Sources and Magnitude of Sampling Error in Redd Counts for Bull Trout

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Abstract.—Monitoring of salmonid populations often involves annual redd counts, but the validity of this method has seldom been evaluated. We conducted redd counts of bull trout Salvelinus confluentus in two streams in northern Idaho to address four issues: (1) relationships between adult escapements and redd counts; (2) interobserver variability in redd counts; (3) sources of interobserver variability; and (4) temporal and spatial variation in spawning activity. We found that estimated adult escapements and redd counts were strongly correlated on a logarithmic scale, but both sources of data probably contained large estimation or observation errors. In particular, redd counts varied significantly among observers in replicate counting trials. Observer counts ranged between 28% and 254% of the best estimates of actual redd numbers. Counting errors included both omissions and false identifications. Correlations between counting errors and redd and habitat characteristics were highly variable and provided limited insights into potential causes of sampling error. Finally, we found significant spatial and temporal variability in spawning activity, which should be considered in establishing index areas for redd counts and the timing of counts. Our results suggest substantial improvements are needed to make redd counts and unbiased estimates of adult escapement more useful for population monitoring.

Bull trout *Salvelinus confluentus* are a conservation concern throughout most of their range in North America (Campbell 1998; U.S. Fish and Wildlife Service 1998, 1999). Much of what is known about the dynamics of bull trout populations comes from redd counts that have been used in a number of contexts, ranging from assessments of population trends and extinction risk (e.g., Rieman and McIntyre 1993; Rieman and Myers 1997) to analyses relating spatial variability in natural processes and human disturbance (e.g., Rieman and McIntyre 1996; Baxter et al. 1999).

Redd counts offer several advantages for population monitoring. They are much less expensive than alternative methods used to inventory bull trout populations (e.g., underwater observation, tagging, trapping, weirs, and genetics). Thus, with limited resources it is possible to conduct redd counts for a greater number of populations over longer periods. Redd counts also may be less disruptive or invasive to bull trout populations than other methods. Finally, many time series of redd counts for bull trout now extend over 15 years, which exceeds available information on popula-

tion size from other sources (Rieman and McIntyre 1993, 1996; Rieman and Myers 1997).

Most time series of redd counts are from populations of predominantly migratory bull trout, which are generally large (400–700 mm fork length; Rieman and McIntyre 1993); the females disturb a considerable amount of substrate during redd construction. These large excavations may be easily observed because spawning generally occurs from August to November (Rieman and McIntyre 1993), and stream discharges are usually low enough to allow good visibility of stream bottoms and redds. The apparent ease of identifying redds has led to a generally uncritical acceptance of redd counts for monitoring populations of migratory bull trout and many other species of salmonids.

The validity of redd counts depends on at least two assumptions: that counts are representative of actual redd numbers (i.e., redds are counted with minimal error) and that numbers of redds reflect population status. We are aware of little evidence to support the first assumption (Rieman and McIntyre 1996; Bonneau and LaBar 1997). Substantial counting errors may obscure important trends (e.g., Rieman and Myers 1997; Maxell 1999) and lead to uncertainty that could compro-

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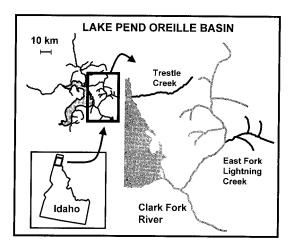


FIGURE 1.—Bull trout study streams, Trestle Creek and East Fork Lightning Creek, in the Lake Pend Oreille basin of northern Idaho.

mise conservation of the species. There is some evidence from other salmonids that provides support for the second premise. Both adult escapement (Hay 1984) and juvenile recruitment (Beard and Carline 1991; Beland 1996) have been positively correlated with redd counts.

Errors in redd counts can result from a number of sources. Variation in redd and habitat characteristics (e.g., redd size, age, density, superimposition, distance to cover, water depth, and substrate composition) may affect the visibility and identification redds, and observers vary in deciding which redds should be counted. Incomplete sampling of spawning areas, either in space or time, also may be important. For example, many redd counts are conducted in standard index areas, requiring the assumption that a fixed proportion of spawning occurs in those areas every year. The timing of redd counts may lead to errors if redds are formed after counting or if redds constructed before counts are made become obscured before counting.

