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ARTICLE

Spatial and Temporal Dynamics in Brook Trout Density: Implications for Population Monitoring

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Abstract
Many potential stressors to aquatic environments operate over large spatial scales, prompting the need to assess and monitor both site-specific and regional dynamics of fish populations. We used hierarchical Bayesian models to evaluate the spatial and temporal variability in density and capture probability of age-1 and older Brook Trout *Salvelinus fontinalis* from three-pass removal data collected at 291 sites over a 37-year time period (1975–2011) in Pennsylvania streams. There was high between-year variability in density, with annual posterior means ranging from 2.1 to 10.2 fish/100 m^2; however, there was no significant long-term linear trend. Brook Trout density was positively correlated with elevation and negatively correlated with percent developed land use in the network catchment. Probability of capture did not vary substantially across sites or years but was negatively correlated with mean stream width. Because of the low spatiotemporal variation in capture probability and a strong correlation between first-pass CPUE (catch/min) and three-pass removal density estimates, the use of an abundance index based on first-pass CPUE could represent a cost-effective alternative to conducting multiple-pass removal sampling for some Brook Trout monitoring and assessment objectives. Single-pass indices may be particularly relevant for monitoring objectives that do not require precise site-specific estimates, such as regional monitoring programs that are designed to detect long-term linear trends in density.

Management decisions for inland freshwater fisheries are often made on a site- or water body-specific basis; however, there is an increasing need to also monitor and assess the regional dynamics, status, and trends of fish populations. This need is due in large part to increases in potential stressors acting over large spatial scales. For example, climate and land use changes, including increases in urbanization, have been found to negatively affect fish assemblages over large spatial extents (Wenger et al. 2008, 2011; Isaak et al. 2012). More recently, the large-scale exploration for and extraction of natural gas in previously

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inaccessible underground reservoirs have expanded throughout the USA (Sutherland et al. 2010; Entrekin et al. 2011), and many of the activities associated with exploration and extraction have the potential to deleteriously affect fish communities (Dauwalter 2013).

Climate change, urbanization (i.e., developed land), and energy development have all been identified as threats to the conservation and management of native Brook Trout *Salvelinus fontinalis* throughout much of the species' native range in the eastern USA (Meisner 1990; Hudy et al. 2008; Weltman-Fahs and Taylor 2013). For instance, in Pennsylvania, a large portion of the state's wild Brook Trout resource is located above large reservoirs of natural gas. Natural gas exploration and extraction from these reservoirs could directly and indirectly affect Brook Trout populations. Thus, quantifying the relationships between Brook Trout density and natural and anthropogenic landscape characteristics is important for predicting potential changes in populations as landscapes are altered.

Although it is challenging given limited fiscal resources and the spatial extent of the Brook Trout's range, monitoring the response of Brook Trout to regional development is necessary to ensure long-term persistence and distribution of the species. Multiple-pass removal sampling is commonly used to estimate abundance and community attributes of stream-dwelling fishes, but it can be time intensive. For example, Sweka et al. (2012) suggested that a 400–450-m reach length was needed to estimate Brook Trout density within 25% of the true density by using three-pass removal sampling in Pennsylvania headwater streams. Although these reach lengths can be effectively sampled by a three- to four-person crew in a single day, sampling is usually limited to a single stream site in a given work day. Because of the time required to complete multiple-pass removal sampling, the use of single-pass sampling as an index of density has been proposed as a cost-effective alternative (Vehanen et al. 2013). Single-pass total catch and CPUE have been shown to be highly correlated with abundance and density estimates from three-pass removal sampling, particularly for small streams (Kruse et al. 1998; Bergman et al. 2011). However, single-pass indices may be imprecise and of limited use as monitoring indicators if catchability varies spatially or temporally (Bergman et al. 2011). Thus, our objectives were to (1) examine relationships between Brook Trout density and natural and anthropogenic landscape characteristics and (2) examine spatial and temporal variation in catchability and the relationship between single-pass and three-pass removal density estimates in an attempt to determine the efficacy of using single-pass CPUE as an index of density for Brook Trout monitoring and assessment.

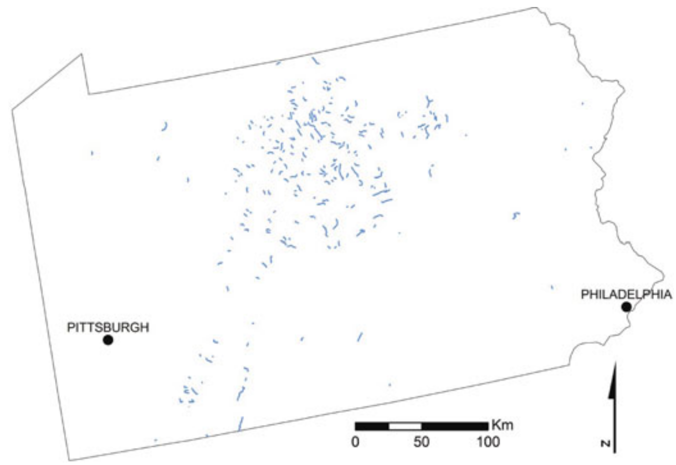

FIGURE 1. Map of Pennsylvania, USA, showing the stream reach line segments of sites where Brook Trout were sampled using three-pass removal methods.

METHODS

Fish sampling.—Three-pass removal data for age-1 and older (>100 mm TL) wild Brook Trout were obtained from the Pennsylvania Fish and Boat Commission (PFBC). Removal data were collected under summer base flow conditions using a three-person crew at 291 sites representing 212 coldwater streams over a 37-year time period (1975–2011). Sample sites were located throughout Pennsylvania, but primarily in the north-central region (Figure 1), which comprises large tracts of forested land and represents the stronghold for Brook Trout in the state. All sample sites were linked to the National Hydrography Dataset Plus version 1 (NHDPlusV1; USEPA and USGS 2005), and no two sample sites were located within the same stream reach (reaches delineated by NHDPlus). All fish sampling involved standard backpack electrofishing procedures established by the PFBC (Detar et al. 2011).

Landscape predictors.—We used the 1:100,000-scale NHDPlusV1 stream reaches as the base spatial unit for data management and analysis. Landscape predictors were summarized within the upstream network catchment for each stream reach (Esselman et al. 2011). We summarized predictors only at the network catchment scale because landscape predictors at the local (i.e., land area draining directly to a reach) and network catchment scales were highly correlated for our relatively small stream systems. In addition, we were particularly interested in cumulative upstream impacts on Brook Trout density. We included natural and anthropogenic landscape predictors that we hypothesized to influence Brook Trout density (Table 1). We predicted that Brook Trout density would be positively correlated with both the percentage of forest cover and the mean elevation and would be negatively correlated with all anthropogenic landscape characteristics. We also predicted that stream width would be an important predictor of Brook Trout capture probability, with smaller, narrower streams having a higher probability of Brook Trout capture than wider streams.

