

Utility and Validation of Day and Night Snorkel Counts for Estimating Bull Trout Abundance in First- to Third-Order Streams

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Abstract.—Despite the widespread use of underwater observation to census stream-dwelling fishes, the accuracy of snorkeling methods has rarely been validated. We evaluated the efficiency of day and night snorkel counts for estimating the abundance of bull trout *Salvelinus confluentus* in 215 sites within first- to third-order streams. We used a dual-gear approach that applied multiple-pass electrofishing catch data adjusted for capture efficiency to estimate true or baseline fish abundance. Our multiple-pass electrofishing capture efficiency models were based on a prior study and used recapture data for known numbers of individually marked fish. Snorkeling efficiency was estimated by comparing day and night snorkel counts with the baseline. We also evaluated the influence of fish size and stream habitat features on snorkeling efficiency. Bull trout snorkeling efficiency was higher at night (mean = 33.2%) than during the day (mean = 12.5%). Beta-binomial regression indicated that bull trout day and night snorkeling efficiencies were positively related to fish size and negatively related to stream width and habitat characteristics. Day snorkeling efficiency also was positively influenced by water temperature and nonlinearly related to underwater visibility, whereas night snorkeling efficiency was nonlinearly related to water temperature and pool abundance. Although bull trout were our target species, day and night snorkeling efficiencies combined for rainbow trout *Oncorhynchus mykiss* and subspecies of cutthroat trout *O. clarkii* averaged 32.3% and 18.0%, respectively. Our ability to detect and accurately count fish underwater was influenced by fish size, species, time of day, and stream habitat characteristics. Although snorkeling is versatile and has many advantages over other sampling methods, the use of raw snorkel counts unadjusted for the effects of these biases will result in biased conclusions. We recommend that biologists adjust underwater count data to minimize the effect of such biases. We illustrate how to apply sampling efficiency models to validate snorkel counts.

For over four decades, biologists have used snorkeling gear to observe stream-dwelling fishes (Ellis 1961; Keenleyside 1962; Northcote and Wilkie 1963). Underwater observation has been applied to assess fish abundance (Pollard and Bjornn 1973), monitor basinwide species distributions (Hankin and Reeves 1988), estimate size structure (Griffith 1981), evaluate habitat use (Fausch and White 1981), and observe behavior (Reed 1967).

Underwater observation offers several advantages over other sampling methods. It is feasible where environmental conditions (i.e., deep or low-conductivity

water) limit the effectiveness of methods like electrofishing (Schill and Griffith 1984; Bonneau et al. 1995). Relatively modest gear requirements reduce equipment costs and adapt the technique well for sampling remote locations (Thurrow 1994). Fewer personnel and less sampling time are required, so cost is reduced and efficiency may be improved (Hankin and Reeves 1988). Since underwater observation is nonlethal and less intrusive, it can also be well adapted for sampling sensitive species that are federally listed under the Endangered Species Act, such as bull trout *Salvelinus confluentus*.

Despite its advantages, underwater observation yields valid estimates of abundance and distribution only when estimators are unbiased (i.e., data are both precise and accurate; Griffith et al. 1984). To ensure that an estimator is unbiased requires an evaluation of

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Received April 7, 2005; accepted August 29, 2005
Published online February 3, 2006

potential violations of estimator assumptions and a comparison of estimator abundances to true abundances (Peterson et al. 2004). If estimators are biased, reliable estimates of fish abundance can still be obtained by applying unbiased estimates of capture efficiency (Buttiker 1992; Bayley and Dowling 1993). It is particularly important to validate snorkeling methods for bull trout because their cryptic behavior (Pratt 1984; Thurow and Schill 1996; Thurow 1997) and affinity for cold water (<16°C), low conductivity (<100 µS/cm), and complex habitat (Goetz 1994; Jakober et al. 2000; Dunham et al. 2003) make them difficult to sample. Consequently, snorkeling may fail to detect bull trout or may underestimate their true abundance (Thurow and Schill 1996).

The precision of snorkeling techniques has been evaluated for a variety of species under a range of conditions. Counts have been replicated temporally within the same unit (i.e., Slaney and Martin 1987) or spatially by replicating multiple units in the same strata (i.e., Hankin and Reeves 1988). Many authors report high precision of counts made by trained, independent snorkelers (Northcote and Wilkie 1963; Griffith 1981; Schill and Griffith 1984; Hicks and Watson 1985; Zubik and Fraley 1988; Teirney and Jowett 1990).

Although replicate counts are often precise, the accuracy of underwater counts has been problematic to assess because the true population density is usually unknown (Hillman et al. 1992). Most prior attempts to measure count accuracy have applied dual-gear approaches that assumed that the nonsnorkeling techniques provided true estimates of population abundance. Biologists have estimated the true population via electrofishing, seining, mark–recapture events, and toxicants. Each of these methods has limitations for calibrating snorkel counts. Electrofishing estimates (Griffith 1981; Hankin and Reeves 1988; Thurow and Schill 1996; Mullner et al. 1998) are themselves biased. Peterson et al. (2004) recommended avoiding the use of uncorrected removal electrofishing data to estimate true population abundance because these estimates tend to overestimate capture efficiency while underestimating population abundance. Seining (Goldstein 1978) has limited application in bull trout rearing areas, which tend to be in first- to third-order streams with complex habitats; seining also requires capture efficiency calibrations. Techniques that combine snorkeling resight of previously marked fish (Slaney and Martin 1987; Zubik and Fraley 1988) rely on electrofishing or angling to mark fish, and both of these capture techniques are size selective. Toxicants can provide unbiased estimates of the true population (Northcote and Wilkie 1963; Hillman et al. 1992) but are rarely used in waters that support native fishes.

In this paper, we examine the utility of snorkel counts for estimating the abundance of bull trout and other salmonids in small streams by applying a dual-gear validation approach. Our specific objectives were to (1) estimate true or baseline fish abundance by use of multiple-pass electrofishing catch data adjusted for capture efficiency, (2) validate (assess the bias and precision of) day and night snorkel counts by comparing them to the baseline to estimate snorkeling efficiency, and (3) examine the influence of stream habitat characteristics, fish species, and fish size on snorkeling efficiency.

Study Area

We evaluated the utility of snorkel counts for estimating bull trout abundance in 215 sites within first- through third-order streams located primarily on federal (National Forest and Bureau of Land Management) lands in central Idaho, southwest Montana, and Washington. Study sites were selected within the known range of bull trout at elevations exceeding 169 m (Table 1). Sites were sampled once during June–October between 1994 and 2002. We sampled sites on the declining limb of the hydrograph, and most sites were sampled near base flow.

Methods

In any evaluation of fish census methods, it is critical to consider the influence of capture efficiency. Failure to account for differences in capture efficiency may introduce bias into the data, which can significantly affect estimates of both abundance (Bayley and Dowling 1993) and distribution (Bayley and Peterson 2001). Here, we define snorkeling efficiency as the

TABLE 1.—Mean, SD, and range of habitat characteristics of the 215 sample sites included in the evaluation of salmonid day and night snorkeling efficiency. Sites were located in central Idaho, southwest Montana, and Washington.

