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[Article]

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

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Abstract.—We developed and evaluated a stratified index redd area method to estimate Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* escapement in several coastal streams in northern California based on the assumption that redd size is related to the number of redds a female builds. Sources of error in redd counts were identified, including the use of logistic regression to classify redd species (necessary due to temporal overlap in the spawning of these species in coastal northern California). Redd area escapement estimates were compared with estimates from more conventional methods and releases above a counting structure. Observer efficiency in redd detection ranged from 0.64 (SE = 0.10) to 0.75 (SE = 0.14) and was significantly associated with streamflow and water visibility (analysis of variance [ANOVA]: $F = 41.8$; $P < 0.001$). Logistic regression reduced uncertainty in redd identification. Redd area and date observed were significant in predicting coho salmon and steelhead redd species (Wald's $z = 11.9$ and 18.09, respectively; $P < 0.001$). Pot substrate and redd area were significant in classifying Chinook and coho salmon redds (Wald's $z = 5.88$ and 4.03; $P = 0.015$ and 0.04, respectively). Stratified index redd area escapement estimates and estimates based on capture–recapture experiments, area-under-the-curve estimates, and known releases above the counting structure (coho salmon only) were not significantly different (ANOVA: $F < 13.6$; $P > 0.06$). Escapement estimates assuming one redd per female were only significantly different from other methods for steelhead (ANOVA: $F = 13.11$; $P = 0.006$). Redd counts were significantly correlated with escapement estimates ($r > 0.82$; $P < 0.04$). Reduction of counting errors and uncertainty in redd identification, biweekly surveys throughout the spawning period, and the use of redd areas in a stratified index sampling design produced precise, reliable, and cost-effective escapement estimates for Chinook salmon, coho salmon, and steelhead.

Accurate estimates of escapement are essential for effective management and conservation of salmonids (Busby et al. 1996; McElhany et al. 2000). In northern California coastal Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* are listed as threatened species under the U.S. Endangered Species Act (U.S. Office of the Federal Register 1997, 1999, 2000). Estimates of abundance at the population level are likely to be an important, though not independent, part of delisting criteria. There is a need for reliable, cost-effective, and precise techniques for monitoring salmonid escapement.

While redd counts are commonly used to index adult escapement and assess population trends (Beland 1996; Rieman and Myers 1997; Isaak et al. 2003), their accuracy as a measure of abundance has rarely been evaluated (Dunham et al. 2001). As the product only of reproductive adults, redd counts provide an index of effective population size (Meffe 1986). Maxell (1999) suggests that the sources of counting errors involved in redd counts be identified and reduced before they will be useful for long-term monitoring. Dunham et al. (2001) suggest that redd counts are less intrusive and expensive than tagging, trapping, underwater observation, weirs, and genetics for inventorying bull trout *Salvelinus confluentus* populations, and that with limited resources more populations can

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be inventoried over a longer period. However, they conclude that substantial improvements are needed to reduce counting errors before redd counts will be useful for population monitoring. The use of redd counts for population monitoring may be further complicated if females make more than one redd. Crisp and Carling (1989) found that female salmonids occasionally make more than one redd, and Reingold (1965) documents a steelhead making two redds in different locations within a stream. Salmonids may also make false or ‘‘test’’ redds, which are abandoned before eggs are deposited (Crisp and Carling 1989).

The use of redd counts for population monitoring may be further complicated if there is uncertainty in redd species identification. Identification of Chinook and coho salmon and steelhead redds in coastal northern California streams is difficult because of overlap in spawning time and redd sizes. Chinook and coho spawn from late October through January, and steelhead spawn from December through March in coastal northern California (Weitkamp et al. 1995; Busby et al. 1996; Myers et al. 1998). Redd surface areas range from 0.84 to 15 m^2 for Chinook salmon, from 0.80 to 8.4 m^2 for coho salmon (Burner 1951), and from 2.4 to 11.2 m^2 for steelhead (Orcutt et al. 1968). Thus, to use redd counts for population monitoring in coastal northern California it was necessary to develop a technique to distinguish redd species.

To resolve some of the weaknesses listed above, we evaluated the amount of bias in estimates due to errors in redd species identification, detection of redds, and duration under variable survey conditions. We used data collected over 2 years in four rivers and three creeks to develop a logistic regression model based on physical redd characteristics and spawning time to distinguish between coho salmon and steelhead redds and tested it with data collected in the third year of the study. To distinguish between Chinook and coho salmon redds, a similar model was developed and evaluated with data collected in two rivers during 1 year. We evaluated the validity and some sources of bias involved with using redd counts and redd sizes to estimate escapement by estimating surveyor efficiency, the duration redds remain visible, and the influence of streamflow and water visibility on redd detection. To determine if redd-based estimates differed from conventional escapement approaches, we examined the relationship between these estimates and estimates based on capture–recapture experiments, area-under-the-curve (AUC) estimates, and counts at the Noyo River Egg Collecting Station (ECS) between 2000 and 2001 and between 2002 and 2003. To test if coho salmon and steelhead redd counts and redd-based escapement estimates are related to true abundance, we examined the relationship between these data collected over 4 years in one river (steelhead only) and 3 years in two rivers and three creeks. To determine if female salmonids make more than one redd we compared the number of redds observed to our AUC and capture–recapture estimates of the number of females. The two-fold purpose of this study was to determine if escapement estimates, based on redd counts or on the assumption that redd size is related to the number of redds a female salmonid makes, can be applied to all three species, and if they are more reliable, cost effective, and precise than conventional approaches.

Methods

Study Area and Data Collection

The streams studied were Caspar, Hare, and Pudding creeks and the Albion, Little, Noyo, and Ten Mile rivers (Figure 1). These streams range in drainage area from 13 to 296 km^2, flow directly into the ocean, are unregulated, and are groundwater fed with peak flows in winter following heavy rains.

All available spawning habitat in Caspar, Hare, and Pudding creeks and Little River was surveyed approximately biweekly from early December 2000 to mid-February 2001 and from early December 2001 to mid-April 2002 and approximately weekly from mid-December 2002 to mid-April 2003. The entire extent of spawning habitat in the Noyo River was surveyed biweekly from late February 2000 to late April 2000 and from early December to mid-April during 2000–2001 and 2001–2001. During 2002–2003 nine segments ranging from 2 to 8 km were surveyed weekly in the Noyo River. The Albion and Ten Mile rivers were surveyed sporadically between 2000 and 2003.

Crews of two walked or kayaked 2- to 9-km-long stream reaches searching for redds, live fish, and carcasses. Streamflow (m^3/s) was estimated from flow rated staff gauges and water visibility quantified as the maximum depth (m) the stream substrate was visible. All redds observed were measured and uniquely marked with labeled flagging, tied to the nearest branch directly upstream of the pot, to avoid double counting. Live fish were identified to species, counted, and fork length and sex visually estimated. Carcasses were identified

