

Observer Error Structure in Bull Trout Redd Counts in Montana Streams: Implications for Inference on True Redd Numbers

CLINT C. MUHLFELD*

Montana Fish, Wildlife and Parks, 490 North Meridian Road, Kalispell, Montana 59901, USA

MARK L. TAPER AND DAVID F. STAPLES

Montana State University, Department of Ecology, 310 Lewis Hall, Bozeman, Montana 59717-3460, USA

BRADLEY B. SHEPARD

Montana Fish, Wildlife and Parks, Montana Cooperative Fishery Research Unit, 1400 South 19th Avenue, Bozeman, Montana 59718-5417, USA

Abstract.—Despite the widespread use of redd counts to monitor trends in salmonid populations, few studies have evaluated the uncertainties in observed counts. We assessed the variability in redd counts for migratory bull trout *Salvelinus confluentus* among experienced observers in Lion and Goat creeks, which are tributaries to the Swan River, Montana. We documented substantially lower observer variability in bull trout redd counts than did previous studies. Observer counts ranged from 78% to 107% of our best estimates of true redd numbers in Lion Creek and from 90% to 130% of our best estimates in Goat Creek. Observers made both errors of omission and errors of false identification, and we modeled this combination by use of a binomial probability of detection and a Poisson count distribution of false identifications. Redd detection probabilities were high (mean = 83%) and exhibited no significant variation among observers (SD = 8%). We applied this error structure to annual redd counts in the Swan River basin (1982–2004) to correct for observer error and thus derived more accurate estimates of redd numbers and associated confidence intervals. Our results indicate that bias in redd counts can be reduced if experienced observers are used to conduct annual redd counts. Future studies should assess both sources of observer error to increase the validity of using redd counts for inferring true redd numbers in different basins. This information will help fisheries biologists to more precisely monitor population trends, identify recovery and extinction thresholds for conservation and recovery programs, ascertain and predict how management actions influence distribution and abundance, and examine effects of recovery and restoration activities.

Accurate estimates of population trends and process variation are crucial to managing for the recovery and conservation of a species (Dennis et al. 1991). Redd counts have been commonly used to monitor trends in salmonid populations (Emlen 1995; Dauble and Watson 1997; Rieman and Allendorf 2001; Gallagher and Gallagher 2005), yet few studies have evaluated the sampling error associated with redd counts (Dunham et al. 2001; Gallagher and Gallagher 2005). Uncertainties in redd counts may include observer error, error due to the timing of counts, and error due to habitat characteristics (Dunham et al. 2001). Therefore, the validity (accuracy and precision) of redd counts for monitoring abundance and ultimately population persistence must be critically assessed, as these factors may influence the ability to detect population responses associated with management activities and recovery programs (Staples et al. 2004; Dennis et al., in press).

Populations of bull trout *Salvelinus confluentus* have declined throughout much of the species' native range (Rieman et al. 1997), and bull trout are currently listed as a threatened species under the Endangered Species Act (U.S. Office of the Federal Register 1998). Declines are largely attributed to habitat degradation and fragmentation (Fraley and Shepard 1989; Rieman and McIntyre 1995; Schmetterling 2003) and interactions with nonnative salmonids (Kitano et al. 1994; Deleray et al. 1999; Rich et al. 2003). In response to the declines, the U.S. Fish and Wildlife Service is charged with developing a recovery program for conserving bull trout; the program must include recovery criteria that can be objectively measured through monitoring programs. Thus, there is a need for dependable, accurate, cost-effective, and legally defensible techniques to monitor population trends and assess status (Maxell 1999; Dunham et al. 2001).

Redd counts have commonly been used to index adult escapement and trends in the abundance and distribution of local and regional bull trout populations (Maxell 1999; Rieman and McIntyre 1995, 1996;

* Corresponding author: cmuhlfeld@mt.gov

Received May 11, 2005; accepted December 26, 2005
Published online May 30, 2006

Rieman and Myers 1997; Staples et al. 2005), and redd count data extend over 20 years for some populations. Redd counts are both less expensive and less invasive than population monitoring methods that require capture and handling of fish (i.e., electrofishing, trapping, genetic analyses, telemetry, and tagging; Dunham et al. 2001). Annual estimates of the number and distribution of redds may provide a valuable index for assessing bull trout population trends due to the temporal and stream-specific nature of spawning (Dunham and Rieman 1999) and the relative ease with which spawning redds can be counted (Maxell 1999). Bull trout spawning occurs from late August through early October, when water temperatures fall below 9°C, and takes place in low-gradient reaches that contain clean gravel, groundwater influence, and cover (Fraley and Shepard 1989). Since 1980, biologists have conducted annual redd counts to estimate escapement of large (>400 mm), migratory (e.g., fluvial and adfluvial) bull trout in several spawning and rearing streams throughout the Flathead River and Swan River basins in Montana (Fraley and Shepard 1989; Rieman and Myers 1997; Deleray et al. 1999). To our knowledge, these data represent the most consistent and extensive monitoring information for bull trout throughout their range.

Despite the widespread use of redd counts to index escapement and monitor population trends, few studies have evaluated the validity of this method for detecting trends in population size (Emlen 1995; Maxell 1999; Staples et al. 2005). Dunham et al. (2001) pointed out that the validity of raw redd counts as an index of population size relies on two key assumptions: (1) redd counts represent actual redd numbers (i.e., redds are counted with minimal error) and (2) the number of redds is related to the actual number of spawning adults. Several researchers reported that redd counts were significantly correlated with adult escapement and thus provided a relatively accurate measure of the number of reproducing individuals in the population (Beland 1996; Dunham et al. 2001; Rieman and Allendorf 2001; Gallagher and Gallagher 2005). Dunham et al. (2001), however, reported a high degree of interobserver variation in bull trout redd counts in two streams in northern Idaho and concluded that substantial improvements are necessary to reduce counting errors before redd counts will be useful for population monitoring. Maxell (1999) also suggested that the sources of counting errors should be known and minimized before redd counts are used for long-term bull trout population monitoring, because counting errors may obscure important population trends, potentially misleading conservation and recovery programs (Rieman and Meyers 1997).

