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[Article]

Validation of Abundance Estimates from Mark–Recapture and Removal Techniques for Rainbow Trout Captured by Electrofishing in Small Streams

AMANDA E. ROSENBERGER*

U.S. Forest Service, Rocky Mountain Research Station, 316 East Myrtle Street, Boise, Idaho 83702, USA; and Center for Ecohydraulics Research, Department of Civil Engineering, College of Engineering, Boise Center, University of Idaho, 800 Park Boulevard, Suite 200, Boise, Idaho 83712, USA

JASON B. DUNHAM[1]

U.S. Forest Service, Rocky Mountain Research Station, 316 East Myrtle Street, Boise, Idaho 83702, USA

Abstract.—Estimation of fish abundance in streams using the removal model or the Lincoln–Peterson mark–recapture model is a common practice in fisheries. These models produce misleading results if their assumptions are violated. We evaluated the assumptions of these two models via electrofishing of rainbow trout *Oncorhynchus mykiss* in central Idaho streams. For one-, two-, three-, and four-pass sampling effort in closed sites, we evaluated the influences of fish size and habitat characteristics on sampling efficiency and the accuracy of removal abundance estimates. We also examined the use of models to generate unbiased estimates of fish abundance through adjustment of total catch or biased removal estimates. Our results suggested that the assumptions of the mark–recapture model were satisfied and that abundance estimates based on this approach were unbiased. In contrast, the removal model assumptions were not met. Decreasing sampling efficiencies over removal passes resulted in underestimated population sizes and overestimates of sampling efficiency. This bias decreased, but was not eliminated, with increased sampling effort. Biased removal estimates based on different levels of effort were highly correlated with each other but were less correlated with unbiased mark–recapture estimates. Stream size decreased sampling efficiency, and stream size and instream wood increased the negative bias of removal estimates. We found that reliable estimates of population abundance could be obtained from models of sampling efficiency for different levels of effort. Validation of abundance estimates requires extra attention to routine sampling considerations but can help fisheries biologists avoid pitfalls associated with biased data and facilitate standardized comparisons among studies that employ different sampling methods.

Estimation of fish population sizes is a fundamental activity for fisheries management and research. The validity of abundance estimates is a function of how well and how consistently they approximate actual fish numbers. Abundance estimates for stream fish often rely on active capture of fish by nets, toxicants, or electrofishing (Murphy and Willis 1996), and it is widely known that no method is 100% effective. Therefore, assessment of fish abundance begins with an assessment of the proportion of the total number of fish present that are captured in a sample, or sampling efficiency. Sampling efficiency for a variety of methods can be affected by habitat complexity (Rodgers et al. 1992; Kruse et al. 1998; Mullner et al. 1998), habitat size (Bayley and Dowling 1993; Kruse et al. 1998; Peterson et al. 2004), fish species and size (Büttiker 1992; Bayley and Dowling 1993; Dolan and Miranda 2003), density of fishes (Simpson 1978; Kruse et al. 1998), and level of effort (Riley and Fausch 1992; Riley et al. 1993; Peterson et al. 2004).

Abundance estimates from electrofishing capture data are most often generated using the removal model or the mark–recapture model (Otis et al. 1978; White et al. 1982; Thompson et al. 1998). The removal model uses catch data from depletion sampling to estimate sampling efficiency and population size. Depletion sampling is accomplished in most cases with one site visit, and re-

* Corresponding author: arosenberger@fs.fed.us
[1] Present address: U. S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis Research Group, 3200 Southwest Jefferson Way, Corvallis, Oregon 97331, USA.

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moval estimates are obtained with available software (e.g., Otis et al. 1978; White et al. 1982). Removal model assumptions are (1) a closed population and (2) equal capture probability for all individuals and all sampling occasions (e.g., depletions, electrofishing passes). Use of effective movement barriers during sampling can satisfy the first assumption, but the second assumption is more difficult to address. Although the time spent actively sampling or the area sampled can be held constant over successive capture occasions, fish that remain after initial passes may be less catchable, resulting in lower sampling efficiency from pass to pass. For example, larger fish are easier to capture than smaller fish (Büttiker 1992; Bayley and Dowling 1993; Dolan and Miranda 2003; Peterson et al. 2004). Also, fish that remain after initial capture occasions may be less catchable because of physiological or behavioral response to the disturbance of the previous passes (Mesa and Schreck 1989). The removal model overestimates sampling efficiency and underestimates population size under conditions of decreasing sampling efficiencies (Zippin 1958; Riley and Fausch 1992). This can be addressed with a generalized removal estimator that adjusts for differences among passes in sampling efficiency; however, this approach requires at least four capture occasions and detection of heterogeneity by use of a goodness-of-fit test (Otis et al. 1978).

The Lincoln–Peterson mark–recapture model is a widely used alternative to the removal model (Thompson et al. 1998). This approach is computationally simple but more field intensive than the removal method. Mark–recapture estimator assumptions are (1) a closed population, (2) random distribution of marked and unmarked individuals, and (3) no difference in capture probability between marked and unmarked fish (White et al. 1982). As with the removal method, the closure assumption can be addressed through adequate use of movement barriers. The remaining assumptions can be addressed by allowing a sufficient recovery period between marking and recapture (e.g., 24 h; Mesa and Schreck 1989; Peterson et al. 2004). Presumably because it is easier to meet these assumptions for stream fish, mark–recapture abundance estimates appear to be less biased when compared to removal estimates (Rodgers et al. 1992).

Unbiased abundance estimates are difficult and time consuming to obtain. This can limit the spatial extent of scientific or management endeavors and can decrease understanding of large-scale patterns of fish abundance (Hankin and Reeves 1988). This problem has led to attempts to obtain unbiased abundance estimates by comparing numbers from a low-intensity but biased method of sampling fish (e.g., snorkeling or single-pass counts) to more intensive and model-based population estimates that are assumed to be unbiased (e.g., multiple-pass removal estimates). If estimates from low-intensity and high-intensity methods are strongly correlated, these studies typically conclude that the numbers from the low-intensity method can be calibrated or used as a relative measure of abundance (Hankin and Reeves 1988; Lobón-Cerviá and Utrilla 1993; Simonson and Lyons 1995; Thurow and Schill 1996; Kruse et al. 1998; Mullner et al. 1998; Joyce and Hubert 2003). Though intuitively and practically appealing, this validation method (an ''index-to-index'' comparison) can be problematic. Factors such as habitat features can contribute to bias in both low- and high-intensity estimates (Thompson 2003), and the relationship between the two indices may vary unpredictably in different contexts (Williams et al. 2004). Validation of abundance estimates instead requires a comparison of the estimate against an unbiased account of fish abundance (an ''index to unbiased estimate'' comparison). Unbiased numbers can be obtained via release of a known number of marked individuals into a site (Rodgers et al. 1992; Peterson et al. 2004) and/or by use of a model with assumptions that can be rigorously tested or addressed.

