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[Article]

Performance of Spawner Survey Techniques at Low Abundance Levels

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Abstract.—Population monitoring is essential to know whether coastal California's Endangered Species Act–listed Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* stocks are progressing toward recovery. In coastal California, salmonids are at the southern edge of their range, and this one of many reasons they are not abundant. This provides unique challenges for monitoring, as different survey methods will result in estimates with different levels of accuracy and precision, which are important for evaluating population trends. For this study we intensively monitored three Mendocino County watersheds to evaluate the reliability of two-stage data for monitoring regional escapement. Under this scheme, regional spawning surveys (stage 1) were calibrated with data from intensively monitored watersheds (stage 2), where escapement was estimated using capture–recapture methods, redd counts, and fish counts. The objective of the study was to evaluate the quality of the stage 2 data for calibrating regional surveys. We evaluated the precision of live-fish capture–recapture estimates and compared these estimates with estimates derived from spawning survey data using carcass capture–recapture, area under the curve (AUC), and redd counts. Live-fish capture–recapture produced escapement estimates with narrower 95% confidence bounds where permanent structures were used to capture fish. Redd counts converted to fish numbers using spawner : redd ratios were chosen for the regional salmonid monitoring method because they were reliable, economical, and less intrusive. Converted redd counts were statistically and operationally similar to live-fish capture–recapture estimates but required fewer resources. The AUC estimates were less reliable than converted redd counts and live-fish capture–recapture methods due to the sensitivity of the estimates of residence time and observer efficiency. Finally, we found that carcass capture–recapture methods were operationally unsuccessful in coastal California streams. On the basis of our results, we recommend that annual spawner : redd ratios from intensively monitored watersheds be used to calibrate redd counts for regional status and trend monitoring of California's coastal salmonids.

Population monitoring is essential to know whether salmon and steelhead populations listed under state and federal Endangered Species acts (ESAs) are progressing towards recovery. This knowledge drives management decisions directing actions designed to conserve and restore salmonid populations and their habitat. These decisions require an adequate level of confidence in estimates of abundance and ability to detect change in abundance over reasonably short time intervals. Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* are all at the southern edge of their range in California (Good et al. 2005) and are species listed under the U.S. ESA (NOAA 1999, 2000, 2005). Coho salmon are also listed under the California ESA (CDFG 2004). For reasons identified in the listings and because of anthropogenic impacts, all of these salmonid populations are at various, but generally low, abundance levels. Sampling salmonids at low abundances results in levels of accuracy and precision very different from those in the survey sampling methods widely used in Oregon, Washington, and British Columbia (Boydstun

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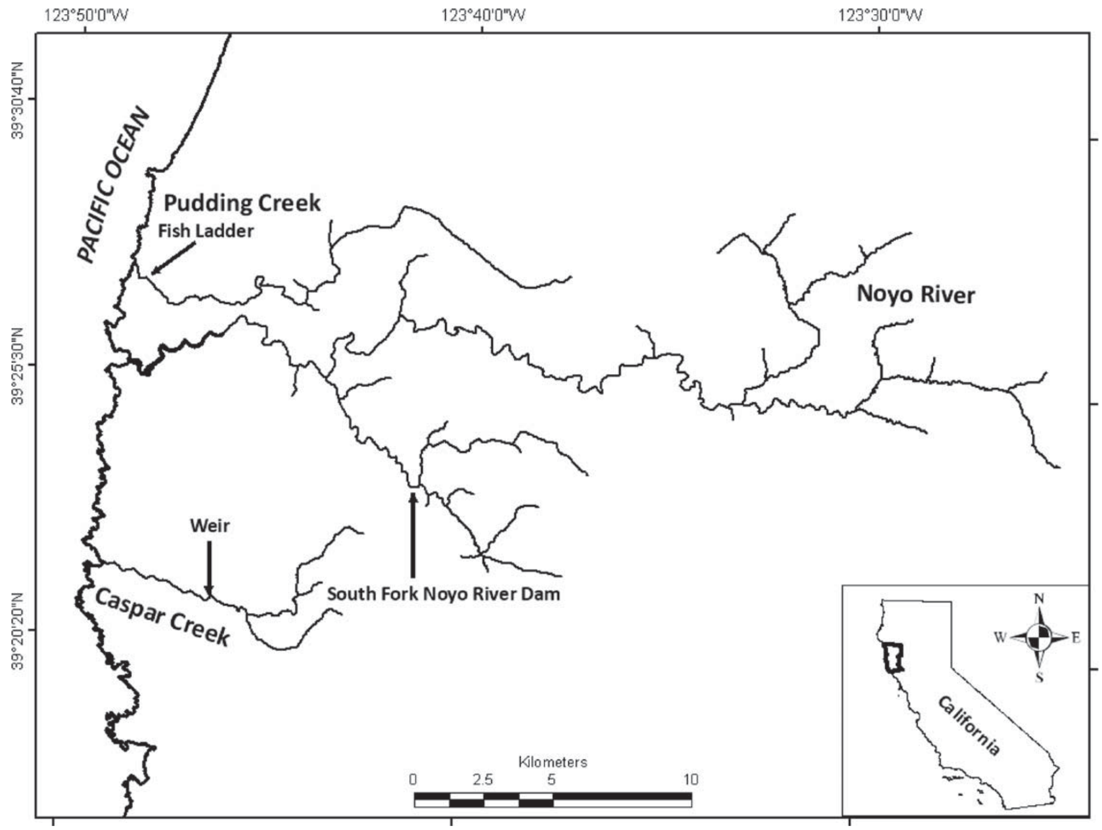

FIGURE 1.—Locations of the study streams. The South Fork Noyo River Dam is the South Fork Noyo River egg collecting station.

and MacDonald 2005). The challenge is to design a practicable and affordable sampling program to monitor the status and trends of these overlapping populations across a very large geographical scale (i.e., Evolutionarily Significant Units) that will also provide estimates accurate enough to direct recovery actions at smaller population scales. Therefore, an evaluation of the performance of different salmon escapement monitoring methods is necessary to determine which methods provide estimates adequate for our management purposes.

