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ARTICLE

Accuracy of Removal Electrofishing Estimates of Trout Abundance in Rocky Mountain Streams

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Abstract

Removal electrofishing is frequently used to estimate fish distribution and abundance in streams because it is simple and requires only one visit to a site. However, because the removal method usually overestimates capture efficiency and therefore underestimates fish abundance, some biologists have questioned its use in favor of less biased methods. In southern Idaho streams in the summers of 2006 and 2007, rainbow trout *Oncorhynchus mykiss*, cutthroat trout *O. clarkii*, and brook trout *Salvelinus fontinalis* were captured with backpack electrofishers using pulsed DC and marked and released in blocknetted sites; on the following day, four-pass electrofishing removals were conducted. Removal electrofishing underestimated the abundance of trout 10 cm and larger by 17% (four passes), 22% (three), and 25% (two); for trout less than 10 cm, the respective underestimates were 27, 27, and 37%. Removal estimates were biased in part because capture efficiency progressively decreased for fish 10 cm and larger from 58% in pass one to 37% (two passes), 30% (three), and 18% (four); a similar decline was not as evident for fish less than 10 cm. Increased channel complexity, in the form of boulder substrate, water depth, and stream shading, increased bias in removal estimates. Linear regression models incorporating these and other variables explained 44–67% of the variation in this bias. Visiting new sites in the summer of 2009 with a new field crew produced similar amounts of removal estimate bias, but predictions based on multiple-regression results did not correct the bias any more accurately than did using a mean correction rate from the original sites. Our results suggest that multiple-pass removal sampling in typical Rocky Mountain streams can produce population estimates that are consistently but not drastically biased and are, therefore, probably adequate for most basic fish population monitoring even without correction, especially if electrofisher settings and crew training balance the need to minimize injury with effective fish sampling.

Backpack electrofishing is one of the most commonly used methods for assessing fish composition and abundance in wadeable streams. Biologists often make multiple electrofishing passes through a particular study site (i.e., the removal-depletion method) and use the catch data to obtain a maximum likelihood estimate of abundance and capture efficiency (Moran 1951; Zippin 1956, 1958). The assumptions for valid removal method estimates are that (1) the population is closed, (2) fishing effort is constant, and (3) capture efficiency remains constant. Placement of block nets can ensure the first assumption (Peterson et al. 2005), although violation of this assumption in small streams is often minor (Young

and Schmetterling 2004), and establishing long sample areas (Bohlin et al. 1989) with upper and lower boundaries at shallow riffles or velocity barriers may help minimize the likelihood of fish moving out of the site. The second assumption can be ensured not by maintaining constant time spent electrofishing or time electricity is applied, but rather by ensuring all habitat is thoroughly electrofished on each pass (Riley and Fausch 1992) because substantially more electrofishing time will be needed in earlier passes when there are more fish to capture.

Regarding the assumption of constant capture efficiency, the removal method tends to (1) produce declining capture efficiency with successive passes and (2) overestimate true capture

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efficiency and thus underestimate true fish abundance (e.g., Mahon 1980; Riley and Fausch 1992). These violations may occur because larger fish are more vulnerable and are thus caught in earlier passes (Mahon et al. 1979; Mahon 1980; Bohlin and Cowx 1990). Also, fish not captured in early removal passes may be continually more likely to seek refuge in subsequent passes by hiding in complex habitat, such as rootwads, large substrate, undercut banks, woody debris, or overhanging vegetation (Mahon et al. 1979; Rodgers et al. 1992; Peterson et al. 2004; Rosenberger and Dunham 2005), or they may inadvertently become lodged there once they are immobilized. It is often difficult to determine when declining capture efficiency is occurring because in small streams fish catch in each pass is often not large enough to accurately estimate actual efficiency (Riley and Fausch 1992). Regardless of how evident a declining capture efficiency is, the effect that fish size may be having on the decline can and should be reduced by partitioning the sample into size-classes and estimating abundance for each size-class separately, provided there are ample fish for partitioning.

Despite these shortcomings, removal electrofishing continues to be widely accepted for monitoring fish populations, largely because it is simple and requires only one visit to a site. Also, biologists may not be fully aware of the level of bias in their data, or may assume the bias is negligible. Previous studies have produced a wide range in estimates of electrofishing removal bias, from as little as 12% (Habera et al. 2010) to as much as 88% (Peterson et al. 2004). The level of bias can be affected not only by channel complexity, but also by factors such as the type of electricity used (AC, DC, or pulsed DC), the electrical intensity of the shocker settings, and the experience of the crew. Because the level of bias can be substantial and is usually unknown, some biologists have questioned whether removal estimates should be used to monitor fish populations unless the bias is corrected (Peterson et al. 2004), either by comparison to unbiased estimates such as from the mark-recapture method or by releasing a known number of marked fish in the sampling site before conducting removal estimates. If the level of bias can be estimated and can be explained by factors affecting the bias, statistical models may be able to correct the bias in other removal estimates by the same or similarly trained crews, if the uncontrollable factors (e.g., fish size, channel complexity) are measured and the controllable factors (equipment and crew training) are largely held constant.

The objectives of this study were to (1) estimate capture efficiency and removal estimate bias from multiple-pass removal electrofishing for trout in small streams, (2) assess what biotic or abiotic factors affected capture efficiency and removal estimate bias, and (3) determine whether predictive models can be built to consistently correct removal estimate bias for future sampling crews trained in a similar fashion to those from which the original estimates of bias were derived.

TABLE 1. Physiochemical characteristics of 23 study streams in southern Idaho that were electrofished to estimate multiple-pass removal estimate bias and capture efficiency.