We attempted to quantify these potential sources of error in a study of redds and populations of migratory bull trout spawning in two tributaries of Lake Pend Oreille in northern Idaho. We determined the utility of index areas for redd counts by examining concordance in the spatial distribution of redd counts within spawning habitats in 1997 and 1998. In 1998 we quantified temporal development of redds to determine rates of redd accumulation during the spawning season and to predict the consequences for timing of redd counts. In 1998 we also quantified interobserver variabil-

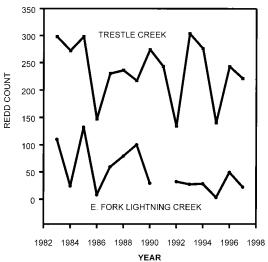


FIGURE 2.—Time series of bull trout redd counts in Trestle Creek and East Fork Lightning Creek, 1982–1998 (Idaho Fish and Game, unpublished data).

ity in redd counts, compared characteristics of redds and redd counts between our two study streams, and tested for associations between redd and habitat characteristics and counting errors. Finally, we tested the assumption that redd counts and population size were related by analyzing relationships between estimates of adult escapements and redd counts.

Methods

Study area.—We studied populations spawning in two streams within the Pend Oreille basin: Trestle Creek and East Fork Lightning Creek (Figure 1). Time series of redd counts suggest Trestle Creek consistently supports one of the largest spawning populations of bull trout in the Lake Pend Oreille system, whereas redd counts in East Fork Lightning Creek have declined significantly since 1983 (Figure 2; Rieman and McIntyre 1993; Rieman and Myers 1997).

Habitat conditions differ between these two streams. Trestle Creek has abundant large wood within the active stream channel, numerous deposits of gravel, complex pool structure, perennial stream flows, and relatively dense canopy over the stream. In contrast, East Fork Lightning Creek has little large wood within the active channel, little gravel or pool complexity, reaches of intermittent summer stream flow, and minimal canopy cover. The two streams effectively span the wide range of habitat conditions experienced by naturally spawning bull trout within the Pend Oreille basin,

and therefore span the conditions that observers likely to experience during redd surveys in the area.

Population survey.-We used mark-resight methods (White 1996) to estimate the number of spawning bull trout in each stream. Fish in each stream were resighted on two occasions with different methods. Initial capture and marking of fish was conducted in the last week of June 1998 in East Fork Lightning Creek and in the third week of July 1998 in Trestle Creek. Fish were captured throughout the occupied length of each stream via snorkeling and dipnetting or by driving fish from holding areas into block seines. Individuals were marked by removing the adipose fin. We completed the first resighting by snorkeling the same areas in the first week of September 1998. A second resighting was accomplished by trapping fish at weirs as they emigrated downstream following spawning. Weirs were placed in each stream in the first week of September 1998 and continuously operated in both streams in September and October 1998. We used the numbers of marked and unmarked fish from each resighting effort to estimate the size of each population of spawning adults; estimates were made via the joint hypergeometric maximum-likelihood estimator in the program NOREMARK (White 1996).

Determining redd accumulation.—In 1998 we counted redds as they appeared in a 2-km study reach in each stream. Study reaches were located in areas with the highest densities of adults observed during snorkeling. Accumulation of redds in Trestle Creek was monitored during seven visits (1 September–14 October) and in East Fork Lightning Creek during five visits (14 September–15 October).

One author (KD) tracked redd accumulations, and the others subsequently corroborated redd locations. Counts from the redd accumulation survey were "best estimates" (as defined by Bonneau and LaBar 1997) that were subject to error. However, we believe that error was minimal because we frequently observed the adults actually constructing redds. Furthermore, our familiarity with channel features in each reach allowed us to detect redd development that otherwise could have been confused with natural hydrologic features. We used our best estimates to serve as valid references for evaluating observer error. Because of conservation concerns, we did not attempt to excavate redds for evidence of egg deposition.