Variable	Mean	SD	Range
Site elevation (m) ^a	1,430	534	169–2,450
Mean wetted width (m)	4.70	1.80	1.9–10.5
Mean cross-sectional area (m ²)	0.81	0.51	0.1–2.5
Map reach gradient (%)	4.49	2.48	0.4–11.8
Wood density (number/m ²)	0.05	0.05	0–0.3
% Pools composition	10.94	10.65	0–50.5
Undercut banks (%)	11.00	15.59	0–93.4
Water temperature (°C)	9.90	2.76	3.0–16.8
Day visibility (m) ^b	2.67	0.98	0.5–7.8
Substrate (%)			
Fines ^a	14.82	11.96	0–67
Gravel	25.24	13.29	0–64
Cobble ^a	28.60	10.59	4–59
Rubble	31.14	18.30	0–78

^a Variables that were not included in candidate models.

^b Day visibility was used to fit night snorkeling efficiency models.

proportion of fish in a given sampling site that are counted (observed) during sampling. Hence, our snorkeling efficiency estimates required a reliable estimate of the true abundance of trout within the sampled area. We used a dual-gear calibration procedure in which a closed population was sampled with a primary gear (snorkeling) followed by a secondary gear (three-pass electrofishing) with a previously investigated ability to estimate the true population. Standard removal electrofishing methods are themselves biased by factors such as fish size and the physical characteristics of the area sampled (Peterson et al. 2004) and so cannot provide reliable estimates of the true population. As an alternative, we estimated snorkeling efficiency by use of electrofishing catch data adjusted for electrofishing capture efficiency as the baseline or true population for comparison with snorkel counts. This dual-gear calibration procedure has been widely used to evaluate various other fish collection methods (Bayley et al. 1989; Bayley and Austen 1990, 2002; Bayley and Dowling 1993; Peterson and Rabeni 2001).

Our intent was to evaluate snorkeling efficiency under conditions commonly encountered within the range of bull trout in the northwestern USA. Consequently, we developed sampling strata based on habitat data from previously sampled bull trout streams in the region. Strata were defined by features including channel wetted width, gradient, large wood density, and length of undercut banks (Peterson and Banish 2002; Peterson et al. 2004). Our objective was to select sample sites that covered a broad range of physical habitat conditions rather than to precisely measure conditions. Sample sites (~100-m long) were selected from within each stratum. To meet the assumption of a closed population, we used 7-mm square-mesh nets secured to the streambed to block off each site prior to sampling. We selected locations with abrupt changes in channel gradient as hydraulic controls for upper and lower boundaries of each site to ensure adequate closure. All block nets were maintained in place until electrofishing was concluded.

Fish were sampled via day snorkeling between 1000 and 1700 hours and night snorkeling between 2230 and 0230 hours within the same 24-h period. Prior to snorkeling, we inspected the sample site to determine the number of snorkelers (1 or 2) needed to complete the survey in a single pass. We assessed maximum stream wetted width, depth, velocity, physical obstructions, and underwater visibility. Shallow habitats (wide riffles and pocket water) typically require more observers than deepwater habitats (Thurrow 1994). For logistical and safety reasons, we completed day snorkel surveys first at most sites. We used identical

sampling techniques during day and night except that night snorkel counts were completed with the aid of a hand-held underwater halogen light. Day snorkelers occasionally used a halogen light to inspect shaded locations. All snorkeling began at the downstream end of each study site and was completed in a single upstream pass. During each count, the snorkelers, who were equipped with wet or dry suits, masks, snorkels, and recording sleeves (Dolloff et al. 1996), proceeded slowly upstream in a zigzag pattern, alternating between streambanks. To avoid double counting, two snorkelers typically moved side by side up the middle of the channel and counted fish outward toward the streambank nearest to them. All salmonids were identified to species and were classified into one of three total length (TL) size-classes: 60–99, 100–199, and over 200 mm. We excluded age-0 fish (<60 mm) because of the difficulty in accurately assessing salmonid young of the year (Griffith 1981). Snorkelers recorded fish count data on their sleeves and paused periodically at the end of a habitat unit or hydraulic control to relay information to a data recorder on the streambank.

After snorkeling was completed, sample sites were undisturbed for an average of 4 h prior to electrofishing surveys. We then resampled the site with three upstream passes of a backpack electrofisher that used unpulsed DC (following Peterson et al. 2004). Block nets were removed after the final electrofishing pass.

Physicochemical measurements.—Prior to the onset of day snorkeling, three measurements of underwater visibility or water transparency were taken via a method similar to the use of a Secchi disk in lentic systems (Thurrow 1994). A plastic silhouette of a salmonid was suspended in the water column in front of the snorkeler, who moved away until the spotting on the silhouette could not be distinguished. The snorkeler then moved back toward the silhouette until the spotting reappeared clearly, and that distance was measured. Visibility was estimated as the average of the three measurements. Visibility was measured in the longest and deepest habitats (i.e., pools or runs) where a snorkeler had the longest unobstructed underwater view. In 2000 and 2002, this procedure was repeated at night prior to snorkeling. Because night visibility was highly correlated with day visibility ($r = 0.813$, $P < 0.001$), we used day visibility as a surrogate for visibility during night snorkeling efficiency modeling procedures.

After block-net removal, we measured physical and chemical stream features at each site. Beginning at the downstream end of each site, transects were established perpendicular to the flow along the centerline of the stream and were spaced at 20-m intervals. At each

transect, we recorded the type of fast- or slow-water habitat (e.g., pool, riffle), measured wetted channel width, and estimated mean water depth by averaging readings at 0.25, 0.50, and 0.75 times the channel width. Cross-sectional area was estimated as the product of wetted width and mean depth. Substrate composition was visually estimated in a 1-m-wide band centered across each transect and categorized as fines (<6 mm), gravel (6–75 mm), cobble (75–150 mm), and rubble (>150 mm). Transect-specific measurements were averaged for each site.

At each site, we counted the number of pieces of woody debris, which we defined as a piece of wood at least 3 m long and 10 cm in diameter lying within an active channel. Wood density was estimated as the total number of wood pieces divided by the wetted surface area of each site. We measured the length of undercut banks along each bank and expressed them as percentages of the total bank length (left and right). Site gradient was estimated from a U.S. Geological Survey 7.5-min (1:24,000 scale) map. We measured conductivity in the center of each site by use of a calibrated hand-held meter. Water temperature was measured at 1-h intervals with a continuously recording thermograph.

Modeling snorkeling efficiency.—For each salmonid species, we estimated the size-class-specific baseline fish abundance at a site by adjusting the three-pass electrofishing catch data with electrofishing capture efficiency models as follows:

$$A_i = \frac{N_i}{\hat{\pi}_i},$$

where A_i is the estimated (adjusted) number of individuals and represents the baseline, $\hat{\pi}_i$ is the predicted electrofishing capture efficiency expressed as a fraction, and N_i is the number of individuals of size-class i collected with three-pass electrofishing. Predicted capture efficiency ($\hat{\pi}_i$) was estimated based on species-specific capture efficiency models and site-specific habitat data. Bull trout capture efficiency was estimated as

$$\hat{\pi}_i = \{1 + \exp[-(0.360 - 0.912 \cdot \text{CRX} + 0.004 \cdot \text{CON} - 0.013 \cdot \text{UCT} - 0.876 \cdot \text{SIZE1} + 0.466 \cdot \text{SIZE3})]\}^{-1},$$

where CRX is the mean wetted stream cross-sectional area (m²), CON is stream conductivity (μΩ), UCT is percent undercut banks, SIZE1 is a binary variable coded as 1 when TL is 60–99 mm and 0 otherwise, and SIZE3 is 1 when TL is 200–350 mm and 0 otherwise (following Peterson et al. 2004; Thurow et al. 2004). Similarly, *Oncorhynchus* spp. capture efficiency was estimated as

$$\hat{\pi}_i = \{1 + \exp[-(0.025 - 0.058 \cdot \text{MWT} - 0.012 \cdot \text{COBB} - 0.019 \cdot \text{POOL} - 0.936 \cdot \text{SIZE1} + 0.155 \cdot \text{SIZE3})]\}^{-1},$$

where MWT is the mean water temperature during sampling (°C), COBB is the percent of the substrate in cobble-sized (75–150-mm diameter) particles, and POOL is the percent of the site comprised of pool habitats. Three-pass electrofishing capture efficiency models based on the recapture of known numbers of individually marked fish were fit by use of the data and techniques detailed in Peterson et al. (2004) and Thurow et al. (2004).

