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An Evaluation of Multipass Electrofishing for Estimating the Abundance of Stream-Dwelling Salmonids

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Abstract.—Failure to estimate capture efficiency, defined as the probability of capturing individual fish, can introduce a systematic error or bias into estimates of fish abundance. We evaluated the efficacy of multipass electrofishing removal methods for estimating fish abundance by comparing estimates of capture efficiency from multipass removal estimates to capture efficiencies measured by the recapture of known numbers of marked individuals for bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarki lewisi*. Electrofishing capture efficiency measured by the recapture of marked fish was greatest for westslope cutthroat trout and for the largest size-classes of both species. Capture efficiency measured by the recapture of marked fish also was low for the first electrofishing pass (mean, 28%) and decreased considerably (mean, 1.71 times lower) with successive passes, which suggested that fish were responding to the electrofishing procedures. On average, the removal methods overestimated three-pass capture efficiency by 39% and underestimated fish abundance by 88%, across both species and all size-classes. The overestimates of efficiency were positively related to the cross-sectional area of the stream and the amount of undercut banks and negatively related to the number of removal passes for bull trout, whereas for westslope cutthroat trout, the overestimates were positively related to the amount of cobble substrate. Three-pass capture efficiency measured by the recapture of marked fish was related to the same stream habitat characteristics that influenced (biased) the removal estimates and did not appear to be influenced by our sampling procedures, including fish marking. Simulation modeling confirmed our field observations and indicated that underestimates of fish abundance by the removal method were negatively related to first-pass sampling efficiency and the magnitude of the decrease in capture efficiency with successive passes. Our results, and those of other researchers, suggest that most electrofishing-removal-based estimates of fish abundance are likely to be biased and that these biases are related to stream characteristics, fish species, and size. We suggest that biologists regard electrofishing-removal-based estimates as biased indices and encourage them to measure and model the efficiency of their sampling methods to avoid introducing systematic errors into their data.

Biologists and managers need reliable methods to assess the abundance and distribution of stream-dwelling fishes. The reliability of such methods is influenced by their ability to capture fishes (henceforth termed capture efficiency). One commonly used method of sampling stream fishes is electrofishing (Reynolds 1996). The capture efficiency of electrofishing, however, is affected by the size and species of fish (Bagenal 1979; Anderson 1995) as well as physical habitat characteristics (Rodgers et al. 1992; Bayley and Dowling 1993). Failure to account for differences in capture efficiency introduces a systematic error or bias into the data that can significantly bias abundance estimates and models (Bayley and Dowling 1993). Presence and absence data are similarly affected by capture efficiency biases because the probability of detecting a species depends, in part, on the probability of capturing individual fish (i.e., efficiency; Bayley and Peterson 2001).

Previous investigations have attempted to reduce the influence of sampling bias by using multiple pass removal (depletion) methods (Zippin 1956; Otis et al. 1978). However, removal estimates are known to be biased by such factors as fish species and size (Buttiker 1992), the number of removal passes and the statistical estimator (White et al. 1982), and fish abundance and the physical characteristics of the area sampled (Ken-

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TABLE 1.—Mean, SD, and range of habitat characteristics of the 43 sites included in the evaluation of removal estimates and modeling electrofishing capture efficiency. Asterisks indicate variables included in candidate models.

Variable	Mean	SD	Range
Site elevation (m)	2,096	258	1,774–2,450
Mean wetted width (m)*	3.44	1.00	2.3–7.4
Mean cross-sectional area (m^2)*	0.47	0.19	0.2–1.3
Map reach gradient (%)	4.67	2.25	2.0–9.9
Wood density (number/m^2)*	0.09	0.07	0.01–0.30
Undercut banks (%)*	27.96	20.89	3–93
Water temperature (°C)*	9.17	2.40	3–14
% Surface turbulence	21.21	9.47	2–40
% Submerged cover	25.16	14.48	5–80
% Pools	8.18	8.59	0–34
% Overhanging vegetation	45.78	26.371	5–98
Conductivity (μohms)*	57.96	48.22	16–203
Substrate (% substrate composition)			
Fines	16.82	9.77	1.7–36
Gravel	21.85	12.16	6.3–60
Cobble*	25.37	8.53	5–44
Rubble	35.96	18.34	1–1,978
Recovery time after marking (h)	31.81	14.55	24–72

nedy and Strange 1981; Riley et al. 1993). Despite these shortcomings, the use of removal estimates continues to flourish in fisheries biology. For instance, a recent search in Science Citation Index (Institute of Scientific Information, Philadelphia, Pennsylvania) identified 49 articles since 1995 that used removal methods to estimate stream fish abundance. The continued use of removal estimators may be related to a general lack of information on the magnitude and causes of bias or to a perceived lack of viable alternatives for estimating fish abundance.

Obtaining reliable estimates of fish abundance and species distribution requires the use of unbiased (statistical) estimators (e.g., mark–recapture, removal). That an estimator is unbiased, however, can be assured only by evaluating potential violations of estimator assumptions under typical sampling conditions and by comparing abundance estimates with known abundances. If estimators are found to be biased, reliable estimates of fish abundance can be obtained by using unbiased estimates of fish capture efficiency (Buttiker 1992; Bayley and Dowling 1993; Anderson 1995). Thus, our objectives were to (1) evaluate the efficacy of electrofishing removal methods for estimating the abundance of stream-dwelling salmonids, (2) examine the influence of stream habitat characteristics, species, and fish size on removal estimates, and (3) evaluate an alternative approach to estimating stream-dwelling salmonid abundance by modeling the efficiency of electrofishing for fish capture.

Study Area

We evaluated the accuracy of electrofishing removal–based estimates of fish abundance and the efficiency of backpack electrofishing in 43 first- through third-order streams located primarily in National Forests and Bureau of Land Management lands in central Idaho and southwest Montana. Because bull trout *Salvelinus confluentus* was the focus of our study, we selected streams within the known range of bull trout and at relatively high elevations (Table 1). We sampled during June–October 1999 and 2000 on the declining limb of the hydrograph, sampling most sites at or near base flow.