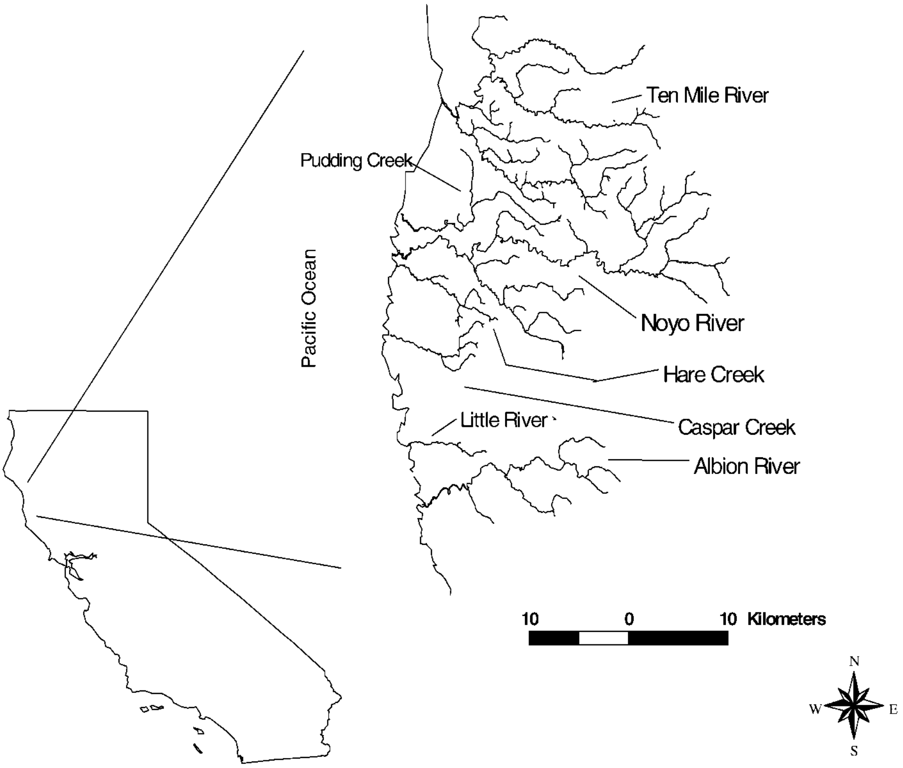

FIGURE 1.—Map showing the locations of the streams surveyed during this study in coastal Mendocino County, California.

to species and sex, measured, inspected for tags, marks, and fin clips, and unmarked carcass were uniquely marked with numbered metal tags. To ensure consistency in data collection and identification of redds and fish, surveyors were provided with 4 h of laboratory training and 2 h of field training at the beginning of each season. In addition, surveyors were rotated so that experienced and inexperienced surveyors were paired.

All newly constructed redds observed were identified to species, treated as unknown, or denoted as test or redds under construction; marked with flagging; counted; and measured during each visit. Tests (redds which appeared incomplete to the observers) and redds under construction were reexamined on consecutive surveys and were reclassified if appropriate based on their apparent completion. Redd measurements consisted of area, substrate, and depth. Pot length (measured parallel to streamflow), pot width (perpendicular to the length axis), and pot depth (the maximum depth of the excavation relative to the undisturbed streambed) were measured, and the dominant pot substrate was visually estimated using a modified Brusven index (Platts et al. 1983). Tailspill length (longitudinally parallel to streamflow) and tailspill width at one-third and two-thirds from the downstream edge of the pot to the end of the tailspill (perpendicular to the length axis) were measured. The dominant tailspill substrate was visually estimated as the undisturbed substrate upstream of the pot following Gallagher and Gard (1999) from December 2000 to April 2001 and in the middle of the tailspill during following years. Redd areas were the sum of pot and tailspill areas calculated by treating the pot as a circle or ellipse and the tailspill as square, rectangle, or triangle. Redd locations were recorded on field maps.

To assess redd longevity and observer efficiency all flagged and newly constructed redds were examined in each survey during 2002–2003. To examine redd longevity, redds were classified as new, measurable, no longer measurable, or no longer apparent. Weekly observer efficiency was estimated as the percentage of known flagged redds (minus those classified as no longer apparent) observed during each survey. Weekly flag observer efficiency for each species was averaged for all

TABLE 1.—Number of known coho salmon and steelhead redds observed by river and year used as a training data set for logistic regression analysis. Numbers in parentheses are assumed known steelhead redds (based on date) added to increase the training data set.

	2000–2001		2001–2002	
Water body	Coho Salmon	Steelhead	Coho Salmon	Steelhead
Albion River	1	3	10	0
Caspar Creek	3	0	11	(14)
Hare Creek	0	0	2	1 (5)
Little River	0	0	5	0 (8)
Noyo River	26	7 (13)	11	9 (33)
Pudding Creek	12	0	2	0 (6)
Ten Mile River	0	0	24	0

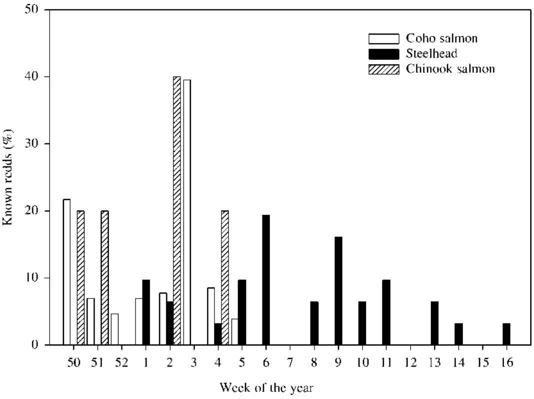

FIGURE 2.—Percent of positively identified Chinook and coho salmon and steelhead redds observed by week in several coastal Mendocino County streams, 2001–2003.

survey segments in each stream throughout the season to estimate total efficiency for the season. Multiple regression was used to examine the relationship between weekly flag-based observer efficiency, streamflow, and water visibility. To further examine observer efficiency, on two occasions during early March 2003 four crews of two followed each other on one survey segment and recorded only newly constructed redds. Average field observer efficiency was calculated by assuming the largest number of redds observed by any one crew was the known number, and the totals from each survey crew observing fewer redds was divided by this number and these averaged.

Classification of Redd Species

Examination of the number of known redds (redds which were positively identified with one species or another building or guarding them) observed by week indicated a large overlap in the time of spawning among the three species of salmonids in this study (Figure 2).

Known coho salmon and steelhead redd data were used as a training data set in logistic regression analysis to differentiate redds by species using data collected in three creeks and four rivers during 2000–2001 and 2001–2002 (Tables 1–2). To develop a training data set for discrimination, the redd data from each river was examined and all known redds identified. Because so few steelhead were observed on redds (Table 1), the number of known steelhead redds in the training data set was increased so that the number of coho salmon and steelhead redds was equal. To do this, we developed a subset of all field-identified steelhead redds containing only redds field identified as steelhead after 16 February (the last date which live or dead coho salmon adults were observed). From this data set, field-identified steelhead redds from each river each year were randomly selected until number of steelhead and known coho salmon redds per river was equal. Because no steelhead redds were observed in the Albion and Ten Mile rivers during 2001–2002 (due to the surveys ending in mid-February), more late-season, field-identified steelhead redds were randomly selected from

TABLE 2.—Average and SE of Chinook salmon, coho salmon, and steelhead redd variables used in the training data set for logistic regression; na = not applicable.

	Coho salmon			Steelhead			Chinook salmon		
Variable	Average	SE	*N*	Average	SE	*N*	Average	SE	*N*
Day	32.4	1.6	102	101.8	2.6	102	28	10.1	5
Distance from ocean (km)	14.4	0.7	86	24.3	1.4	99	40.9	3.2	5
Fork length (cm)	67.9	1.1	81	71.7	2.9	20			
Pot depth (m)	0.21	0.01	95	0.14	0.01	102	0.12	0.01	5
Pot substrate (cm)	2.1–4.5	na	102	2.1–4.5	na	102	15.2	1.3	5
Redd area (m^2)	6.03	0.34	102	1.78	0.14	102	6.72	0.87	5
Tail spill substrate (cm)	2.0–4.5	na	61	1.3–3.7	na	75	6.75	0.99	5

the other rivers to equalize the number of known redds (Table 1).

