

# CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, SPAWNING ESCAPEMENT BASED ON MULTIPLE MARK-RECAPTURE OF CARCASSES

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## ABSTRACT

Mark-recapture data from a population of chinook salmon, *Oncorhynchus tshawytscha*, carcasses were collected for escapement estimates in a northern California stream. Escapement was taken to be immigration into the population of carcasses. Results from three methods of estimating total immigration into this population—Jolly-Seber, Manly and Parr, and Jolly-Seber with a modified data set—were compared to a weir count. Sources of violations of modeling assumptions, age-dependent catchability, and survival were identified, but the estimates appeared to be relatively insensitive to these. The effect of lower sampling intensity, which exacerbates effects of age-dependent catchability, was evaluated through simulation. The third method appears to be the best of the three because 1) it requires the least sampling effort, 2) it is the most robust with respect to violations of the assumption of equal catchability, and 3) it enables reanalysis of previously collected data. Standard errors and 95% confidence intervals of estimates obtained by the third method were computed by simulation. Since the distribution of estimates is asymmetrical, these confidence limits are preferred over standard expressions.

Pacific salmon fisheries are currently managed by attempting to allow a specified number of fish to escape the fishery, migrate upstream and spawn. Proper management therefore requires accurate estimates of this escapement. Since Pacific salmon die immediately after spawning, escapement can be estimated from the number of carcasses that accumulate during a spawning season. The California Department of Fish and Game (CDF&G) estimates escapement of chinook salmon, *Oncorhynchus tshawytscha*, each year using the methods of Schaeffer (Schaeffer 1951; Darroch 1961) and Peterson (Seber 1982) to analyze mark-recapture data from surveys of accumulated carcasses. Since the fish enter the stream to spawn during the sampling periods, the assumption of a closed population required by the Peterson estimate does not hold. The Schaeffer method is designed to estimate numbers from a stratified two sample experiment in which fish are tagged at different locations (or different times at one location as fish migrate upstream) and are sampled at the same locations (or an upstream point) at a later time. CDF&G carcass surveys, on the other hand, involve sampling the same unstratified stretch of spawning stream several times. The results described here are part of an attempt to develop an accurate, efficient, and robust procedure for estimating escapement from carcass data. A

technique that allows not just estimates for current and future years, but also could be used to analyze mark-recapture data taken by CDF&G in past years was desired.

Parker (1968) and Stauffer (1970) used standard Jolly-Seber methods to estimate spawning run sizes from mark-recapture data obtained from carcass counts. However, they did not examine departures from modeling assumptions by collecting appropriate data in the field or statistically testing assumptions. Also, an independent count of the population size was unavailable, hence actual errors in their estimates could not be computed. In addition, carcasses were carefully replaced where they had been found after sampling and tagging, hence captured carcasses would have a high probability of being recaptured. Thus, their results were probably biased because of heterogeneous capture probabilities.

To develop the estimation technique a mark-recapture experiment was performed in the Bogus Creek spawning area of the Upper Klamath River drainage during the 1981 chinook salmon spawning run. As a check on the estimates, a counting weir was placed at the mouth of Bogus Creek. Salmon were counted while they were in the weir trap, and were subsequently released upstream. This mark-recapture study differed from the usual mark-recapture studies of fish and wildlife populations in that the population was composed of carcasses (i.e., individuals enter the population by dying and leave by predation and decay). Thus, the age of a carcass,

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as used here, refers to time since death rather than time since recruitment.

The procedures followed here differed from previous CDF&G surveys in that more data were taken than were actually needed for the estimate so that departures from model assumptions could be examined. The additional data enabled simulation of the sampling procedure to estimate bias and variances, and allowed us to determine the sources of failure of assumptions. We were also able to develop estimates from which some sources of bias had been removed.

## METHODS

The study was conducted on a chinook salmon spawning area of a small northern California

stream, Bogus Creek (Fig. 1). The stream was sampled over a 6.5-mi reach from a counting weir upstream to Bogus School road. Sampling was begun on 15 September 1981, at the very beginning of the spawning run, and discontinued on 12 November 1981, by which time very little spawning activity was apparent. The stream was sampled weekly during that period; sampling took 2 d during the peak of the run, with one half of the stream being sampled per day. The stream was sampled by two people walking upstream and capturing with a gaff any carcasses seen. Data on each capture were described as follows:

Place of capture: Edge top, edge bottom, middle top, middle bottom, snagged, dry or buried.