Methods

To evaluate the efficiency of electrofishing under sampling conditions typically encountered in the region, we developed sampling strata based on stream size and habitat characteristics, using data previously collected throughout the region (R. Thurow, unpublished data; Peterson and Wollrab 1999). For example, one stratum consisted of small mean wetted width (<3-m), low-gradient (<3%) streams with high wood density (>0.15-m^2). Sampling sites approximately 100 m long were randomly selected from within each stratum. Before sampling, each site was blocked off with 7-mm-square mesh nets that were secured to the streambed. To ensure adequate closure, we selected locations with abrupt changes in channel gradient as hydraulic controls for upper and lower boundaries of each site. During the 2000 field season, a second set of block nets (henceforth termed double block nets) was placed approximately 3 m immediately above and below the up- and downstream block nets, respectively, to evaluate potential fish escape from the sample units. Because the block nets were in place for several days, they were regularly cleaned of debris and inspected with snorkel gear to ensure they were barriers to fish passage. All block nets remained in position until electrofishing sampling was concluded.

An evaluation of removal estimates and efficiency of fish capture requires an unbiased estimate of the true number of fish in a site. Fisheries biologists have used three basic approaches to obtain these estimates: (1) stocking a known number of fish into a site (Rodgers et al. 1992); (2) using a dual gear procedure, often with one gear being lethal (Bayley and Austen 2002); and (3) collecting fish within a site, marking, and returning them (Riley et al. 1993). Each method has potential problems. For example, fishes stocked in a new environment may respond differently from resident fishes, and resident fishes (if present) could influence the vulnerability of stocked individuals, biasing evaluations. We chose the last approach (i.e., marking and releasing) because we believed it to be the easiest to implement, given our limitations in working with sensitive native species. The effects of handling and marking, however, could affect fish behavior (Mesa and Schreck 1989), altering their vulnerability to capture and thus biasing our capture efficiency estimates. To evaluate this potential bias, we varied the time between marking and returning fish and the subsequent electrofishing multipass sampling of each site (henceforth termed recovery time).

Salmonids were initially sampled within blocked-off sites by using a backpack electrofisher with unpulsed direct current (DC) and one upstream and downstream pass. All captured fish were held in live wells containing ambient stream water. At the conclusion of shocking, each salmonid was anesthetized with MS-222, identified, and measured (total length [TL], to the nearest 10 mm), and a portion (<1 cm^2) of the dorsal or caudal fin was clipped in a manner that would not restrict fish movement but could readily be identified. After recuperating, all fish were released back into the site systematically to ensure uniform dispersal. Marked fishes were allowed to disperse for a randomly assigned recovery time of 24, 48, or 72 h.

After the assigned recovery time, marked and unmarked fishes were sampled within each site during multiple upstream passes with a gasoline powered backpack electrofisher. We used unpulsed DC to reduce the risk of injuring fish and generated 400–500 V with a gas-powered Smith-Root backpack electrofisher using a single 28-cm hoop anode and cable cathode. At least three and four electrofishing passes was completed at each site in 1999 and 2000, respectively. Additional electrofishing passes were made if necessary until the catch-per-pass declined by 75% or more between successive passes. All captured fish were placed in live wells and held at stream margins. At the completion of each pass, fish were identified to species, checked for marks, and measured for TL (nearest 10 mm). Because we processed fish after each pass, approximately 0.5 h elapsed between successive electrofishing passes. During the 2000 field season, the area between the double block nets then was electrofished to determine whether any marked fish had escaped from the blocked-off site. All captured fish were identified, measured, checked to see if they had been marked, and released immediately.

Physicochemical measurements.—At each study site, after electrofishing and the subsequent removal of block nets, we measured physical and chemical stream features that might affect electrofishing efficiency. Beginning at the downstream end of each site, transects were established perpendicular to the flow along the centerline of the stream and spaced at 20-m intervals. At each transect, we recorded the type of habitat (e.g., pool, riffle), measured wetted channel width, and estimated mean water depth by averaging readings at one-fourth, one-half, and three-fourths of the channel width. Cross-sectional area was estimated as the product of wetted width and mean depth. Substrate composition was visually estimated in a 1-m-wide band centered across each transect and categorized as follows: fines (<6 mm in diameter), gravel (6–75 mm), cobble (75–150 mm), and rubble (>150-mm). Transect-specific measurements were averaged for each site. Based on a previous assessment (Thurow et al. 2001), most of these measurements were estimated to be within 40% of the true mean values with 95% confidence.

In each site, we counted the number of pieces of woody debris, which we defined as a piece of wood at least 3 m long and 10 cm in diameter, lying within an active channel. Wood density was estimated as the total number of wood pieces divided by the wetted surface area of each site. For the entire site, we estimated the percent cover for each of four cover types (submerged, turbulent, overhead, undercut). We measured the length of undercut banks and overhead vegetation along each bank and expressed these as percents of the total bank length (left and right). We visually estimated (to the nearest 10%), the percent of the reach that had turbulence and submerged cover. We defined turbulence as abrupt changes in water velocity typically observed at changes in gradient (riffles), near physical obstructions to flow (wood or boulders), and along irregular shorelines. Submerged cover included large boulders, bedrock, and large wood. Site gradient was estimated from a U.S. Geological Survey 7.5-min (1:24,000) map. Conductivity was measured in the center of each site by using a calibrated hand-held meter. Water temperature was measured at 1-h intervals with a continuously recording thermograph.

Evaluation of removal estimates.—Because fish length affects the efficiency of many collection methods (Bagenal 1979; Reynolds 1996), species were placed into three TL size-classes before analyses: one, 70–99 mm; two, 100–199 mm; and three, 200–350 mm. The three size-class ranges were chosen to facilitate the incorporation of capture efficiency models into existing standardized sampling protocols (Thurow 1994) and because fish larger than 350 mm TL were not encountered during sampling.