In logistic regression analysis, the species making a redd was the dependent variable and the variables listed in Tables 1 and 2 were independent variables. Survey date was changed to day with the first survey date set as one. Modeling with logistic regression continued iteratively, removing those variables least significantly associated with predicting species and rerunning the regression. The final model was tested by applying it to all known redds observed during 2002–2003 and further evaluated by applying it to known steelhead redds measured in the American River during 2002–2003 (J. Hannon, U.S. Bureau of Reclamation, unpublished data). The following equation was applied to all redds observed to reclassify them as steelhead or coho–Chinook:

$$\begin{aligned}\text{Logit } P &= -4.074 + (0.13 \cdot \text{day}) \\ &\quad - (0.918 \cdot \text{redd area}); \\ \text{steelhead} &\geq 0.5; \\ \text{otherwise, coho or Chinook salmon.} & \qquad (1)\end{aligned}$$

Chinook salmon redds were only positively identified during 2002–2003. Equation (1) predicted all known Chinook salmon redds observed during 2002–2003 to be coho salmon redds. All known Chinook and coho salmon redds during 2002–2003 were used in logistic regression analysis following a procedure similar to that used to develop equation (1). The resulting equation (equation 2) was used to classify redds as Chinook or coho salmon, that is,

$$\begin{aligned}\text{Logit } P &= -5.962 + (0.441 \cdot \text{pot substrate}) \\ &\quad + (0.253 \cdot \text{redd area}); \\ \text{Chinook salmon} &\geq 0.5; \quad \text{otherwise, coho salmon.} \\ & \qquad (2)\end{aligned}$$

This model was evaluated by comparing the number of known redds in the original data set misclassified by equation (2).

Escapement Estimates

Redd area.—Escapement estimates based on redd data were made by expanding total redd counts by the male-to-female ratio and by a method which assumes the number of redds a female makes is related to the size of the redd (redd area method). Escapement estimates assuming one redd per female were made by multiplying the number of redds by the male-to-female ratio observed in each river and summing this with the number of redds. Because Susac and Jacobs (1999) found steelhead redds per female to range from 0.5 to 4.45 and results reported herein were within this range, we assumed the number of redds per steelhead female to range from one to four.

To estimate the number of female steelhead based on redd area and a range of one to four redds per female, we estimated the number of females from redd area by multiplying the maximum-sized known steelhead redd by three-quarters, one-half, and one-quarter. Redds larger than 4.6 m^2 were assumed to represent one female. Each redd between 3.05 and 4.6 m^2 was assumed to represent three quarters of a female, redds between 1.52 and 3.04 m^2 were assumed to represent one half of a female, and redds smaller than 1.52 m^2 were assumed to represent one quarter of a female. Coho salmon redd area escapement estimates were based on findings from releases above the ECS during 1996, where it was estimated that females make between one and four redds and redd areas larger than 5.1 m^2 represent one female, redds between 2.1 and 5.0 m^2 represent one half a female, and redds smaller than 2.0 m^2 represent one-quarter of a female (M. Maahs, Salmon Trollers Marketing Association, unpublished data). Female coho salmon and steelhead redd area escapement estimates were multiplied by the male-to-female ratio observed in each stream each year and summed with female estimates to estimate populations. Observer efficiency estimated during 2002–2003 and predicted for 2000–2001 and 2001–2002 was used to expand redd counts and redd area estimates. Uncertainty in redd identification was derived from logistic regression, and field uncertainty was calculated from observer uncertainty in species making redds.

Stratified index.—To determine whether escapement estimates could be made with reduced sampling effort using a stratified index approach (Irvine et al. 1992), steelhead and coho salmon redd area densities in the Noyo River during 2001–2002 were plotted against sample reach (Figure 3a). Figure 3a indicated that after nine reaches the variance around the mean did not substantially decrease. Nine reaches were selected, and the average density was calculated and multiplied by the total length of spawning habitat in each category to estimate steelhead escapement for 2000, 2000–2001, and 2001–2002. Coho salmon escapement was estimated by the stratified index approach for the Noyo River during 2001–2002. Coho salmon and

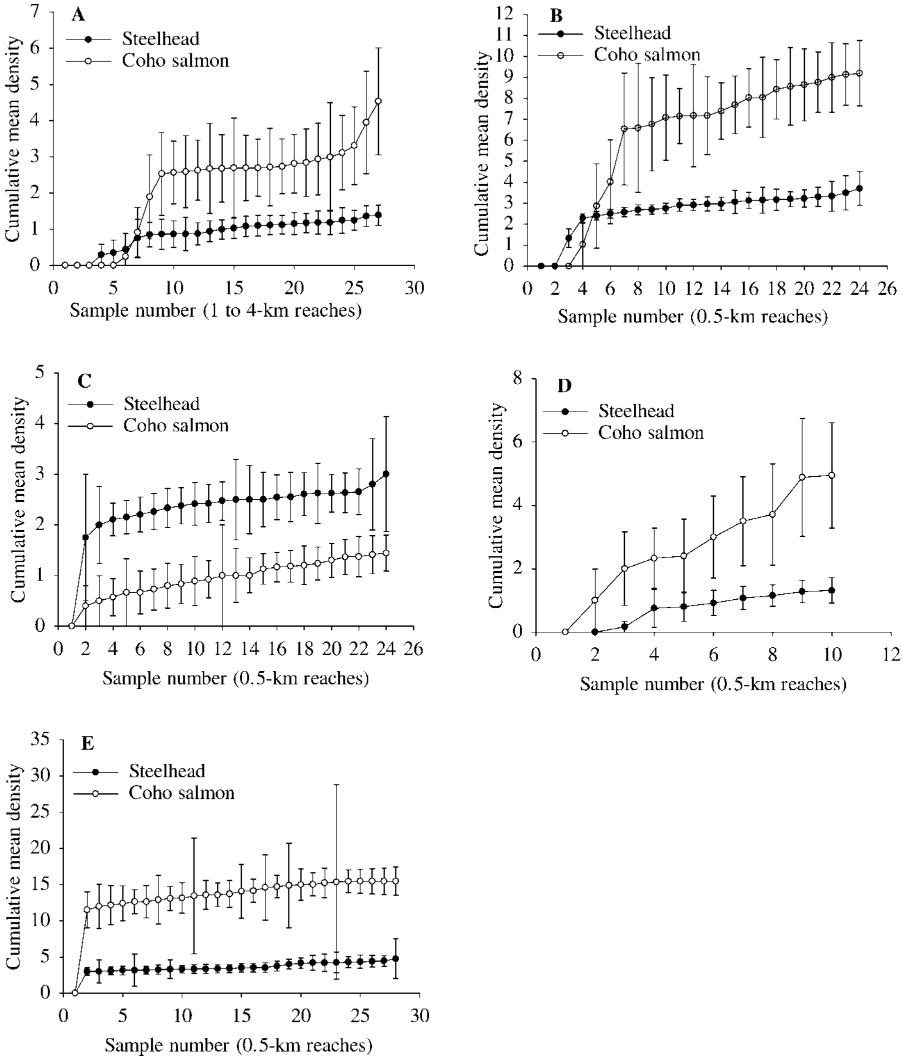

FIGURE 3.—Cumulative mean density of coho salmon and steelhead (±SE) plotted against the number of sample reaches for **(A)** the Noyo River, **(B)** Caspar Creek, **(C)** Hare Creek, **(D)** the Little River, and **(E)** Pudding Creek.

steelhead escapement was estimated with a stratified index approach in Caspar, Hare, and Pudding creeks and Little River for 2001–2002. Specifically, we divided the streams into 0.5-km segments, developed performance curves of redd area densities (Figure 3b–e), randomly selected the number of segments indicated by the performance curves, and multiplied the average density by the length of spawning habitat in each stream. These estimates were compared with estimates from surveying the entire river and capture–recapture estimates. To further evaluate this method during 2002–2003, only nine reaches were surveyed in the Noyo River and resulting escapement estimates compared to capture–recapture estimates.