Variable	Mean	SD	Range
Reach length (m)	105.9	15.8	71–159
Mean wetted width (m)	3.1	0.9	1.7–5.4
Mean depth (m)	0.12	0.04	0.06–0.21
Reach gradient (%)	3.7	2.3	1.6–9.5
Conductivity ($\mu\text{S}/\text{cm}$)	111	91	45–416
Pieces of instream wood	19	24	1–104
Mean width of overhanging vegetation (m)	0.26	0.22	0–0.84
Percent of reach with undercut banks	10	9	0–32
Percent of reach that was shaded	33	20	4–90
Percent of reach with unstable banks	5	11	0–44
Percent substrate composition			
Fines	7	6	0–21
Sand	12	8	0–34
Gravel	34	19	6–72
Cobble	29	16	5–69
Boulder	16	11	0–49
Bedrock	2	5	0–19
Mean water temperature ($^{\circ}\text{C}$)	10	3	6–14

METHODS

We chose 23 sampling locations in southern Idaho streams representative of those in which we routinely conduct removal electrofishing to monitor fish populations. Our study sites were typically narrow, shallow, moderately shaded, and predominated by gravel and cobble substrate, but we attempted to sample streams with a variety of physiochemical characteristics (Table 1). We sampled fish and made habitat measurements in summer (at or near base flow conditions) of 2006 and 2007.

Field measurements.—The target length for the study sites was 100 m, but length varied depending on effective locations for placing upper and lower block nets. An additional set of block nets were established about 3 m outside the study site block nets at a subset of sites to estimate escapement rates of marked fish. The salmonid catch composition included brook trout *Salvelinus fontinalis* (50%), rainbow trout *Oncorhynchus mykiss* (47%), and cutthroat trout *O. clarkii* (3%).

Once block nets were set, two samplers conducted a fish-marking run by electrofishing the site with a generator-powered backpack electrofisher (Smith-Root Model 15D) with a 1.8-m electrical pole and 28-cm aluminum ring (1.0-cm thickness) for the anode and a trailing 3-m braided stainless steel rat tail (0.5-cm thickness) for the cathode. During the marking run we attempted to catch and mark only a small portion (i.e., about

10–20%) of the trout standing stock and took care to minimize fish injuries that could affect capture efficiency during later runs. Thus, we used the lowest possible electrofisher power output that produced sufficient taxis that some fish could be netted (usually 400–500 V of pulsed DC at 40–50 Hz and a 1–2-ms pulse width). Trout were captured, measured for total length (TL; cm), marked with an adipose fin clip, allowed to recover in a bucket, and then returned to the stream near the point of capture once the sampler with the electrofishing unit had moved upstream of the area.

On the following day, a crew of three samplers conducted four-pass electrofishing removals in the site (with block nets still in place) using the same backpack electrofisher. Electrofisher settings varied by study site, and our protocol for determining appropriate settings was based on professional experience, and recommendations from the manufacturer. In short, on the Model 15D backpack unit, the user can change pulse rate (typically 10-Hz increments), pulse width (typically in 0.5–1.0-ms increments), and voltage (100-V increments) to manipulate the amount of electrical output (power) in the water. The Model 15D unit makes a continuous audio tone when it is operating, but as the settings are increased and the unit approaches a power output of 100 W (average power), the tone switches from continuous to intermittent. Manufacturer's suggestions and personal experience in the study area (Meyer et al. 2006) indicate that slightly less than 100 W of average power typically produces adequate fish taxis to the anode, although we also visually assessed fish response to ensure fish were reaching taxis but not tetany, and (infrequently) made further adjustments to the unit settings accordingly.

To determine the proper settings at any given site, we tested the settings well below the site boundary. We started with low settings of about 30 Hz, 0.5-ms pulse width, and 300 V and increased voltage (one increment at a time) to about 700 V. If the audio tone did not change, we dialed back to 300 V and increased pulse width one increment, and repeated the process. If settings reached 3-ms pulse width and 700 V and the audio tone had still not changed from solid to intermittent, then pulse width and voltage were returned to their initial settings, pulse frequency was increased by one increment, and the process was repeated. We chose 60 Hz as the upper limit of pulse rate to minimize fish injury, and in this study never failed to achieve an intermittent audio tone at settings ≤ 60 Hz, ≤ 3 -ms pulse width, and ≤ 700 V (in other work we have used settings up to 70 Hz, 6-ms pulse width, and 800 V). Once the intermittent tone was achieved, we reduced volts by one increment and started our electrofishing session within the study site. Voltage sometimes had to be reduced another 100 V in deeper pools to avoid overloading the generator. We followed this more flexible protocol, as suggested by Rosenberger and Dunham (2005), rather than a stricter, standardized protocol, in order to more closely emulate typical sampling by fisheries biologists.

Immobilized fish were netted and retained in buckets until the entire site was sampled, then held outside the site in live wells

(separated by passes) until all four removals were completed. The area between each set of double block nets (for sites where these were used) was thoroughly electrofished during each pass. Escape rates were estimated to be $<1\%$. Trout were identified to species, measured (TL; cm), checked for an adipose clip, and released within the study site following completion of all electrofishing.

For each site we measured several physiochemical variables, some of which we thought might affect trout capture efficiency. Gradient (%) was determined using the software All Topo Maps version 2.1 for Windows (iGage Mapping Corporation, Salt Lake City, Utah); the distance (m) between the two contour lines that bounded the study site was traced (average traced distance was about 1 km), and gradient was calculated as the elevational increment between those contours divided by the traced distance. Specific conductivity ($\mu\text{S}/\text{cm}$) was measured with a calibrated hand-held conductivity meter accurate to 2%. Water temperature ($^{\circ}\text{C}$) was measured with a handheld digital thermometer at the beginning and end of electrofishing and the average was used to characterize temperature during sampling.

