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CONTENTS

NOTES

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ANALYSIS OF TWO MARK-RECAPTURE METHODS TO ESTIMATE THE FALL CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SPAWNING RUN IN BOGUS CREEK, CALIFORNIA

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Carcass survey data for the 1981 chinook salmon spawning run into Bogus Creek, a small tributary to the Klamath River in northwestern California, were analyzed by the Schaefer and Jolly-Seber methods and compared to the actual run-size determined at a dam near the creek mouth. Age 2 fish (grilse) were recaptured as carcasses at a significantly lower rate than older age (adult) fish. Both methods produced close estimates of the adult run. The grilse run was not estimated by the Jolly-Seber Method due to low sample size. Ideas for further study are presented.

INTRODUCTION

Chinook salmon spawning runs into the major natural spawning areas of the Central Valley of California have been estimated by the California Department of Fish and Game (DFG) since 1973 based on carcass tagging and recovery data analyzed by the Schaefer Method (Taylor 1974). The Jolly-Seber Method (see Ricker 1975) has been recommended by Sykes and Botsford (1986) for estimating California salmon spawning runs, and has been used on some Washington streams by the Washington Department of Fisheries (R. De Vore, Wash. Dept. Fish., pers. comm.).

I compared the Schaefer and Jolly-Seber methods for estimating the 1981 chinook salmon spawning run into Bogus Creek, a small tributary to the Klamath River in northwestern California. A small dam near the creek mouth was used to count and characterize the run. A tag-recapture experiment using salmon carcasses was conducted above the dam to develop estimates by the two methods. This is the same data set used by Sykes and Botsford (1986), except that the data have been partitioned into adults and grilse and estimates developed for the Schaefer as well as the Jolly-Seber Method.

STUDY AREA

Bogus Creek enters the Klamath River at river km 304 next to the Iron Gate Salmon and Steelhead Hatchery at an elevation of about 670 m (Fig. 1). The creek drains an area of 140 km^2 and heads at an elevation of about 2400 m. The main stem is about 24 km in length. Fall-run chinook salmon enter from September through November with spawning occurring soon after creek entrance. Most spawning occurs from the mouth to about km 8, the mouth of Cold Creek. The mean drop in gradient along the principal spawning area is about 15 m/km. Creek flows at the mouth during the fall spawning season are generally 0.4 to 0.6 m^3/sec. The deepest pools are generally less than about 2 m. Riparian growth is dense along the entire stream course.

METHODS

Dam Count

A wooden drop-board dam and fish ladder, located about 300 m upstream from

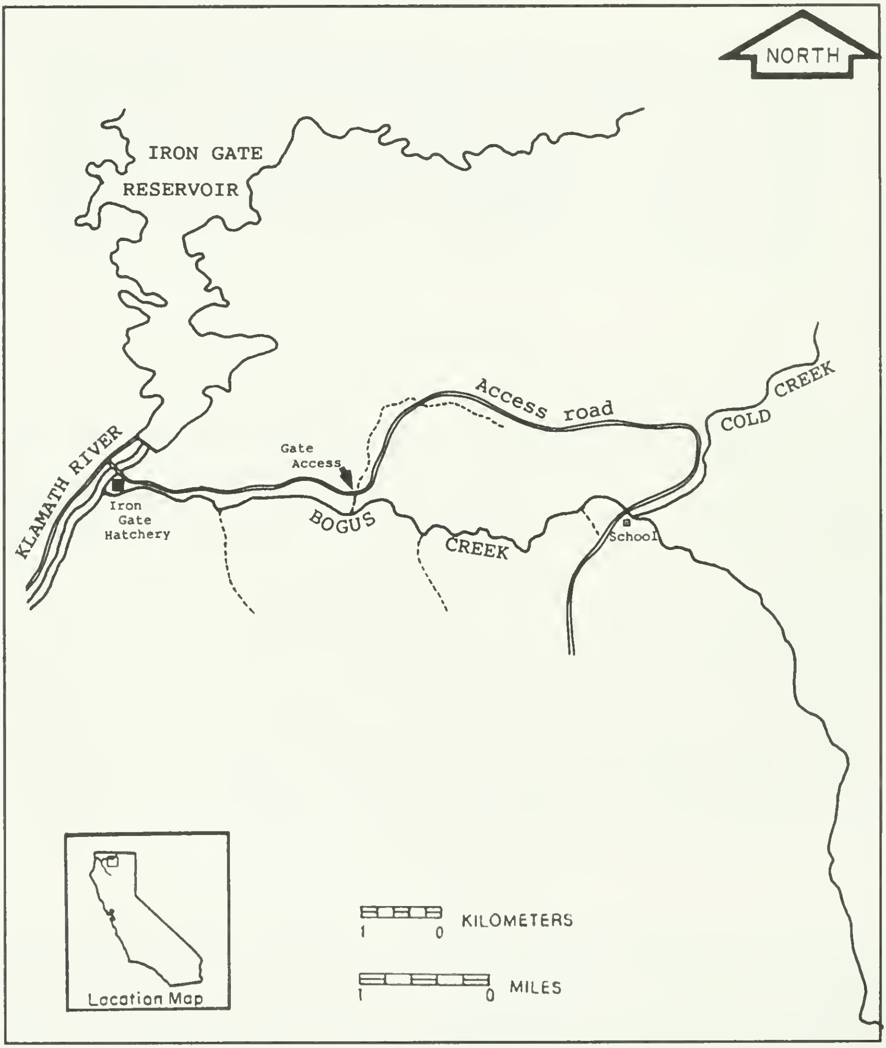

Figure 1. Map and Location of Bogus Creek Survey Area, California.

the creek mouth, were used to count and characterize the run above the dam. The dam was about 0.9-m high and extended across the entire stream width. Depth of water at the base of the dam was insufficient for fish to jump over it. The ladder was operated daily throughout the run from about one hour before sunrise to one hour after sunset. Each salmon was visually identified to species (a few coho salmon, *O. kisutch*, spawn in Bogus Creek), gender and class. Chinook salmon under about 56 cm total length were classified as grilse, while longer fish were classified as adults, male or female.

Carcass Survey

The carcass survey was conducted upstream of the counting facility throughout the period of salmon spawning and dying. The entire length of creek from the dam to Clear Creek was walked by two samplers one day each week searching the stream and shoreline for dead salmon. A long handle gaff was used to retrieve carcasses from the deeper pools and for general carcass handling purposes. All initial carcass recoveries (new recoveries) were identified to species, gender, class (grilse or adult) and condition. Carcasses with firm flesh and at least one clear eye (no milky color) were classified as "fresh," while all others were classified as "decayed." Carcasses were then either cut in two with a machete or tagged with a commercially available serially numbered jaw tag. Tagged carcass recaptures were examined for tag number, while all cut carcasses were disregarded from further sampling. All tagged carcasses were returned to moving water in the close vicinity of where the carcass was found. (This is the procedure used by the DFG, and the carcass deposition is assumed to be similar to that of a naturally dying or dead fish).

Tags were applied to all carcasses recovered during the first week of tagging. Roughly every other carcass recovered during the second week was given a tag and about 86% of the carcasses recovered during the third and fourth weeks were tagged. It was not necessary to tag carcasses recovered during the fifth and last week of sampling. Fork lengths (FL) were taken of all chinook salmon carcasses recovered on one day during the study.

Estimation Models

Schaefer Method. The modified Schaefer Model (Schaefer 1951) used to estimate chinook salmon run sizes, E, for Central Valley streams is as follows:

$$E = N_{ij} = R_{ij}(T_iC_j/R_iR_j) - T_i \tag{1}$$

where:

N_{ij} = Population size in tagging period i recovery period j,

R_{ij} = number of carcasses tagged in the ith tagging period and recaptured in the jth recovery period,

T_i = number of carcasses tagged in the ith tagging period,

C_j = number of carcasses recovered and examined in the jth recovery period,

R_i = total recaptures of carcasses tagged in the ith tagging period, and
R_j = total recaptures of tagged carcasses in the jth recovery period.

This model differs from the original in that the number of tags applied the previous period, beginning with estimation period 2, are subtracted from the population estimate for the current period. Schaefer's original model was based on sampling without replacement (tagging and sampling for tags were geographically separated) while under carcass salmon survey conditions sampling occurs with replacement. (Memo from S. Taylor, DFG, to R. Heimann, DFG, 29 August 1974).

In the analysis based on fresh carcasses, sample size by period (C_j) did not include recaptures of carcasses that had been classified as decayed when tagged (i.e., they never would have been tagged under the fresh carcass tagging procedure).

Jolly-Seber Method. The Jolly-Seber Method is used to analyze mark recapture data when four or more samples are taken, and tag recaptures per sample period number three or more (Ricker 1975). The estimate of the total spawning population, E, is:

$$E = N_1 + D_1 + D_2 \ldots + D_j \tag{2}$$

where:
N_1 = Number of carcasses in the population in period 1, the first period of spawning and dying, and
D_i = number of carcasses that joined the population between periods i and i+1, with j as the last survey period.

