha) and Ponca (326 ha) were eutrophic (both with a trophic state index [TSI] of 57) and had average Secchi disk depths of 47 and 78 cm, respectively. Lakes Okemah (270 ha) and Okmulgee (270 ha) were mesotrophic (TSI of 46 and 48, respectively) and had average Secchi disk depths of 78 and 116 cm, respectively; whereas, Lakes Lone Chimney (223 ha) and Greenleaf (372 ha) were eutrophic (TSI of 53 and 52, respectively) average Secchi disk depths of 67 and 111 cm, respectively.

Fish surveys.—Fish were sampled at eight randomly selected sites in May 2010 at each reservoir. Sampling locations were randomly selected by first developing a buffer within the inside of each lake and then randomly generating points using ArcGIS version 10.2 (2013; Environmental Systems Research Institute, Redlands, California). We sampled fish using tandem hoop nets (three nets per series, each 3.4 m long with 25-mm bar mesh and seven 0.8-m hoops [Miller Net and Twine, Memphis, Tennessee]) (Buckmeier and Schlechte 2009). To prevent fish escape, cords of the crow-foot throats in the cod end of each hoop net were joined by nylon zip ties (Porath et al. 2011). Eight series (one per site) were deployed on the same day during the sampling period to standardize effort among reservoirs. Nets were baited with 1 kg of ground cheese logs (Boatcycle, Henderson, Texas) and fished parallel to shore at depths less
than 4 m for 72 h. Sites were sampled a second time within at least 7 d of the first sampling event to meet the assumptions of a closed population and constant abundance for the detection models. We identified fish to species and recorded catch, expressed as number of fish per series.

Landscape data.—We used environmental data collected from online sources to develop a model-based hypothesis to evaluate species-specific relationships to landscape factors. We measured land use surrounding each sampling location and at the reservoir scale to account for environmental correlation. We hypothesized that developed areas (e.g., residential) would tend to have more Green Sunfish *Lepomis cyanellus*, Largemouth Bass *Micropterus salmoides*, Bluegills *L. macrochirus*, and Channel Catfish, given that these species

FIGURE 1. Location of sample sites (solid dots) within six study reservoirs (McMurtry, Ponca, Okemah, Okmulgee, Lone Chimney, and Greenleaf) in Oklahoma.
are commonly stocked to provide fishing opportunities in more developed locations. Additionally, we hypothesized that undisturbed sites (e.g., forested) would tend to have more White Crappies *Pomoxis annularis*, a species that shows a strong affinity to cover like woody debris (Pope and Willis 1997). Additionally, we predicted a negative correlation between agriculture and cover-oriented species, and thereby, a positive correlation with noncover-oriented species like Channel Catfish and Common Carp *Cyprinus carpio* (Jones and Stuart 2007).

Land use surrounding each lake was summarized using the latest 30-m resolution land cover data (2006) from the Multi-Resolution Land Characteristics Consortium (Fry et al. 2011) and processed in ArcGIS version 10.2 (Environmental Systems Research Institute). We considered the fish collections were contemporaneous with the “current” land cover data. Land use data were “clipped” to a 1-km buffer around the boundary of each reservoir, and land cover classes were tabulated for the whole lake and at 150-m buffers around each sampling site. Land cover types were grouped into the following classes: developed, agriculture, grassland, shrub, wetland, and forest.

**Reservoir habitat.**—Physiochemical properties were measured at the site, regional, and reservoir scales to account for intercorrelation. We hypothesized that sunfishes (Centrarchidae) would occur more often at sites associated with clear water and less nutrient input (Shoup et al. 2012); therefore, clearer and less productive systems would tend to have fewer Channel Catfish and other benthic species that have evolved life history characteristics to persist in more turbid systems (Stewart 2013). Secondly, we predicted that species would show a positive correlation with water temperature, given the onset of spawning for many reservoir fishes during the time of sampling (Etnier and Starnes 1993).