Size: Small (<65 cm), medium minus (65-69 cm),

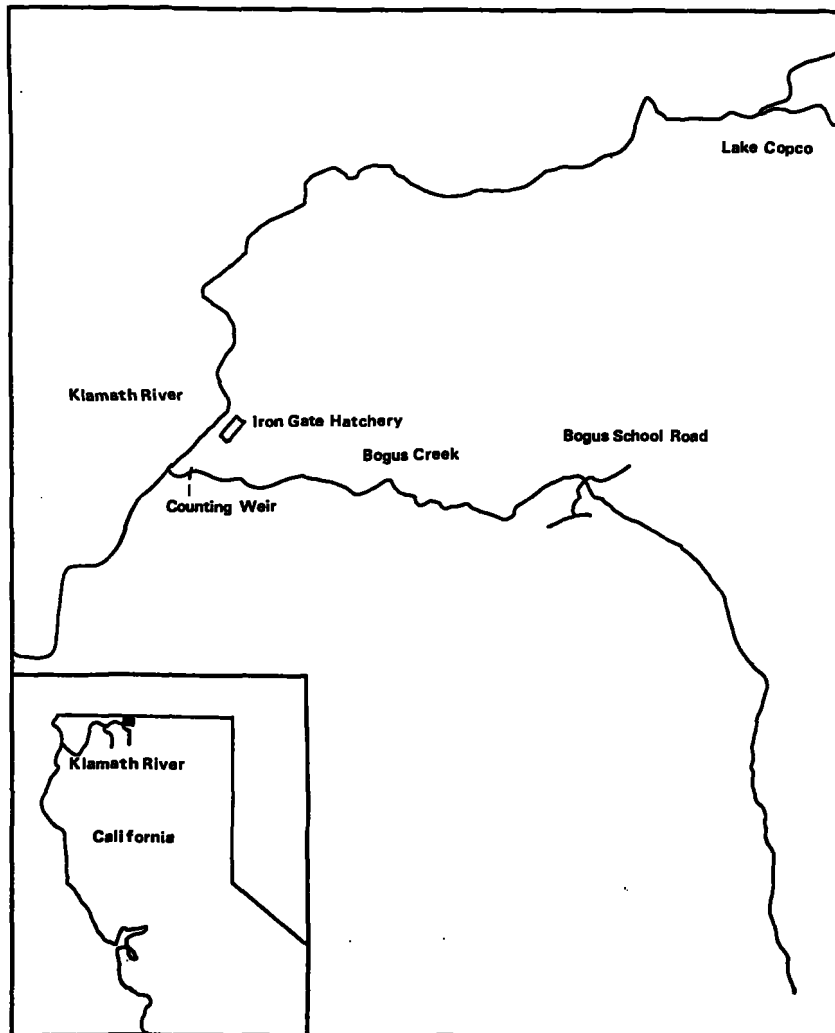


FIGURE 1.—Study area in northern California.

medium (70-80 cm), medium plus (81-85 cm), or large (>85 cm).

Sex: Male or female.

Condition: Alive, fresh (eyes clear), decayed minus (eyes cloudy, flesh firm), decayed (flesh soft), decayed plus (flesh very soft), or skeleton (flesh falling off).

Carcasses were individually tagged with fingerling fish tags which were attached around the maxillary bone. Data on place of release for each released carcass were recorded as follows:

Pool, pool/riffle, or riffle.

The presence or absence of obstructions which would trap and remove a carcass.

The speed of water flow.

Thus movements of individual carcasses and their condition, both of which might affect catchability and survival, could be examined on an individual basis. During the sampling process about one-third of the unmarked, captured carcasses was randomly removed from the population by cutting the fish in two. This was done because of limited time available for recording data. These individuals were considered "trap mortalities" (i.e., they are counted in the sample size but not in the total releases for that time period). Because the mark-recapture methods used allow for capture loss, removal of these fish has no effect on errors other than lowering sample sizes.

Two existing methods, those of Jolly and Seber (Seber 1982) and Manly and Parr (1968), and a third, a modified Jolly-Seber method, were used to estimate population sizes, recruitment, survival, and their standard errors (when expressions were available). The corrected estimates of Seber (1982) were used for the Jolly-Seber method. When survival was estimated as greater than unity, or immigration as <0.0, those values were replaced with 1.0 and 0.0 respectively in subsequent calculations. In the third method, standard Jolly-Seber estimates were calculated after modifying the mark-recapture data so that all decayed (decayed minus or worse) carcasses (marked and unmarked) were assumed to have been destroyed upon capture. This method simulates the way CDF&G has traditionally collected data.

After these estimates had been calculated, the estimated escapement,  $E$ , was calculated as the number present at the first sample period, plus the number of individuals immigrating during each subsequent period.

$$\hat{E} = n_1 + ((\hat{N}_2 - R_1 * \hat{\Phi}_1)/(\hat{\Phi}_1)^5) + \hat{D}_2 + \hat{D}_3 + \hat{D}_4 \quad (1)$$

where  $n_1$  = the number sampled at the first sample time,

$R_1$  = the number tagged and released at the first sample time,

$\hat{N}_2$  = the estimated population size at sample time two,

$\hat{D}_i = \hat{B}_i/(\hat{\Phi}_i)^5$ ,

$\hat{\Phi}_i$  = the survival rate from  $i$  to  $i + 1$ , and

$\hat{B}_i$  = the estimated number of carcasses still present at the sample time  $i + 1$  which immigrated between  $i$  and  $i + 1$ .