Three basic quantities must first be calculated:
(1) The estimate of the number of tags available for recapture in each survey, B_i:

$$B_i = (T_i+1)K_i/(R_i+1) + M_i+1 \tag{3}$$

where:
T_i = Number of carcasses tagged in period i,
K_i = sum of all tag recaptures made later than period i of carcasses tagged before period i,
R_i = sum of tag recaptures of carcasses tagged in tagging period i, and
M_i = sum of recaptures of tagged carcasses in period i (from all tagging periods).

(2) The estimate of the total number of carcasses in the population immediately prior to each survey, N_i:

$$N_i = B_i(C_i+1)/(M_i+1) \tag{4}$$

where:
C_i = Number of carcasses examined for tags in tagging period i.

(3) The "survival" rate of tagged carcasses, S_i, from period i to period i+1 (required to estimate carcass "recruitment") is estimated by:

$$S_i = B_{i+1}/(B_i-M_i+T_i) \tag{5}$$

Finally, to calculate D_i:

$$D_i = (N_{i+1}-S_i[N_i-C_i+T_i])/\ S_i \tag{6}$$

The expression S_i is applied to correct for fish entering the creek and disappearing between surveys (see Sykes and Botsford 1986).

The Jolly-Seber Method described by Ricker (1975) does not provide direct estimates of S_1, B_j, or N_1. Here these parameters are estimated as follows:

(i) To estimate survival of carcasses from period 1 to period 2, I used the formula of Seber (1973, p. 200):

$$S_1 = B_2/T_1 \tag{7}$$

(ii) To estimate the number of carcasses in the population at the start of the first survey, I assumed equal sampling rates between periods 1 and 2. Thus,

$$N_1 = N_1C_1/C_2\ \ S_1 \tag{8}$$

(iii) To estimate B_j, the number of tags in the population just before the last survey, I assumed the proportion of tags recovered in the last survey was the same as the estimated proportion in the population the previous period. Thus,

$$B_j = B_{j-1}M_j/M_{j-1} \tag{9}$$

In the analysis based on fresh carcasses, sample size each period, C_i, was reduced by the number of tagged carcass recoveries that were classified as decayed when their tags were applied (i.e., they never would have been tagged under the fresh carcass tagging procedure).

Confidence Intervals. Confidence intervals were not developed for this study as there is no explicit formula for the Schaefer Method and the Jolly-Seber procedure is highly cumbersome. Their approximate widths can be inferred from a study by Law (1994) based on stochastic modeling.

RESULTS

Sampling Conditions

Sampling conditions were conducive to accurate run-size counting at the dam and recovery of carcasses throughout the primary spawning area. No significant storm events were encountered and the bottoms of the deepest pools were generally visible from above the stream surface at all times. Stream flows were estimated to have fluctuated between 0.4 and 0.6 m^3/sec. throughout the period of salmon spawning and dying. There were few root wads, no log jams and no extensive areas of undercut bank where carcasses could become lodged and not retrieved.

Dam Count

The first and last fall chinook salmon of the 1981 run were counted through the Bogus Creek ladder on 16 September and 6 November, respectively. The run totaled 3,642 fish, including 2,730 (75%) adults and 912 (25%) grilse (Table 1). The adult run was composed of 1,113 (41%) males and 1,617 (59%) females. The adult and grilse runs peaked during the weeks ending 10 October 24 October, respectively.

Carcass Survey

The carcass survey was conducted during the weeks ending 17 October through 14 November 1991. A total of 2,503 carcasses, 69% of the run, was recovered for tagging or cutting (Table 2). The adult sample of 2,065 carcasses comprised 76% of the adult run while the grilse sample of 438 carcasses comprised 48% of the grilse run. The grilse recovery rate was 63% of the adult recovery rate and the difference was significant ($X^2 = 243.2$; 1 df; $P < 0.001$). For adult salmon, the dam count showed 41% (1,113) of the adult run was males and 59% (1,617) was females. The carcass survey of adult fish produced 38% (776) males and 62% (1,289) females. This difference was significantly different from the dam proportions ($X^2 = 35.83$; 1 df; $P < 0.001$).

Fresh carcasses were sampled during the weeks ended 17 October through 14 November and peaked during the week ended 24 October (Table 2). Decayed carcasses were sampled during the weeks ended 17 October through 14 November and peaked during the week ended 7 November. A total of 1,683 carcasses was sampled during the two consecutive weeks ended 31 October and 7 November. This total

Table 1. Bogus Creek chinook salmon dam count by week, 1981 season.

	Adults				Salmon
Week ending	Male	Female	Total	Grilse	Total
19 Sep	0	0	0	0	0
26 Sep	12	22	34	3	37
3 Oct	113	267	380	56	436
10 Oct	487	750	1,237	225	1,462
17 Oct	343	403	746	219	965
24 Oct	116	146	262	238	500
31 Oct	37	23	60	142	202
7 Nov	5	6	11	29	40
Totals	1,113	1,617	2,730	912	3,642

Table 2. Bogus Creek chinook salmon carcass tagging and cutting data by week in numbers of carcasses, 1981.[1]

Class	17 Oct	24 Oct	31 Oct	7 Nov	14 Nov	Total
Tagged Fresh Carcasses						
Grilse	7	16	51	41	0	115
Females	24	81	89	53	0	247
Males	22	54	39	23	0	138
Adults	46	135	128	76	0	385
Totals	53	151	179	117	0	500
Tagged Decayed Carcasses						
Grilse	0	13	77	130	0	220
Females	14	82	284	309	0	689
Males	16	62	174	177	0	429
Adults	30	144	458	486	0	1,118
Totals	30	157	535	616	0	1,338
Total Carcasses Tagged						
Grilse	7	29	128	171	0	335
Females	38	163	373	362	0	936
Males	38	116	213	200	0	567
Adults	76	279	586	562	0	1,503
Totals	83	308	714	733	0	1,838
Cut Fresh Carcasses						
Grilse	0	18	6	4	2	30
Females	0	96	16	1	2	115
Males	0	49	8	1	1	59
Adults	0	145	24	2	3	174
Totals	0	163	30	6	5	204
Cut Decayed Carcasses						
Grilse	0	15	13	19	26	73
Females	0	92	71	37	38	238
Males	0	65	35	25	25	150
Adults	0	157	106	62	63	388
Totals	0	172	119	81	89	461
Total Cut Carcasses						
Grilse	0	33	19	23	28	103
Females	0	188	87	38	40	353
Males	0	114	43	26	26	209
Adults	0	302	130	64	66	562
Totals	0	335	149	87	94	665

cont.

Table 2. cont.

Class	17 Oct	24 Oct	31 Oct	7 Nov	14 Nov	Total
Total Fresh Carcasses						
Grilse	7	34	57	45	2	145
Females	24	177	105	54	2	362
Males	22	103	47	24	1	197
Adults	46	280	152	78	3	559
Totals	53	314	209	123	5	704
Total Decayed Carcasses						
Grilse	0	28	90	149	26	293
Females	14	174	355	346	38	927
Males	16	127	209	202	25	579
Adults	30	301	564	548	63	1,506
Totals	30	329	654	697	89	1,799
Total Carcasses						
Grilse	7	62	147	194	28	438
Females	38	351	460	400	40	1,289
Males	38	230	256	226	26	776
Adults	76	581	716	626	66	2,065
Totals	83	643	863	820	94	2,503

[1]Entries are first time recoveries. Multiple recapture data are not shown.

included 1,342 adults and 341 grilse representing 49% and 37% of the adult and grilse runs, respectively. The mean lengths of fresh carcasses recovered on 23 October 1981 were 68.1 cm FL for females and 74.5 cm FL for males (Appendix I). To facilitate analysis, carcass tagging and recapture data were organized by class and condition, week of tagging, and week of recapture (Table 3).

Population Estimates

Schaefer Method. For adult chinook, the Schaefer estimate was high by 17% based on total carcasses and low by 15% based on fresh carcasses (Table 4). The grilse estimates by this method were high by 14% and 27% based on total and fresh carcasses, respectively.

Jolly-Seber Method. The adult chinook salmon estimate by the Jolly-Seber Method based on total carcasses was within 1% of the actual run size (Table 4). Based on fresh carcasses, the adult estimate was low by 18%. Grilse data were insufficient to make an estimate as only two tags (from total tagged carcasses) were recaptured during the week ended 17 October, leaving only three sampling periods for estimation purposes (a minimum of four sampling periods required).

Table 3. Bogus Creek chinook salmon tagging and recapture data by carcass condition and week in numbers of fish[1].