During net setting, water transparency was measured at each sample site with a Secchi disk (cm). To measure reservoir productivity, surface water samples were collected annually from four regions of each reservoir in July 2010 to estimate chlorophyll *a* (*μg/L*) concentrations. Water samples were filtered within 24 h of collection using 0.7-μm glass fiber filters (Whatman, grade GF/F) and frozen, and chlorophyll *a* concentrations were estimated with an Optimal Technologies Ratio-2 fluorometer (APHA 2005).

**Statistical analysis.**—We used hierarchical Bayesian multispecies mixture modeling to make inferences on the probability of detection (p) and abundance (N) of fishes captured using hoop nets, effectively estimating values of species-specific parameters simultaneously and essentially increasing efficiency of the modeling exercises. Only species caught at more than 2% of the sampling locations were considered to avoid biased model parameter estimates for rare species due to insufficient information (Kirsch and Peterson 2014). The model structure used was a binomial-mixture model that accounted for imperfect detection using spatially replicated counts *y* for species *k*, site *i*, and survey *t* by compiling a species-by-site-by-survey abundance matrix, where *y* are observations that follow a binomial distribution denoted as

\[ y_{ikt} | N_{ik}, p_{ik} \sim \text{Binomial}(N_{ik}, p_{ik}) \]
Capture efficiency (per individual detection probability, \( p_{itk} \)) accounts for incomplete detection and reduces the uncertainty in the estimated abundance of the target species at the sample sites (MacKenzie et al. 2002; Royle 2004). The modeling approach assumes that detection probability is constant for all individuals, the population is demographically closed, and that abundance at each site did not change during the sampling period (Royle 2004); we believe that we met this assumption given that sites were resampled within a 2–7-d period. We modeled detection probability using a logit transformation represented as

\[
\logit(p_{itk}) = \gamma_{0,k} + \sum_{r=1}^{s} \gamma_{h,k}x_{r,itk},
\]

where \( x_{r,itk} \) are the reservoir habitat predictors \( r = 1, 2, \ldots, s \) for species \( k \) measured at site \( i \) at time \( t \), and \( \gamma_{0,k} \) and \( \gamma_{h,k} \) are species-specific parameter estimates.

The estimated abundance \( N_{ik} \) for each fish species is treated as a random effect and estimated as a function of a hierarchical model that accounts for site-specific random effects (Snijders and Bosker 1999; Gelman and Hill 2007). Abundance was estimated by assuming a negative binomial distribution, accomplished by adding a hierarchical element \( \epsilon_i \) to the likelihood of a Poisson distribution through a random effect to account for overdispersion, denoted as

\[
N_{ik}|\epsilon_i, E_{ik}, \lambda_{ik} \sim \text{Poisson}(\lambda_{ik} \epsilon_i), \epsilon_i \sim \text{gamma}(\theta, \theta),
\]

where \( \theta > 0 \). The resulting probability distribution marginal to \( \epsilon_i \) is

\[
P(N_{ik} = n_{ik}|E_{ik}, \lambda_{ik}, \theta) = \frac{\Gamma(n_{ik} + \theta)}{\Gamma(n_{ik} + 1)\Gamma(\theta)} \left( \frac{\lambda_{ik}}{\lambda_{ik} + \theta} \right)^{n_{ik}} \left( 1 - \frac{\lambda_{ik}}{\lambda_{ik} + \theta} \right)^{\theta},
\]

with the \( E(N_{ik}) = \lambda_{ik} \) and \( V(N_{ik}) = \lambda_{ik} + (\lambda_{ik})^2/\theta \), where \( \theta \) is the parameter of extra-Poisson variation with large values of \( \theta \) consistent to variability similar to the Poisson distribution. As \( \theta \to \infty \) the distribution of \( N_{ik} \) converges to a Poisson random variable, and \( \lambda_{ik} \) is expressed as a log-link function of environmental factors as

\[
\log(\lambda_{ik}) = \alpha_{0,k} + \sum_{v=1}^{w} \alpha_{v,k} x_{v,i} + \delta_i,
\]

where \( x_{v,i} \) are land use predictors \( v = 1, 2, \ldots, w \) measured at site \( i \), \( \alpha_{0,k} \), and \( \alpha_{v,k} \) are species-specific parameter estimates. The \( \gamma \) and \( \alpha \) terms are the fixed-effect coefficients, and \( \delta \) is the random effect or exchangeable error term that is \( N \sim (0, \sigma) \).