Redds were classified, based on presence or absence of an obvious tailspill, as "true" redds or "potential" redds, albeit in normal redd enumeration practices in the Pend Oreille basin such distinctions are not made (C. Corsi, Idaho Department of Fish and Game, personal communication). Individual redds were flagged and locations were recorded on reach maps. Reach maps were handdrawn to scale and included representations of prominent channel features. We also placed labeled markers at 100-m intervals throughout the study area (also marked on maps) to orient observers.

Measuring spatial distribution of redds.—Total redd counts were conducted in the third week of October 1997 and 1998. As with snorkeling and fish capture, redd counts were conducted over the entire length of known bull trout spawning areas in Trestle and East Fork Lightning creeks. The spatial distribution of redds was recorded in each stream and compared with known locations of the redds we counted during the same period in 1997. We tested for between-year variation in the spatial distribution of redds using a two-sample Kolmogorov—Smirnov test.

Interobserver variability.—From 17 to 21 October 1998, observers counted redds within study reaches in Trestle Creek (N=15 observers) and East Fork Lightning Creek (N=13). None of these observers had prior knowledge of redd locations within study reaches, and before the study, all markers indicating redd locations were removed. Before replicate redd counts were conducted, we trained observers. They received a 1-h presentation and discussion of redd counting and redd identification on the evening before counts were conducted, and on the day the redds were counted, they were given a 1–2 h training session in the field that included actual bull trout redds in each study stream.

Observers were provided with maps of the study reaches on which they marked redd locations. Observers were instructed to count all redds without distinguishing potential and true redds. Each study section was divided into 19 (Trestle Creek) or 20 (East Fork Lightning Creek) subreaches approximately 100 m long. We mapped each subreach to scale on individual sheets of paper. Study reaches were immediately resurveyed following completion of replicate redd counts to account for any new redds that were constructed during counts.

We compared redds identified by observers to our best estimates to assess the numbers of redds correctly identified, those that were missed (omissions), and stream features incorrectly identified as redds (false identifications). Scoring of redd

counts was occasionally complicated by close proximity or superimposition of redds. Due to the difficulty of identifying these individual redds, we analyzed subreach-level summaries of the data.

We used Wilcoxon's rank-sum tests to identify between-stream differences in various components of sampling error. Omissions and false identifications were summarized as percentages of actual redd counts in both streams. To compare the precision of redd counts, we generated absolute residual deviations from mean observed redd counts in each stream. The magnitude of residuals was then compared between streams.

Relative bias in redd counts was calculated as the difference between observed and actual redd counts converted to a percentage of the actual redd count. Observer error was defined in two ways: (1) apparent error or the absolute value of relative bias (percent) in redd counts, and (2) total error or the sum of omissions and false identifications, standardized as a percentage of the actual redd count. Apparent and total errors were compared between streams.

Surveys of habitat and redd characteristics.— Surveys of habitat and redd characteristics were conducted immediately after the interobserver variability study and included median gravel size at redd tailspills, distance of redds to nearest cover, cover type, water depth at redd tailspill, area of suitable gravel adjacent to redds, redd tailspill area, redd density, and redd superimposition. Median gravel size was visually estimated as the width of the second longest axis of a gravel particle and included the following categories: 2, 2.8, 4, 5.6, 8, 11.2, 16, 22.4, 32, 44.8, 64, 89.6, 128, 179, 256, 358, 512, 716, and 1,024 mm or greater. Gravel sizes were estimated in the center of redd tails within the area of a 25 \times 25-cm quadrat. Suitable gravel around redds was defined as gravel with a median diameter greater than 8 mm up to 64 mm (compare Baxter and McPhail 1996). Area of suitable gravel was defined as the product of length and width (m) of continuous substrate of suitable gravel within the wetted stream channel. Cover was considered to be anything within the wetted channel that could conceal spawning bull trout, such as large wood pieces, live roots, rocks, undercut banks, deep water (>1 m), and turbulence. Water depths were recorded in the center of redd tails. Redd tailspill length and width (m) were multiplied to estimate redd tailspill area. Superimposition of redds was defined as overlapping redd pits or tailspills resulting from construction of multiple redds in the same area.