The objective of this study was to evaluate whether the accuracy and precision of estimates from intensively monitored (small spatial scale) streams could be used for calibrating regional (large spatial scale) survey sampling at conditions of low salmonid abundance. Intensively monitored streams were chosen where the use of weirs was judged suitable to estimate numbers of spawning adults by using capture–recapture methodologies. We evaluated the precision of our capture–recapture estimates based on live fish and compared these to estimates derived from spawning survey data using (1) redd counts, where redds were converted to adult numbers using spawner : redd ratios; (2) repeated live-fish counts utilizing area-under-the-curve (AUC) estimation techniques (Hilborn et al. 1999); or (3) salmon carcass capture–recapture techniques (Boydstun 1994). Findings of this study will provide advice for sampling salmonids at low abundance and will help shape coastal California's salmonid monitoring program.

Study Area

This study evaluated these three estimation methods for sampling in three streams in coastal Mendocino County (Figure 1) as described by Boydstun and McDonald (2005). The three study streams (Figure 1) were selected on the basis of existing facilities, equipment, ease of access, and prior monitoring knowledge. Three different types of adult capture structures were used: (1) a flashboard dam and fish ladder on Pudding Creek; (2) a concrete dam structure

TABLE 1.—Coho salmon and steelhead spawner : redd ratios for some coastal Mendocino County streams, 2004–2008. The lower and upper 95% confidence limits are given along with the point estimates; nd = no data.

Site and year	Number of coho salmon per redd: Lower limit	Point estimate	Upper limit	Number of steelhead per redd: Lower limit	Point estimate	Upper limit
South Fork Noyo River						
2004	1.45	1.65	1.65			
2005	1.70	3.27	5.08			
2006	7.74	11.40	21.78			
2007	1.52	2.28	4.04	0.27	0.71	28.36
2008	nd	nd	nd	0.28	0.46	1.05
Pudding Creek						
2004	1.35	2.02	3.98	0.31	1.11	1.82
2005	2.18	2.68	3.85	1.03	1.62	2.15
2006	8.40	9.33	10.83	0.49	1.29	4.59
2007	2.68	3.65	5.46	1.47	2.98	14.51
2008	1.35	2.02	3.98	0.90	1.05	3.39
Caspar Creek						
2006	1.37	3.32	121.00	0.11	0.14	0.55
2007	0.62	1.20	4.36	1.22	2.47	12.17
2008	nd	nd	nd	0.17	0.36	0.61
All sites, average						
2004	1.40	1.84	2.83	0.31	1.11	1.82
2005	1.94	2.98	4.46	1.03	1.62	2.15
2006	5.84	8.01	51.20	0.28	0.67	8.16
2007	1.61	2.38	4.62	0.90	1.72	14.05
2008	1.35	2.02	3.98	0.45	0.62	1.68
Grand mean[a]	1.61	2.35	4.06	0.62	1.22	6.92

[a] Coho salmon ratios do not include 2006 data.

(the Noyo River Egg Collecting Station) on the South Fork Noyo River; and (3) a floating board resistance weir (Stewart 2002) in Caspar Creek (Figure 1). In Caspar Creek and the South Fork Noyo River, spawning habitat occurs directly above the capture structures. In Pudding Creek a 5-km-long pond is above the capture structure. Adult fish have been observed within a few hours after tagging on the spawning grounds in all three streams. These streams are dominated by coniferous redwood forests, range in drainage area from 22 to 42 km^2, flow directly into the ocean, and are groundwater-fed with peak flows in winter following heavy rains.

Methods

Live-fish capture–recapture abundance estimation.—We used live-fish capture–recapture methods, as described by Gallagher and Gallagher (2005), to estimate escapement in our intensively monitored streams. These estimates were used as the standard against which escapement estimates based on other methods were measured. The other methods included live-fish counts, redd counts and measurements, and carcass capture–recapture. Abundance data were collected in Pudding Creek and the South Fork Noyo River from 2004 to 2008 and in Caspar Creek from 2006 to 2008. Fish captured at the trapping sites described above were marked and released with week-specific individually numbered bicolored floy tags. Recaptures were based on live-fish observations made during spawning surveys (Szerlong and Rundio 2008). To evaluate tag loss, fish were also marked with weekly stream-specific operculum punches.

Spawning ground redd survey abundance estimation.—To estimate escapement, we used redd count and measurement data collected during spawning surveys following Gallagher and Knechtle (2003) and Gallagher et al. (2007). Over- and undercounting errors in redd counts (bias-corrected) were reduced following Gallagher and Gallagher (2005). These efforts included a formal written protocol, training of field staff, pairing experienced and inexperienced observers, marking and reexamining marked redds, estimating observer efficiency for each reach, measuring redds, using predictive models to determine redd species, having a test category for ambiguous redds (these were removed from further analysis), and surveying biweekly. Surveys were conducted approximately fortnightly from early December to late April each year in all spawning habitats in each stream.