Recapture week	Tagging Week					
	17 Oct	24 Oct	31 Oct	7 Nov	14 Nov	Total
Fresh Grilse						
17 Oct	(7)					-
24 Oct	2	(16)				2
31 Oct		4	(51)			4
7 Nov			35	(41)		35
14 Nov			2	12	(0)	14
Subtotals	2	4	37	12	0	55
Decayed Grilse						
17 Oct	(0)					-
24 Oct		(13)				0
31 Oct		2	(77)			2
7 Nov		6	40	(130)		46
14 Nov			4	18	(0)	22
Subtotals	0	8	44	18	0	70
Total Grilse						
17 Oct	(7)					-
24 Oct	2	(29)				2
31 Oct		6	(128)			6
7 Nov		6	75	(171)		81
14 Nov			6	30	(0)	36
Subtotals	2	12	81	30	0	125
Fresh Adults						
17 Oct	(46)					-
24 Oct	23	(135)				23
31 Oct	4	48	(128)			52
7 Nov	4	34	80	(76)		118
14 Nov	1	6	6	13	(0)	26
Subtotals	32	88	86	13	0	219
Decayed Adults						
17 Oct	(30)					-
24 Oct	20	(144)				20
31 Oct	0	53	(458)			53
7 Nov	3	38	299	(486)		340
14 Nov	1	2	6	107	(0)	116
Subtotals	24	93	305	107	0	529

cont.

Table 3. cont.

Recapture week	Tagging Week 17 Oct	24 Oct	31 Oct	7 Nov	14 Nov	Total
Total Adults						
17 Oct	(76)					-
24 Oct	43	(279)				43
31 Oct	4	101	(586)			105
7 Nov	7	72	379	(562)		458
14 Nov	2	8	12	120	(0)	142
Subtotals	56	181	391	120	0	748
Total Grilse and Adults						
17 Oct	(83)					-
24 Oct	45	(308)				45
31 Oct	4	107	(714)			111
7 Nov	7	78	454	(733)		539
14 Nov	2	8	18	150	(0)	178
Totals	58	193	472	150	0	873

[1] Number of fish tagged shown in parentheses. Subtotals and totals are exclusive of numbers tagged

Table 4. Bogus Creek chinook salmon run size estimates and dam counts, 1981 season.

Method	Carcasses used	Class	Estimate	Deviation from actual
Schaefer	Total	Adults	3,181	+17%
		Grilse	1,039	+14%
	Fresh	Adults	2,324	-15%
		Grilse	1,160	+27%
Jolly-Seber	Total	Adults	2,743	<1%
		Grilse	no est.	-
	Fresh	Adults	2,236	-18%
		Grilse	no est.	-
Dam count	-	Adults	2,730	-
		Grilse	912	-

DISCUSSION

Dam count and carcass survey data showed that grilse were recovered in the carcass survey at 63% of the adult recovery rate and the difference was statistically significant. The smaller size of grilse probably contributed to their lower recapture rate. Smaller salmon probably disappear from the stream at a faster rate than larger salmon, and also are probably less visible in the stream or along the stream bank, even in fresh condition. The fact most grilse are males may also have contributed to the difference because of possible gender-related spawning behavior. In the carcass survey, grilse appeared to be most abundant in the upper sections while larger males were most abundant lower down in the creek. Recovery conditions possibly varied between stream sections and could have contributed to the discrepancy.

The lower recovery rate of adult males (88% of the adult female recovery rate) was statistically significant and may have been due to sex misidentification at the counting dam. In the carcass survey, salmon gender in the 60-70 cm range was not always obvious. In many cases, gonadal tissue had to be examined to determine gender.

The run at the creek mouth extended over seven weeks and required approximately 50 person-days of effort. It is noteworthy that 49% of the adult run and 37% of the grilse run were sampled during the weeks ended 31 October and 7 November. These high percentages may indicate a close relation between total run size in Bogus Creek and the number of carcasses in the creek at the peak of spawning. If so, spawning escapement monitoring costs could be reduced by conducting a carcass count during a few days of the year rather than counting the entire run.

Both methods produced a reasonably close (generally within 20%) estimate of the Bogus Creek chinook salmon run. The Schaefer estimate based on fresh carcasses was low by 15%, while the Jolly-Seber estimate based on total carcasses was nearly the same as the actual count. For grilse, the Schaefer estimate was closer to the actual count based on total carcasses (high by 14%) than the estimate based on fresh carcasses (high by 27%). No estimate of the grilse escapement was possible by the Jolly-Seber Method because of low sample size.

The survey procedure followed in 1981 should have been extended one week longer to recover tags applied in week 4. The Jolly-Seber Method depends on tag recoveries one and two weeks following tagging. No sampling was conducted during the second week following tagging week 4. The effect of this shortfall in sampling probably had a minor effect on the estimates by either method as the majority of new recruits to the carcass population had accrued by recovery week 3.

The close agreement between the two methods and the actual Bogus Creek run size for adult fish was likely due to large sample sizes and high first week survival rates of tagged carcasses. Simulation modeling by Law (1994) shows that population estimates by both methods quickly converge on the true run size, as each of these factors exceeds about 50%. In this study, based on total tagged adult chinook salmon, 76% of the run was sampled in the carcass survey and, of these, 73% received a tag. The first week survival rate of carcasses, based on the Jolly-Seber S_1 estimate, was about 0.80.

Bogus Creek survey conditions differ from survey conditions in a large stream. Virtually all carcasses are recoverable in Bogus Creek while a small proportion of the carcasses in a large stream, such as the Feather or American rivers in the Central Valley, are available for sampling. In a large stream, many carcasses are deposited in deep water or other inaccessible areas and are never available for sampling. In this situation, it is critical that the tagged carcasses randomly mix with the untagged ones. This requires releasing of tagged carcasses in moving water upstream from where they were recovered so that, hopefully, they will randomly mix with the untagged carcasses. The condition of random mixing of tagged and untagged carcasses is more easily met in a stream the size of Bogus Creek than it is in a river the size of the Feather River.

Sykes and Botsford (1986) analyzed the Bogus Creek data set by the Jolly-Seber and Manly and Parr methods. They did not compare Jolly-Seber and Schaefer estimates nor did they present separate estimates for grilse and adults. It is shown here that it is important to separate adults from grilse in carcass survey data because of lower recapture rate of grilse. It is also shown that both the Jolly-Seber and Schaefer methods both can produce close estimates of salmon spawning populations in a small stream situation.

RECOMMENDATIONS

(i) Several seasons of instantaneous carcass counts should be conducted on Bogus Creek during the weeks of 31 October and 7 November to compare the carcass counts with the actual run sizes at the creek mouth. A close relation between the carcass survey and dam counts could reduce the cost of estimating the run by conducting a few days of carcass counts each year.

(ii) Further analysis of the Jolly-Seber and Schaefer methods should be done to determine the accuracy of the model under different carcass "survival" rates and sampling regimes (complete, incomplete, systematic, etc.). Simulation modeling of a hypothetical salmon population might be used in such an analysis.

(iii) The accuracy of tag recapture models should be evaluated on different sizes of salmon streams, particularly large ones. Streams with counting facilities would be used. A "correction factor" may be required for large stream estimates because of imperfect mixing of tagged and untagged carcasses or incomplete population sampling.

(iv) Recapture rates for grilse and adult carcasses should be determined for other streams. Streams with counting facilities would again be used. Combining grilse and adults in survey data will overestimate the run if tagged grilse are recaptured at a lower rate than adults. The adult estimate is further inflated if the grilse percentage is underestimated due to a lower probability of initial capture.

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Appendix 1. Length frequencies of Bogus Creek chinook salmon measured for fork length on 23 October 1981.

cm	Males	Females	Total	cm	Males	Females	Total
45	1	0	1	73	0	3	3
47	1	0	1	74	3	4	7
51	1	0	1	75	1	1	2
54	1	1	2	76	1	0	1
55	1	0	1	77	1	0	1
59	1	6	7	78	1	1	2
60	2	2	4	79	1	2	3
61	0	3	3	80	0	1	1
62	2	5	7	81	1	1	2
63	0	2	2	82	0	1	1
64	1	7	8	83	3	1	4
65	2	6	8	84	2	0	2
66	2	6	8	86	3	1	4
67	1	10	11	87	3	0	3
68	0	10	10	88	2	0	2
69	0	6	6	89	3	0	3
70	1	6	7	90	1	0	1
71	2	11	13	91	1	0	1
72	3	5	8	99	1	0	0
				Totals	50	102	152
				Means	74.5	68.1	70.2

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SIMULATION STUDY OF SALMON CARCASS SURVEY CAPTURE-RECAPTURE METHODS

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Population estimates are made on a hypothetical salmon (*Oncorhynchus* sp.) spawning run by a capture-recapture survey of fish carcasses by simulation. The Petersen, Schaefer, and Jolly-Seber models are used under various combinations of survival rates, catch rates, and tag rates. All model estimates are least affected by different levels of tag rates. The Schaefer model population estimates are sensitive to changes in survival and catch rates. The Petersen model consistently overestimates the population. The Jolly-Seber model more closely estimated the simulated population. Great care must be taken in assessing the aptness of models in capture-recapture studies.