While annual counts of bull trout redds may be

a practical method for monitoring bull trout populations, the observer error structure has not been well explored and no attempts have been made to adjust counts to more accurately estimate the true number of bull trout redds. An understanding of the observer error structure is necessary for using the counted number of redds to calculate an estimate of the true redd number with associated uncertainty. We evaluated observed counts of bull trout redds by experienced observers in two tributaries to the Swan River, Montana. Our objectives were to (1) describe the observer error structure in bull trout redd counts; (2) develop simple procedures for bias correction and construction of confidence intervals; and (3) apply these corrections and confidence intervals to historical annual redd counts made in Swan River tributaries from 1982 to 2004. We close with a discussion of factors that are likely to affect redd count observer error, our perspective on the validity of using redd counts as an index for assessing population trends, and recommendations for future work.

Methods

Study area.—In 2004, we determined the temporal and spatial distribution of bull trout redds and assessed observer variation in redd counts in Lion and Goat creeks, which are tributaries to the Swan River in northwestern Montana (Figure 1). The Swan River–Swan Lake system is recognized as a regional stronghold for bull trout throughout their historic range (Rieman and Myers 1997; Rieman et al. 1997), and the study streams support relatively strong migratory bull trout populations in the upper Flathead River and Swan River systems in Montana (Fraley and Shepard 1989; Deleray et al. 1999; Muehlfeld and Marotz 2005). Both streams flow through cedar valley bottoms that contain complex stream habitat consisting of pools and riffles with abundant amounts of large woody debris (LWD). From 1982 to 2004, the number of redds counted by annual surveys averaged 102 in Lion Creek (range = 26 in 1985 to 190 in 1997) and 51 in Goat Creek (range = 17 in 1992 to 91 in 2001). Habitat complexity and redd densities in the two study streams represent moderate to difficult conditions for counting redds in the Swan River and Flathead River systems (Tom Weaver, Montana Fish, Wildlife, and Parks [MFWP], personal communication).

Bull trout exhibit a migratory life history strategy (e.g., fluvial and adfluvial) in the upper Flathead River and Swan River systems (Fraley and Shepard 1989), although a resident form may exist. Bull trout grow to maturity in the lake or river system and then begin spawning migrations during May–July, traveling 88–250 km upriver to natal tributaries. Spawning occurs during late August through early October (Fraley and

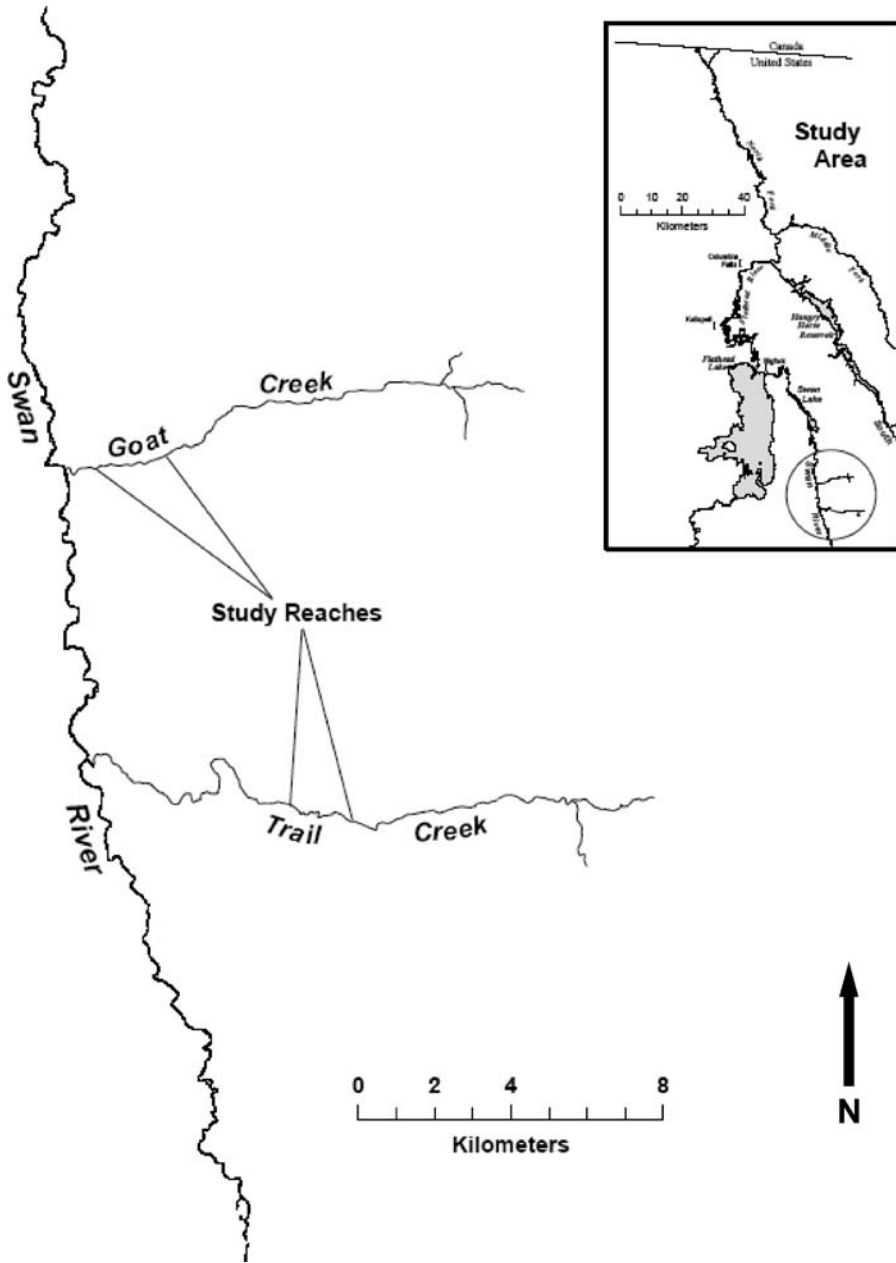


FIGURE 1.—Study streams and sample reaches in the Swan River drainage, Montana.