We evaluated the use of the number of fish per redd (spawner : redd ratio) to convert bias-corrected redd counts into fish numbers. We calculated spawner : redd ratios by dividing capture–recapture abundance estimates for coho salmon and steelhead by the bias-corrected redd counts for all available data (Table 1).

TABLE 2.—Coho salmon residence times in three coastal Mendocino County streams; na = not available.

		Residence time (d)		
Site and year	*n*	Lower limit	Point estimate	Upper limit
South Fork Noyo River				
2003–2004	119	25.97	28.09	30.22
2004–2005	21	21.14	26.81	32.48
2005–2006	4	18.25	19.14	37.39
2006–2007	1	na	21.00	na
Pudding Creek				
2003–2004	19	28.99	32.63	36.27
2004–2005	10	11.33	21.10	30.87
2005–2006	6	14.38	25.00	35.62
2006–2007	2	12.72	25.00	32.72
2007–2008	1	na	24.00	na
Caspar Creek				
2005–2006	1	na	16.00	na
2007–2008	1	na	24.00	na
All sites, average				
2003–2004	138	27.48	30.36	33.24
2004–2005	31	16.23	23.95	31.68
2005–2006	11	15.03	21.73	28.42
2006–2007	3	20.00	23.30	29.00
2007–2008	2	na	24.00	na
Grand mean	185	24.43	26.21	27.98

TABLE 3.—Steelhead residence times in some coastal Mendocino County streams; na = not available.

		Residence time (d)		
Site and year	*n*	Lower limit	Point estimate	Upper limit
Noyo River main stem				
1999–2000	3	24.76	38.00	51.24
2002–2003	2	0.00	28.0	75.41
2005–2006	1	na	48.00	na
Grand mean[a]	6	17.84	30.87	43.83
Noyo River tributaries				
1999–2000	8	6.99	12.13	17.26
2000–2001	3	6.55	16.67	26.78
2001–2002	1	na	15.00	na
2002–2003	4	2.40	13.25	24.10
2004–2005	2	0.00	10.00	27.24
2006–2007	1	na	19.00	na
2007–2008	8	13.35	25.67	37.98
Pudding Creek				
2003–2004	8	3.00	9.37	15.75
2004–2005	3	22.43	28.33	34.24
2006–2007	2	6.40	47.00	87.60
2007–2008	1	na	34.00	na
Caspar Creek				
2006–2007	1	na	21.00	na
2007–2008	5	3.60	30.40	57.20
Grand mean, tributaries, 2000–2005[a]	29	11.33	15.43	19.54
Annual average[a]				
2006–2007	4	11.01	20.00	28.99
2007–2008	13	20.27	27.80	36.20
Grand mean	53	16.60	21.00	25.40

[a] Bootstrap 95% confidence limits.

These estimates were then used to convert redd counts into fish numbers in each stream, using multiyear and annual multistream average spawner : redd ratios. Transferability of the spawner : redd ratios among streams and over years was evaluated using analysis of variance (ANOVA). Spawner : redd ratios were used to convert bias-corrected redd counts into fish numbers for each stream.

Repeated live-fish count (AUC) abundance estimation.—Spawning population estimates were derived from live-fish observations by dividing the number of fish-days (estimated using the AUC) by residence time and multiplying by observer efficiency (English et al. 1992; Hilborn et al. 1999; Szerlong and Rundio 2008). Coho residence time was estimated from the time between the initial capture and tagging of live fish and their recapture as fresh carcasses (clear eyes and no fungus, hence assumed to be recently deceased; Table 2). Because steelhead are iteroparious, we estimated steelhead residence time as the time between capture and recapture of tagged fish in Pudding and Caspar creeks and the Noyo River (Table 3). Steelhead were recaptured at our capture structures and in smolts traps in these three streams. We estimated steelhead residence time separately for the main stem Noyo River and tributaries and evaluated these data for estimating escapement with AUC. We evaluated the utility of using annual three-stream average and multiyear average residence time estimates for estimating escapement with AUC. Transferability of residence time among streams and over years was evaluated using ANOVA. Observer efficiency, the ratio of total number of fish observed to the total number of fish present (Korman et al. 2002), was estimated as the total number of marked fish observed during spawning surveys divided by the total number of marked fish present.

Carcass capture–recapture abundance estimation.—Chinook and coho salmon escapement was also estimated by carcass capture–recapture methodology (marked independently of the floy tag experiments described above). All carcasses observed during spawning surveys were marked with uniquely numbered metal tags (Gallagher and Knechtle 2003). We examined the carcass mark–recapture data by survey reach to determine whether this method was useful for producing reach-specific escapement estimates. When detected during spawning surveys, carcasses were inspected for metal tags, floy tags, and operculum punches to estimate tag loss and residence time.