Candidate hierarchical models were fit using covariates standardized with a mean of zero and SD of one, and only predictor variables that had a correlation coefficient \( r < 0.60 \) were used in the same model to reduce intercorrelation due to potential multicollinearity (Dormann et al. 2013). Correlated predictor variables \( r \geq 0.60 \) were not used in the same model but were still considered when developing models based on a priori hypotheses. Models were implemented in WINBUGS software, version 1.4 (Spiegelhalter et al. 2003) using Markov chain–Monte Carlo (MCMC) algorithms to generate posterior distributions of the parameters. Noninformative priors (i.e., diffuse priors) were used and models were fit using three parallel chains simulated for 500,000 iterations with a burn-in of the first 200,000 iterations. To determine convergence, we used the Gelman–Rubin diagnostic convergence statistics, the examination of chain histories, and the posterior density plots (Gelman and Rubin 1992).

We ranked models based on a priori hypotheses relative to site- and reservoir-specific factors on detection and abundance (Table 1). We used an information theoretic approach (Burnham and Anderson 2002) to rank the set of competing hypotheses by calculating deviance information criteria (DICs; Spiegelhalter et al. 2002). We assumed models with \( \Delta \text{DIC} \leq 4 \) were plausible and the degree of evidence for one model over another was calculated from deviance weights (i.e., Akaike weights based on DIC statistics: Burnham and Anderson 2002). We also sought to determine whether the composite relative abundance (number of fish per hoop-net series; Michaletz and Sullivan 2002; Stewart and Long 2012) differed among species and impoundments using an ANOVA at the \( \alpha \leq 0.05 \) significance level, where abundance was log(count + 1) transformed.

**RESULTS**

Overall, we caught 7,212 individual fish representing 12 species. Relative abundance was significantly different among species \( (F_{9, 40} = 17.04, P < 0.01) \), but there was not a significant reservoir \( (F_{5, 40} = 6.52, P = 0.16) \) or species × reservoir interaction effect \( (F_{5, 36} = 0.81, P = 0.77) \). The majority of the catch was Channel Catfish \( (n = 3,326, 46\% \text{ of total catch}) \), followed by Bluegill \( (n = 1,843, 25\% \text{ of total catch}) \), and White Crappie \( (n = 1,018, 14\% \text{ of total catch}) \) (Tables 2, 3). Though not statistically different, some species were caught in higher abundances at reservoirs having very different habitat characteristics. For example, Bluegill catch was highest at Lake Okmulgee (62.25 fish/series), Common Carp was highest at Lake Lone Chimney (2.63 fish/series), and catches of Green Sunfish and Longear Sunfish \( L. \) megalotis were highest at Lake Ponca (9.88 fish/series and 21.00 fish/series, respectively). Redear Sunfish \( L. \) microlophus and Warmouth \( L. \) gulosus catches were highest at Lake Greenleaf (51 fish/series and 3 fish/series, respectively), Channel Catfish catch was highest at Lake Okemah (154 fish/series), and White Crappie catch was highest at Lake McMurtry (78 fish/series).

Detection probabilities \( (p) \), estimated from an unconditional model, were different among species. Overall, detection probabilities were highest for Channel Catfish (69%), Bluegill
(60%), White Crappie (55%), Redear Sunfish (43%), and Longear Sunfish (38%) (Table 2). Estimated detection probability was highest for Bluegill at Lakes Lone Chimney (54%) and Ponca (61%), Channel Catfish at Lakes Okemah (84%) and Ponca (71%), Longear Sunfish at Lake Ponca (65%), Redear Sunfish at Lake Okemah (51%), and White Crappie at Lake McMurtry (57%).

