Understanding the Significance of Redd Counts: a Comparison between Two Methods for Estimating the Abundance of and Monitoring Bull Trout Populations

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Abstract.—For salmonids that exhibit multiple life history forms within a single population, it may be necessary to evaluate the inconsistencies associated with population monitoring techniques. We compared mark–resight population estimates with those based on annual redd counts for bull trout Salvelinus confluens in eastern Oregon. Our data suggest that across years, the trends in population estimates based on expanded redd count data and those based on the mark–resight method may be similar within basins. Across basins, however, there appear to be inconsistencies between mark–resight population estimates for different size-classes of bull trout and the expanded redd count data. In some systems, only the larger, potentially migratory fish are represented in redd counts, whereas in others some combination of small resident and large, potentially migratory fish is represented. The disparity between redd counts and population estimates for the reproductive population suggests that caution be invoked when choosing the monitoring techniques used to set recovery or monitoring goals for bull trout populations.

The trend in abundance of the reproductive portion of a population is often one of the most important characteristics in the recovery and conservation of a species, yet the estimation of this trend can be a deceivingly difficult task. This task is especially complicated for species exhibiting multiple life history forms that coexist within a single population unit and that are behaviorally cryptic (e.g., bull trout Salvelinus confluens; Maxell 1999). In addition to species-specific challenges, managers are often resource limited and must rely on monitoring techniques that (1) are cost and time effective, (2) are specifically focused on the demographic portion of the population of interest (e.g., reproductive adults), and (3) have not been adequately validated with alternative approaches. Given these limitations, the accuracy and precision of population monitoring techniques must be critically evaluated, as these factors can affect our ability to assess the impacts of implemented management and recovery actions on long-term species persistence.

A considerable number of salmonid populations have experienced significant declines throughout their native ranges (Frissell 1993; Thurow et al. 1997). Bull trout have been listed as threatened in the United States since 1998 and have been designated as a species of special concern since 1995 in Canada. Bull trout require cold water temperatures (Selong et al. 2001; Dunham et al. 2003) and are often associated with complex habitats (Rieman and McIntyre 1993, 1996; Nelson et al. 2002). Resident bull trout remain in their headwater natal streams for their entire life cycle and are thought to remain relatively small (<300 mm; Goetz 1989; Buchanan et al. 1997). Migratory bull trout remain in their natal streams for 1–3 years before migrating to a larger stream or lake and ultimately returning to their natal streams to spawn (Rieman and McIntyre 1993).

Like many anadromous salmonids, bull trout population monitoring is often based on annual redd counts, where biologists visit the spawning
grounds once or several times over the duration of the spawning event and count redds visually based on conditions such as the disturbance of gravel and nest structure. Bull trout return to natal headwater systems and spawn over a concentrated time period from about mid-August through November, making redd counts a cost- and time-effective monitoring tool for managers. Despite the cost and time effectiveness of this method, observer variability can reduce the accuracy and precision (Dunham et al. 2001) of redd counts and the ability to detect changes in population trends (Maxell 1999). In addition to observer variability, redd counts may be ineffective for monitoring bull trout populations where both small (i.e., resident) and large (potentially migratory) fish coexist within a single population unit. Finally, factors such as size differences in redd scour sites between small resident and large, potentially migratory fish; redd superimposition; and delineation between test digs and redds can reduce the level of certainty in using redd counts to monitor populations (Maxell 1999; Dunham et al. 2001). Therefore, it is necessary to evaluate which portion of the population is represented by redd count data and to determine how reliable this information is for gauging the achievement of target recovery goals.

The purpose of this paper is to evaluate the use of redd counts as a population monitoring tool for bull trout populations exhibiting multiple life history forms. In particular, we are interested in (1) examining which components of the population (e.g., small resident and/or large, potentially migratory fish) are represented in redd counts and (2) determining whether the relationship between abundance estimates from redd counts and from mark–resight methods is consistent across basins and years. The majority of previous research evaluating the precision and accuracy of bull trout redd counts has occurred for populations dominated by large migratory fish (e.g., Dunham et al. 2001), yet many bull trout populations contain both resident and migratory forms (Buchanan et al. 1997). Further, recovery goals are ambiguous in terms of the relative contribution of life history forms.

