

North American Journal of Fisheries Management 40:840–851, 2020

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ISSN: 0275-5947 print / 1548-8675 online

DOI: 10.1002/nafm.10443

ARTICLE

Multipass Electrofishing Sampling Efficiency for Stream Crayfish Population Estimates

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Abstract

We estimated the efficiency of electrofishing for collecting crayfishes in southern Appalachian Mountain streams (Alabama, USA). We conducted electrofishing depletion surveys at 20 sites in five large, species-rich streams in two drainages. We collected five crayfish species during the depletion surveys. On average, catchability was 34%, with depletion surveys collecting 73% of the individuals that were estimated to reside within stream sections. Catchabilities were lower for pass 1 than for the subsequent passes in 21% of the depletion surveys. The number of species that was collected increased during the second electrofishing pass, indicating that conducting two electrofishing passes may be more effective than a single electrofishing pass is for estimating the richness of crayfish species. Crayfish catchability by electrofishing was higher in streams with higher conductivities, longer crayfish, higher water temperatures, and lower percentages of adult males. Our results show that multipass electrofishing can precisely assess population density for various crayfish species in species-rich, large-stream habitats and that multipass electrofishing provides more precise estimates of species richness for crayfish than single-pass electrofishing does.

Numerous studies illustrate the importance of crayfishes to aquatic ecosystems, with crayfishes serving as ecosystem engineers and playing major roles in food web dynamics (Statzner et al. 2003; Usio and Townsend 2004). While the ecological importance of crayfishes is evident (Chambers et al. 1990; Lodge et al. 1994; Momot 1995), we still struggle with accurately assessing crayfish community structures and population characteristics (e.g., density). For crayfishes and other organisms, efficient sampling methods are critical for accurately and precisely estimating biotic

assemblage structures including species richness, composition, and relative abundances (Maher et al. 1994; Growns et al. 1996; Kennard et al. 2006) and for making informed ecosystem management decisions (Kennard et al. 2006).

Electrofishing is a common sampling method that is used to assess the structure of crayfish populations both quantitatively and qualitatively (Usio and Townsend 2000; Adams 2013; Larson and Olden 2016; Adams et al. 2018; Budnick et al. 2018). However, few studies have assessed the efficiency of electrofishing for sampling crayfish

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Received December 12, 2019; accepted March 26, 2020

(Bernardo et al. 1997; Rabeni et al. 1997; Alonso 2001; Reid and Devlin 2014). In all but one of these studies (Rabeni et al. 1997), small streams (2–6 m wide) with a majority of pool habitats were sampled, and the studies focused on streams with one crayfish species present (Bernardo et al. 1997; Rabeni et al. 1997; Alonso 2001). Only one study has assessed the efficiency of electrofishing depletion sampling for crayfish in large streams (drainage area $\geq 91 \text{ km}^2$; stream width $>7 \text{ m}$) with mostly riffle and run habitats and multiple crayfish species (Reid and Devlin 2014). No study has assessed how stream characteristics affect sampling efficiency. Because electrofishing efficiency varies depending on the characteristics of the sampled habitat, species diversity, and species-specific characteristics (e.g., avoidance, size) (Bohlin et al. 1989; Zalewski and Cowx 1990), understanding how and why electrofishing efficiency varies is critical for effective sampling. Understanding the efficiency of electrofishing in species-rich streams with diverse stream habitats will allow investigators to choose methods that account for biases and provide the most accurate and precise data.

In this study, we assessed electrofishing efficiency for crayfish via depletion surveys in relatively large streams (drainage areas $\geq 91 \text{ km}^2$) in the biotically diverse southern Appalachian Mountains. We assessed electrofishing efficiency relative to the size variation and sex of the sampled crayfish and stream habitat characteristics. Our goal was to assess the precision of the population and community structure estimates that were obtained by electrofishing in large, species-rich streams and to assess the number of electrofishing passes that is necessary to provide the most precise estimates. Our objectives were to determine electrofishing efficiency by (1) assessing crayfish catchability (the probability of collecting all individuals) among multiple electrofishing passes, (2) assessing differences between collected and estimated species density (number of individuals/ m^2), (3) estimating the number of electrofishing passes that is needed to precisely assess species richness, and (4) assessing the effect of crayfish assemblages and the environmental characteristics of the stream on the catchability of crayfish by electrofishing.

Study Area

The study sites were in the Bear Creek (Tennessee River basin) and Cahaba River (Mobile River basin) drainages in the southern Appalachian Mountain region of Alabama, USA (Figure 1). The region is the northern hemisphere center of crayfish diversity, with some of the most biotically diverse streams in the world (Crandall and Buhay 2008). We sampled five, wadeable, perennial streams. The streams were typical of the rocky, mountainous streams that are found throughout the southern Appalachian Mountain region (Barnett 2019). They

flowed through predominantly forested environments intermixed with agricultural, residential, and urban land uses (Thom et al. 2013). The Bear Creek drainage sites were in the Fall Line Hills physiographic province, in Franklin and Colbert counties, and the Cahaba River drainage sites were in the Ridge and Valley physiographic province, in Shelby and Jefferson counties (Sapp and Emplaincourt 1975).