Adjusted or baseline fish abundance (A_i) rounded down to the nearest whole number and the number of fish (>60 mm) counted during snorkeling (C_i) were used as dependent variables (i.e., the number of trials and successes, respectively), and snorkeling efficiency was modeled as a function of various predictors as follows:

$$\frac{C_i}{A_i} = f(\text{predictors}),$$

where $f(\text{predictors})$ represents the predictors used in the beta-binomial regression modeling procedure described below. Size-classes were binary coded (0, 1) for the 60–99 and 200–350-mm TL size-classes, and the 100–199-mm TL size-class was used as the statistical baseline. The number of snorkelers used was binary coded to examine the effect of two snorkelers on capture efficiency; the use of one snorkeler was the statistical baseline. Observations during full- and new-moon phases were binary coded to examine the influence of moon phase on night snorkeling efficiency. Data for cutthroat trout *O. clarkii* also were binary coded to examine the differences between snorkeling efficiencies for cutthroat trout and rainbow trout *O. mykiss*. Pearson's product-moment correlations were run on all pairs of continuous predictor variables (i.e., physical and chemical measurements) prior to analyses. To avoid multicollinearity, predictor variables that were strongly correlated ($r^2 > 0.20$) were not used together in the modeling procedure.

We initially fitted capture 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). To account for the overdispersion, we modeled capture efficiency by use of beta-binomial regression fitted with R statistical software (Ihaka and Gentleman 1996) and Lindsey's (2001) nonlinear regression and repeated measurements libraries. Beta-binomial regression is similar to logistic regression except that the variance is modeled as a beta

distribution that accounts for extra variance (Prentice 1986), and this variance can be directly incorporated in estimating fish detection probabilities (Peterson and Rabeni 2001) and confidence intervals (Peterson et al. 2004). Thus, we used beta-binomial regression to examine the influence of physical and chemical variables and other factors (Tables 1, 2) on day and night snorkeling efficiency.

The goal of our snorkeling efficiency modeling was to obtain the simplest, best-fitting (predicting) models given our data. Thus, we used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the fit of beta-binomial regression models that related sample site characteristics, number of snorkelers, and fish body size to snorkeling efficiency. We began our modeling by constructing a global regression model for each salmonid species based on observations (Riley et al. 1993; Thurow and Schill 1996) that suggest salmonid snorkeling efficiency is significantly influenced by stream habitat characteristics, fish body size, and species. We also included variables that represented the number of day and night snorkelers and the moon phases in the night snorkeling efficiency models. We then fit all possible subsets of the global model (including all first-order interactions) via beta-binomial regression. To assess the fit of each candidate model, we calculated Akaike's information criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989). The AIC is an entropy-based measure used to compare candidate models (Burnham and Anderson 1998). We assessed the relative fit of each candidate model by calculating Akaike weights (Burnham and Anderson 1998), which can range from 0 to 1; the best-fitting candidate model is the one with the highest Akaike weight.

We based all inferences and predictions on the best-fitting model. The precision of coefficients for the best-fitting model was assessed by calculating 90% confidence intervals based on a *t*-statistic with degrees

of freedom equal to $n - 1$. The relative importance of individual predictor variables also was estimated as the sum of Akaike weights for candidate models in which each predictor occurred (Burnham and Anderson 1998). The ratio of the weights for two candidate models also can be used to assess the relative evidence favoring one model over another (Burnham and Anderson 1998). Thus, importance weights were only calculated for the predictor variables that occurred in one or more candidate models that had weights within 10% of the largest weight, which is similar to the general rule of thumb (i.e., 1/8 or 12%) suggested by Royall (1997) for evaluating strength of evidence. We defined these models (with weights within 10%) as the confidence set, following Burnham and Anderson (1998). We assessed goodness of fit for global models by examining residual probability plots. We examined dependence among size-classes by ordering the residuals by sample site and size-class and conducting a Wald-Wolfowitz runs test (Bayley 1993).

We assessed the relative bias and precision of the best-fitting day and night snorkeling efficiency models for each species using 10-fold cross validation. Cross-validation estimates are nearly unbiased estimators of out-of-sample model performance (Fukunaga and Kessel 1971) and provide a measure of overall predictive ability without excessive variance (Efron 1983). Tenfold cross validation has been found to be optimal for estimating the expected error rate of a given model (Brieman and Spector 1992). Hence, it should provide an estimate of the ability of the models to estimate snorkeling efficiency under conditions similar to those under which the models were parameterized. During this procedure, the site-specific data were randomly placed into 10 groups, data from one group were excluded, the beta-binomial regression model was fit with data from the remaining nine groups, and the capture efficiency for sites in the excluded group were predicted. This procedure was repeated for each group

TABLE 2.—The distribution of bull trout, rainbow trout, and cutthroat trout observations based on number of snorkelers or moon phases during snorkel efficiency evaluations at 215 sites in Idaho, Montana, and Washington. For snorkeler number, specific means, SDs (in parentheses), and ranges of site dimensions are included for comparison.

Variable	Percent of observations	Wetted width (m)		Cross-sectional area (m ²)	
		Mean	Range	Mean	Range
Number of snorkelers					
One	76.7	4.23 (1.59)	1.9–10.4	0.70 (0.46)	0.1–2.6
Two	23.3	6.27 (1.58)	3.5–10.5	1.19 (0.49)	0.4–2.3
Moon phase					
New	25.1				
First quarter	18.1				
Last quarter	34.4				
Full	22.3				

(i.e., a total of 10 times), and error was estimated as the difference between the predicted and measured (i.e., number recaptured/number marked) efficiency. For each species, relative model bias was estimated as the mean difference and precision as the root mean square error across samples. The proportion of snorkeling efficiencies falling within the predicted 90% confidence intervals also is reported.

Results

Snorkeling efficiency evaluations were conducted at 215 sample sites that covered a relatively wide range of habitat characteristics (Table 1). Most evaluations (77%) were conducted with one snorkeler; these sample sites were, on average, narrower than sites that required two snorkelers (Table 2). Bull trout were present in 88% of sample sites, cutthroat trout were present in 31%, and rainbow trout were present in 37% (Table 3). Bull trout, cutthroat trout, and rainbow trout were detected at 68, 20, and 29% of sample sites, respectively, during day snorkeling, whereas they were detected at 83, 27, and 29% of sites, respectively, during night snorkeling. We collected brook trout *S. fontinalis* at 4% of sites, which was insufficient for evaluating snorkeling efficiency. Hence, we confined our analyses to bull, cutthroat, and rainbow trouts.