Fish abundance (marked and unmarked) in each blocked-off section was estimated by using two different removal estimators, depending on the maximum number of electrofishing passes (White et al. 1982). We used the constant capture probability estimator (Zippin 1956) to estimate species and size-class specific abundance for sites with three removal passes, and the generalized removal estimator (model M_{bh}; Otis et al. 1978) for sites sampled with at least four electrofishing passes. The constant probability estimator assumes that capture efficiency is the same for each removal pass, whereas the generalized removal estimator adjusts for heterogeneity in capture efficiency (e.g., decrease or increase) between successive removal passes and should provide more accurate estimates (White et al. 1982). Goodness-of-fit was assessed for each removal estimate by a chi-square test as implemented in program CAPTURE (Rexstad and Burnham 1991).

The numbers of marked fish recovered were sufficient to estimate capture efficiency, which we define as the proportion (or percentage) of fish, in a given area, that are captured during sampling. Thus, we examined the adequacy of the removal technique by estimating the capture efficiency of electrofishing for each species two ways. To estimate the *measured* capture efficiency for each site, we divided the number of marked individuals in a size-class that were recaptured by the corresponding total number that had been marked. *Removal* capture efficiencies were estimated as the total catch in three removal passes divided by the removal estimate of total abundance. We used three-pass total catches to facilitate comparisons with published efficiency estimates. Bias of the removal estimates was calculated as the difference between removal and measured capture efficiency. Thus, positive values indicated overestimation of removal capture efficiency and negative values indicated underestimation. The number of marked fishes was not sufficient at all sites (i.e., mean: nine individuals per species' size-class) to calculate removal abundance estimates for only marked fish.

We used linear regression analysis (Neter et al. 1990) to examine the relationships among removal estimate bias and site characteristics, fish body size (size-class), and the maximum number of removal passes. Three size groups were categorized by assigning dummy variables (0, 1) to size-class one and three; size-class two was retained as the baseline. Pearson correlations were run on all pairs of predictor variables (i.e., site characteristics) before modeling. To avoid multicollinearity, a subset of seven uncorrelated predictor variables (all $r^2 < 0.20$) was selected for inclusion in our candidate models (Table 1). We also assessed the normality of the distribution of removal bias estimates, using Lilliefor's test (Lilliefor 1967).

We used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the fit of linear regression models relating site characteristics, fish body size, and maximum number of removal passes to removal estimate bias. We began our modeling by constructing a global regression model for each species based on our observations (Thurow and Schill 1996) and those of other investigators (Riley et al. 1993) suggesting that salmonid capture efficiency and removal estimates are significantly influenced by habitat characteristics, body size, and number of removal passes. We then fit all possible subsets of the global model (including all first-order interactions) by using linear regression. To assess the fit of each candidate model, we calculated Akaike's information criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989).

To incorporate model selection uncertainty and presumably increase model accuracy, we computed model-averaged estimates of the individual coefficients and their standard errors by using Akaike weights (Burnham and Anderson 1998). Model-averaged coefficients and standard errors were calculated only for the predictor variables that occurred in the best-fitting model. The precision of model-averaged coefficients was assessed by calculating 90% confidence intervals based on a t-statistic with $n - 1$ degrees of freedom. Goodness-of-fit was assessed for global models by examining residual and normal probability plots (Neter et al. 1990). Dependence among size-classes was examined by ordering the residuals by sample site and size-class and conducting a Wald–Wolfowitz runs test (Bayley 1993).

Preliminary analyses suggested significant biases in the removal efficiency estimates. We were concerned that this could have been the result of our field procedures (e.g., marking fish), low capture efficiency, or large reductions in capture efficiency (heterogeneity) between removal passes. To investigate potential sources of bias, we simulated five-pass removal sampling for various combinations of first-pass capture efficiencies and reductions in capture efficiency among four subsequent passes assuming a population of 100 fish. Using the program CAPTURE (Rexstad and Burnham 1991), we conducted 1,000 replicate simulations for 231 combinations of 11 first-pass efficiencies set from 10% to 60% by 5% increments (i.e., 10, 15, . . . 60%) and 21 levels of reduction in capture efficiency for sequential passes (e.g., pass 1–2) set from 0 change to 2 times lower for each pass by 0.05 increments. For example, during the 1,000 replicate simulations of 10% first-pass capture efficiencies and a reduction in capture efficiency of 1.20 per pass (e.g., pass two = 0.10/1.20), simulated capture efficiencies were 8, 7, 5, and 4% for passes 2–5, respectively. Note that simulated pass-specific capture efficiencies less than 2% were set at 2%, which was approximately the lowest average efficiency we observed. For each replicate simulation, the number of fish caught during a pass was estimated as a binomial random variate (with parameters N, p), where N is the simulated number of fish remaining in a site and p is pass-specific capture efficiency. Fish abundance was estimated by using the simulated sampling data and the best-fitting removal estimator that had been automatically selected by CAPTURE, based on the chi-square goodness-of-fit test (White et al. 1982). Bias was calculated as the simulated removal estimate of fish abundance minus 100 (the known abundance). Thus, negative values indicated underestimation of fish abundance and positive values indicated overestimation.

Evaluation of fish escape.—A potential source of bias in our study was the effect of fish escaping from the blocked-off sites. To examine this, we estimated the escape rate of fishes by using as dichotomous dependent variables the number of marked fish captured between the double blocknets and the total number of marked fish (i.e., the number of success and trials, respectively). We initially fit logistic regression models (Agresti 1990) that related escape rate to recovery time and site characteristics. However, an examination of the dispersion parameters for the global logistic regression model indicated that the data were overdispersed (i.e., the variance exceeded the presumed binomial). To account for the overdispersion, we modeled fish escape rate with quasi-likelihood regression, which is similar to logistic regression with an additional element, the extra-binomial variance (Agresti 1990).