In this expression the initial number present at time period 1 is conservatively taken to be the sample size at time period 1 ( $n_1$ ). The number immigrating during the subsequent period is taken to be the estimated population at time period 2, minus the number of tagged fish which had been accounted for in the first sample. Immigration during the next two periods are standard estimates. Each immigration rate is divided by the square root of the survival rate (the survival rate for half the sample period), to account for fish that enter the population and leave it between sampling periods, and thus are never sampled (Stauffer 1970).

Estimates of immigration during the last time period are not computed in standard multiple mark-recapture experiments; however, this immigration ( $B_4$  here) can be estimated from the standard Jolly-Seber expression (Seber 1982), if the final numbers ( $N_5$ ) and survival rate ( $\Phi_4$ ) can be estimated. If survival varies little from sample to sample,  $\Phi_4$  can be estimated by assuming that mortality is equal to the value estimated over an earlier period in this study. Since survival varied little between sampling periods and the  $\chi^2$  test of Seber (1982) failed to reject the null hypothesis of constant survival ( $\chi^2 = 0.4648$ ,  $df = 2$ ), we estimated survival from period 3 to period 4 as the average of  $\hat{\Phi}_1$ ,  $\hat{\Phi}_2$ , and  $\hat{\Phi}_3$ . To estimate  $N_5$ , we estimated the capture probability at sample period 5 ( $P_5$ ) as the ratio of the number of carcasses released at sample 4 and recaptured at sample 5 ( $r_4$ ) to the number released at sample 4 ( $R_4$ ) times survival to sample 5 ( $\hat{\Phi}_4$ ),

$$\hat{P}_5 = r_4/(R_4 * \hat{\Phi}_4). \quad (2)$$

We then estimated the population size at sample 5

( $\hat{N}_5$ ) as the sample size ( $n_5$ ) divided by the capture probability ( $\hat{P}_5$ ).

Standard errors and 95% confidence limits for the third method were obtained by simulation. The sampling process was simulated by generating a population of carcasses based on population size estimates from the third method. We then sampled the population by comparing a uniformly distributed random number with the appropriate probability of capture [see Sykes (1982) for a more detailed description of the simulation process, and a Fortran program].

From each simulation we calculated Jolly-Seber estimates of survival, immigration, population sizes, and their standard errors. An estimate of  $E$  was then calculated as above. This simulation process was repeated 1,000 times. In addition to calculating the average and standard error of each of these estimates, 95% confidence limits were calculated by Buckland's (1980) method 1. To obtain 95% confidence limits by this method, one adds the difference between the average of the 25th and 26th lowest estimates (out of 1,000) and the average value to the field estimate to obtain the upper bound and subtracts the difference between the average of the 25th and 26th highest estimates and the average value to obtain the lower bound.

All three methods assume that all individuals are equally catchable. The methods based on the Jolly-Seber model also assume that all individuals have equal probabilities of survival. Since violation of these assumptions could result in biased estimates, we determined whether catchability and survival varied and the effects of these on the estimates.

Several statistical tests can be used to check for differential catchability and mortality, but only among animals that are already marked. Two  $\chi^2$  tests, which compare expected frequencies of capture histories with actual frequencies (Seber 1982; Jolly 1982) were calculated from the unmodified field data. The test of Leslie and Carothers (Carothers 1971) was not performed because of the small number of sampling periods. Since both tests yielded expected values less than unity, pooled  $\chi^2$  values were also calculated, using a conservative df value of  $df = (\text{number of pools} - 1)$ . For Seber's test, all values less than unity were pooled; for Jolly's, each value less than unity was pooled with the next highest value.

Following Leslie et al. (1953, cited by Seber 1982) we tested for homogeneity of catchability and survival by comparing estimates of population parameters obtained by different methods. These methods differ in sensitivity to survival and capture heterogeneity, hence the presence of heterogeneity

should cause differences in estimates of the same parameter by the different methods. We tested the unmodified field data by calculating the following parameter estimates as per Leslie et al. (1953):

- $\hat{v}_i$ : the estimated number of new marks released at time  $i$
- $\hat{\phi}_i$ : the estimated survival for the subpopulation of marked carcasses, and
- $\hat{N}_i$ : the number of marked carcasses.

and compared them with, respectively,

- $v_i$ : the actual number of new marks released at time  $i$
- $\hat{\phi}_i$ : the Jolly-Seber estimate of survival, and
- $\hat{M}_i$ : the Jolly-Seber estimate of the number of marked carcasses.

If differential catchability or survival, when present, results in significant bias, these estimates will be different.