Statistical analysis.—We fitted a Bayesian hierarchical model for three-pass successive removal data to elucidate spatial and temporal variation in Brook Trout density and capture probability as well as to determine the effects of land use and cover type on density. The basic model was described in

TABLE 1. Natural and anthropogenic landscape characteristics (with data source) used to predict Brook Trout density in Pennsylvania streams. All metrics were summarized at the network catchment scale.

Landscape characteristic	Mean	SD	Min	Max	Source
Catchment area (km^2)	22.0	73.0	1.8	1,170.7	USEPA and USGS 2005
Mean elevation (m)	561.4	85.9	255.3	818.2	USGS 2006
Impervious surface (%)	0.15	0.37	0.0	3.2	USGS 2008
Road density (m/km^2)	1,018.6	617.2	0.0	4,501.8	U.S. Bureau of the Census 2000
Developed land (%)	0.02	0.03	0.0	0.37	USGS 2008
Agriculture (%)	0.04	0.09	0.0	0.54	USGS 2008
Forest (%)	0.89	0.11	0.38	1.0	USGS 2008

detail by Parent and Rivot (2013); however, a brief description of the model follows. The sampling distributions of the catch data followed a binomial distribution

$$C^1_{i,j} \sim \text{Binomial}\,(\nu_{i,j}, \pi_{i,j}),$$
$$C^2_{i,j} \sim \text{Binomial}\,\left(\nu_{i,j} - C^1_{i,j}, \pi_{i,j}\right),$$
$$C^3_{i,j} \sim \text{Binomial}\,\left(\nu_{i,j} - \left(C^1_{i,j} + C^2_{i,j}\right), \pi_{i,j}\right),$$

where $C^n_{i,j}$ is the catch on the nth pass ($n = 1$, 2, or 3) for the ith site in the jth year; $\nu_{i,j}$ is the initial population size; and $\pi_{i,j}$ is the capture probability, which is assumed to remain constant among passes. The model is parameterized where the initial population size depends on the expected fish density ($\delta_{i,j}$; fish/m^2) and the surface area of the sample site ($S_{i,j}$). Thus, the initial population size is assumed to follow a Poisson distribution,

$$\nu_{i,j} \sim \text{Poisson}\,(\delta_{i,j} \times S_{i,j}).$$

The effects of predictors on the expected mean density and the probability of capture were modeled on the log$_e$ and logit scales, respectively, as

$$\mathbb{E}(\log_e(\delta_{i,j})) = \alpha_{\delta j} + \beta_{\delta 1} X_{i,j},$$
$$\mathbb{E}(\text{logit}(\pi_{i,j})) = \alpha_{\pi j} + \beta_{\pi 1} X_{i,j},$$
$$\begin{pmatrix} \log_e(\delta_{i,j}) \\ \text{logit}(\pi_{i,j}) \end{pmatrix} \sim N\left(\begin{pmatrix} \mathbb{E}\left(\log_e(\delta_{i,j})\right) \\ \mathbb{E}\left(\text{logit}(\pi_{i,j})\right) \end{pmatrix}, \begin{pmatrix} \sigma^2_\delta & \rho_{\delta\pi}\sigma_\delta\sigma_\pi \\ \rho_{\delta\pi}\sigma_\delta\sigma_\pi & \sigma^2_\pi \end{pmatrix} \right),$$

where $\alpha_{\delta j}$ and $\alpha_{\pi j}$ are random year effects for density and probability of capture, respectively. We assumed that $\alpha_{\delta j} \sim N(\mu_\delta, \sigma^2_{\alpha\delta})$ and $\alpha_{\pi j} \sim N(\mu_\pi, \sigma^2_{\alpha\pi})$, where μ_δ is the overall mean density, μ_π is the overall mean probability of capture, and $\sigma^2_{\alpha\delta}$ and $\sigma^2_{\alpha\pi}$ are the among-year variances in density and probability of capture, respectively. Random year effects for density and probability of capture were included because we predicted that annual variation in climate and streamflow—factors that might influence all sites similarly in a given year—would result in annual variation in these two parameters. The fixed effects of $\beta_{\delta 1}$ and $\beta_{\pi 1}$ describe the relationship between predictor $X_{i,j}$ and the log$_e$(density) or logit(probability of capture). A bivariate normal distribution was used to quantify residual variation and the correlation between density and probability of capture (σ^2_δ, σ^2_π, and $\rho_{\delta\pi}$). The aforementioned model allowed us to quantify among-year variability in density and the probability of capture. However, to further test for temporal trends in density and capture probability, we explicitly modeled the random year effects (random intercepts) as a function of time (i.e., we added the year of sampling as a predictor variable for the random year intercepts). Noninformative priors were used for all parameters. The models were fitted by using Bayesian estimation, and the program JAGS was used for all analyses (Plummer 2011). Three parallel chains were run with different initial values to generate 150,000 samples from the posterior distributions for each analysis after discarding the first 80,000 samples. We retained every third sample for a total of 70,000 samples.

Candidate models.—Two kinds of models were fitted: (1) an unconditional model to quantify unconditional spatial and temporal variability using all of the data ($n = 346$ removal sampling occasions across 291 sites); and (2) a set of landscape-based models to examine landscape correlates of density. The landscape models were restricted to sites that were sampled between 1991 and 2011 ($n = 267$); this was done to ensure that the sampling events bracketed the years when land use and land cover were derived (Homer et al. 2007). The landscape metrics that were considered as predictors of Brook Trout density included mean elevation, catchment area, percent developed and agricultural land use, percent forest cover, percent impervious surface, and road density (Table 1). As expected, many of the landscape metrics were highly correlated. To address the issue of collinearity, we first fitted models containing a single landscape predictor for Brook Trout density. Second, we fitted two- and three-predictor models, which included predictors that had a correlation coefficient (r) less than 0.60. Mean stream width was included as a predictor of capture probability in all candidate models because we expected it to be an important determinant of capture probability. Because the use of information-theoretic criteria (e.g., Akaike's information criterion and deviance information criterion) for hierarchical model selection is not straightforward, largely because of difficulty in determining the effective number of parameters, we assessed statistical "significance" by examining whether or not the 95% credible intervals (CRIs) for estimated coefficients overlapped zero. After selecting a top-ranked model, we evaluated the predictive performance by withholding approximately 15% of the sites (40 sites), refitting the model, and predicting the density at the 40 holdout sites. The posterior distributions for the observed and predicted densities were then plotted (for details, see Supplement A in the online version of this article).