Ten equally spaced transects were established within each study site from which the remaining measurements took place. Mean wetted stream width (m) was calculated from the average of all transect widths. Mean depth was calculated for each transect using measurements at 1/4, 1/2, and 3/4 of the distance across the channel, the sum of which was divided by four to account for zero depths at the stream margins for trapezoidal-shaped channels (Platts et al. 1983; Arend 1999); mean depth for the site was calculated from the averages for each transect. Percent substrate composition was visually estimated as the percent of substrate within 1 m upstream of the transect that was silt (<0.06 mm), sand (0.06–1.99 mm), gravel (2–63 mm), cobble (64–256 mm), boulder (257–4,096 mm), or bedrock ($>4,097$ mm). Percent unstable banks, undercut banks, and stream shading were also visually estimated within 1 m upstream of each transect. The mean width of overhanging vegetation (i.e., any vegetation within 2 m of the water surface) extending from the bank out into the wetted channel was measured at three locations (at the transect, and 0.5 and 1.0 m upstream from the transect) for each bank (left and right) and averaged for an overall mean at that transect. All habitat measurements were averaged across all transects for an overall mean for the study site. Finally, we counted the total number of pieces of wood in the site (≥ 10 cm in diameter and ≥ 1 m in length) that was within the bankfull channel.

Estimates of abundance and capture efficiency.—Maximum likelihood estimates of trout abundance and 95% confidence intervals (CIs) were calculated for two-pass, three-pass, and four-pass removals using the MicroFish software package (Van Deventer and Platts 1989), which assumes equal capture efficiency for all passes. Because electrofishing is inherently size selective (Reynolds 1996), we separated our estimates into trout less than 10 cm and 10 cm and longer, but limited catch data

at many sites precluded further partitioning. Similarly, separate population estimates are often not possible for each species present in small trout streams because of low abundance, thus we combined capture data for all species before generating population estimates.

We assessed how biased our removal estimates were in two ways. First, we calculated the abundance of marked trout in each site with the removal method, based on the number of marked trout captured in two-pass, three-pass, and four-pass removals. Measured bias for removal estimates at a site was calculated as $1 - M_e/M_k$, where M_e is the number of marked fish estimated (by the removal method) to be present and M_k is the number known to be present. Measured capture efficiency for each pass was the number of marked fish captured divided by the known number at large (i.e., the original number released minus the cumulative catch from previous removal passes).

For a comparative assessment of bias in our removal estimates, we assumed that the Lincoln–Petersen mark–recapture (M–R) model as modified by Chapman (1951) was an unbiased estimator of total abundance because in nearly all cases the M–R sample size criterion of Robson and Reiger (1964) was met, which ensures that M–R estimates are less than 2% biased. We calculated the maximum likelihood estimate of trout abundance for each site using the removal method, which was based on catch data from two-pass, three-pass, and four-pass removals. We also calculated an M–R estimate of abundance by combining catch data from all four removal runs into bins of marked (R) and unmarked (M) fish, using the original marking run as the initial capture of fish (C). Modeled bias for removal estimates at a site was calculated as $1 - N_r/N_{mr}$, where the total number of trout estimated to be present are N_r by the removal method and N_{mr} by the M–R method. Modeled capture efficiency was the number of trout captured during each removal pass, divided by the number estimated to be at large (i.e., the M–R estimate for total abundance minus the cumulative catch from previous removal passes).

Data analyses.—Previous research has shown that electrofishing capture efficiency in streams may be influenced by factors such as fish size (Sullivan 1956; Mahon et al. 1979), stream size (Kennedy and Strange 1981; Rosenberger and Dunham 2005), and channel complexity (Peterson et al. 2004; Rosenberger and Dunham 2005; but see Riley and Fausch 1992). Accordingly, we calculated mean fish length (for trout ≥ 10 cm only) at each site and assumed that as mean length increased fish would be easier to see and more completely immobilized, resulting in increased capture efficiency and reduced removal estimate bias. Similarly, we assumed that as stream wetted width, gradient, and channel complexity (in the form of trout cover such as water depth, undercut banks, boulder substrate, overhanging vegetation, and instream wood) increased fish could more easily escape or would be more difficult to see or net, and thus, capture efficiency would decrease and removal estimate bias would increase. Finally, we assumed that decreased water

temperature would cause trout to be more lethargic and respond to the electric field more slowly, thus making them more difficult to catch and increasing removal estimate bias. Because conductivity affects power output in the water, but electrofisher settings at least partially mitigate that effect, we assumed that conductivity would have little impact on capture efficiency and removal estimate bias (but see Pusey et al. 1998).

We plotted the physiochemical variables against removal estimate bias for the 23 study sites and detected no data abnormalities or nonlinearity. Multicollinearity among the physiochemical variables was assessed with variance inflation factors, but no values were greater than 10, suggesting that collinearity was acceptably low in our data set (Neter et al. 1989).

We assessed whether the amount of bias in four-pass removal estimates was related to physiochemical variables via multiple regression in an information-theoretic approach (Burnham and Anderson 1998). To assess the strength of all candidate regression models relating stream characteristics to removal estimate bias, we used Akaike's information criterion (AIC; Akaike 1973) with the bias correction for small sample sizes (AIC_c; Burnham and Anderson 1998). The most plausible models (and the only ones we present) were judged to be those for which AIC_c values were within about 2.0 of the best model (Burnham and Anderson 2004). We calculated AIC_c weights (w_i) to judge the relative plausibility of each of the most plausible models, and R^2 was used to assess the amount of variation explained by the models. Because w_i indicated that no individual model was clearly best, we calculated model-averaged parameter estimates based on all the most plausible models, following the formulas in Burnham and Anderson (1998).