Data analysis.—Mark–recapture escapement was estimated using the Schnabel method, and confidence intervals (CIs) were obtained from the Poisson distribution (Krebs 1989). We evaluated tag loss following Krebs (1989). Relationships between redd counts and escapement estimates were examined by using correlation. The spawner : redd ratio expanded redd count and AUC escapement estimates were compared to the capture–recapture data using ANOVA, treating years as replicates. Root mean square errors among methods were compared to evaluate the best method for estimating regional escapements; lower values were considered more precise. To evaluate precision in our escapement estimates, we also evaluated 95% CI half-widths. Narrower 95% CIs (and thus smaller SD) were deemed more precise and reliable than wider bounds. Finally, we compared population estimates, residence time, and spawner : redd ratios with ANOVA or the Kruskal–Wallis test (K–W) when the kurtosis was significantly different from zero ($P < 0.05$). We accepted statistical significance at P less than 0.05, although endangered species management often accepts statistical significance at the P less than 0.10 level (Good et al. 2005).

Results

Capture–Recapture

The methods used for carcass capture–recapture were not useful for any species because too few fish were marked and recovered. For coho salmon, the carcass capture–recapture estimates were orders of magnitude lower than live-fish estimates (data not presented); also, because we encountered few carcasses, we were unable to produce these estimates for any stream in 2008. Nor were we able to produce reach-level carcass capture–recapture escapement estimates necessary for regional monitoring. For Chinook salmon, although we were able to estimate mean escapement in the Noyo River during 2007 as 4 fish (95% CI, 2–157 fish), we were unable to estimate Chinook salmon escapement with carcass capture–recapture during 2006 or 2008.

Live-fish capture–recapture using brightly colored floy tags in situations where permanent structures were used to capture coho and steelhead produced escapement estimates with narrower 95% CI bounds than those from our temporary weir. We did not capture and mark any live Chinook salmon at any of our weirs and were therefore unable to evaluate the methodology for this species. For coho salmon, the capture–recapture escapement estimates had 95% CI half-widths that were 70% of the point estimates for both Pudding Creek and the South Fork Noyo River (Figure 2A). Additionally, in 2 of 5 years the Pudding Creek 95% CI half-widths were no more than 30% of the point estimates. In contrast, the 95% CI half-widths for coho salmon at Caspar Creek, a floating board resistance weir, was more than 100% over 2 years. Because coho salmon returns were low in 2008 (the lowest in the study period), we did not observe any tagged fish during spawning surveys in Caspar Creek and the South Fork Noyo River. As a consequence, we were unable to produce reliable CI estimates for the capture–recapture escapement estimates for these streams. For steelhead, the capture–recapture escapement estimates had wider 95% CIs than did those for coho salmon in all three streams (Figure 2B). Furthermore, in only two instances were the steelhead 95% CI half-widths less than 50% of the point estimates; half the time, they were more than 100%. We were not able to produce capture–recapture escapement estimates for steelhead in the South Fork Noyo River during 2006 because no fish were captured and marked there that year. Throughout all years of the study, the CIs were narrower for coho salmon than for steelhead at the permanent capture structures. However, the temporary weir on Caspar Creek had narrower CI estimates for steelhead than for coho salmon (Figure 2A, B).

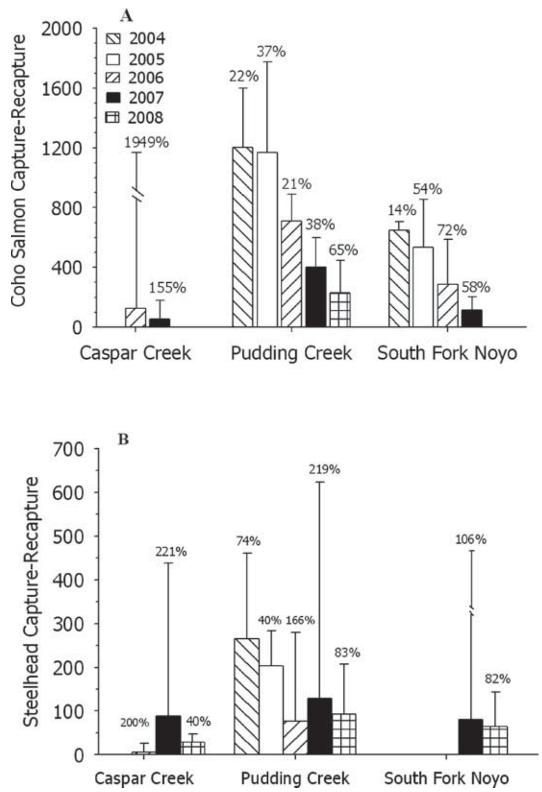

FIGURE 2.—**(A)** Coho salmon and **(B)** steelhead capture–recapture escapement estimates for three life cycle monitoring streams in Mendocino County, 2004–2008. The thin lines are 95% confidence intervals; the percentages are the widths of those intervals relative to the point estimates.