We used the information-theoretic approach (outlined above) to evaluate the relative fit of various candidate models in relating escape rate to recovery time and physical habitat characteristics. The global model contained recovery time (after marking) and a combination of physical habitat features that potentially influenced fish movement and our ability to effectively block off sites (Table 1). The low numbers of escapees (10 bull trout from 19 sites, 1 westslope cutthroat trout *Oncorhynchus clarki lewisi*) prevented us from examining the influence of fish body size and species on fish escape; hence data were pooled over species and size classes. We fit the global model and all subsets via quasi-likelihood logistic regression. To assess the fit of each candidate model, we then calculated quasi-likelihood AIC_c ($QAIC_c$; Burnham and Anderson 1998) and computed model-averaged estimates of the predictor variables in the best-fitting model, their standard errors, and 90% confidence intervals, using Akaike weights. We also calculated scaled odds ratios (Hosmer and Lemeshow 1989) for each predictor variable to facilitate interpretation. The odds ratio scalars corresponded to what we believed to be relevant unit changes in the predictors. Goodness-of-fit was assessed for the global model by examining deviance residuals and normal probability plots (Agresti 1990).

Measured capture efficiency modeling.—We initially fit three-pass electrofishing measured capture efficiency models using logistic regression with the number of individuals recaptured in three passes and the total number of marked individuals as dichotomous dependent variables. As above, an examination of the dispersion parameters from the global models indicated that the data were overdispersed. To account for the overdispersion, we modeled three-pass electrofishing capture efficiency using beta-binomial regression (Prentice 1986) fit with *R* statistical software (Ihaka and Gentleman 1996). Beta-binomial regression is similar to logistic regression and quasi-likelihood regression in that it uses dichotomous dependent variables, but differs in that variance is modeled as a beta distribution (rather than a binomial) to account for extra-binomial variance Additionally, a dispersion parameter is estimated during beta-binomial regression (Prentice 1986) that can be used to estimate detection probabilities (Peterson et al. 2002) and confidence intervals of sampling efficiency estimates. Marked individuals that escaped and were captured outside of the sampling unit (i.e., between the double blocknets, described above) were not used for the capture efficiency modeling. As above, we used the information-theoretic approach and all-subsets selection to evaluate the fit of three-pass capture efficiency models. The global models were identical to those used in evaluation of removal estimate bias (Table 1). However, we also included recovery time after marking to examine effect of previous capture and handling (for marking) on fish vulnerability to capture. Model-averaged estimates, confidence intervals, and scaled odds ratios were estimated as described above. Beta-binomial dispersion parameters were estimated by using the species-specific global models. Goodness-of-fit and dependence among length-groups also was assessed for each global efficiency model as detailed above.

Predicted three-pass capture efficiency was calculated as

$$\hat{p} = [1 + \exp(-\beta_0 + \beta_i x_i \ldots)]^{-1}, \qquad (1)$$

where $\hat{p}$ is the predicted capture efficiency as a fraction, β_0 is the constant, β_i are the model coefficients, and x_i are the corresponding variable values. Abundance estimates can be derived by dividing the number of fish collected during three-passes by the estimated capture efficiency, $\hat{p}$ (Bayley and Austen 2002). Approximate 95% confidence limits were calculated from the predicted efficiency from equation (1), estimated fish abundance ($\hat{n}$), and the beta-binomial dispersion parameter (γ) as follows:

$$\hat{p}(\text{upper}) = \left\{1 + \exp\left[-\left\{\log_e\left(\frac{\hat{p}}{1-\hat{p}}\right) + 1.96\left[\sqrt{\frac{\hat{p}(1-\hat{p})}{\hat{n}}\left(1 + \frac{(\hat{n}-1)\gamma}{1+\gamma}\right)}\right]\right\}\right]\right\}^{-1}, \qquad (2)$$

where $\hat{p}$(upper) is the upper 95% confidence limit. The lower confidence limit was obtained by changing the sign preceding 1.96.

We assessed the relative bias and precision of the best-fitting measured capture efficiency model for each species by using leave-one-out cross validation. Cross-validation estimates are nearly unbiased estimators of model performance (Fukunaga and Kessel 1971) and provide a measure of overall predictive ability without excessive variance (Efron 1983). Hence, they should provide an estimate of the adequacy of the three-pass capture efficiency models. During this procedure, one sample site was omitted from the data, the beta-binomial regression model was fit with the remaining observations, and the capture efficiency and 95% confidence intervals for the omitted site were predicted by using equations (1) and (2). This procedure then was repeated for each of the 42 sites. Error was then estimated as the difference between the predicted and measured (i.e., number recaptured/number marked) efficiency. For each species, relative model bias was estimated as the mean difference, and precision was the square root of the mean of the squared differences across samples. The proportion of measured efficiencies falling within the predicted 95% confidence intervals also is reported.

Results

On average, our sampling sites were in small (3.4-m-wide), cold (<14°C), low-conductivity (57-μΩ) streams at high elevations (>1,770 m; Table 1). The 43 electrofishing efficiency evaluation sites covered a relatively wide range of habitat characteristics.

A sufficient number of bull trout in all size classes, and westslope cutthroat trout in size classes two and three, were marked and collected during subsequent multiple removal electrofishing to obtain reliable estimates of measured capture efficiency. Rainbow trout *O. mykiss* and brook trout also were collected at 8 sites, but 63% of catches consisted of a single individual of each of these two species. Hence, we confined our analyses to bull trout and westslope cutthroat trout.