The correlation between measured bias and modeled bias for removal estimates was strong for trout less than 10 cm ($r = 0.94$) and 10 cm and larger ($r = 0.88$). Because of this relationship, we constructed multiple-regression models only for measured bias for trout 10 cm and larger because measured bias was based on an adequate sample size of marked fish at each site (mean = 18). However, the number of marked trout less than 10 cm was low at most sites (mean = 5), so for this size-class, estimates of measured bias at individual study sites was not always reliable due to small sample sizes. Consequently, for trout less than 10 cm we constructed multiple-regression models only for modeled bias.

Predicting removal estimate bias at new sites.—We visited five sample sites in 2009 and repeated our sampling methods to test whether the model-averaged parameters could adequately correct the bias in removal estimates at future sampling locations. The bias in removal estimates predicted by global models (which included all model-averaged parameters) was compared with measured bias for trout 10 cm and larger and with modeled bias for trout less than 10 cm. Because some of the model-averaged parameters occurred in only one or a few of the best models, we also used only the best model for each size-class to predict the bias in removal estimates.

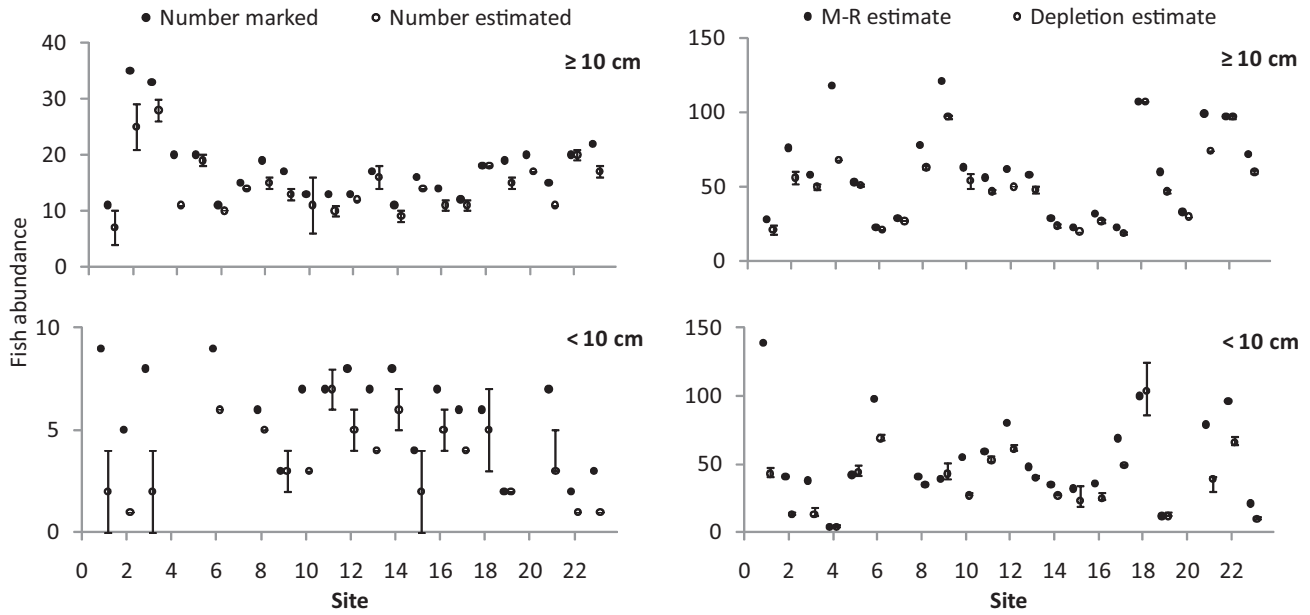


FIGURE 1. Depictions of electrofishing four-pass removal estimate bias for two size-classes of trout in 23 study sites in southern Idaho. The left-hand panels show the number of marked trout estimated to be present by the removal method versus the number known to be present (i.e., measured bias); the right-hand panels show the total number of trout estimated to be present by the removal method versus the number derived from the mark-recapture (M-R) method (i.e., modeled bias).

RESULTS

For trout 10 cm and larger, measured bias averaged 0.17 for four-pass, 0.22 for three-pass, and 0.25 for two-pass removals, whereas modeled bias averaged 0.16, 0.22, and 0.28. Sample sizes were too small to reliably calculate measured bias for trout less than 10 cm, but modeled bias was 0.27 (four pass), 0.27 (three), and 0.37 (two).

For trout 10 cm and larger, 95% CIs around four-pass removal estimates for marked fish (Figure 1, left panels) included the actual number of marked fish for only 6 of 23 study sites, compared to 5 of 19 study sites for trout less than 10 cm (none were marked at 4 sites). Similarly, 95% CIs around four-pass removal estimates for all fish (Figure 1, right panels) included the M-R estimate for 4 of 23 study sites for trout 10 cm and larger and for 4 of 19 study sites for trout less than 10 cm.

Removal estimates were constantly lower than mark-recapture estimates (Figure 2). Nevertheless, removal and mark-recapture estimates were highly correlated both for trout 10 cm and larger ($r = 0.94$) and for trout less than 10 cm ($r = 0.70$).

Removal estimates were negatively biased because of inflated capture efficiency estimates and because capture efficiency decreased with successive passes. For trout 10 cm and larger, the first electrofishing pass captured an average of 58% of the fish estimated to be present (Figure 3). Subsequent measured capture efficiency for remaining fish decreased to 37% in pass two, 30% in pass three, and 18% in pass four. A similar decline in modeled capture efficiency with successive passes was not as evident for trout less than 10 cm (41, 26, 28, and 30% for passes one through four).