Correlation between redd counts and redd and habitat characteristics.—We summarized redd and habitat characteristics within each subreach as means (suitable gravel area, redd tailspill area, distance to cover, gravel size in redd tailspill, depth at redd tailspill, redd age), as the percentage of redds that were true redds and percentage of superimposed redds, or as total number of redds (redd density). To standardize for variation in redd density, we summarized counting errors (omissions and false identifications) as percentages of actual redd numbers in each subreach. We tested for correlations between redd counting errors and redd density using absolute numbers of counting errors.

Using Spearman's rank correlation, we examined, for each observer in each stream, correlations between counting errors and habitat and redd characteristics. For each redd and habitat characteristic within each stream, correlation coefficients for all observers were summarized for both types of counting errors. For each resulting distribution of correlation coefficients, we used a one-sample *t*-test to test the null hypothesis that the mean of the distribution of coefficients was equal to zero. Distributions of correlation coefficients were tested for normality with the Shapiro–Wilk test (Cody and Smith 1991).

Redd counts and spawning escapement.—We used data from this study and previous work enumerating bull trout redds and spawning adults (Ratliff et al. 1996; Westover and Conroy 1997; Chirico and Westover 1998; Clayton 1998) to relate redd counts to adult escapement estimates. We used linear regression of log-transformed data to predict adult escapements from redd counts. Ratios of the number of spawning adults to redd counts (spawner: redd ratios) also were calculated for each data set.

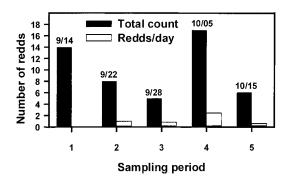
Results

Population Survey

We captured and marked 50 adult bull trout with adipose fin clips in East Fork Lightning Creek and 307 fish in Trestle Creek. Mark-resight population estimates (Table 1) indicated there were about five times more bull trout spawning in Trestle Creek than in East Fork Lightning Creek. After weirs were installed, we observed 25 fish migrate into East Fork Lightning Creek and 102 into Trestle Creek. Weirs were installed directly after the snorkel resighting, so snorkel counts probably underestimated the population slightly.

TABLE 1.—Summary of resighting surveys of marked bull trout in Trestle and East Fork Lightning creeks. Symbols follow White (1996): m = total number of sightings of marked bull trout, and u = total number of sightings of unmarked bull trout. Population estimates for individual resighting surveys (snorkel and weir) were calculated using the Lincoln–Peterson estimator. Population estimates for the combined results of both surveys were calculated using the joint hypergeometric maximum-likelihood estimator (White 1996).

Resighting method	m	и	Popula- tion estimate	95% confidence interval				
East Fork Lightning Creek								
Snorkel	17	77	268	180-355				
Weir	19	91	282	196-367				
Combined			283	229-368				
		Trestle	Creek					
Snorkel	125	348	1,157	1,024-1,290				
Weir	138	554	1,534	1,366-1,703				
Combined			1,387	1,288–1,506				



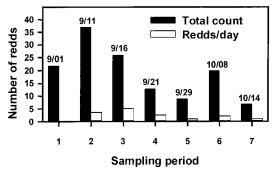
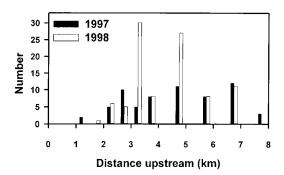


FIGURE 3.—Number of new bull trout redds or existing redds with recent excavation activity counted during five sampling periods for East Fork Lightning Creek (top panel) and Trestle Creek (bottom panel) in 1998 and rates of accumulation (redds per day). The last date of known activity is noted above each dark bar.



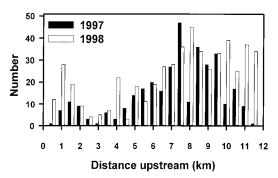


FIGURE 4.—Spatial distribution of bull trout redds within East Fork Lightning Creek (top panel) and Trestle Creek (bottom panel) in 1997 and 1998.