Capture–recapture method.—Steelhead escapement in the Noyo River was estimated using the Petersen capture–recapture method during 2000, 2000–2001, 2001–2002, and 2002–2003 (Krebs 1989). During 2000 steelhead were captured, marked, and recaptured using gill nets set in the lower river, at the ECS, in fyke traps set throughout the river, and by anglers. During 2000–2001 a weir was operated in the lower river and fish were captured, marked, and recaptured at the weir, at the ECS, in fyke traps set throughout the river, by anglers, and during spawning surveys. During 2001–2002 and 2002–2003 steelhead were captured, marked, and recaptured by angling, at the ECS, in fyke traps set throughout the river, and during spawning surveys.

Coho salmon populations were estimated by capture and recapture of carcasses during spawning surveys in all streams following the Jolly–Seber method, or the Schnabel method when recaptures were less than seven (Krebs 1989). During 2002–2003 live coho salmon were captured and tagged in the lower Noyo River using gill nets and recaptured during spawning surveys; we estimated escapement using the Peterson method. Known numbers of coho salmon were released above the Noyo River ECS during 2000–2001, 2001–2002, and 2002–2003.

Area-under-the-curve estimates.—Spawning population estimates each year were also derived from live fish observations using the AUC method (English et al. 1992; Hilborn et al. 1999). Steelhead stream residence time (rt) was estimated separately for tributaries and main-stem sections by averaging observations of fish on redds, time between capture and recapture of tagged fish, and from data from Shapovalov and Taft (1954) and Korman et al. (2002), and was 12.6 and 41.3 d, respectively. Coho salmon rt was 11 d (Beidler and Nickelson 1980). Chinook rt of 9.3 d was the average of values presented by Parken et al. (2003) and Neilson and Geen (1981). Observer efficiency (v), the ratio of total fish seen to the total present (Korman et al. 2002), was estimated by dividing the total number of fish of each species observed during spawning surveys by the capture–recapture estimates each season. Thus, confidence intervals for AUC and capture–recapture estimates were interrelated.

Data analysis.—Physical characteristics of redds and associated variables were compared by means of correlation, logistic regression, and Mann–Whitney U- or t-tests. Significance of variables in predicting redd species was based on examination of the significance of Wald's z-values. Population estimates were compared with ANOVA or the Kruskal–Wallis ANOVA on ranks when standard kurtosis P-values were less than 0.05. Correlation was used to determine whether redd counts or redd area escapement estimates were related to capture–recapture or AUC escapement estimates by treating year- and river-specific data for each species as samples. Relationships between redd sizes and female fork lengths were examined by correlation. Statistical significance was accepted at P less than 0.05.

Results

Steelhead redd observer efficiency based on flag recaptures during 2002–2003 was 0.74 (SE = 0.02) and was very similar to the field observer efficiency of 0.75 (SE = 0.14). Coho salmon redd observer efficiency based on flag recaptures was 0.64 (SE = 0.10). There was no difference in the percentage of redds smaller than 1.5 m^2 and redds larger than 1.5 m^2 observed more than once (t = 1.06; P = 0.31; df = 16); however, the power of this test was low (β = 0.06). Weekly streamflow and water visibility were significant in predicting weekly flag-based observer efficiency (ANOVA: F = 41.8; $P < 0.001$; df = 66), and the resulting equation (equation 3) was used to predict observer efficiency for 2000–2001 and 2001–2002, that is,

$$\begin{aligned}\text{Observer efficiency} = 0.435 & \\ - (0.00278 \times \text{streamflow}) & \\ + (0.256 \times \text{visibility}). & \quad (3)\end{aligned}$$

Predicted observer efficiency was 0.74 (SE = 0.03) for 2000–2001 and 0.67 (SE = 0.02) for 2001–2002. Treating weeks as samples, predicted and estimated observer efficiency was not different among years (ANOVA: H = 3.62; P = 0.17; df = 2).

The percentage of steelhead redds still measurable after 2 weeks was 73.4%, whereas only 39% of coho salmon redds and 43% of Chinook salmon redds were still measurable after 2 weeks during 2002–2003. If surveys were conducted monthly only 25% of steelhead redds, 18% of coho salmon redds, and 14% of Chinook salmon redds would still have been measurable. After 8 weeks only 1% of steelhead, 0.2% of coho salmon, and no Chinook salmon redds were still measurable.

Classification of Redd Species

Logistic regression reduced uncertainty in redd identification. Field uncertainty in redd identification was 16% during 2000, 22.4% during 2000–2001, 18.2% during 2001–2002, and 11.1% during 2002–2003. The apparent error rate from logistic regression was 3.9% (i.e., in the training data set known-species redds [Tables 1–2], only 8 out of 204 redds were misclassified by logistic regression). When this model (equation 1) was applied to all redds observed during 2000–2001 and 2001–2002, no redds were classified as coho after 16

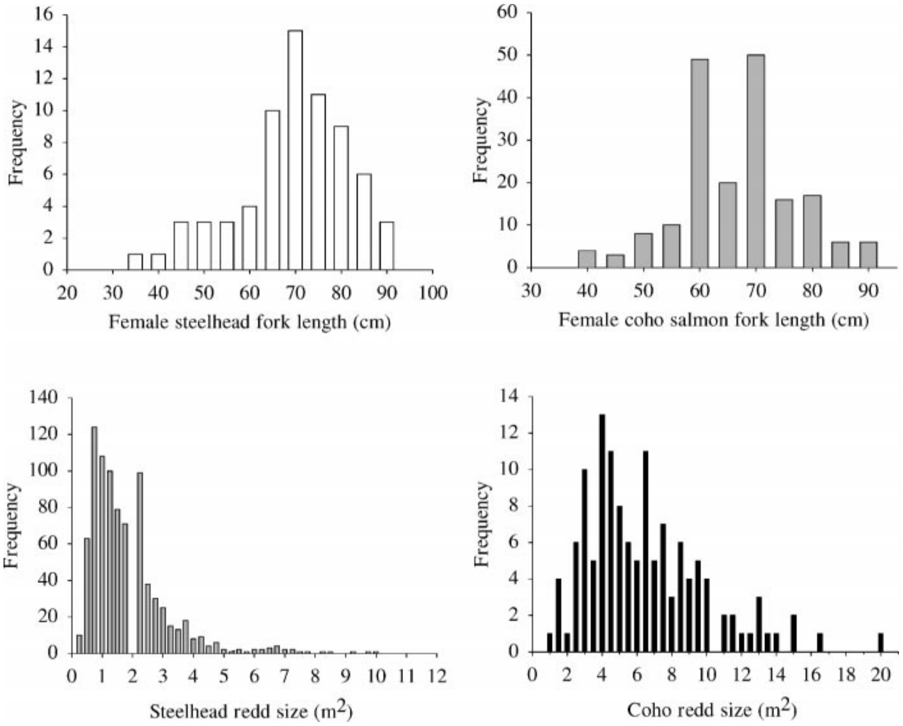

FIGURE 4.—Frequency distributions for female coho salmon and steelhead fork length (upper panels) and redd size (lower panels) in several coastal Mendocino County streams, 2001–2003.