Shepard 1989). Juveniles rear in natal spawning and rearing streams for 1–4 years and then emigrate (primarily during high spring flows) to the river or lake (e.g., subadult phase; Shepard et al. 1984; Muhlfeld and Marotz 2005).

Observer variation in redd counts.—Seven weekly surveys were conducted to track the accumulation of migratory bull trout redds in 2-km study reaches in

both Lion Creek (7 September–18 October) and Goat Creek (7 September–19 October). Study reaches were chosen to reflect typical spawning habitat conditions in each stream. Each week, the same experienced observer walked in the middle of the stream, mapping locations of individual redds. Each redd was flagged and numbered, and locations were recorded on field maps and with a handheld Global Positioning System

unit. Redds were recorded if a definite pit and tailspill were visible (Burner 1951; Crisp and Carling 1989), and spawning fish were frequently observed and noted. Counts from the accumulation study served as the best estimate of the "true" number of redds.

We assessed the variation in bull trout redd counts among seven experienced observers in the study reaches of Lion and Goat creeks on 6 October 2004. We selected observers that had counted bull trout redds for at least 10 years (mean = 18 years; range = 10–26 years). For comparative purposes, we followed the field methodology reported by Dunham et al. (2001). Briefly, all flags that identified redd locations were removed prior to the replicate counts, and none of the observers had prior knowledge of redd locations. Each study reach was divided into 10 subreaches that were approximately 200 m long, and the upper limit of each subreach was marked with flagging on both banks and on tree limbs across the channel. Detailed maps of each reach were drawn to scale, and key channel and habitat features were noted, including subreach boundaries, LWD pieces, debris jams, large boulders, islands, side channels, braids, and point bars. Prior to the replicate counts, observers were given a brief presentation on redd identification. Observers were provided maps of each study reach (broken into 200-m subreaches) and independently walked in the middle of the stream and marked redd locations on the maps. The next day, the independent observer that tracked redd accumulations (i.e., true redd number) re-surveyed the study reaches and evaluated observer error for each individual observer's counts in each subreach.

The redd numbers and locations identified by each observer were compared with the true numbers and locations to assess (1) the number of true redds that were correctly identified, (2) the number of true redds that were missed (omissions), and (3) false counts of areas of gravel that were not bull trout redds (false identifications). These two types of counting errors imply that an observed redd count is actually the sum of two random processes: the number of true redds detected plus the number of false identifications recorded. False identifications were classified as being caused by flow hydraulics, scrapes (incomplete redds), superimposed areas, and animal or human prints.

Based on our observation of two distinct types of observer error, we modeled observed redd counts as the sums of two independent, discrete random variables: the number of actual redds that were detected plus the number of false identifications. The simplest assumption possible regarding the detection of true redds is that each redd has an independent and equal chance of being detected. This assumption implies that observed redds will be binomially distributed. The simplest

assumption for false identifications is that false identifications occur with uniform probability along the stream—that is, each small increment of stream length has an equal and independent probability of holding a false identification. This assumption implies that false identifications should have Poisson distributions.

The adequacy of these models can be tested by seeing whether either the observed means or variances in counts (either among subreaches, observers, or streams) differ significantly from what is expected based on the models. Failure of these dispersion tests would suggest that more complex models for these random processes should be investigated. The binomial distribution is useful in this context because it directly incorporates the parameter of most interest (the true number of redds in the stream) and a parameter for detection rates that can be adjusted if detection rates are not constant (i.e., a beta binomial distribution). The Poisson distribution is appropriate because false identification rates were uncorrelated with the number of redds present and were constant among reaches and observers (see below), which suggests that false identifications are solely a function of the length of stream sampled. A negative binomial could be used if false count rates were found to be different among streams or observers.

Data analysis.—Potential associations between the number of true redds and both omissions and false identifications within each subreach were evaluated by use of Pearson's correlation analysis. We used a *t*-test to determine between-stream differences ($\alpha = 0.05$) in estimated detection probabilities averaged across observers. Because false identifications were uncorrelated with redd density, we used sample means of Poisson counts to test for differences in false identification rates between streams (Zar 1996).

To test whether detection probabilities were constant among reaches and observers, we calculated the variances of the estimated probability (*p*) of detecting a true redd (1) among 200-m subreaches in each creek after averaging *p* across all observers for every subreach where there was at least one true redd and (2) among observers pooled across the two creeks. We evaluated whether the observed variance of *p* among subreaches or among observers was overdispersed by simulating a bootstrapped distribution (Efron and Tibshirani 1993; Davison and Hinkley 1997) of the variability in *p*-estimates given a constant *p*. Overdispersion of estimated variances (i.e., the observed variability in *p* is higher than expected) would indicate that detection probabilities were changing among different subreaches or among observers. To test for overdispersion among observers, we simulated a true

redd number (T) of 55 and a p of 0.83, representing Goat and Lion creeks combined. A binomial model was used to generate 10,000 samples, each with seven observations. Observed detection probabilities and their variance were calculated for each sample to obtain a bootstrapped distribution for the variance of seven estimates of p given a constant p . We then compared the observed variance in estimates of p among observers to the bootstrapped distribution. Similarly, we simulated a bootstrapped distribution of the variance of p -estimates among subreaches (pooled across observers); in this case, each of the 10,000 samples consisted of 20 estimates of p from a binomial with p equal to 0.826 and T varying according to the true number of redds in each section. We performed a similar simulation analysis to evaluate overdispersion in false identifications among observers and reaches.

With this dual error structure, observed redd counts are modeled as

$$R = A + F, \quad (1)$$

where R is the counted number of redds, A follows the binomial distribution (T, p), and F follows the Poisson distribution (λd), λ being the rate of false counts per kilometer and d the distance sampled (km).

Redd count data simulated with this binomial/Poisson model indicated that redd counts (and the log of redd counts) were approximately normally distributed; the closeness of this approximation and whether raw or log counts were more "normally distributed" depended on the number of true redds and the rate of false counts.