METHODS

Crayfish sampling.—We conducted electrofishing depletion surveys to estimate electrofishing efficiency for collecting crayfishes. The surveys took place in summer (July and August) 2015–2017 at 20 sites, four along each of five streams (Figure 1). Within each site, we isolated one stream section (30–105 m long) with block nets (5-mm mesh seines) to prevent crayfishes from leaving the sites. The section lengths were a minimum of three times the wetted stream width, and the sections were lengthened, if necessary, to encompass a representative of each habitat type in the site. We partitioned the sampling effort between macrohabitats (i.e., riffle, runs, pools) based on the percentage of each macrohabitat within the blocked sections. A minimum of three successive electrofishing passes were made in each section. In 2017, if the total number of crayfish that was collected did not decrease from the second to third pass, we conducted a fourth pass.

We used a Smith-Root backpack electrofisher (model 12A programmable output wave, battery-powered electrofisher set at 50–60 Hz, 4–5 ms pulse width, 300–400 V [Table 1]; Vancouver, Washington) with a circular anode that was covered with 3-mm meshed netting. The electrofisher settings were adjusted at each site based on stream conductivity and temperature. We manipulated the electrofisher settings until the electrofisher sound was a continuous beep, and we then decreased the voltage by 100 V to get a broken beep (Smith-Root 1996; Hoese and Reader 2011). We used as low a voltage as possible to prevent the loss of crayfish chelae (Alonso 2001). The sampling crew consisted of three people: the electrofisher operator who also collected crayfish and two dip netters who collected crayfish by using 41 × 23 cm dip nets with 3-mm mesh.

We electrofished for 4–10 s/m of stream in each macrohabitat (electrofishing time range: 145–650 s/site). We electrofished the entire stream width while slowly moving upstream and trying to catch all of the crayfish in the blocked section. If stunned crayfish were seen along the stream bottom but could not be collected easily with the dip nets, the electrofisher operator would stop and lift the anode out of the water, and individuals would collect the stunned crayfish by hand. While all of the blocked

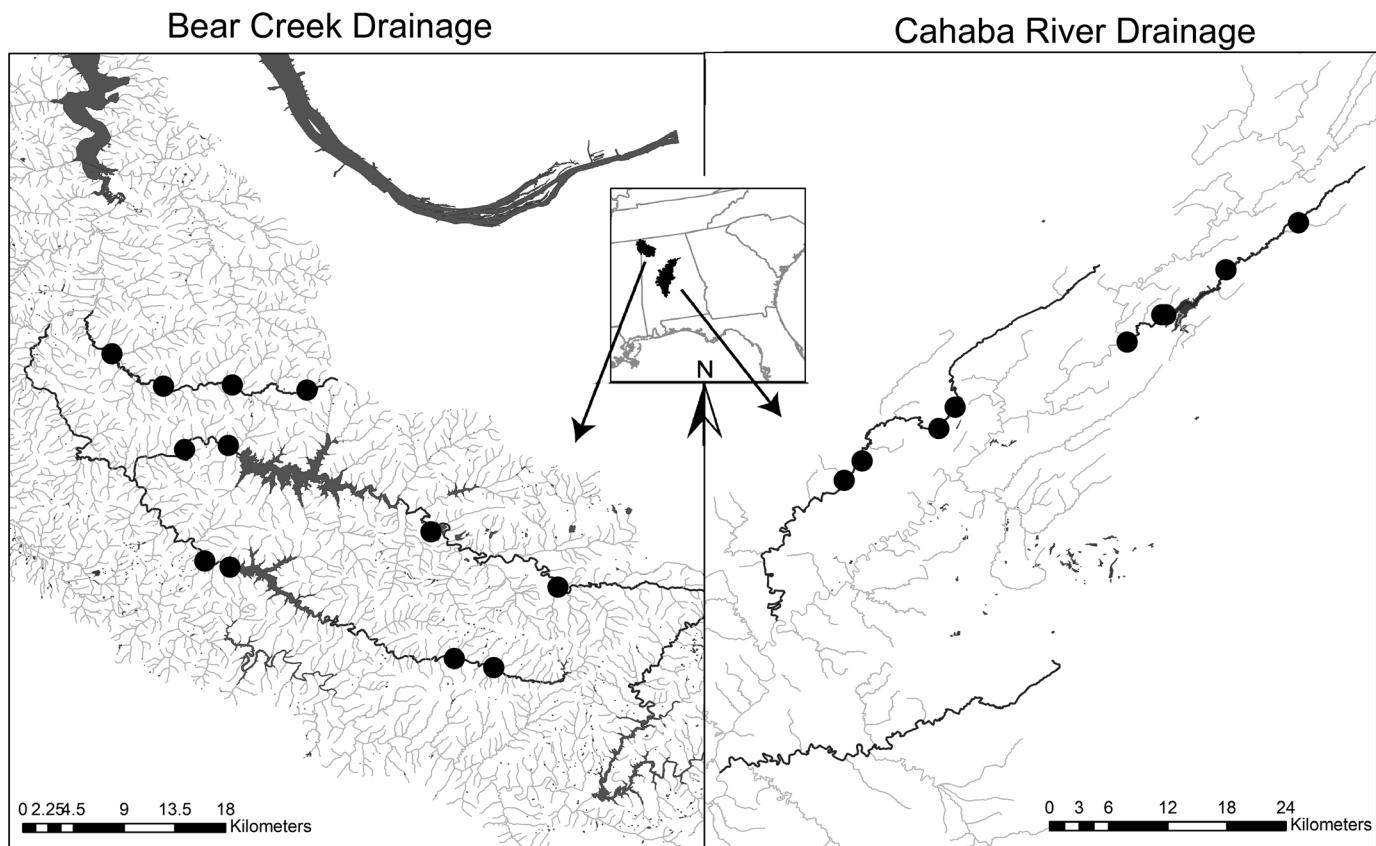


FIGURE 1. Map of the Bear Creek and Cahaba River drainages, Alabama, with collection sites represented by filled circles. The inset shows the drainage locations that are within the southeastern United States.