The decline in measured capture efficiency for trout 10 cm and larger was concurrent with a decreasing mean length of fish

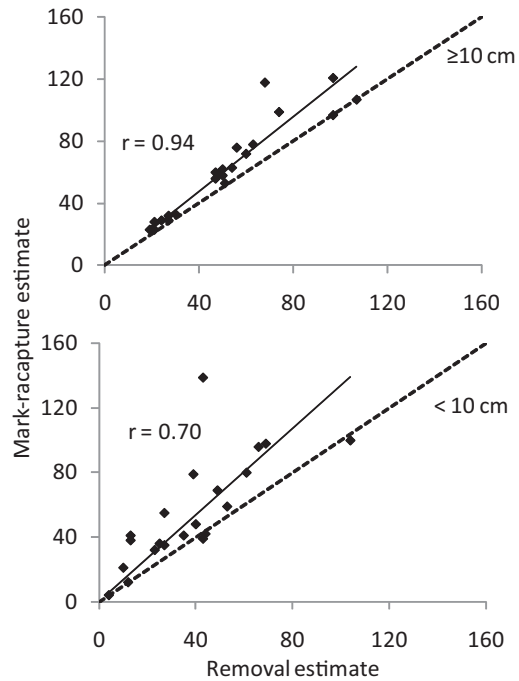


FIGURE 2. Relationships between removal and mark-recapture trout abundance estimates at 23 study sites in southern Idaho. The solid lines depict the linear regression fits, the dashed lines 1:1 relationships. The regressions were forced through the origin.

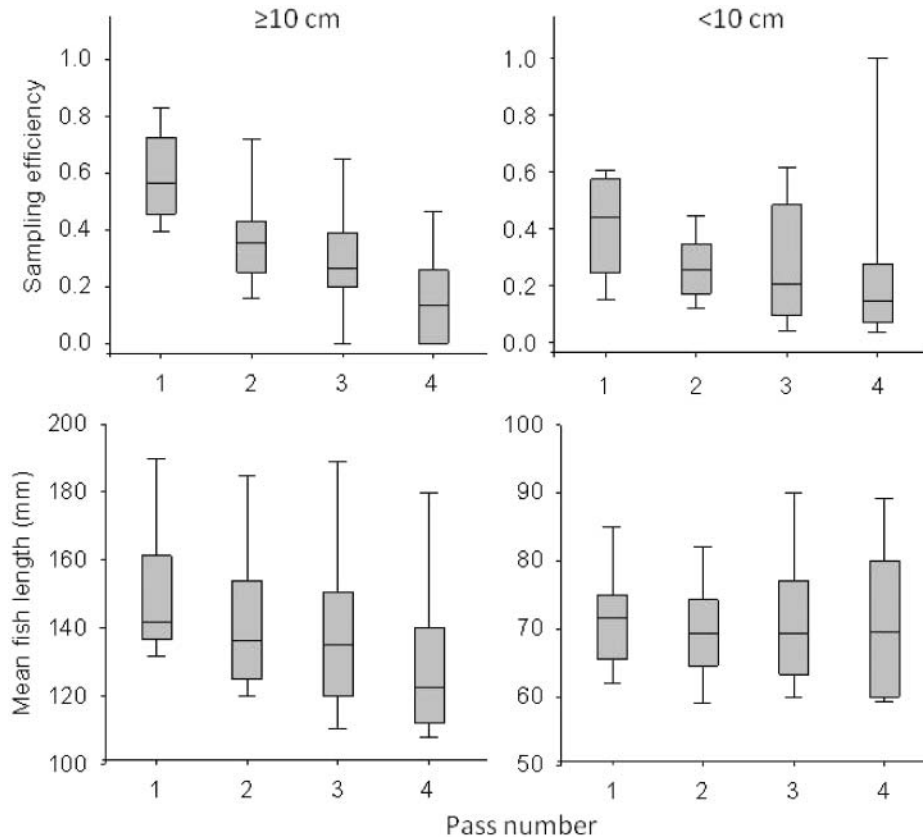


FIGURE 3. Box plots of electrofishing capture efficiency and mean trout length for four-pass removal electrofishing in 23 study sites in southern Idaho. Capture efficiency was either (1) measured as the number of marked trout captured during each removal pass divided by the known number at large (trout ≥ 10 cm; left panels) or (2) modeled as the number of trout captured during each removal pass divided by the number estimated (by the unbiased mark-recapture method) to be at large (trout < 10 cm; right panels).

captured decreasing with each successive pass (Figure 3). In fact, the correlation coefficient between mean fish length and pass number was negative for 22 of the 23 study sites, and fish averaged 11, 15, and 17 mm smaller in passes two, three, and four compared with pass one. In contrast, there was no concurrent decline in mean fish length with successive passes for trout less than 10 cm (for which fish averaged only 0.4 mm smaller in pass four than in pass one), and the correlation coefficient between mean fish length and pass number was negative for only 7 of 19 study sites for which a coefficient could be calculated.

For trout 10 cm and larger, all of the most plausible multiple-regression models relating physiochemical variables to removal estimate bias contained percent boulder substrate, mean depth, and mean fish length (Table 2). The percentage of undercut banks, water temperature, and mean wetted width each appeared in one of the four most plausible models. These models explained 63–67% of the variation in removal estimate bias. Based on model-averaged parameter estimates, there was a positive relationship between removal bias and boulder substrate, mean depth, and fish length (Table 3). Thus, removal estimate bias increased as fish length and channel complexity (i.e., more boulder substrate and increased water depth) increased.