Accumulation and Spatial Distribution of Redds

In 1998 we observed peak spawning activity in early October in East Fork Lightning Creek and in mid-September in Trestle Creek (Figure 3). Redd counts totaled 101 for East Fork Lightning Creek and 535 for Trestle Creek. Interannual variation in the spatial distribution of redds differed significantly in Trestle Creek (Kolmogorov–Smirnov test, P < 0.02) but not in East Fork Lightning Creek. In Trestle Creek, the most obvious annual change was an increase of spawning activity in the upper reaches of Trestle Creek in 1998 (Figure 4).

Interobserver Variability

Overall, variation in counts among observers was large. Redd counts within the 2-km study reaches in East Fork Lightning Creek ranged between 14 and 127, or 28–254% of the best estimate of 50 redds, and between 49 and 201 in Trestle Creek, or 40–162% of the best estimate of 124 redds (Figure 6).

Observers frequently committed both omissions and false identifications. In East Fork Lightning Creek, the mean percentage of false identifications was significantly higher (mean = 40%, range =

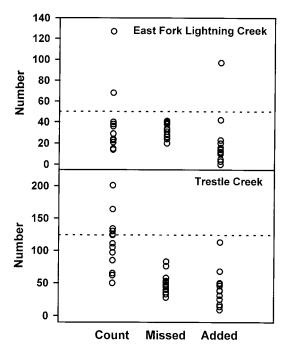


FIGURE 5.—Number of bull trout redds counted and counting errors (omissions or "missed" and false identifications or "added") in East Fork Lightning Creek and Trestle Creek. Dashed horizontal lines refer to best estimates of redd numbers.

0–194%) than in Trestle Creek (29%, 7–91%; P = 0.04). The mean percentage of omissions was also significantly higher in East Fork Lightning Creek (66%, 40–82%) than in Trestle Creek (45%, 23–67%; P = 0.002).

Precision of redd counts, as indicated by residual variability, was lower on average in Trestle Creek (mean residual deviation = 34 redds), than in East Fork Lightning Creek (19 redds). This difference was marginally significant (P=0.05). Relative bias in redd counts ranged from -72% to 154% of actual redd numbers in East Fork Lightning Creek (mean = -25%), and in Trestle Creek it ranged from -61% to 62% (mean = -15%). Differences in relative bias between these streams were not significant.

Mean relative error (the absolute value of relative bias) was 54% (range = 20-154%) in East Fork Lightning Creek and 30% (range = 0-62%) in Trestle Creek; these differences were not significant. Mean total error in redd counts was 106% (range = 52-234%) in East Fork Lightning Creek and 74% (range = 54-120%) in Trestle Creek. Total error in Trestle Creek was significantly lower than in East Fork Lightning Creek (P = 0.001).

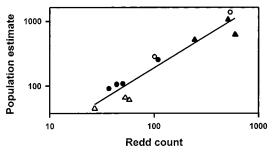


FIGURE 6.—Relationship between redd count and estimated population size of spawning bull trout: Open circles are data from this study, filled circles are data from Ratliff et al. (1996), filled triangles are data from Westover and Conroy (1997) and Chirico and Westover (1998), and open triangles are data from Clayton (1998).

Apparent error and total error in redd counts were not significantly correlated.

Correlation Between Redd Counts and Redd and Habitat Characteristics

Correlations between redd counting errors and redd and habitat characteristics varied widely (Tables 2, 3). Rates of false identification error consistently increased with increasing redd tailspill

TABLE 2.—Summary of Spearman's rank correlations between redd or habitat characteristics and numbers of false identifications for 13 observers in East Fork Lightning Creek and 15 observers in Trestle Creek; NA = not applicable.

Variable ^a	Mean	Rangeb	P				
East Fork Lightning Creek							
Redd density ^c	-0.18	0.69	0.0097				
Percent true redds	-0.16	0.75	0.0147				
Percent superimposed redds	NA	NA	NA				
Suitable gravel area	0.11	0.59	0.0664				
Redd tailspill area	0.26	0.74	0.0012				
Distance to cover	0.02	0.45	0.6315				
Gravel size in redd tailspill	-0.08	0.95	0.2095				
Depth at redd tailspill	-0.06	1.11	0.5172				
Redd age	-0.06	0.80	0.3522				
Trestle Creek							
Redd density	0.16	0.68	0.0035				
Percent true redds	0.39	0.94	0.0002				
Percent superimposed redds	0.01	0.89	0.8589				
Suitable gravel area	0.31	0.97	0.0001				
Redd tailspill area	0.42	0.65	0.0001				
Distance to cover	-0.06	0.92	0.3400				
Gravel size in redd tailspill	0.38	1.21	0.0001				
Depth at redd tailspill	0.08	0.84	0.1749				
Redd age	0.26	0.75	0.0009				

^a Correlation using percentage of false identifications, except where otherwise noted.