In this study, we describe electrofishing sampling efficiency for rainbow trout *Oncorhynchus mykiss* in small mountain streams. Our objectives were to assess the accuracy of modeled abundance estimates and to evaluate multiple calibration approaches that adjust catch data or removal estimates to reflect valid measures of abundance. Our study involved the following: (1) determination of site-scale correlates of sampling efficiency; (2) testing of mark–recapture and removal model assumptions; (3) comparison of two-, three-, and four-pass removal estimates with less-biased measures of fish abundance; (4) examination of correlates of removal estimate bias; and (5) assessment of the feasibility of calibrating removal catch data to reflect valid measures of fish abundance by use of predictions from models of sampling efficiency and removal estimate bias. For calibration models, we considered cumulative catch data from one, two, three, or four passes to determine whether and how much an increase in sampling effort (measured as the number of passes completed) im-

TABLE 1.—Characteristics of 31 study sites in headwater tributaries of the Boise River and Panther Creek, Idaho, sampled to estimate rainbow trout abundance in 2002–2003.

Variable	Mean	SD	Range
Site elevation (m)	1,511	208	1,134–2,034
Site length (m)	103.9	8.7	90.0–132.9
Mean wetted width (m)	2.9	0.9	1.5–4.8
Mean depth (m)	0.10	0.03	0.06–0.15
Mean cross-sectional area (m^2)	0.32	0.16	0.10–0.63
Conductivity (μS/cm)	49.6	26.8	11.1–116.0
Temperature (°C)	12.9	3.3	7.2–20.0
Gradient	0.06	0.03	0.004–0.14
Total length of undercut banks (m)	5.5	8.9	0–41.2
Instream wood (total count)	17	16	0–64
Substrate (% composition)			
Fine	3.4	4.8	0–19.9
Sand	9.0	6.8	0–24.1
Gravel	31.3	17.8	6.4–80.2
Cobble	30.9	12.3	0.7–53.4
Boulder	25.4	13.8	0–50.0
Embedded	16.1	9.9	0–34.2
Median length of fish > 60 mm (mm)	105	21	72–136
Recovery period after marking (h)	24.0	7.0	15.4–47.3

proved model predictions. We discuss our results in light of developing validation protocols that can produce standardized estimates of fish abundance.

Methods

Study area.—We conducted our study in the Salmon–Challis National Forest and the Boise National Forest in central and southwestern Idaho. Study sites were located in small, headwater tributaries of the Middle, North, and South forks of the Boise River and in Panther Creek, a tributary of the Salmon River. This study is part of an ongoing project examining the effects of wildfire on aquatic systems, and streams were selected to represent the range of characteristics that we expect to encounter for the duration of this larger project (Table 1). Sites within those streams were selected based on accessibility. We sampled during July–September of 2002 and 2003 at or near base flow conditions.

Field methods.—Each site was approximately 100 m in length (Table 1). Prior to sampling, crews blocked off the upstream and downstream ends of the site with 7-mm-mesh nets secured to the streambed at habitat unit breaks. To evaluate potential bias from escapement (violation of the closed-population assumption), we equipped a subset of our sites with double block nets at both ends (n = 11 sites; following Peterson et al. 2004). After block nets were in place, we conducted a single electrofishing pass by use of a backpack electrofisher (Smith-Root, Inc., Vancouver, Washington; model LR-24 or 12B) with pulsed DC. Crews adjusted voltage, pulse, and frequency to maximize capture probability without causing fish injury (settings range: voltage = 400–700, frequency = 30–50 Hz, pulse width = 2–8 ms). Rainbow trout from the initial marking pass were anesthetized with tricaine methanesulfonate (MS-222) and were measured for fork length to the nearest millimeter. Rainbow trout greater than 60 mm in length were marked by a fin clip taken from the dorsal tip of the caudal fin. Live wells with ambient stream water held all captured fish during processing. Crews returned marked individuals throughout the length of the closed site to encourage random dispersal. Fish that did not appear healthy were released below the site and were not included in the marked fish population. The marked population served as an unbiased baseline abundance estimate (Riley et al. 1993; Peterson et al. 2004).

After the marking pass and at least one overnight recovery period, crews carried out four-pass depletion sampling within the closed site. To assist in evaluation of potential bias from changes in fish behavior after marking and handling (violation of the equal capture probability assumption of the mark–recapture model), crews varied the time between marking and the first removal (recapture) pass (hereafter, recovery period; range = 15.4–47.3 h). After completion of each removal, fish were identified, checked for marks, and measured for fork length to the nearest millimeter. If double block nets were present, crews sampled between nets to detect marked fish that escaped from the original site. All block nets remained in position for the duration of removal sampling. Live wells held all captured fish at stream margins outside of the site until all four passes were completed. Times between removal passes were variable and did not include an explicit ''resting period'' to allow fish to recover from previous electrofishing activity. All available habitats within the site were sampled. We could have implemented a more strict protocol to ''standardize'' sampling effort (e.g., shocking time, time between passes, shocker settings), but our point was to emulate common practice for fishery biologists in the region. We reasoned that this approach would provide the most useful and generally applicable information.

For each site, we recorded its length (m), slope (%; measured with a stadia rod and hand level), elevation (m), maximum depth (cm), and mean temperature (°C) from measurements taken at the beginning and end of each pass. We also counted instream wood (>10 cm in diameter and >1 m in length) and aggregates (more than four pieces of wood acting as a single component). In addition, crews placed transect lines perpendicular to the channel over the length of the site, with a spacing of 5 m. For each transect, crews measured wetted channel width (m) and mean depth (cm; Overton et al. 1997). At seven points along each transect, dominant substrate characteristics within a 10-cm-diameter circle were determined. Substrate categories were defined based on an Udden–Wentworth grain-size scale following Buffington and Montgomery (1999): 1 = silt (<0.0625 mm); 2 = sand (0.0625–2.0 mm); 3 = gravel (2–64 mm); 4 = cobble (>64–256 mm); 5 = boulder (>256 mm); and 6 = bedrock. Larger particles were ''embedded'' if predominantly surrounded by silt or sand. The total length of undercut banks over 10 cm in depth, height, and length were recorded if they intersected horizontal transects.

Data Analysis

Objective 1: evaluation of site-scale correlates of sampling efficiency.—With logistic regression, we modeled overall (cumulative, four-pass) sampling efficiency based on site-scale habitat and fish population characteristics in the Statistical Analysis System (SAS 2001). Mean cross-sectional area, total length of undercut banks, and total wet debris were $\log_{10}$ transformed to meet normality assumptions. Pearson's product-moment correlations were run on all pairs of predictor variables prior to modeling to test for collinearity (maximum observed correlation coefficient $r = 0.53$). We estimated overall sampling efficiency in two ways: (1) the cumulative four-pass catch of marked fish was divided by the number of marked fish released into the site and (2) the cumulative four-pass catch of fish over 60 mm (marked and unmarked) was divided by the mark–recapture abundance estimate of fish over 60 mm. We used the Lincoln–Peterson mark–recapture model as modified by Chapman (1951). Cumulative four-pass catch of marked fish served as the number of recaptures for mark–recapture estimates. When we used the known number of marked fish released, our baseline measure of fish abundance, we could directly measure sampling efficiency by using the number of recaptures; therefore, we describe marked fish sampling efficiency as ''measured sampling efficiency,'' following Peterson et al. (2004). We use the term ''mark–recapture sampling efficiency'' for estimated sampling efficiency based on mark–recapture estimates divided by the total number of captured fish over 60 mm.