Since only marked (and thus decayed) carcasses are considered in the statistical tests discussed thus far, these tests do not address the potential for age-dependent catchability. To evaluate possible effects of age-dependent catchabilities we "corrected" the sample size  $n_i$  by reducing it to account for the fact that fewer fresh (shiny, silver colored) carcasses would have been captured if they had not been more visible than decayed (dull brown colored) carcasses. We then recalculated the escapement estimates using the corrected sample size. We used two ratios of average fresh to decayed catchability: 2.0 and 1.4. Since visibility only differed among carcasses on the stream bed, and only 30% of the captures were on the stream bed, these values represented actual ratios for carcasses on the stream bed of approximately 6.7 and 4.7, respectively.

To evaluate the potential advantage of increasing the efficiency of the third method by lowering the sampling effort we examined the effect of lowered sampling intensity on behavior of the three estimators. Lower effort would most likely result in less searching on the bottom of the stream for carcasses. We therefore simulated lowered sampling by generating new capture histories for each individual according to the following set of rules: 1) If an individual was buried at a capture event, that and all subsequent captures were ignored, 2) captures of decayed carcasses on the stream bed and surface were ignored according to comparison of a uniform random number with the appropriate decrease in capture probability, and 3) the next cap-

ture of an individual whose previous bottom capture was ignored was considered to be a bottom capture, as movement was probably the result of the previous capture event.

### RESULTS

Total escapement estimates for the three methods and the weir count of fish moving into the spawning area are presented in Table 1. All three methods result in escapement estimates that are close to the weir count. The third method is the most efficient

TABLE 1.—Estimates of total escapement and the estimates used to compute them for each of the three methods.

	Jolly-Seber	Manly and Parr	Method 3
$\hat{N}_2$	999	1,076	1,063
SE $\hat{N}_2$	95	128	139
$\hat{N}_3$	2,302	2,312	1,886
SE $\hat{N}_3$	166	184	161
$\hat{N}_4$	1,845	1,853	1,452
SE $\hat{N}_4$	67	72	93
$\hat{B}_2$	1,801	1,740	1,459
SE $\hat{B}_2$	174	( <sup>1</sup> )	183
$\hat{B}_3$	150	136	371
SE $\hat{B}_3$	128	( <sup>1</sup> )	179
$\hat{\phi}_2$	0.7617	0.7789	0.7297
SE $\hat{\phi}_2$	0.353	( <sup>1</sup> )	0.439
$\hat{\phi}_3$	0.7878	0.7940	0.8578
SE $\hat{\phi}_3$	0.0305	( <sup>1</sup> )	0.0548
$\hat{n}_1$	87	87	87
$[\hat{N}_2 - R_1 \hat{\phi}_1] / \hat{\phi}_1^{0.5}$	1,042	1,139	1,142
$\hat{D}_2$	2,062	1,970	1,708
$\hat{D}_3$	169	151	401
$\hat{D}_4$	84	91	170
$\hat{E}$	3,445	3,438	3,508

Weir count: 3,642

<sup>1</sup>Estimate of these standard errors are not available.

in the sense that it requires the least sampling effort.

For the third method, Jolly-Seber estimates and associated estimated standard errors, computed from the survey data along with the average value, standard errors, and 95% confidence limits obtained from simulation, are presented in Table 2. Estimated standard errors and simulated standard errors are in close agreement, except that the distribution of estimates around the mean value is clearly asymmetrical. Since they are based on simulation of the actual process rather than approximate analytical expressions, confidence limits obtained from simulation are presumably more realistic than those estimated by the methods of Jolly and Seber.

The sum of the estimated escapement by time  $i + 2$  is plotted with the sum of the weir count at time  $i$  in Figure 2. Since the numbers of fish which migrated through the weir correlates well with the estimated number of fish that died 2 wk later, most salmon probably spawned and died within 2 wk of having entered the stream. Since the estimate of immigration during the last sampling interval seems to fit the known number of fish immigrating, the assumption of constant survival seems to be a good one. It is clear that our criteria for stopping sampling when most spawning activity had ceased resulted in an estimate of the complete run. Sampling for another week would have removed the need to make any assumptions in estimating  $B_4$ , but since this value will always be small in relation to the total escapement, the increase in accuracy does not seem worth the additional effort.

Data regarding the condition of carcasses at the time of capture reflect a declining trend in catch-

TABLE 2.—Estimates of escapement ( $\hat{E}$ ), population size ( $\hat{N}$ ), immigration ( $\hat{B}$ ), survival ( $\hat{\phi}$ ), and associated standard errors obtained from a Jolly-Seber analysis of data for method three. Also shown are the computed mean, standard error, and 95% confidence intervals obtained by simulation.