 $^{^{\}rm b}$ Because correlation coefficients range from -1 to 1, the maximum range is 2.

^c Correlation using absolute number of false identification.

TABLE 3.—Summary of Spearman's rank correlations between redd or habitat characteristics and omission error rates for 13 observers in East Fork Lightning Creek and 15 observers in Trestle Creek.

Variable ^a	Mean	Rangeb	P			
East Fork Lightning Creek						
Redd density ^c	0.81	0.37	0.0001			
Percent true redds	-0.14	0.70	0.0241			
Percent superimposed redds						
Suitable gravel area	-0.42	0.86	0.0001			
Redd tail area	-0.15	0.77	0.0425			
Distance to cover	-0.33	0.64	0.0001			
Gravel size in redd tail	-0.33	0.61	0.0001			
Depth at redd tail	-0.18	0.97	0.0435			
Redd age	0.35	0.44	0.0001			
Trestle Creek						
Redd density ^c	0.74	0.46	0.0001			
Percent true redds	-0.30	0.71	0.0001			
Percent superimposed redds	-0.50	0.45	0.0001			
Suitable gravel area	-0.06	0.85	0.3246			
Redd tail area	0.08	0.64	0.1481			
Distance to cover	0.07	0.73	0.1141			
Gravel size in redd tail	0.05	0.93	0.4102			
Depth at redd tail	-0.18	0.72	0.0018			
Redd age	0.21	0.71	0.0008			

^a Correlation using percentage of omissions, except as otherwise noted.

area and, to a lesser extent, suitable gravel area. In both streams, rates of omission error increased with increasing redd density and age of redds and with shallower water depths at redd tailspills. Substantial variability among observers in the direction and magnitude of these correlations was obvious when the range of correlation coefficients was considered (Tables 2, 3).

Redd Counts and Spawning Escapement

Total redd counts and the estimated number of spawning bull trout were strongly correlated across all data sets. Linear regression of log-transformed data revealed that variation in redd counts was strongly correlated with estimated numbers of spawning bull trout ($r^2 = 0.90$, P < 0.0001; Figure 6). A logarithmic transformation was necessary to equalize variance heterogeneity. The mean number of adults per redd was 2.16 (range = 1.03-3.33). Based on our population estimates and total redd counts, spawner: redd ratios were 2.59 in East Fork Lightning Creek and 2.80 in Trestle Creek.

Discussion

Temporal and Spatial Distribution of Redds

Based on the temporal accumulation of redds in both East Fork Lightning Creek and Trestle Creek,

we suggest that final redd counts should not be conducted until at least the latter half of October; that will include most of the spawning activity, although some redd development probably continues into November. We observed some spawning activity and small numbers of unspawned adults migrating upstream over weirs in late October. Waiting beyond October to count redds is risky because of increased probability of high stream flows and snowfall (C. Corsi, Idaho Department of Fish and Game, personal communication) that may obscure redds and produce difficult and hazardous sampling conditions.

Annual variation in the distribution of redds within Trestle Creek suggests use of index areas may be problematic in some streams. If redd counts are conducted only on limited segments of spawning habitats (as with index areas), apparent temporal changes in redd numbers may actually be due to changes in the spatial distribution of spawning activity.

Interobserver Variability

We found that total redd counts varied widely among observers. Similarly, Bonneau and LaBar (1997) found redd counts by 11 observers in the same 3-km reach of Trestle Creek ranged from 14 to 85 (23–137% of their best estimate of 62 redds) and from 14 to 51 (29–104% of their best estimate of 49 redds) in East Fork Lightning Creek. In this study, we partitioned sources of interobserver variability in redd counts into omissions and false identifications. Both types of error were common, and because observers often committed both, they tended to cancel each other out.