We used an information-theoretic approach (Burnham and Anderson 2002) for hypothesis testing and model selection. We began by constructing a global model based on information from previous studies to select site-scale features (Table 1) that were most likely to influence sampling efficiency. Candidate models were subsets of the global model and were based on frequently cited combinations of variables that affect electrofishing sampling efficiency. We categorized these variables into four groups: stream size, cover, mean stream temperature, and fish size. We used mean cross-sectional area (the product of mean stream depth and width) as our measure of stream size (Peterson et al. 2004). Cover included total length of undercut banks, total count of instream wood, and percent cobble. Median fork length of captured fish over 60 mm was used as an overall measure of fish size. We anticipated that stream size and cover would reduce sampling efficiency, whereas an increase in stream temperature and median fish length would improve sampling efficiency. After testing the significance of the global model and model assumptions, we selected the most likely model using Akaike's information criterion (AIC; Akaike 1973) corrected for small-sample bias (AIC_c; Burnham and Anderson 2002). The relative plausibility of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002). If model selection did not indicate overwhelming evidence for a single candidate model, we created an averaged composite model by averaging predictor variables across all candidate models for which Akaike weights were more than one-eighth of the largest weight (as recommended by Royall 1997). We used a weighted mean based on Akaike weights to calculate averaged model parameter estimates (Burnham and Anderson 2002).

Objective 2: evaluation of mark–recapture and removal model assumptions.—To evaluate the closed-population assumption of the mark–recapture model, we compared mark–recapture estimates with and without escapees (marked fish found outside of the site between double block nets). We corrected mark–recapture estimates for escapement in all subsequent analyses.

Electrofishing can alter fish behavior for up to 24 h (Mesa and Schreck 1989), which could be exacerbated by handling and fin clip removal. An inadequate recovery period would result in an unequal capture probability between marked and unmarked fish, violating a mark–recapture model assumption. We used logistic regression to examine the relationship between recovery period (range = 15.4–47.3 h; mean ± SD = 23.2 ± 6.8 h) and measured sampling efficiency. A lack of relationship would signify that marking had a negligible effect on sampling efficiency and was not a significant source of mark–recapture estimate bias.

The removal estimator obtained from the program CAPTURE (White et al. 1982) was used to estimate within-site abundance of marked rainbow trout and all rainbow trout over 60 mm (White et al. 1982). We obtained separate removal estimates of fish abundance based on two, three, or all four passes. For four-pass removal estimates only, we used the generalized removal model that can account for heterogeneity in sampling efficiency among passes detected by use of a goodness-of-fit test (Otis et al. 1978; White et al. 1982). We were able to use the generalized removal model to estimate only the total abundance of fish over 60 mm in the site (number marked: range = 2–60, mean ± SD = 17 ± 13; number of marked fish recovered: range = 2–43, mean ± SD = 12 ± 9). In all other cases, we used the Zippin removal estimator, which assumes equal capture probability among removal passes.

Violation of the constant-capture probability assumption is the most likely source of bias in removal estimates (White et al. 1982). Therefore, for each electrofishing depletion pass, we compared estimated sampling efficiency based on the removal model (henceforth, removal model sampling efficiency) with measured sampling efficiency. We also examined whether measured sampling efficiency was heterogeneous over all four successive passes by use of a log-likelihood *G*-test (significance level α adjusted for multiple tests by use of the Dunn–Sidak correction; adjusted α = 0.001; Sokal and Rohlf 1995). Results from these direct tests on measured sampling efficiency were compared in a case-by-case manner to results from the generalized model goodness-of-fit tests on four-pass removal data of all fish over 60 mm (Zippin 1958; Otis et al. 1978; White et al. 1982). The comparison served as an assessment of how well the goodness-of-fit test detected sizeable heterogeneity when present.

Objective 3: evaluation of removal estimate bias.—We measured removal estimate bias in two ways: (1) by comparison of marked fish removal estimates to the known number of marked fish returned to the closed site and (2) by comparison of removal estimates of all fish over 60 mm to mark–recapture estimates of all fish over 60 mm. The first comparison was a more exact assessment of estimate bias but was limited in terms of the range of fish abundance (see above). The second comparison had potential for inaccuracy but better emulated the range of fish densities typical of our study area (12–155 individuals captured per 100-m site). To examine the effect of effort on bias, we made these comparisons separately for two-, three-, and four-pass removal estimates.

Objective 4: site-scale correlates of removal estimate bias.—We used linear regression to examine the relationship between four-pass removal estimate bias and site characteristics. We expressed and modeled bias of removal estimates in two ways: (1) marked fish removal estimates divided by the known number of marked fish returned to the closed site and (2) removal estimates of all fish larger than 60 mm divided by the mark–recapture estimate of all fish larger than 60 mm. Because factors influencing sampling efficiency can similarly affect removal estimate bias (Peterson et al. 2004), we considered the same habitat variables that were included in sampling efficiency models. For model selection, averaging, and inference, we used the Burnham and Anderson (2002) information-theoretic approach described previously. We examined equality of variances through visual examination of residuals, Levene's test of homogeneity of variances on absolute residual deviations, and correlations between absolute residual deviations and model variables.

Objective 5: model prediction of fish abundance.—We evaluated three approaches for unbiased prediction (calibration) of fish abundance: (1) models of sampling efficiency, (2) direct calibra-

TABLE 2.—Parameter estimates for best-fitting logistic regression models of overall sampling efficiency based on known numbers of marked rainbow trout released in a site (measured sampling efficiency) and mark–recapture abundance estimates (mark–recapture sampling efficiency). Sites were located in headwater tributaries of the Boise River and Panther Creek, Idaho, and were sampled in 2002–2003 (CL = confidence limit).

Parameter or variable	Parameter estimate	Lower 95% CL	Upper 95% CL
Measured sampling efficiency			
Intercept	1.62	2.25	1.02
Log_{10} mean cross-sectional area	−2.09	−3.73	−0.46
Mark–recapture sampling efficiency			
Intercept	0.61	−1.05	2.28
Log_{10} mean cross-sectional area	−1.58	−3.51	0.35
Mean temperature	−0.02	−0.14	0.10
Median length of fish > 60 mm	0.01	−0.01	0.03

tion of catch without consideration of site-scale correlates of sampling efficiency, and (3) calibration of removal estimates via models of removal estimate bias, with and without habitat covariates. For simplicity and to avoid falsely inflating measures of predictive power, calibration models with site-scale covariates included only those covariates that influenced sampling efficiency in previous analyses (objectives 1 and 4). In all cases, mark–recapture estimates were used as baseline measures of fish abundance. Although these estimates are more subject to error than known numbers of marked fish released, they better reflect the typical range of abundances in our study area.

