# Development of Bull Trout Sampling Protocols 

## Final Report

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### 1.0 INTRODUCTION

This report describes results of research conducted in Washington in 2000 through Interagency Agreement \#134100H002 between the U.S. Fish and Wildlife Service (USFWS) and the U.S. Forest Service Rocky Mountain Research Station (RMRS). The purpose of this agreement is to develop a bull trout (Salvelinus confluentus) sampling protocol by integrating and interpreting various types and sources of bull trout sampling efficiency, habitat association, and probability of detection databases. In this report, we also contrast Washington results with related research conducted by RMRS scientists and cooperators in Idaho during 1999 and 2000.

Extensive interest in development of bull trout sampling protocols stems from the problematic aspects of sampling bull trout. Behavior of bull trout, their specific habitat requirements, and population characteristics make them difficult to sample. Bull trout appear to have an affinity for stream reaches colder than $15^{\circ} \mathrm{C}$ (Goetz 1994; Rieman and Chandler 1999) and many populations reside in streams with low conductivities ( $<100 \mu \mathrm{~S} / \mathrm{cm}$ ) and high water clarity. Their coloration and cryptic behavior may make bull trout difficult to see (Thurow and Schill 1996). Bull trout frequent areas with instream overhead cover and coarse substrate (Pratt 1984). Juvenile bull trout are closely associated with the streambed and may be concealed within substrate (Thurow 1997). Bull trout tend to be found in relatively low densities (Schill 1992) and populations may be clustered in specific areas of suitable habitat. As a result, common sampling techniques like electrofishing and snorkeling may fail to detect bull trout or underestimate their true abundance (Thurow and Schill 1996).

Consequently, a critical feature to consider when designing a bull trout sampling or monitoring protocol is the influence of sampling efficiency. In addition to gear type, fish sampling efficiency influenced by the size and species of fish (Bagenal 1977; Reynolds 1983; Riley et al. 1993) as well as physical habitat features (Bayley and Dowling 1993; Peterson 1996). Failure to account for differences in sampling efficiency introduces an error or bias into the data, which can significantly affect abundance estimates (Bayley and Dowling 1993). Presence and absence estimates are similarly affected by sampling efficiency because the probability of detecting a species is a function of its probability of capture and its density, both of which are influenced by habitat features that vary. Therefore, gear and habitat-specific sampling efficiency estimates are required for estimating bull trout detection probabilities and sample size
requirements (Peterson et al. 2001). This report describes results of our efforts to derive sampling efficiency estimates in a range of streams supporting bull trout in Washington and Idaho.

### 1.1 Objectives

USFWS Washington Research

1. To compare the probability of detecting bull trout and other salmonids using day snorkeling, night snorkeling, and successive capture or mark-recapture electrofishing with an unbiased estimate of the true population.
2. To evaluate the influence of the marking procedure on recovery rates of marked fish.
3. To describe the influence of physical channel features including stream size, water temperature, conductivity, channel complexity, and abundance of cover on probabilities of detecting bull trout and other salmonids.
4. To compare probabilities of detection for different salmonid species and size classes.

## RMRS Idaho Research

1-4. As listed above.
5. To evaluate block net effectiveness.
6. To estimate the precision of measures describing physical channel features.

### 2.0 METHODS

### 2.1 USFWS Washington Field Protocols

The crew protocols described below were designed to estimate population abundance and size structure through recovery of marked individuals and to predict probabilities of detection under different conditions. Attachment A provides more detailed descriptions of sampling methods. The ultimate goal of this research is to develop protocols for estimating the sampling effort and techniques required to achieve a desired level of accuracy in detecting the presence/absence of native salmonids. As a central hypothesis we suggest that probabilities of detecting bull trout are influenced by the sampling method, sampling effort, physical features of the sampling unit, fish density, and fish size.

### 2.1.1 Sampling unit selection

Crews were instructed to select sampling units in areas that support relatively high densities of age $1+$ bull trout. A density of $>10$ fish per 100 m of channel length was a target. If
possible, crews selected units with a range of physical habitat conditions. Our intent was to capture relatively gross differences in conditions (high, medium, low hydraulic complexity, for example) rather than attempting to precisely measure conditions. We attempted to select areas that were readily accessible so more time was spent sampling and less in hauling equipment to the sites. Crews paced an approximately 100 m sampling unit and selected hydraulic controls for upper and lower boundaries. In every fourth unit, crews paced a 50 m sampling unit. Sampling unit locations were marked on a topographic map.

### 2.1.2 Block nets and thermographs

Block nets were installed at upper and lower unit boundaries and nets inspected using snorkeling gear to insure they were barriers to movement. In some locations, crews selected adjacent sampling units separated by a block net (i.e. 3 block nets in 2 sampling units). Block nets were held for approximately 4 days so care was taken to insure they remained fish tight. Nets were cleaned regularly until all fish sampling was completed. Crews installed a thermograph at the lowermost net and recorded hourly temperatures during the sampling period.

### 2.1.3 Pre-survey fish marking

Crews used electrofishing gear to capture and mark age $1+$ salmonids in each unit. They completed one upstream pass and one downstream pass using unpulsed Direct Current (DC) where feasible to reduce the potential for injuring fish. The waveform and voltage were recorded with starting and ending times and water temperatures. Captured fish were placed in live wells, anesthetized, measured, and the species and total lengths recorded to the nearest 10 mm size groups. Crews notched or paper punched the dorsal or caudal fins in a manner that was visible to snorkelers. In adjacent units, differential marks were applied. Crews varied the time since marking from 24-72 hours before initiating abundance surveys. To reduce the likelihood of injury, when large ( $>400 \mathrm{~mm}$ ) bull trout were encountered during the pre-survey marking, crews terminated the survey and selected another sampling unit.

### 2.1.4 Abundance survey

Day-Snorkeling.-- Crews inspected the sample unit and selected the number of snorkelers necessary to survey the unit in a single pass. Only snorkelers who participated in species identification and size estimation training were to complete counts (Thurow 1994). The units were snorkeled during the daytime between 1000 and 1700 by moving slowly upstream.

Snorkelers counted the total number of salmonids by species, estimated size classes to the nearest 100 mm size group, and recorded marks. A data recorder on shore carried a small halogen light that the snorkelers accessed to facilitate spotting fish hidden in shaded locations. Crews recorded starting and ending times, water temperatures with a calibrated hand-held thermometer, and the divers who completed counts.

Snorkelers measured the underwater visibility of a salmonid silhouette at three locations using a secchi disk-like approach as follows. One crewmember suspended the silhouette in the water column and a snorkeler moved away until the marks on the object could not be distinguished. The snorkeler moved back toward the object until it reappears clearly and measured that distance. Visibility was measured in the longest and deepest habitats (i.e. pools or runs) where a diver had the longest unobstructed underwater view. Crews also recorded whether a snorkeler could see from bank to bank underwater.

Crews also recorded the presence of non-salmonid fishes during day and night snorkel surveys and electrofishing surveys and noted whether fish were juveniles or adult. The presence of amphibian adults or juveniles was similarly noted by species.

Night-Snorkeling.-- A nighttime snorkel survey was completed in the same unit between 2230 and 0430. Crews used the identical technique applied during the daytime survey with the aide of a halogen light. Starting and ending times and water temperatures were recorded. On occasions crews varied the sequence by completing the nighttime survey first and the daytime survey the following day.

Electrofishing.-- After the day and night snorkeling were completed, crews electrofished the unit using unpulsed Direct Current (DC) where feasible to reduce the potential for injuring fish. Crews completed four upstream passes and record the waveform, voltage, and frequency and starting and ending times and water temperatures. Fish captured during individual passes were placed in live wells along the stream margins. Crews were instructed to sample slowly and deliberately, especially near cover components and to observe captured fish and adjust voltages to reduce the risk of injuring fish. Crews were instructed that fish may be increasingly susceptible to handling stress as water temperatures increase above $16{ }^{\circ} \mathrm{C}$ so during warm days, sampling was sometimes conducted in the early morning and late evening to reduce the risk of injury. Fish were anesthetized, measured, and the species and total lengths and marks of all
salmonids recorded to the nearest 10 mm size groups. Data were recorded by individual pass. Crews were instructed to complete a $5^{\text {th }}$ pass if the catch in the 4 th pass did not decline by $75 \%$ or more from the $3^{\text {rd }}$ pass (i.e. $4^{\text {th }}$ pass catch is $25 \%$ or less of the $3^{\text {rd }}$ pass).

### 2.1.5 Physical and chemical data

Conductivity.-- A calibrated conductivity meter was used to measure conductivity in each unit.

Channel dimensions and substrate.-- As previously stated, our intent was to capture and classify gross differences in physical habitat conditions. As a result, we used an abbreviated habitat inventory procedure. Crews measured unit physical attributes by establishing transects at 10 m intervals in 50 m units and at 20 m intervals in 100 m units. In every $3^{\text {rd }} 100 \mathrm{~m}$ unit, transects were established at 10 m . To establish transects, crews used a string machine or tape to measure the unit along the centerline of the stream. At each transect, crews recorded the type of habitat, measured wetted channel width perpendicular to the flow, measured mean and maximum depth, visually classified the substrate into four size classes, and completed a wolman pebble count (Wolman 1954).
Habitat types- are discrete channel units influenced by flow pattern and channel bed shape. We classified habitats as slow (pools) or fast (riffles, pocket-water, runs, or glides).

Mean depth.-- was calculated by measuring the depth at approximately $1 / 4,1 / 2$, and $3 / 4$ the channel width and dividing the sum by four to account for zero depth at each bank (Platts et al. 1983). Crews also measured the maximum depth at each transect and at the deepest location in the entire unit.

Substrate.-- in a one meter band parallel to the transect, crews estimated the percent of the substrate in four substrate size classes: fines ( $<6 \mathrm{~mm}$ ), gravel ( $6-75 \mathrm{~mm}$ ), cobble ( $75-150$ mm ), and rubble ( $>150 \mathrm{~mm}$ ). Also at each transect, crews sampled 10 substrate particles as follows: They selected 10 evenly spaced locations across the transect. If the stream was too narrow, crews evenly space 5 locations on the transect and 5 more about 1 meter upstream. Crews walked to a location and pointed their index finger on the substrate at the toe of their boot while looking away (Wolman 1954). The first particle touched was measured and recorded by size class.

Bankfull width.-- This is a notoriously difficult variable to measure in streams. There are several indicators commonly used to mark the level of bankfull width within stream channels. Crews were instructed to measure bankfull width at two "representative" locations within each site. Locations were chosen where bankfull width was determined, according to the list of indicators in Harrelson et al. (1994).

Pools.-- In the stream segment between each transect, crews counted the number of pools and measured the length of pools. Pools were defined as either having a length greater than or equal to the wetted channel width, or occupying the entire wetted width. Crews recorded the dominant pool-forming feature in the unit: boulder, large wood, meander, bedrock, beaver, artificial, or other (described).

Large Wood.-- In the stream segment between each transect crews counted the number of pieces of large woody debris (LWD). LWD was defined as a piece of wood, lying above or within the active channel, at least 3 m long by 10 cm in diameter. Crews also recorded the number of large aggregates (more than four single pieces acting as a single component) and rootwads.