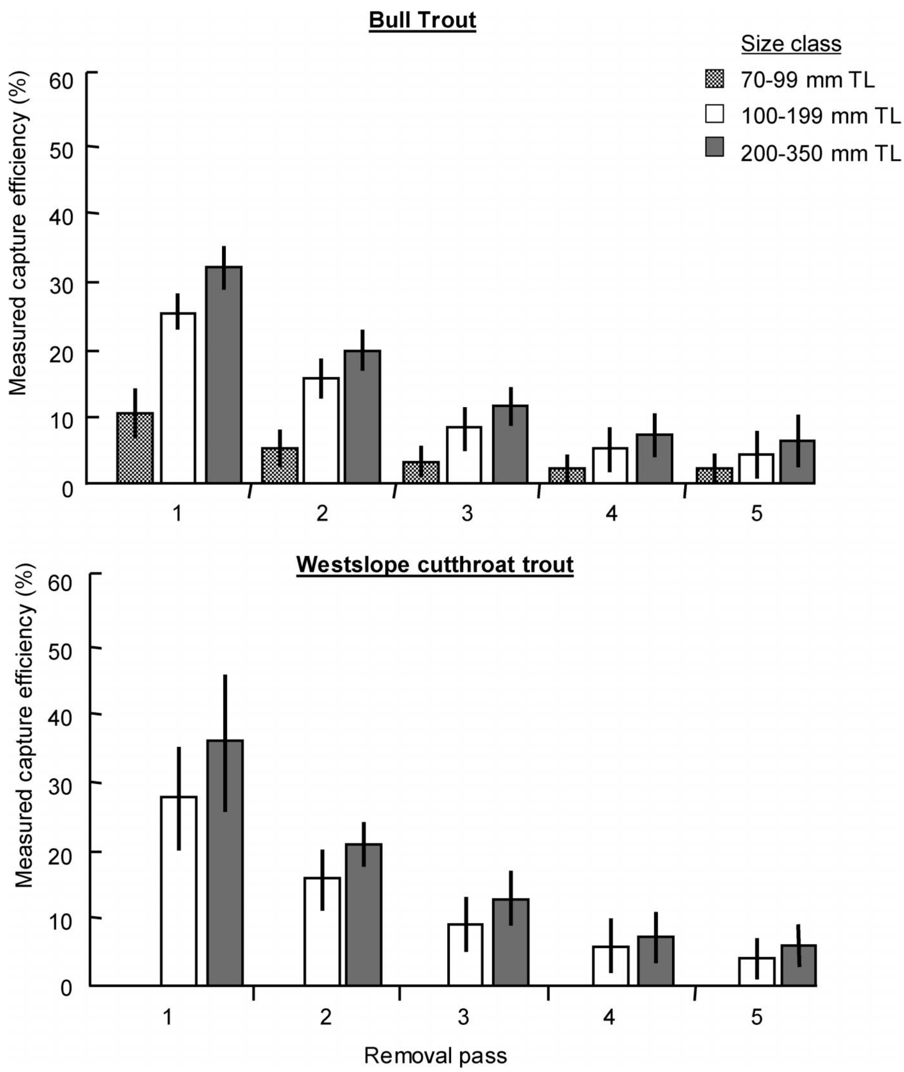

FIGURE 1.—Mean measured electrofishing capture efficiency and standard errors (vertical lines) for three total length (TL) size-classes of bull trout (top) and westslope cutthroat trout (bottom) by removal pass. Measured capture efficiency was estimated by using a known number of marked and recaptured individuals weighted by the number of marked individuals.

Measured capture efficiency estimates indicated that westslope cutthroat trout capture efficiency for size classes two and three was, on average, 8% greater than bull trout capture efficiency, across removal passes (Figure 1). For both species, capture efficiency was greatest for the largest size-class and the first removal pass. Measured capture efficiency for bull trout during the second removal pass was on average 1.72 times less than during the first pass (i.e., pass 1/pass 2) and measured efficiencies during passes 2–5 were 1.79, 1.59, and 1.15 times less, respectively, than during the previous pass, across size classes (Figure 1). For westslope cutthroat trout, measured capture efficiencies during passes 2–5 were respectively 1.69, 1.82, 1.92, and 1.96 times less than during the previous pass, across size classes (Figure 1).

Evaluation of Removal Estimates

Chi-square goodness-of-fit tests indicated lack-of-fit ($P < 0.05$) in 12% and 22% of bull trout and cutthroat trout removal estimates, respectively, that did not appear to be related to the number of removal passes (Table 2). Three-pass removal ef-

TABLE 2.—Total number of removal estimates (*N*), number failing goodness-of-fit tests (in parenthesis), and mean and standard error (in parenthesis) of estimated difference between removal and measured capture efficiency (calculated as removal minus measured efficiency) of three-pass electrofishing for bull trout and westslope cutthroat trout by maximum number of removal passes and total length size-class.

Size class (mm)	Bull trout		Westslope cutthroat trout	
	N	Mean	*N*	Mean
3 removal passes				
70–99	10 (3)	0.74 (0.09)		
100–199	14 (1)	0.58 (0.04)	6 (1)	0.18 (0.12)
200–350	11 (0)	0.39 (0.07)	8 (3)	0.40 (0.13)
Average		0.57		0.29
4 removal passes				
70–99	13 (3)	0.51 (0.10)		
100–199	17 (1)	0.40 (0.04)	4 (1)	0.42 (0.30)
200–350	12 (2)	0.36 (0.09)	3 (1)	0.33 (0.10)
Average		0.43		0.38
5 removal passes				
70–99	8 (2)	0.64 (0.09)		
100–199	12 (0)	0.34 (0.06)	3 (0)	0.25 (0.38)
200–350	11 (1)	0.23 (0.06)	3 (0)	0.25 (0.17)
Average		0.40		0.25

ficiency was consistently higher than measured efficiency across species and size classes (Table 2). On average, removal efficiency estimates were 86% and 83% for bull trout and westslope cutthroat trout across size classes, respectively, and were 46% and 30%, respectively, greater than measured efficiency. Because removal efficiency was estimated from removal abundance estimates (i.e., three-pass total catch divided by removal abundance estimate), this suggests that the removal estimates underestimated abundance, on average, by 116% and 60% for bull trout and westslope cutthroat trout, respectively, across size classes.

Examination of the residuals from the global model of electrofishing removal bias for bull trout indicated that the model adequately fit the data and had no obvious outliers. The best-fitting model of electrofishing removal bias contained mean cross-sectional area, undercut banks, maximum number of removal passes, and size classes one and three (Table 3). Removal bias was positively related to size-class one and negatively to size-class three. That is, relative to size-class two, removal estimates of capture efficiency were overestimated for the smaller size-class and underestimated for the larger size-class. Mean cross-sectional area and undercut banks also had relatively strong positive relationships with removal bias (e.g., larger area

TABLE 3.—Model-averaged parameter estimates for best-fitting linear regression model of bull trout and westslope cutthroat trout removal model bias. Size-class 2, with total lengths (TL) of 100–199 mm, was used as the baseline in the regression; CL = confidence limit.