The dual error structure in redd counts leads to a change in redd count bias depending on the frequency of true redds in the sampled tributary. This occurs because although the number of true redds missed in a redd count is a function of the actual number of true redds present in the stream, the number of false counts is dependent only on the length of stream sampled. At certain frequencies of redds, the number of true redds missed will exactly equal the number of false counts added (i.e., $T[1 - p] = \lambda d$), and thus the expected value of the observed redd count will equal the true number of redds. However, at very low redd frequencies, there will be relatively few missed redds relative to the expected number of false counts (i.e., $T[1 - p] < \lambda d$), because false counts are only dependent on the length of stream sampled. In this case, the expectation of the observed redd count will be larger than the number of true redds. Conversely, observed redd counts are expected to be lower than true redd numbers when redds are numerous. At such high redd frequencies, many more true redds are missed than are added due to false counts (i.e., $T[1 - p] > \lambda d$).

Application to Swan River drainage redd counts.—The parameter of interest is T in a stream for which there are data on R . Under the dual error structure, the expected value of an observed redd count is $Tp + \lambda d$ and its associated variance is $Tp(1 - p) + \lambda d$. If λ and p are assumed to be known and constant, the pseudo-likelihood (Hall 1990) estimate of the mean number of true redds given an observed count (T') is equal to $(R - \lambda d)/p$, and its associated variance is $[T'p(1 - p) + \lambda]/p^2$. Confidence intervals can be calculated with standard methods under the assumption that redd counts are approximately normally distributed.

Bull trout redd counts have been made annually since 1982 in approximately 34 km of spawning habitats in Lion, Goat, Elk, and Squeezer creeks in the Swan River drainage (Deleray et al. 1999). Final counts were conducted in October in Goat and Lion creeks after weekly assessments of spawning activity at known spawning areas to ensure that most of the spawning adults spawned. We used these annual redd counts to estimate the expected true numbers of redds and to calculate their associated confidence intervals based on mean estimates of p and λ from the present study.

Results

Timing of Spawning

Bull trout spawning activity peaked in September, and redd construction ended in early October. In 2004, bull trout spawning activity peaked in late September in Goat Creek and probably during early September in Lion Creek, and no new redds were observed after early October (Figure 2). We were unable to determine exactly when bull trout began spawning in Lion Creek, as we counted 22 redds on the first survey (7 September), which was the maximum number of newly observed redds that were detected during the study period. Bull trout spawned as mean daily temperatures gradually declined below 8°C in Goat and Lion creeks, and no new redds were encountered once the mean daily temperatures declined below 6°C. We counted a total of 45 redds in Lion Creek and 10 redds in Goat Creek in the study reaches.

Observer Variation in Redd Counts

The variation in bull trout redd counts among observers was low in Goat (range = 9–13) and Lion (range = 35–48) creeks in 2004. Redd counts within the 2-km study reach in Goat Creek were 90–130% of the best estimate of 10 redds; counts in Lion Creek were 78–107% of the best estimate of 45 redds (Figure 3). Although variation in counts was low, observers made

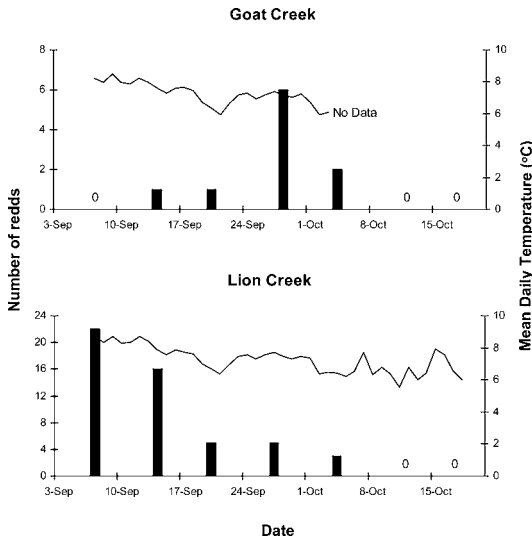


FIGURE 2.—Bull trout redd accumulations (bars) versus mean daily water temperature (°C; lines) in Goat and Lion creeks, Montana, during fall 2004.

errors both of omission and false identification, and these errors often offset each other (Figure 3).

The true number of redds within subreaches was not correlated with the number of false identifications, supporting the assumption of the independence of these processes ($r = 0.18$; $P > 0.1$); however, the true redd number was strongly correlated with the number of omissions ($r = 0.80$; $P < 0.01$; Figure 4), as predicted by the assumption of a binomial distribution. The redd detection probability averaged across observers within subreaches ranged from 0.71 to 1.00 and was not significantly correlated ($r = -0.37$; $P > 0.1$) with the actual number of redds (Figure 5). Redd detection probabilities averaged across observers were relatively high in both streams—0.82 (SD = 0.09) in Lion Creek and 0.84 (SD = 0.08) in Goat Creek—and were not significantly different between the two creeks (t -test: $P = 0.50$). The overall mean detection probability for observers was 0.83 (SD = 0.08). Observer detection probabilities were slightly overdispersed relative to the bootstrapped distribution of variance in p estimates ($P = 0.08$), indicating that redd detection probabilities might have differed slightly among observers. Variation in detection probabilities was not overdispersed among subreaches ($P = 0.32$).