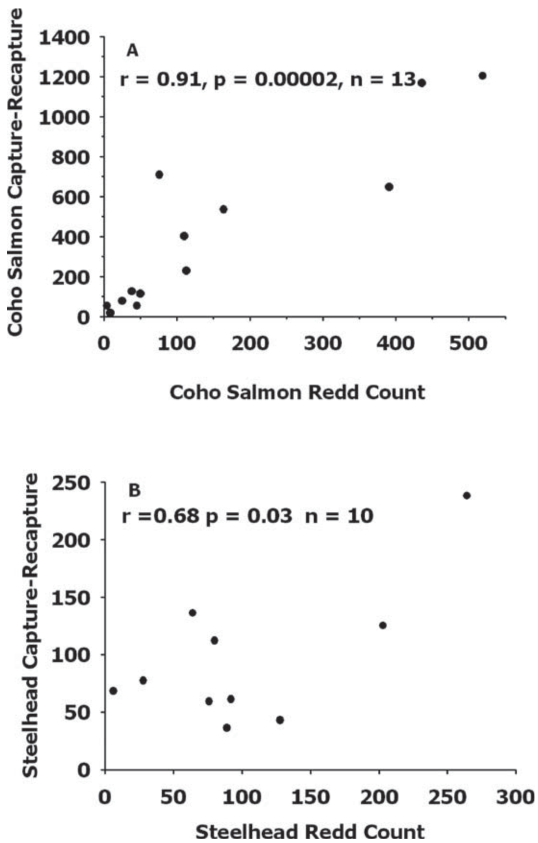

FIGURE 3.—Relationships between capture–recapture escapement estimates and redd counts for **(A)** coho salmon and **(B)** steelhead in coastal Mendocino County.

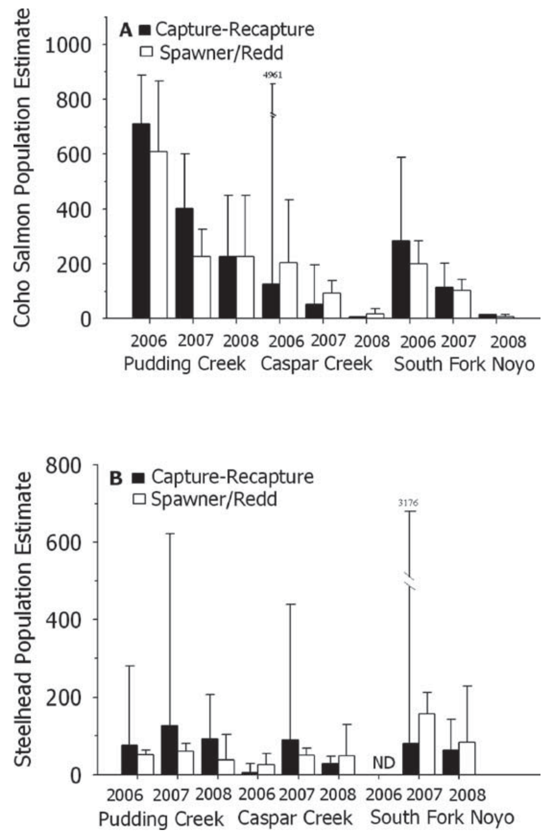

FIGURE 4.—Capture–recapture and spawner : redd ratio population estimates for **(A)** coho salmon and **(B)** steelhead in three life cycle monitoring streams in coastal Mendocino County, 2006–2008. The thin lines are 95% confidence intervals; ND = no data.

Live adult coho salmon and steelhead did not lose their marks. However, tag loss probability for fresh coho salmon carcasses averaged 0.28 for floy tags and 0.68 for operculum punches (torn or missing operculum) over 3 years. Tag loss probability for the few tagged steelhead carcasses observed averaged 0.25 for floy tags and 0.75 for operculum punches over 3 years. As an illustration of the durability of floy tag as a marking technique, three steelhead kelts tagged in downstream traps in spring were recaptured fresh from the ocean at our weirs the following winter. Despite spending nearly a year at sea, these fish retained their floy tags. In contrast, their operculum punches, although still obvious, had regenerated.

Redd Methods

Redd counts were significantly positively correlated with the capture–recapture escapement estimates for coho salmon (r = 0.91, P < 0.001, n = 13) and for steelhead (r = 0.68, P = 0.03, n = 10; Figure 3). We found that escapement estimated from the redd counts expanded by the annual spawner : redd ratios overlapped the capture–recapture estimates in all cases (Figure 4).

The spawner : redd ratios for coho salmon (Table 1) were not significantly different among streams when years were treated as replicates (ANOVA: $F_{2,\ 11}$ = 0.19, P = 0.83). The power of this test (β) was low (β = 0.08). Similarly, steelhead spawner : redd ratios were not significantly different among streams (ANOVA: $F_{3,\ 12}$ = 1.21, P = 0.35, β = 0.08). Neither were the coho (K–W: H = 10.24, df = 7, P = 0.17) or steelhead (K–W: H = 7.79, df = 8, P = 0.45) spawner : redd ratios significantly different among seasons when streams were treated as replicates, even though the 2006 coho salmon spawner : redd ratios in Pudding Creek and the South Fork Noyo River were much larger than in other years. Based on examination of the root mean square error, annual average spawner : redd ratio–based