Cover Components.-- Crews measured the total length of the unit from the lower to the upper block net by summing the number of transects and adding the length of the final segment. For the entire unit, crews estimated the percent cover for each of four cover types (submerged, turbulent, overhead, undercut). Crews measured the length and average width of undercut and overhanging vegetation along each bank and recorded it. Overhead cover within 0.5 m of the water surface was included. Crews estimated (to the nearest $10 \%$ ), the percent of the reach that had turbulence and submerged cover. Turbulence develops where abrupt changes in water velocity occur. Turbulence was typically observed at changes in gradient (riffles), near physical obstructions to flow (LWD or boulders), and along irregular shorelines. Submerged cover included large boulders, bedrock, LWD, etc. Crews classified the contribution of wood to the overall complexity of the unit in one of four classes: 1) Wood contributes little to stream habitat complexity, mostly small ( $10-30 \mathrm{~cm}$, median diameter) single pieces; 2 ) Wood has combinations of single pieces and small accumulations, providing cover and some complex habitat; 3) Wood present with medium (30-50 cm, median diameter) and large ( $>50 \mathrm{~cm}$, median diameter) pieces providing accumulations and debris jams, with good cover and complex habitat within the low
flow channel (during reduced stream discharge in mid-late summer and early fall, the low flow channel is generally equivalent to the active channel); or 4) Wood present as large single pieces, accumulations, and jams that provide good cover and complex habitat at all discharge levels.

Reach Gradient.-- Two methods were applied to estimate gradient: 1) from a topographic map or DEM; and 2) gradient was measured in the field with a hand level as follows. Observer B stood along the bank at the start of the unit and held a survey rod vertically at the waters surface (using a rock to steady the rod). Observer $A$ stood about 25 m upstream and used the level to shoot an elevation on the survey rod. After recording the downstream elevation, observer $B$ moved along the same bank to the 50 m transect in the unit and observer $A$ shot an elevation to that location. These elevations and the unit length were used to calculate gradient. In 100 m units, a second gradient measurement was made and recorded between the 50 m transect and the end of the unit. If channel meanders in a sampling unit prevented sighting 50 m , crews used the level to collect elevations in a many segments as required to estimate the total reach gradient.

### 2.2 RMRS Idaho Crew Protocols

Crews in Idaho applied the identical protocols listed above and in Attachment A. In addition, they tested the precision of measuring stream physical characteristic and the effectiveness of block nets. To test measurement precision, crews initially measured the physical variables immediately after sampling fish. Separate crew members returned to the sampling unit and measured the physical variables a second time. To test the effectiveness of block nets, crews placed two block nets at the ends of each sampling unit. After the completion of biological sampling, the areas between both sets of two nets were electrofished and all fish captured were inspected for marks.

### 2.3 Statistical Analyses

### 2.3.1 Evaluation of habitat measurements

Imprecise or inaccurate habitat measurements could reduce our ability (power) to detect important influences on sampling efficiency and could affect the adequacy of sampling
efficiency models. Thus, we estimated the precision of stream habitat measures for each site sampled according to Snedecor and Cochran (1967) as:

$$
\begin{equation*}
P=\sqrt{\frac{t^{2} C V^{2}}{N}} \tag{1}
\end{equation*}
$$

where $P$ is the precision expressed as a percentage of the mean, $C V$ is the within site coefficient of variation for a habitat measure, $t$ is a constant that varies with confidence level $(t=1.96$ at the $95 \%$ confidence level), and $N$ is the number of measurements taken within a unit (e.g., $N=3$ for visibility estimates). Precision at the $95 \%$ confidence level was only calculated for habitat variables that were estimated via several measurements within a unit (e.g., transect measurements).

We assessed the repeatability of all habitat measurements by (1) calculating the difference between original (measured during calibration) and remeasured estimates and expressing these as a percentage of the original estimates and (2) by examining the consistency of class-level assignments (e.g., wood class rating). Remeasurements were only conducted in Idaho; hence, repeatability could only be assessed for habitat data collected during Idaho calibrations.

### 2.3.2 Evaluation of removal estimates

Because fish length affects the efficiency of many collection methods (Bagenal 1977;
Reynolds 1996), species were placed into 3 total length (TL) size classes prior to analyses: size class $1,70-100 \mathrm{~mm}$; size class $2,100-200 \mathrm{~mm}$; and size class $3 \mathrm{TL}>200 \mathrm{~mm}$.

Fish abundance in each blocked-off section was estimated using two different removal estimators (White et al. 1982). The first assumed a constant capture probability among successive passes (Zippin 1956) and the second allowed for heterogeneity in catchability between pass 1 and subsequent passes (Otis et al. 1978). Size class-specific removal estimates were made using catch data for each size class from sites in Idaho. An insufficient number of fish were collected in Washington streams during 2000 to estimate size class-specific removal estimates. Therefore, removal estimates also were calculated using the combined (summed) catch of all size classes at a site. Goodness-of-fit was assessed for each removal estimate via a chi-square test (White et al. 1982).

We define sampling efficiency as the proportion (or percentage) of fish, in a given area, that are captured or observed during sampling. Thus, we examined the adequacy of the removal technique for estimating bull trout sampling efficiency by estimating the efficiency of each method (snorkeling, electrofishing) two ways. First, sampling efficiencies were estimated by dividing the number of recaptured (resighted) individuals by the number marked. Relative efficiencies then were estimated by dividing the day and night snorkeling counts and electrofishing total catch for 3 passes by the estimate of fish abundance from the best fitting removal model. Because of the very small and unequal numbers of marked fish in Washington streams and its effect on measured sampling efficiency, mean sampling efficiency and $95 \%$ percent confidence intervals were estimated via maximum likelihood (Agresti 1990) for each method by location (i.e., state), species, and size class.

### 2.3.3 Modeling sampling efficiency

The number of recaptured (or resighted) and marked individuals were used as dichotomous dependent variables (i.e., the number of success and trials, respectively) for the beta-binomial regression modeling procedure, described below. Marked individuals captured outside of the sampling unit (i.e., between the second set of blocknets at Idaho sites, described above) were not used for the sampling efficiency modeling (see Evaluation of Procedural Bias, below). Size classes were dummy coded $(0,1)$ for size class 2 and 3 with size class 1 as the baseline. Pearson correlations were run on all pairs of predictor variables (i.e., physical/chemical measurements) prior to analyses. To avoid multicollinearity, predictor variables that were significantly correlated $(\underline{P}<0.1)$ were not used together in the modeling procedure.

We initially fit sampling efficiency models using logistic regression (Agresti 1990). A preliminary examination of the dispersion parameters for logistic regression models indicated that the data were overdispersed (i.e., the variance exceeded the presumed binomial). The excess variance also appeared to be related to the number of marked fish in the site (e.g., Figure 1). The best means of accounting for this type of overdispersion is to use a technique that models the variance as a function of the number of marked individuals (Liang and McCullagh 1993). Betabinomial regression is similar to logistic regression in that it uses dichotomous dependent variables, but differs from it in that variance is modeled as a beta distribution that accounts for extra variance related to the number of marked individuals (Prentice 1986). Thus, we used beta-
binomial regression to examine the influence of physical and chemical variables (Table 1) on sampling efficiency for day and night snorkeling and 3-pass backpack electrofishing in each region (Washington and Idaho).

We used the information-theoretic approach, described by Burnham and Anderson (1998), to evaluate the relative plausibility of beta binomial models relating habitat characteristics and fish body size to sampling efficiency for each method. We began our modeling by constructing a set of candidate logit models based on our observations (Thurow and Schill 1996) and those of other investigators (Riley et al. 1993) that suggest that salmonid sampling efficiency is significantly influenced by habitat characteristics and body size. We also included time after marking in our candidate models to examine effect of previous capture and handling (for marking) on bull trout vulnerability during sampling. The subset of uncorrelated physical and chemical variables and time after marking was used to construct the global model (i.e., model containing all of the predictors). From this model, we constructed a subset of 29 candidate models that contained various combinations of the predictors (contained in the global model). The candidate models were then fit with the beta binomial models. To assess the fit of each candidate model, we calculated Akaike's information criteria (AIC; Akaike 1973) with the small-sample bias adjustment $\left(\mathrm{AIC}_{\mathrm{c}}\right.$; Hurvich and Tsai 1989). AIC is an entropy-based measure used to compare candidate models for the same data (Burnham and Anderson 1998), with the best fitting model having the lowest $\mathrm{AIC}_{\mathrm{c}}$. The relative plausibility of each candidate model was assessed by calculating $\Delta \mathrm{AIC}_{\mathrm{c}}$ weights as described in Burnham and Anderson (1998). These weights can range from 0 to 1 , with the most plausible (i.e., best fitting) candidate model having the greatest $\Delta \mathrm{AIC}_{\mathrm{c}}$ weight.

To incorporate model-selection uncertainty, we computed model-averaged estimates of the model coefficients and their standard errors as described by Buckland et al. (1997) and Burnham and Anderson (1998). Briefly, the coefficients and standard errors from each candidate model were weighed by their associated $\Delta \mathrm{AIC}_{\mathrm{c}}$ weights and summed across models. The ratio of the $\Delta \mathrm{AIC}_{\mathrm{c}}$ weights for 2 candidate models also can be used to assess the evidence for one model over another (Burnham and Anderson 1998). Thus, model-averaged coefficients and standard errors were only calculated for the predictor variables that occurred in one or more candidate models with $\Delta \mathrm{AIC}_{\mathrm{c}}$ weights within $10 \%$ of the largest $\Delta \mathrm{AIC}_{\mathrm{c}}$ weight. Reliability of these model-
averaged predictors was assessed by calculating $95 \%$ confidence intervals based on a $t$-statistic with $n-1$ degrees of freedom. Predictors were considered reliable if the confidence intervals did not contain 0 . All predictor variables were standardized prior to model fitting with a mean $=0$ and standard deviation $=1$ to allow for ease of interpretation and comparison. Beta-binomial regression dispersion parameters were estimated for each method using the global model (Burnham and Anderson 1998). Goodness-of-fit was assessed for each global model by examining residual and normal probability plots (Agresti 1990).

### 2.3.4 Evaluation of model accuracy

Relative bias of the best fitting model for each method, as indicated by the $\Delta \mathrm{AIC}_{c}$ weights (above), was assessed via leave-one-out cross validation. Cross validation estimates are nearly unbiased estimators of out-of-sample model performance (Funkunaga and Kessel 1971) and provide a measure of overall predictive ability without excessive variance (Efron 1983). Hence, they should provide an adequate estimate of the relative bias of the efficiency models. During this procedure, one observation was left out of the data, the beta-binomial model was fit with the remaining $n-1$ observations, and the sampling efficiency for the left out observation was predicted. Error was then estimated as the difference between the predicted and measured (i.e., number recaptured/ number marked) efficiency.

The cross-validation error rates of the sampling efficiency models fit to the state-specific data (i.e., Idaho and Washington) provide an estimate of state-specific model accuracy.

However, we were concerned that the models could be region-specific due to localized physical and chemical characteristics, which would limit their usefulness. Thus, we evaluated the out-ofregion accuracy of the best fitting sampling efficiency models (above) by using the Idaho models to predict the efficiency in Washington streams and vice versa.

### 2.3.5 Evaluation of procedural bias

We were concerned that our sampling efficiency procedures could have biased our sampling efficiency estimates. One such source of bias is the effect of handling on fish behavior and consequently, their vulnerability to capture. We evaluated this possible source of bias by including time after marking in the beta binomial regression above. Another source of bias is the possible effect of fish escape from the blocked-off sites. To examine this the potential influence, we estimated the escape rate using the number of marked fish captured between the second set of
blocknets and the number of marked fish as dichotomous dependent variables. We then fit quasi-likelihood logistic regression models (Bayley 1993) relating escape rate to time after marking and uncorrelated habitat characteristics. We used the information-theoretic approach (outlined above) to evaluate the relative plausibility of various candidate models.