Parameter	Estimate	Upper 90% CL	Lower 90% CL
Bull trout			
Intercept	0.580	0.961	0.200
Mean cross-sectional area	0.371	0.624	0.118
Undercut banks	0.002	0.004	0.001
Maximum number of passes	−0.071	−0.009	−0.133
70–99 mm TL	0.193	0.311	0.075
200–350 mm TL	−0.100	−0.011	−0.189
Westslope cutthroat trout			
Intercept	0.320	1.008	−0.369
Cobble substrate	0.014	0.027	0.001
200–350 mm	−0.051	0.120	−0.222

= greater bias). In contrast, the maximum number of removal passes was negatively related to removal bias, which indicated that the bias was smaller when a greater number of removal passes were used.

Examination of the residuals from the global model of electrofishing removal bias for westslope cutthroat trout indicated that it too adequately fit the data. The best-fitting model of removal bias contained percent cobble substrate and size-class three (Table 3). Percent cobble substrate had a positive relationship with removal bias (e.g., more cobble = greater bias), and size-class three was negatively related to removal bias. However, the coefficient for size-class three was imprecise and the confidence interval contained zero, thus limiting our inference.

Electrofishing removal simulations indicated that the generalized removal estimator (model M_{bh}) was the best-fitting estimator when the reduction in capture efficiency per pass (i.e., heterogeneity) was greater than zero. Nonetheless, the reduction in capture efficiency per pass tended to have a greater influence on removal bias than did first-pass efficiency (Figure 2). At relatively high first-pass efficiencies (>35%) and low reduction in efficiency per pass (<1.10), the removal estimates were nearly unbiased. However, removal estimates were highly biased at the average measured sampling efficiency values observed for bull trout and westslope cutthroat trout during this study (Figure 2). Additionally, the magnitude and direction of bias (e.g., underestimate of abundance and overestimate of efficiency) were consistent with our comparisons of measured efficiency and removal three-pass electrofishing efficiency.

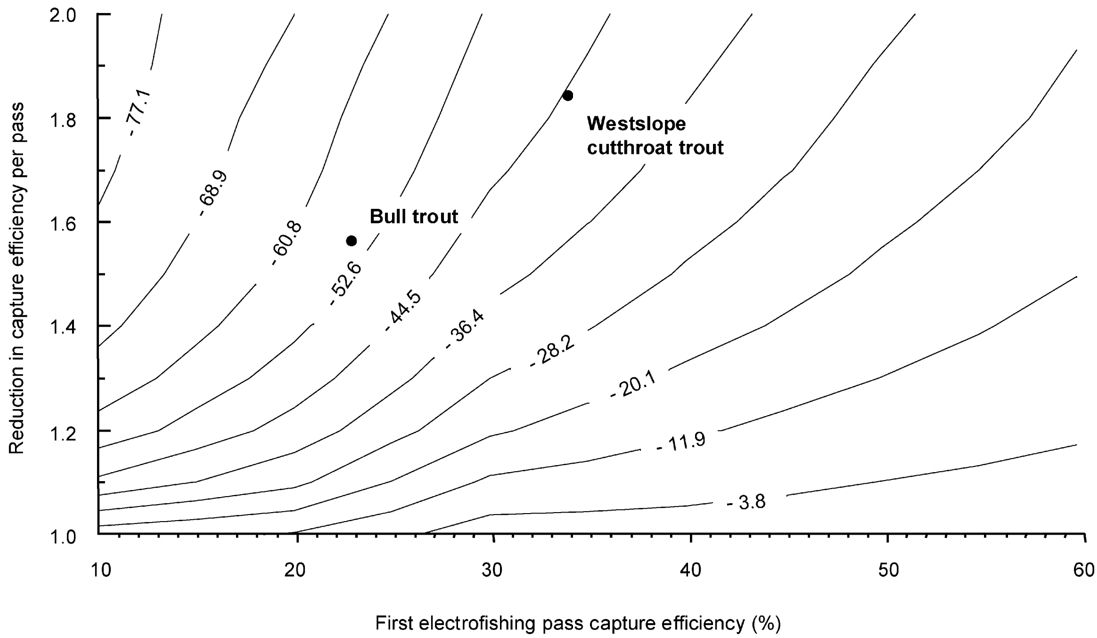

FIGURE 2.—Contour lines showing magnitude and direction of bias (estimated abundance minus known abundance) in the generalized removal estimator based on 1,000 simulations of different combinations of first-pass capture efficiencies and reductions in capture efficiency among four subsequent passes for a population of 100 fish. A reduction in capture efficiency of 1.0 represents no change in capture efficiency from removal pass to pass. The labeled points are the average measured values for bull trout and westslope cutthroat trout sampled during this study.

Evaluation of Fish Escape

Residuals from the global model of fish escape from the blocked-off sites indicated that the model adequately fit the data. The best-fitting model contained recovery time after marking, which was strongly, positively related to fish escape from the blocked-off area. The standardized odds ratio indicated that the escape rate was 269% greater with every 24-h increase in recovery time. Nonetheless, estimated escape rates at 24, 48, and 72 h were 0.7, 1.8, and 4.9%, respectively, or less than 1 marked fish in the 24-h (0.03 individuals) and 48-h (0.62) recovery times and approximately 1 fish in the 72-h period.

Measured Capture Efficiency Modeling

Deviance residuals from the global model of three-pass measured capture efficiency for bull trout indicated that the model adequately fit the data. The best-fitting model of measured capture efficiency for bull trout contained cross-sectional area, undercut banks, and both size-classes (Table 4). Scaled odds ratios suggested that bull trout measured capture efficiency was most strongly and negatively related to size-class one and was, on average, 27% that of size-class two fishes (the baseline). Mean cross-sectional area and undercut banks also had strong negative relationships with measured capture efficiency (Figure 3). Measured capture efficiency, on average, decreased by 30% with each 0.20 m^2 increase in mean cross-sectional area and by 26% with each 20% increase in undercut banks (Table 4).