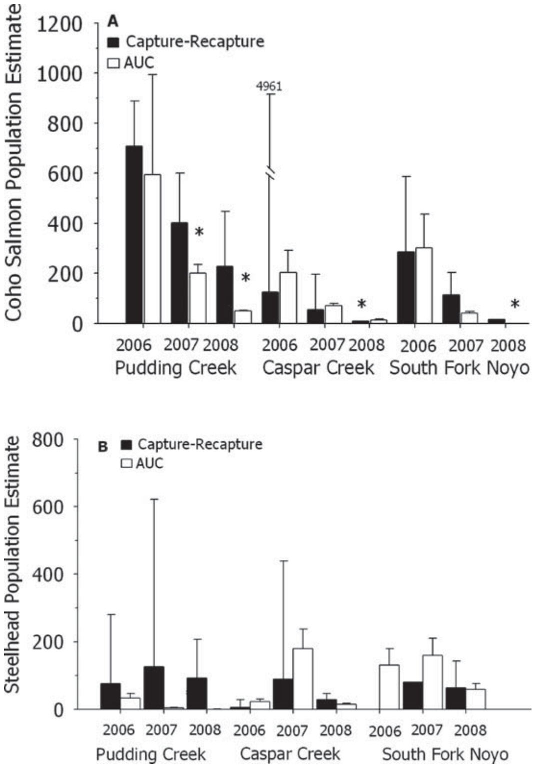

FIGURE 5.—Capture–recapture and AUC population estimates for **(A)** coho salmon and **(B)** steelhead in three life cycle monitoring streams in coastal Mendocino County, 2006–2008. The thin lines are 95% confidence intervals; asterisks indicate no overlap between intervals.

escapement estimates (coho = 111.3, steelhead = 46.8) were more precise than escapement estimated by using the mean of all years' data (coho = 191.9, steelhead = 55.9). Because the spawner : redd ratios varied among years, and because using annual average ratios produced more precise escapement estimates than did using the mean of all years' data, we used annual average spawner : redd ratios. Steelhead spawner : redd ratios had wider 95% CI bounds than did coho salmon as a result of the precision of the capture–recapture estimates (Figure 2; Table 1).

Area under the Curve

The results from the first 2 years suggested that AUC escapement was best estimated by using the multiple-year average residence time and annual observer efficiency calculated as the total number of marked fish observed divided by the total number marked and released (Figure 5). Coho salmon residence time was not significantly different among streams or over years (ANOVA: $F_{6,\ 174} = 1.71$, $P = 0.12$, $\beta = 0.27$; Table 2). For coho salmon, observer efficiency averaged 0.19 (SE = 0.01) and was not significantly different among streams (ANOVA: $F_{3,\ 8} = 2.70$, $P = 0.11$, $\beta = 0.30$). However, observer efficiency was significantly different over years (ANOVA: $F_{3,\ 9} = 4.31$, $P = 0.044$, $\beta = 0.53$). Steelhead residence time in the main stem Noyo River was significantly different from that in all other sites (K–W: $H = 22.61$, df = 13, $P = 0.046$; Table 3). Without the main stem Noyo River observations, steelhead residence time was not significantly different among streams and years (K–W: $H = 13.99$, df = 9, $P = 0.12$). When years were treated as replicates, steelhead residence time was not significantly different among main stem reaches of the Noyo River (ANOVA: $F_{1,\ 3} = 1.04$, $P = 0.38$, $\beta = 0.06$). Residence time also was not different between Noyo River tributaries and the other small streams in this study (K–W: $H = 19.43$, df = 11, $P = 0.06$). Therefore, we used tributary residence time estimates for tributary and small stream estimates and main stem residence time for main stem estimates. Observer efficiency for steelhead averaged 0.18 (SE = 0.05) and was not significantly different among streams or over years (ANOVA: $F_{1,\ 5} = 0.33$, $P = 0.5$, $\beta > 0.30$).

The AUC escapement estimates for coho salmon developed using these data overlapped the capture–recapture escapement estimates for all streams in 2006 and for Caspar Creek and the South Fork Noyo River in 2007, but they did not overlap in any stream in 2008 (Figure 5A). When we treated years as replicates, coho salmon capture–recapture and AUC escapement estimates were not significantly different (ANOVA: $F_{1,\ 16} = 3.58$, $P = 0.09$, $\beta = 0.28$). For steelhead, AUC and capture–recapture escapement estimates overlapped in two of three streams during 2008 and for all other years and streams except not for Pudding Creek in 2007 (Figure 5B). Steelhead capture–recapture and AUC escapement estimates were not significantly different (ANOVA: $F_{1,\ 14} = 0.18$, $P = 0.68$, $\beta = 0.05$). Examination of the root mean square error indicated that the spawner : redd ratio–based escapement estimates (coho = 78.2, steelhead = 57.9) were more precise than the AUC escapement estimates (coho = 112.7, steelhead = 67.2).

Discussion

At low salmonid abundance, we found that redd counts converted to fish numbers using spawner : redd ratios were the best choice for estimating regional salmonid populations: They were reliable, cost effective, less intrusive, and conceptually intuitive. Converted redd counts were statistically and operationally similar to live-fish capture–recapture estimates but overall required fewer resources to conduct and were less invasive to ESA-listed fish. The AUC estimates were largely influenced by their sensitivity to residency time and observer efficiency estimates; consequently, we found they were less reliable than converted redd counts and live-fish capture–recapture methods. Finally, carcass capture–recapture methods tested at low abundance were found to be operationally unsuccessful.

Our results suggest that redd counts were reliable indices for monitoring low-abundance salmonid escapement. Thus redd counts alone could serve as an index of annual escapement. Others (Jacobs et al. 2001; Gallagher and Gallagher 2005) have found that redd counts are significantly correlated with capture–recapture estimates. Being the product of reproductive adults only, counts of salmon redds provide an index of effective population size (Meffe 1986). Dunham et al. (2001) suggest that, operationally, redd counts are less intrusive and expensive than using tagging, trapping, underwater observation, weirs, and genetics to inventory bull trout populations, and therefore more populations can be inventoried over a longer period with limited resources. Redd counts are widely utilized to provide indirect estimates or indices of spawning escapement on rivers that lack counting facilities (Murdoch et al. 2009a). Because our findings corroborate the findings of previous studies for use at low abundance, we too suggest using redd counts for regional monitoring rather the AUC method, the latter being more commonly used in Oregon for coho salmon (Jacobs et al. 2001).