TABLE 1. Median (SD) values for environmental parameters and electrofishing voltage from multipass electrofishing surveys. Four sites were sampled in each stream. The abbreviations are as follows: DO = dissolved oxygen; D16 = size (mm) at which 16% of substrate particles were smaller; D84 = size (mm) at which 84% of particles were smaller.

	Little Bear	Cedar	Rock	Little Cahaba	Shades
Water temperature (°C)	21.5 (2.8)	25.8 (1.8)	22.2 (1.7)	23.4 (2.5)	26.7 (1.0)
DO (mg/L)	8.0 (0.2)	7.0 (1.2)	5.0 (1.8)	6.7 (0.2)	6.1 (1.0)
Conductivity ($\mu\text{S}/\text{cm}$)	96.5 (54.7)	272.0 (85.0)	160.8 (52.9)	326.7 (86.3)	211.0 (29.7)
pH	7.54 (0.13)	7.79 (0.85)	7.38 (0.41)	7.62 (0.03)	7.35 (0.14)
Wetted width (m)	6.6 (2.5)	10.4 (3.5)	6.9 (1.3)	11.3 (5.1)	11.9 (2.9)
Depth (cm)	9.9 (5.1)	16.5 (5.7)	11.3 (8.7)	18.8 (12.2)	15.7 (1.7)
Width to depth ratio	0.67 (0.38)	0.76 (0.18)	0.54 (0.51)	0.80 (0.47)	0.69 (0.19)
D16	1.1 (1.2)	7.7 (5.7)	1.4 (16.1)	21.7 (32.6)	0.2 (0.9)
D84	1,300.4 (1,000.1)	249.3 (932.0)	48.8 (978.8)	180.3 (942.4)	1,021.7 (1,137.0)
Aquatic vegetation (%)	12.0 (13.2)	17.3 (9.3)	16.0 (11.7)	11.7 (3.3)	7.9 (8.2)
Canopy cover (%)	63.9 (20.9)	59.7 (17.2)	56.1 (20.7)	61.1 (10.2)	77.4 (20.9)
Discharge (m^3/s)	2.9 (1.3)	7.5 (3.9)	0.2 (0.6)	11.8 (11.7)	10.6 (8.3)
Electrofisher voltage (V)	400 (50)	300 (50)	400 (0)	300 (0)	300 (0)

areas were electrofished, greater sampling effort was spent in areas with complex cover (e.g., vegetation, wood) than in open areas where few crayfish appeared. Because

assemblage comparisons should be based on standardized samples (e.g., standardized for area, volume, number of individuals, catch per time) (Gotelli and Colwell 2001;

Colwell et al. 2004), we standardized both area and time sampled. To standardize time sampled, we calculated a minimum electrofishing time (4 s/m) for each site based on the electrofishing effort that was necessary to sample several sites during the preliminary sampling. Because this time was surpassed during the first electrofishing pass during each survey, we sampled all of the passes in the depletion surveys by using the electrofishing time that was needed to adequately sample during the first electrofishing pass. The electrofishing time did not include the times that the electrofisher was stopped and individuals hand-collected crayfish.

Immediately after each pass, crayfish statistics were recorded and most of the crayfish were released outside of the blocked section. We recorded crayfish species, life stage (i.e., adult, juvenile), sex, adult reproductive form (form I male [reproductive], form II male [nonreproductive], female [without eggs], and ovigerous female [bearing eggs]), and postorbital carapace length. We preserved the crayfish that were not released in the field in $\geq 70\%$ ethanol for further laboratory analyses.

Environmental measurements.—To understand what environmental factors were associated with electrofishing efficiency, we measured water quality parameters (water temperature, conductivity, dissolved oxygen [DO], and pH), channel characteristics (wetted width, depth, and percentage of canopy cover), substrate characteristics (substrate sizes and percentage of aquatic vegetation) and stream discharge (Table 1). Before sampling, we measured the water quality parameters at one location within each site with a Hydrolab Quanta (Hach-Hydrolab, Loveland, Colorado). We calibrated the Hydrolab before each sampling round (yearly sampling) for all of the parameters and daily for DO. The channel characteristics were measured at four equidistant locations 10 to 68 m apart. Depth was measured midchannel and 10 cm from the right and left edges. Canopy cover was also measured midchannel with a convex spherical densiometer. Using Wolman pebble count procedures (Wolman 1954; Harrelson et al. 1994), we documented streambed composition across the bankfull channel width. We measured one pebble (mm), blindly selected at our boot tip, at a minimum of 100 points, distributed among at least 10 diagonal transects (10 points were equally spaced along each transect) within each site. Between adjacent sampling points, we visually estimated the percentage of streambed that was covered by vegetation. We calculated stream discharge (m^3/s) by using the transect method (Harrelson et al. 1994) with a Marsh-McBirney Flo-Mate 2000 and topsetting rod (Hach, Loveland, Colorado) at one location per site.

Crayfish catchability and density analyses.—To determine electrofishing efficiency, we estimated each crayfish species' catchability (the probability of collecting all of the individuals that were estimated within stream section) and

species density (the number of individuals/ m^2) for each site by using the maximum weighted likelihood method (Carle and Strub 1978). This maximum-likelihood algorithm assumes a constant catchability and constant effort in each survey and was selected because of its statistical robustness. We tested the constant probability of capture among passes assumption by using a chi-square-based statistic (Seber 1982). We ran all of the analyses with the FSA package (Ogle et al. 2018) in R software version 3.4.2 (R Core Team 2013).