To evaluate the relationship between first-pass CPUE (catch/min) and density, we fitted a linear regression model with $\log_e$(first-pass catch/min) as the predictor and $\log_e$(density), estimated from the complete data set, as the response variable. This analysis was restricted to sampling occasions that had first-pass effort (electrofishing time, min) information ($n = 343$ occasions). The relationship between first-pass catch per minute and density was plotted after the data were retransformed, and 80% and 95% prediction intervals were calculated (Stow et al. 2006).

Power analyses were performed to compare the utility of using first-pass catch per minute (i.e., density predicted from the relationship between first-pass catch per minute and density) versus the density estimated from three-pass removal sampling in two monitoring scenarios. For conciseness, we focus our two scenarios on monitoring and assessment of a single stream because our goal is to elucidate when a first-pass catch index may be useful and when it may not be useful rather than to determine an optimal monitoring design for any particular management objective. First, we examined the difference (in terms of statistical power) between using first-pass catch per minute and three-pass removal estimates to evaluate a management action (e.g., habitat improvement) that was designed to increase Brook Trout density in a stream. Specifically, this scenario (scenario 1) consisted of sampling Brook Trout prior to implementation of the management action (hereafter, pre-management), sampling Brook Trout again after the management action occurred (hereafter, postmanagement), and comparing the two estimates. If the 95% CRI of the difference between the pre- and postmanagement estimates did not contain zero, then the estimates were considered statistically different. Briefly, the power analysis consisted of using a simple removal model to generate samples from the posterior distributions for Brook Trout density (mean = 0.03 fish/100 m^2; 95% CRI = 0.02–0.04 fish/100 m^2) and capture probability (mean = 0.74; 95% CRI = 0.61–0.84) using three-pass depletion data collected from a Pennsylvania stream. Next, we used the posterior samples of density and capture probability to generate 250 simulated data sets for each of 10 potential population responses to a management intervention designed to increase Brook Trout density. The 10 hypothetical population responses were modeled as percent increases in density (10, 15, 20, 30, 40, 50, 60, 70, 80, and 90% increases; i.e., the effect sizes) for a total of 2,500 simulated data sets. Each of these simulated data sets consisted of catches for each of the three electrofishing passes during postmanagement sampling. For each simulated data set, we then estimated postmanagement density by using all of the three-pass catch data, and we predicted density by using the linear regression model with $\log_e$(first-pass catch/min) as the predictor and $\log_e$(density) as the response variable, as described above. For each of the 250 simulations and for each of the potential population responses and two approaches to estimating density, we tallied the number of times in which the 95% CRI of the difference between pre- and postmanagement densities did not contain zero (i.e., when the two estimates were considered statistically different). We report power as the proportion of simulations during which statistically different results were detected.

For the second management scenario (scenario 2), we examined the difference (in terms of statistical power) between the density predicted from the first-pass catch per minute–density relationship and the density estimated using three-pass removal data to detect a significant linear temporal trend in Brook Trout density within a stream. The simulation approach used for the power analysis was similar for that described for scenario 1; however, instead of estimating the power to detect differences in pre- versus postmanagement densities across a range of effect sizes, we evaluated the power to detect a 5% annual increase in Brook Trout density over a 10-, 20-, 25-, or 30-year period by using point estimates (posterior means) of density over time for both the density predicted from the first-pass catch per minute–density relationship and the density estimates obtained by using catch data from all three passes. For each of the 250 simulations and for both approaches to estimating density, we fitted a linear regression model to the time-series of $\log_e$ transformed density, examined whether the slope estimate was positive, and determined whether the 95% CRI for the slope (trend) parameter overlapped zero. We report power as the proportion of simulations in which statistically significant and positive trend results were detected.

RESULTS

Three-pass removal data from the 291 stream sites resulted in a total of 346 population estimates because 55 sites (16%) were sampled multiple times over the course of the time series. The number of times a given site was sampled ranged from 1 to 6. Seventeen sites were sampled twice, one site was sampled three times, two sites were sampled four times, five sites were sampled five times, and two sites were sampled six times (the remaining sites were sampled once). The mean site length was 288 m (SD = 54; range = 97–451 m), and mean site width was 4.0 m (SD = 1.6; range = 1.2–11.9 m). The mean stream surface area was 1,151 m^2 (SD = 580; range = 285–3,927 m^2). The overall estimated mean density of age-1 and older Brook Trout was 5.7 fish/100 m^2 (range = 0.24–37.2 fish/100 m^2, 95% CRI = 4.6–7.1 fish/100 m^2, $\hat{\sigma}^2_\delta = 0.83$; Figure 2A). The overall estimated mean probability of capture was 0.72 (range = 0.52–0.85, 95% CRI = 0.71–0.74, $\hat{\sigma}^2_\pi = 0.18$; Figure 2B).