We also examined the possible effects of marking and handling on bull trout sampling efficiency via a cross-comparison method as follows:

Step 1: Estimate sampling efficiency $\left(\pi_{m}\right)$ for each method $(m)$, site combination using the betabinomial efficiency models.
Step 2: Estimate the number of unmarked fish in a site using the method- specific estimates of the number of unmarked fish and the sampling efficiency as:

$$
\begin{equation*}
T_{m}=N_{m} / \pi_{m} \tag{2}
\end{equation*}
$$

where: $T_{m}=$ efficiency adjusted estimate of the number of unmarked bull trout, $\pi_{m}=$ predicted sampling efficiency as a fraction, and $N_{m}=$ the number of unmarked bull trout collected or counted with method $m$.
Step 3: Cross-calculate estimates of the sampling efficiency of each method by dividing the raw (actual) count /catch of unmarked fish by the efficiency adjusted estimates of unmarked fish of the other sampling methods. This results in 3 sampling efficiency estimates per method: (1) the efficiency estimate which is the ratio of recaptured (resighted) to marked individuals and (2-3) two cross-calculated efficiency estimates which are the ratio of the number of unmarked fish counted with that method to the efficiency adjusted estimates of the number of unmarked fish for the other two methods. For example, the two crosscalculated estimates for day snorkeling would be calculated by dividing $N_{d}$ by $T_{n}$ and $T_{e}$, where $N_{d}=$ the number of unmarked bull trout counted during day snorkeling, $T_{n}=$ efficiency adjusted estimate of the number of unmarked bull trout for night snorkeling, and $T_{e}=$ the efficiency adjusted estimate of the number of unmarked bull trout for 3-pass electrofishing.
Each of the three estimates then was averaged across sites and $95 \%$ log-based confidence intervals (Buckland et. al. 1997) calculated to assess the relative accuracy of the methods. Large differences among the three efficiency estimates for each method would indicate that marking/ handling affected the vulnerability of marked fishes differently among methods or through time.

### 3.0 RESULTS

Washington crews initiated sampling in 68 sites in 2000. The complete protocols were applied in 39 sites due to unpredictable problems, such as blocknet failure during intensive rainfall events. There also were difficulties in retaining complete population closure at 3 adjacent sites in which fish marked in one of the three sample units were recaptured in another. To minimize the influence of this potential source of bias, these 3 sites were combined into a single site for analysis. The resulting data consisted of 33 sites in which bull trout were marked, 5 sites with marked brook trout (Salvelinus fontinalis), 11 sites with marked cutthroat trout (Oncorhynchus clarki spp.) and 11 with marked rainbow trout (Oncorhynchus mykiss). Of these salmonids, only bull trout were collected in sufficient number to rigorously evaluate removal estimates and model sampling efficiency. Hence, we focused the analysis of sampling efficiency to bull trout, but provide mean sampling efficiency estimates for the other species collected.

In 1999 and 2000, Idaho crews applied the complete protocols in 43 sites. Bull trout were the target species for these efforts. Consequently, all of the data ( 43 sites) in Idaho were included in the analysis of sampling efficiency.

### 3.1 Regional Contrasts

Washington streams tended to be wider and deeper, with smaller gradients, less wood, and a much smaller percentage of undercut banks than their Idaho counterparts (Table 1). Additionally, Washington streams tended to have greater visibility and lower conductivities. Because many of these factors are believed to influence sampling efficiency, these differences suggest that estimated sampling efficiencies and the influences thereon, are likely to vary among regions.

Regional calibrations also differed substantially in the number of marked fish used during the calibration procedures. In Washington, fewer individuals (mean=8.2) were marked for each calibration. For example, individuals size class $1(70-100 \mathrm{~mm})$ and $3(\geq 200 \mathrm{~mm})$ were marked in 8 and 9 of the 33 calibrations, respectively (Figure 2). In contrast, Idaho calibrations had a much larger number of marked individuals (mean $=27$ ) across size classes (Figure 2). The accuracy and precision of logistic (and beta-binomial) models can be significantly influenced by the number of marked fish. Hence, the Washington data collected to date might be insufficient
for developing robust sampling efficiency models for the relatively unique combinations of habitat characteristics (compared to Idaho).

### 3.2 Evaluation of Habitat Measurements

The evaluation of Idaho habitat measurements indicated that several of the measurements were relatively precise. Width and depth measurements were generally within $20 \%$ of the true value for each site (Table 2). However, the substrate measures were quite variable. For instance, the estimate of fine substrate was only within $75 \%$ of its true value. Among the substrate measures, cobble estimates were the most precise and were, on average, within $39 \%$ of the true values.

Estimates of the number of required transects suggested it was probably not feasible to be within $10 \%$ of the true mean for most habitat measures (Table 2). For example, 80 and 31 transects would be required to be within $10 \%$ of the true means for cobble and mean maximum depth, respectively. However, several on the measures would be within $20 \%$ of the true means with the use of 15-20 transects, including mean wetted width, mean depth, and percent cobble substrate (Table 2).

Examination of the re-measured habitat data from 8 sites in Idaho indicated that some of the measures were fairly reliable, such as length, width, and gradient (both measures), which differed less than $25 \%$ from the original measurements (Table 3). Some measurements, however, were quite variable- particularly the pool measures, undercut banks, and overhanging vegetation, which varied more than $50 \%$ between measurements. The substrate composition and wood density measures fell somewhere in the middle of these two extremes (Table 3). One notable exception was the Wolman count for substrate composition, which tended to be less repeatable when compared to the "visual" estimates of percent substrate composition.

### 3.3 Evaluation of Removal Estimates

Sampling efficiency as estimated from the recapture (resight) of marked individuals differed significantly from estimates calculated relative to removal estimates. On average, relative day snorkeling efficiency estimates were $177 \%$ greater, relative night snorkeling $259 \%$ greater, and 3-pass electrofishing 149\% greater than those estimated via resight of marked fish (Table 5). These differences also were relatively consistent among sites. For example, relative
efficiency of 3-pass electrofishing was estimated to be $163 \%$ and $136 \%$ greater than recapture estimates at Washington and Idaho, respectively (Table 5).

Relative efficiency estimates were very similar to those previously reported for salmonids (e.g., Thurow and Schill 1996). This suggested that our relative efficiency results were not anomalous. Rather, the differences may have been due to potential biases associated with removal estimators. In general, removal estimates can be biased by very low efficiencies, large changes in efficiency among removal passes, and low fish abundance (White et al. 1982). Of these, the estimates of sampling efficiency based on the recapture of marked individuals suggested that sampling efficiency was relatively low on the first sampling pass and dropped significantly in subsequent passes in both Washington and Idaho streams (Figure 3). The drop in efficiency also appeared to have a similar effect across size classes. Interestingly, this is somewhat counter to the current hypothesized mechanisms for heterogeneity among removal passes (see White et al. 1982). Goodness-of-fit tests were designed to detect the potential influence of these factors, but these only indicated lack-of-fit ( $\mathrm{P}<0.1$ ) in $25 \%$ of our removal estimates. However, these tests can be influenced by the same factors that can bias removal estimates. Therefore, we sought to examine the effect that the observed efficiencies (mark and recapture) could have on removal estimates and their goodness-of-fit tests.

To examine the potential biases on removal estimates, we simulated 4-pass removal sampling in which sampling efficiency was identical to that estimated by recapture of marked fish during our study in Idaho, across size classes: $24 \%$ on the first pass, $14 \%$ on the second, $8 \%$ on the third, and $5 \%$ on the fourth. Simulations were conducted with fish abundances set from 10 to 250 by increments of 10 fish (i.e., $10,20,30 \ldots 250$ ) and 1,000 replicates per abundance value. The number of fish captured on each pass was modeled as a binomial variate with a mean equal to the pass-specific sampling efficiency values above.

Simulation results indicated that the constant and heterogeneous removal models consistently overestimated sampling efficiency for all passes (Figure 4). In general, there was a relationship between fish abundance and the size of the bias, which tended to level off at an abundance of 100 or more fish. Between the two models, the generalized removal estimator (heterogeneous efficiency) was the best (Figure 4), but still overestimated 3-pass sampling efficiency (on average) by 44\%. Interestingly, simulated the 3-pass sampling efficiency bias
was similar, but slightly lower then the measured bias for bull trout in both regions (Figure 4). Additionally, the goodness-of-fit tests indicated lack-of-fit ( $\mathrm{P}<0.10$ ) in $28 \%$ of simulations.

Sampling efficiency estimates for brook trout, cutthroat trout, and rainbow trout - based on the recapture of marked fish- were similar to those obtained for bull trout (Table 6). Of these 3 species, brook trout had the greatest day and night snorkeling sampling efficiency on average ( $15.8 \%$ and $42.2 \%$, respectively) and rainbow trout the greatest 3-pass electrofishing efficiency (63.1\%). The 3-pass electrofishing sampling efficiency for all of these species also was well below the recommended $80 \%$ required for adequate removal estimates for small populations (Bohlin 1982). Therefore, removal estimates for these species are likely to be biased under similar sampling conditions.

### 3.4 Modeling Sampling Efficiency

Beta-binomial models of day snorkeling efficiency indicated that the most plausible model for estimating efficiency differed among Washington and Idaho streams. The best model for Washington contained maximum depth, water temperature, visibility, time after marking, and fish size (Table 7), whereas the best Idaho model contained unit length, water temperature, visibility, undercut banks, cobble substrate, and fish size (Table 8). Interestingly, few variables were reliable ( $95 \%$ confidence intervals did not contain zero) for the Washington model compared to the Idaho model. The most notable being fish size, which was relatively precise in the Idaho model but not in the Washington model. Visibility also had a negative effect on day snorkeling efficiency in Washington streams and a small, positive effect in Idaho streams. These differences suggest that the very different sampling conditions in Washington (e.g., much greater visibility) have markedly different influences on sampling efficiency compared to Idaho.

The low AIC weights of the candidate night snorkeling efficiency models for both regions (Washington and Idaho) suggest that no single model best fits the data (Tables 9 and 10). That is, no variables could be completely ruled-out as potential predictors. The most plausible model for Washington streams contained wood density and fish size class. However, none of the coefficients were reliable (Table 9). The best fitting Idaho model contained mean wetted width, visibility, gradient, and fish size class 2 and 3. Among these, mean wetted width and fish size (both classes) had relatively precise coefficients and were negatively and positively related with sampling efficiency, respectively (Table 10).

Similar to night snorkeling, then beta-binomial models for 3-pass electrofishing indicated that no single model best fits the Washington data. Among these models, the model containing conductivity, undercut banks, wood density, and size class fit the data best (Tables 11). None of these variables were reliable enough to base sound inferences. However, the coefficient for mean wetted with was relatively precise and indicated that it was negatively related to 3-pass electrofishing efficiency. In contrast, the Idaho model containing mean wetted width, maximum depth, percent undercut banks, and fish size was the most plausible, given the data (Table 12). Of these predictors, sampling efficiency was negatively related to mean depth and undercut banks, and positively related to fish body size. The coefficient for mean wetted width, however, was relatively imprecise.