False identifications and omissions were more frequent in East Fork Lightning Creek. We were unable to attribute this difference to a specific cause. Although counting errors were more common in East Fork Lightning Creek, precision of redd counts was lower in Trestle Creek. Densities of redds were much higher in Trestle Creek, and this may suggest that precision of redd counts decreases as redd numbers increase.

Our analysis of individual redds produced an noteworthy finding: Estimates of counting error that compare total known redds versus total redds observed may be misleading. For example, we detected no difference between the two streams when apparent error (i.e., observed — actual number of redds) was considered, but when comparing true error (i.e., total omissions + false identifications) East Fork Lightning Creek was significantly greater, primarily because of a lower omission error in

^b Because correlation coefficients range from −1 to 1, the maximum range is 2.

^c Correlations using absolute number of omissions.

Trestle Creek. Both sources of error are significant and should be considered in evaluating redd counts.

Effects of Redd and Habitat Characteristics

We found no evidence to suggest a single common cause for errors in redd counts, but counts by some individuals were strongly correlated with certain redd or habitat characteristics (Tables 2, 3). As may be expected, omissions were more numerous in subreaches with higher densities of redds, where there were more opportunities to commit omissions. The number of false identifications was more difficult to interpret, and did not show a consistent relationship with redd density between streams.

Rates of omission error in both streams were often related to redd age, suggesting that older redds were more difficult for observers to identify. This result suggests multiple surveys may be needed throughout the spawning season. The practice of counting redds only once near the end of the spawning season may increase the chance that older redds formed at the beginning of the season are not detected.

Redd counting errors were often correlated with the percentage of true redds, but the magnitude of correlation varied substantially between streams and observers (Table 3) and correlations were difficult to interpret. For example, observers were generally more likely to correctly identify redds when the percentage of potential redds was higher. We expected potential redds to be more difficult to detect, and the correlations we observed may be spurious because of the influences of unmeasured variables. The question of whether redd counts should be focused only on true redds may depend in part on the ability of observers to reliably survey and distinguish potential redds and the probability that such redds are used for spawning by females (Barlaup et al. 1994). Without excavation of redds to find eggs, it will be difficult to distinguish true and potential redds.

In general, counting behavior varied substantially among observers, as indicated by the wide range of correlation coefficients observed in the analysis between streams and among observers within streams. With one exception, observers frequently committed both types of counting error, but the relative frequency of each was variable. Overall, omissions were most frequent, leading to underestimating redd numbers. Some individuals, however, were more prone to making false iden-

tifications, as evident from their consistent overestimates of redd numbers.

Our results suggest that complex interactions are likely between redd counts by different individuals and redd and habitat characteristics, which vary both within and among streams. Furthermore, other variables not considered in this study (e.g., variation in stream discharge, turbidity, and weather) may be important, especially in the context of annual variation in sampling conditions.

Improving Redd Counts

Bonneau and LaBar (1997) suggested the 20-min training session given to observers in their study was insufficient and led to high levels of interobserver variability in redd counts. In our study, we provided much more extensive classroom and field training, yet observer variability in redd counts was still large. This suggests even further training is needed to improve redd counts, or alternatively, that high interobserver variability in counts is unavoidable.

One obvious consideration in redd counts is the relative experience of observers. Bonneau and Labar (1997) found that interobserver variation in redd counts was high for all their observers, regardless of experience. In our study, many observers had little or no prior experience with redd counts. We considered an observer to be experienced if they had previously counted bull trout redds in the study streams and had experience working with bull trout in the area. For Trestle Creek, 3 of 15 observers were experienced, but of the three observers with the fewest counting errors only one was experienced. Similarly, 2 of 13 observers in East Fork Lightning Creek were experienced, but of two observers with the fewest counting errors only one was experienced. Although experience in redd counting should not be discounted, it is important to have an objective basis for evaluating the ability of observers to count redds, and to have a common training program.