The model selection procedure identified five models that showed detection and abundance of fish were significantly related to water clarity (Secchi disk depth), water temperature, and land use characteristics (Table 4). The best overall model included Secchi disk depth, water temperature, maximum reservoir depth, shoreline length, and reservoir surface area (Figures 2–4). Detection probabilities for Bluegill, Longear Sunfish, Largemouth Bass, Redear Sunfish, and Warmouth increased with increasing water clarity (Figure 2), whereas detection probabilities decreased for Channel Catfish, Common Carp, Green Sunfish, and White Crappie. For example, estimated detection probabilities for Channel Catfish, White Crappie, and Bluegill at a Secchi disk depth of 20 cm were 15% (95% CI = 14.42–16.62), 24% (95% CI = 23.20–25.20), and 8% (95% CI = 6.5–10.5), respectively; while

### TABLE 2. Fish species, sample characteristics, and mean conditional detection probabilities (p_jN ± 95% credibility intervals) observed within the six Oklahoma reservoirs.

<table>
<thead>
<tr>
<th>Species</th>
<th>Catch</th>
<th>Relative abundance (Number of fish/series)</th>
<th>CV</th>
<th>p_jN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Channel Catfish <em>Ictalurus punctatus</em></td>
<td>3,326</td>
<td>69.29</td>
<td>1.27</td>
<td>69 ± 1</td>
</tr>
<tr>
<td>White Crappie <em>Pomoxis annularis</em></td>
<td>1,018</td>
<td>21.21</td>
<td>1.37</td>
<td>55 ± 3</td>
</tr>
<tr>
<td>Bluegill <em>Lepomis macrochirus</em></td>
<td>1,843</td>
<td>37.15</td>
<td>0.64</td>
<td>60 ± 3</td>
</tr>
<tr>
<td>Longear Sunfish <em>L. megalotis</em></td>
<td>259</td>
<td>5.40</td>
<td>1.44</td>
<td>38 ± 9</td>
</tr>
<tr>
<td>Common Carp <em>Cyprinus carpio</em></td>
<td>40</td>
<td>0.83</td>
<td>0.75</td>
<td>8 ± 6</td>
</tr>
<tr>
<td>Green Sunfish <em>L. cyanellus</em></td>
<td>99</td>
<td>2.06</td>
<td>1.88</td>
<td>15 ± 10</td>
</tr>
<tr>
<td>Redear Sunfish <em>L. microlophus</em></td>
<td>629</td>
<td>13.1</td>
<td>1.51</td>
<td>43 ± 3</td>
</tr>
<tr>
<td>Largemouth Bass <em>Micropterus salmoides</em></td>
<td>13</td>
<td>0.27</td>
<td>1.03</td>
<td>11 ± 10</td>
</tr>
<tr>
<td>Warmouth <em>L. gulosus</em></td>
<td>34</td>
<td>0.71</td>
<td>1.56</td>
<td>15 ± 11</td>
</tr>
<tr>
<td>Flatehead Catfish <em>Pylodictis olivaris</em>²</td>
<td>5</td>
<td>0.10</td>
<td>1.60</td>
<td></td>
</tr>
<tr>
<td>Saugye (Walleye <em>Sander vitreus</em> × Sauger <em>S. canadensis</em>)²</td>
<td>4</td>
<td>0.08</td>
<td>2.46</td>
<td></td>
</tr>
<tr>
<td>Spotted Sucker <em>Minotrema melanops</em>²</td>
<td>2</td>
<td>0.04</td>
<td>2.45</td>
<td></td>
</tr>
</tbody>
</table>

² Indicates species not included in N-mixture analysis.

### TABLE 3. Fish species and sample characteristics observed within the six Oklahoma reservoirs. Catch is the number of fish caught by species and CPUE is described as the number of fish per hoop-net series.