### 3.5 Evaluation of Model Accuracy

Cross-validation of the Idaho sampling efficiency models indicated that they were relatively unbiased. For example, the mean difference between predicted and known efficiency was less than $2 \%$ across methods (Table 13). However, cross-validated differences between predicted and known efficiency for Washington streams were $347 \%$ greater. Assuming the threshold densities in Peterson et al. (2001), the Washington sampling efficiency biases would lead to an underestimation of required sample sizes for an $80 \%$ bull trout detection probability of: $47 \%$ for day snorkeling and $31 \%$ for night snorkeling, whereas sample sizes for 3-pass electrofishing would be overestimated by $24 \%$. In addition, the high variability of the differences for Washington and Idaho efficiency models, as indicated by the relatively high root mean square error, suggest that they were somewhat imprecise (Table 13).

Cross- region (state) validation of the Washington and Idaho models indicated that neither could adequately estimate sampling efficiency in the other state. On average, the Idaho model underestimated sampling efficiency for night snorkeling in Washington streams by 13\% and overestimated efficiency of day snorkeling and 3-pass electrofishing by $14 \%$ and $10 \%$, respectively (Table 13). These, in turn, translate into required sample size errors of $46 \%$ (underestimate), 108\% (overestimate), and 35\% (underestimate) for day and night snorkeling and 3-pass electrofishing, respectively. The greater errors for Washington predictions of Idaho efficiency (Table 13) would only lead to greater detection errors. These high error rates indicate
that neither model is should be applied outside the range of conditions under which they were calibrated.

The low cross-validation accuracy of the Washington models and the imprecision of the coefficients, particularly for the well-documented effect of fish length on sampling, suggests that these data are likely not adequate for developing robust sampling efficiency models. High variance influences the ability to statistically detect relationships, can affect the precision of models, and can only be overcome by collecting additional samples. There are several methods for estimating number of samples required to statistically detect an effect of obtain a desired level of precision. To estimate the latter, researchers generally use statistical power tests (Agresti 1990). Statistical power tests of individual predictors in a regression are significantly influenced by presence of other predictors in the model (Table 15); hence, they are conditionally dependent. The model-averaged standard errors from the AIC procedure are conditionally independent (Burnham and Anderson 1998). Thus, they can provide a relatively unbiased index of the number of samples needed to obtain precise estimates of individual regression coefficients.

Using the model-averaged standard errors for each sampling efficiency model (Tables 7 12) and equation (1), we estimated the number of samples needed to obtain regression coefficients with mean values within $20 \%$ on their true means. On average, required sample sizes were quite high and variable among coefficients (Table 15). In Washington streams, average sample size requirements for day snorkeling, night snorkeling, and 3-pass electrofishing were 699,182 , and 229 , respectively, whereas they were 46,105 , and 7080 , respectively for Idaho streams. Interestingly, the largest estimated sample sizes were for variables known to have significant effects of sampling efficiency. For example, 951 samples would need to be collected from Washington streams to obtain a coefficient for size class 2 that is within $20 \%$ of the true value.

### 3.6 Evaluation of Procedural Bias

The quasi-likelihood logistic regression model of escape rate to recovery time indicated the best fitting model contained only time after marking (Table 16). However, none of the variables were statistically significant $(\mathrm{P}<0.05)$. The best fitting model predicted that, on average, the escape rates at 24,48 and 72 hours are $0.7 \%, 2.0 \%$ and $5.0 \%$, respectively, which translates to less than 1 marked fish in the 24 hour ( 0.03 individuals) and 48 hour ( 0.62 ) recovery
times and approximately 1 fish in the 72 hour period. Thus, it is unlikely that escaping individuals had a large effect on the sampling efficiency estimates, especially considering that marked individuals that had escaped were not included in the Idaho sampling efficiency modeling (above).

The cross-comparison of the 3 sampling efficiency estimates for all methods indicated that they were similar to the mark-recapture (resight) estimates (Figure 5). In fact, all were well within the $95 \%$ CI of the all of the mark-recapture based estimates. This suggested that either there was no detectable effect of marking on bull trout vulnerability or that this effect did not differ among methods or through time.

### 4.0 DISCUSSION

The bull trout sampling efficiencies in Washington and Idaho, as estimated from the recapture of marked individuals, were substantially lower than previously reported (e.g., Thurow and Schill 1996 and references therein). However, our electrofishing efficiency estimates were similar to those reported for several warmwater species (Mahon 1980; Bayley and Dowling 1993). These discrepancies were likely a result of the use of bull trout removal estimates as the baseline for estimating the efficiency of electrofishing and snorkeling methods for previous studies (Thurow and Schill 1996) in contrast to the use of known (true) abundances for this study and the warmwater studies. Indeed, removal simulations suggested that, on average, estimated 3-pass efficiency would be positively biased $45 \%$, which was similar to the observed bias of $49 \%$ and $53 \%$ for Washington and Idaho, respectively. The positive bias in removal sampling efficiency estimates would result in underestimates of "true" fish abundance and hence, positively biased estimates of snorkeling efficiency. The simulation results also suggest that goodness-of-fit tests were very poor indicators of badly fitting removal estimates, particularly when fish abundances are low (White et al. 1982). Thus, they are probably useless for detecting biased removal estimates. To avoid biased sampling efficiency estimates, we suggest that future efforts use known numbers of fish as the baseline for estimating sampling efficiency for all methods.

Although bull trout sampling efficiency was similar (on average) in Washington and Idaho streams, the influences thereon differed between regions. For example, visibility was
positively related to day snorkeling efficiency in Idaho and negatively related in Washington. These differences also caused the low cross-region prediction accuracy of the sampling efficiency models and were likely due to the different conditions under which each method was calibrated. For example, the much greater visibility in Washington streams may have allowed fish to detect and flee from divers at longer distances and thereby lowered the efficiency. In contrast, the lower visibility in Idaho streams may have prevented divers from seeing (and counting) fish, so that efficiency was greater at moderate visibility (compared to Washington). The adequacy of any predictive model depends upon the range and combinations of conditions under which the model was parameterized. Thus, the differences in sampling conditions between regions and the low cross-region accuracy indicate that Idaho models are probably inadequate for predicting sampling efficiency and determining sample sizes for detecting bull trout in Washington streams.

The forgoing discussion illustrates the need to calibrate sampling efficiency models under conditions that are representative of those encountered during normal sampling. For example, shaded sections in Figure 6 show the various combinations of undercut banks and gradient and conductivity for which current sampling efficiency models (Washington and Idaho) should not be applied. The degree to which the combinations of habitat characteristics in the Washington data represent the universe of sampling conditions could not be ascertained due to the lack of readily available data. Therefore, we recommend evaluating the universe of sampling conditions encountered in Washington streams and develop strata to base future sampling efficiency studies.

The accuracy of the Washington models was also relatively low compared to the Idaho models. Indeed, the cross-validation procedure suggest that sampling efficiency and required sample size estimates for bull trout detection would be consistently underestimated for day and night snorkeling and overestimated for electrofishing. The relatively poor performance of the Washington models was probably due in part to low statistical power and precision. Ten fewer sites were collected in Washington (compared to Idaho) and the number of individuals marked per site was approximately $1 / 3$ of that in Idaho streams. The effect of sample size on power and precision is well known (Snedecor and Cochran 1967) and will not be covered here. Much less known is the influence of the number of marked fish (i.e., size of the binomial index) has on the
power and precision of logistic regression (e.g., Figure 7). To illustrate, assume that sampling efficiency for a fish species is $33 \%$. If a single fish is marked for each calibration, the fish is either captured or not (i.e., measured efficiency is $0 \%$ or $100 \%$ ). Therefore, it would take (on average) three calibrations to determine the correct sampling efficiency, $33 \%=(0 \%+0 \%+$ $100 \%) / 3$. If three fish were marked, we would expect (on average) to capture one on each calibration $(1 / 3=33 \%)$. Thus, it would take one calibration to correctly estimate efficiency when three fish are marked versus three calibrations when one fish is marked. To increase the accuracy of sampling efficiency models in Washington streams, we suggest conducting more calibrations and marking a greater number of individuals per calibration. We further recommend that field personnel attempt to mark at least 20 individuals with a minimum of 5 per size class for each calibration.

The power of statistical modeling and precision of sampling efficiency models is also influenced by the accuracy of the field-measured variables. During our modeling, we attempted to use only data that could be estimated with at least $35 \%$ precision. The only exception being percent undercut banks, which had a very low repeatability but was an important predictor in the Idaho model. Nonetheless, attempts should be made to increase the precision of habitat measurements by collecting additional samples per calibration. Our estimates of the number of required transects suggest that only feasible level of precision would be $20 \%$, which would require 15-20 transects. In addition, Wolman counts of substrate composition were relatively imprecise and less repeatable when compared to the "visual" estimates of percent substrate composition. Given that Wolman counts are generally more time consuming (and expensive) to collect, we suggest that future sampling efficiency efforts use visual substrate estimates. Finally, the class-level assignments wood class rating and dominant habitat type differed $63 \%$ among measurements. These types of subjective assignments are generally difficult to repeat and have low accuracy (e.g., Roper and Scarnecchia. 1995); hence we recommend that future studies refrain from using class-level assignments.

### 5.0 SUMMARY

Results of this research indicate that sampling efficiency for bull trout is much lower than previously reported. This was likely a result of the use of biased removal estimates in previous sampling efficiency studies. Sampling efficiency in Washington streams was similar to that in Idaho streams and averaged $12.5 \%$ for day snorkeling, $27.5 \%$ for night snorkeling and $30.0 \%$ for 3-pass electrofishing. However, the effect of physical and chemical variables on efficiency differed among States, which resulted in low predictive ability of Idaho models when applied to streams in Washington and vice versa. The predictive accuracy of Washington sampling efficiency models were also relatively low due to small sample sizes and fewer numbers of fish marked per calibration. These results indicate that the Idaho models are likely not be adequate for estimating sampling efficiency in Washington streams and that current Washington models are relatively inaccurate and possibly biased. We recommend future bull trout sampling efforts in Washington seek to model sampling efficiency with a larger number of samples and more marked fish. Sampling efficiency models must be calibrated under conditions in which normal sampling will be conducted. Thus, we further recommend that future sampling efficiency work in Washington also seek to determine the sampling universe and develop strata to ensure a more thorough coverage of the range of conditions.