Calibration from sampling efficiency.—We used logistic regression models predicting cumulative mark–recapture sampling efficiency after one, two, three, and four passes. To have a measure of how well our regression models predicted new observations, we used leave-one-out cross validation for predictions of sampling efficiency for each occasion. These modeled estimates of sampling efficiency against known catch were used to predict fish abundance (predicted fish abundance = known catch divided by predicted sampling efficiency). These predictions were plotted against mark–recapture estimates, and the strength of that relationship (R^2) indicated the predictive power of the sampling efficiency model under a leave-one-out scenario.

Direct calibration of catches.—We also used linear regression to predict mark–recapture abundance estimates based on fish catches alone. We used a similar leave-one-out validation approach via calculation of prediction sum of squares (PRESS) residuals (Myers 1990). The PRESS residuals are estimated by withholding a single observation (y_i) and calculating a y_i residual by subtracting the observed value from that predicted by a regression model constructed with the remaining observations ($n - 1$). We compared PRESS residuals with residuals estimated from the overall means model with an R^2-like statistic (R^2_{pred}) that indicates the overall predictive performance (Myers 1990). We examined equality of variances through visual examination of residuals, the Levene's test of homogeneity of variances on absolute residual deviations, and correlations between absolute residual deviations and model variables.

Calibration of biased removal estimates.—To examine whether two-, three-, and four-pass removal estimates were good predictors of unbiased fish abundance measures, we used linear regression models of removal estimate bias with and without site-scale covariates. To assess the predictive abilities of these models, we used the PRESS residuals to calculate R^2_{pred} as described above. Model assumptions were tested as described above.

Results

Objective 1: Evaluation of Site-Scale Correlates of Sampling Efficiency

We constructed two logistic regression models: one modeled the measured sampling efficiency (cumulative number of marked fish recaptured over four passes divided by the number of marked fish released into the site) and the other modeled mark–recapture sampling efficiency (cumulative catch of fish longer than 60 mm over four passes divided by the mark–recapture estimate of fish over 60 mm). The most likely model of measured sampling efficiency included only mean cross-sectional area, our measure of stream size (Table 2). Ninety-five percent confidence intervals (CIs) around the mean cross-sectional area parameter estimate and the model intercept did not overlap zero. The most likely model for mark–recapture sampling efficiency included stream size, mean temperature, and median fish length; however, in all cases, 95% CIs overlapped zero, indicating unpredictable effects on mark–recapture sampling efficiency (Table 2). Strong evidence for both models (high Akaike weights) precluded model averaging.

Objective 2: Evaluation of Mark–Recapture and Removal Model Assumptions

Our measure of escapement was probably negatively biased due to two unknowns: (1) any fish that escaped from one block net may have escaped from both and (2) it is almost certain that we did not capture 100% of fish between block nets. Escapement that was detected did not present a substantial source of bias. Although escapement was observed in 5 out of the 11 sites for which double block nets were set, no more than one fish escape was detected per site, representing only 3% of the 164 marked rainbow trout in those sites. Correcting for escapement did not greatly change mark–recapture estimates (corrected estimate divided by uncorrected estimate: mean ± SD = 0.95 ± 0.05).

We found no evidence to suggest that the second assumption of equal capture probability of marked and unmarked individuals was violated over the range of recovery periods in our study. Logistic regression indicated that differences in recovery period ranging between 15.4 and 47.3 h did not affect measured sampling efficiency (recovery period parameter estimate = 0.007; 95% CI range = −0.04 to 0.06). Further, measured sampling efficiency and recovery period were not correlated.

The removal model generally overestimated sampling efficiency (Figure 1). For the first pass, measured sampling efficiency exceeded removal model sampling efficiency for only 1 of 35 sites. In addition, measured sampling efficiency successively declined over removal passes (Figure 1). Chi-square goodness-of-fit tests of the generalized removal model performed by the program CAPTURE for each site (White et al. 1982) indicated that, with only four exceptions, capture efficiency was constant and the removal model was appropriate. In contrast, log-likelihood *G*-tests performed on measured sampling efficiencies indicated that, for 17 of the 35 sites sampled, capture probabilities were heterogeneous and removal model assumptions were not met ($G \geq 16.42$, df ≤ 2, $P < 0.001$). Thus, in 13 out of these 17 occasions, the generalized removal model failed to detect and adjust for sizeable changes in sampling efficiency over successive passes.

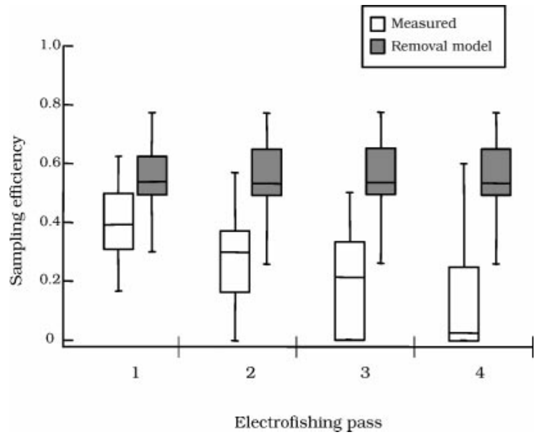

FIGURE 1.—Box plots of electrofishing sampling efficiency over four consecutive depletion passes, expressed as measured sampling efficiency (percent recapture of a known number of marked rainbow trout released into the site minus escapement) and removal model sampling efficiency (calculated in CAPTURE; Otis et al. 1978; White et al. 1982). Fish were sampled in the headwater tributaries of the Boise River and Panther Creek, Idaho, in 2000–2003.

Objective 3: Evaluation of Removal Estimate Bias

Of the 36 sites for which we obtained four-pass marked fish removal estimates, we could calculate three- and two-pass estimates for only 27 and 26 of the sites, respectively. The reason for model failure was an increase in marked fish catch from one pass to the next, indicating low and inconsistent sampling efficiency over successive passes. Regardless of how many passes were included in the model, removal estimates of marked rainbow trout were negatively biased (Figure 2). Bias decreased as effort increased (marked fish removal estimate divided by known number of marked fish released: two-pass mean ± SD = 0.63 ± 0.22; three-pass mean ± SD = 0.67 ± 0.26; four-pass mean ± SD = 0.75 ± 0.21). Confidence intervals around four-, three-, and two-pass marked fish removal estimates encompassed the number of marked fish released for only 37, 22.5, and 26.7% of the sites, respectively (Figure 2). Confidence intervals around three-pass removal estimates were the most narrow (coefficient of variation [CV] of the 95% CI: two-pass CV = 1.7; three-pass CV = 1.1; four-pass CV = 1.6).