Bias-corrected coho salmon and steelhead redd counts converted to fish numbers using annual spawner : redd ratios produced escapement estimates that were similar to capture–recapture estimates. Although the statistical power of the ANOVA comparisons was low, the 95% CIs overlapped, and the root mean square error comparisons suggested that spawner : redd ratio escapement estimates were more similar to the capture–recapture estimates than were AUC estimates. Coho salmon average spawner : redd ratios had 95% CI half-widths of less than 70% over 3 years (Table 1). The 95% CI half-widths for the multiyear spawner : redd ratios were less than 50% for coho and less than 64% for steelhead (Table 1). Because we did not capture and tag any live Chinook salmon, we were not able to calculate spawner : redd ratios for this species. Boydstun and McDonald (2005) wrote that Chinook redds are expanded by a factor of 2.5 in Washington State. Alternatively, Chinook redd counts can be converted to escapement by using the observed sex ratio and an estimate of 1.01 redds per female (Murdoch et al. 2009b).

Because coho salmon and steelhead spawner : redd ratios developed for this study were not different among streams or over years, we could use them for converting regional redd counts into escapement in our study; our findings suggest that these ratios should prove useful for long-term regional monitoring. The number of steelhead per redd in coastal Mendocino County was not different from that reported by Susac and Jacobs (2002) for coastal Oregon rivers; they were, however, slightly less than twice the 1.2 female steelhead per redd reported by Duffy (2005). Although we observed between-year and between-stream variations in coho salmon and steelhead spawner : redd ratios, these variations were not significantly different, probably because following strict field and laboratory protocols reduced the bias in redd counts. Dunham et al. (2001) found considerable annual variation in bull trout spawner : redd ratios in Idaho, which they attributed to life history variation or bias in redd counts. Al-Chokhachy et al. (2005) attributed variation in bull trout spawner : redd ratios to differences in contributions from different life history forms. Steelhead spawner : redd ratios ranged from 1.04 to 3.15 in coastal Oregon over 3 years (Jacobs et al. 2001). Annual spawner : redd ratios can be viewed as conversion factors for converting redd counts into escapement; as such, they incorporate annual variation in survey conditions related to environmental conditions (e.g., high or low flows or turbidity levels). For example, during 2006, coho salmon spawner : redd ratios were much larger than other years (Table 1) because of difficult survey conditions, but expanded redd counts were not different from capture–recapture escapements (Figure 2). Calibrated redd counts are important for answering questions of status and are conceptually easier than using redd areas (Gallagher and Gallagher 2005) or simply assigning an arbitrary conversion factor such as multiplying redds by 2.5. We recommend using annual spawner : redd ratios to convert redd counts into escapement estimates.

The live-fish capture–recapture methodology developed for this study produced reasonable coho salmon escapement estimates for the permanent counting structures in Pudding Creek and the South Fork Noyo River and provided information for reducing bias in, and calibration of, the regional escapement estimates. However, the coho salmon escapement estimates made using the floating board weir in Caspar Creek, although improved in 2007 compared to 2006, still lacked precision relative to the estimates in the other two streams. The structure of the Schnabel estimator (sum of recaptures plus one in the denominator, Krebs 1989) enabled us to estimate coho escapement during 2008. However, because no marked fish were observed in two of three streams, we could not derive the upper bounds of the 95% CIs for these streams. Krebs (1989) states that population estimates for management should be accurate to ±25% and preliminary surveys should be accurate to ±50%. Jacobs and Nickelson (1998) suggest that ±30% should be the target precision level for monitoring coho salmon Gene Conservation Units in Oregon. Jacobs et al. (2001) defined ±30% as the target precision levels for steelhead redd count estimates in Oregon. In four of five years the precision in the live coho capture–recapture estimates for Pudding Creek was less than 50% and in two of these years it was no more than 25%. Precision in the coho salmon capture–recapture estimates in the South Fork Noyo River have been less than 60% over 3 years and less than 25% for one season. Low coho salmon returns during the last year of the study period resulted in low precision of the capture–recapture estimates.

The precision of steelhead capture–recapture estimates was low because of the low numbers of marked and recaptured fish. We were able to generate steelhead capture–recapture estimates for all years and streams except for the South Fork Noyo River in 2006. Precision of five of our steelhead capture–recapture estimates was less than 85% and for two estimates was less than 50%. For comparison, Jacobs and Nickelson (1998) estimated basin level precision in escapement estimates between 80% and 99%. Additionally, Korman et al. (2002) suggest that precision in tagging studies can be improved by selecting survey dates with the best possible survey conditions and by increasing the number of tags present (i.e., marking more fish). Because steelhead enter streams in low numbers during high flows, they are difficult to capture, tag, and reobserve. From our estimates of precision for steelhead capture–recapture estimates, as well as the work of others, we believe managers may have to accept larger uncertainties in escapement estimates or use redd area estimates (Gallagher and Gallagher 2005).