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Table 1. Means, coefficients of variation (CV), and ranges of stream habitat measurements and other predictors, by region (ID = Idaho, WA = Washington). Predictors with abbreviations (Abbr.) were uncorrelated and were used in the candidate sampling efficiency models.

| Predictor | Abbr. | Mean |  | CV |  | Range |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | WA | ID | WA | ID | WA | ID |
| Unit elevation (m) |  | 900.95 | 2095.77 | 0.378 | 0.123 | 169-1425 | 1774-2450 |
| Unit length (m) | Unit_Lng | 104.60 | 81.97 | 0.517 | 0.263 | 44-301 | 36-134 |
| Bankfull width (m) | Bfwid | 12.01 | 5.24 | 0.505 | 0.313 | 0.2-31.3 | 3.0-10.5 |
| Mean wetted width (m) | Mwid | 6.41 | 3.44 | 0.282 | 0.290 | 3.5-10.3 | $2.3-7.4$ |
| Mean depth (m) | Mdep | 0.22 | 0.14 | 0.259 | 0.304 | 0.1-0.4 | 0.1-0.2 |
| Mean maximum depth (m) |  | 0.36 | 0.27 | 0.211 | 0.290 | 0.2-0.5 | 0.1-0.4 |
| Field measured gradient (\%) | Reach_Gr | 3.18 | 4.32 | 0.664 | 0.364 | 0.5-8.8 | 2.2-7.3 |
| Channel entrenchment |  | 2.03 | 2.32 | 0.310 | 0.354 | 1-3 | 1-3 |
| Mean water temperature ( $\left.{ }^{0} \mathrm{C}\right)$ | Mwt | 9.08 | 9.17 | 0.244 | 0.262 | 4.5-13.8 | 3.0-13.5 |
| Mean visibility- day (m) | Mvsbd | 3.54 | 2.23 | 0.243 | 0.282 | 2.0-5.0 | 1.1-3.4 |
| - night | Mvsbn | - | 2.31 | - | 0.19 | - | 0.4-1.0 |
| Conductivity ( $\mu \mathrm{ohms}$ ) | Conduct | 41.79 | 57.96 | 0.657 | 0.832 | 9-77 | 16-203 |
| \% Surface turbulence |  | 24.88 | 21.21 | 0.807 | 0.447 | 4-75 | 2-40 |
| \% Submerged cover |  | 27.14 | 25.16 | 0.749 | 0.576 | 5-85 | 5-80 |
| \% undercut banks | Pctuct | 0.88 | 27.96 | 1.598 | 0.747 | 0-7 | 3-93 |
| \% overhanging vegetation |  | 1.69 | 45.78 | 1.207 | 0.576 | 0-7 | 5-98 |
| Wood class rating* |  | 2.54 | 3.11 | 0.480 | 0.370 | 1-4 | 1-4 |
| Wood density (no./m2) | Denlwd | 0.04 | 0.09 | 1.243 | 0.766 | 0.01-0.21 | 0.01-0.30 |
| \% fine |  | 9.54 | 16.82 | 1.129 | 0.581 | 0-40 | 2-36 |
| \% gravel |  | 25.91 | 21.85 | 0.506 | 0.556 | 6-50 | 6-61 |
| \% cobble | Pctcobb | 32.56 | 25.37 | 0.273 | 0.336 | 17-47 | 5-44 |
| \% rubble |  | 32.04 | 35.96 | 0.699 | 0.510 | 1-76 | 1-78 |
| Number of habitat types |  | 1.78 | 2.33 | 0.803 | 0.348 | 1-9 | 1-4 |
| Total pool lengths (m) |  | 9.40 | 6.49 | 0.913 | 1.019 | 0-40 | 0-24 |
| \% pools |  | 10.43 | 8.18 | 0.918 | 1.050 | 0-40 | 0-34 |
| Voltage (electrofishing) |  | 563.63 | 497.67 | 0.523 | 0.069 | 100-1000 | 400-600 |
| Time after marking fish (h) | Timafmrk | 24.57 | 31.81 | 0.118 | 0.457 | 21-39 | 24-72 |

Table 2. Mean, standard deviation, and range of the precision of site-specific habitat measurements expressed as a percentage of the true mean and mean number of transects needed to be measured at each site to be within 30,20 , and $10 \%$ of the true means at the $95 \%$ confidence level ( $\mathrm{N}=43$ sample units).

| Predictor | $\underline{\text { Mean }}$ |  | $\underline{\text { SD }}$ |  | Range |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Mean wetted width | 19.9 |  | 7.05 |  | $8-35$ |  |
| 3 |  | $\frac{20 \%}{5}$ | $\frac{10 \%}{21}$ |  |  |  |
| Bankfull width | 11.15 | 7.43 | $3-21$ | 2 | 2 | 7 |
| Mean maximum depth | 23.78 | 12.52 | $5-52$ | 4 | 8 | 31 |
| Mean depth | 19.9 | 7.05 | $8-35$ | 3 | 5 | 21 |
| \% fine | 75.14 | 39.27 | $27-196$ | 34 | 76 | 302 |
| \% gravel | 48.16 | 24.25 | $13-118$ | 14 | 30 | 123 |
| \% cobble | 39.6 | 20.38 | $11-101$ | 9 | 20 | 80 |
| \% rubble | 52.14 | 34.2 | $15-142$ | 16 | 36 | 147 |
|  |  |  |  |  |  |  |

Table 3. Percent difference between original and resurvey habitat measurements for Idaho streams ( $\mathrm{N}=8$ sample units).

| Predictor | Mean | $\underline{\text { SD }}$ | Range |
| :--- | :---: | :---: | :---: |
| Unit length | 3 | 4 | $0-11$ |
| Bankfull width | 13 | 15 | $2-49$ |
| Mean wetted width | 13 | 13 | $1-42$ |
| Mean depth | 21 | 9 | $6-35$ |
| Mean maximum depth | 21 | 13 | $3-42$ |
| Field measured gradient | 9 | 7 | $3-21$ |
| Conductivity | 8 | 7 | $0-21$ |
| \% Submerged cover | 39 | 28 | $0-100$ |
| \% Surface turbulence | 48 | 38 | $0-100$ |
| \% undercut banks | 126 | 82 | $28-200$ |
| \% overhanging vegetation | 93 | 71 | $27-200$ |
| Wood density | 40 | 24 | $11-77$ |
| \% fine | 46 | 41 | $11-123$ |
| \% gravel | 50 | 21 | $29-90$ |
| \% cobble | 38 | 32 | $7-92$ |
| \% rubble | 33 | 31 | $11-86$ |
| Wolman count $\quad<8 \mathrm{~mm}$ | 85 | 60 | $21-200$ |
| Wolman count $\quad 8-15 \mathrm{~mm}$ | 131 | 78 | $4-200$ |
| Wolman count $16-32 \mathrm{~mm}$ | 63 | 44 | $0-145$ |
| Wolman count $33-63 \mathrm{~mm}$ | 85 | 83 | $0-200$ |
| Wolman count $64-127 \mathrm{~mm}$ | 43 | 36 | $0-103$ |
| Wolman count $128-255 \mathrm{~mm}$ | 39 | 32 | $0-100$ |
| Wolman count $>256 \mathrm{~mm}$ | 35 | 25 | $9-80$ |
| Number of habitat types | 30 | 28 | $0-67$ |
| Total pool lengths | 58 | 67 | $3-200$ |
| \% pools | 57 | 68 | $3-200$ |
|  |  |  |  |

Table 4. Variability of class-level assignments for 8 remeasured sample units in Idaho.

| Predictor | \% Agreement |  | \% Error |
| :--- | :---: | :---: | :---: |
|  |  | 38 |  |
| Wood class rating | 100 |  | 63 |
| Reach type | 50 |  | 50 |
| Channel entrenchment | 75 |  | 25 |

Dominant habitat type 38

Table 5. Mean sampling efficiency estimates and $95 \%$ confidence limits (CL) based on the recapture of marked individuals and relative to removal estimates, by location, method, and size class. Removal estimates were calculated using the generalized removal estimator (White et al. 1987).


[^0]${ }^{2}$ Size class 1 estimate based on the recapture of a single marked individual on 2 occasions.

Table 6. Mean sampling efficiency estimates and $95 \%$ confidence limits (in parenthesis) for brook trout, cutthroat trout, and rainbow trout based on the recapture of marked individuals

Size class (mm) Day snorkeling Night snorkeling 3-pass electrofishing

## Brook trout (N=5)

$70-100 \quad 0.010(0.000-1.000) \quad 0.667(0.154-0.957) \quad 0.250(0.034-0.762)$
$100-200 \quad 0.063(0.009-0.335) \quad 0.375(0.179-0.623) \quad 0.118(0.030-0.368)$
$\geq 200$
ALL 0.158 (0.052-0.392) 0.421 (0.226-0.644) 0.143 (0.047-0.361)

## Cutthroat trout ( $\mathbf{N}=11$ )

| $70-100$ | $0.010(0.000-1.000)$ | $0.010(0.000-1.000)$ | $0.077(0.011-0.391)$ |
| ---: | :--- | :--- | :--- | :--- |
| $100-200$ | $0.186(0.096-0.330)$ | $0.395(0.262-0.546)$ | $0.333(0.215-0.477)$ |
| $\geq 200$ | $\underline{0.071(0.010-0.370)}$ | $\underline{0.214(0.071-0.494)}$ | $\underline{0.109(0.053-0.212)}$ |
| ALL | $0.122(0.065-0.218)$ | $0.297(0.204-0.411)$ | $0.308(0.216-0.418)$ |

## Rainbow trout ( $\mathbf{N}=11$ )

| $70-100$ | $0.100(0.025-0.324)$ | $0.765(0.514-0.909)$ | $0.300(0.141-0.527)$ |
| ---: | :--- | :--- | :--- |
| $100-200$ | $0.049(0.028-0.084)$ | $0.255(0.205-0.313)$ | $0.636(0.574-0.693)$ |
| $\geq 200$ | $\underline{0.000(0.000-0.000)}$ | $\underline{0.182(0.046-0.507)}$ | $\underline{0.204(0.117-0.332)}$ |
| ALL | $0.086(0.058-0.125)$ | $0.348(0.294-0.405)$ | $0.631(0.573-0.685)$ |

Table 7. Predictor variables, AICc, $\Delta \mathrm{AICc}, \Delta \mathrm{AICc}$ weights ( $w$ ) for the set of candidate models (i) and model-averaged estimates of beta-binomial regression coefficients and upper and lower $95 \%$ confidence limits (bottom) for day snorkeling sampling efficiency for bull trout in Washington streams. $\triangle \mathrm{AICc}$ weights are interpreted as relative plausibility of candidate models. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | AICc | $\triangle \mathrm{AICc}$ | $\underline{w}_{i}$ |
| :---: | :---: | :---: | :---: |
| Mmaxd Mwt Mvsbd Timafmrk Size2 Size3 | 97.27 | 0.00 | 0.228 |
| Mvsbd Timafmrk Size2 Size3 | 97.88 | 0.61 | 0.168 |
| Mvsbd Mwt Reach_Gr Denlwd Size2 Size3 | 98.72 | 1.45 | 0.110 |
| Mvsbd Denlwd Size2 Size3 | 99.16 | 1.90 | 0.088 |
| Mwt Mvsbd Denlwd Size2 Size3 | 99.52 | 2.25 | 0.074 |
| Mwt Mvsbd Timafmrk Size2 Size3 | 99.96 | 2.69 | 0.059 |
| Mvsbd Size2 Size3 | 100.12 | 2.85 | 0.055 |
| Mwid Mmaxd Mvsbd Size2 Size3 | 100.33 | 3.06 | 0.049 |
| Mwt Mvsbd Size2 Size3 | 100.81 | 3.54 | 0.039 |
| Mvsbd Pctuct Size2 Size3 | 101.36 | 4.09 | 0.029 |
| Mwt Mvsbd Pctcobb Size2 Size3 | 102.11 | 4.85 | 0.020 |
| Mwt Mvsbd Pctuct Size2 Size3 | 102.40 | 5.13 | 0.017 |
| Mwid Size2 Size3 | 103.71 | 6.44 | 0.009 |
| Mwt Mvsbd Pctuct Pctcobb Denlwd Size2 Size 3 | 103.73 | 6.46 | 0.009 |
| Unit_Lng Mwt Mvsbd Pctcobb Size2 Size3 | 103.92 | 6.65 | 0.008 |
| Unit_Lng Mwid Mmaxd Mwt Mvsbd Size2 Size3 | 103.94 | 6.67 | 0.008 |
| Mwid Mmaxd Reach_Gr Size2 Size3 | 104.52 | 7.25 | 0.006 |
| Mwid Mmaxd Pctcobb Size2 Size3 | 105.36 | 8.09 | 0.004 |
| Unit_Lng Mwid Size2 Size3 | 105.51 | 8.24 | 0.004 |
| Unit_Lng Mwt Mvsbd Pctuct Pctcobb Size2 Size3 | 105.76 | 8.50 | 0.003 |
| Unit_Lng Mwid Mmaxd Size2 Size3 | 106.05 | 8.79 | 0.003 |
| Mwid Mmaxd Denlwd Size2 Size3 | 106.16 | 8.89 | 0.003 |
| Mwid Mmaxd Reach_Gr Mwt Mvsbd Pctuct Pctcobb Size2 |  |  |  |
| Size3 | 106.42 | 9.15 | 0.002 |
| Unit_Lng Mwid Mmaxd Reach_Gr Mwt Mvsbd Pctuct Pctcobb |  |  |  |
| Denlwd Timafmrk Size2 Size3 | 106.42 | 9.16 | 0.002 |
| Mwid Mmaxd Pctuct Pctcobb Denlwd Timafmr Size2 Size3 | 106.92 | 9.66 | 0.002 |
| Size2 Size3 | 113.68 | 16.41 | 0.000 |
| Pctuct Size2 Size3 | 115.16 | 17.89 | 0.000 |
| Denlwd Size2 Size3 | 115.28 | 18.01 | 0.000 |
| Mwt Size2 Size3 | 115.49 | 18.22 | 0.000 |
| Mmaxd Pctuct Pctcobb Denlwd Size2 Size3 | 119.75 | 22.48 | 0.000 |