Methods

We used mark–resight techniques to provide population estimates for different sizes and life history forms and contrasted these estimates with expanded redd counts for several different bull trout populations. Mark–resight data, which has been firmly established as an accurate and precise population estimation technique (Minta and Man-
mm passive integrated transponder tag, and released at the point of capture. After marking was completed, daytime snorkel surveys were performed in each of the sampled reaches to collect mark–resight data. The time interval between marking surveys and snorkeling surveys for each reach ranged from approximately 1 week to 1 month. Although Bonneau et al. (1995) suggested that night surveys may be more appropriate for bull trout, we have observed no consistent differences in fish counts between day versus night snorkel surveys (Budy et al. 2004); this is probably a result of cold water temperatures in these systems (Thurow and Schill 1996). All snorkel surveys were conducted during daylight hours beginning 2 h after sunrise and ending 2 h before sunset. To avoid potential bias that could result from double counting of fish as they migrate upstream to spawn, snorkeling surveys in each study site began at the uppermost reach and continued downstream to the lower limit of the study site. In each reach, snorkelers proceeded upstream while estimating and enumerating all marked and unmarked bull trout into 50-mm size categories beginning 2 h after sunrise and ending 2 h before sunset. To avoid potential bias that could result from double counting of fish as they migrate upstream to spawn, snorkeling surveys in each study site began at the uppermost reach and continued downstream to the lower limit of the study site. In each reach, snorkelers proceeded upstream while estimating and enumerating all marked and unmarked bull trout into 50-mm size categories beginning with 120-mm fish.

Within each site, marking and snorkeling data from reach units were pooled and were used to calculate annual population estimates for all tagged fish (hereafter referred to as the total population estimate, POPTOT). We used a modified Petersen mark–recapture estimator (Seber 1982), \( \hat{N} = \{((M + 1)(C + 1))/((R + 1)) - 1 \} \), where \( M \) is the number of marked fish, \( C \) is the total number of fish sighted in snorkeling surveys, and \( R \) is the number of tag resights. Normal approximation confidence intervals (95%; Krebs 1999) were calculated for each population estimate but were not possible for some years and sites because of a low number of resighted fish. The sampling rate (percentage of the study area sampled) was used to expand the mark–resight population estimates and corresponding variance to the entire study area.

Each of the four population estimates was further delineated into different size categories based on demographic information regarding the size at sexual maturity and the size range of fish considered migratory. Size-based population estimates were calculated by separating the number of marked, sighted, and resighted fish into the corresponding size categories. Resident bull trout in the Pacific Northwest can reach sexual maturity at 150 mm (Hemmingsen et al. 2001). Data from sacrificed fish in the SFWW suggests that bull trout are sexually mature at or below 200 mm (Budy et al. 2004); limited data from NFU, BCS, and LIC suggests similar (200 mm) or smaller sizes at sexual maturity (P. Budy, unpublished data). We therefore calculated a second, more conservative, population estimate for all bull trout larger than 220 mm (hereafter referred to as POP220), which includes both small resident and large, potentially migratory fish. Finally, it has also been proposed that bull trout larger than approximately 300 mm are likely to be migratory in fluvial systems (Goetz 1989; Rieman and McIntyre 1993; Nelson et al. 2002). Therefore an additional conservative population estimate was calculated for bull trout larger than 370 mm (hereafter referred to as POP370), which may include both migratory and/or larger resident fish. This segregation of classes enabled us to better assess the contribution of each size-class or life history form to the overall population and to compare these compartmentalized and total population estimates to expanded annual redd counts.

The Petersen mark–recapture model is a closed-population estimator, such that violations of the closure assumption may significantly bias annual population estimates. Marked animals emigrating from the study site between the onset of marking and the end of snorkeling surveys may lead to positive bias in the population estimates. We monitored the number of emigrating individuals during this period in the SFWW (Budy et al. 2004); emigration rates were low and should have had little effect on population estimates. Although emigration rates in the other three systems are unknown, juveniles (<200 mm) comprise the majority of bull trout that emigrate downstream during this period. Upstream migration is dominated by adult bull trout (Fraley and Shepard 1989; Hemmingsen et al. 2001; Nelson et al. 2002), which would be quantified in our snorkel surveys. There may also be bias associated with fish moving between the individual reaches. However, by pooling our mark–resight data and considering emigration rates (see above), we assume that we sufficiently met the assumption of closure temporally at the study site level.