For trout less than 10 cm, there was less consistency and more uncertainty in the inclusion of independent variables for the most plausible multiple-regression models (Table 2). Percent boulder substrate and stream shading occurred in all of the top four models and were positively related to removal estimate bias (Table 3), but no other variables were consistently included in the most plausible models. The most plausible models for trout less than 10 cm explained less of the total variation in removal estimate bias (44–58%) than did those for the larger size-class.

The mean bias for four-pass removal estimates in 2009 was the same (mean = 0.17) as in 2006–2007 for trout 10 cm and larger, and was similar for trout less than 10 cm (0.27 in 2006–2007 and 0.31 in 2009). However, model-averaged parameter estimates from the most plausible models did not accurately predict fish abundance when corrected for removal estimate bias, removal estimate corrections being off by an average of 26% for trout 10 cm and larger and 58% for trout less than 10 cm. In contrast, predictions using only the single most plausible model for each size-group were much better at correcting removal estimates for trout 10 cm and larger (mean difference = 6%) and for trout less than 10 cm (mean difference = 28%). However, the single most plausible model was no better at correcting the

TABLE 2. Multiple-regression model results relating stream characteristics to removal estimate bias. The bias for trout ≥ 10 cm was based on known numbers of marked fish (i.e., measured bias) and that for trout < 10 cm on comparison with mark-recapture estimates (i.e., modeled bias). Only the most plausible models (i.e., those with ΔAIC_c scores within about 2.0 of the best model) are presented. Variables appear in their order of contribution to the strength of the model.

Variables	R^2	AIC_c	ΔAIC_c	w_i
Trout ≥ 10 cm				
Boulder substrate, mean depth, mean fish length	0.63	-97.20		0.43
Boulder substrate, mean depth, mean fish length, undercut banks	0.67	-96.04	1.16	0.24
Boulder substrate, mean depth, mean fish length, water temperature	0.66	-95.43	1.77	0.18
Boulder substrate, mean depth, mean fish length, mean wetted width	0.65	-95.02	2.18	0.15
Trout < 10 cm				
Boulder substrate, stream shading, instream wood	0.54	-64.81	0.00	0.14
Stream shading, boulder substrate, undercut banks	0.52	-63.90	0.92	0.09
Boulder substrate, stream shading	0.45	-63.87	0.95	0.09
Boulder substrate, stream shading, instream wood, mean depth	0.59	-63.76	1.06	0.08
Mean wetted width, stream shading	0.44	-63.63	1.18	0.08
Boulder substrate, overhanging vegetation, mean depth	0.51	-63.54	1.27	0.07
Mean depth, overhanging vegetation, stream shading, boulder substrate	0.58	-63.36	1.45	0.07
Overhanging vegetation, stream shading, boulder substrate	0.50	-63.30	1.51	0.06
Mean depth, stream shading, boulder substrate	0.50	-63.12	1.70	0.06
Stream width, stream shading, boulder substrate	0.50	-63.07	1.75	0.06
Gradient, instream wood, stream shading, boulder substrate	0.57	-63.06	1.75	0.06
Instream wood, undercut banks, stream shading, boulder substrate	0.57	-62.99	1.83	0.05
Overhanging vegetation, undercut banks, stream shading, boulder substrate	0.57	-62.93	1.89	0.05
Mean depth, instream wood, boulder substrate	0.49	-62.83	1.99	0.05

new removal estimates than if we assumed the new estimates were biased by the average of the original sites, these corrections being off by 8% for 10 cm and larger and 17% for trout less than 10 cm.

DISCUSSION

Our results suggest that removal electrofishing in small Rocky Mountain streams with moderate channel complexity can produce abundance estimates that only slightly underestimate true abundance. Previous research has produced varying levels of bias in multiple-pass removal estimates for a variety of salmonid species and conditions (Table 4). Negative bias has been reported to be as little as 12% for three-pass removals of rainbow trout in small Appalachian streams (Habera et al. 2010) to as much as 88% for three-pass removals of bull trout *S. confluentus* and cutthroat trout in Idaho (Peterson et al. 2004). Our estimates of three-pass removal estimate bias of 22% for trout 10 cm and larger and 27% for trout less than 10 cm are at the middle of the range for published studies, most such estimates being between 12% and 39% for all size-classes and between 12% and 23% for larger fish. Removal estimate bias is typically higher for smaller size-classes (Table 4), and we found that subsequent removal estimate corrections for smaller fish were less accurate as well.

The removal estimates were biased because capture efficiency declined with successive passes, and this may happen for several reasons. Most obvious is the fact that electrofishing is size selective, and for typical removal electrofishing surveys at sites with moderate fish densities, the relatively small number of fish caught in each pass often precludes splitting abundance estimates into enough size-classes to completely account for this size selectivity. We found that for trout 10 cm and larger, fish size declined in successive passes concurrently with the decline in capture efficiency (Figure 3), and this has been observed previously (e.g., Mahon et al. 1979). However, although mean fish length occurred in all the top models for trout 10 cm and larger, it was only weakly correlated to removal estimate bias ($r = 0.04$). Mean length is arguably a poor index of size selectivity, but correlation to removal bias was no stronger for other metrics, such as the magnitude of reduction in mean fish length from the first to fourth pass ($r = 0.07$). For trout less than 10 cm, no decline in fish size was evident between successive passes because they were mostly all in the same age-class and, as Figure 3 indicates, their variation in fish length was too small for any meaningful decline to occur. Based on our results, we concur with the conclusion of Mahon (1980) that changing catchability is not primarily caused by size selectivity.