There was no significant difference ($P = 0.23$) in false identification rates between Lion (average = 1.0 false identification/km) and Goat creeks (0.75 false identifications/km). Variation in false identification rates among subreaches ($P = 0.46$) or among observers ($P = 0.22$) was not significantly different than the

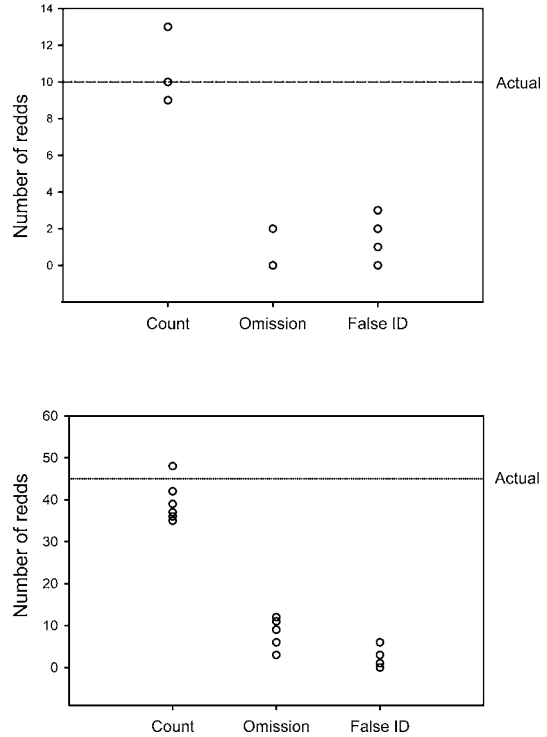


FIGURE 3.—Counts of bull trout redds, actual redds missed by observers (omission), false redd identifications made by observers (false ID), and actual numbers of redds (horizontal dotted lines) in Goat (top panel) and Lion creeks (bottom panel), Montana. There were seven observers in each creek, and some of the points overlap.

bootstrapped distribution of variance in λ , indicating that false identification rates were relatively consistent among stream reaches and among observers.

Applications to Swan River Drainage Redd Counts

For the Swan River drainage data, the frequency at which missed redds equaled false counts was approximately 5 redds/km. Because true redd frequencies have generally been quite high in bull trout spawning areas monitored within the Swan River basin since 1982, only the 1985 redd count is larger than the estimated expected number of true redds in these spawning areas (Figure 6). The 1982 redd count (193) was nearly equal to the estimated mean (200), suggesting that the point at which the direction of bias shifts is close to 190 redds in these monitored spawning areas. Many counts were much lower than the estimated mean number of redds. For example, the 1998 index count (612) was not only much less than the estimated mean true number (711) but also was lower than the lower end of the estimated 95% confidence interval for true redds (683). We should

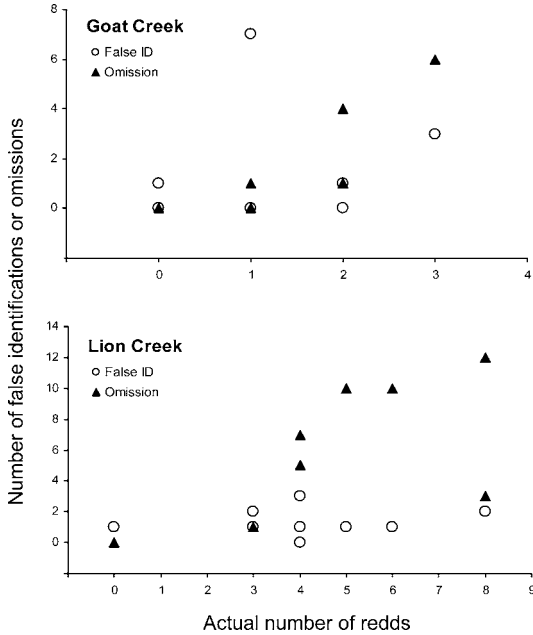


FIGURE 4.—Number of false identifications (false ID) and omissions of bull trout redds, summed across observers ($N = 7$ for both Goat and Lion creeks), versus the actual number of redds in Goat (top panel) and Lion Creek (bottom panel) subsections. Subsections were classified by the number of actual redds for each creek.

note that this analysis is contingent on assumptions that true detection probabilities and false count rates were similar to those we estimated in Lion and Goat creeks and have remained constant over time.

Discussion

Redd counts have been commonly used to monitor trends in bull trout populations, and these data have often been used to develop recovery and monitoring

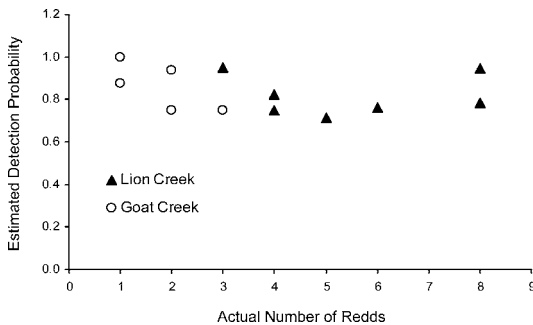


FIGURE 5.—Average estimated probability of detection of bull trout redds versus the actual number of redds for each subsection in Lion and Goat creeks, Montana. Five subsections had no true redds and were omitted.

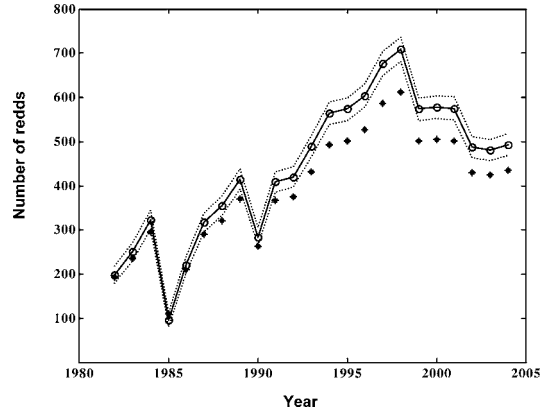


FIGURE 6.—Estimated true bull trout redd numbers for historic index redd counts in the Swan River drainage, Montana. Stars represent index redd counts, open circles mean estimated true redd numbers, and dotted lines 95% confidence intervals for the true redd numbers.

programs for this threatened species. However, few studies have examined the uncertainties in observed counts to assess whether redd counts are a valid technique for monitoring population abundance over time. We assessed variability in migratory bull trout redd counts among experienced observers in northwestern Montana and found substantially lower observer variability in bull trout redd counts than that seen in previous studies (Bonneau and LaBar 1997; Dunham et al. 2001). These results suggest that redd counts may be a viable tool for monitoring trends in migratory bull trout populations if experienced observers are used to conduct the counts.