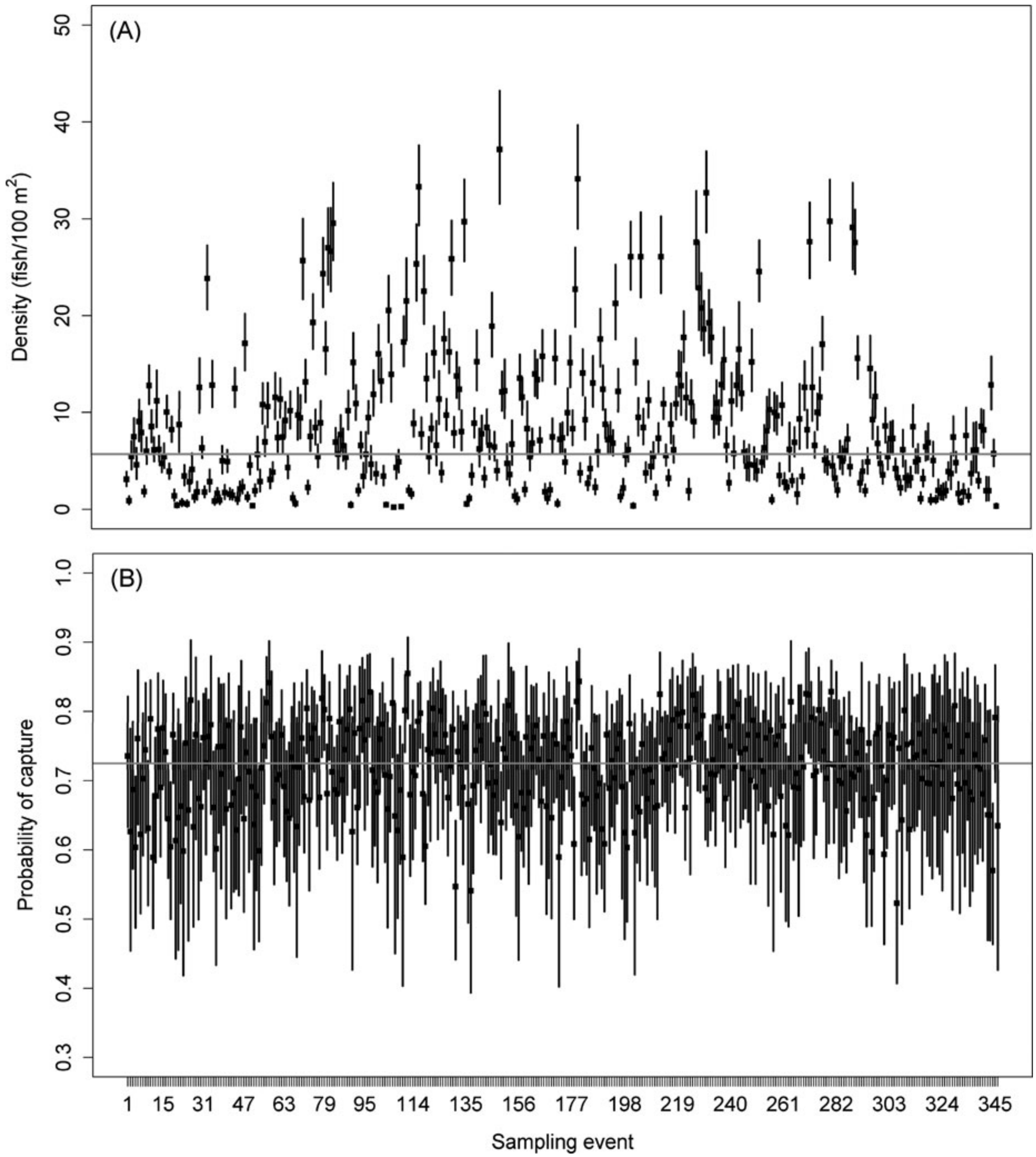

FIGURE 2. Estimated Brook Trout (**A**) density and **(B)** probability of capture from three-pass removal data for 346 sampling events in Pennsylvania streams. Squares are posterior means, vertical lines are 95% credible intervals, and the horizontal gray line represents the grand mean.

The number of sites sampled per year ranged from 1 to 29. Data were not available for the years 1976–1979 and 1985 (Figure 3A). Estimated annual average density (across all sites) was variable and ranged from 2.1 to 10.2 fish/100 m^2 ($\hat{\sigma}_{\alpha\delta}$ = 0.51, 95% CRI = 0.33–0.75; Figure 3A), whereas the estimated annual mean capture probability did not vary substantially, ranging from 0.71 to 0.74 ($\hat{\sigma}_{\alpha\pi}$ = 0.08, 95% CRI = 0.005–0.17; Figure 3B). The slope parameters describing the effect of time (i.e., a temporal trend) on average annual density and probability of capture overlapped zero, suggesting no apparent temporal trends in either parameter (trend parameter estimate for density = −0.033, 95% CRI = −0.264 to 0.193; trend parameter estimate for capture probability = −0.022, 95% CRI = −0.097 to 0.052; Figure 3).

The top-ranked landscape-based model included the predictors of mean elevation and percent developed land (Table 2;