	Field estimate	Simulation value			
		Mean	SE	Upper 95% C.I.	Lower 95% C.I.
$\hat{N}_2$	1,063	1,041	145	+222	-344
SE $\hat{N}_2$	139	138	43	+66	-100
$\hat{N}_3$	1,886	1,889	166	+289	-360
SE $\hat{N}_3$	161	165	28	+46	-62
$\hat{N}_4$	1,452	1,458	94	+167	-199
SE $\hat{N}_4$	93	94	19	+33	-43
$\hat{\phi}_2$	0.7297	0.7327	0.0459	+0.0892	-0.0929
SE $\hat{\phi}_2$	0.0439	0.0447	0.0021	+0.0039	-0.0046
$\hat{\phi}_3$	0.8578	0.8559	0.0551	+0.1003	-0.1127
SE $\hat{\phi}_3$	0.0548	0.0554	0.0090	+0.0145	-0.0205
$\hat{B}_2$	1,459	1,446	193	+360	-415
SE $\hat{B}_2$	183	189	29	+46	-68
$\hat{B}_3$	371	377	143	+307	-252
SE $\hat{B}_3$	179	143	22	+36	-53
$\hat{E}$	3,508	3,503	100	+186	+192

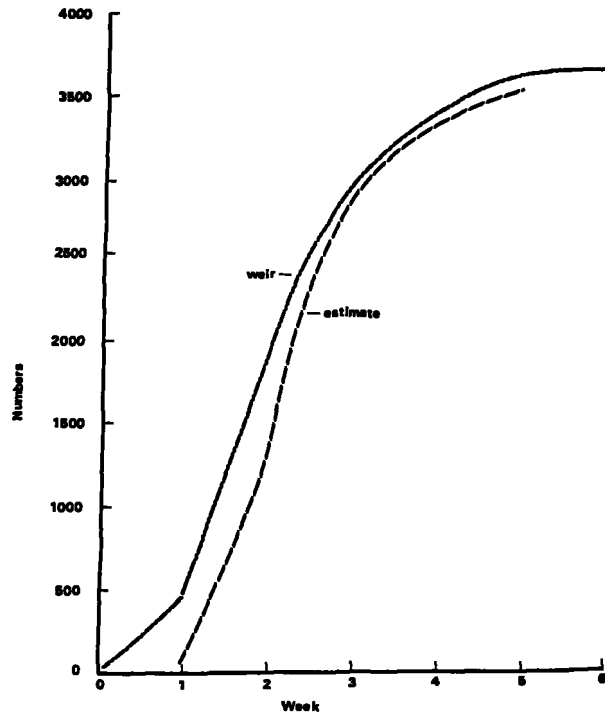


FIGURE 2.—Total numbers of fish immigrating as of week  $i$  by the weir count and total numbers of fish estimated by method three to have died as of week  $i + 2$ .

ability and/or survival with condition among "marked" (and thus decayed) animals (Fig. 3). For each week, smaller and more decayed carcasses appear to have lower recapture rates. (Note that since this figure represents catchability at and after the earliest time of recapture, these data do not reflect catchabilities of fresh fish. Also, recapture rates for week 3 are higher than those for week 4 because there is one more opportunity for recapture.) These low recapture rates can be the result of either lower survival or lower catchability of smaller and more decayed carcasses. The effects of these differences in catchability on absolute numbers of recaptures would be small because of the small number of carcasses in the lower capture probability categories. Note also in Figure 3 that recapture rates of fresh carcasses vary less with size than decayed carcasses.

The expected and actual values for the tests for differential catchability and mortality, the contribution of each difference to the  $\chi^2$  value, and the normal and pooled  $\chi^2$  values are presented in Tables 3 (Seber 1982) and 4 (Jolly 1982), respectively. Although the fit between expected and observed values appears to be quite good, the total differences are statistically significant, hence catchability is not strictly homogeneous.

The comparison of estimated and actual parameters as suggested by Leslie et al. (1953, cited by

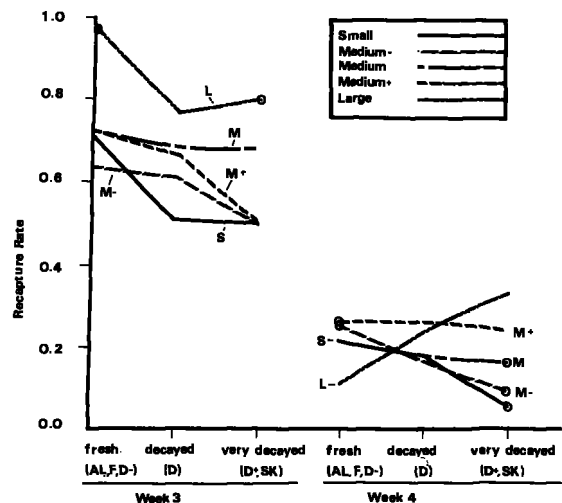


FIGURE 3.—Fraction of marked fish recaptured by size, condition, and week of release. Circled data points have sample sizes of numbers of fish recaptured  $< 10$ . Where  $< 5$  fish were released, that point was not plotted. Note that all fish are decayed upon recapture. The "fresh" category here includes alive, fresh and decayed minus; the "decayed" category includes decayed and the "very decayed" category includes decayed plus and skeleton.