We developed linear models to examine catchability differences among species and streams and to estimate the relationship between the collected and estimated crayfish densities. This relationship can estimate crayfish densities from electrofishing collections in streams with similar conditions. To test whether catchability varied among species and streams, we developed a linear mixed-effect "catchability" model, fit with maximum-likelihood estimation. In the catchability model, \log_e catchability was the response variable, species and streams were the independent variables, and year was a random effect. The interactions between the independent variables were not included in the model. Because *Cambarus striatus* and *Faxonius compressus* were collected at few (≤ 3) of the 20 sites, they were not included in the catchability model. The analyses were performed with the lmerTest package (Kuznetsova et al. 2015) in R, using Tukey's honestly significant difference post hoc tests for comparing the means. Histograms of the model residuals did not depart from normality. The relationship between the collected and estimated crayfish densities was estimated by using linear regression analyses.

Species richness analyses.—To estimate the number of electrofishing passes that were needed to precisely assess species richness, we compared the differences between the numbers of species that were collected during each pass by using a linear, mixed-effect "species" model. In the species model, the number of species that was collected was the response variable, electrofishing pass and stream were independent variables, and site was a random effect. The interaction of electrofishing pass and stream was included in the model to understand whether changes in the number of species by pass differed among streams. The analyses were performed with the lmerTest package in R, using Tukey's honestly significant difference post hoc tests for comparing the means. Histograms of the model residuals did not depart from normality.

Analyses of environmental and crayfish assemblage effects on catchability.—We created linear mixed-effect "environmental" models to determine whether crayfish assemblages and stream environmental characteristics were associated with the catchability of crayfish when electrofishing. We used the environmental models to relate catchability with \log_e channel characteristics, \log_e water quality parameters (water temperature, conductivity, and

DO), pH, log_e stream discharge, log_e substrate characteristics (streambed vegetation and substrate metrics), crayfish species, median crayfish size, and percentages of adults and adult males. We averaged the streambed vegetation and channel characteristics across each site. Two substrate metrics were derived from the pebble counts from each subreach: the particle size at which 16% (D16) of the particles were smaller and that at which 84% of the particles were smaller (D84) (Olsen et al. 2005). In the model, crayfish catchability was the response variable and the lack of independence among the sites that were sampled within a stream was accounted for by treating stream as a random effect. We included the interactions between the crayfish species and crayfish parameters (i.e., crayfish size, percentages of adults, and percentages of males) in the full model to understand whether the crayfish parameters correlated with catchability differently among the crayfish species. We used the MuMIn R package (Barton and Anderson 2002) to analyze all of the possible models, using the corrected Akaike information criterion (AIC_c) for model selection (Burnham and Anderson 2004). Delta AIC_c values ≤ 2 represented the best-supported models (Hurvich and Tsai 1989). For each predictor variable, relative variable importance was calculated based on the variable's appearance in the AIC_c-best models (Burnham and Anderson 2004). Predictors with relative variable importance >0.5 were considered important. The proportions of variance explained by the fixed effects (marginal R^2) and by the fixed and random effects (conditional R^2 s) were used to assess the fit of each model (Nakagawa and Schielzeth 2013; Johnson 2014). The histograms of model residuals did not depart from normality.

RESULTS

We collected 510 crayfish (including five species) in 20 electrofishing depletion surveys. We caught from 1–99 crayfish per survey ($\bar{X} = 26/\text{survey}$), and the postorbital carapace lengths of the crayfish ranged from 3.8–39.2 mm ($\bar{X} = 11.6 \text{ mm}$). We conducted four electrofishing passes in 8 of the 20 electrofishing depletion surveys due to increases in the total numbers of crayfish that were collected from the second to third passes. The crayfish were collected in large ($\bar{X} = 11 \text{ m}$ wetted width), warm ($\bar{X} = 24.3^\circ\text{C}$), low conductivity ($\bar{X} = 207.4 \mu\text{S}/\text{cm}$) streams, with a relatively wide range of habitat characteristics (Table 1).

Crayfish Catchability and Density Estimates

Catchability differed among the species ($F_{3, 32} = 3.22$, $P = 0.04$) and streams ($F_{4, 32} = 4.62$, $P < 0.01$). The mean ($\pm 95\%$ CI) overall catchability was $34 \pm 3\%$ ($N = 34$), with *F. validus* in Rock Creek having the lowest catchability (3%) and *F. erichsonianus* in Little Cahaba River having the highest catchability (71%). *Cambarus striatus*

was collected at one site and had 44% catchability. Catchability was similar for all of the species except *F. compressus* and *F. validus* (Figure 2). Catchability for *F. compressus* was significantly higher than that for *F. validus*. For each species, catchabilities were lower for pass 1 than for the other passes in 8–42% ($\bar{X} = 21\%$) of the depletion surveys. Catchability was also higher in Little Cahaba River than in Rock and Shadys creeks (Figure 3).

The estimated densities ranged from 0.00–2.69 individuals/m² ($\bar{X} = 0.15/\text{m}^2$). Crayfish densities were highest in Rock Creek ($0.59 \pm 0.36/\text{m}^2$, [mean $\pm 95\%$ CI]) and lowest in Cedar Creek ($0.02 \pm 0.01/\text{m}^2$). During the depletion surveys, we captured, on average, 73% of the individuals that were estimated to be within the stream sections. The relationship between the collected and estimated densities was best represented by a polynomial regression model (Figure 4).