Table 7. continued

|  |  | Upper <br> Parameter |  | Lower <br> Estimate |
| :--- | ---: | ---: | ---: | ---: |
|  | $\underline{95 \% \mathrm{CL}}$ | $\underline{95 \% \mathrm{CL}}$ |  |  |
| Intercept | -0.513 | 6.890 | -7.915 |  |
| Mwid | 0.315 | 0.789 | -0.160 |  |
| Mmaxd | -10.428 | -0.162 | -20.693 |  |
| Reach_Gr | -0.329 | 0.021 | -0.680 |  |
| Mwt | -0.081 | 0.177 | -0.338 |  |
| Mvsbd | -5.442 | -2.083 | -8.801 |  |
| Pctuct | -0.139 | 0.519 | -0.798 |  |
| Denlwd | -16.075 | 3.930 | -36.079 |  |
| Timafmrk | 0.236 | 0.456 | 0.016 |  |
| Size2 | 0.332 | 2.377 | -1.714 |  |
| Size3 | 0.535 | 2.989 | -1.919 |  |

Table 8. Predictor variables, AICc, $\Delta \mathrm{AICc}, \Delta \mathrm{AICc}$ weights ( $w$ ) for the set of candidate models (i) and model-averaged estimates of beta-binomial regression coefficients and upper and lower 95\% confidence limits (bottom) for day snorkeling sampling efficiency for bull trout in Idaho streams. $\triangle \mathrm{AICc}$ weights are interpreted as relative plausibility of candidate models. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | AICc | $\triangle \mathrm{AICc}$ | $\underline{w}$ |
| :---: | :---: | :---: | :---: |
| Unit_Lng Mwt Mvsbd Pctuct Pctcobb Size2 Size3 | 569.40 | 0.00 | 0.645 |
| Unit_Lng Mwt Mvsbd Pctcobb Size2 Size3 | 571.82 | 2.42 | 0.193 |
| Unit_Lng Mwid Mmaxd Reach_Gr Mwt Mvsbd Pctuct Pctcobb |  |  |  |
| Denlwd Timafmrk Size2 Size3 | 573.04 | 3.64 | 0.105 |
| Mwt Mvsbd Pctcobb Size2 Size3 | 577.42 | 8.01 | 0.012 |
| Mwt Mvsbd Pctuct Pctcobb Denlwd Size2 Size3 | 577.43 | 8.03 | 0.012 |
| Mwid Mmaxd Reach_Gr Mwt Mvsbd Pctuct Pctcobb Size2 |  |  |  |
| Size3 | 577.65 | 8.25 | 0.010 |
| Mwt Size2 Size3 | 578.35 | 8.94 | 0.007 |
| Mwt Mvsbd Denlwd Size2 Size3 | 579.11 | 9.71 | 0.005 |
| Mwt Mvsbd Size2 Size3 | 580.31 | 10.91 | 0.003 |
| Mvsbd Mwt Reach_Gr Denlwd Size2 Size3 | 580.75 | 11.34 | 0.002 |
| Unit_Lng Mwid Mmaxd Mwt Mvsbd Size2 Size | 581.49 | 12.09 | 0.002 |
| Mwt Mvsbd Pctuct Size2 Size3 | 581.79 | 12.38 | 0.001 |
| Mwt Mvsbd Timafmrk Size2 Size3 | 582.08 | 12.67 | 0.001 |
| Mmaxd Mwt Mvsbd Timafmrk Size2 Size3 | 583.65 | 14.24 | 0.001 |
| Mwid Mmaxd Pctcobb Size2 Size3 | 584.31 | 14.90 | 0.000 |
| Size2 Size3 | 585.50 | 16.10 | 0.000 |
| Mwid Size2 Size3 | 585.63 | 16.22 | 0.000 |
| Mmaxd Pctuct Pctcobb Denlwd Size2 Size3 | 586.16 | 16.76 | 0.000 |
| Mvsbd Size2 Size3 | 586.24 | 16.83 | 0.000 |
| Unit_Lng Mwid Size2 Size3 | 586.40 | 17.00 | 0.000 |
| Mwid Mmaxd Mvsbd Size2 Size3 | 586.80 | 17.40 | 0.000 |
| Denlwd Size2 Size3 | 587.39 | 17.99 | 0.000 |
| Pctuct Size2 Size3 | 587.43 | 18.03 | 0.000 |
| Mvsbd Denlwd Size2 Size3 | 588.10 | 18.70 | 0.000 |
| Mvsbd Pctuct Size2 Size3 | 588.19 | 18.79 | 0.000 |
| Mvsbd Timafmrk Size2 Size3 | 588.20 | 18.80 | 0.000 |
| Unit_Lng Mwid Mmaxd Size2 Size3 | 588.36 | 18.96 | 0.000 |
| Mwid Mmaxd Reach_Gr Size2 Size3 | 588.73 | 19.33 | 0.000 |
| Mwid Mmaxd Denlwd Size2 Size3 | 588.80 | 19.40 | 0.000 |
| Mwid Mmaxd Pctuct Pctcobb Denlwd Timafmrk Size2 Size3 | 588.98 | 19.58 | 0.000 |

Table 8. continued

|  | Upper <br> Parameter |  | Lower |  |
| :--- | ---: | ---: | ---: | :---: |
| Intercept | Estimate | 95\% CL | $95 \% \mathrm{CL}$ |  |
| Unit_Lng | -2.558 | -2.064 | -3.052 |  |
| Mwid | 0.486 | 0.806 | 0.166 |  |
| Mmaxd | -0.371 | -0.016 | -0.726 |  |
| Reach_Gr | 0.075 | 0.348 | -0.199 |  |
| Mwt | -0.287 | 0.011 | -0.585 |  |
| Mvsbd | 0.380 | 0.641 | 0.118 |  |
| Pctuct | 0.214 | 0.464 | -0.035 |  |
| Pctcobb | -0.256 | -0.010 | -0.503 |  |
| Denlwd | 0.400 | 0.652 | 0.148 |  |
| Timafmrk | -0.330 | 0.053 | -0.714 |  |
| Size2 | 0.323 | 0.710 | -0.063 |  |
| Size3 | 0.943 | 1.582 | 0.304 |  |
|  | 1.441 | 2.069 | 0.813 |  |

Table 9. Predictor variables, AICc, $\Delta \mathrm{AICc}, \Delta \mathrm{AICc}$ weights ( $w$ ) for the set of candidate models ( $i$ ) and model-averaged estimates of beta-binomial regression coefficients and upper and lower $95 \%$ confidence limits (bottom) for night snorkeling sampling efficiency for bull trout in Washington streams. $\triangle \mathrm{AICc}$ weights are interpreted as relative plausibility of candidate models. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | AICc | $\underline{\triangle A I C c}$ | $\underline{W}_{\underline{i}}$ |
| :---: | :---: | :---: | :---: |
| Denlwd Size2 Size3 | 223.92 | 0.00 | 0.194 |
| Mvsbn Pctuct Size2 Size3 | 225.18 | 1.26 | 0.103 |
| Pctuct Size2 Size3 | 225.38 | 1.47 | 0.093 |
| Mvsbn Size2 Size3 | 225.80 | 1.89 | 0.076 |
| Mwid Mmaxd Denlwd Size2 Size3 | 226.14 | 2.23 | 0.064 |
| Size2 Size3 | 226.60 | 2.69 | 0.051 |
| Mwid Mmaxd Mvsbn Size2 Size3 | 226.87 | 2.95 | 0.044 |
| Mwt Size2 Size3 | 227.30 | 3.39 | 0.036 |
| Mwid Mmaxd Reach_Gr Size2 Size3 | 227.48 | 3.56 | 0.033 |
| Mvsbn Timafmrk Size2 Size3 | 227.50 | 3.58 | 0.032 |
| Reach_Gr Size2 Size3 | 227.51 | 3.59 | 0.032 |
| Mwt Mvsbn Pctuct Size2 Size3 | 227.55 | 3.63 | 0.032 |
| Mvsbn Reach_Gr Size2 Size3 | 227.61 | 3.69 | 0.031 |
| Mwt Mvsbn Size2 Size3 | 227.78 | 3.86 | 0.028 |
| Unit_Lng Size2 Size3 | 227.88 | 3.96 | 0.027 |
| Mwid Size2 Size3 | 228.06 | 4.15 | 0.024 |
| Unit_Lng Mwid Mmaxd Size2 Size3 | 228.86 | 4.94 | 0.016 |
| Mwt Mvsbn Timafmrk Size2 Size3 | 229.10 | 5.18 | 0.015 |
| Mwid Mmaxd Pctcobb Size2 Size3 | 229.10 | 5.18 | 0.015 |
| Mwid Mvsbn Reach_Gr Size2 Size3 | 229.58 | 5.66 | 0.011 |
| Mwid Mvsbn Reach_Gr Denlwd Size2 Size3 | 229.77 | 5.86 | 0.010 |
| Mwt Mvsbn Pctcobb Size2 Size3 | 230.14 | 6.22 | 0.009 |
| Mmaxd Mwt Mvsbn Timafmrk Size2 Size3 | 230.26 | 6.34 | 0.008 |
| Unit_Lng Mwid Mmaxd Mwt Mvsbn Size2 Size3 | 231.74 | 7.83 | 0.004 |
| Mwt Mvsbn Pctuct Pctcobb Denlwd Size2 Size3 | 231.81 | 7.89 | 0.004 |
| Unit_Lng Mwt Mvsbn Pctcobb Size2 Size3 | 232.19 | 8.28 | 0.003 |
| Unit_Lng Mwt Mvsbn Pctuct Pctcobb Size2 Size3 | 232.36 | 8.45 | 0.003 |
| Mwid Mmaxd Pctuct Pctcobb Denlwd Timafmr Size2 Size3 | 232.55 | 8.64 | 0.003 |
| Mwid Mmaxd Reach_Gr Mwt Mvsbn Pctuct Pctcobb Size2 |  |  |  |
| Size3 | 238.65 | 14.74 | 0.000 |