Analysis of the deviance residuals from the global model of westslope cutthroat trout three-pass measured capture efficiency indicated that model fit was adequate. The best-fitting model for westslope cutthroat three-pass measured electrofishing efficiency contained percent cobble and size-class three (Table 4). Measured capture efficiency for westslope cutthroat was related negatively to percent cobble substrate and positively to fish body size (Figure 4). Measured capture efficiency of size-class three was, on average, 84% greater than size-class two (Table 4). Efficiency also decreased by 37% for each 10% increase in cobble substrate.

Cross-validation of the three-pass measured capture efficiency models indicated that they were relatively unbiased; mean differences between pre-

TABLE 4.—Model-averaged parameter estimates for best-fitting beta-binomial regression model of bull trout and westslope cutthroat trout 3-pass electrofishing measured capture efficiency. Size class 2, with total lengths (TL) of 100–199 mm, was used as the baseline in the regression; CL = confidence limit.

Parameter	Estimate	Upper 90% CL	Lower 90% CL	Odds ratio unit change	Odds ratio
Bull trout					
Intercept	0.985	1.477	0.493		
Mean cross-sectional area	−1.798	−1.102	−2.494	0.20	0.698
Undercut banks	−0.015	−0.009	−0.021	20	0.743
70–99 mm TL	−1.325	−0.849	−1.802	1	0.266
200–350 mm	0.187	0.354	0.020	1	1.206
Dispersion[1]	0.092				
Westslope cutthroat trout					
Intercept	0.219	3.261	−2.822		
Cobble substrate	−0.032	−0.002	−0.063	10	0.725
200–350 mm	0.608	1.211	0.005	1	1.837
Dispersion[a]	0.127				

[a] Estimated using the global model (all predictors).

dicted and measured efficiency for bull trout and westslope cutthroat trout were −0.4% and 0.6%, respectively (Table 5). Cross-validated root mean square errors also indicated predicted efficiency was relatively precise for bull trout (19.8%) but poor for westslope cutthroat trout (36.9%). However, a greater than expected proportion of measured efficiencies fell outside the predicted 95% confidence intervals (Table 5), mainly because of the relatively large number of observations with no recaptures.

Discussion

Three-pass electrofishing-measured estimates of capture efficiency in this study (range, 20–57%) were considerably lower than previously reported (range, 45–100%) for other stream-dwelling salmonids (Riley and Fausch 1992; Thompson and Rahel 1996; Thurow and Schill 1996; Heimbuch et al. 1997; Kruse et al. 1998 and references therein) but similar to those reported for warmwater stream fishes (range, 7–69%; Bayley and Dowling 1990). This apparent discrepancy is probably influenced by the different methods used to estimate capture efficiencies. We used known numbers of

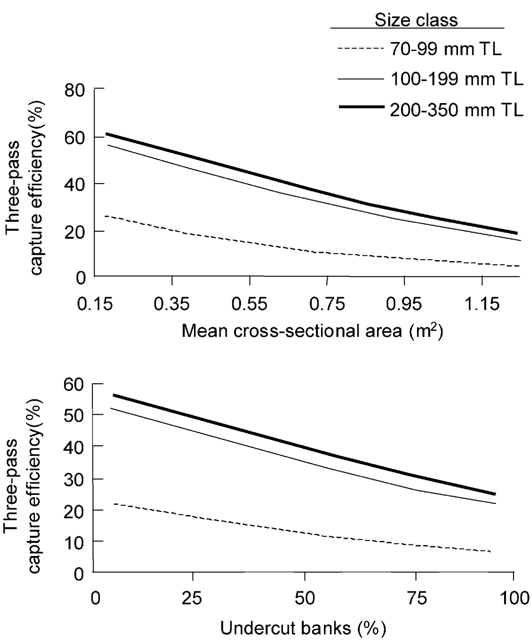

FIGURE 3.—Predicted three-pass electrofishing capture efficiencies for three TL size-classes of bull trout versus stream cross-sectional area (top) and percent undercut banks (bottom). Predictions based on best-fitting beta binomial model and assuming percent undercut banks of 28% (top) and cross-sectional area of 0.47 m^2 (bottom).

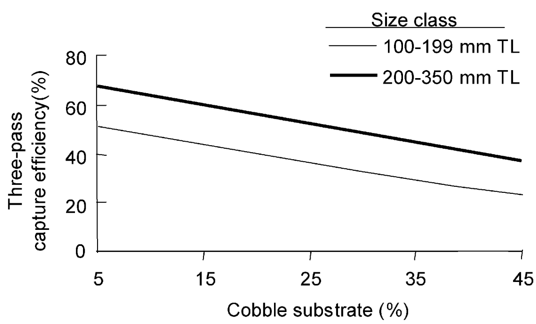

FIGURE 4.—Predicted three-pass electrofishing capture efficiencies for two TL size-classes of westslope cutthroat trout versus percent cobble substrate. Predictions are based on best-fitting beta binomial model (Table 4).

TABLE 5.—Cross-validation results for best-fitting beta-binomial regression model of bull trout and westslope cutthroat trout three-pass electrofishing measured capture efficiency.

Observation	Number of observations	Mean error	Root mean squared error	Predictions within 95% confidence intervals
Bull trout				
All observations	120	−0.004	0.198	72.5
Excluding observations with no recaptures	92	−0.036	0.195	94.6
Westslope cutthroat trout				
All observations	28	0.006	0.369	64.3
Excluding observations with no recaptures	19	−0.187	0.331	94.7

marked individuals as our benchmark for estimating measured capture efficiency. Similarly, Bayley and Dowling (1990) used the estimated number of individuals based on secondary collections with a high-efficiency method (rotenone), adjusted for differences in the capture efficiency of rotenone. In contrast, capture efficiency for the other previously cited studies was simply based on the number of individuals captured divided by the removal estimates as baseline (i.e., removal efficiency estimates). Low capture probabilities and violation of model assumptions, such as heterogeneity in catchability discussed below, may yield misleadingly high estimates of capture probability (White et al. 1982). Thus, our estimates of measured capture efficiency are probably more accurate representations of salmonid capture efficiencies encountered in relatively small coldwater streams.