Species Richness Estimates

The number of species that was collected in the depletion surveys ranged from 1–4 species/survey ($\bar{X} = 2$ species/survey). Species richness was highest at the sites in Rock Creek (3.0 ± 0.4 , mean $\pm 95\%$ CI) and lowest at the sites in Shadys Creek (1.3 ± 0.3) and Little Cahaba River (1.3 ± 0.3). The sampled species richness increased after the first pass (comparisons were completed by ANOVA models of pass 1 with passes 2, 3, and 4, all P values < 0.05 ; Table 2), with no statistically significant differences detected among subsequent passes (comparisons of passes 2, 3, and 4, P -values range = 0.44–0.81).

Environmental and Crayfish Assemblage Effects on Catchability

Crayfish catchability varied by stream and species, suggesting that stream environmental factors and crayfish characteristics influenced catchability. Water quality, crayfish size, and crayfish sex were correlated with crayfish catchability. Catchability was higher in the streams with higher conductivities, higher water temperatures, larger crayfish, and fewer adult males (Table 3). The fixed effects explained 45% of the variation in the dependent variable, indicating that unmeasured independent variables may substantially influence electrofishing efficiency.

DISCUSSION

Reliability and confidence in the population and community structure estimates that are obtained by commonly used sampling methods, such as electrofishing, are critical to making informed ecosystem management decisions (Kennard et al. 2006). Numerous factors (e.g., stream and population characteristics) influence the effectiveness of

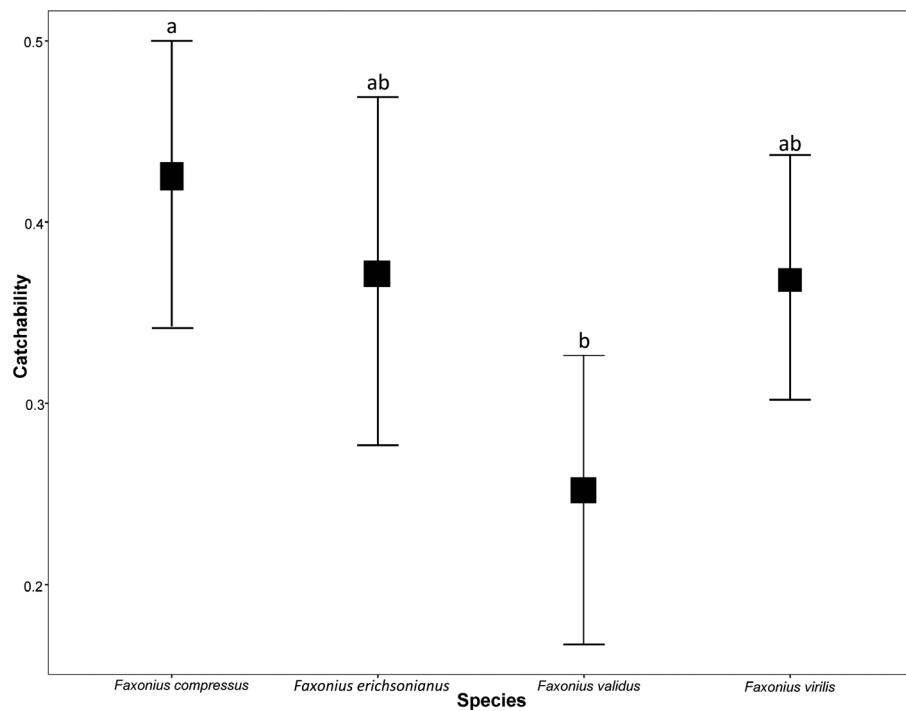


FIGURE 2. Comparisons of mean catchability (probability of collecting all of the individuals) $\pm 95\%$ CI among species. The different letters above the bars indicate significant differences ($P < 0.05$) in catchability. Log_e transformed data were used in linear mixed-effects catchability models.