Unit_Lng Mwid Mmaxd Reach_Gr Mwt Mvsbn Pctuct
$\begin{array}{lllll}\text { Pctcobb Denlwd Timafmrk Size2 Size3 } & 244.25 & 20.34 & 0.000\end{array}$

Table 9. continued

| Parameter | Estimate | $\begin{gathered} \text { Upper } \\ 95 \% \mathrm{CL} \end{gathered}$ | Lower 95\% CL |
| :---: | :---: | :---: | :---: |
| Intercept | -2.173 | 0.323 | -4.668 |
| Unit_Lng | 0.003 | 0.009 | -0.004 |
| Mwid | -0.034 | 0.205 | -0.274 |
| Mmaxd | 4.098 | 8.900 | -0.704 |
| Reach_Gr | -0.089 | 0.103 | -0.281 |
| Mwt | 0.061 | 0.273 | -0.151 |
| Mvsbn | -1.370 | 0.463 | -3.203 |
| Pctuct | 0.217 | 0.451 | -0.018 |
| Denlwd | 6.605 | 12.654 | 0.557 |
| Size2 | 1.031 | 2.467 | -0.406 |
| Size3 | 2.017 | 3.639 | 0.395 |

Table 10. Predictor variables, $\mathrm{AICc}, \Delta \mathrm{AICc}, \Delta \mathrm{AICc}$ weights ( $w$ ) for the set of candidate models $(i)$ and model-averaged estimates of beta-binomial regression coefficients and upper and lower $95 \%$ confidence limits (bottom) for night snorkeling sampling efficiency for bull trout in Idaho streams. $\triangle$ AICc weights are interpreted as relative plausibility of candidate models. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | AICc | $\triangle \mathrm{AICc}$ | $\underline{\underline{w}}$ |
| :---: | :---: | :---: | :---: |
| Mwid Mvsbn Reach_Gr Size2 Size3 | 2664.53 | 0.00 | 0.221 |
| Mwid Mmaxd Denlwd Size2 Size3 | 2665.30 | 0.77 | 0.150 |
| Mwid Size2 Size3 | 2665.44 | 0.91 | 0.140 |
| Unit_Lng Mwid Mmaxd Mwt Mvsbn Size2 Size3 | 2665.80 | 1.27 | 0.117 |
| Mwid Mvsbn Reach_Gr Denlwd Size2 Size3 | 2665.84 | 1.31 | 0.115 |
| Mwid Mmaxd Reach_Gr Size2 Size3 | 2666.86 | 2.34 | 0.069 |
| Mwid Mmaxd Mvsbn Size2 Size3 | 2667.04 | 2.51 | 0.063 |
| Unit_Lng Mwid Mmaxd Size2 Size3 | 2667.45 | 2.92 | 0.051 |
| Mwid Mmaxd Pctcobb Size2 Size3 | 2669.57 | 5.04 | 0.018 |
| Mvsbn Reach_Gr Size2 Size3 | 2669.82 | 5.29 | 0.016 |
| Mwid Mmaxd Pctuct Pctcobb Denlwd Timafmrk Size2 Size3 | 2670.85 | 6.32 | 0.009 |
| Mmaxd Mwt Mvsbn Timafmrk Size2 Size3 | 2671.51 | 6.98 | 0.007 |
| Mvsbn Size2 Size3 | 2672.33 | 7.80 | 0.004 |
| Mvsbn Timafmrk Size2 Size3 | 2672.39 | 7.86 | 0.004 |
| Mwid Mmaxd Reach_Gr Mwt Mvsbn Pctuct Pctcobb Size2 |  |  |  |
| Size3 | 2672.73 | 8.20 | 0.004 |
| Mwt Mvsbn Timafmrk Size2 Size3 | 2673.10 | 8.57 | 0.003 |
| Mwt Mvsbn Size2 Size3 | 2673.27 | 8.74 | 0.003 |
| Mvsbn Pctuct Size2 Size3 | 2674.66 | 10.14 | 0.001 |
| Mwt Mvsbn Pctcobb Size2 Size3 | 2674.76 | 10.23 | 0.001 |
| Mwt Mvsbn Pctuct Size2 Size3 | 2675.67 | 11.14 | 0.001 |
| Unit_Lng Mwid Mmaxd Reach_Gr Mwt Mvsbn Pctuct Pctcobb Denlwd Timafmrk Size2 Size3 | 2677.08 | 12.56 | 0.000 |
| Unit_Lng Mwt Mvsbn Pctcobb Size2 Size3 | 2677.54 | 13.01 | 0.000 |
| Unit_Lng Mwt Mvsbn Pctuct Pctcobb Size2 | 2680.25 | 15.72 | 0.000 |
| Mwt Mvsbn Pctuct Pctcobb Denlwd Size2 Size3 | 2680.25 | 15.73 | 0.000 |
| Reach_Gr Size2 Size3 | 2686.72 | 22.19 | 0.000 |
| Pctuct Size2 Size3 | 2687.19 | 22.66 | 0.000 |
| Unit_Lng Size2 Size3 | 2687.88 | 23.36 | 0.000 |
| Mwt Size2 Size3 | 2688.42 | 23.89 | 0.000 |
| Size2 Size3 | 2689.27 | 24.74 | 0.000 |


| Denlwd Size2 Size3 | 2691.81 | 27.29 | 0.000 |
| :--- | :--- | :--- | :--- |

Table 10. continued

| Parameter | Estimate | $\begin{gathered} \hline \text { Upper } \\ 95 \% \mathrm{CL} \\ \hline \end{gathered}$ | Lower $95 \% \mathrm{CL}$ |
| :---: | :---: | :---: | :---: |
| Intercept | -1.004 | -0.841 | -1.167 |
| Unit_Lng | 0.043 | 0.191 | -0.105 |
| Mwid | -0.233 | -0.073 | -0.393 |
| Mmaxd | -0.063 | 0.058 | -0.185 |
| Reach_Gr | 0.088 | 0.193 | -0.018 |
| Mwt | -0.128 | -0.004 | -0.252 |
| Mvsbn | 0.094 | 0.246 | -0.058 |
| Pctuct | 0.026 | 0.151 | -0.099 |
| Denlwd | -0.099 | 0.033 | -0.231 |
| Size2 | 0.676 | 0.884 | 0.469 |
| Size3 | 1.022 | 1.237 | 0.806 |

Table 11. Predictor variables, $\mathrm{AICc}, \Delta \mathrm{AICc}, \Delta \mathrm{AICc}$ weights ( $w$ ) for the set of candidate models ( $i$ ) and model-averaged estimates of beta-binomial regression coefficients and upper and lower $90-95 \%$ confidence limits (bottom) for 3-pass electrofishing sampling efficiency for bull trout in Washington streams. $\Delta \mathrm{AICc}$ weights are interpreted as relative plausibility of candidate models. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | AICc | $\triangle \mathrm{AICc}$ | $\underline{\underline{w}}$ |
| :---: | :---: | :---: | :---: |
| Conduct Pctuct Denlwd Size2 Size3 | 170.31 | 0.00 | 0.114 |
| Mwid Mmaxd Denlwd Conduct Size2 Size3 | 171.16 | 0.84 | 0.075 |
| Pctuct Pctcobb Denlwd Size2 Size3 | 171.22 | 0.90 | 0.073 |
| Conduct Pctuct Size2 Size3 | 171.79 | 1.48 | 0.055 |
| Mwid Mmaxd Denlwd Size2 Size3 | 171.81 | 1.49 | 0.054 |
| Mwid Mmaxd Reach_Gr Size2 Size3 | 171.97 | 1.66 | 0.050 |
| Unit_Lng Mwid Size2 Size3 | 172.02 | 1.71 | 0.049 |
| Mwid Mmaxd Conduct Pct_Surt Size2 Size3 | 172.22 | 1.90 | 0.044 |
| Mwid Mmaxd Conduct Pctuct Denlwd Size2 Size3 | 172.48 | 2.17 | 0.039 |
| Mwid Mmaxd Conduct Pctcobb Size2 Size3 | 172.59 | 2.28 | 0.037 |
| Mwid Mmaxd Conduct Pctuct Size2 Size3 | 172.62 | 2.31 | 0.036 |
| Mwid Mmaxd Conduct Pct_Surt Timafmrk Size2 Size3 | 172.72 | 2.40 | 0.034 |
| Conduct Pctuct Pctcobb Size2 Size3 | 172.97 | 2.66 | 0.030 |
| Timafmrk Size2 Size3 | 173.06 | 2.74 | 0.029 |
| Conduct Pct_Surt Denlwd Size2 Size3 | 173.08 | 2.76 | 0.029 |
| Mmaxd Pctuct Pctcobb Denlwd Size2 Size3 | 173.19 | 2.88 | 0.027 |
| Size2 Size3 | 173.54 | 3.23 | 0.023 |
| Mwid Mmaxd Denlwd Pct_Surt Size2 Size3 | 173.81 | 3.49 | 0.020 |
| Mwid Mmaxd Pctuct Size2 Size3 | 173.88 | 3.57 | 0.019 |
| Unit_Lng Mwid Mmaxd Size2 Size3 | 173.90 | 3.58 | 0.019 |
| Mwt Conduct Pct_Surt Size2 Size3 | 173.97 | 3.66 | 0.018 |
| Mwid Mmaxd Conduct Pctuct Pctcobb Size2 | 174.92 | 4.60 | 0.011 |
| Mwid Mmaxd Reach_Gr Conduct Pct_Surt Den Size2 Size3 | 175.13 | 4.81 | 0.010 |
| Mwid Mmaxd Pctuct Pctcobb Size2 Size3 | 175.28 | 4.97 | 0.010 |
| Mwid Mmaxd Pctuct Pctcobb Denlwd Timafmrk Size2 Size3 | 176.12 | 5.80 | 0.006 |
| Mmaxd Mwt Conduct Pct_Surt Size2 Size3 | 176.17 | 5.85 | 0.006 |
| Unit_Lng Mwid Mmaxd Mwt Conduct Pct_Surt Size2 Size3 | 176.23 | 5.91 | 0.006 |
| Mwid Mmaxd Reach_Gr Mwt Conduct Pct_Surt Size2 Size3 | 182.99 | 12.67 | 0.000 |
| Unit_Lng Mwid Mmaxd Reach_Gr Mwt Conduct Pct_Surt Pctuct Pctcobb Denlwd Timafmrk Size2 Size3 | 184.35 | 14.04 | 0.000 |

Table 11. continued

| Parameter | Estimate | Upper 95\% CL | Lower 95\% CL |
| :---: | :---: | :---: | :---: |
| Intercept | -1.607 | 0.860 | -4.073 |
| Unit_Lng | 0.002 | 0.008 | -0.005 |
| Mwid | -0.234 | -0.006 | -0.461 |
| Mmaxd | 2.686 | 8.006 | -2.634 |
| Reach_Gr | 0.158 | 0.363 | -0.047 |
| Mwt | 0.034 | 0.248 | -0.180 |
| Conduct | 0.015 | 0.028 | 0.001 |
| Pct_Surt | 0.005 | 0.025 | -0.015 |
| Pctuct | 0.276 | 0.852 | -0.300 |
| Pctcobb | -0.028 | 0.021 | -0.078 |
| Denlwd | -10.516 | 4.398 | -25.430 |
| Timafmrk | -1.622 | 0.659 | -3.904 |
| Size2 | 0.750 | 2.159 | -0.659 |
| Size3 | -0.337 | 1.184 | -1.858 |