February, the last day live or carcass coho salmon were observed. All known steelhead and coho salmon redds observed during 2002–2003 were correctly predicted to species by equation (1). Three of 44 known steelhead redds (6.8%) observed in the American River during 2002–2003 were misclassified by equation (1).

For discrimination of steelhead and coho salmon, only redd area and the date redds were observed were significantly associated with predicting species (Wald's z = 11.9 and 18.09, respectively; $P < 0.001$). Year and river were not significantly associated with predicting species (Wald's $z = 0.02$, $P = 0.88$; and $z = 0.08$, $P > 0.93$, respectively). Distance from the river mouth was not significant in predicting species (Wald's $z = 0.53$; $P = 0.47$). For redds where fish were observed in enough detail to estimate fish length, fork length was not significantly correlated with pot size ($r = 0.05$; $P = 0.62$) or redd size ($r = 0.06$; $P = 0.57$) and was not significantly associated with predicting species (Wald's $z = 0.98$; $P = 0.32$). Steelhead and coho salmon fork lengths were not different in 2000–2001 ($u = 6787$; $P = 0.05$) nor in 2001–2002 ($t = 1.27$, $p = 0.21$; Table 2), were not normally distributed (K–S = 0.15, $P < 0.001$; and K–S = 0.12, $P < 0.009$, respectively), and were skewed towards larger size fish (Figure 4a). Steelhead and coho salmon redd sizes were not normally distributed (K–S < 0.11; $P < 0.02$) and were skewed towards smaller redds (Figure 4b).

The apparent error rate for classification of Chinook and coho salmon redds (equation 2) was 5.9%. Only pot substrate and redd area were significant in classifying Chinook and coho salmon redds (Wald's z = 5.88 and 4.03; P = 0.015 and 0.04, respectively). Only five Chinook salmon redds were positively identified during 2002–2003, so it was not possible to examine river and year effects on predicting redd species or relationships between redd size and female size. The low number of known redds used in the training data set for logistic regression and the lack of multiple years' data limited the evaluation of this model.

Escapement Estimates

The uncertainty associated with each method of estimating coho salmon escapement, while generally higher for capture–recapture and AUC estimates, overlaps the point estimates, suggesting

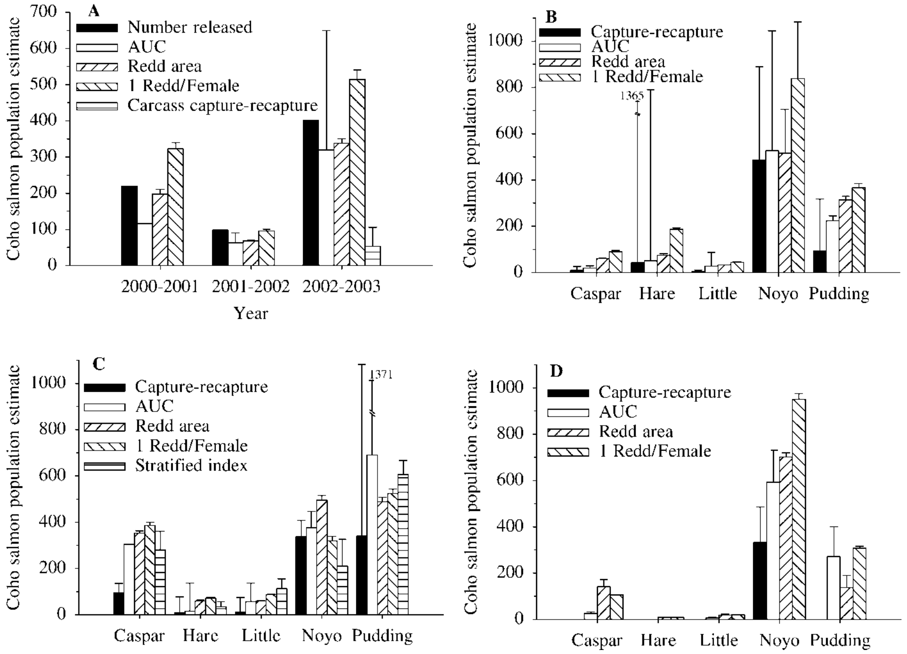

FIGURE 5.—Coho salmon population estimates in several coastal Mendocino County streams, 2000–2003. Panel **(A)** shows estimates for the area above the Noyo River egg collecting station in several time periods; panels **(B−D)** show estimates for various sites during 2002–2003, 2001–2002, and 2000–2001, respectively. The thin lines are 95% confidence intervals for the carcass capture–recapture estimates and observer uncertainty in the area-under-the-curve (AUC) estimates, the uncertainty in redd identification for the redd area and one-redd-per-female estimates, and the SE for the stratified index redd area estimates.

that all methods were similar (Figure 5a–d). Treating years as samples known numbers of coho salmon released above the ECS were not significantly different from AUC and redd area escapement estimates (ANOVA: $F = 6.54$, $P = 0.06$, df = 8; Figure 5a) nor were they different from estimates based on assuming one redd per female (ANOVA: $F = 6.30$; $P = 0.06$; df = 8). However, the power of these tests was low ($\beta = 0.51$ and 0.50, respectively). The coho salmon carcass based capture–recapture estimate above the ECS, made only during 2002–2003 because of low numbers of recaptures in other years, was much lower than the known release and other estimates (Figure 5a). Treating years as samples and including data from all streams, coho salmon carcass-based population estimates were not significantly different from redd area estimates (ANOVA: $F = 3.13$, $P = 0.12$, df = 30; Figure 5b–d). The power of this test ($\beta = 0.24$) was low. Coho salmon carcass-based estimates were significantly lower than assuming one redd per female (ANOVA: $F = 13.57$; $P = 0.04$; df = 15; $\beta = 0.90$). Coho salmon AUC and redd area estimates did not significantly differ (ANOVA: $F = 0.35$; $P = 0.57$; df = 36), but the power was low ($\beta = 0.05$). Escapement estimates based on one redd per female were not different from AUC estimates (ANOVA: $F = 3.39$; $P = 0.09$; df = 30), yet the power of this test was low ($\beta = 0.05$). Treating rivers as samples, stratified index based escapement estimates for coho salmon during 2001–2002 were not significantly different from AUC estimates (ANOVA: $F = 0.41$, $P = 0.54$, df = 30, $\beta = 0.05$; Figure 5b).