<table>
<thead>
<tr>
<th>Reservoir</th>
<th>Lone Chimney</th>
<th>Greenleaf</th>
<th>McMurtry</th>
<th>Okemah</th>
<th>Okmulgee</th>
<th>Ponca</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Catch</td>
<td>CPUE</td>
<td>Catch</td>
<td>CPUE</td>
<td>Catch</td>
<td>CPUE</td>
</tr>
<tr>
<td>Channel Catfish</td>
<td>394</td>
<td>49.3</td>
<td>76</td>
<td>9.5</td>
<td>742</td>
<td>92.8</td>
</tr>
<tr>
<td>White Crappie</td>
<td>211</td>
<td>26.4</td>
<td>29</td>
<td>3.6</td>
<td>622</td>
<td>77.8</td>
</tr>
<tr>
<td>Bluegill</td>
<td>137</td>
<td>17.1</td>
<td>452</td>
<td>56.5</td>
<td>77</td>
<td>9.6</td>
</tr>
<tr>
<td>Longear Sunfish</td>
<td>10</td>
<td>1.25</td>
<td>36</td>
<td>4.5</td>
<td>9</td>
<td>1.3</td>
</tr>
<tr>
<td>Common Carp</td>
<td>21</td>
<td>2.6</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>1.4</td>
</tr>
<tr>
<td>Green Sunfish</td>
<td>3</td>
<td>0.4</td>
<td>14</td>
<td>1.8</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Redear Sunfish</td>
<td>7</td>
<td>0.9</td>
<td>404</td>
<td>50.5</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td>1</td>
<td>0.1</td>
<td>5</td>
<td>0.63</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Warmouth</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>2.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Flatehead Catfish²</td>
<td>3</td>
<td>0.4</td>
<td>1</td>
<td>0.1</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Saugye²</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0.4</td>
</tr>
<tr>
<td>Spotted Sucker²</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

² Indicates species not included in N-mixture analysis.
estimated detection at 140 cm depth was 3% (95% CI = 2.5–4.5), 2% (95% CI = 1.5–3.5), and 15% (95% CI = 13.34–17.34), respectively. An increase in water temperature resulted in an increase in detection of Largemouth Bass, Redear Sunfish, and Warmouth, while detection decreased for the remaining species (Bluegill, Channel Catfish, Common Carp, Green Sunfish, Longear Sunfish, and White Crappie; Figure 3). For example, estimated detection probabilities for Longear Sunfish, Green Sunfish, and Redear Sunfish at 17°C were 16% (95% CI = 15.5–17.5), 30% (95% CI = 27–33), and 2.5% (95% CI = 2.4–2.6), respectively; while estimated detections at 28°C were 2% (95% CI = 1–3), 2% (95% CI = 1.5–2.5), and 6% (95% CI = 4–8), respectively. The best model predicted an increase in abundance for

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Abundance (λ) and detection (p) covariates</th>
<th>DIC</th>
<th>w_i</th>
<th>E_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(λ(\text{Max}<em>\text{depth}, \text{Surface}</em>\text{area}, \text{Shoreline}<em>\text{length})p(\text{Secchi}</em>\text{depth}, \text{Temperature}))</td>
<td>790.0</td>
<td>0.51</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>(λ(\text{Percent}<em>\text{ag}, \text{Chl}</em>\text{a}, \text{Secchi}<em>\text{depth}, \text{Percent}</em>\text{grassland}, \text{Percent}<em>\text{urban})p(\text{Secchi}</em>\text{depth}, \text{Temperature}))</td>
<td>792.8</td>
<td>0.13</td>
<td>4.06</td>
</tr>
<tr>
<td>3</td>
<td>(λ(\text{Percent}<em>\text{forest}, \text{Max}</em>\text{depth}, \text{Secchi}<em>\text{depth}, \text{Percent}</em>\text{urban})p(\text{Secchi}_\text{depth}, \text{Temperature}))</td>
<td>792.8</td>
<td>0.13</td>
<td>4.06</td>
</tr>
<tr>
<td>4</td>
<td>(λ(\text{Percent}<em>\text{forest}, \text{Shoreline}</em>\text{length}, \text{Percent}<em>\text{urban})p(\text{Secchi}</em>\text{depth}, \text{Temperature}))</td>
<td>792.9</td>
<td>0.12</td>
<td>4.26</td>
</tr>
<tr>
<td>5</td>
<td>(λ(\text{Percent}<em>\text{ag}, \text{Chl}</em>\text{a}, \text{Max}<em>\text{depth}, \text{Secchi}</em>\text{depth})p(\text{Secchi}_\text{depth}, \text{Temperature}))</td>
<td>793.5</td>
<td>0.09</td>
<td>5.75</td>
</tr>
</tbody>
</table>