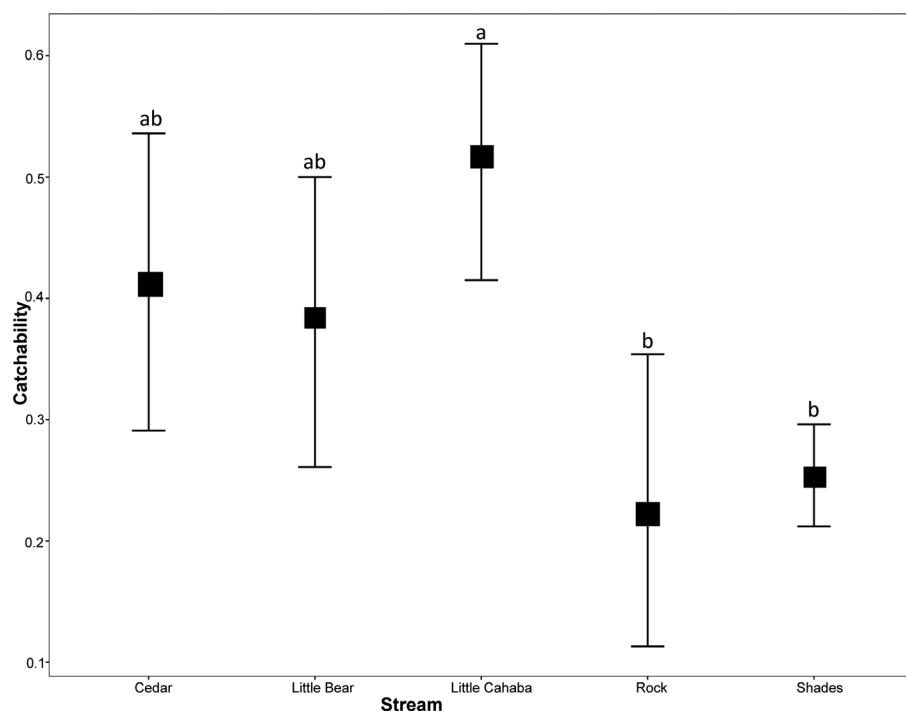


FIGURE 3. Comparisons of mean catchability $\pm 95\%$ CI among streams. The different letters above the bars indicate significant differences ($P < 0.05$) in catchability. Log_e transformed data were used in linear mixed-effects catchability models.

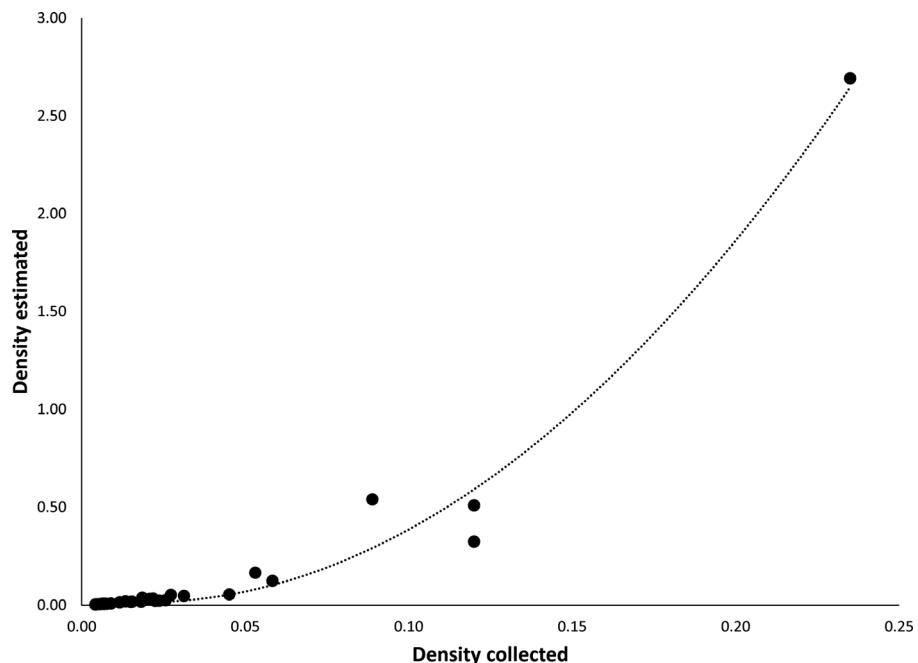


FIGURE 4. Polynomial regression model describing the relationship between the collected and estimated crayfish densities (N/m^2) (estimated density = $56.29[\text{collected density}]^2 - 2.12[\text{collected density}] + 0.030$, $r^2 = 0.98$).

TABLE 2. Accumulation of sampled crayfish species for each electrofishing pass during the multipass surveys. CR = county road; Hwy = highway.

Stream	Site	Pass			
		1	2	3	4
Cedar	CR 63	1	2	2	2
	CR 90	1	3	3	3
	Hwy 24	1	2	2	
	Hwy 247	2	2	2	
Little Bear	Hwy 59	1	3	3	3
	Hwy 24	2	2	2	
	Murphy	1	1	2	
	Stone	1	2	2	
Rock	McCullum	1	3	3	3
	Carpenter	2	4	4	4
	Henry	1	2	2	
	Coon Dog	2	2	2	
Little Cahaba	Below dam 1	0	1	1	1
	Below dam 2	0	1	1	
	Bailey Road	1	2	2	
	Hwy 119	1	1	2	
Shades	Dickey Springs	1	2	2	2
	CR 53	1	1	1	
	Ross Bridge	0	2	2	2
	Hwy 150	0	2	2	

electrofishing and its ability to accurately assess crayfish populations. To understand electrofishing effectiveness, Rabeni et al. (1997) and Alonso (2001) evaluated the efficacy of crayfish population estimates that were obtained from multipass electrofishing in small streams (mean width = 2.5 m) with one crayfish species. Multipass electrofishing increased crayfish catchability relative to single-pass electrofishing, resulting in more precise crayfish population estimates (Rabeni et al. 1997; Alonso 2001; Gladman et al. 2010). However, multipass electrofishing was not as precise in large (mean width 5.3 m), relatively species-rich (7 species) Ontario streams due to an increase in the number of crayfish that were captured after the first pass or because too few individuals were collected to estimate the population sizes (Reid and Devlin 2014). In contrast to these previous studies, we assessed the precision of the crayfish population estimates that were obtained by multipass electrofishing in large, species-rich streams in the southern Appalachian Mountains, and we concurrently examined how the stream and population characteristics influenced these estimates. Multipass electrofishing provided more precise species richness estimates after two electrofishing passes as well as precise population estimates, collecting 73% of individuals that were estimated to be within the stream sections. The precision of electrofishing was correlated with stream and population characteristics, indicating that stream and population characteristics must be taken

TABLE 3. Stream and crayfish variables that best explained the catchability (Carle and Strub 1978) of crayfish during the multipass electrofishing surveys. The results include variables from the environmental models that were within two AIC_c units of the best model. Only estimates of important variables ($RI > 0.50$), averaged across models, are displayed. N = number of models within 2 AIC_c units of the best model; SE = standard error; RVI = relative variable importance (variables with RVI of 1.00 were included in all of the best models).