On average, snorkeling efficiency was highest at night for the largest size-class across species (Figure 1). Night snorkeling efficiency was higher than day snorkeling efficiency across species and size-classes (Figure 1). We estimated that snorkeling efficiency was on average lowest (mean 6%) for small bull trout during the day and highest (mean 46%) for large bull trout at night. Efficiencies were similar for rainbow trout and cutthroat trout. However, day snorkeling efficiencies for the smallest size-classes of rainbow and cutthroat trouts were on average 2.2 times higher than the efficiency for small bull trout (Figure 1).

Bull Trout

Residuals from the global models of bull trout day and night snorkeling efficiency indicated that the models adequately fit the data. A Wald–Wolfowitz runs test of residuals ordered by size-class and sample also indicated no detectable dependence among size-classes for the day ($Z = -0.605$, $P = 0.273$) and night ($Z = -0.980$, $P = 0.163$) snorkeling global models.

Beta-binomial models of bull trout day snorkeling efficiency indicated that the best-fitting model contained day visibility and its quadratic term (day visibility squared), mean water temperature and its quadratic term, wood density, rubble substrate, and fish body size (Table 4). Importance weights for these seven predictors were, on average, 1.53 times greater

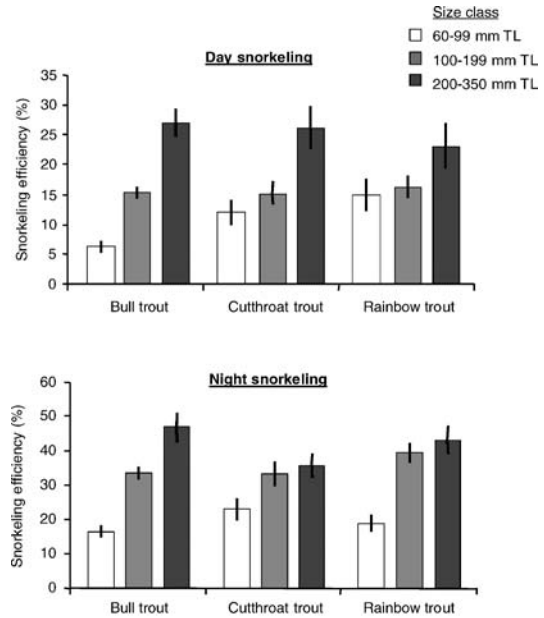


FIGURE 1.—Mean day and night snorkeling efficiencies ($\pm$ SE [vertical bars]) for three total length (TL) size-classes of bull, cutthroat, and rainbow trouts at 215 sites in Idaho, Montana, and Washington. Efficiency was estimated by comparing snorkel counts to baselines derived by efficiency-adjusted electrofishing abundance estimates.

than the next-best predictor, percent undercut banks (Table 5). Day snorkeling efficiency was positively related to body size and negatively related to wood density and rubble substrate (Table 4). However, the relationships between day visibility, mean water temperature, and bull trout day snorkeling efficiency were relatively complex. We estimate that day snorkeling efficiency was positively related to visibility when visibility was less than 3.1 m, whereas it decreased when visibility exceeded 3.1 m (Figure 2). Similarly, day snorkeling efficiency was positively related to water temperatures at temperatures below 13°C, but snorkeling efficiency did not improve when temperatures exceeded 13°C (Figure 2).

The best-fitting bull trout night snorkeling efficiency model was similar to the day snorkeling model and contained mean water temperature and its quadratic term, pool composition and its quadratic term, rubble substrate, and fish body size (Table 4). Akaike importance weights for these six predictors were, on average, 1.51 times greater than the next-best predictor, the full-moon binary indicator variable (Table 5). Night snorkeling efficiency was negatively related to rubble substrate and positively related to body size (Table 4). Similar to day snorkeling, bull trout night snorkeling

TABLE 3.—Distribution of observations of bull, rainbow, and cutthroat trouts at 215 sties in Idaho, Montana, and Washington.

Salmonid species	Percent of observations	Percent of sites at which species were detected during snorkeling	
		Day	Night
Bull trout only	39.1	41.4	44.2
Cutthroat trout only	2.3	6.0	4.2
Rainbow trout only	8.8	14.0	10.2
Bull and cutthroat trouts	21.9	12.1	20.9
Bull and rainbow trouts	20.9	12.6	16.7
Cutthroat and rainbow trouts	0.9	0.0	0.0
All three species	6.0	2.3	1.4

efficiency was nonlinearly related to mean water temperature, and the highest efficiency was at 9–10°C (Figure 3). Night snorkeling efficiency also was nonlinearly related to pool composition and was highest when pools comprised 25–30% of the sample site. Although the full-moon binary indicator variable was not included in the best-fitting model, it affected night snorkeling efficiency, as evidenced by a weight that was, on average, 1.46 times greater than the other excluded parameters (Table 5).

Other Salmonids

The initial fits of the combined cutthroat trout and rainbow trout day snorkeling efficiency models indicated little difference in observability between the two species. Candidate models containing the species binary indicator variable were never among the best-fitting models, and the Akaike importance weights for

the cutthroat trout binary indicator variable were among the lowest for the considered predictors. Consequently, the data for the two species were pooled (i.e., one data point per species size-group per sample site), and beta-binomial models were fit to the pooled data (henceforth, *Oncorhynchus* spp.; Table 5).

Examination of the residuals from the day and night snorkeling efficiency global models for *Oncorhynchus* spp. indicated that the models adequately fit the data and had no obvious outliers. The Wald–Wolfowitz runs test of the residuals ordered by size-class and sample also indicated no detectable dependence among size-classes for the day ($Z = -0.355$, $P = 0.365$) and night ($Z = -0.699$, $P = 0.244$) snorkeling global models. Therefore, we assumed that model fit was adequate for the candidate models.

The best-fitting beta-binomial model of *Oncorhynchus* spp. day snorkeling efficiency contained mean

TABLE 4.—Parameter estimates, SEs, and upper and lower 90% confidence limits (CLs) for best-fitting beta-binomial regression models of single-pass day and night snorkeling efficiency for bull trout in Idaho, Montana, and Washington. The 100–199-mm TL size-class was used as the statistical baseline in the regression.

Variable	Estimate	SE	Lower 90% CL	Upper 90% CL
Day snorkeling				
Intercept	–4.689	0.918	–6.194	–3.184
Day visibility	1.055	0.363	0.459	1.650
(Day visibility) ²	–0.170	0.060	–0.268	–0.071
Mean water temperature	0.360	0.143	0.125	0.594
(Mean water temperature) ²	–0.012	0.007	–0.024	–0.001
Wood density	–3.106	0.927	–4.627	–1.586
Rubble substrate	–0.021	0.003	–0.026	–0.016
60–99-mm TL	–1.207	0.148	–1.450	–0.964
200–350-mm TL	1.002	0.159	0.741	1.263
Dispersion	0.156	0.040		
Night snorkeling				
Intercept	–3.687	0.648	–4.750	–2.624
Mean water temperature	0.655	0.157	0.398	0.912
(Mean water temperature) ²	–0.035	0.009	–0.050	–0.020
Pool composition	0.029	0.011	0.010	0.047
(Pool composition) ²	–0.001	0.000	–0.001	0.000
Rubble substrate	–0.007	0.002	–0.011	–0.003
60–99-mm TL	–1.293	0.107	–1.469	–1.118
200–350-mm TL	0.816	0.140	0.587	1.044
Dispersion	0.151	0.030		

TABLE 5.—Akaike importance weights for variables in the confidence set of beta-binomial regression models for bull trout and *Oncorhynchus* spp. single-pass day and night snorkeling efficiency. Values in bold italics identify variables in best-fitting models. Importance weights for the cutthroat trout binary indicator variable are from an analysis of cutthroat trout and rainbow trout efficiencies and are shown for comparison.