Observer Variation in Redd Counts

Our results and the findings of Dunham et al. (2001) suggest that experience may influence observer error in bull trout redd counts. Observers in our study had 10–26 years of experience (mean = 18 years) monitoring migratory bull trout redds in the Swan River and Flathead River systems, whereas most observers in the Dunham et al. (2001) study were novices. Dunham et al. (2001) suggested that observer inexperience, among other factors, probably accounted for their high counting error rates. Similarly, Hemmingsen et al. (2001b) found that variation in observed bull trout redd counts was higher for novice observers than for experienced surveyors in Oregon streams. Redd frequencies were also different between Dunham et al.'s (2001) study reaches and ours, as we studied observer error in streams that contained lower redd frequencies (5 redds/km in Goat Creek and 22.5 redds/km in Lion Creek) as compared to the study in Idaho (up to 62 redds/km). Also, our study and Dunham et

al.'s (2001) study found that detection error commonly occurred in areas where superimposition was prevalent, which is common within and among salmonid species (Hayes 1987; Essington et al. 1998; Taniguchi et al. 2000). Thus, redd superimposition may have been less common in our study streams, making it easier for observers to identify individual redds. Other factors include (but are not limited to) the color and size of the substrate (Kondolf and Wolman 1993; Kondolf et al. 1993; Hemmingsen et al. 2001a), stream productivity (Hemmingsen et al. 2001a; Moore et al. 2004), habitat complexity (Dunham et al. 2001; Wissmar and Craig 2004), water visibility and flow (Gallagher and Gallagher 2005), redd age (Dunham et al. 2001; Gallagher and Gallagher 2005), redd size (Hemmingsen et al. 2001a), and, possibly, weather conditions and the physical and mental state of the observers. Nonetheless, we believe that observer experience in counting bull trout redds is the primary factor influencing observer error, because experience enables observers to discern actual redds from streambed features, such as scour and alluvial deposits, and to distinguish redds of sympatric species (Taniguchi et al. 2000) such as introduced brook trout *S. fontinalis* (Kitano et al. 1994) based on redd size, depth, and substrate characteristics (Gallagher and Gallagher 2005).

Life history variation may limit the utility of redd counts as abundance monitoring tools. In our study, redd counts occurred in streams dominated by migratory bull trout that excavated large areas of the streambed due to their large body size (>400 mm; Fraley and Shepard 1989; Rieman and Myers 1997; Deleray et al. 1999). In contrast, in systems that contain small resident fish, redds may go undetected due to their small size and location in the watershed (e.g., steep headwater areas versus low-gradient, alluvial valley bottom reaches) or they may be classified as test digs or small disturbances in the gravel (Al-Chokhachy et al. 2005). The difficulty in detecting redds constructed by small resident fish may therefore prevent or limit managers from accurately monitoring adult abundance. Nonetheless, our results suggest that redd counts may be a viable tool for monitoring trends in migratory bull trout populations.

Uncertainties in redd counts may be related to error associated with the timing of redd counts. We found that bull trout spawning activity peaked in September and that redd construction ended in early October. Similarly, Dunham et al. (2001) observed peak bull trout spawning activity in September and early October in two streams in northern Idaho. Many long-term monitoring programs rely on annual redd count data that are presumed to be collected at or near the end of

the spawning season (Beland 1996; Rieman and Myers 1997; Isaak et al. 2003). Our results suggest that counts in the Swan River system should not be conducted until October to ensure that most of the spawning adults have spawned. However, salmonid life history traits, such as migration timing, may vary among individual spawning populations (Gresswell et al. 1994; Rieman and McIntyre 1996) due to physical and biological characteristics of the environment (i.e., aspect, temperature; Gresswell et al. 1997). Therefore, the timing of redd counts should be determined for each population of interest through periodical surveys to ensure that most of the reproductive adults are represented in the counts. Also, we recommend that counts be conducted no later than late October in the Swan River system to reduce possible counting error due to flow conditions, water visibility, the formation of algal growth and aufwuchs (Hemmingsen et al. 2001a; Moore et al. 2004), redd age (Dunham et al. 2001; Gallagher and Gallagher 2005), and several other factors mentioned herein. Dunham et al. (2001) found that observers tended to miss older redds, something that we also observed but did not quantify in our study. Gallagher and Gallagher (2005) found that observer efficiency in counting redds of Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* was significantly associated with streamflow and water visibility. In many bull trout streams in the Pacific Northwest, flows and turbidity may increase in the fall because of rain or snowmelt conditions (Rieman and McIntyre 1996), which may preclude accurate identification of bull trout redds by reducing visibility.

Dunham et al. (2001) recognized two sources of observer error in bull trout redd counts: omissions and false identifications. We found that these two types of errors have different distributions; we used a best-fit approach to combine these distributions based on a binomial probability of detection and a Poisson count distribution of false identifications. We found that redd detection probabilities were high (mean = 83%) and quite constant among observers. We performed several statistical tests that evaluated the appropriateness of the binomial and Poisson distributions, only finding weak evidence that detection rates differed among observers. Nevertheless, our statistical analyses revealed that the binomial/Poisson redd count model is an appropriate approximation of redd count observer error; however, the potential for high interobserver variability reiterates the importance of using experienced observers.

Application to Swan River Drainage Redd Counts

We found that modeled error rates could be applied to monitoring redd counts to correct for sampling error,

thus deriving more accurate estimates of redd numbers. The bias in raw redd counts will depend on the frequency of true redds because omissions are proportional to true redd numbers, while false identifications appear to be independent of redd frequency. For the observers we tested in the Swan River drainage, our results suggested that at true redd frequencies of 5 redds/km, redd counts accurately estimated the true number of redds because errors of omission and false identification canceled each other out. Conversely, at redd frequencies lower than 5 redds/km, sample counts overestimated the true number of redds, and at frequencies higher than 5 redds/km, sample counts underestimated actual redd numbers. Although the errors of omission and false identification cancelled each other out in our study streams, we did not evaluate redd frequencies lower than 5 redds/km. Future research should investigate observer errors in areas with low redd frequencies to determine whether observer error rates differ from our estimates.