The AUC method is sensitive to the time between surveys, estimates of residence time, and observer efficiency (Hilborn et al. 1999), which should be estimated annually for each stream (English et al. 1992; Manske and Schwarz 2000). Capture–recapture experiments provided reasonable estimates of residence time and observer efficiency, and we used both annual three-stream average and multiyear average residence time estimates. Because steelhead residence time differed between main stem and tributary reaches, we used separate residence time estimates for observations in different areas. Korman et al. (2002) found that steelhead residence time (called survey life) for fish tagged lower in the system (e.g., main stem observations) was significantly longer than that of fish tagged in the upper parts of their study area. Neilson and Geen (1981) found that early arriving Chinook salmon had longer residence time than those arriving later in the season. Because our data indicated that residence time was not significantly different among streams or over years, and because combining the data increased sample size and thus decreased the variance, we used multiyear estimates.

The AUC method generally produced escapement estimates that were not different than our capture–recapture estimates during the first 2 years of the study; during the last year of the study, however, the AUC estimates were very different. Lestelle and Weller (2002) found that for coho salmon in Washington AUC escapement estimates were more reliable than redd count estimates at high spawner abundance, whereas redd counts were better at low spawner abundance. During the present study, coho salmon escapement decreased over the study period and was lowest during 2008 (Figures 4A, 5A). Low abundance influenced observer efficiency, which, coupled with variation in estimates of residence time, affected the precision of the AUC estimates. We believe that low abundance is the main difference between coastal California and areas to the north where the AUC is commonly used. Our field staff observed that live coho may be more readily detected than redds during surveys conducted when conditions are marginal (e.g., high flows and turbidity). Therefore, live-fish observations may have utility for producing escapement estimates during wet years or years of high abundance. In contrast, average annual spawner : redd ratio conversions of redd counts into escapement were not different from capture–recapture estimates for any stream. The AUC escapement estimates should be evaluated annually for reliability relative to that of capture–recapture experiments made over a longer number of years.

Carcass capture–recapture methodology (described by Crawford et al. 2007) was operationally unsuccessful in estimating salmonid escapement in this study, an outcome we believe would be the case in all of coastal northern California. We were able to produce coho carcass capture–recapture estimates for only two of three streams during 2007 and these estimates were orders of magnitude lower than our live-fish estimates. This was because we observed too few coho salmon carcasses in any of the reaches surveyed during the study to develop these estimates. Removal by predators and high flows can decrease the chance of finding carcasses, and Cederholm et al. (1989) found that the occurrence of buried carcasses was greatly underestimated. Although stream flows during the coho spawning periods in 2007 and 2008 were generally low, carcass counts did not produce reliable escapement estimates, and buried carcasses were unlikely to be responsible for this result. Surveys were conducted about every 10 d, the frequency recommended by Crawford et al. (2007). Our results contradict the findings of Boydstun (1994), who observed no difference between Chinook carcass capture–recapture estimates and total live-fish counts in Bogus Creek, California. The characteristics of Bogus Creek, however, are quite unlike any of the streams we studied. A small Klamath River tributary in the transition zone between the Cascade Range and the Great Basin, it supports a high density of Chinook spawners. For Chinook salmon during our study, we were able to produce carcass capture–recapture estimates in only one of the three study years. Clearly, additional work is needed to evaluate regional sampling for monitoring Chinook salmon in coastal California. Although our carcass capture–recapture efforts did not produce effective abundance estimates, they were nonetheless valuable because they provided observers with hands-on experience in species identification and differentiation of the sexes. Therefore we recommend continued field efforts at carcass capture–recapture, but suggest that escapement estimates not be based on these data. Because carcasses lost both types of marks applied on live fish and because so few carcasses were observed, we suggest mark–recapture studies use resightings of live fish rather than carcass recoveries for streams with low abundances of coho salmon and steelhead trout.

The main purpose for constructing and operating the floating board weir in Caspar Creek was to examine the utility of using this type of temporary structure for capturing and tagging salmonids; if successful, it would give some flexibility as to where on the landscape intensively monitored streams can be located. With continued improvement in design and operation, the weir showed promise for capturing and tagging coho salmon and steelhead. After 3 years, however, the 95% CIs for coho salmon were still more than 100% of the point estimates; in contrast, the variance about the steelhead estimates improved over time (Figure 2B). This may be a result of flow variance in Caspar Creek; because the stream flows overtopped and flowed around the weir during storm events, some fish passed through without detection. We located the weir at the lowest point in the stream with access and chose the most conducive site to place it, but the bank still required considerable modification to produce a uniform channel needed for optimal operation. In Scott Creek, California, Bond et al. (2008) located a similar floating board weir in a section of stream with confining railroad levees on both banks. Using this different configuration, they were able to produce steelhead escapement estimates with 95% CIs of no more than 20% of the point estimates over the past few years (Sean Hayes, NOAA Fisheries, Santa Cruz, California, personal communication). In this study, capture–recapture estimates had narrower 95% CIs where permanent structures were used to capture and tag adult fish. Our experience with the Caspar weir, and the findings of Bond et al. (2008), suggest that site location is critical to the success of these types capture structures.

Finally, we found that redd counts converted to fish numbers using spawner : redd ratios or simply redd counts themselves were the most efficient regional salmonid survey method at low abundance conditions. The converted redd counts or the redd counts were more similar to the more intense and expensive capture–recapture counts than were other methods because of the nature of rare populations. In addition, the redd methods were a less invasive method of population estimation for ESA-listed species near extinction.

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