Seber 1982) is presented in Table 5. The close agreement between both sets of estimates indicates any

TABLE 3.—Expected  $E(b_w)$  and actual ( $b_w$ ) numbers of individuals with the specific capture history  $w$  and the contribution of the difference between these values to the  $\chi^2$  test of Seber (1982). The listed capture histories indicate the fish was caught only at those times.

$w$	$E(b_w)$	$b_w$	$[E(b_w) - b_w]^2/E(b_w)$
2	120.22	116	0.1480
3	247.59	248	0.0007
4	589.01	588	0.0017
1,2	17.78	22	1.0000
1,3	2.37	2	0.0585
1,4	4.56	7	1.3121
1,5	0.30	2	9.4810
2,3	34.88	36	0.0362
2,4	66.97	68	0.0160
2,5	4.46	8	2.8045
3,4	359.38	355	0.0535
3,5	23.95	19	1.0225
4,5	150.07	153	0.0572
1,2,3	5.16	4	0.2603
1,2,4	9.91	9	0.0827
1,2,5	0.66	0	0.6801
1,3,4	3.44	2	0.6052
1,3,5	0.20	0	0.2295
1,4,5	1.16	0	1.1806
2,3,4	50.62	58	1.0749
2,3,5	3.37	5	0.7843
2,4,5	17.06	10	2.9266
3,4,5	91.56	102	1.1894
1,2,3,4	7.49	5	0.8267
1,2,3,5	0.50	0	0.4490
1,2,4,5	2.52	4	0.8636
1,3,4,5	0.88	0	0.8774
2,3,4,5	12.90	10	0.6511
1,2,3,4,5	1.91	2	0.0045
Pooled	$\chi^2 = 28.68$	df = 14	$\alpha = 0.025$
	$\chi^2 = 17.06$	df = 10	$\alpha = 0.10$

TABLE 4.—Expected and actual numbers of individuals caught at sample  $i$  and  $j$  ( $m_{ij}$ ), regardless of their capture history before  $i$  and after  $j$ , and the contribution of the difference between these values to the  $\chi^2$  test for equal catchability and survival of Jolly (1982).

$i,j$	$E(m_{ij})$	$m_{ij}$	$[E(m_{ij}) - m_{ij}]^2/E(m_{ij})$
1,3	6.95	4	1.2510
2,3	117.05	120	0.0743
1,4	5.74	7	0.2752
2,4	96.74	91	0.3410
3,4	529.51	534	0.0380
1,5	0.31	2	9.2562
2,5	5.20	8	1.5064
3,5	28.49	24	0.7066
Pooled	$\chi^2 = 13.44$	df = 3	$\alpha = 0.005$
	$\chi^2 = 6.34$	df = 2	$\alpha = 0.05$

differential catchability or survival that does exist (as indicated by  $\chi^2$  tests and differential recapture rates) does not significantly bias resultant estimates.

Values of  $\hat{E}$  computed from data "corrected" for age-dependent catchability are presented in Table 6. Again, it appears that if age-dependent catchability is present, it has little effect on the estimates. Also, that our estimates correlate well with the weir count estimates, whereas "corrected" estimates are

TABLE 5.—Estimates of the number of marks released ( $v_i$ ), survival ( $\phi_i$ ), and the marked population size ( $n_i$ ) for the standard Jolly-Seber method and the same estimates ( $\hat{v}_i, \hat{\phi}_i, \hat{n}_i$ , respectively) for the test for equal catchability and survival of Leslie et al. (1953, cited by Seber 1982).

Sample	$v_i$	$\hat{v}_i$	SE $\hat{v}_i$	$\phi_i$	$\hat{\phi}_i$	$\hat{N}_i$	$\hat{N}_{i-1}$
1	84	—	—	0.7995	—	67	—
2	311	—	—	0.7617	—	288	319
3	724	680	44	0.7878	0.7969	797	796
4	741	756	214	—	—	1,201	1,234
5	—	—	—	—	—	—	—

far too low, indicates that this bias was probably not present in our sampling process. Thus biases encountered here are insignificant, both in relation to possible imprecision in estimating the percent run and area covered, and the estimated standard errors.

Estimates computed to evaluate the effects of lowering sampling intensity are shown in Table 7. Simulations are listed according to the percent of top and the percent of bottom captures ignored for that simulation. The estimates obtained by the third

TABLE 6.—Escapement estimates obtained by correcting for differential catchability of fresh and decayed carcasses for three methods of estimating escapement. For each correction, the ratio of the average fresh to decayed catchabilities that was assumed to obtain the corrected estimate is given.