INTRODUCTION

Boydstun (1994) estimated the fall chinook salmon (*Oncorhynchus tshawytscha*) spawning run into Bogus Creek, Klamath River, California, by carcass survey. Carcasses were tagged and released for subsequent recapture. Data were collected during five weekly capture and five weekly recapture periods. The Schaefer (Schaefer 1951) and Jolly-Seber (Seber 1982) models were used to estimate the run (population). These were compared to a weir count made at the creek mouth. Different survey protocols for tagging fresh carcasses only and total carcasses (fresh and nonfresh) were used. Both models closely estimated the true run size. Simulation was recommended for further assessment of the two techniques.

This study is based on a hypothetical salmon population with a predetermined distribution of die-off ("recruitment") and fixed carcass carry-over ("survival") rates. Three models -- Petersen (see Ricker 1975) , Schaefer, and Jolly-Seber -- were used for population estimation. The relative biases of population estimates of each model was studied under different combinations of specified ranges of survival rates, catch (capture) rates and tag rates.

METHODS

PASCAL programs were written to simulate capture-recapture matrices and to compute population estimates using the Petersen, Schaefer, and Jolly-Seber models at specified ranges of survival rates, catch rates, and tag rates. Confidence limits of population estimates were also computed. Population estimates and confidence bounds, expressed as a percentage deviation from the known hypothetical true population, were plotted against a specified range of survival rates while holding the catch rate and tag rate fixed. Similar plots were made for specified ranges of catch rates and tag rates, respectively. Sensitivity of the population estimations to changes of survival rates, catch rates and tag rates was studied. The relative merits and applications of each model for estimating salmon spawning runs are discussed.

Estimation Models

The details of Schaefer and Jolly-Seber models are described by Schaefer (1951) and Seber (1982). The Petersen model was a rather crude application as the conditions for a closed population obviously were not met. Its inclusion is only for comparative purposes since the Petersen model continues to be used by some biologists for population estimation in carcass surveys.

The Petersen population estimate (Ricker 1975) is:

$$N = \frac{T \times C}{M}$$

where:

N = the population estimate;

T = the sum of T_i, the number of carcasses tagged in the i^{th} tagging period;

C = the sum of C_j, the number of carcasses captured and recaptured in the j^{th} recovery period; and

M = the sum of M_{ij}, the number of carcasses recovered with tags from the i^{th} tagging and j^{th} recovery period.

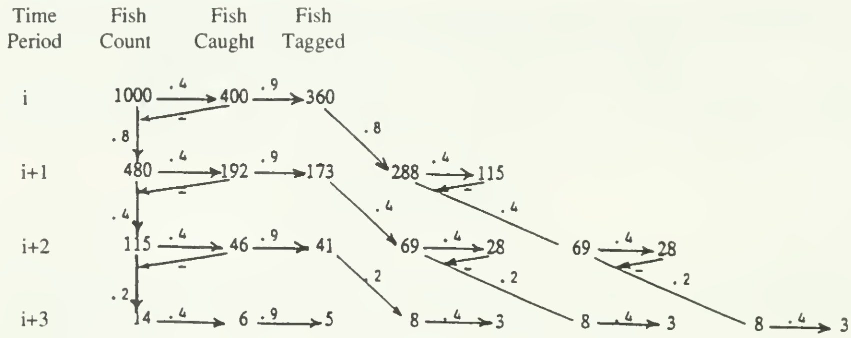
Hypothetical Salmon Population and Construction of Data Matrix

A hypothetical salmon spawning run of 5,000 fish was chosen with the following die-off schedule (recruitment of carcasses):

Recapture Period	Number Recruited	% of Total
1	500	10
2	1,000	20
3	2,000	40
4	1,000	20
5	500	10
All	5,000	100

To avoid having to adjust for carcasses being recruited and disappearing between recapture periods, abrupt ("knife edge") spawning and dying was assumed to occur immediately prior to each recapture period (Sykes and Botsford 1986).

An example of the construction of one element of a capture-recapture data matrix consisting of 1,000 carcasses entering the stream is shown in Figure 1. The catch rate was 40%. Survival rate for periods 1, 2, and 3 were 80%, 40%, and 20%, respectively.



Capture-recapture matrix

Recovery Period	Tag Periods i	i+1	i+2
i+1	115		
i+2	28	28	
i+3	3	3	3

Figure 1. Simulated capture-recapture data matrix for one cohort of carcasses.

No carcass "survived" beyond period 4. Decimal numbers next to arrows are multiplicative fractions; a " - " symbol next to an arrow indicates subtraction. Ninety percent of all recovered carcasses were tagged. The 10% captured carcasses that were not tagged were removed to simulate the chopping of untagged carcasses recovered to remove them from future tagging or counting. For example, the number of untagged carcasses remaining in the stream at the beginning of period 2 is 1,000 minus 400; then multiply the result by 80% to give 480. These data are constructed based on total-carcass tagging (fresh and nonfresh). The resultant captured carcasses that are tagged at various periods are tabulated to form a lower triangular matrix. Subsequent recruitment of carcasses were similarly computed and added to the lower triangular matrix corresponding to their capture-recapture periods. In generating the hypothetical capture-recapture data matrix, homogeneity of tagged and untagged carcasses with respect to catchability are assumed for all except one set of simulations.

Population Estimates and Confidence Intervals for Each Estimation Model

Population estimates and confidence limits were computed by simulation. For each combination of survival rate, catch rate, and tagging rate, 1,000 simulations were carried out. Stochastic variations for each of the selected rate parameters were generated using a random uniform distribution function. In addition to calculating the average of each population estimate, 90% confidence limits were calculated by Buckland's (1980) Method 1. The lower 90% confidence limit was the average of the

Table 1. Summary of salmon population simulations and corresponding figures in this paper.

Objective	Figure	First period survival rate(%)	Catch rate(%)	Tag rate(%)	Carcass type	Disposition of untagged carcass. caught
1. Changing Surv. Rates	2(a)	11% to 80%	30%	100%	Total	Not Returned
2. Changing Surv. Rates	2(b)	11% to 80%	30%	100%	Fresh	Not Returned
3. Changing Surv. Rates	2(c)	11% to 80%	90%	100%	Total	Not Returned
4. Changing Catch Rates	3(a)	80%	11% to 80%	30%	Total	Not Returned
5. Changing Catch Rates	3(b)	80%	11% to 80%	90%	Total	Not Returned
6. Changing Catch Rates	3(c)	80%	11% to 80%	90%	Fresh	Not Returned
7. Changing Tag Rates	4(a)	80%	30%	11% to 80%	Total	Not Returned
8. Changing Tag Rates	4(b)	80%	90%	11% to 80%	Total	Not Returned
9. Changing Tag Rates	4(c)	80%	90%	11% to 80%	Fresh	Not Returned
10. Changing Catch Rates	5(a)	80%	11% to 80%	90%	Total	Returned
11. Changing Catch Rates	5(b)	80%	11% to 80%	90%	Fresh	Returned
12. Changing Surv. Rates	5(c)	11% to 80%	30%(recruit) 36%(tagged)	100%	Total	Not Returned

50th and 51st smallest values. The upper 90% confidence limit was the average of the 50th and 51st largest values. All population estimates and confidence limits were expressed as a percentage deviation from the true population total of 5,000 fish. Both fresh-carcass-only tagging and total-carcass tagging surveys were simulated. Carcasses that carried over for more than one period were considered nonfresh. All tagged carcasses recaptured were removed. Table 1 is a summary of salmon population simulations carried out in this study.

Changes in Survival Rate

Population estimates were computed for a range of survival rates. The first period survival rates were set to vary from 11 to 80% in 1% increments. The second and third period survival rates were each 50% of the previous survival rate. All carcasses were assumed lost after three periods; hence, we considered the fourth period survival rate as zero. Two series of simulations were carried out at catch rates of 30%. One series simulated total-carcass tagging. The other series simulated fresh-carcass tagging only. A third series of total-carcass tagging simulations was made at catch rate of 90% All captured carcasses were tagged.

Changes in Catch Rate

Population estimates were computed for a range of catch rates from 11 to 80% in 1% increments. The first four periods survival rates were fixed at 80, 40, 20, and 0%, respectively. Two series of simulations were carried out at tag rates of 30% and 90%, with total-carcass tagging. A third series of simulations was made at tag rate of 90%, for tagging fresh carcasses only. Captured carcasses that were not tagged were removed.

Changes in Tag Rate

Population estimates were computed for a range of tag rates from 11 to 80% in 1% increments. The first four periods survival rates were fixed at 80, 40, 20, and 0%, respectively. Two series of simulations were carried out at catch rates of 30% and 90%, with total-carcass tagging. A third series of simulations was made at catch rate of 90% for tagging fresh carcasses only. All captured carcasses that were not tagged were removed.

Returning of Untagged Carcasses

Two series of simulations were made with catch rates range from 11 to 80% in 1% increments. Tag rate was 90%. The first series was for total-carcass tagging while the second series was for fresh-carcass tagging only. All captured carcasses that were not tagged were returned.

Differences in Catch Rate of Recaptures

Tagged carcasses may be more readily recaptured than untagged carcasses since they were available for capture and tagging in the first place. One series of simulations for total-carcass tagging was carried out for a range of first period survival rate from 11 to 80% at 1% increments. Catch rate of recruit was at 30% while catch rate of carcasses was 36%. Tag rate was 100%.