Annual redd counts were performed by state, federal, or tribal biologists in each of the four basins by use of streamside surveys. For the SFWW and NFU, redd counts began in mid-August and continued until the end of October. Counts were performed biweekly in the areas with the highest density of reds (including major tributaries) and monthly otherwise. In BSC and LIC, redd surveys were conducted twice during the spawning season.
Table 1.—Methodologies used to estimate the number of bull trout per redd in the Columbia River basin and corresponding estimates. The average of these five values (2.68 spawners/redd) was used to expand redd count data for comparison with population estimates from mark–resight data.

<table>
<thead>
<tr>
<th>Method</th>
<th>Spawners per redd</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weir counts</td>
<td>1.2</td>
<td>Baxter and Westover (2000)</td>
</tr>
<tr>
<td></td>
<td>2.1</td>
<td>Sankovich et al. (2003)</td>
</tr>
<tr>
<td>Weir counts</td>
<td>2.3</td>
<td>Ratliff et al. (1996)</td>
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<tr>
<td>Weir with fish counter</td>
<td>3.5</td>
<td>Taylor and Reasoner (2000)</td>
</tr>
<tr>
<td></td>
<td>4.3</td>
<td>Taylor and Reasoner (2000)</td>
</tr>
<tr>
<td>Average</td>
<td>2.68</td>
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in index areas of historically high spawning densities. Newly encountered redd sites were flagged to avoid the potential double counting of redds in subsequent surveys.

We expanded the annual redd counts for the comparisons with mark–resight population estimates that follow. Since, no estimates of spawners per redd were available for the systems of interest, annual redd counts were expanded by the number of spawners per redd based on (1) an average of the various basin values (from the Columbia River basin) (Table 1; 2.68 spawners/redd, hereafter referred to as POPREDDS) and (2) the range of values available (Table 1; 1.2–4.3 spawners/redd), which were used to calculate lower and upper confidence bounds. While we acknowledge that there is great uncertainty in converting the number of redds to the number of reproductive fish, we have chosen a wide range of values for expansion to account for this uncertainty and capture the variability expected across systems.

Results

Sampling rates varied by location and year: SFWW was sampled at 22% in 2002, 46% in 2003, and 48% in 2004; BSC and LIC (2002) were each sampled at a 20% sample rate; and NFU was sampled at 52% in 2003 and 37% in 2004. Total population estimates based on mark–resight data for each system were substantially larger than the corresponding POPREDDS. This pattern is not surprising given that the POPTOT estimates included subadult and adult bull trout, whereas redd counts presumably include only adult, sexually mature fish. However, when we further delineated the populations into POP220 and POP370, the redd-based population estimates were not consistently lower or higher across the four basins.

For the SFWW (Figure 1a), POPREDDS was most similar to POP370; this pattern was consistent across the 3 years of data for the SFWW. Further, POPREDDS was well below the lower bound for the POP220 group for each year, suggesting that across years the smaller resident adult bull trout were not included in annual redd counts. The average annual POP220 estimate (2,392 fish; 2002–2004 average) was considerably larger than POPREDDS regardless of which ratio of spawners per redd was used. In addition, the total annual redd counts in the SFWW included tributaries of the SFWW, which we know contain resident bull trout, while the mark–recapture population estimates did not include resident fish from the tributaries. Thus, our population estimates from mark–resight techniques were potentially biased low at the basin level (although consistently so between years), and the discrepancy between redd-count-based and mark–resight-based estimates was probably even greater than what is presented here.

In the NFU (Figure 1b), POPTOT estimates were substantially larger than POPREDDS, a pattern similar to that seen for the SFWW. However, unlike the SFWW, POPREDDS were consistently larger than POP370 estimates across the 2 years of NFU data and appeared to include a portion of the population of smaller residents (we were unable to calculate mark–resight confidence intervals because of low sample sizes). These results suggest that redd counts represented both a portion of the smaller resident group and larger migratory fish in the NFU, a pattern that differed from that of the SFWW.