The uncertainty associated with estimating steelhead escapement by the capture–recapture method and the AUC was large and overlaps that of other methods, suggesting that all methods gave similar results (Figure 6a–c). Treating years as samples steelhead capture–recapture escapement estimates in the Noyo River (Figure 6a) were not significantly different from redd area or stratified index-based estimates (ANOVA: $F = 1.20$ and 0.15; $P = 0.35$ and 0.73, respectively; df = 12). The power of these tests was low ($\beta < 0.06$). Steelhead capture–recapture estimates were significantly different from those based on one redd per female (ANOVA: $F = 11.85$; $P = 0.04$; df = 8), but the tests power was low ($\beta = 0.60$). The AUC escapement estimates from the Noyo River were

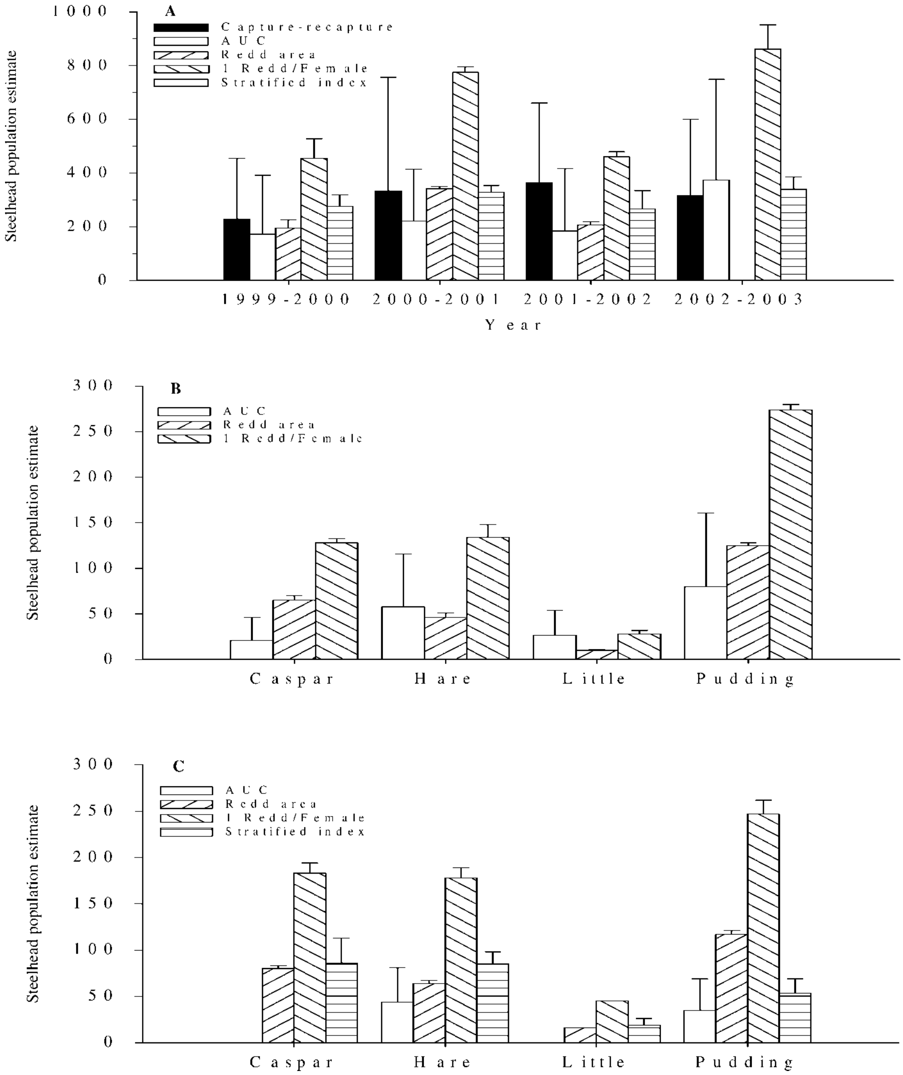

FIGURE 6.—Steelhead population estimates in several Mendocino county streams, namely, **(A)** the Noyo River from 1999–2000 to 2002–2003, **(B)** four streams in 2002–2003, and **(C)** four streams in 2001–2002. The thin lines are 95% confidence intervals for the capture–recapture and area-under-the-curve (AUC) estimates, the uncertainty in redd identification for the redd area and one-redd-per-female estimates, and the SE for the stratified index redd area estimates.

not significantly different from those of the redd area (ANOVA: $F = 0.64$; $P = 0.48$; df = 8), assuming one redd per female (ANOVA: $F = 7.88$; $P = 0.07$; df = 8), or stratified index estimates (ANOVA: $F = 0.19$; $P = 0.69$; df = 8). However, the power of these tests was low ($\beta < 0.44$). Treating years as samples and including all streams data, AUC escapement estimates were not significantly different from redd area estimates (ANOVA: $F = 0.64$, $P = 0.48$, df = 21; Figure 6a–c). The AUC estimates were significantly different from assuming one redd per female (ANOVA: $F = 13.11$; $P = 0.006$; df = 21; $\beta = 0.88$). The AUC escapement estimates were not significantly different from stratified index estimates (ANOVA: $F = 0.04$; $P = 0.85$; df = 17). However, the power of these tests was low ($\beta = 0.05$).

As with the coho salmon and steelhead escapement estimates, the uncertainty associated with the different Chinook salmon escapement estimate methods overlapped, was large for the capture–recapture and AUC methods, and indicates that all

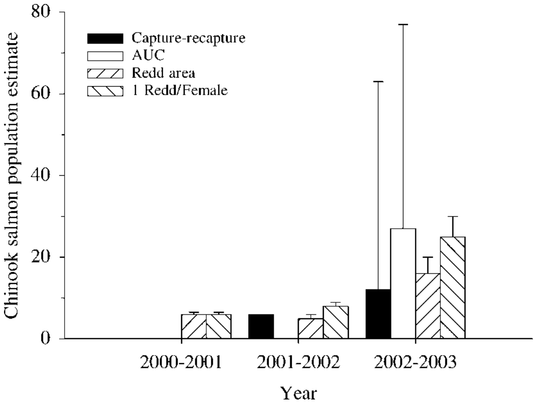

FIGURE 7.—Chinook salmon population estimates in the Noyo River from 2000–2001 to 2002–2003. The thin lines are 95% confidence intervals for the capture–recapture and AUC estimates and the uncertainty in redd identification for the redd area and one-redd-per-female estimates.

methods produced similar estimates (Figure 7). Chinook salmon were only observed in the Albion (2002–2003 only) and Noyo rivers. The Albion River was not surveyed completely in 2002–2003 such that it was not possible to make escapement estimates. Only two Chinook salmon carcasses were marked and none were recaptured during 2000–2001 such that capture–recapture estimates were not made for this season. Although sample sizes were small ($n = 2$), treating years as samples, Chinook salmon capture–recapture estimates did not differ significantly from redd area estimates (ANOVA: $F = 0.36$; $P = 0.66$; df = 4) or from estimates based on one redd per female (ANOVA: $F = 1.86$; $P = 0.40$; df = 4). The power of these tests was low ($\beta = 0.05$ and 0.11, respectively).

Based on capture–recapture and AUC estimates, coho salmon and steelhead females appear to make more than one redd. Coho salmon females released above the ECS averaged 1.25 (SE, 0.15) redds per female (range = 1.02–1.54) over 3 years. Based on capture–recapture estimates of coho salmon carcasses the average number of redds per female over 3 years in all streams was 4.61 (range = 1.80–7.04). The average number of redds per coho salmon female based on AUC estimates over 3 years in all streams was 1.70 and ranged from 0.50 to 3.19. The average number of steelhead redds per female over 3 years based on capture–recapture estimates was 1.93 (SE = 0.47) and ranged from 1.02 to 2.43. The average number of steelhead redds per female based on AUC estimates over 3 years in all streams was 3.46 and ranged from 1.80 to 6.91. In the Noyo River over 2 years Chinook salmon averaged one redd per female.

Redd counts significantly reflect Chinook and coho salmon and steelhead escapement (Figure 8a–c). Treating years as samples, coho salmon redd counts and known numbers of females above the ECS were significantly correlated ($r = 0.99$; $P = 0.04$). Treating years as samples and including all streams data, coho salmon redd counts and capture–recapture escapement estimates were significantly correlated ($r = 0.83$, $P = 0.001$, $n = 11$; Figure 8a). Similarly, coho salmon redd counts were significantly correlated with AUC escapement estimates ($r = 0.83$; $P < 0.001$; $n = 14$). Treating years as samples and including data from all streams, steelhead redd counts were significantly correlated with AUC escapement estimates ($r = 0.82$, $P = 0.003$, $n = 10$; Figure 8b). With only 2 years of data for Chinook salmon it was not possible to correlate redd counts with capture–recapture estimates, although they appear related (Figure 8c).