Model	Marginal- R^2	Conditional- R^2	N	Estimate	SE	RI
Catchability	0.45	0.83	4			
% Adult males				-0.041	0.012	1.00
Average crayfish size (mm)				0.187	0.061	1.00
Water temperature (°C)				0.825	0.259	1.00
Conductivity (μS/cm)				0.780	0.336	0.80
Dissolved oxygen (mg/L)						0.43

into account when making management decisions based on electrofishing collections.

In the current study, the mean catchability for crayfish (34%) was similar to the catchabilities that were estimated in large, species-rich Ontario streams (30%; Reid and Devlin 2014), but lower than the catchabilities in small European streams 46–60% (Bernardo et al. 1997; Alonso 2001; Gladman et al. 2010). The lower catchabilities in larger streams may be attributed to sampling streams with larger rocks, multiple macrohabitats, and lower conductivities (Penczak and Rodriguez 1990; Paller 1995; Alonso 2001; Gladman et al. 2010; Reid and Devlin 2014). These complex habitats create conditions where some crayfish may avoid capture due to complex cover (e.g., macrophyte and large rocks) and large sampling areas. Although site widths were compared among the surveys, we did not have sufficient statistical power to detect differences. Catchability was higher when we sampled in warmer waters. Ectothermic organisms are often more active in warmer temperatures, making them easier to catch (Somers and Stetchy 1986; SFCC 2007). Catchability was also higher when fewer adult males and more large crayfish were present (Zalewski and Cowx 1990; Alonso 2001). Adult males are often able to secure and retain shelter better than juveniles and adult females are (Rabeni 1985; Nakata and Goshima 2003), decreasing the chances of collecting all of the crayfish in stream sections with higher abundances of adult males (Portt et al. 2006; Gladman et al. 2010). Additionally, electrofishing may create negatively biased estimates for age-0 and juvenile crayfish, with larger crayfish being more susceptible to electrofishing than smaller crayfish are. Our results only indicate changes in overall catchability; thus, differences between catchabilities of crayfish forms (e.g., juveniles, form 1 males) were not assessed.

To increase the efficiency of electrofishing and precisely assess species abundance in streams, more than one electrofishing pass may be needed (Holdich 2002; Kennard et al. 2006). Crayfish often become more susceptible to capture after being disturbed during the first electrofishing

pass (Reid and Devlin 2014), and wider streams with complex habitats that may hold a considerable fraction of the resident crayfish offer more areas for them to avoid capture during a single electrofishing pass. Penczak and Rodriguez (1990) also found that catchability was lower in lotic than lentic habitats. Conducting multiple electrofishing passes increases the chances of crayfish being dislodged from cover (e.g., under rocks, in vegetation, in woody debris) and subsequently collected. Because crayfish respond erratically (e.g., quickly swimming out of the electrical field, walking along bottom, lying narcotized on stream bottom) to electrofishing (Westman et al. 1978; Burba 1993), electrofishing through the same areas multiple times increases the collectors' familiarity with the area and their ability to recognize the places that crayfish may use as refuge. Therefore, the likelihood that collectors will see and collect the crayfish also increases. Because catchabilities for crayfish vary greatly by species (i.e., 3–71% catchability in the current study), conducting multiple passes (instead of spending more time sampling new areas) increases the chances of collecting the crayfish species with low catchabilities. In the current study, the first electrofishing pass from four sites within a stream did not account for all of the species that were collected within a stream by using multipass electrofishing. Species richness also did not differ between the second electrofishing pass and subsequent passes; thus, two electrofishing passes were adequate for assessing species richness for crayfish. In even larger or more diverse streams, additional passes may be necessary. Conducting more than one pass also allows managers to estimate population densities, which cannot be estimated with single-pass electrofishing. Improving species detection by increasing electrofishing passes should increase the chances of collecting less abundant, rare species and give managers more accurate assessments of species distributions and population estimates.

This study presents the first comparison of crayfish catchability among species. Although Reid and Devlin (2014) sampled streams with multiple crayfish species, they only assessed the catchability of one species. In the current study,

catchability varied by species, with *F. validus* having the lowest catchability and *F. compressus* having the highest catchability. The availability and vulnerability of target fauna are two factors that affect catchability (Arreguín-Sánchez 1996). Because *F. validus*, *F. erichsonianus*, and *F. virilis* were the most abundant crayfishes in sampled streams (Z. C. Barnett, unpublished data), it is unlikely that the availability of individuals varied greatly between these species. Nonetheless, the vulnerability of the crayfish, which is influenced by the behavior of the species, may have caused differences in catchability among the sampled species. The typical escape response, use of different macrohabitats (e.g., riffle, run, pool) and cover types (e.g., woody debris, macrophyte), level of aggression, and burrowing behavior of various crayfish species may influence their catchability. Similarly, Penn (1984) described how the level of aggregation and schooling patterns of shrimp influence their catchability by trawls. Furthermore, using single-pass electrofishing to assess the relative abundance crayfish may give misleading results, with less abundant, highly catchable species (i.e., *F. compressus*) having a higher relative abundance than more abundant, less catchable species have (i.e., *F. validus*).