The reduction in measured capture efficiency among subsequent electrofishing passes observed in this study (average, 1.71 times lower per pass) was similar to, but greater than, the average 1.30 times lower per pass we estimated from the data in Mahon (1980 Appendix A). These differences may have been due, in part, to Mahon's assumption of 100% capture efficiency for rotenone, which actually averages less than 70% and also is influenced by fish species, body size, and characteristics of stream habitat (Bayley and Dowling 1990). The relatively consistent reduction in measured capture efficiency per pass among species and size-classes also suggests that fish may have been responding to the sampling procedure. For example, fishes may attempt to avoid capture by concealment in areas that are difficult to sample, such as undercut banks and larger substrate, or by attempting to avoid the anode. This is consistent with our observations of the effect of undercut banks, cobble substrate, and stream size on measured capture efficiency. If such behavioral responses to electrofishing occur, they also bring into question the validity of removal estimates from unblocked stream sections (Hankin and Reeves 1988), where fish are unrestricted in their ability to flee during the sampling process.

Fishery biologists often rely on goodness-of-fit tests to determine the adequacy of removal estimators for estimating fish abundance (White et al. 1982). Our study suggests, however, that these goodness-of-fit tests are insufficient for determining the adequacy of removal estimators for estimating stream-fish abundance. We found that both the constant probability and generalized removal estimators significantly underestimated the abundance of bull trout and westslope cutthroat trout. Yet, significant lack-of-fit ($P < 0.05$) was detected in only 12% and 22% of bull trout and cutthroat trout removal estimates, respectively. The statistical power of goodness-of-fit tests is influenced by the abundance of fishes in a site and the true capture efficiency (Riley and Fausch 1992), the same factors that potentially bias removal estimates. Further, goodness-of-fit tests only measure how well the removal model (estimator) fits the data, not how well the model represents the true underlying sampling process (White et al. 1982). The only means of evaluating the adequacy of an estimation technique is to compare estimates with known or unbiased estimate of fish abundance. Therefore, we recommend that biologists use known or unbiased estimates of fish abundance when evaluating the adequacy of techniques for estimating populations. We also suggest that biologists avoid using capture efficiency estimates and models that rely on removal estimates of capture efficiency and abundance (e.g., Thurow and Schill 1996; Kruse et al. 1998; Mullner et al. 1998; Mitro and Zale 2000; Roni and Fayram 2000) because these are likely to be biased to various (unknown) degrees.

Our results and those of previously cited studies indicate that removal estimators tend to overestimate capture efficiencies and underestimate fish population sizes. Biologists may be tempted to continue to use biased removal estimates with the belief that the biases (e.g., underestimation of population sizes) will result in more ‘‘conservative’’ policies for resource management. We are concerned about this belief for three reasons. First, overestimates of capture efficiency are likely to lead to insufficient sampling effort, thus increasing the chances of falsely concluding that a species is absent. For instance, removal and measured three-pass electrofishing efficiency for bull trout size-class one averaged 93% and 19.5%, respectively. Assuming a mean abundance of 0.5 per sample unit and a random (Poisson) distribution, the corresponding sample sizes for 95% detection probabilities would be 7 and 31 samples, respectively. Clearly, reliance on estimates of removal sampling efficiency would probably lead to insufficient sampling and poor resource management decisions. Second, removal estimates are biased by factors that affect fish distribution and abundance, thereby confounding studies of fish habitat requirements and potentially causing studies to misidentify critical habitats. For example, bias in the estimate of bull trout removal efficiency was positively related to undercut banks, indicating that removal estimates of abundance are underestimated (biased) in streams with more undercut banks. Models of bull trout abundance fit using this biased abundance data could falsely lead to the conclusion that undercut banks are unimportant to bull trout or, alternatively, that undercut banks are negatively influencing bull trout. Such conclusions could lead to poor management decisions regarding the enhancement or protection of stream habitats. Third, removal estimates are biased by factors such as species and body size, confounding multispecies and population demographic studies.

Interestingly, the factors affecting removal estimate bias and electrofishing-measured capture efficiency were very similar. This suggests that any factor that affects capture efficiency is likely to bias removal estimates of fish abundance. The results of our simulation provided some insight into the probable mechanisms: Bias of removal-based estimation increased with decreasing first-pass capture efficiency. Thus, any factor affecting the first-pass capture efficiency would probably influence the accuracy of the removal estimate (within the ranges simulated). Increasing the number of removal passes may decrease the bias, but more passes will be more costly and the bias may still be considerable. For example, simulated 10-pass removal sampling of a population of 100 fish with efficiencies of 35%, 25%, and 15% for passes 1–3, respectively, and 5% each for passes 4–10, still underestimates population size by 25% on average. Indeed, no removal estimator can accurately estimate fish abundance when capture efficiency decreases consistently among passes, unless the number of passes is increased until all fishes are collected (White et al. 1982). Given our observations of decreasing efficiency with successive passes, we believe that the option of collecting all fish may be cost-prohibitive.

As a more cost-effective alternative, we suggest that biologists develop sampling efficiency models by using known or unbiased estimates of fish abundance under the range of conditions typically encountered. As described above, there are perhaps three basic approaches for biologists to apply to obtain unbiased sampling efficiency estimates for their streams: (1) by stocking a known number of fish into a site; (2) by using a dual gear procedure; and (3), as we have done in this study, by collecting fish within a site, marking them, and returning them. The optimal approach will depend on a variety of factors including the target species, access, and the physical-chemical characteristics of the streams. However, our results should provide some useful guidelines when developing study plans.

We found no detectable effects of marking and handling on measured capture efficiency after a 24-h recovery and dispersal period, which is consistent with previous studies of fish behavior and physiology (Mesa and Schreck 1992). We also found that the number of fish that escaped from a blocked-off stream reach increased with recovery time, leading us to estimate that 4.9% of fish, on average, escape by 72 h. To maximize recovery time and minimize the potential for escape, we recommend that researchers use a recovery time between 24 and 48 h. We also caution researchers against using shorter recovery times because we believe that efficiency estimates could be biased as a result of behavioral and physiological changes associated with electrofishing and handling (Schreck et al. 1976; Mesa and Schreck 1992). Finally, we encourage biologists to evaluate their methods for sampling and population estimation and, if necessary, revise them to improve data quality.

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