RESULTS

Examples of Population Estimates

The population estimate of one simulation based on the hypothetical population of 5,000 carcasses, using the Schaefer model is shown in Table 2. Catch rate was 40%. Survival rates for each consecutive period were 80%,40% 20%, and 0%, respectively. Tag rate was 90%. The Schaefer model based on total-carcass tagging gave an estimate of 8,893 fish, approximately 78% greater than the true population of 5,000. The Jolly-Seber estimate of 4,539 fish (Table 3) is about 91% of the true population. The Petersen model gave a population estimate of 12,557, which is 251% of the true population.

Simulations with fresh-carcass-only tagging by the Schaefer (Table 4) and Jolly-Seber (Table 5) models were 152% and 83% of true population value, respectively. The Petersen model estimate was 184% of the true population. In the following studies of the effects of changes of different rate parameters, the Petersen model consistently showed substantially larger overestimation of total population than either the Schaefer model or the Jolly-Seber model. Hence, the results of the Petersen estimates have been excluded from further discussion.

Effects of Changes in Survival Rates

At a relatively low catch rate of 30%, the Schaefer model shows a nine-fold overestimation of the population at about 10% first period survival rate (Figure 2a). With increasing survival rates, the population estimates decrease until there is a 100% overestimation at the 80% survival rate. All 90% confidence intervals do not cover the true population value. The Jolly-Seber model underestimates the true population value for the range of first period survival rates of 11 to 80%. The 90% confidence intervals cover the true population value from first period survival rates of 11 to 23% (Figure 2a). Precision of estimation increases with survival rates for both models. When only fresh carcasses were tagged, both models show very slightly lowered population estimates than total-carcass tagging estimates (Figure 2b).

At a high catch rate of 90% both models show higher precision of population estimation with shorter 90% confidence intervals (Figure 2c). The Schaefer model also shows less overestimation while the Jolly-Seber model shows accurate and precise estimation for the range of first period survival rates from 11 to 80%.

Effects of Changes in Catch Rates

At a low tag rate of 30%, the Schaefer model shows 140% overestimation of the population at about 10% catch rate (Figure 3a). All 90% intervals do not cover the true population value. The Jolly-Seber model underestimates the true population. Ninety percent confident intervals cover the true population value for 11 to 30% of catch rate. At a high tag rate of 90%, there is only a slight increase of precision of estimation for both models for the entire range of catch rates from 11 to 80% (Figure 3b). There is a reduction of bias and an increase of precision for the population estimates with increasing catch rates.

Fresh-carcass-only tagging lowers the population estimates for both models (Figure 3c). This makes the Schaefer model estimates closer to the true population, although all 90% confidence limits still do not cover the true population value. The Jolly-Seber model underestimates the population for the entire range of catch rates and the 90% confidence intervals do not cover the true population value.

Effects of Changes in Tag Rates

Population estimates are rather insensitive to tag rate changes from 11 to 80% and catch rates at 30% or 90% (Figure 4a,b). Only slight increases in precision are observed for both models with increasing tag rates. The Schaefer model consistently overestimates the population while the Jolly-Seber model shows rather precise and accurate population estimation. Fresh-carcasses-only tagging has no significant effect on population estimates for either model (see Figure 4c for 90% catch rate example).

Table 2. Salmon population estimation using the Schaefer Model by tagging of total carcasses with all captured untagged carcasses removed.

Capture-recapture data matrix

Week of Recovery (j)	Week of Tagging (i) 1	2	3	4	5	6	7	Tagged fish Recvrd R(j)	Total fish Recvrd C(j)	Ratio C(j)/R(j)
2	58	0	0	0	0	0	0	58	554	9.55
3	14	129	0	0	0	0	0	143	1158	8.10
4	2	29	260	0	0	0	0	291	1124	3.86
5	0	3	59	174	0	0	0	236	725	3.07
6	0	0	7	34	92	0	0	133	286	2.15
7	0	0	0	3	17	17	0	37	66	1.78
8	0	0	0	0	2	2	2	6	8	1.33
R(i)	74	161	326	211	111	19	2	<- Tagged fish recovered		
M(i)	180	446	914	750	441	138	26	<- Total fish tagged		
$\frac{M(i)}{R(i)}$	2.43	2.77	2.80	3.55	3.97	7.26	13.00	<- Ratio		

Population estimation

Week of Recovery (j)	Week of Tagging (i) 1	2	3	4	5	6	7	Total
2	1348	0	0	0	0	0	0	1348
3	276	2894	0	0	0	0	0	3170
4	19	310	2816	0	0	0	0	3145
5	0	26	508	1900	0	0	0	2434
6	0	0	42	260	786	0	0	1088
7	0	0	0	19	120	220	0	360
8	0	0	0	0	11	19	35	65
Subtotal	1642	3230	3366	2179	917	240	35	11608
Tagged	0	-466	-914	-750	-441	-138	-26	-2715
					Estimated total			8893

Catch Rate: 0.40
Tag Rate: 0.90
First four periods survival rates: (0.8, 0.4, 0.2, 0.0)

Effects of Returning Untagged Carcasses Captured

If untagged carcasses were not removed upon initial capture, but returned for further recapture, the Schaefer model for total carcass tagging shows only slight changes of population estimation for the range of catch rates from 11 to 80% (compare Figures 5a and 3b). The Jolly-Seber model underestimates the population with catch

Table 3. Salmon population estimation using the Jolly-Seber Model by tagging of total carcasses only, with all captured untagged carcasses removed.

Capture-recapture data matrix

Week of Recovery (j)	Week of Tagging (i) 1	2	3	4	5	6	7	Tagged fish Recvrd R(j)	Total fish Recvrd C(j)
1	0	0	0	0	0	0	0	0	200
2	58	0	0	0	0	0	0	58	554
3	14	129	0	0	0	0	0	143	1158
4	2	29	260	0	0	0	0	291	1124
5	0	3	59	174	0	0	0	236	725
6	0	0	7	34	92	0	0	133	286
7	0	0	0	3	17	17	0	37	66
8	0	0	0	0	2	2	2	6	8
R(i)	74	161	326	211	111	19	2	<- Tagged fish recovered	
M(i)	180	446	914	750	441	138	26	<- Total fish tagged	

Population estimation

Week of Tagging	Survival rates	Pop. prior to week	New recruits
1	0.5622	346	774
2	0.4899	958	1517
3	0.5283	1934	1166
4	0.4147	2059	565
5	0.4684	1263	161
6	0.2448	620	10
7	0.1586	125	0
8	0.0000	14	0
		Estimated total	4539

Catch Rate: 0.40

Tag Rate: 0.90

First four periods survival rate: (0.8, 0.4, 0.2, 0.0)

rates less than 65% but it overestimates the population with catch rates greater than 65%. Fresh-carcasses-only tagging show similar effects for both models (compare Figure 5b and 3c). The Jolly-Seber model underestimates the population with catch rates less than 60% but it overestimates the population with catch rates greater than 60%.

Table 4. Salmon population estimation using the Schaefer Model by tagging of fresh carcasses only, with all captured untagged carcasses removed.

Capture-recapture data matrix

Week of Recovery (j)	Week of Tagging (i) 1	2	3	4	5	Tagged fish Recvrd R(j)	Total fish Recvrd C(j)	Ratio C(j)/R(j)
2	58	0	0	0	0	58	554	9.55
3	14	115	0	0	0	129	1144	8.87
4	2	28	230	0	0	260	1093	4.20
5	0	3	55	115	0	173	664	3.84
6	0	0	7	28	58	93	245	2.63
7	0	0	0	3	14	17	46	2.71
8	0	0	0	0	2	2	4	2.00
R(i)	74	146	292	146	74	<- Tagged fish recovered		
M(i)	180	360	720	360	180	<- Total fish tagged		
M(i)/R(i)	2.43	2.47	2.47	2.47	2.43	<- Ratio		

Population estimation

Week of Recovery (j)	Week of Tagging (i) 1	2	3	4	5	Total
2	1348	0	0	0	0	1348
3	302	2515	0	0	0	2817
4	20	290	2384	0	0	2695
5	0	28	521	1088	0	1637
6	0	0	45	182	372	599
7	0	0	0	20	92	112
8	0	0	0	0	10	10
Subtotal	1670	2833	2950	1290	474	9217
Tagged	0	-360	-720	-360	-180	-1620
				Estimated total		7597

Catch Rate: 0.40

Tag Rate: 0.90

First four periods survival rates: (0.8, 0.4, 0.2, 0.0)

Effects of Differences in Catch Rate of Recaptures

When catch rates of recaptured carcasses are higher than catch rates of new recruits by 20%, there is a general lowering of population estimates by both models for different combinations of survival rates, catch rates, and tag rates (see Figure 5c for typical example and compare with Figure 2a).

Table 5. Salmon population estimation using the Jolly-Seber Model by tagging of fresh carcasses only, with all captured untagged carcasses removed.