The data for BSC (Figure 1c) resembled those of the SFWW, and LIC data (Figure 1d) were similar to NFU data. In BSC, POPREDDS was most similar to POP370; like the SFWW, expanded redd counts for BSC apparently did not include smaller resident bull trout (e.g., POP220 was substantially different than POPREDDS). However, in LIC, which is in the same basin as BSC, POPREDDS was most similar to POP220, suggesting that redd counts in LIC included both smaller resident and larger migratory fish. These results again suggest a considerable inconsistency in the portion of the
FIGURE 1.—Bull trout population estimates for (a) the South Fork Walla Walla River (SFWW), (b) the North Fork Umatilla River (NFU), (c) Lick Creek (LIC), and (d) Big Sheep Creek (BSC) in eastern Oregon. In each figure, the total population estimate (POPTOT), the population of fish larger than 220 mm (POP220), and the population of fish larger than 370 mm (POP370) were calculated from mark–resight data. Confidence intervals are not shown for estimates where sample size was too low. The number of redds for each corresponding year (POPREDDS) was expanded by the number of spawners per redd; the lower error bound was 1.2 spawners/redd, the upper error bound was 4.3 spawners/redd, and the average was 2.68 spawners/redd.

reproductive population that is represented in redd count data across basins.

Discussion

Although redd counts provide a cost- and time-efficient method of monitoring salmonid populations, we have demonstrated that there is significant variability between basins regarding which components of the population are best represented by redd counts. In some systems, only the larger, potentially migratory fish are represented in redd counts, while in others some combination of small...
resident and large, potentially migratory fish is represented. Ultimately, our data suggest that within-system trends between redd counts and population estimates may be similar, suggesting that redd counts may be a viable tool for monitoring trends once these data are validated and once the potential biases are better understood. However, the differences in the patterns we observed across systems indicate that these trends may be basin specific, possibly indicating different patterns of life history expression (Dunham et al. 2001), a factor that may limit the utility of redd counts as abundance monitoring tools.

Specifically, the majority of research that has investigated the variability of bull trout redd counts has occurred in systems dominated by very large migratory bull trout (e.g., Rieman and McIntyre 1996). Within these systems, redds can be easily detected because of the size of the excavation made by these large bull trout (Rieman and Myers 1997). However, in systems with both resident (smaller) and migratory (larger) bull trout, the characteristics of redds constructed by small residents may increase the imprecision of the counts. For example, redds constructed by smaller fish may go undetected due to their size and location, may be categorized as test digs, or may be considered as small disturbances in the gravel (e.g., from large ungulates). Under these conditions, the difficulty in detecting redds constructed by small resident fish may prevent managers from accurately monitoring the reproductive population.

While our data illustrate inconsistencies in the component of the population represented by redd counts, there are limitations and uncertainties in our approach. First, the sampling error associated with redd counts has not been quantified in the basins used in our comparisons. These uncertainties, which have been demonstrated by Dunham et al. (2001), may include observer error, errors associated with the timing of the counts, difficulties associated with detecting redds in well-covered habitats, and the habitat characteristics of the redds. Ideally, these errors should be quantified within any system where redd counts are used as population monitoring tools. Second, we do not have more comprehensive information regarding the size at sexual maturity or the sexually mature percentage of the population for the POP220 and POP370 groups. To address these uncertainties, we used a range of values and conservative cutoffs for each group (220 and 370 mm) based on limited data from sacrificed fish (Budy et al. 2004) and adjacent basins (Hemmingsen et al. 2001). Finally, we acknowledge that there is uncertainty associated with the inefficiencies of snorkel data used in our mark–resight population estimates. In particular, the cryptic behavior of bull trout can reduce sampling efficiency in snorkel surveys (Thurow et al. 2001, 2004). However, we assumed that there would be no differences in the snorkel sampling efficiency of marked and unmarked fish, such that our estimates would not be significantly affected.

Management Implications

Our results illustrate the need to evaluate population estimation techniques for salmonid species containing multiple life history forms. In particular, we suggest that alternative monitoring approaches (i.e., in a subset of streams within basins) may be necessary to accurately determine the best overall strategy for effectively monitoring fish populations with redd counts. While redd counts may provide a cost-effective technique for estimating population size in some systems, a significant portion of the population (e.g., smaller, potentially resident, mature fish) may be grossly underrepresented when there is a high proportion of larger migratory fish. Further, because the difference between adult population estimates and redd counts varies in direction across different systems (i.e., sometimes population estimates are greater than expanded redd counts and vice versa), we must exercise caution when using these redd count data to set targets for recovery goals or in assessing the status of a population relative to a recovery target. Ultimately, it is necessary to understand which components of the population are represented in the redd count data and how those components relate to a specified recovery goal or criterion.

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