Variable	Bull trout		<i>Oncorhynchus</i> spp.	
	Day	Night	Day	Night
Mean wetted width	0.298	0.419	0.313	0.462
Mean cross-sectional area	0.275	0.364	0.330	0.387
Map reach gradient	0.287	0.431	0.287	0.277
Mean water temperature	0.996	0.691	1.000	0.583
(Mean water temperature) ²	0.593	0.468	0.222	0.197
Day visibility	0.630	0.401	0.533	0.291
(Day visibility) ²	0.629	0.363	0.524	0.287
Undercut banks	0.549	0.271	0.295	0.270
Wood density	0.876	0.305	0.311	0.443
Gravel substrate	0.329	0.335	0.276	0.352
Rubble substrate	1.000	0.706	0.327	0.785
Pool composition	0.352	0.816	0.965	0.698
(Pool composition) ²	0.211	0.775	0.591	0.500
Full moon		0.517		0.303
60–99-mm TL	1.000	1.000	0.697	1.000
200–350-mm TL	1.000	1.000	0.773	0.576
Cutthroat trout binary indicator variable			0.275	0.308

water temperature, day visibility and its quadratic term, pool composition and its quadratic term, and fish body size (Table 6). Importance weights for these six

variables were, on average, 2.20 times greater than the next-best fitting variable, mean cross-sectional area (Table 5). Day snorkeling efficiency was positively related to mean water temperature and body size. The *Oncorhynchus* spp. day snorkeling efficiency also was nonlinearly related to day visibility and pool composition (Figure 4). We estimated that day snorkeling efficiency was highest when visibility was 2.5–3.5 m and when pools comprised 20–30% of the sample site.

The best-fitting beta-binomial model of *Oncorhynchus* spp. night snorkeling efficiency contained mean water temperature, rubble substrate, pool composition and its quadratic term, and fish body size (Table 6). The Akaike importance weights for these predictors also were the largest among the variables considered (Table 5). The *Oncorhynchus* spp. night snorkeling efficiency was positively related to water temperature and body size but was negatively related to rubble substrate. Night snorkeling efficiency also was nonlinearly related to pool composition and was highest when pools comprised approximately 20% of the sample site (Figure 5).

Cross validation of the snorkeling efficiency models indicated that they were relatively unbiased; mean differences between predicted and measured efficiency were 0.4% and 0.1% for bull trout and *Oncorhynchus* spp., respectively (Table 7). However, a larger than expected proportion of efficiencies fell outside the predicted 90% confidence intervals (Table 7). This was primarily a result of the relatively large number of sites with no individuals detected during snorkeling.

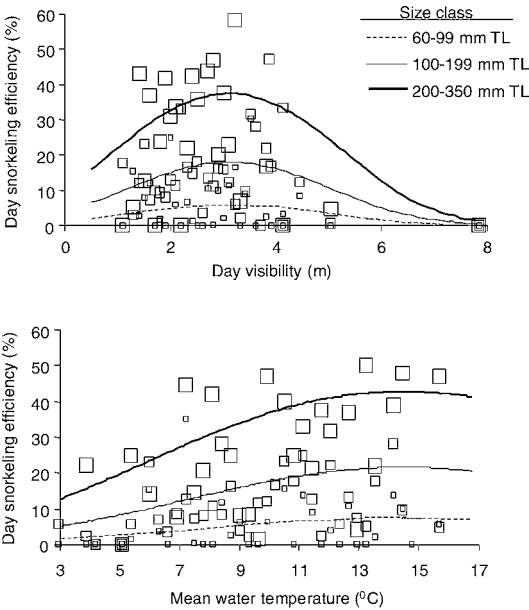


FIGURE 2.—Predicted bull trout day snorkeling efficiencies for three total length (TL) size-classes versus day underwater visibility (top panel) and mean water temperature (bottom panel) at 215 sites in Idaho, Montana, and Washington. Predictions were based on the best-fitting beta-binomial model and assumed the average values for wood density, rubble substrate, water temperature (top), and daytime underwater visibility (bottom) shown in Table 1.

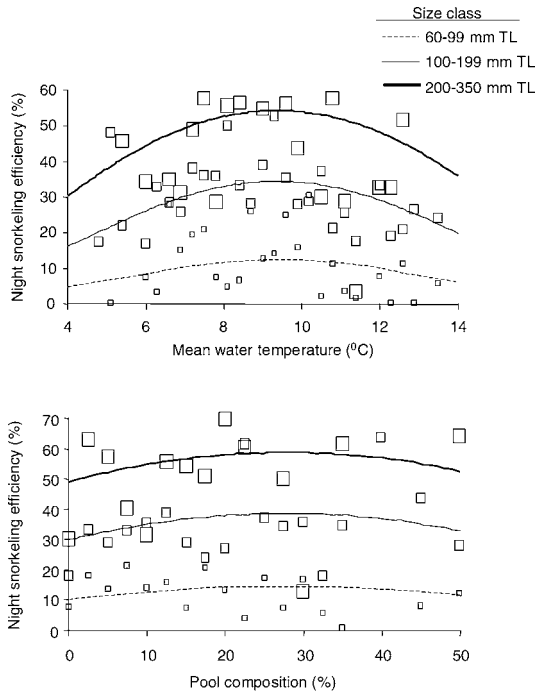


FIGURE 3.—Predicted bull trout night snorkeling efficiencies for three total length (TL) size-classes versus mean water temperature (top panel) and pool composition (bottom panel). Predictions were based on the best-fitting beta-binomial model and assumed the average values for rubble substrate, pool composition (top), and mean water temperature (bottom) show in Table 1.

Discussion

Our estimated day and night snorkeling efficiencies were lower than most values reported in the literature. During day surveys, we observed an average of 12.6, 16.7, and 18.3% of the age-1 and older bull, cutthroat, and rainbow trouts, respectively, present as estimated by electrofishing (adjusted for capture efficiency). Other studies reported that day snorkel counts averaged 78.3% and 74.9% of the age-1 and older bull trout estimated by use of electrofishing (Shepard and Graham 1983 and Thurow and Schill 1996, respectively). Mullner et al. (1998) combined day snorkel counts of cutthroat, rainbow, and brook trouts and cutthroat trout-rainbow trout hybrids and observed an average of 65% of the trout estimated by depletion electrofishing. Day snorkelers observed an average of 96.3% and 90.8% of the juvenile rainbow trout and steelhead (anadromous rainbow trout), respectively, that were estimated by means of electrofishing (Hankin and Reeves 1988; Hillman and Chapman 1993). Similarly, day snorkelers observed an average of 94.8% and 74.1% of the age-1 and older cutthroat trout estimated by electrofishing and mark-resight (snorkeling) methods, respectively (Shepard and Graham 1983; Slaney and Martin 1987). Griffith (1981) and Zubik and Fraley (1988) reported that snorkeling was even more efficient; they saw more cutthroat trout while day snorkeling than a dual-gear method (electrofishing and mark-resight) estimated as being present.