The information in this study was used to correct bias in a historical redd count data set with associated uncertainty. Estimates of true redd numbers in the Swan River population show that observed redd counts are likely to be lower than the actual number of redds present. In contrast, in systems with low redd abundances, redd counts may overestimate the true redd number due to false positives. These findings may have strong implications for evaluating a population's current status, especially for populations at low abundances, such as many bull trout populations throughout the species' range. Threatened populations will probably be present at low abundances with concomitant low redd frequencies, where redd counts could tend to overestimate the number of true redds. Overestimation of the true population when a population is low and potentially declining may have serious consequences for fish managers trying to conserve threatened populations. This conclusion is conditional on the p and λ estimates from the study streams in the Swan River system and the validity of applying them elsewhere.

Habitat complexity and the availability of suitable spawning habitat may influence observer error in bull trout redd counts. We evaluated observer counts in complex stream habitat (i.e., abundant amounts of LWD) that contained high redd densities. Observer error rates may differ under a wider range of habitat conditions. For example, in the North Fork Flathead River system, redd counts are conducted in streams that (1) contain relatively lower redd abundances, (2) do not contain as much wood, and (3) are interspersed with long tracts of unsuitable bull trout spawning habitat; however, these areas are included in annual monitoring

counts. Therefore, future evaluations of observer error should focus on bull trout streams that vary in habitat conditions; to avoid overestimating the number of false identifications, our estimates of observer error should be applied only to the monitoring of reaches where surveyors actually count redds.

It is important to recognize that the pseudo-likelihood confidence intervals that we constructed do not incorporate uncertainty in the estimates of p and λ and consequently will have lower coverage than their nominal levels. Uncertainty in the rate of false counts will have the largest effect on uncertainty and bias in estimates of true redd abundances for threatened populations, while uncertainty in detection rates will have a stronger influence on estimates and intervals for populations with higher abundances.

Ferrari and Taper (in press) used a joint-likelihood method to incorporate external data on the magnitude of measurement error into the time series analysis of redd counts. The joint-likelihood approach constructs more accurate confidence intervals than pseudo-likelihood and might be applicable to the more realistic models of observation error used in this paper. Another potential method for incorporating uncertainty in p and λ in redd estimate confidence intervals would be to resample p and λ from their sampling distributions and to calculate confidence limits for each sampled pair of parameters by use of the pseudo-likelihood approach described in this paper. Quantiles of the distribution of these individual limits may be useful in constructing confidence intervals with better statistical properties. This should be investigated in future studies.

Our study did not assess the relationship between adult abundance and redd number, which is another potential source of error when redd counts are used to estimate adult abundance (Dunham et al. 2001). However, several researchers have reported that redd counts were significantly correlated with the abundances of spawning bull trout (Dunham et al. 2001; Rieman and Allendorf 2001) and other salmonid species (Beland 1996; Gallagher and Gallagher 2005) and thus provide a relatively accurate measure of the number of reproducing adults in the population. While we recognize that this is a problem, we believe that redd number and the number of reproductive adult females are highly correlated, as was documented for Atlantic salmon *Salmo salar* (De Gaudemar et al. 2000), suggesting that redd counts can provide a useful measure of reproductive adult female abundance and the demographic potential of the population.

Overall, our corrected redd counts with confidence intervals indicated that redd frequencies have increased in the Swan River drainage since 1982. The Swan River represents arguably one of the strongest

metapopulations of bull trout within the species' current range. The corrected counts will be useful to ascertain and more accurately predict how density-dependent and density-independent factors influence the distribution and abundance of bull trout in the Swan River system (Baxter et al. 1999) through population viability analysis and viable population monitoring (Staples et al. 2004, 2005). This may be especially important because MFWP recently discovered non-native lake trout *S. namaycush* in Swan Lake (MFWP, Kalispell, unpublished data), and it will be important to track potential changes in bull trout abundance after this discovery.

Conclusions and Recommendations

We recognized two sources of observation error and applied estimates of these to historical redd counts to obtain more accurate estimates of escapement. While we observed minimal differences between streams and observers in counting error rates, the spatial scale of our study was small. This study should be repeated under different environmental and habitat conditions, levels of observer experience, and temporally over many spawning seasons. Our study streams contained complex habitats that contained numerous bull trout redds and thus represented difficult conditions for evaluating observation error. Because we found that observer variation in redd counts was lower than those of previous studies, we recommend that long-term monitoring programs use experienced observers to collect annual redd count data. Further, inexperienced observers should undergo extensive field training with experienced observers to track individual redds and redd accumulations over as much of the spawning season as possible to ensure consistency and accuracy in data collection and allow calibration of results from inexperienced observers.

In summary, we found that observer variation in migratory bull trout redd counts was low for experienced observers in Montana streams. When coupled with the results of Dunham et al. (2001), which show that redd counts and escapement are significantly related, our data indicate that redd counts can accurately monitor migratory bull trout populations for recovery and conservation programs if experienced observers conduct the annual counts. We found that errors of omission and false identification have different consequences that may obscure the ability to detect population trends. We also found that modeled error rates could be applied to redd count data to correct for sampling error and to derive more accurate estimates of redd number and its associated confidence interval. Consequently, future studies should assess both sources of error to allow valid inference on true

redd counts in different river systems. This information will help fisheries biologists to more precisely monitor population trends, identify recovery and extinction thresholds for conservation and recovery programs, ascertain and predict how management actions influence distribution and abundance, and examine the effects of recovery and restoration activities.

Acknowledgments

We thank Bonneville Power Administration and Montana Fish, Wildlife and Parks for providing funding. We thank Steve Glutting, Rick Hunt, Durae Daniels, Brian Marotz, Jon Cavigli, Mark Deleray, Scott Rumsey, John Fraley, Scott Hawxhurst, and Tom Weaver for their assistance in counting redds and implementation of this study.