Discussion

We were able to account for and reduce many sources of bias and uncertainty in redd counts. By marking redds and reexamining flagged redds on subsequent surveys we were able to account for undercounting errors (i.e., missed redds). Because flag and field observer efficiency was not different, it appears that marked (flagged) and unmarked (no flags and assumed to be new) redds were equally detectable as were small and large redds. Rather than examine sources of individual variation in redd counts, we estimated it for all surveys and averaged it for the season, which tends to minimize the effects of individual errors (Krebs 1989). Dunham et al. (2001) attributed variability in redd counts to differences among individual surveyors and redd and habitat characteristics, yet did not examine the effect of streamflow or turbidity. In this study, water visibility and streamflow had a strong effect on redd detection, and we were able to use these variables to predict observer efficiency for years it was not field estimated. Although we did not account for overcounting redds (false identifications), several factors suggest this was not a concern for this study. The survey protocol had a redd classification category called ‘‘test,’’ and surveyors were instructed to use this for redds or channel features that looked like redds but uncertainty existed as to whether these features actually were redds. Redds classified as test were reexamined on subsequent surveys and if they had not

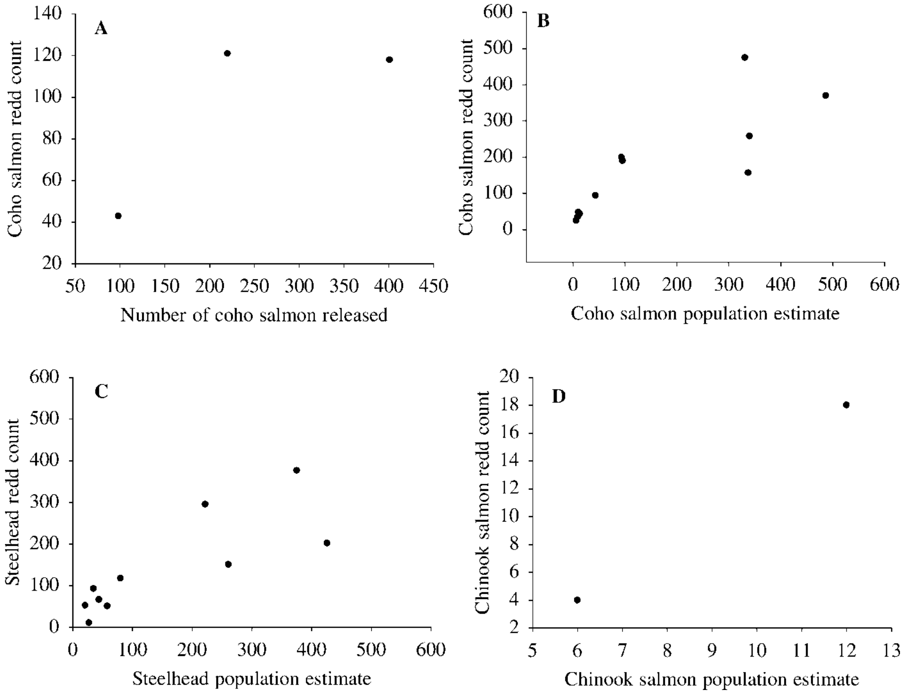

FIGURE 8.—Relationships between redd counts and salmonid population estimates in several Mendocino County streams, 2000–2001 and 2002–2003. Individual panels are as follows: **(A)** redd counts relative to the number of coho salmon released above the Noyo River egg collecting station; **(B)** redd counts relative to capture–recapture estimates for coho salmon for five streams; **(C)** redd counts relative to area-under-the-curve (AUC) estimates for steelhead for five streams; and **(D)** redd counts relative to capture–recapture estimates for Chinook salmon.

changed were left in this category; these redds were not included in further analysis. Field crews worked in pairs and were instructed to confer on redd species identification. All redds, including those field classified as test, were measured, and, as part of the measuring process, surveyors examined redds in some detail and were less likely to include channel features which were not actually redds.

The length of time redds remain visible and measurable can cause counting errors and may affect the use of redd counts for population monitoring. Dunham et al. (2001) found redd age was significantly associated with counting errors, and some redds in their study were over 4 weeks old. They and other researchers (Beland 1996; Rieman and Myers 1997; Isaak et al. 2003) counted redds once or twice at the assumed end of the spawning season. In this study we surveyed weekly or biweekly throughout the season such that the oldest redds encountered would have been aged less than 13 d. Observer efficiency was not different between years, and escapement estimates based on redd counts were not different from AUC or capture–recapture estimates among years, suggesting that biweekly surveys encountered redds as well as weekly surveys. Since redds disappeared and a large percentage were not measurable after as little as 2 weeks, we recommend that surveys be conducted less than 13 d apart or as soon after large flow events as possible throughout the spawning season. Surveying weekly rather than biweekly will increase the cost of these surveys. Survey periodicity should be within the residence time of the species of interest so that AUC can also be estimated. Surveying once at the end of the spawning season for all species (over 4 months) would not produce realistic results. Even if surveys were conducted once after Chinook and coho salmon spawning occurred and again at the end of steelhead spawning, the results would be of little use. A larger percentage of steelhead redds remained measurable longer than Chinook and coho salmon redds because most steelhead spawn later than coho and Chinook salmon, after the usual time of large streamflow events.

Classification of Redd Species

The discrimination function from logistic regression reduced species uncertainty by an average of 15% and thus decreased this source of error in the use of redd counts for population monitoring. The apparent error rate from logistic regression of 3.9% was lower than that reported by other researchers using multivariate techniques to classify salmonid redds. Fukushima and Smoker (1998) found water depth and velocity and stream gradient significant in discriminating sockeye and pink salmon redds, but report an error rate of 33%. Zimmerman and Reeves (2000) found water depth and substrate significant in separating anadromous and resident steelhead redds using stepwise discrimination and report an error rate greater than 28%.

The model based on steelhead and coho salmon redd area and date of spawning appears spatially and temporally robust for distinguishing between the two species and may be applicable to other streams where these species co-occur. All known steelhead and coho salmon redds observed during 2002–2003 were correctly classified by equation (1), and only 6.8% of known steelhead redds in the American River were misclassified. Year and river were not significant in predicting redd species. The physical features of redds which contribute to species identification (i.e., size and date of spawning) appear to be consistent over a large geographic area, suggesting they are driven by some biologically inherent characteristics of the species and not by stream geomorphic or watershed features. Steelhead redds may be smaller than coho and Chinook salmon redds because steelhead are iteroparous. Female steelhead and coho salmon fork lengths were not significantly different and redd sizes were not related to fish size. Female steelhead may not expend all their energy making redds because they survive to spawn again in later years, whereas coho and Chinook salmon die after spawning. While Burner (1951) observed that salmon continue to dig above the nest pockets of redds after spawning activity ceased, Briggs (1953) states that both male and female steelhead drift downstream after spawning is complete.