Capture-recapture data matrix

Week of Recovery (j)	Week of Tagging (i) 1	2	3	4	5	6	7	Tagged fish Recvrd R(j)	Total fish Recvrd C(j)
1	0	0	0	0	0	0	0	0	200
2	58	0	0	0	0	0	0	58	554
3	14	115	0	0	0	0	0	129	1144
4	2	28	230	0	0	0	0	260	1093
5	0	3	55	115	0	0	0	173	664
6	0	0	7	28	58	0	0	93	245
7	0	0	0	3	14	0	0	17	46
8	0	0	0	0	2	0	0	2	4
R(i)	74	146	292	146	74	0	0<- Tagged fish recovered		
M(i)	180	360	914	146	73	0	0<- Total fish tagged		

Population estimation

Week of Tagging	Survival rates	Pop. prior to week	New recruits
1	0.5366	330	748
2	0.5269	914	1472
3	0.5252	1851	1015
4	0.5118	1765	485
5	0.4093	1014	79
6	1.0000	296	0
7	0.7207	51	0
8	0.0000	4	0
		Estimated total	4129

Catch Rate: 0.40
Tag Rate: 0.90
First four periods survival rate: (0.8, 0.4, 0.2, 0.0)

DISCUSSION

Population estimates are least sensitive to changes in tag rates for all three models. The Petersen model consistently overestimates the population and shows much higher bias than both the Schaefer and the Jolly-Seber models for all combinations of rate parameters studied. The Schaefer model also overestimates the population, particularly at low survival and low catch rates. The Jolly-Seber model shows remarkably concise and accurate estimates for various combinations of rate parameters studied, although it underestimates the population at low survival and low catch rates. Fresh-carcasses-

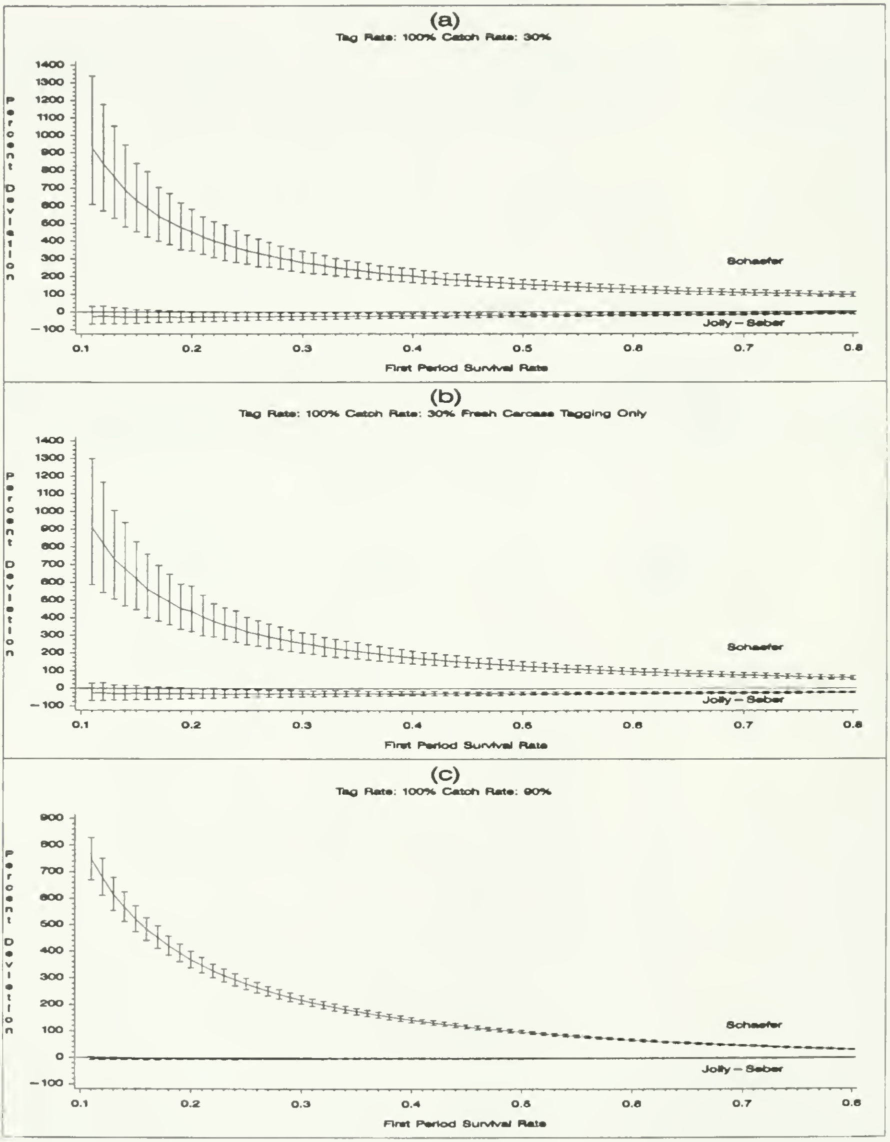


Figure 2. (a),(b),(c) Comparison of percentage deviations of simulated salmon population estimates from the true population value at different catch rates and increasing survival rates with 90% confidence intervals using Schaefer and Jolly-Seber models.

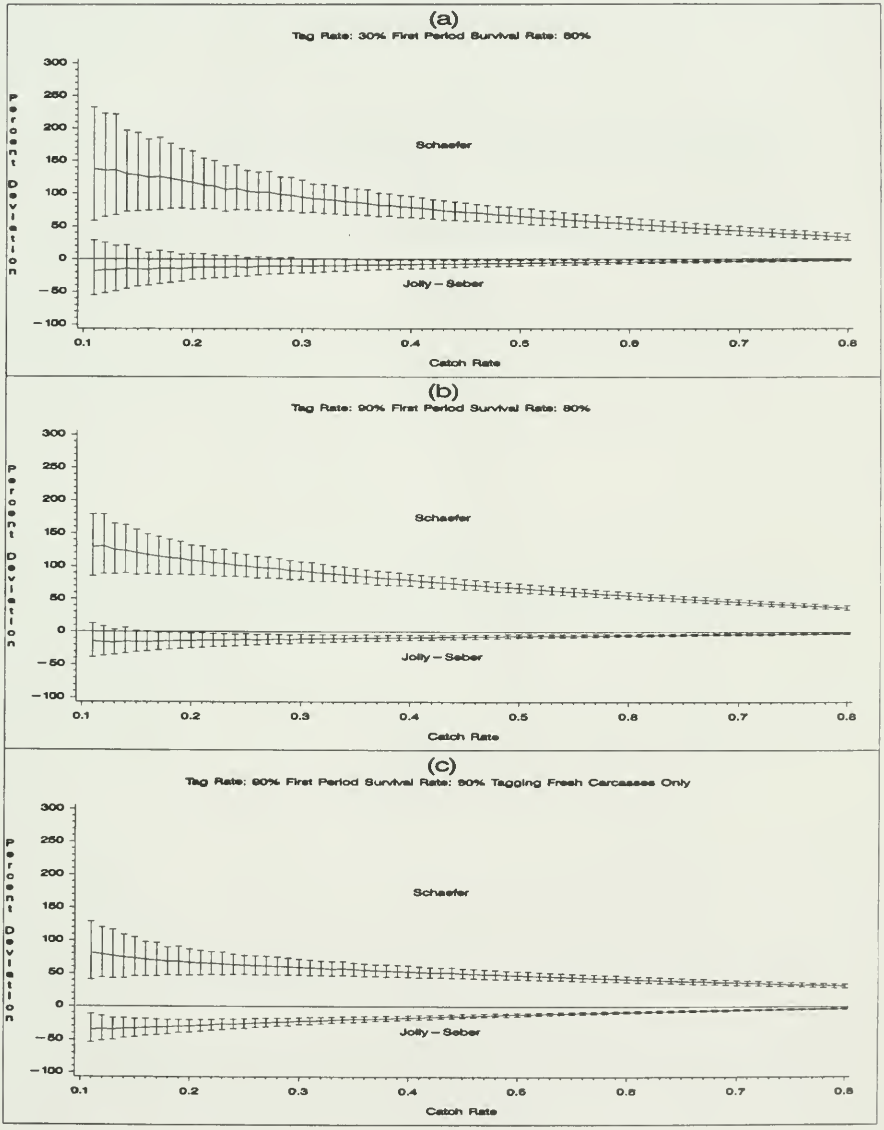


Figure 3. (a),(b),(c) Comparison of percentage deviations of simulated salmon population estimates from the true population value at different tag rates and increasing catch rates with 90% confidence intervals using Schaefer and Jolly-Seber models.