References

- Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. *North American Journal of Fisheries Management* 25:1505–1512.
- Baxter, C. V., C. A. Frissell, and R. F. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. *Transactions of the American Fisheries Society* 128(5):854–867.
- Beland, K. F. 1996. The relationship between redd counts and Atlantic salmon (*Salmo salar*) parr populations in the Dennys River, Maine. *Canadian Journal of Fisheries and Aquatic Sciences* 53:513–519.
- Bonneau, J. L., and G. LaBar. 1997. Interobserver and temporal bull trout redd count variability in tributaries of Lake Pend Oreille, Idaho. Department of Fisheries and Wildlife, University of Idaho, Completion Report, Moscow.
- Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. *U.S. Fish and Wildlife Fishery Bulletin* 52:97–110.
- Crisp, D. T., and P. A. Carling. 1989. Observations of the siting, dimensions, and structure of salmonid redds. *Journal of Fish Biology* 34:119–134.
- Dauble, D. D., and D. G. Watson. 1997. Status of fall Chinook salmon populations in the mid-Columbia River, 1948–1992. *North American Journal of Fisheries Management* 17:283–300.
- De Gaudemar, B., S. L. Schroder, and E. P. Beall. 2000. Nest placement and egg distribution in Atlantic salmon redds. *Environmental Biology of Fishes* 57:37–47.
- Davison, A. C., and D. V. Hinkley. 1997. *Bootstrap methods and their application*. Cambridge University Press. Cambridge, UK.
- Deleray, M., L. Knotek, S. Rumsey, and T. Weaver. 1999. Flathead Lake and river fisheries status report. Montana Department of Fish, Wildlife and Parks, Federal Aid in Fish Restorations, Report F-78-R-1-5, Kalispell.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for

- endangered species. *Ecological Monographs* 61:115–143.
- Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. In press. Estimating density dependence, process noise, and observation error. *Ecological Monographs*.
- Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9:642–655.
- Dunham, J., B. Rieman, and K. Davis. 2001. Sources and magnitude of sampling error in redd counts for bull trout. *North American Journal of Fisheries Management* 21:343–352.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York.
- Emlen, J. M. 1995. Population viability of the Snake River Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 52(7):1442–1448.
- Essington, T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences* 55(10):2310–2316.
- Ferrari, M., and M. L. Taper. In press. Improving estimates of process variation in time series using external information on measurement error. *Environmental and Ecological Statistics*.
- Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and river system, Montana. *Northwest Science* 63:133–143.
- Gallagher, S. P., and C. M. Gallagher. 2005. Discrimination of Chinook salmon, coho salmon, and steelhead redds and evaluation of the use of redd data for estimating escapement in several unregulated streams in northern California. *North American Journal of Fisheries Management* 25:284–300.
- Gresswell, R. E., W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. *Canadian Journal of Fisheries and Aquatic Sciences* 5(Supplement 1):298–309.
- Gresswell, R. E., W. J. Liss, G. L. Larson, and P. J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. *North American Journal of Fisheries Management* 17:1046–1064.
- Hall, P. 1990. Pseudo-likelihood theory for empirical likelihood. *Annals of Statistics* 18:121–140.
- Hayes, J. W. 1987. Competition for spawning space between brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* 44(1):40–47.
- Hemmingsen, A. R., S. L. Gunckel, J. K. Shappart, B. L. Bellerud, D. V. Buchanan, and P. J. Howell. 2001a. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon, 1997. Annual Report to the Bonneville Power Administration, Project 199505400, Portland, Oregon.
- Hemmingsen, A. R., S. L. Gunckel, B. L. Bellrud, and P. J. Howell. 2001b. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon, 1998. Annual Report to the Bonneville Power Administration, Project 199505400, Portland, Oregon.
- Isaak, D. J., R. F. Thurow, B. E. Rieman, and J. B. Dunham. 2003. Temporal variation in synchrony among Chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 60:840–848.
- Kitano, S., K. Maekawa, S. Nakano, and K. D. Fausch. 1994. Spawning behavior of bull trout in the upper Flathead drainage, Montana, with special reference to hybridization with brook trout. *Transactions of the American Fisheries Society* 123(6):988–992.
- Kondolf, G. M., M. J. Sale, and M. G. Wolman. 1993. Modification of fluvial gravel size by spawning salmonids. *Water Resources Research* 29:2265–2274.
- Kondolf, G. M., and M. G. Wolman. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 27:2275–2285.
- Maxell, B. A. 1999. A prospective power analysis on the monitoring of bull trout stocks using redd counts. *North American Journal of Fisheries Management* 19:860–866.
- Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia* 139:298–308.
- Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. *North American Journal of Fisheries Management* 25:797–810.
- Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. *North American Journal of Fisheries Management* 21:756–764.
- Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath basins. *North American Journal of Fisheries Management* 17:1111–1125.
- Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society* 124:285–296.
- Rieman, B. E., and J. D. McIntyre. 1996. Spatial and temporal variability in bull trout redd counts. *North American Journal of Fisheries Management* 16:132–141.
- Rieman, B. E., and D. L. Myers. 1997. Use of redd counts to detect trends in bull trout (*Salvelinus confluentus*) populations. *Conservation Biology* 11:1015–1018.
- Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. *North American Journal of Fisheries Management* 23:721–731.
- Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the Upper Flathead River Basin, Montana. Montana Department of Fish, Wildlife, and Parks, Final Report for EPA under Contract Number R008224–01–5, Helena.
- Staples, D. F., M. L. Taper, and B. Dennis. 2004. Estimating population trend and process variation for PVA in the presence of sampling error. *Ecology* 85:923–929.

- Staples, D. F., M. L. Taper, and B. B. Shepard. 2005. Viable population monitoring. *Conservation Biology* 19(6): 1908–1916.
- Taniguchi, Y., Y. Miyake, T. Saito, H. Urabe, and S. Nakano. 2000. Redd superimposition by introduced rainbow trout, *Oncorhynchus mykiss*, on native charrs in a Japanese stream. *Ichthyological Research* 47:149–156.
- U.S. Office of the Federal Register. 1998. Endangered and threatened wildlife and plants; determination of threatened status for the Klamath River and Columbia River distinct population segments of bull trout. *Federal Register* 63:111(10 June 1998):31647–31674.
- Wissmar, R. C., and S. D. Craig. 2004. Factors affecting habitat selection by a small spawning charr population, bull trout, *Salvelinus confluentus*: implications for recovery of an endangered species. *Fisheries Management and Ecology* 11:23–31.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd edition. Prentice-Hall, Englewood Cliffs, New Jersey.