Because redd counts are prone to errors, training should include the tracking of individual redds, as well as tracking of redd accumulations over as much of the spawning season as possible. This will facilitate identifying individual redds and produce best estimates of actual redd numbers. Tests of an observer's ability to count redds should be conducted until the observer attains relatively consistent counts with minimal error, relative to best estimates. Training of observers should focus on factors that create redd counting errors, cognizant of

the fact that the influence of redd and habitat characteristics on observer error may differ among streams or observers.

Expanded training and sampling protocols will improve the reliability of redd counts, but costs would increase, which might compromise budgetary abilities to monitor other streams. An alternative would be to conduct more intensive (and presumably more precise) redd counts on less regular intervals (e.g., biennial or longer). Training costs also could be reduced by ensuring that highly experienced personnel are continuously involved in counting redds, as is the case on many streams in western Montana, where a single individual has counted redds for over 15 years (T. Weaver, Montana Department of Fish, Wildlife, and Parks, personal communication).

Spawning Escapement and Redd Counts

To be useful for population monitoring, redd counts must be related to actual numbers of spawning adults. Across all data sets, redd counts were positively correlated with population estimates of spawning adults, but only on a log scale. In practice, redd counts often are related to spawning escapement by using a previously determined or assumed ratio of number of spawning adults to redds. The number of spawning adults per redd ranged from 1.03 to 2.80 in the data sets we analyzed, and both spatial variation and interannual variation in spawner: redd ratios were evident. This degree of variation suggests that life history patterns vary strongly among populations (e.g., Barlaup et al. 1994) or that estimates of spawning escapement based on redd counts are biased or imprecise approximations of true escapements.

Conclusions

Results of this work and that of Bonneau and LaBar (1997) suggest that sampling error is a potentially significant factor influencing the spatial and temporal variability of redd counts (see also Rieman and McIntyre 1996). Sampling error tends to distort patterns of spatial and temporal variability in redd counts, and redd counts may therefore only be useful for detecting relatively substantial changes in bull trout populations (Maxell 1999). Because significant and widespread declines in bull trout redd counts have been detected (Rieman and Myers 1997), it is possible that they represent severe population declines.

Given the uncertainty associated with (1) potential sampling error in redd counts, (2) relations between redd counts and spawning escapements,

and (3) natural variation in population dynamics (including the possibility of significant time lags in the response of fish populations to environmental changes), it seems likely that management actions based on redd counts may be limited to those reflecting substantial changes in population sizes, which will be more difficult for management to reverse. Therefore, it would be desirable to have a more sensitive indicator of population declines.

Results of our work indicate a need to substantially improve the reliability of redd counts. Although redd counts have been the least invasive and expensive method of monitoring bull trout populations, limited reliability of counts could reduce those advantages. Nevertheless, we suggest redd counts be further evaluated. With such additional information, we should be able to determine whether other monitoring approaches (e.g., genetics or direct population estimates of juveniles or adults) may be needed in place of or in addition to redd counts.

Acknowledgments

This project could not have been completed without assistance from the following individuals and institutions: D. Horan, K. Gillogly, D. Lee, B. Long, D. Myers, D. Oswald, K. Overton, and R. Thurow (Rocky Mountain Research Station); M. Davis, S. Dekome, and M. Gibbs (Panhandle National Forests): C. Corsi and J. Scott (Idaho Fish and Game); G. LaBar and students A. Dux, T. Kisaka, K. McGrath, J. Neal, T. Reischel, P. Stormo, and D. Vidergar (University of Idaho); S. Adams, K. Knudsen, P. Spruell, and Z. ("J.") Wilson (University of Montana); S. Gunckel (Oregon State University); and S. Berkeley, D. Berkley, and K. Pratt. JBD was supported by a Research Joint Venture Agreement between the University of Nevada-Reno and U.S. Department of Agriculture Rocky Mountain Research Station. Work on bull trout was authorized by U.S. Fish and Wildlife Service (recovery permit TE8044480-0), U.S. Army Corps of Engineers (stream alteration permit 981201700), and Idaho Department of Fish and Game (collecting permit no. F-63-92). Many thanks to S. Adams, C. Baxter, C. Corsi, B. Harvey, and P. Howell for insightful comments on earlier versions of this manuscript.

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