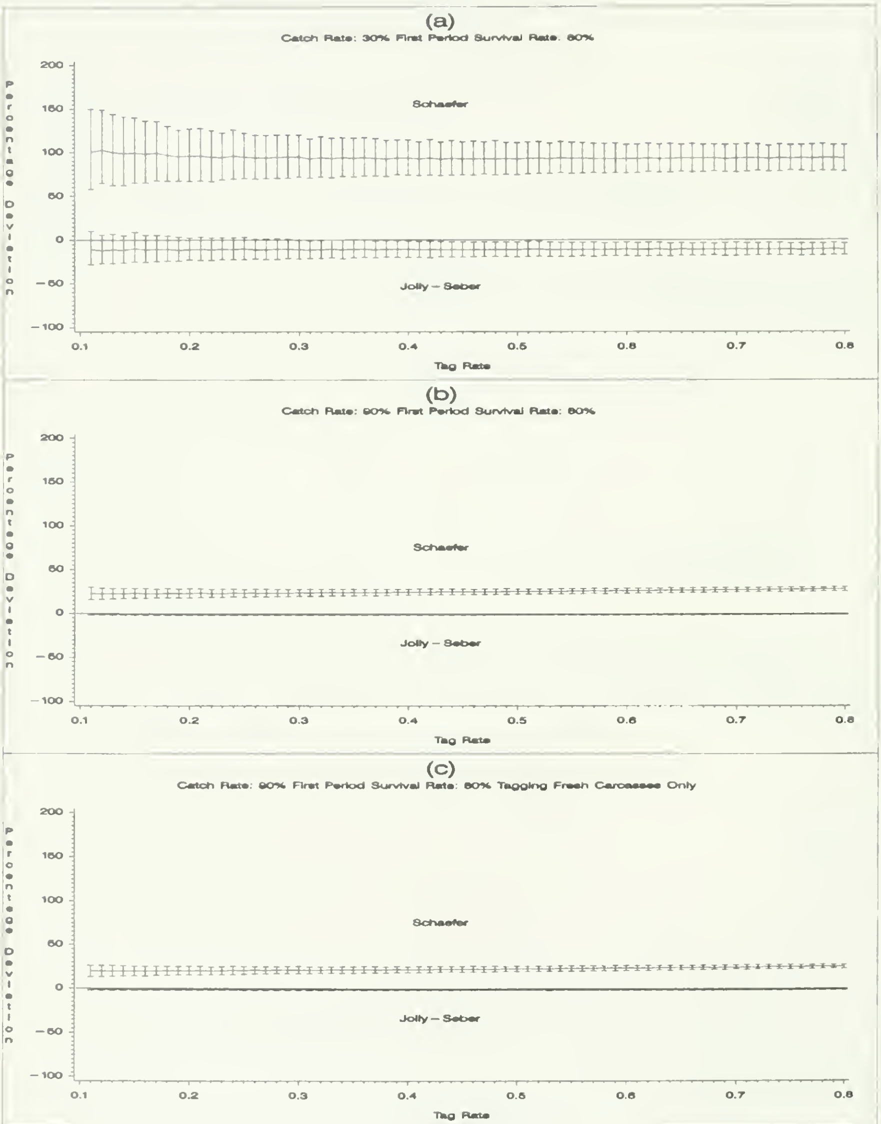


Figure 4. (a),(b),(c) Comparison of percentage deviations of simulated salmon population estimates from the true population value at different catch rates and increasing tag rates with 90% confidence intervals using Schaefer and Jolly-Seber models.

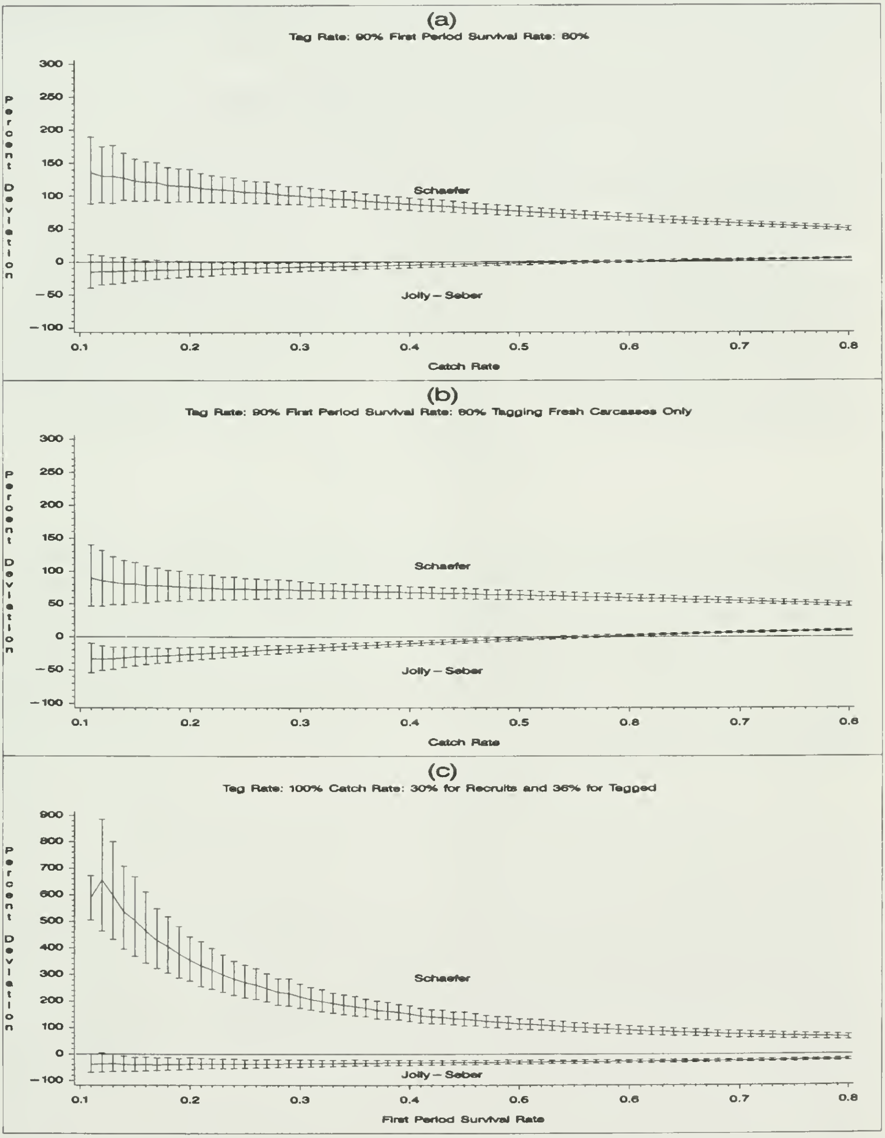


Figure 5. Comparison of percentage deviations of simulated salmon population estimates from the true population value with 90% confidence intervals, (a), (b) at 90% tag rate, 80% first period survival rate and increasing catch rates , (c) at 100% tag rate, 30% catch rate for recruits, 36% catch rate for tagged carcasses, and increasing survival rates, using Schaefer and Jolly-Seber models.

only tagging shows only slight effects on population estimates for all models.

When captured untagged carcasses were returned for future recapture, the Schaefer model shows little change of estimation. The Jolly-Seber model overestimates the population with catch rates greater than about 60%. Also if catch rates are higher for recaptures than new recruits both Schaefer and Jolly-Seber model show lower population estimates.

The Bogus Creek situation reported by Boydstun (1994) is almost ideal for capture-recapture studies with independent verification by weir count. Very few carcasses escaped capture-recapture sampling. The catch rate was fairly high (>70%). This simulation study shows that the Jolly-Seber method most closely estimates the simulated population size in all comparisons.

Some biologists believe that carcass surveys on larger rivers, such as the Klamath River, yield population estimates that are too low using the Jolly-Seber model. It is possible that the basic assumption of equal mixing of tagged carcasses with all carcasses at large may be violated. In that case, recaptured carcasses may constitute a different subpopulation. Field studies should be conducted to ascertain the appropriateness of models in such situations.

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RECENT EVIDENCE FOR THE FORMATION OF ANNUAL GROWTH INCREMENTS IN THE OTOLITHS OF YOUNG PACIFIC SARDINES (*SARDINOPS SAGAX*)

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Periodicity of annuli in the sagittal otoliths of sardines (*Sardinops sagax*) was determined using two methods: for juvenile fish by demonstrating a relationship between the formation of the first annulus and the back-calculated hatch date; and for age 2 fish by examination of seasonal changes in the condition of the otolith edge. The potential exists for systematic aging errors associated with variability in the timing of the spawning peak, but this source of error was thought to be minor in recent years. Annual monitoring of the timing of the spawning peak was suggested as a way to identify changes in the magnitude of the error.