Consistent with many other studies (Goetz 1994; Bonneau et al. 1995; Jakober 1995; Thurow and Schill

TABLE 6.—Parameter estimates, SEs, and upper and lower 90% confidence limits (CLs) for best-fitting beta-binomial regression models of single-pass day and night snorkeling efficiency for *Oncorhynchus* spp. (cutthroat and rainbow trouts) in Idaho, Montana, and Washington. The 100–199-mm TL size-class was used as the statistical baseline in the regression.

Variable	Estimate	SE	Lower 90% CL	Upper 90% CL
Day snorkeling				
Intercept	−5.746	0.725	−6.935	−4.557
Mean water temperature	0.208	0.030	0.159	0.257
Day visibility	0.835	0.420	0.146	1.524
(Day visibility) ²	−0.135	0.073	−0.255	−0.015
Pool composition	0.104	0.022	0.068	0.139
(Pool composition) ²	−0.002	0.001	−0.003	−0.001
60–99-mm TL	−0.459	0.163	−0.726	−0.193
200–350-mm TL	0.914	0.293	0.433	1.394
Dispersion	0.191	0.072		
Night snorkeling				
Intercept	−1.001	0.316	−1.519	−0.484
Mean water temperature	0.066	0.026	0.023	0.109
Pool composition	0.049	0.016	0.023	0.074
(Pool composition) ²	−0.001	0.001	−0.002	0.000
Rubble substrate	−0.009	0.003	−0.013	−0.004
60–99-mm TL	−1.182	0.115	−1.371	−0.994
200–350-mm TL	0.413	0.209	0.071	0.755
Dispersion	0.182	0.052		

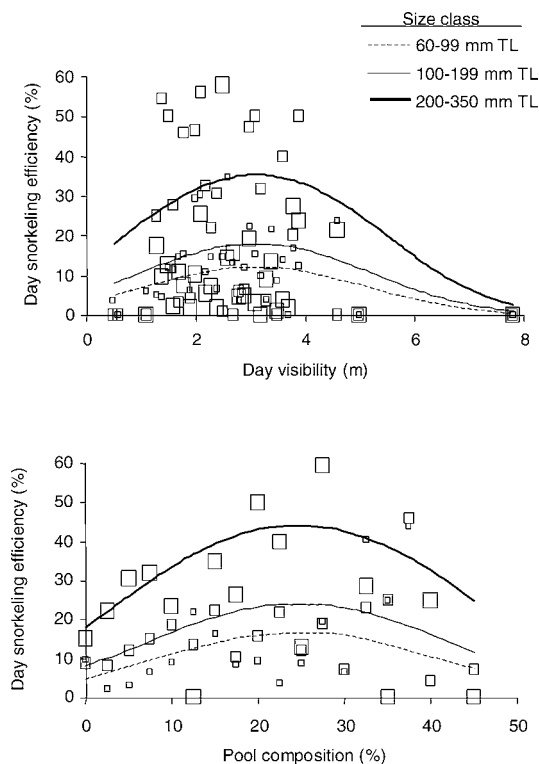


FIGURE 4.—Predicted day snorkeling efficiencies for three total length (TL) size-classes of rainbow and cutthroat trouts versus daytime underwater visibility (top panel) and pool composition (bottom panel). Predictions were based on the best-fitting beta-binomial model and assumed the average values for mean water temperature, pool composition (top), and day visibility (bottom) shown in Table 1.

1996), our night snorkeling efficiencies exceeded day snorkeling efficiencies. Our measured night snorkeling efficiencies (average of 32.2, 30.8, and 33.9%, for age-1 and older bull, cutthroat, and rainbow trouts, respectively) were, however, also less than those reported elsewhere. Jakober (1995) and Thurow and Schill (1996) applied unadjusted electrofishing estimates of the true population and reported night snorkeling efficiencies for bull trout of 80% and 77%, respectively. Few other studies have examined night snorkeling efficiency based on estimates of the true population as the baseline. Goetz (1994) attempted a dual-gear approach but reported that night snorkeling counts were 1.9 times more effective than electrofishing in detecting bull trout. Bonneau et al. (1995) similarly reported that electrofishing was ineffective in sampling bull and cutthroat trouts in small, low-conductivity streams, and therefore they were unable to apply a dual-gear approach.

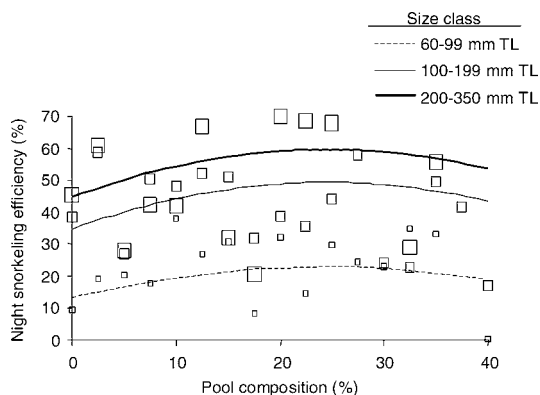


FIGURE 5.—Predicted night snorkeling efficiencies for three total length (TL) size-classes of rainbow and cutthroat trouts versus pool composition. Predictions were based on the best-fitting beta-binomial model and assumed the average values for mean water temperature and rubble substrate shown in Table 1.

Several factors may influence the discrepancies between our data and most reports of day and night snorkeling efficiencies. Perhaps most importantly, there may be errors in estimates of the true trout population. With the exception of Slaney and Martin (1987) and Zubik and Fraley (1988), all of the studies cited above used electrofishing estimates unadjusted for the effects of sampling bias as their true population estimates. Peterson et al. (2004) demonstrated that the use of electrofishing data unadjusted for sampling efficiency to estimate true population abundance is biased because these estimates tend to overestimate capture efficiency (snorkeling in this case) while underestimating population abundance. Hence, we believe that our lower estimates of snorkeling efficiency are more accurate representations of actual efficiency than those derived from unadjusted electrofishing estimates. In the only other snorkeling evaluation that we found to more rigorously estimate the true trout population, Hillman et al. (1992) used a fish toxicant (sodium cyanide) and reported an average day snorkeling efficiency very similar to ours (21.8%) for juvenile rainbow trout and steelhead.

Handling and marking could affect fish behavior, altering fish vulnerability to capture and biasing capture efficiency estimates. However, for the efficiency data applied in this study, Peterson et al. (2004) reported no detectable effects of marking and handling on capture efficiency after a 24–72-h recovery, which is consistent with previous studies of fish behavior and physiology (Mesa and Schreck 1989). Bohlin and Sundstrom (1977) similarly detected no marking effect after 24 h.

TABLE 7.—Tenfold cross-validation mean error, root mean square error (RMSE), and percent of predictions within 90% confidence intervals (CIs) for best-fitting beta-binomial regression models of bull trout and *Oncorhynchus* spp. single-pass snorkeling efficiency.