We compared removal estimates of rainbow trout over 60 mm with mark–recapture estimates for 38 sites. Removal estimates tended to be lower than mark–recapture estimates, except for very low numbers of rainbow trout (Figure 3). If we

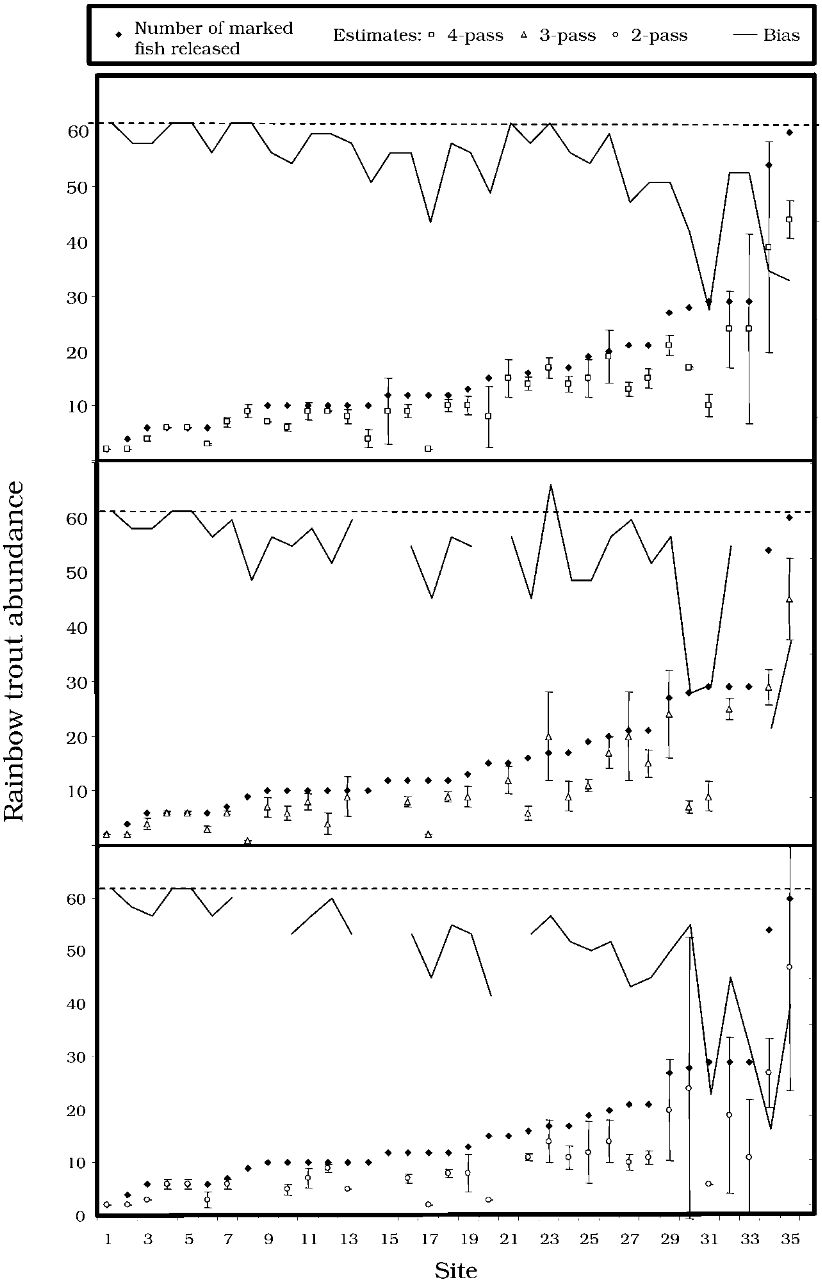

FIGURE 2.—Abundance of marked rainbow trout at 36 sites in Boise River and Panther Creek, Idaho, tributaries sampled in 2002–2003. Abundance is expressed as the known numbers of marked fish released and as four-, three-, and two-pass marked fish removal estimates with 95% confidence intervals. Lines indicate the magnitude of removal estimate bias (removal estimate less marked fish released). Gaps in removal estimates are from instances when the removal model failed.

eliminated occasions when the mark–recapture estimate was less than 10 individuals, we saw a similar pattern of negative bias as described above. Again, bias declined with increased sampling effort (removal estimate/mark–recapture estimate: two-pass mean ± SD = 0.62 ± 0.31; three-pass mean ± SD = 0.71 ± 0.25; four-pass mean ± SD = 0.77 ± 0.19; Figure 3). Confidence intervals