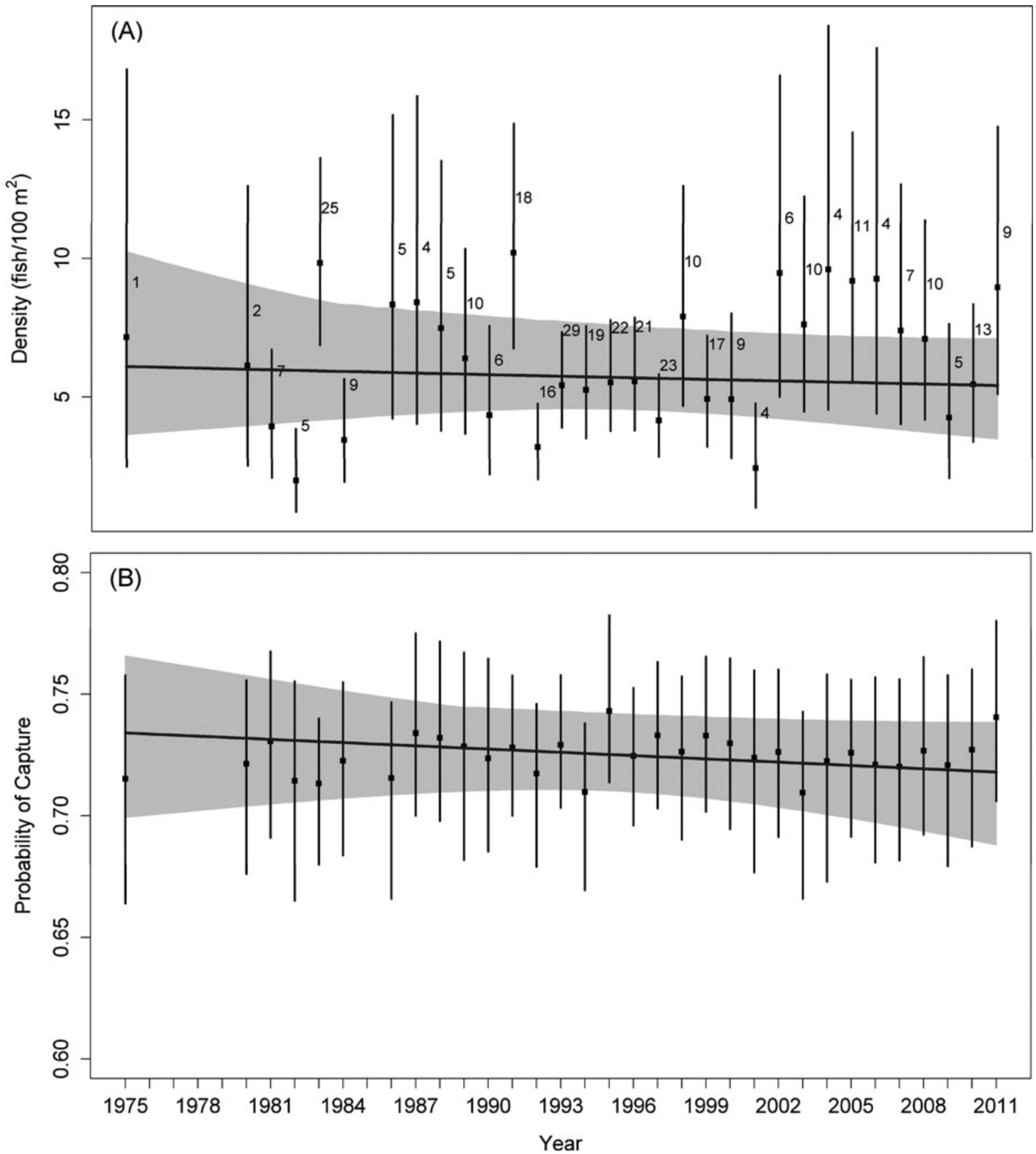

FIGURE 3. Estimated annual average **(A)** density and **(B)** capture probability of Brook Trout from three-pass removal data for 346 sampling events in Pennsylvania streams. Squares are posterior means; vertical lines are 95% credible intervals. Horizontal lines are hierarchical regression fitted lines; shaded regions are 95% credible regions. The numbers adjacent to estimates in panel (A) represent the number of sampling events that occurred in each year. Note the missing data for the years 1976–1979 and 1985.

posterior mean for the correlation between density and capture probability for this model = 0.02, 95% CRI = −0.20 to 0.23). Percent developed land was negatively correlated with Brook Trout density, and elevation was positively correlated with Brook Trout density (Figure 4A). As expected, mean stream width was negatively correlated with the probability of capture (Figure 4B). The top-ranked model predicted, on average, a Brook Trout density of 11 fish/100 m^2 (95% CRI = 7–16 fish/100 m^2) at high-elevation (∼800 m) sites with no developed land and a density of 2 fish/100 m^2 (95% CRI = 1–3 fish/100 m^2) at sites with 37% developed land (the highest network catchment land use percentage observed in

TABLE 2. Estimated posterior means (corresponding 95% credible intervals in parentheses) for predictors in the candidate landscape-based models of variation in Brook Trout density and capture probability. Brook Trout densities were estimated based on three-pass removal data from 267 sites (Pennsylvania Fish and Boat Commission data). All candidate models included mean stream width as a predictor of capture probability. Models are ranked according to the number of estimated coefficients with 95% credible intervals that did not overlap zero (shown in bold italics). See Table 1 for a description of predictors (NI = predictor was not included in the model).

Model	Predictor of capture probability	Predictors of Brook Trout density						
	Stream width	Developed land	Forest	Impervious surface	Agriculture	Catchment area	Mean elevation	Road density
1	***−0.182 (−0.269, −0.095)***	***−0.291 (−0.535, −0.044)***	NI	NI	NI	NI	***0.163 (0.046, 0.281)***	NI
2	***−0.180 (−0.268, −0.150)***	***−0.267 (−0.513, −0.018)***	NI	NI	NI	−0.087 (−0.203, 0.029)	***0.159 (0.041, 0.276)***	NI
3	***−0.175 (−0.264, −0.085)***	NI	NI	NI	NI	NI	***0.201 (0.087, 0.315)***	NI
4	***−0.188 (−0.274, −0.100)***	***−0.393 (−0.635, −0.153)***	NI	NI	NI	NI	NI	NI
5	***−0.179 (−0.267, −0.091)***	NI	NI	NI	NI	***−0.123 (−0.241, −0.006)***	NI	NI
6	***−0.176 (−0.266, −0.087)***	NI	NI	NI	−0.005 (−0.137, 0.127)	NI	***0.200 (0.084, 0.316)***	NI
7	***−0.177 (−0.267, −0.088)***	NI	NI	−0.280 (−0.294, 0.613)	NI	NI	***0.195 (0.079, 0.312)***	NI
8	***−0.178 (−0.267, −0.090)***	NI	0.063 (−0.076, 0.201)	NI	NI	NI	***0.196 (0.082, 0.310)***	NI
9	***−0.184 (−0.273, −0.096)***	NI	0.086 (−0.054, 0.227)	NI	NI	NI	NI	NI
10	***−0.185 (−0.272, −0.096)***	NI	NI	−0.695 (−1.698, 0.284)	NI	NI	NI	NI
11	***−0.184 (−0.273, −0.096)***	NI	NI	NI	NI	NI	NI	−0.043 (−0.143, 0.056)
12	***−0.154 (−0.252, −0.056)***	NI	NI	NI	−0.135 (−0.285, 0.016)	NI	NI	NI

our study) and low elevation (mean catchment elevation = 255 m; Figure 4A). However, based on predictions for holdout sites, the model tended to underpredict Brook Trout density for sites with high observed densities. There was also a high amount of uncertainty for several holdout sites (as indicated by wide predicted posterior distributions; Supplementary Figure 1).

First-pass Brook Trout CPUE ranged from 0.02 to 6.8 fish/min (SD = 1.19) and was correlated with the three-pass removal density estimates (Figure 5). The estimated slope of the relationship between $\log_e$(first-pass catch/min) and estimated $\log_e$(density) was 0.93 (95% CRI = 0.88–0.98), and the estimated intercept was −3.03 (95% CRI = −3.07 to −2.98). Log_e(first-pass catch/min) explained 80% of the variation in $\log_e$(density). Despite the correlation between $\log_e$(first-pass catch/min) and $\log_e$(density), the corresponding 80% and 95% prediction intervals were fairly wide, indicating that first-pass CPUE was a relatively imprecise index.

The power analysis for management scenario 1, which compared the predicted density from the first-pass catch per minute–density relationship and the estimated density from three-pass removal sampling to evaluate a management action, highlighted the low statistical power (near zero over the range of effect sizes examined) of using predicted density from the first-pass CPUE index (Figure 6A). The low power resulted from the large amount of uncertainty in the predicted densities (e.g., Figures 5, 6B). When using three-pass removal estimates, a power of 0.80 was achieved at a postmanagement density increase of approximately 55%. For this scenario, estimation of density by using three-pass removal data led to a large increase in power relative to using predicted density from first-pass catch per minute; the increase in power was largely a function of the increase in precision gained by performing three passes to estimate density. Conversely, in scenario 2, the power to detect a long-term linear trend—a management objective that does not necessarily require precise estimates at any given site—was similar when using either the predicted density from first-pass catch per minute or the estimated density from three-pass removal sampling. The statistical power required for both the predicted and estimated densities to detect a 5% annual increase in density over 10-, 20-, 25-, and 30-year sampling time frames was approximately 0.07, 0.54, 0.86, and 0.98, respectively.