Taxon	Snorkeling period	Mean error	RMSE	Predictions within 90% CIs	Nonzero predictions within 90% CIs
Bull trout	Day	0.002	0.203	44	91
	Night	0.003	0.247	65	90
<i>Oncorhynchus</i> spp.	Day	−0.002	0.236	37	71
	Night	0.001	0.268	68	86

Differences in the complexity of instream habitat can profoundly affect snorkeling efficiency. Physical habitat characteristics, individually and in combination, significantly affected our day and night snorkeling efficiencies for bull, rainbow, and cutthroat trouts. Wood density, for example, negatively influenced bull trout day snorkeling efficiency. Rubble substrate negatively influenced bull trout day and night snorkeling efficiencies. All of these factors contribute to the complexity of the sample site by increasing fish concealment cover and potentially decreasing the ability of snorkelers to detect fish. Jakober et al. (2000) similarly observed that bull trout and cutthroat trout preferred large woody debris and large substrate for cover during both day and night. He noted that in sites with smaller substrates, fish preferred areas with wood and undercut banks. Although the undercut bank variable was not included in our best-fitting model, it did influence sampling efficiency, as evidenced by a larger importance weight relative to the other excluded parameters. One unexpected result was the nonlinear relationship between pool composition, bull trout night snorkeling efficiency, and *Oncorhynchus* spp. day and night snorkeling efficiency. The highest snorkeling efficiencies occurred in sites where pools comprised 20–30% of the area. We hypothesize that in shallower areas with few pools and abundant concealment cover, salmonids are more difficult to detect. In small streams with periodic, discrete pools that are longitudinally interspersed with shallower habitats, age-1 and older salmonids tend to be most abundant in pools (Thurow and Schill 1996) and may be more readily observed if snorkelers take care to gradually enter pools while moving upstream. In very large and long pools at night, salmonids may detect the dive light and flee before being counted. A similar fright response may occur during the day for *Oncorhynchus* spp. that remain higher in the water column.

Differences in water temperature may also explain the discrepancies in snorkeling efficiency results (Thurow and Schill 1996). At water temperatures less than 9–10°C, the concealment behavior of salmonids is

well documented (Cunjak 1988; McMahon and Hartman 1989; Contor and Griffith 1995; Thurow 1997). At these temperatures, salmonids become photonegative and conceal themselves during the day (Rimmer et al. 1983), while some fish emerge at night. This diurnal concealment and nocturnal emergence is well documented for a variety of salmonids, including bull trout and the *Oncorhynchus* spp. we studied (Jakober et al. 2000). Consistent with other studies, water temperature was positively related to the snorkeling efficiencies we measured for bull trout and *Oncorhynchus* spp. Because bull trout were the target species for our evaluations, we selected most sample sites in cold, high-elevation streams at the periphery of rainbow trout and cutthroat trout distributions. Thus, low water temperatures probably resulted in diurnal concealment, making fish less vulnerable to detection. Consequently, our day snorkeling counts were much lower than our night counts. In contrast, at water temperatures greater than 10°C, day and night snorkeling counts of bull and cutthroat trouts have reportedly been very similar (Bonneau et al. 1995; Thurow and Schill 1996).

The nonlinear response of bull trout night snorkeling efficiency to water temperature is more complex. The left limb of the curve (Figure 3) is consistent with the documented concealment of bull trout and other salmonids at water temperatures less than 9–10°C. The right limb of the curve, however, suggests an optimal night emergence or foraging water temperature range above which increasing numbers of bull trout remain concealed. Although, to our knowledge, this has not previously been reported, it appears to be somewhat consistent with the fundamental thermal niche of 10.2–14.2°C reported for bull trout as well as the observed high probabilities of bull trout occurrence and maximum densities at temperatures less than 13°C (Selong et al. 2001).

Underwater counts require adequate water clarity, and researchers have suggested minimum criteria ranging from 1.5 to 4.0 m (Gardiner 1984; Griffith et al. 1984; Zubik and Fraley 1988; Hillman et al. 1992). Underwater visibility significantly affected our mea-

sured day snorkeling efficiencies for bull, rainbow, and cutthroat trouts. Unlike other studies, however, that cited increased numbers of fish observed with increasing visibility, we observed day snorkeling efficiencies for all three species that were nonlinearly related to underwater visibility. For bull trout, the highest snorkeling efficiencies occurred in sites with visibilities less than 3.1 m, whereas for *Oncorhynchus* spp. the highest snorkeling efficiencies occurred in sites with visibilities from 2.5 to 3.5 m. Similar to the observed nonlinear response to pool composition, we hypothesize that in sites with high water clarity and complex habitat, salmonids may detect the snorkeler and flee before being counted.

Consistent with other studies, we found a strong positive relationship between snorkeling efficiency and fish body size across all three species and both methods (Griffith 1981; Helfman 1983; Hillman et al. 1992). Larger individuals are more visible to snorkelers, making them easier to detect and count, whereas smaller individuals may more readily conceal themselves.

Snorkeling efficiency also varied among the three salmonid species we studied. Day and night snorkeling efficiencies were lowest for bull trout smaller than 100 mm, and night snorkeling efficiency was highest for 200–350-mm bull trout. There were no detectable differences in snorkeling efficiency between rainbow and cutthroat trouts across sampling methods. Although the presence of hybrids and the misidentification of rainbow and cutthroat trouts could influence the lack of detectable differences, we hypothesize that similarities in snorkeling efficiency for rainbow and cutthroat trouts are real and correctly reflect similarities in behavior and morphology. This is consistent with previous evaluations of capture efficiency for warm-water fishes (Bayley and Austen 1990, 2002; Peterson and Rabeni 2001); generally, in these studies, capture efficiency did not detectably differ between closely related species. Capture efficiency and presumably snorkeling efficiency are influenced by morphological and behavioral traits. In our case, although rainbow trout tend to prefer moderate or faster water velocities (Everest 1969) and cutthroat trout tend to prefer pools (Ireland 1993), both rainbow and cutthroat trouts behave similarly by maintaining positions in the water column above the substrate or other submerged cover. However, some forms such as westslope cutthroat trout *O. clarkii lewisi* may be coldwater adapted (Liknes and Graham 1988) relative to rainbow trout, whose broad distribution suggests their tolerance of a wide range of conditions (Thurrow et al. 1997), potentially resulting in different concealment temperature thresholds between the species. Although additional species-specific cap-

ture efficiency information is needed, the fact that similar species may have similar efficiencies suggests that previous capture efficiency studies may be useful starting points for evaluating capture efficiencies of other species.

Implications for Sampling Strategies

Gear sampling efficiency can profoundly affect data quality. As we report here, fish size, species, and physical stream features influence snorkeling efficiency for salmonids. Failure to account for these differences could lead to spurious conclusions in observational or experimental studies as well as in attempts to monitor population abundance and distribution. For example, models relating salmonid abundance, as estimated via snorkel counts, to stream habitat characteristics would probably be biased by water temperature and visibility. Because stream temperature and underwater visibility often vary with stream discharge (Figure 6), snorkeling efficiency and, hence, snorkel counts are likely to be negatively biased during high-discharge years and positively biased during low-discharge years, thus leading to erroneous conclusions. Even if physical stream conditions can be assumed to be constant from location to location or through time, the effect of fish length on snorkeling efficiency is likely to bias bull trout demographic studies. Bull trout presence and absence data are similarly affected by snorkeling efficiency because the probability of detecting a species depends upon its probability of capture (efficiency) (Bayley and Peterson 2001). Thus, we strongly discourage the use of raw snorkel counts, and we agree with Anderson (2001) that such indices are unreliable.