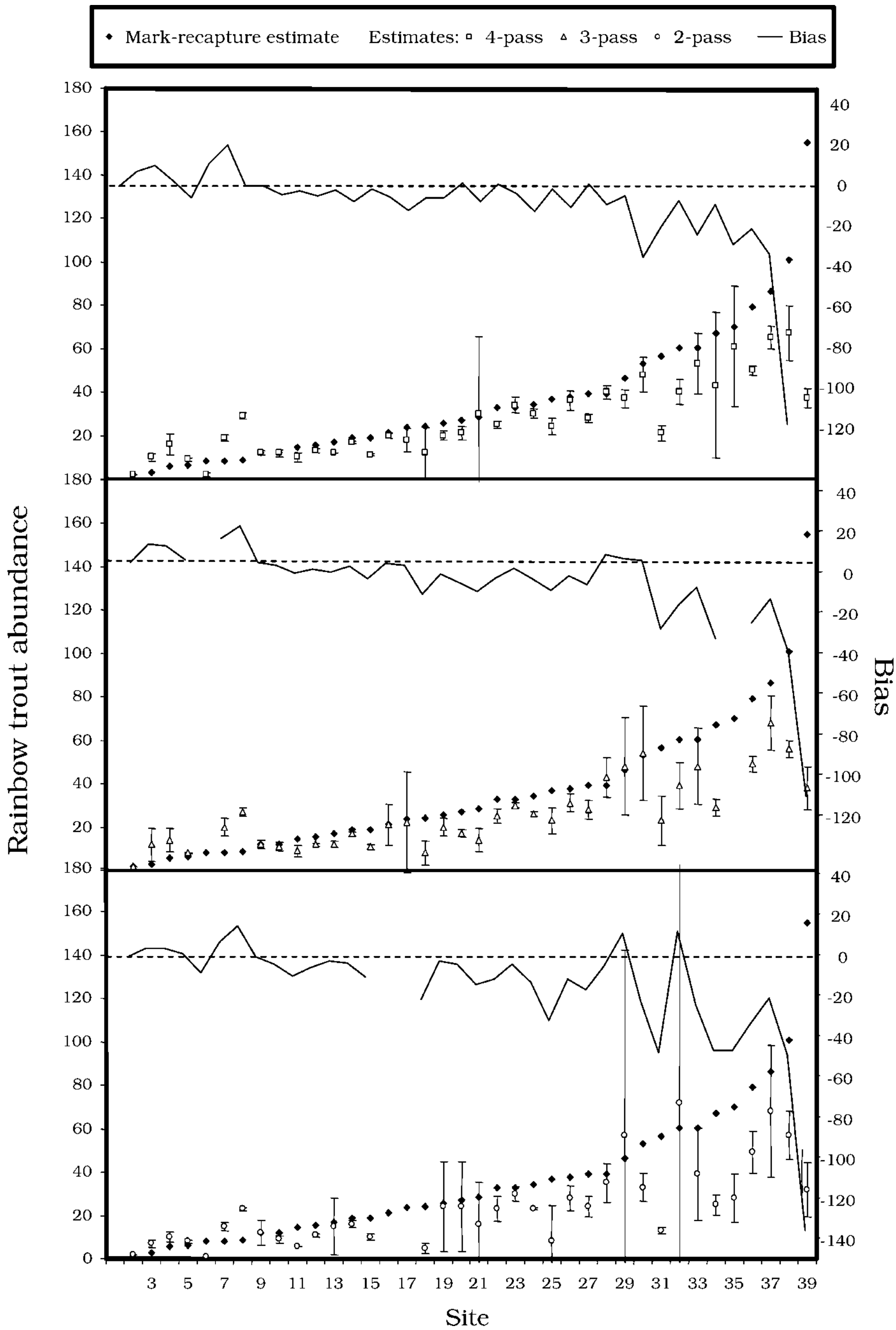

FIGURE 3.—Abundance of rainbow trout larger than 60 mm at 38 sites in Boise River and Panther Creek, Idaho, tributaries sampled in 2002–2003. Abundance is expressed as mark–recapture estimates and as four-, three- and two-pass removal estimates with 95% confidence intervals. Lines indicate the magnitude (*n*) of difference between the two estimates (removal estimate less mark–recapture estimate). Gaps in removal estimates are from instances when the removal model failed.

TABLE 3.—Model-averaged parameter estimates for best-fitting linear regression models of four-pass removal estimate bias based on known numbers of marked rainbow trout released in a site and mark–recapture abundance estimates. Sites were located in the Boise River and Panther Creek, Idaho, and were sampled in 2002–2003 (CL = confidence limit).

Variable	Parameter estimate	Lower 95% CL	Upper 95% CL
Bias based on percent of marked fish released			
Intercept	0.639	0.315	0.962
Log_{10} mean cross-sectional area	−0.463	−0.787	−0.139
Log_{10} total length of undercut bank	0.006	0.000	0.011
Log_{10} instream wood	−0.003	−0.005	0.000
% Cobble substrate	0.002	−0.001	0.005
Mean temperature	−0.004	−0.010	0.002
Median length of fish > 60 mm	0.003	0.000	0.005
Bias based on percent of mark–recapture estimate			
Intercept	0.970	0.716	1.225
Log_{10} mean cross-sectional area	−0.358	−0.671	−0.045
Log_{10} total length of undercut bank	0.006	−0.002	0.013
Log_{10} instream wood	−0.008	−0.011	−0.004
% Cobble substrate	−0.002	−0.006	0.003
Mean temperature	0.001	−0.002	0.003
Median length of fish > 60 mm	0.000	0.000	0.001

around four-, three-, and two-pass removal estimates only occasionally encompassed mark–recapture estimates (30, 31, and 36%, respectively; Figure 3). Confidence intervals were again most narrow for three-pass removal estimates (CV of 95% CI: four-pass CV = 1.5; three-pass CV = 0.98; two-pass CV = 2.0).

Results suggested that mark–recapture estimates were unbiased except for estimates of less than 10 individuals. Low escapement and no evidence of unequal capture probability among marked and unmarked individuals indicated that model assumptions were effectively addressed. Further, the pattern of removal estimate bias was the same whether the marked fish released or mark–recapture estimates less than 10 were used as baseline measures of abundance. For the bias and calibration models described later, we used mark–recapture abundance estimates as baseline measures of fish abundance. We were less certain of mark–recapture estimates than the number of marked fish remaining in a site; however, these calibration models are more widely applicable because mark–recapture estimates better reflect the range of abundances typical of our study area.

Objective 4: Site-Scale Correlates of Removal Estimate Bias

The averaged model of four-pass marked fish removal estimate bias indicated that mean cross-sectional area contributed to negative bias (Table 3). All other parameters, with the exception of the model intercept, had CIs that overlapped zero, indicating an inconsistent or negligible effect on bias. In the averaged model of four-pass removal estimate bias based on mark–recapture estimates as baseline measures of fish abundance, we saw a similar pattern of a positive intercept and increased negative bias with an increase in cross-sectional area. In addition, instream wood was positively related to estimate bias in this model. All other variables included in the averaged model had CIs around parameter estimates that overlapped zero (Table 3).

Objective 5: Model Prediction of Fish Abundance

The models in the previous section indicated that only mean cross-sectional area and instream wood appreciably affected overall sampling efficiency or removal estimate bias. Therefore, logistic models intended for calibration purposes included only those two site-scale covariates (Table 4). Using mark–recapture estimates as baseline measures of fish abundance, we employed a leave-one-out approach to predict sampling efficiency for each level of effort; these sampling efficiencies were used to generate predicted fish abundances (Table 4; Figure 4). When plotted against validated mark–recapture estimates, predicted fish abundances strongly correlated with mark–recapture estimates, regardless of sampling effort. With increased effort taken into account, the amount of variation explained by models increased, prediction intervals decreased, and slope and intercept values were closest to 1 and 0, respectively (Figure 4). Direct linear calibration of total catch to un-

TABLE 4.—A summary of parameter estimates (with lower 95% confidence limit [CL], upper 95% CL) from logistic regressions used to predict cumulative sampling efficiency of rainbow trout after one, two, three, or four electrofishing passes in sites sampled during 2002–2003 within the Boise River and Panther Creek, Idaho. Leave-one-out predictions from these models were used to generate the predictions of fish abundance estimates in Figure 4.

Variable	Number of passes			
	4	3	2	1
Intercept	1.47 (0.53, 2.48)	1.25 (0.36, 2.19)	0.61 (−0.17, 1.42)	−0.31 (−1.02, 0.39)
Log_{10} mean cross-sectional area	−0.51 (−1.04, 0.004)	−0.31 (−0.80, 0.18)	−0.37 (−0.81, 0.06)	−0.35 (−0.74, 0.04)
Log_{10} instream wood	−0.47 (−0.72, −0.24)	−0.39 (−0.62, 0.17)	−0.35 (−0.54, −0.15)	−0.26 (−0.43, −0.09)

biased mark–recapture estimates without consideration of site-scale covariates of sampling efficiency resulted in much poorer calibration, particularly for low levels of effort (Table 5).