The logistic regression equation developed to distinguish between Chinook and coho salmon redds was encouraging and, although more known redd data will probably improve this relationship, it appears that these species redds can be identified based on physical characteristics. Chinook and coho salmon redds differed in pot substrate and redd size. The difference in redd size may be because Chinook salmon are larger than coho salmon. Although we found that steelhead and coho salmon fork lengths and redd sizes were not related, we were unable to examine this relationship for Chinook salmon because so few fish were observed on redds. The difference in pot substrate size between these species may be because Chinook salmon excavate their nests deeper than coho salmon (DeVries 1997) or because they prefer different substrate sizes (Hampton and Aceituno 1988). However, pot depths were not different between the two species in this study (Table 2). Redd size and substrate used to differentiate Chinook and coho salmon redds were not different from that reported in other areas (Burner 1951), suggesting that equation (2) may be useful in other areas where these species overlap. This model will need further evaluation and more data to validate its applicability over multiple years or in other systems.

Escapement Estimates

Redd area.—Although we did not quantitatively evaluate the assumption that redd size is related to the number of redds a female salmonid makes (e.g., the redd area method), several of our results suggest that this was valid. Redd area escapement estimates were not different from known numbers of coho salmon released above the ECS. The redd area and stratified redd area escapement estimates were not significantly different from other methods, except assuming one redd per female which overestimated escapement. The number of redds per female was greater than 1.0 for all methods and were within the range used in the redd area method. Redd size was not related to female size. Fork lengths were not normally distributed and were skewed towards larger fish, whereas redd sizes were skewed towards smaller redds (Figure 4), suggesting redd size is related to female effort. The redd area method accounts for multiple redds per female and smaller redds have lower importance in escapement estimates.

The redd area method is sensitive to the female: male ratio, the size and range of redds, and errors in counting and measuring redds. We used female to male ratios based on live fish observations in each stream, or when too few fish were observed, we assumed it was one to one. Average coho salmon and steelhead redd sizes were very similar each year, and we only used known redd areas for estimating the female effort ranges. Training of surveyors and efforts to reduce redd counting errors described above helped reduce these potential sources of error.

Stratified index.—Of the methods examined in this study, Chinook and coho salmon and steelhead escapement was most precisely, cost effectively, and reliably estimated using redd areas in a stratified index approach. Irvine et al. (1992) found that stratified index estimates were always similar to capture–recapture estimates. Stratified index escapement estimates were not significantly different from redd area, capture–recapture, or AUC estimates, but were significantly different from estimates assuming one redd per female for steelhead. When tested in the third year of the study, stratified index estimates were not different from AUC, capture–recapture, or redd area escapement estimates. Although the power of these tests was low and the uncertainty associated with the point estimates high, they overlapped for all escapement estimates except for the steelhead estimates that assumed one redd per female (Figures 5–6). Uncertainty associated with the stratified index estimates was lower than that of AUC and capture–recapture estimates. The one redd per female and redd area estimates were total counts, and their uncertainty was that associated with redd identification such that these methods did not provide statistical descriptions of uncertainty. Krebs (1989) states that total counts are often of dubious reliability and recommends sample counts for population estimation. The stratified index estimates can be viewed as a specialized form of block sampling where the stream segments are blocks and the entire length of spawning habitat in a stream is the census zone. The mean and variance is calculated from the blocks and multiplied by the census zone. The use of performance curves reduced cost by reducing the amount of the census zone (i.e., spawning habitat in each stream) by about 60%, allowing more coverage with the same effort while reducing variance in escapement estimates. This method was shown to work for a variety of water years and streams, is not susceptible to mechanical failure, and fish are not handled, tagged, or their movements impeded. This approach may be useful and applicable to examine and monitor metapopulation dynamics (Rieman and McIntyre 1996) important for the recovery of these threatened species (Isaak et al. 2003). Redd counts and escapement from stratified redd areas was significantly correlated with fish released above the ECS (coho) and capture–recapture estimates, thus these estimates track population trends (Figure 8). This, combined with reduced uncertainty from improvements in redd counts and redd identification and realistic confidence bounds from the stratified index approach, suggests it may be useful for monitoring and detecting long term trends (Maxell 1999).

Capture–recapture estimates.—The capture–recapture estimates had large confidence bounds owing to low numbers of marked and recaptured fish, and carcass-based estimates appeared to underestimate populations (Figures 5–7). Carcass population estimates require unique individual marks, a short duration between surveys, and survey of the entire river to increase the chance of recapturing marked fish. Increasing the periodicity of surveys during 2002–2003 allowed coho salmon carcass-based estimates above the ECS, yet this drastically underestimated escapement and did not greatly decrease uncertainty in the escapement estimates for other streams (Figure 5). To observe, tag, and recover enough carcasses to reduce the uncertainty with these estimates might require surveys on a daily basis because high flows between surveys can bury, wash away, or otherwise decrease the chance of finding carcasses (Cederholm et al. 1989). Too few steelhead carcasses were observed to estimate escapement using the capture–recapture method. Live fish capture–recapture programs require active capture techniques which are susceptible to mechanical failure in moderate-to-high water years, and that fish are tagged, handled, and their movements impeded. Permanent or temporary counting structures are expensive to build, maintain, and operate; are susceptible to mechanical failure; and, coupled with extensive permitting and access requirements, limit their use over a large geographic area. Shapovalov and Taft (1954) could not operate traps on Waddell Creek, California, during high flows, and seining to capture steelhead in the Rouge River, Oregon, was limited by high flows (Everest 1973).

Area-under-the-curve estimates.—The AUC estimates were not different from total counts of coho salmon above the ECS or from capture–recapture estimates of Chinook salmon, coho salmon, and steelhead. This suggests that the use of residence time from the literature for Chinook and coho salmon and estimated for steelhead in the Noyo River and applied to other streams in this study was not unrealistic. However, observer efficiency and residence time should be estimated annually for each stream and estimated throughout each season (English et al. 1992; Manske and Schwarz 2000) because the AUC method is very sensitive to these variables (Hilborn et al. 1999).

English et al. (1992) found the AUC method is also sensitive to variability in survey time. The AUC confidence bounds in this study were estimated from observer efficiencies which were tied to the capture–recapture estimates. One of the major shortcomings of the AUC is that it lacks a rigorous statistical method for calculating confidence bounds and when estimated requires intensive bootstrap computer simulation and independent capture–recapture estimates for their calculation (Korman et al. 2002; Parkin et al. 2003). Where the AUC has been used to estimate salmonid escapement, residence time and observer efficiency have been estimated using independent capture–recapture programs (Shardlow et al. 1987; Jones et al. 1998, Korman et al. 2002; Parken et al. 2003) which are capable of estimating escapement without the use of the AUC. Because of the need to better define estimates of residence time and observer efficiency (Manske and Schwarz 2000) and the need for intensive simulation to estimate statistical descriptors of uncertainty, the AUC may prove too cumbersome for long-term monitoring of salmonids in coastal northern California.

Reduction of counting errors and uncertainty in redd identification, combined with biweekly surveys throughout the spawning period of Chinook and coho salmon and steelhead, allowed us to estimate escapement in a stratified index sampling design using redd areas. This resulted in precise, reliable, and cost-effective escapement estimates compared with more conventional approaches. We recommend that surveys be conducted 7–13 d apart, that observer efficiency in redd counts be estimated for each survey and averaged for the season, that redd identification be based on the logistic regression models presented here (with continued development and testing of the Chinook–coho salmon model as data become available), and that escapement be estimated using redd areas in a stratified index approach. The relationship between redd size and the number of redds a female builds needs further evaluation. This approach appears promising for long term monitoring of individual populations and metapopulations (Isaak et al. 2003) in a randomized block design similar to that applied to salmonids in Oregon (Jacobs et al. 2001). Evaluations of the power of the data from stratified index redd area escapement estimates for long-term trend detection should be conducted.

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