FIGURE 2. Estimated mean conditional detection probabilities \(p_j/N\) in relation to Secchi disk depth (cm) for commonly captured fish species in six Oklahoma reservoirs using hoop nets. The middle lines are posterior means and the shaded regions are 95% credible intervals.
Channel Catfish, Bluegill, and Longear Sunfish as shoreline length increased. Also, abundance of Channel Catfish, White Crappie, Bluegill, Common Carp, and Redear Sunfish increased with reservoir depth. Finally, abundance of most sunfish species (except Bluegill and Redear Sunfish) increased with surface area.

Models based on land use (i.e., percentage residential development, shrub land, and agriculture) were less likely than the best model that only included reservoir variables. Abundance of Channel Catfish, Common Carp, and Green Sunfish decreased as the percentage of agricultural land increased, whereas abundance of most sunfish species significantly increased based on species-specific slope estimates of the candidate models (Figure 4). Channel Catfish and White Crappie abundance significantly decreased with increased chlorophyll $a$ concentrations, while the remaining sunfish species and Common Carp abundance increased. Other landscape covariates like percentage of forest, grassland, and urban cover were important, though only a few significant associations were evident. For example, abundance of White Crappie significantly decreased as the percentage of forest increased, and abundance of Bluegill, Redear Sunfish, and Warmouth significantly decreased as the percentage of grassland increased; whereas, abundance of Channel Catfish, Common Carp, Green Sunfish, and Redear Sunfish significantly decreased as urban cover increased.

DISCUSSION

The present study is one of the first to examine factors influencing capture efficiency of tandem hoop nets in freshwater systems, and illustrates the utility of a generalization of a mixture model to account for additional species and extra-Poisson variation. Moreover, this study demonstrates the efficiency of hoop nets used to sample multiple fish species based
on a multispecies modeling approach. We observed a wide range of detectability estimates, discrediting universal gear effectiveness and assumptions of perfect detection (Royle 2004), indicating that the use of raw count data can be misleading due to the inherent bias associated with sampling gears and detection error (MacKenzie et al. 2002; Royle 2004). In many cases, counts from a single sampling event are used to infer population size and habitat associations, and to determine an appropriate number of nets needed to effectively sample the population (Michaletz and Sullivan 2002; Stewart and Long 2012). Not accounting for factors that influence detection probabilities could result in information loss (MacKenzie et al. 2002; Royle 2004), requiring the development of a model framework that concurrently estimates both abundance and detection (Royle 2005). Under this framework, a researcher could account for both imperfect detection and spatial variation in count data to attain a robust estimate of relative abundance to determine factors influencing a species distribution, and in our case, the distribution of multiple species.