In general, removal estimates generated at different levels of electrofishing effort were more correlated with each other than they were with the less-biased mark–recapture estimates, suggesting that calibrating low-effort removal indices to reflect high-effort removal indices not only retains bias but also leads to false confidence of estimate precision (Table 6). Regardless of whether habitat variables were included in calibration models, two- and three-pass removal estimates were poor predictors of mark–recapture estimates compared to four-pass removal estimates (Table 7), and none

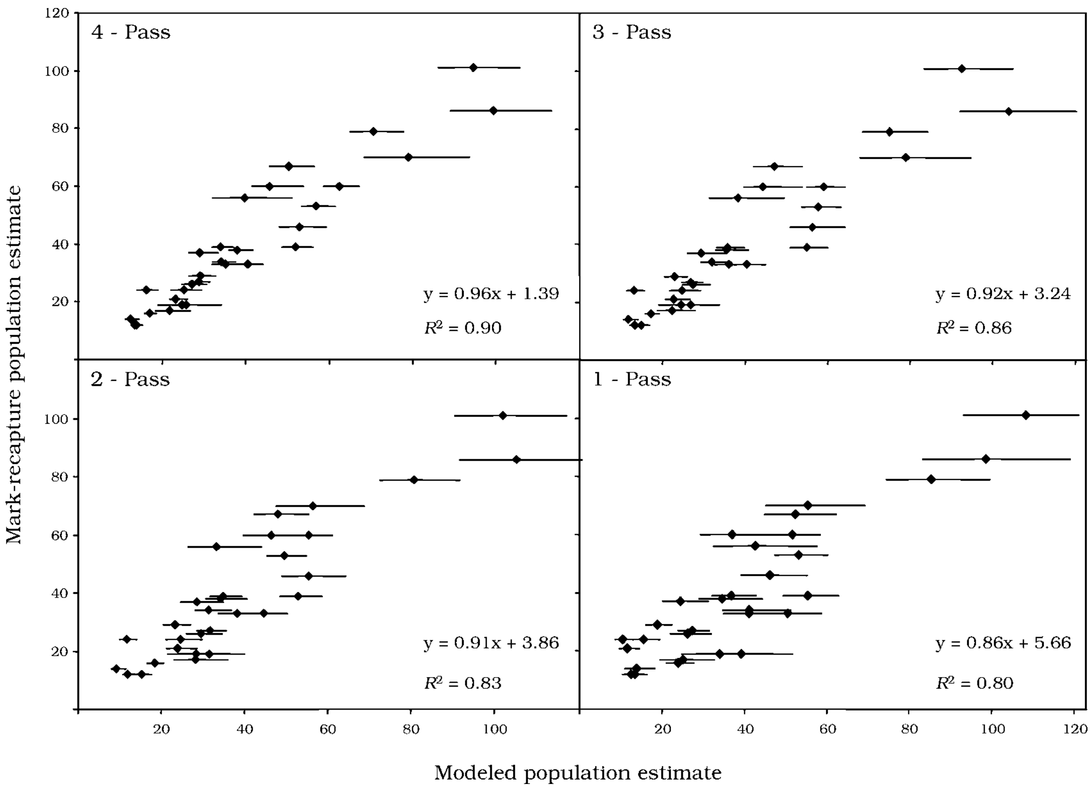

FIGURE 4.—The relationship between mark–recapture abundance estimates of rainbow trout in Boise River and Panther Creek, Idaho, tributaries (2002–2003) and predicted fish abundance based on logistic regression models (predicted abundance = known catch/predicted sampling efficiency). Predictions are based on a leave-one-out validation approach, and error bars represent prediction intervals around the estimate. Separate models were constructed for each level of sampling effort (one-, two-, three-, and four-pass cumulative catch). Equations for best-fitting trend lines and R^2 values are also presented.

TABLE 5.—Parameter estimates (with lower 95% confidence limit [CL], upper 95% CL) from linear regression models used to predict mark–recapture estimates based on cumulative rainbow trout catch after one, two, three, or four electrofishing passes in sites sampled during 2002–2003 within the Boise River and Panther Creek, Idaho. Prediction sum of squares residuals, indicating relative model predictive performance based on a leave-one-out validation approach, were used to generate R^2_{pred}, which reflects model prediction capability (Myers 1990).

Variable	Number of passes			
	4	3	2	1
Intercept	−0.07 (−7.42, 7.28)	1.05 (−6.83, 8.92)	2.81 (−6.18, 11.79)	6.25 (−3.45, 15.95)
Cumulative catch	1.43 (1.20, 1.66)	1.51 (1.24, 1.78)	1.70 (1.33, 2.07)	2.25 (1.68, 2.82)
R^2_{pred}	0.82	0.78	0.72	0.64

of the models equaled the logistic regression models in prediction performance.

Discussion

Our results indicated that the abundance estimates generated by the removal model were negatively biased and influenced by local habitat features. In contrast, we found that rainbow trout abundances could be rigorously assessed with the mark–recapture model as long as sufficient numbers of fish were recaptured. With information on sampling efficiency and accurate abundance baselines based on the mark–recapture model, we were able to develop calibrated estimates of abundance from fish catches or biased removal estimates. Strong predictive models ($R^2 > 0.80$) that included site-scale covariates produced unbiased abundance estimates with relatively low effort (e.g., a single electrofishing pass); however, model predictions improved with increased sampling effort (e.g., number of removals).

Sampling Efficiency and Site-Scale Correlates of Efficiency

Our sampling approach yielded low sampling efficiency (mean measured sampling efficiency for the first pass = 44%) that decreased with successive removal passes. Stream size had a consistent negative effect on sampling efficiency, but the importance of this feature depended on whether known numbers of marked fish released at a site (strong negative effect) or mark–recapture estimates (negative effect, but 95% CIs of the parameter estimate overlapped zero) were used as baseline measures of abundance. This difference may reflect the larger range of abundances entered into the mark–recapture sampling efficiency model or the increased potential for error in mark–recapture estimates. This underscores the importance of adhering to the common sense of avoiding model extrapolation beyond the range of data used to create the model; users should not hazard to apply models to situations for which they were not developed.

TABLE 6.—Pearson's *r* correlation matrix between biased four-, three-, and two-pass removal estimates and validated mark–recapture population estimates of rainbow trout within sites in headwater tributaries of the Boise River and Panther Creek, Idaho, sampled in 2002–2003.

Fish abundance estimate	Removal method		
	Two-pass	Three-pass	Four-pass
Two-pass removal		0.76	0.70
Three-pass removal	0.76		0.89
Four-pass removal	0.70	0.89	
Mark–recapture	0.61	0.75	0.84

Evaluation of Model Assumptions and Removal Estimate Bias

Multiple lines of evidence suggest that our mark–recapture estimates were reliable measures of fish abundance. Presumably, this is because it was feasible to adhere to model assumptions (i.e., closed population and equal capture probability between marked and unmarked individuals). Observed escapement had a negligible effect on mark–recapture estimates. Peterson et al. (2004) reported similarly low escapement (<1 marked fish per day), which was positively correlated with recovery period. An overnight resting period was sufficient to generate no detectable relationship between recovery time and marked fish sampling efficiency. This result indicated that marked individuals had recovered sufficiently within the range of recovery periods (15.4–47.3 h) to have the same likelihood of capture as unmarked individuals. In addition, patterns of removal estimate bias were the same whether the known number of marked fish released or the mark–recapture estimates were used as baseline measures of fish abundance. The exception to this was for sites with very low abundances (<10 fish); in such cases, mark–recapture estimates appeared to be positively biased. This was not surprising; Otis et al. (1978) and White

TABLE 7.—Parameter estimates (with lower 95% confidence limit [CL], upper 95% CL) from linear and multiple-regression models used to predict mark–recapture estimates based on four-, three-, and two-pass removal of rainbow trout in sites sampled during 2002–2003 within the Boise River and Panther Creek, Idaho, with and without site-scale habitat covariates included in the models. Prediction sum of squares residuals were used to generate R^2_{pred}, which reflects the leave-one-out prediction capability of a model (Myers 1990).