The total collections from the electrofishing depletion surveys collected around 70% of the estimated crayfishes within the blocked stream sections. Achieving population estimates that are within 20% of the true population is often the goal in invertebrate studies (Elliot 1971; Cummins 1975) and requires capturing half of the population (Rabeni et al. 1997). To estimate population size with 90% probability, $\geq 75\%$ of the population needs to be captured (Zippin 1958; Robson and Regier 1964). Although true population densities are unknown, our electrofishing-depletion approach, conducting three or more electrofishing passes, provided population estimates that were within 20% of the estimated population, with close to 90% probability. In New Zealand streams, the abundances that were estimated by electrofishing depletion surveys were also similar to electrofishing mark–recapture survey estimates and provided 2–4 times greater abundance estimates than hand-netting depletion surveys did (Rabeni et al. 1997).

A potential bias in our study was that our catchability maximum-likelihood algorithm assumed a constant effort and catchability in each survey. By sampling the same stream length for the same amount of time during all of the passes, effort was kept constant throughout each survey. More time may be needed to collect aquatic fauna during the first electrofishing pass due to depletion occurring during subsequent passes (Riley and Fausch 1992). Thus, we assumed that using the sampling time that was necessary to adequately sample during the first electrofishing pass would lead to adequately sampling the crayfish during all of the passes. However, catchability and the number of species that was collected increased during our

second pass. Standardizing time by using the time that was needed to adequately sample the first pass may have decreased our chances of collecting all of the crayfish in subsequent passes. Because constant effort can be accomplished by sampling the same area during each pass without standardizing time (Riley and Fausch 1992), assuming that the area is thoroughly sampled, an alternative would be to standardize only the sampling area in future studies. Additionally, catchability between the passes differed in 21% of our surveys. Nonetheless, the catchability maximum-likelihood algorithm is the most robust and common method used and previous studies show that the constant catchability assumption is difficult to fulfill (Alonso 2001; Peterson et al. 2004). Without constant catchability, depletion surveys can incorrectly estimate population sizes, with underestimation common when catchability decreases between passes and overestimation common when it increases (Schnute 1983; Riley and Fausch 1992). Thus, our population size estimates may have overestimated the sampled crayfish populations. Nonetheless, estimating populations with at least three-pass surveys results in estimates that are substantially less biased (Riley and Fausch 1992).

Seasonality may have affected the abundance and richness of the crayfish that were collected. Crayfish are often more active in warmer waters and during their mating seasons (primarily spring through early summer and fall; Holdich 2002). Although we did not sample during crayfish mating seasons, because temperature regulates activity level in crayfish (Capelli and Magnuson 1974; Somers and Stetchy 1986), sampling during the summer, when waters were warmest, increased the chances of higher crayfish activity. Additionally, Barnett et al. (2017) noted that as temperature increased, abundance increased for crayfish in the Lower Mississippi Alluvial Valley region, Mississippi, USA. Nonetheless, we only collected one genus (*Faxonius*) during the surveys (although *Cambarus* spp. were documented previously from the sampled sites; Barnett, unpublished data). To increase the chances of collecting other genera and yield higher richness and more precise population estimates, sampling during crayfish mating seasons may be needed.

Sampling large streams with one electrofishing unit may have increased the escape probability of the crayfish in this study (Meador et al. 2003). In wide streams (width > 4 m) the electrical field from one electrofisher does not affect crayfish across the entire stream width (Kimmel and Argent 2006; Rabeni et al. 2009). Thus, more than one electrofisher unit is often used to ensure complete coverage of the channel (Kimmel and Argent 2006; Rabeni et al. 2009). Due to logistical constraints (e.g., number of people available to sample), we used one electrofisher unit to sample the streams in this study. The capture probability in this study (34%) was lower than catchabilities that have been reported in small (width < 4 m) streams (46–60%; Bernardo et al. 1997; Alonso 2001; Gladman et al. 2010),

where one electrofishing unit would adequately cover an entire channel. Conducting multiple electrofishing passes with multiple electrofishing units will likely increase the capture probability and provide more accurate population estimates for crayfish.

Suitable sampling efficiency, accuracy, and precision is essential for estimating population densities and community structures as well as conducting species assessments and informed stream ecosystem management. The results from this study, along with those of previous studies (Rabeni et al. 1997; Alonso 2001; Gladman et al. 2010), show that electrofishing depletion sampling can precisely assess crayfish populations in numerous habitat types for multiple crayfish species. Nonetheless, stream and population characteristics play a part in the effectiveness of electrofishing. Understanding how these factors influence the catchability of sample populations will lead to increased electrofishing efficiency, more precise population assessments, and better management decisions.

ACKNOWLEDGMENTS

We thank the following individuals for their assistance with the field collections: G. McWhirter, M. Bland, and C. Smith (U.S. Forest Service [USFS]); S. McGregor, R. Bearden, S. Stanley, and P. Nenstiel (Geological Survey of Alabama); C. Johnson (Alabama Department of Environmental Management); D. Butler (Cahaba Riverkeeper); C. Mangum (Weyerhaeuser); E. Liles and K. Forbes (University of Mississippi); B. Simms (American Fisheries Society Hutton Scholar); and E. Choice (USFS volunteer). We are grateful to M. Copeland (U.S. Department of Agriculture Natural Resource Conservation Service) for assisting with contacting landowners and to the many landowners who granted us stream access from their properties. We also thank C. Sabatia for statistical advice and the reviewers for providing comments to improve the manuscript. This work was supported by the USFS Southern Research Station, The University of Mississippi, and the Birmingham Audubon Society. The products that are mentioned do not constitute endorsement by the USFS or The University of Mississippi. There is no conflict of interest declared in this article.

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