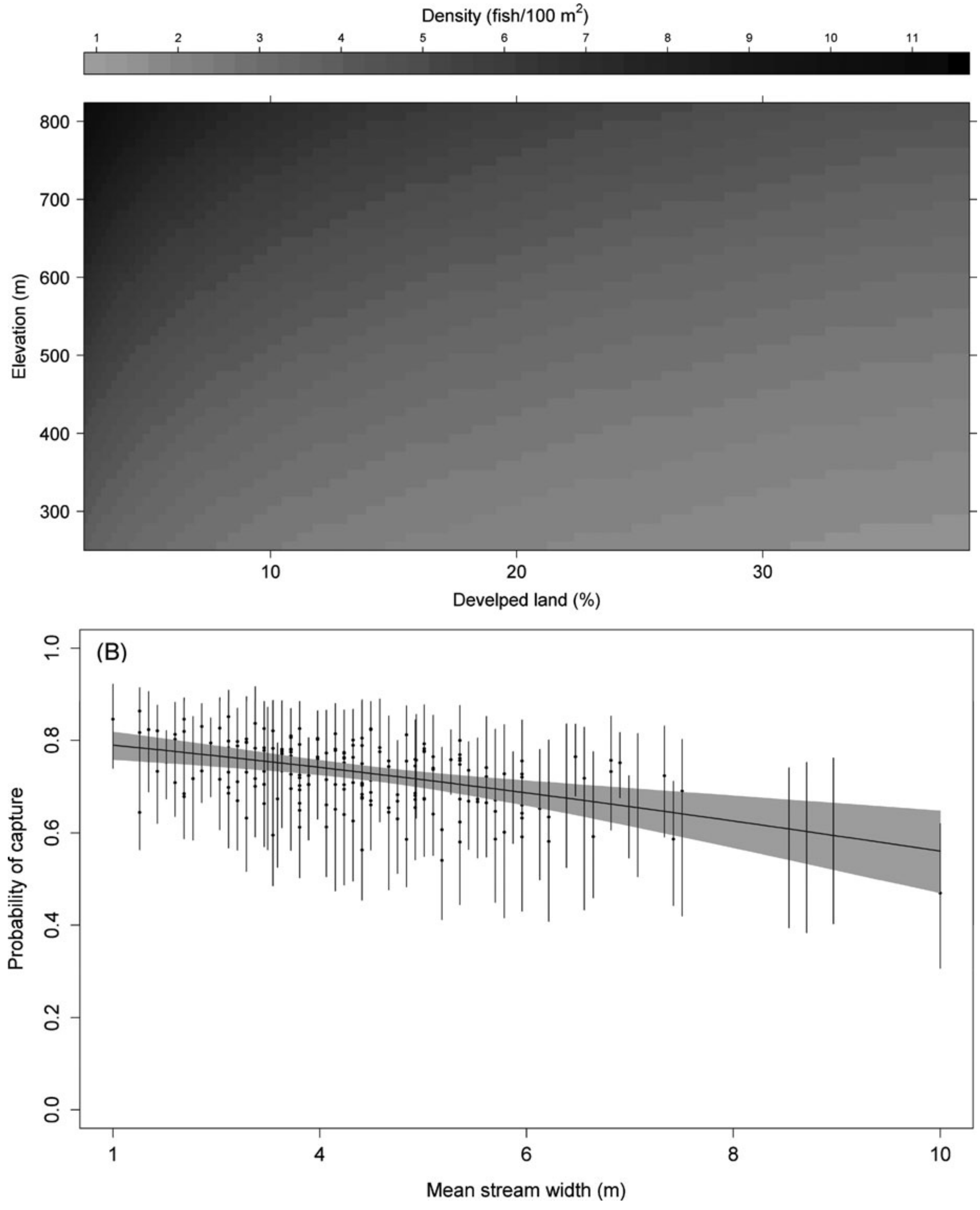

FIGURE 4. **(A)** Brook Trout density predictions (fish/100 m^2) from the top-ranked hierarchical model in relation to the percentage of developed land in the network catchment and mean elevation; and **(B)** the relationship between stream width and Brook Trout capture probability. The predicted surface in panel (A) shows the posterior means. In panel (B), points represent posterior means, vertical lines are 95% credible intervals, and the shaded region is the 95% credible region around the fitted line.