Variable	Number of passes		
	4	3	2
Site-scale habitat covariates included			
Intercept	−9.7 (−19.7, 0.27)	−5.6 (−20.6, 9.5)	−1.2 (−18.7, 16.3)
Abundance estimate	1.3 (1.1, 1.4)	1.3 (1.0, 1.6)	1.0 (0.7, 1.3)
Log_{10} cross-sectional area	−2.0 (−4.4, 0.4)	0.6 (−3.1, 4.3)	1.5 (−3, 5.9)
Log_{10} instream wood	4.3 (1.2, 7.4)	4.4 (−0.3, 9)	7.3 (1.8, 12.8)
R^2_{pred}	0.85	0.56	0.40
Site-scale habitat covariates excluded			
Intercept	1.5 (−5.6, 8.7)	4.2 (−6.1, 14.5)	17.4 (6.4, 28.1)
Abundance estimate	1.3 (1.1, 1.5)	1.3 (1.0, 1.6)	0.9 (0.6, 1.2)
R^2_{pred}	0.83	0.65	0.40

et al. (1982) cautioned that mark–recapture estimates are unreliable when sampling efficiency, population size, and the number of recaptures are low.

As noted in other work, the removal model appears to be a misleading and biased method for assessing stream fish abundance. We observed negative and habitat-mediated bias of removal estimates. Low and decreasing sampling efficiency from pass to pass was a likely culprit (White et al. 1982; Riley and Fausch 1992; Peterson et al. 2004). Increased effort improved, but did not eliminate, this bias. For four-pass removal estimates, we attempted use of the generalized removal model that can account for this heterogeneity (Otis et al. 1978); however, the model's goodness-of-fit test typically failed to detect decreased sampling efficiency. This may be due to the low power of this test for the range of fish abundances within our sites. Accordingly, we do not recommend use of the generalized model to account for four-pass sampling efficiency heterogeneity in sites with similar fish abundances.

The confidence intervals around removal estimates rarely encompassed baseline measures of fish abundance. Even though four-pass estimates were the least biased, CIs were narrower for three-pass estimates than for four-pass estimates. This suggests that in similar cases, the size of a CI around a removal estimate is not a good indicator of the estimate's reliability (Hankin and Reeves 1988). In addition, characteristics of our sampling sites affected removal estimate bias. Marked fish removal estimate bias was related to stream size; when mark–recapture estimates were used as a baseline, stream size and instream wood were related to removal estimate bias. This pattern is similar to what was observed in the sampling efficiency analyses, indicating that factors that decrease sampling efficiency can, in turn, increase removal estimate bias (also see Peterson et al. 2004).

Readers should bear in mind that our measured sampling efficiencies were low, and removal estimate bias may not be nearly as much of a problem in cases when sampling efficiency is high (e.g., 80% or more). However, the sampling efficiency we observed was not unusually low in the context of similar studies. Although we used pulsed instead of constant DC to increase electrofishing sampling efficiency (Bohlin et al. 1989), our first-pass measured sampling efficiency fell within the range of unpulsed DC electrofishing sampling efficiency reported for other salmonids when the numbers of marked fish at a site were known (20–57%; Peterson et al. 2004). Our sampling efficiency also fell within the range reported for AC electrofishing of warmwater stream fishes when catch was compared to rotenone-based numbers adjusted for incomplete capture (7–69% during use of an electrofisher and electric seine; Bayley and Dowling 1993). Alternating current is more effective than DC but has greater potential for fish injury (Bohlin et al. 1989).

Use of Models to Predict Abundances via Count Data or Removal Estimates

Our results suggest that calibration based on sampling efficiency models with habitat covariates and a sufficient amount of sampling effort can be used to reliably predict fish abundance. Direct calibration also successfully corrected catch data and removal estimate bias, and calibration with habitat features taken into account improved model precision.

We used three approaches to model fish abundance: (1) a model of sampling efficiency, which was then used to predict the number of fish in the site (modeled fish abundance = catch/predicted sampling efficiency), (2) direct calibration of catch data using linear regression, and (3) calibration of biased removal estimates using linear regression with and without site-scale covariates of estimate bias. We observed a strong relationship between unbiased mark–recapture estimates and predicted fish abundance based on sampling efficiency models. This relationship was strongest for models that included all four electrofishing passes; however, a reasonable level of accuracy could be obtained from low-effort models with habitat covariates (Figure 4). This is an encouraging result; many studies that encompass large areas of stream measure fish abundances with single-pass, low-effort methods. However, models that directly calibrated catch data without site-scale covariates or that calibrated biased removal estimates (with and without habitat covariates) were precise ($R^2 > 0.80$) only for catches resulting from the highest level of effort (four electrofishing passes).

Retrospective calibrations of biased data that consider site-scale covariates of sampling efficiency (e.g., stream size) will be more accurate, particularly if they are applied to low-effort abundance estimates or catch data. Other variables not considered in this study that may affect sampling efficiency include additional site features (e.g., visibility) and crew ability. The latter is particularly difficult to quantify (e.g., Dunham et al. 2001). To consider crew ability, a consistent designation of crew assignments may be helpful (Dolloff et al. 1993). Alternatively, if this is not possible, calibration models could be based on a broad range of crew assignments, as was done here. Less precise calibrations may result, but they are likely to apply more broadly among different observers.

Conclusions

Our objective was to determine the most valid and efficient sampling and calibration approach for our sampling context. An assessment of sampling efficiency and estimate bias at different levels of effort with and without site-scale covariates allowed us to determine the most cost-effective way of obtaining reliable abundance data in terms of effort, precision, and bias. It was necessary to use known abundances of marked fish or unbiased mark–recapture estimates as baselines for evaluating sampling efficiency and calibrating removal abundance estimates. Whereas removal estimates were highly correlated for different levels of effort (e.g., single- versus multiple-pass removal estimates), all were biased when compared to a valid baseline.

The problem of obtaining a valid approach for sampling fish has led to calls for the creation of standardized sampling protocols for entire regions (e.g., states) and habitat types (e.g., ponds and streams); these standardized protocols would allow biologists to concentrate resources on improving fish populations rather than routine monitoring considerations (Bonar and Hubert 2002). Whereas there is much value in the concept of standardization, practical implementation will require an understanding of the validity of estimator assumptions and the range of sampling efficiencies for all species of interest. By definition, a standardized sampling approach is one that yields estimates that have a common meaning (i.e., common uncertainty, expressed as systematic error [bias] and random error [precision]; Taylor and Kuyatt 1994). This view of standardization is one in which use of a common sampling method or protocol is less important than how well and how predictably the estimates approximate reality. We recommend routine use of a standard *validation* protocol based on the level of certainty needed to address study objectives. With reliable information on bias and precision of removal (or other) estimates of fish abundance, researchers and managers can determine whether population estimates fall within a predetermined acceptable level of error based on research or management objectives, regardless of the sampling approach used (e.g., Freese 1960; Gregoire and Reynolds 1988).

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