The among-species variability in the mean conditional detection probabilities \( (p_i|N) \) and habitat variables likely reflects the selection of habitat types in areas where species are better adapted (Werner et al. 1977; Savino and Stein 1982). Several models and theories of habitat use suggest habitat tends to be used to maximize profitability, which is a trade-off between foraging efficiency and predator avoidance (Savino and Stein 1982). For instance, our hypothesis that the sunfish species would show a positive association with water clarity was supported by the models. For example,
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detection of species like Bluegill, Largemouth Bass, Redear Sunfish, and Warmouth increased with water clarity; this relationship is expected given that these species are commonly associated with vegetation that is only abundant in impoundments with clear water (Savino and Stein 1982). However, Channel Catfish, White Crappie, and Common Carp were less detectable in clear water, suggesting that, at least for Channel Catfish and White Crappie, clear-water impoundments differentially benefit their known predators like Largemouth Bass (Marzolf 1957; Krummrich and Heidinger 1973; Spinelli et al. 1985; Michaeletz and Sullivan 2002) or competitors like Bluegill (Michaeletz 2006). Additionally, increased detectability of Common Carp in turbid water is not surprising, but Common Carp can influence the catch of other species, for example, by increasing the catch of White Crappie and decreasing the catch of Bluegill (Egertson and Downing 2004). Our results illustrate a similar pattern but it is likely not directly related to carp abundance, given the significant habitat relationships observed with White Crappie and Bluegill abundance were not necessarily related to Common Carp but due to differential habitat use.

Our data indicate that freshwater fish abundance was also related to land use variables. The abundance of freshwater fish was consistently negatively related to increased percentage of urban land use, suggesting that the impact of modified landscapes to adjacent habitat in the riparian zone negatively impact some fish in the community. Developed reservoirs are commonly associated with reduced diversity and availability of habitat types for fish (Christensen et al. 1996; Jennings et al. 1996); thus the homogenization of habitat structures (e.g., fishing piers and rip-rap) might not benefit all species and explain the negative relationships observed in this study. Conversely, the abundance of sunfishes was positively associated with the percentage of agriculture, likely a result of increased nutrient productivity that increases zooplankton prey biomass (Werner et al. 1977; Savino and Stein 1982). Though we did not examine zooplankton abundance, we think this is a likely explanation because of the similar trend observed between abundance of most sunfish species and chlorophyll $a$ (Hinch and Collins 1993). The negative relationship between Channel Catfish abundance and percentage agriculture might be related to the reduction in coarse woody debris (Francis and Schindler 2006; Sass et al. 2006). Negative relationships between coarse woody debris and both percent agriculture and urbanization were evident at the study reservoirs based on prior habitat evaluations (Stewart 2013); thus, human impacts have likely reduced an important source of habitat for Channel Catfish that provides refuge for young of year and spawning sites for adults (Paragamian 1990; Coon and Dames 1991; Hubert 1999).

Because Channel Catfish and Bluegill overlap in diet these species may compete for resources, and competition could potentially increase when Channel Catfish are stocked in high numbers (Michaeletz 2006). In order for interspecific competition to exist species must overlap with their use of diet and habitat (Michaeletz 2006), but our results suggest that Channel Catfish and Bluegill occupy different habitats, which may provide an explanation of why some studies have found no evidence of competition between these species (Michaeletz 2006; Leonard et al. 2010). For instance, Channel Catfish abundance was higher in turbid, less disturbed (e.g., less urbanization and agriculture) reservoirs with more littoral zone (increased shoreline length); whereas, Bluegill were more abundant in clear-water, nutrient-rich impoundments with generally have less shoreline and an increased percentage of agriculture. These results indicate that habitat characteristics of a reservoir might only benefit sunfishes or Channel Catfish, but not both, in regard to the obvious antithesis between species-specific abundance–habitat relationships.

The identified habitat features may play an important role in explaining the distribution of reservoir fish. The impact of land use can greatly affect the aquatic ecosystem, and we were able to identify landscape relationships that were significantly related to the abundance of freshwater fish, but these potential interactions warrant further evaluation. Additionally, we found that fine-scale water physiochemistry can significantly influence the capture efficiency of fish, often differently among species, and we further stress the importance of quantifying and then incorporating detection estimates into the species distribution modeling framework. Because of changing capture efficiency, sampling more than once within a relative short period would be an improvement on the typical approach that samples a location a single time. By considering habitat features and factors influencing detection, fishery managers can develop multispecies models that evaluate factors influencing detectability of not just one species but all species encountered, regardless of the sampling gear used.

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REFERENCES


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