There is more evidence that the spatial distribution of fish in streams (due to habitat selection and territoriality) and their avoidance reaction from previous passes is likely to cause

TABLE 3. Parameter estimates from model averaging and the top models among best-fitting linear regression models relating four-pass removal estimate bias to stream conditions. Removal estimate bias was based on known numbers of marked fish (trout ≥ 10 cm) or on comparison with mark–recapture estimates (trout < 10 cm), including the number of models in which each parameter occurs (k).

Variable	k	Estimate	SE
Trout ≥ 10 cm (model averaging)			
Intercept	4	-0.4255	0.2248
Boulder substrate	4	0.0061	0.0017
Mean depth	4	1.7549	0.6117
Mean fish length	4	0.0021	0.0011
Undercut banks	1	0.0034	0.0020
Water temperature	1	-0.0092	0.0072
Mean wetted width	1	-0.0365	0.0293
Trout ≥ 10 cm (top model)			
Intercept		-0.4805	0.2201
Boulder substrate		0.0060	0.0016
Mean depth		1.7853	0.6071
Mean fish length		0.0023	0.0011
Trout < 10 cm (model averaging)			
Intercept	14	-0.199	0.162
Boulder substrate	13	0.010	0.193
Stream shading	12	0.005	0.178
Mean depth	5	1.817	0.764
Instream wood	5	0.003	0.077
Overhanging vegetation	4	0.306	0.138
Undercut banks	3	0.007	0.040
Mean wetted width	2	0.107	0.041
Trout < 10 cm (top model)			
Intercept		-0.115	0.095
Instream wood		0.003	0.002
Stream shading		0.004	0.002
Boulder substrate		0.010	0.003

declining capture efficiency with successive passes. Indeed, fish occupying the simplest habitat will be most easily caught in early passes, and it will become ever more difficult in subsequent passes to capture fish occupying the most complex habitat. Fish not captured in the first pass may also seek refuge in complex habitat (Peterson et al. 2004) or be more wary of the electrical current, further exacerbating the problem. Heggberget and Hesthagen (1979) found that two-pass depletion estimates for Atlantic salmon and brown trout were underestimated by as much as 50% because of electrical current avoidance on the second pass. In some instances, some fish (regardless of size) have a low or essentially zero capture probability no matter how many passes are made (Bohlin and Cowx 1990). The decline in capture efficiency in successive passes has been shown to be less pronounced when time between passes is larger (Cross and Stott 1975; Peterson and Cederholm 1984), suggesting (1)

that disturbance stress from previous passes caused the decline, and (2) that the amount of channel complexity is therefore a primary determinant of the amount of bias in removal estimates (Kennedy and Strange 1981; Peterson et al. 2004; Rosenberger and Dunham 2005).

Channel complexity in our study influenced removal estimate bias, and this was especially true for the percentage of boulder substrate, which appeared in all but one of the most plausible regression models and positively influenced removal estimate bias for both size-classes (i.e., more boulder substrate resulted in more bias in the removal estimates). Both juvenile and adult salmonids are often concentrated near boulder substrate (e.g., Baltz et al. 1991; Gries and Juanes 1998; Meyer and Gregory 2000). Moreover, stream temperatures in our study averaged 10°C during our surveys, which is near the threshold at which juvenile and adult trout conceal more regularly within boulder substrate (Chapman and Bjornn 1969; Griffith and Smith 1993; Meyer and Gregory 2000) and adopt a winter-type behavior. Whether our test fish were concealing within or inhabiting areas consisting of boulder substrate, once they experienced an electric current some fish were likely to become immobilized and lodged between or underneath boulders and thus were less likely to be seen or captured.

Although channel complexity explained much of the variation in removal estimate bias, the ability of model-averaged parameter estimates to predict the bias for new surveys was low. In contrast, the best regression model by itself predicted removal estimate bias for the new surveys more accurately for both size-classes, but even the top model corrected the bias no better than simply using the mean correction from the original data. Considering that (1) removal estimate bias was relatively low, (2) a mean correction factor calibrated the removal estimates as well as any regression models, and (3) the relationship between the removal estimates and the unbiased mark–recapture estimates was strong (Figure 2), our results suggest that correcting removal estimate bias may be inconsequential for most managers conducting routine fishery monitoring and evaluation. We argue that if the bias can be held reasonably constant over the years by providing consistent crew training, then monitoring surveys based on removal estimates should be satisfactory for most management decisions requiring some level of monitoring data, with the understanding that the estimate is probably slightly negatively biased at some unknown level.

Peterson et al. (2004) argued that obtaining reliable estimates of abundance and species distribution requires use of an unbiased estimator. However, associated reductions in the number of sites surveyed may outweigh the benefit from using an unbiased estimator when sampling throughout large watersheds to obtain basinwide population estimates, especially if the bias is consistent. Using the unbiased M–R method (which requires 2 d of sampling the same site) would effectively reduce the total number of surveys conducted by nearly one-half because travel time is often the most limiting factor for survey crews, especially when sites are distributed randomly across the landscape.

TABLE 4. Summary of studies measuring the amount of abundance underestimation in removal electrofishing (i.e., removal bias) based on known numbers of fish in the site (known) or presumably unbiased mark–recapture techniques (M–R). Species include brown trout *Salmo trutta* (BnT), coho salmon (CS), Atlantic salmon *S. salar* (AS), bull trout (BuT), cutthroat trout (CT), rainbow trout (RT), brook trout (BkT). Abbreviations for electrical current settings are as follows: AC = alternating current, DC = direct current, and PDC = pulsed direct current.