Because bull trout night snorkeling efficiency was much greater than day snorkeling efficiency, some biologists may be tempted to discard the latter. However, efficiency should not be the only factor to consider when evaluating sampling methods (Bayley and Austen 2002). Sample designs need to also consider safety, costs, and logistics. Day snorkeling is inherently safer than night snorkeling, especially in streams with steep gradients, large substrate, woody debris, and cold temperatures (Thurrow and Schill 1996). It is also logistically easier to access sampling sites during the day. Consequently, although night snorkeling may be more effective in detecting the number of fish per site, day snorkeling is safer and allows sampling of many more sites than are possible to sample by night snorkeling.

Biologists may similarly be tempted to discard both day and night snorkeling in favor of electrofishing. Electrofishing surveys also have disadvantages; just as

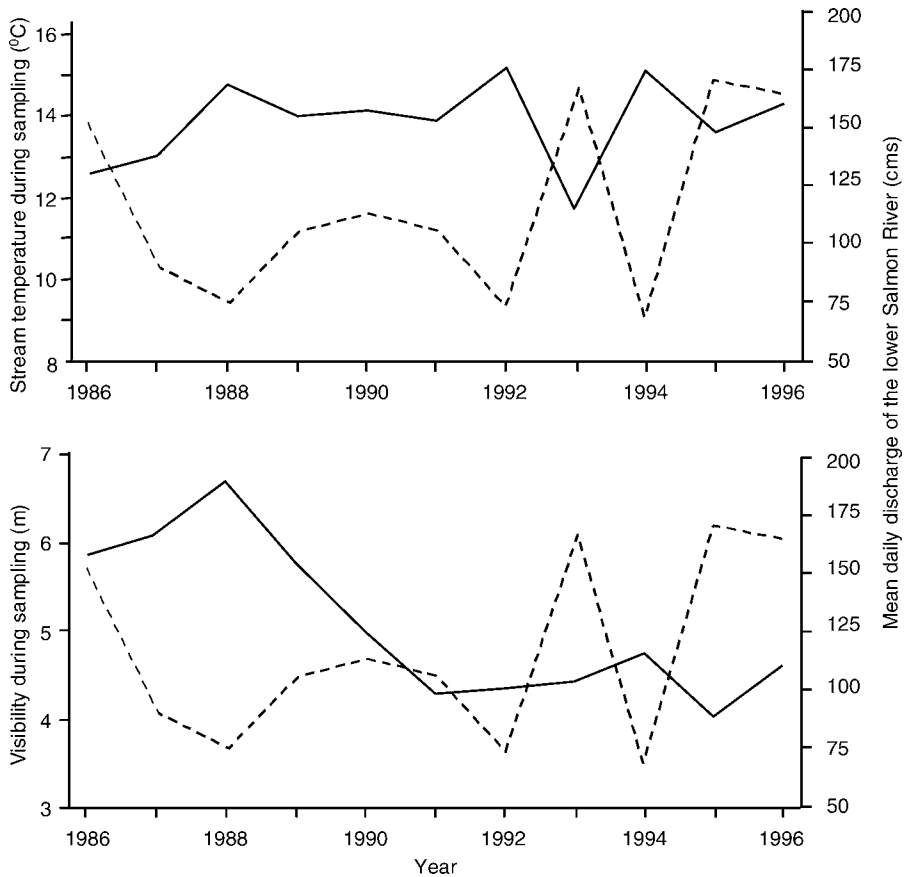


FIGURE 6.—Mean water temperature (solid line; top panel) and mean day underwater visibility (solid line; bottom panel) from 12 fish monitoring sites (Rieman et al. 1999) in the Salmon River Basin, Idaho, and mean discharge (cubic meters per second; broken lines in both panels) for the lower Salmon River during snorkel sampling from 1986 to 1996 (U.S. Geological Survey station 133155000 near French Creek, Idaho).

raw snorkeling counts are biased, unadjusted electrofishing removal methods are similarly biased, so both methods require estimates of sampling efficiency in order to be reliable estimators. Results from the 215 sites we surveyed illustrate a cost of about 2 person-hours per 100-m site to day or night snorkel and 9 person-hours per site to complete a three-pass electrofishing survey. If we assume that travel time to sites was equivalent for snorkeling and electrofishing, 40 person-hours would be required to snorkel 20 sites, whereas 180 person-hours would be needed to electrofish the same 20 sites. Mullner et al. (1998) similarly reported that snorkeling required fewer personnel and less time than depletion electrofishing. As previously noted, electrofishing may also be unsuitable for collecting fish in many of the cold, low-conductivity streams within the range of bull trout (Goetz 1994; Bonneau et al. 1995).

Unbiased estimates of bull trout abundance (number/site) or density (number/area) can be calculated by dividing snorkel counts by the estimated efficiency, provided that there are sufficient numbers of individuals present to ensure detection. Indeed, we found that the accuracy of the day and night snorkeling models was similar when at least one bull trout was detected. Very low efficiencies, such as those for day snorkeling detection of small bull trout, will likely result in high sample variance and must also be considered when designing sampling protocols. Rodgers et al. (1992) concluded that because the relative accuracy of snorkel estimates can change from stream to stream, it is important to regularly calibrate snorkel counts against other methods of estimating population size. While we agree that calibration is necessary, we further suggest that a method is needed for estimating baseline or true population abundance to ensure accurate calibrations.

A dual-gear approach that applies sampling efficiencies to estimate the baseline population has the potential to provide a rigorous method for validating snorkel counts.

Acknowledgments

Idaho and Montana crew members C. Adams, T. Adams, G. Burak, B. Clark, A. Corn, T. Essington, L. Leatherbury, B. McLean, C. Rabe, M. Rayton, J. Richardson, W. Thorson, B. Turley, D. Weigel, and F. Wong, and Washington crew members S. Adams, S. Bruce, B. Bryant, B. Boelts, S. Burdick, T. Buroker, K. Christie, D. Cox, D. Donovan, J. Kelly, N. Martins, R. Mohr, D. Morrow, R. Nauer, J. Rhone, J. Shultz, and F. Taylor provided valuable field assistance. C. Larsen (Rocky Mountain Research Station [RMRS]) and Washington Department of Fish and Wildlife (WDFW) employees M. Hallock and P. Mongillo supervised Washington field crews. C. Clancy (Montana Department Fish, Wildlife, and Parks) and M. Jakober (U.S. Forest Service [USFS]) provided key oversight in Montana. K. McDonald (USFS), J. Delavergne (U.S. Fish and Wildlife Service [USFWS]), S. Craig (USFWS), J. Polos (USFWS), and T. Jackson (WDFW) provided oversight in Washington. Funding for this research was provided by RMRS and also through Interagency Agreement numbers 134100-H002 and 134100-2-H001 between the USFWS and RMRS. We thank USFWS employees S. Spaulding, S. Butts, and K. Benkert for their support in developing and managing the agreements. This manuscript was improved with suggestions from B. Shepard, M. Jakober, and three anonymous reviewers.

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