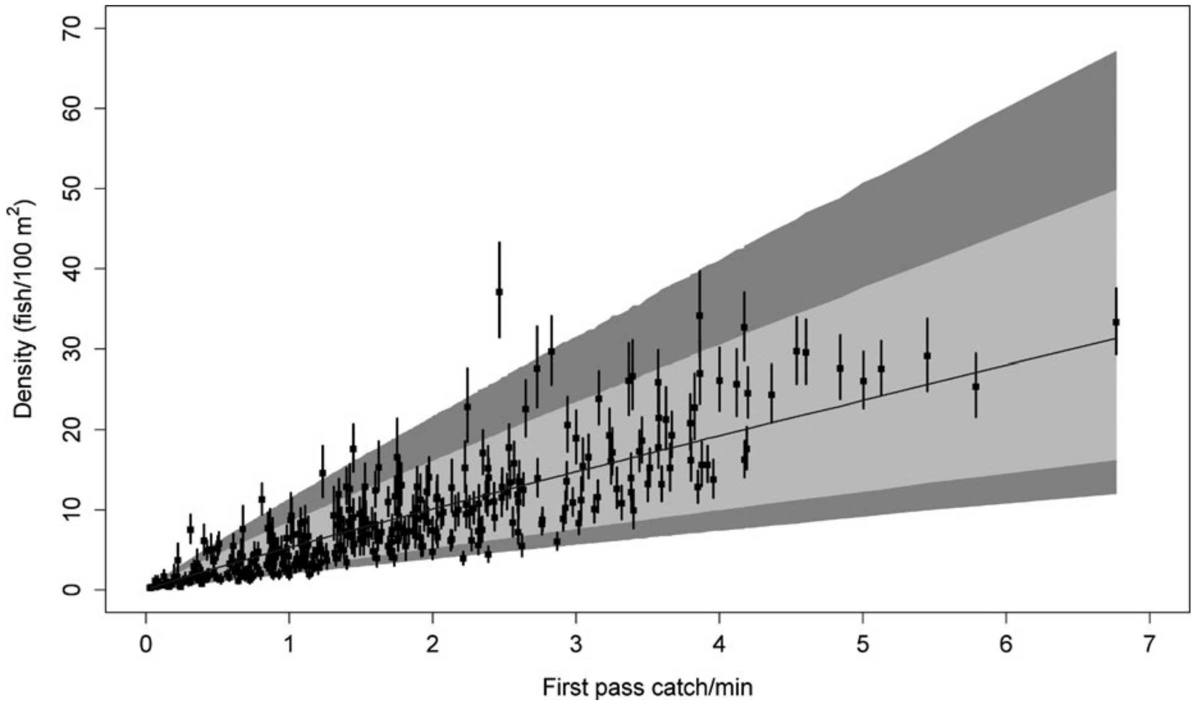

FIGURE 5. Relationship between first-pass catch per minute and estimated density of Brook Trout from three-pass removal sampling for 343 stream sampling events in Pennsylvania. Squares are posterior mean estimated abundances; vertical lines are 95% credible intervals from a hierarchical model. Dark- and light-shaded regions correspond to 95% and 80% prediction regions, respectively, around the retransformed posterior mean predictions ($r^2 = 0.80$).

DISCUSSION

We quantified the spatial and temporal variability in age-1 and older Brook Trout density and capture probability, examined landscape correlates of density, and examined the relationship between first-pass catch per minute and density estimates from three-pass removal sampling. We found substantial variability in Brook Trout density among sites and years. This was expected because Brook Trout density at any given site or year can be related to local biotic (e.g., density-dependent processes) and abiotic (e.g., physical habitat) factors, such as annual variation in streamflow (Deschênes and Rodríguez 2007; Grossman et al. 2010). This high annual variation in abundance is common for inland trout populations (Dauwalter et al. 2009). Because our analysis included a relatively large number of sample sites, the range of estimated Brook Trout densities observed in this study could be used by managers to help refine current management objectives and expectations as they relate to the fish densities that might be expected as a result of fisheries management actions, restoration efforts, or water quality protection. Managers can also use the results from the top-ranked landscape-based model to help anticipate the effects of landscape development on Brook Trout densities across a range of elevations.

We did not observe a regional decreasing trend in Brook Trout density: annual densities were variable and relatively uncertain. This does not suggest that the number of streams supporting self-sustaining Brook Trout has not declined over the 37-year period of interest. In fact, much of the historical Brook Trout habitat in Pennsylvania no longer supports self-sustaining populations (Hudy et al. 2008), and it is likely that localized losses have occurred in recent years as a result of land development and other stressors. Rather, our results illustrate that within streams supporting Brook Trout populations, the annual average density of fish has not systematically declined. In addition, because the stream sites used in this study were not randomly selected, our inferences about temporal trends cannot be generalized to all Brook Trout streams in Pennsylvania. However, because of the negative relationship between Brook Trout density and development, we would predict that for relatively undeveloped catchments, future increases in development may be followed by declining regional trends in density.

The percentage of developed land cover in the network catchment was found to have a negative effect on Brook Trout density, but the exact mechanisms are unknown. We did not find effects of road density or impervious surface cover on Brook Trout density (95% CRIs overlapped zero; these variables were correlated with developed land cover); however, other studies have documented negative associations between these factors and Brook Trout density. Stranko et al. (2008) reported that Brook Trout densities in Maryland declined as the impervious surface percentage increased in the catchment, and Pépino et al. (2012) observed that highway crossings with low and intermediate passability had a negative effect on Brook Trout density. The effects of development on Brook Trout in our study and on coldwater fishes in general likely result from several