Assumed fresh/decayed Catchabilities	Corrected escapement		
	Jolly-Seber	Manly and Parr	Method 3
Original estimate	3,445	3,438	3,508
1.4/1.0	3,446	3,471	3,274
2.0/1.0	3,321	3,319	3,262

TABLE 7.—Escapement estimates obtained by simulation of reduced sampling effort for three methods of estimating escapement. For each simulation the fraction of decayed top carcass captures and the fraction of decayed bottom carcass captures ignored is given.

Fraction of decayed Carcass captures ignored		Escapement estimate		
Top	Bottom	Jolly-Seber	Manly and Parr	Method 3
Original estimate		3,445	3,438	3,508
0.0	0.4	3,740	3,765	3,676
0.0	1.0	3,944	4,058	3,777
0.2	0.4	3,890	3,917	3,977
0.4	0.6	4,844	4,934	4,364

method are less biased than those obtained by the other two methods.

## DISCUSSION

The estimates of total immigration are all remarkably close to the weir count. This accuracy is even more remarkable in light of the fact that CDF&G has traditionally used a correction factor of 0.95 to account for an estimated 5% of the spawning grounds that is not sampled on Bogus Creek. Inclusion of this factor brings all of the estimates to within 1.4% of the weir count. Since the third method provides a high degree of precision (Table 2) at much less sampling cost, it is preferable over the other two methods. We can compare the precision of the third method with the Jolly-Seber and Manly and Parr methods by comparing the standard error estimates that are available for those two methods (Table 1). The Jolly-Seber method is more precise in estimates of  $N$ ,  $B$ , and  $\Phi$ . This is expected, since both the Manly and Parr method and the third method use fewer individuals in estimates than the Jolly-Seber method does. However, the precision of the third method is more than adequate: 95% confidence intervals are +5.3% and -5.5% of the escapement estimate.

The detected violations of assumptions, age-dependent catchability and heterogeneity of capture probabilities and survival, are those that would be expected on the basis of physical considerations.

Survival of carcasses is a function of two processes: fresh carcasses being removed by carnivores, and old carcasses decaying and becoming buried in the stream bed. Rates of disappearance could thus be affected by condition, and therefore age and size, of carcasses. Older carcasses and smaller carcasses, which decay more quickly and are buried more easily than larger carcasses, would be expected to have lower survival rates.

Catchability is a function of both visibility and location, both of which would be expected to vary with condition and size of carcasses. This causes two different types of problems: age-dependent catchability and size-dependent catchability. Shiny, fresh carcasses were much more visible on the bottom of the stream than the brown, decayed carcasses. Carcasses on the stream surface were in general visible regardless of their condition. Since carcasses lost their high visibility in about a week, no marked carcasses will be in this high visibility category, and unmarked carcasses will on the average be more catchable than marked carcasses. This can be thought of as age-dependent catchability. Size-dependent catchability stems from the fact that decayed individuals that were large were more visible than those that were small. This can be viewed as capture heterogeneity. Since fresh fish were high visible regardless of their size, this heterogeneity existed only among decayed individuals. Based on these considerations we would expect catchability to vary with age and size according to Figure 4.



While both Jolly's (1982) and Seber's (1982) tests indicate differential catchability and/or mortality are present, the issue of real importance is the amount of any resulting bias. Manly (1970) concluded that if age-specific mortality is present in a sampled population, Manly and Parr (1968) estimates should fare better than those of Jolly and Seber (Seber 1982). Both methods, however, are biased for the case in which mortality increases with age; in fact, Manly's (1970) estimates of bias for additions ( $B$ ) are greater for Manly and Parr estimates than for Jolly-Seber estimates for those simulations with parameters closest to our population. Survival, population size, and catchability estimates were negatively biased by only 1 or 2%. Seber (1982) pointed out that Jolly-Seber estimates should be relatively unbiased even with differential mortality if mark status and mortality were not correlated. Both estimators, then, should have relatively unbiased estimates of survival and catchability for "marked" animals. A positive bias in estimates of immigration,  $B$ , (and consequently in  $\hat{E}$ ) would arise primarily from applying mortality of marked animals to the entire population, when marked animals are in general older, and thus have lower survival than unmarked animals.

The age-dependent catchability detected in this study would be expected to result in a positive bias in the estimate of total escapement,  $E$ . Because each capture sample includes fresh, recently immigrated individuals, and recapture samples include older, decayed individuals, we expect  $N$  to be overestimated (i.e.,  $n/N > m/M$  in Jolly-Seber and  $pN < n$  in Manly and Parr), which results in estimates of  $B$  and  $E$  being positively biased also. Since bias from age-dependent catchability in  $N$  decreases as  $M$  ap-

proaches  $N$ , and removing carcasses after capture in the third method decreases the ratio of marked to total carcasses, we would expect the third estimator to be more biased by age-dependent catchability problems than the first two methods.