Electrofisher and settings				Fish captured					
Type of current	Hz	Pulse width (ms)	Volts	Species	Size or age	Number of passes	Removal bias	Based on known number or M–R	Reference
PDC	60		650–700	BnT	5.0–8.4 cm	3	0.19	Known	Bohlin and Sundstrom (1977)
PDC	60		650–700	BnT	>8.5 cm	3	0.13	Known	Bohlin and Sundstrom (1977)
PDC	50	5.5	400	CS	Age 0	3	0.14	Known	Peterson and Cederholm (1984)
DC			800	CS	Age 0	2	0.33	Known	Rodgers et al. (1992)
DC				AS	Age 1	4	0.23	Known	Riley et al. (1993)
DC			400–500	BuT, CT	All	3	0.88	Known	Peterson et al. (2004)
PDC	30–50	2–8	400–700	RT	>6 cm	3	0.33	Known	Rosenberger and Dunham (2005)
AC	60		600	RT	4.0–9.9 cm	3	0.31	Known	Habera et al. (2010)
AC	60		600	RT	≥10 cm	3	0.12	Known	Habera et al. (2010)
PDC	60	3.3	990	RT	4.0–9.9 cm	3	0.39	Known	Habera et al. (2010)
PDC	60	3.3	990	RT	≥10 cm	3	0.13	Known	Habera et al. (2010)
PDC	60	0.5–2.0	300–700	RT, BkT, CT	<10 cm	3	0.27	M–R	This study
PDC	60	0.5–2.0	300–700	RT, BkT, CT	≥10 cm	3	0.22	Known	This study

Sweka et al. (2006) found that basinwide estimates of Atlantic salmon parr using removal electrofishing was 11–17% lower than the true population because of bias from using removal estimates; however, decreasing the number of sample sites by half would have doubled the variance in their overall estimate of abundance. The number of sites surveyed may be even more important for obtaining presence–absence information on rare species because nearly twice as many locations can be sampled with depletion electrofishing than M–R electrofishing, which would more clearly delineate occupancy. Moreover, the likelihood of capturing rare species within each site sampled is similar for depletion and M–R sampling. For example, given our data on declining capture efficiency by pass, if a rare species was present in a particular 100-m site at an abundance of only two fish in each of our size-classes, the likelihood of catching at least one of these fish with three depletion passes would be 97% for the larger fish and 90% for the smaller fish. In comparison, the corresponding probabilities for one mark and one recapture run would be 97% and 88%, respectively.

An instance in which it is probably important to correct removal estimate bias is during studies to determine fish habitat requirements. As Peterson et al. (2004) point out, removal estimates are usually biased by the same factors affecting fish

abundance. In our example, removal estimate bias increased as undercut banks, boulder substrate, instream wood, and other measurements of channel complexity increased. Trout abundance is strongly associated with channel complexity (McMahon and Hartman 1989; Horan et al. 2000), so fish habitat models constructed with biased abundance data would underestimate the strength of the fish habitat relationships at a rate commensurate to the level of bias in the abundance estimates.

The range mentioned above in estimates of removal estimate bias among previous studies (Table 4) is substantial, and we believe that certain external, largely controllable factors, such as crew training and electrofisher settings, play a role in this variability. For example, we trained electrofisher operators on our crew to carry the anode in one hand and a dip net in the other. As Habera et al. (2010) point out, the operator has the best (and often only) chance of netting some fish. Additionally, training and operational procedures that inordinately emphasize minimizing fish injury may result in a reluctance to use output settings high enough to adequately immobilize fish for fear of causing injuries. For example, Peterson et al. (2004) used straight DC to minimize fish injury, but their resultant removal bias was much higher than other previous studies (Table 4).

Although we advocate limiting power to no more than is necessary for effective electrofishing, concern about minimizing fish injury must be balanced with the need to effectively capture fish. Regardless of how much electrofishing injury occurs in a particular study site, when viewed in a population context, such injury is typically expected to be inconsequential (Schill and Beland 1995). During intensive fish sampling across the landscape, biologists typically electrofish less than 1% of a particular study area (e.g., Meyer et al. 2006, 2009; Dambacher et al. 2009), so population-level impacts from electrofishing injury would be considered minimal in most cases. Despite assuming unrealistically high electrofishing mortality estimates of 25%, Elle and Schill (2000) estimated population-level mortality from electrofishing for all recorded electrofishing operations in Idaho averaged less than 0.5% in 1995 and 1996. We therefore discourage biologists from allowing fish injury concerns to compromise the utility of removal electrofishing. Although minimizing injury by using less effective output settings may infrequently be necessary when sampling extremely at-risk or range-restricted species, removal electrofishing should be considered a poor choice for most fish sampling scenarios where biologists are unwilling to use electrofisher settings that adequately achieve fish taxis.

In summary, our results and those of others suggest that removal electrofishing abundance estimates can be expected to be biased by about 15–25% (i.e., abundance is underestimated by 15–25%) if more than two passes are made. Clearly, the removal method is not as accurate as other population estimation methods such as M–R techniques, and studies that forego correcting removal estimate bias will underestimate true fish abundance. Although correcting removal estimate bias in most instances is not overly burdensome and should be more routinely incorporated into removal electrofishing sampling regimes, using uncorrected removal estimates that are slightly negatively biased (but to an unknown degree) can still be useful in a number of instances for monitoring fisheries populations. For example, depletion electrofishing will accurately portray trend as long as the bias remains relatively constant over time, which with proper crew training can be achieved and can readily be evaluated. Occupancy assessments with removal electrofishing will be as unbiased as M–R electrofishing methods. Even for extrapolating population abundance across the landscape, we believe that with rigorous capture efforts biases will be relatively small (and in a known direction) and reasonably consistent year to year, and therefore, the added effort needed for obtaining unbiased M–R estimates may be outweighed by the sacrifice of visiting fewer sample sites.

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