Table 12. Predictor variables, $\mathrm{AICc}, \Delta \mathrm{AICc}, \Delta \mathrm{AICc}$ weights ( $w$ ) for the set of candidate models ( $i$ ) and model-averaged estimates of beta-binomial regression coefficients and upper and lower $95 \%$ confidence limits (bottom) for 3-pass electrofishing sampling efficiency for bull trout in Idaho streams. $\triangle \mathrm{AICc}$ weights are interpreted as relative plausibility of candidate models. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | AICc | $\triangle \mathrm{AICc}$ | $\underline{\underline{w}}$ |
| :---: | :---: | :---: | :---: |
| Mwid Mmaxd Pctuct Size2 Size3 | 759.76 | 0.00 | 0.410 |
| Mwid Mmaxd Conduct Pctuct Size2 Size3 | 761.63 | 1.87 | 0.161 |
| Mwid Mmaxd Pctuct Pctcobb Size2 Size3 | 761.66 | 1.90 | 0.159 |
| Mwid Mmaxd Conduct Pctuct Denlwd Size2 S | 763.37 | 3.61 | 0.068 |
| Mwid Mmaxd Conduct Pctuct Pctcobb Size2 | 763.58 | 3.82 | 0.061 |
| Mmaxd Pctuct Pctcobb Denlwd Size2 Size3 | 763.64 | 3.88 | 0.059 |
| Mwid Mmaxd Pctuct Pctcobb Denlwd Timafmr Size2 Size3 | 765.27 | 5.50 | 0.026 |
| Unit_Lng Mwid Mmaxd Size2 Size3 | 766.87 | 7.10 | 0.012 |
| Mwid Mmaxd Denlwd Size2 Size3 | 767.98 | 8.21 | 0.007 |
| Mwid Mmaxd Reach_Gr Size2 Size3 | 768.05 | 8.29 | 0.007 |
| Mwid Mmaxd Conduct Pct_Surt Size2 Size3 | 768.60 | 8.84 | 0.005 |
| Mmaxd Mwt Conduct Pct_Surt Size2 Size3 | 768.67 | 8.91 | 0.005 |
| Mwid Mmaxd Conduct Denlwd Size2 Size3 | 768.92 | 9.16 | 0.004 |
| Mwid Mmaxd Conduct Pctcobb Size2 Size3 | 769.01 | 9.25 | 0.004 |
| Mwid Mmaxd Denlwd Pct_Surt Size2 Size3 | 769.84 | 10.07 | 0.003 |
| Mwid Mmaxd Conduct Pct_Surt Timafmrk Size2 Size3 | 770.48 | 10.72 | 0.002 |
| Unit_Lng Mwid Mmaxd Mwt Conduct Pct_Surt Size2 Size3 | 770.64 | 10.88 | 0.002 |
| Mwid Mmaxd Reach_Gr Conduct Pct_Surt Den Size2 Size3 | 772.05 | 12.29 | 0.001 |
| Conduct Pctuct Denlwd Size2 Size3 | 773.06 | 13.30 | 0.001 |
| Mwid Mmaxd Reach_Gr Mwt Conduct Pct_Surt Size2 Size3 | 773.13 | 13.37 | 0.001 |
| Unit_Lng Mwid Mmaxd Reach_Gr Mwt Conduct Pct_Surt Pctuct Pctcobb Denlwd Timafmrk Size2 Size3 | 773.29 | 13.52 | 0.000 |
| Pctuct Pctcobb Denlwd Size2 Size3 | 773.29 | 13.53 | 0.000 |
| Conduct Pctuct Pctcobb Size2 Size3 | 774.28 | 14.51 | 0.000 |
| Conduct Pctuct Size2 Size3 | 774.75 | 14.99 | 0.000 |
| Conduct Pct_Surt Denlwd Size2 Size3 | 779.85 | 20.09 | 0.000 |
| Mwt Conduct Pct_Surt Size2 Size3 | 780.50 | 20.74 | 0.000 |
| Unit_Lng Mwid Size2 Size3 | 780.57 | 20.81 | 0.000 |
| Size2 Size3 | 781.08 | 21.32 | 0.000 |
| Timafmrk Size2 Size3 | 782.03 | 22.26 | 0.000 |

Table 12. continued

|  |  | Upper | Lower |  |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | :---: | :---: | :---: | :---: | :---: |
| Parameter |  | Estimate | $95 \% \mathrm{CL}$ |  |  |  |  | $95 \% \mathrm{CL}$ |  |
| Intercept | -1.641 | -1.105 | -2.177 |  |  |  |  |  |  |
| Mwid | -0.154 | 0.032 | -0.341 |  |  |  |  |  |  |
| Mmaxd | -0.339 | -0.164 | -0.513 |  |  |  |  |  |  |
| Conduct | 0.025 | 0.189 | -0.139 |  |  |  |  |  |  |
| Pctuct | -0.285 | -0.104 | -0.466 |  |  |  |  |  |  |
| Pctcobb | 0.003 | 0.170 | -0.163 |  |  |  |  |  |  |
| Denlwd | 0.052 | 0.250 | -0.145 |  |  |  |  |  |  |
| Size2 | 1.308 | 1.874 | 0.743 |  |  |  |  |  |  |
| Size3 | 1.625 | 2.257 | 0.993 |  |  |  |  |  |  |

Table 13. Mean difference and root mean squared difference (in parenthesis) between predicted and measured sampling efficiencies by method and region. Cross-validation sampling efficiency predictions were calculated via leave-one-out technique and cross- region predictions were predicted for Idaho using the Washington models and vice versa.

| Day snorkeling |  | Night snorkeling |  | 3-pass electrofishing |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| WA | ID | WA | ID | WA | ID |

Cross-validation $0.059(0.294) 0.003(0.107) 0.079(0.338) 0.016(0.162)-0.080(0.262)-0.004(0.217)$
Cross- region $\quad 0.135(0.395)-0.200(0.423)-0.127(0.344) 0.063(0.259) 0.101(0.366) 0.540(0.648)$

Table 14. Estimated number of samples to achieve $80 \%$ power $(\alpha=0.05)$ for logistic regression model of 3-pass electrofishing efficiency in Washington streams. Sample sizes were estimated using the SAS macro, UnifyPow.sas (SAS 1999), and models fit with each of the 3 predictors individually and the combinations listed below.

|  | Individual | Undercut and <br> conductivity | Undercut and <br> wood density | All <br> predictors |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Percent undercut | $>500$ |  | 712 |  | 89 |  |
| Conductivity | 73 |  | 69 | - | 138 |  |
| Wood density | 183 |  | - | 147 | 102 |  |
|  |  |  |  | 159 |  |  |

Table 15. Mean and range of required sample sized to obtain $20 \%$ precision (with $95 \%$ confidence) of sampling efficiency model coefficients shown in Tables 7-12.

|  | Washington |  | Idaho |  |
| :--- | :---: | :---: | :---: | :---: |
|  | $\underline{\text { Mean }}$ | $\underline{\text { Range }}$ | Mean | $\underline{\text { Range }}$ |
| Day snorkeling | $>500$ | $10->500$ | 46 | $5-336$ |
| Night snorkeling | 182.3 | $16-1218$ | 105 | $2-590$ |
| 3-pass electrofishing | 229 | $22-989$ | 7080 | $4-62202$ |

Table 16. Predictor variables, $\mathrm{QAICc}, \mathrm{Q} \triangle \mathrm{AICc}, \mathrm{Q} \Delta \mathrm{AICc}$ weights (w) for the set of candidate models $(i)$ and model-averaged estimates of quasi-likelihood regression coefficients and upper and lower 95\% confidence limits (bottom) for escape of marked bull trout in Idaho streams. Q $\Delta$ AICc weights are interpreted as relative plausibility of candidate models. Models were fit to standardized data to allow comparison among predictors. Predictor variable abbreviations can be found in Table 1.

| Candidate Model | QAICc | Q $\triangle$ AICc | $\underline{W}_{\text {i }}$ |
| :---: | :---: | :---: | :---: |
| Timafmrk | 69.91 | 0.00 | 0.400 |
| Mwid | 71.38 | 1.48 | 0.191 |
| Timafmrk Mwid | 72.30 | 2.40 | 0.121 |
| Timafmrk Unit_Lng | 72.98 | 3.08 | 0.086 |
| Unit_Lng | 73.76 | 3.86 | 0.058 |
| Reach_Gr | 73.93 | 4.03 | 0.053 |
| Mwid Unit_Lng | 74.75 | 4.84 | 0.036 |
| Timafmrk Mwid Unit_Lng | 76.17 | 6.26 | 0.017 |
| Timafmrk Mwid Reach_Gr | 76.21 | 6.30 | 0.017 |
| Timafmrk Unit_Lng Reach_Gr | 76.89 | 6.98 | 0.012 |
| Mwid Reach_Gr Unit_Lng | 78.60 | 8.70 | 0.005 |
| Timafmrk Mwid Reach_Gr Unit_Lng | 80.79 | 10.89 | 0.002 |
| Mwid Mwt Reach_Gr Unit_Lng | 81.73 | 11.82 | 0.001 |
| Timafmrk Mwid Mwt Reach_Gr Unit_Lng | 85.68 | 15.77 | 0.000 |
| Parameter | Estimate | $\begin{gathered} \text { Upper } \\ 95 \% \mathrm{CL} \\ \hline \end{gathered}$ | Lower 95\% CL |
| Intercept | -4.211 | -3.204 | -5.218 |
| Timafmrk | 0.994 | 2.289 | -0.300 |
| Mwid | 0.426 | 1.038 | -0.185 |
| Mwt | -0.635 | 0.490 | -1.760 |
| Reach_Gr | 0.002 | 0.833 | -0.830 |
| Unit_Lng | -0.143 | 0.661 | -0.946 |



Figure 1. Residuals from global logistic regression model for 3-pass electrofishing efficiency in Idaho streams. Broken lines depict positive relationship between variance and number of marked fish.


Figure 2. Frequency histograms of the number of marked fish per calibration (sample unit) in Washington (top) and Idaho (bottom) streams, by size class.


Figure 3. Mean estimated sampling efficiency and standard errors (vertical bars) for each electrofishing pass in Washington (top) Idaho (bottom) streams, by size class. Sampling efficiency was estimated using known number of marked and recaptured individuals.


Figure 4. Relationship between fish abundance and 3-pass sampling efficiency bias (predicted actual) of removal estimates for constant (heavy solid line) and heterogeneous (thin line) capture efficiency removal models. Solid lines represent the mean values from 1000 simulations and broken lines represent mean bias measured for bull trout in Washington (WA) and Idaho (ID).


Figure 5. Cross-comparison of estimated average sampling efficiency, with log-based $95 \%$ confidence limits (black bars), of day and night snorkeling and 3-pass backpack electrofishing (EF) for bull trout 70-200 mm total length. Method-specific resight (snorkeling) or recapture efficiencies were estimated as the ratio of the number of recaptured or resighted individuals to number of marked individuals. Method-specific baselines were based on efficiency-adjusted estimates of the number of unmarked fish.


Figure 6. Pair wise plots of selected habitat variables measured in Idaho and Washington streams. Shaded areas represent combinations of habitat characteristics for which existing efficiency models should not be applied.


Figure 7. Example of the effect of the number of marked fish per calibration on statistical power and required sample size estimates for sampling efficiency evaluation. Estimates are for an equal number of small and large marked fish and large fish sampling efficiency $200 \%$ greater than for small fish.


[^0]:    ${ }^{1}$ Size specific estimates could not be calculated with Washington data.