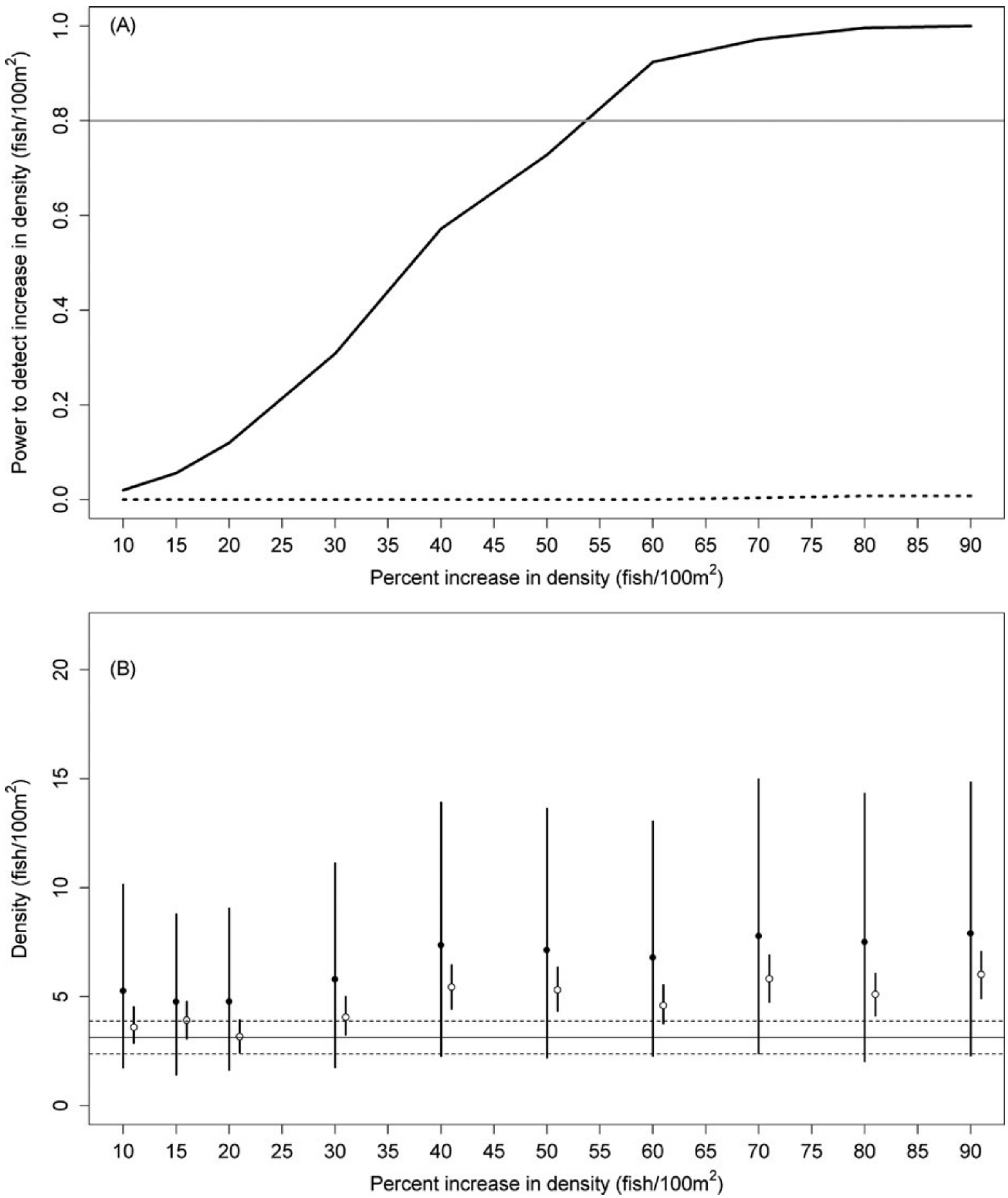

FIGURE 6. **(A)** Power curves evaluating the power to detect significant increases in Brook Trout density over a range of effect sizes (percent increases) by comparing densities estimated via three-pass removal before and after a management action (solid line; scenario 1 in Methods) or densities predicted from first-pass catch per minute (dashed line). A difference between pre- and postmanagement densities was considered significant if its 95% credible interval did not contain zero. Horizontal line represents a power of 0.80, which is shown for reference. Panel **(B)** illustrates results from a single simulation. The horizontal solid line is the pre-management posterior mean density (dashed lines = 95% credible interval) estimated from three-pass removal sampling; the open circles are postmanagement density estimates (vertical lines = 95% credible intervals) from three-pass removal sampling; and the shaded circles are densities (vertical lines = 95% predictive intervals) predicted from first-pass catch per minute by using a regression model. Note the negative bias in the three-pass removal estimator in panel (B) (Sweka et al. 2006).

direct and indirect effects on stream characteristics, including increased water temperature, increased sediment loading, and altered hydrologic regimes associated with the loss of forest cover, increases in road density (and potentially road crossings over streams), and increases in impervious surface percentages (Wang et al. 1997).

The inability of a landscape-based model to predict density at all sites with reasonable accuracy (Supplementary Figure 1) and precision is not surprising, as our top-ranked model did not account for other biological and abiotic factors that interact to ultimately determine Brook Trout density in any given stream. However, the top-ranked model was still useful for illustrating the average relationship between developed land and Brook Trout density and will be useful for managers as they attempt to anticipate the effects of development on Brook Trout density.

Unlike fish density estimates, the probability of capture did not vary substantially among sites or among years, and the small variation that existed among sites was negatively correlated with mean stream width. A negative correlation between capture probability and mean stream width was expected and has been reported in other studies for a variety of trout species (e.g., Kruse et al. 1998). Hense et al. (2010) also found that Brook Trout capture probability was negatively correlated with mean stream width, and they estimated a capture probability of 0.72 for adult Brook Trout, the same as our overall mean estimate of 0.72.

The low spatiotemporal variability, in combination with the correlation between first-pass catch per minute and estimated density from three-pass removal sampling, suggests that single-pass catch per minute could serve as a surrogate for three-pass removal density estimates to support some local and large-scale objectives for Brook Trout monitoring in small Pennsylvania streams. However, the evaluation of statistical power for the two management scenarios highlights the need to explicitly define the goal of the monitoring and assessment program. For example, if an assessment of a stream or set of streams requires relatively precise estimates of density (e.g., scenario 1; Figure 6), then predicting density from the first-pass catch may not be advisable. Rather, the increase in precision achieved by performing three passes may be well worth the additional sampling effort. However, if the goal is long-term trend detection (at a single site or regionally across sites) and if a precise estimate of density at any single stream is not required to meet management objectives, then predicting density from first-pass catch per minute may be sufficient. This may be particularly important for regional long-term trend monitoring programs in which there is a need to minimize the amount of time spent sampling at any single site so that more sites can be sampled across the region of interest. We expect that the number of sites that could be sampled in a single workday by using single-pass removal would at least double in comparison with three-pass removal, thus providing the ability to evaluate Brook Trout population trends in more streams and across a broader spatial extent. Bergman et al. (2011) also concluded that single-pass CPUE could provide a reliable index of adult trout abundance in Wisconsin streams, but that study did not address the uncertainty in estimating abundance with first-pass catch.

Lastly, the results of our power analyses support previous studies' power analyses, highlighting the fact that statistical power to detect changes in status or temporal trends is quite low over management-relevant time frames and for relatively small effect sizes. For example, our power analysis suggested that it takes more than 20 years to achieve a power of at least 0.80 for detecting an annual 5% increase in density. Dauwalter et al. (2009) also found that for many trout populations, the number of years required to detect a 5% annual change (in this case, a decline) with a power of 0.80 or greater and an α of 0.05 could be more than 20 or 30 years. In addition, a literature review by Wagner et al. (2013) found that the mean number of years required for detection of a trend magnitude less than 5% per year with a power of at least 0.80 was 19 years. The relatively long duration (or large effect sizes) required to detect significant temporal trends is common for freshwater fish and habitat metrics and emphasizes the critical role of translating management questions to monitoring objectives as part of the overall management process (Wagner et al. 2013). Thus, the ultimate efficacy of using single-pass catch as an index of Brook Trout density will be dictated by the specific goals and objectives of any given monitoring program.

As changes to the landscape continue and as aquatic habitats are altered under a changing climate, the ability to make inferences about local and regional dynamics of fish populations is of increasing importance. The use of hierarchical models like those employed here allows for the estimation and evaluation of spatial and temporal variability in parameters that are of interest to both management and conservation while also allowing for the elucidation of correlates that may be influencing the observed dynamics. As generating regional inferences becomes increasingly important, the fiscal resources needed for monitoring over large spatial scales will likely be reduced over time (and even if fiscal resources do not decrease, cost-effective approaches are still desirable). Thus, the development of cost-effective assessment techniques that use indices of density (or abundance) will also increase in importance. For example, a change in sampling technique from multiple-pass electrofishing to single-pass electrofishing may allow field crews to sample more sites or water bodies in a given day and increase the overall spatial coverage of sampling efforts, thus enabling stronger inferences to be made about the region of interest. However, the validity of these indices should be evaluated within the context of specific management objectives and on a species-by-species basis to ensure their efficacy.

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