However, the simulations of lower sampling intensity, which would exacerbate the effects of age-dependent catchability, show that the estimate obtained by the third method is more robust with regard to lowered sampling intensity. This unexpected result is probably due to compensating effects which decrease bias in  $E$ . The two most important components of  $E$  are the second ( $(N_2 - R_1 \hat{\Phi}_1)/\hat{\Phi}_1^5$ ) and third ( $\hat{D}_2$ ). In the standard estimates these values both increase with increases in the number of captures ignored. In the third method, however, the second component increases, but the third decreases. This is because as catchability declines, fewer marks are captured and "removed", hence more carcasses are available for later capture. This is not the case in the first two methods because marked carcasses are not removed at capture. Since in the third method the composition of  $M$  and  $N$  is relatively unchanged at the second sample period, but at the third sample period,  $M$  increases relative to  $N$  (because of the increase in the number of decayed marks present), the estimate of population size at the third sample period will be less biased than the estimate for the second sample period. This results in a negative bias in the estimated immigration from time period two to three. This compensation makes the third method more robust with respect to age-dependent catchability problems than the other two methods. Bias in the estimates is not severe until large numbers of capture events are ignored (Table 7). While all three methods produce accurate estimates, even when lowered sampling exacerbates differential catchability problems, the magnitude of the bias relative to standard errors can be substantial. For this reason, samples must be carefully taken if estimates from different streams or different years (which will have different biases because of different conditions) are to be compared statistically.

Heterogeneity of capture probabilities affects Jolly-Seber and Manly and Parr estimates in the same manner. Since in the Jolly-Seber method the individuals marked and released at sample  $i$ ,  $R_i$ , are on the average younger than the individuals marked and released prior to sample  $i$ ,  $M_i$  is a low estimate (i.e.,  $r/R > z/(M - m)$ , or  $M > (Rz/r) + m$ ). This decreases the positive bias in  $N$  which is caused by age-dependent catchability. Since bias in  $M$  increases as more individuals are marked, we expect

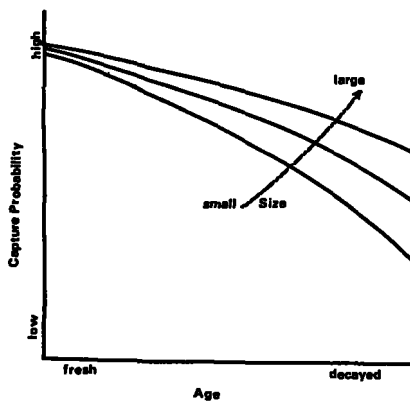


FIGURE 4.—Expected changes in capture probabilities with age at different sizes.

estimates of  $M$  from the third method to be less biased than those from the first two.

Usually, capture heterogeneity leads to the more catchable animals joining the marked population, and we expect marked animals to be more catchable than unmarked animals. Capture heterogeneity, however, is only prevalent among decayed individuals who are all less catchable than fresh, unmarked individuals. Thus, capture heterogeneity, by placing the more catchable decayed individuals in the marked population, results in the capture probability of marked animals being closer to the capture probability of unmarked animals. This reduces the negative bias in population size ( $N$ ), immigration ( $B$ ), and escapement ( $E$ ) estimates, which was caused by age-dependent catchability. Again, the third method, by removing decayed individuals and decreasing the fraction of the population which is decayed, will not be affected by capture heterogeneity as strongly as the other two methods.

Manly and Parr estimators will have the same ameliorating affects because of capture heterogeneity as their Jolly-Seber counterparts. Since the estimate of catchability,  $p$ , should be accurate for the more catchable animals, estimated survival should be accurate for that group. Bias would result from correlations between catchability and survival. Also, since  $p$  is estimated for marked (and thus decayed) individuals, using the more catchable decayed individuals to estimate  $p$  brings the estimated catchability closer to the actual catchability of the unmarked individuals. Again, this reduces the bias in  $\hat{N}$ ,  $\hat{B}$ , and  $\hat{E}$  which is caused by age-dependent catchability.

There are other approaches to estimating parameters from populations with age-dependent survival and capture rates. By placing carcasses in two readily identifiable age classes, fresh (and thus <1 wk old) or decayed (and thus older than 1 wk), Pollock's (1981) modified Jolly-Seber analysis of the data could have been made. Since this method requires recaptures of decayed individuals, it could not be used to analyze data from previous surveys, and it would require more sampling effort in future surveys than the method 3 estimate. If different age classes have sufficiently different capture or survival rates, then this method will provide more accurate estimates. If not, then it will yield the same estimate as the third method, but would have higher variances, as more parameters are estimated.

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