INTRODUCTION

Studies of the dynamics of fish populations often require information on age composition. Growth increments in the hard parts of fishes, especially the otoliths, have been routinely used to determine age and year class. Confirmation of the temporal periodicity of growth increment formation is necessary to demonstrate the validity of age estimates. This has been accomplished using various body structures in many species of fish. Yoklavich and Boehlert (1987) demonstrated daily growth increments in otoliths of black rockfish (*Sebastes melanops*), and Butler (1987) found daily growth increments in otoliths of known-age sardines (*Sardinops sagax*). Thomas (1983) used seasonal variation in the condition of otolith margins to determine annuli periodicity in South African pilchards (*Sardinops ocellata*). Aguayo, et al. (1987) also verified the formation of annuli by examining the condition of otolith margins from 5-6 year-old Chilean sardines (*Sardinops sagax*). Taubert and Tranquilli (1982) used validated daily growth increments in otoliths of largemouth bass (*Micropterus salmoides*) to determine the periodicity of another structure (annuli) of unknown periodicity, by counting daily growth increments between suspected annuli. Unfortunately, documentation of periodicity (validation) is usually either implied or assumed for many other species (Beamish and McFarlane 1983). Periodicity of suspected daily growth increments was refuted under certain growth conditions in known-age herring (*Clupea harengus*) by Geffen (1982) and McGurk (1984), demonstrating that growth increments do not always correspond to discrete time units and emphasizing the need for validation.

Sardines were aged using scales and otoliths in the 1930s and reached a maximum age of 13+ at that time (Mosher and Eckles 1954). Walford and Mosher (1943) used marginal increment width to imply periodicity of annulus formation in otoliths of sardines from the California fishery during the late 1930s. However, significant changes have occurred in the sardine stock and in oceanographic regimes associated with the California Current during the past five decades (Barnes et al. 1992), and it should not be assumed that Walford and Mosher (1943) demonstrate validation of annuli in sardines under current conditions.

Sardines are multiple batch spawners (Blaxter and Hunter 1982), with some spawning occurring during the entire year. Peak periods may vary between years (Blaxter and Hunter 1982). Historically, the population spawned primarily in the spring (based on larval abundance), until it collapsed in the early 1950s (Smith 1972). Following the collapse, spawning occurred in the summer, autumn, and winter quarters. During more recent years (1978-1986), inshore spawning was concentrated during the summer quarter, with the exception of an autumn peak during 1984 (Watson 1992).

It is not possible to determine the periodicity of major growth increments in sagittal otoliths of young-of-the-year sardines by counting daily growth increments between the primordium and the first major mark in otoliths because, due to the protracted spawning period, all fish of a year class are not hatched on the same date. Therefore, we explore the relationship between hatch date of individual sardines (back calculated from date of capture by counting total daily growth increments) and presence or absence of an annulus. We also present changes in the condition of the growth increment on the otolith margin as evidence for the annual formation of one translucent and one opaque growth increment in otoliths of age 2 sardines.

METHODS AND MATERIALS

Data from two independent sources were used for this study. Young-of-the-year specimens were obtained from California Department of Fish and Game (CDFG) surveys conducted during the autumn of 1984 to collect young fish of the coastal pelagic species complex found in the Southern California Bight. Specimens of older sardines (initially presumed to be age 2 based upon otolith annuli) were obtained from a random-stratified port sampling of southern California commercial landings made during 1988 and 1989 (Barnes et al. 1992). The port samples represented about 30.5 percent of all sardine landings in southern California during the study period.

Age 0 and Age 1 Sardines

John L. Butler (National Marine Fisheries Service, pers. comm.) estimated the ages in days by counting daily growth increments in the otoliths of 132 young sardines collected as a result of the CDFG surveys off southern California during late September-early October of 1984 and provided us with the data and the whole, mounted otoliths. Although some otoliths had been polished so that daily growth increments could be counted to determine age in days, it did not affect our ability to discern the translucent and opaque growth increments. Butler (1987) had previously determined that daily growth increments were deposited in the otoliths of laboratoryreared larval and juvenile sardines. Using criteria set by Williams and Bedford (1974), we examined the whole (sometimes polished) sagittal otoliths for annuli on a black background under reflected light at 18x magnification. An annulus is defined as the sequential interface between an inner translucent (dark) growth increment and a distal opaque (white) growth increment (Collins and Spratt 1969). This particular sequence coincides with an increase in growth in the late spring when the opaque growth increment begins to form.

Age 2 Sardines

The 1986 year class was chosen for analysis of marginal growth increment condition because it was the most numerous in our port samples (n = 981), and by limiting the data to only one year class we restricted the expression of any potential age effect on the seasonality of annulus formation, similar to the approach used by Walford and Mosher (1943). Also, by selecting only age 2 fish, we avoided potential problems associated with determining edge type on otoliths with narrower margins from older, slower-growing fish. Samples were collected during the 12-month period between June 1988 and May 1989, and year class assigned using the criteria and techniques previously described. Since we assumed a hatch date of 1 July for sardines, the collection period primarily coincided with age 2 for the 1986 year class. Outer margins were classified as follows (modified from Jensen 1965): T = Translucent; O = Opaque; w = wide; n = narrow. Opaque narrow and wide classifications were pooled (On & Ow), as were translucent narrow and wide (Tn & Tw). Otoliths with margins that were in transition from opaque wide to translucent narrow exhibited some characteristics of both classifications, and were designated: Transition - Ow/Tn. A similar designation was used for otoliths that were in transition from translucent wide to opaque narrow (Transition - Tw/On). Margin widths at the posterior region of the otolith were compared by eye to the preceding increment of the same basic classification (i.e.: translucent or opaque), and if the increment at the margin was less than 20 percent of the previous increment, that increment was considered narrow; otherwise it was considered wide.

RESULTS AND DISCUSSION
Age 0 and Age 1 Sardines

Based on daily growth increments, the "juvenile" sardines collected in September and October 1984 ranged from 62 to 515 days of age. Individuals ranged in size from 45 mm standard length (SL) (71 days old) to 208 mm SL (342 days old). Hatch dates were determined by subtracting the age in days from the date of capture, and were distributed (Fig. 1) from 21 April 1983 to 31 July 1984. Individual fish hatched from April to August 1983 had one annulus and those hatched from November 1983 through July 1984 had none. The five fish which hatched between September 18 and October 7 had either one annulus (three fish) or no annulus (two fish). Fish hatched after the onset of the deposition of the translucent growth increment in October and

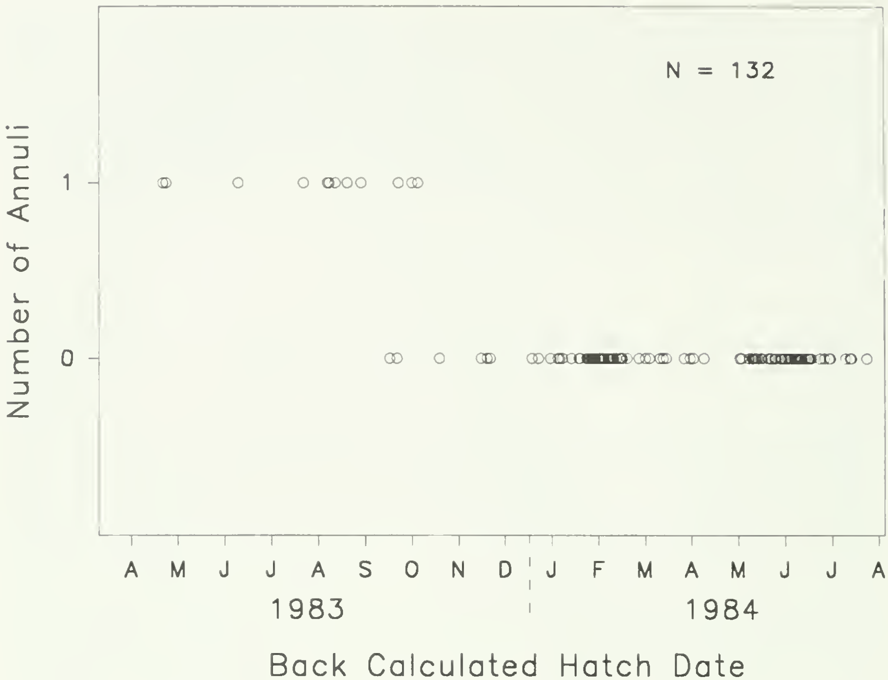

Figure 1. Hatch date and number of annuli for 132 sardines collected during September/October 1984. Number of annuli corresponds to year class: 0 = 1984 year class; 1 = 1983 year class.

November did not form a translucent increment during the first winter of life, possibly because larval and juvenile otolith growth tends to be opaque, precluding expression of the winter increment. Under the preceding conditions, the presence of an annulus indicates hatching occurred before mid-September 1983. Absence indicates hatching occurred after mid-October 1983. Therefore, annuli in sardine otoliths may be used to assign fish to specific year classes, at least during the first 1.5 years of life. Using these criteria, a year class would be composed of all fish hatched during the autumn of one year through the summer of the next year, rather than the common tenet that a year class is all fish hatched in a calendar year. Due to the timing of annulus formation, fish hatched during the last quarter of the year are subject to aging error; i.e., they may be incorrectly assigned to the following year class. Fortunately, most spawning activity during recent years occurred during the summer months (Watson 1992), suggesting that the timing of annulus formation in the autumn represents a minor source of aging error. When sardine year classes are designated by calendar year, it is in accordance with the dominant summer spawning period.

Age 2 Sardines

Further evidence of the formation of annuli in otoliths of age 2 sardines was found

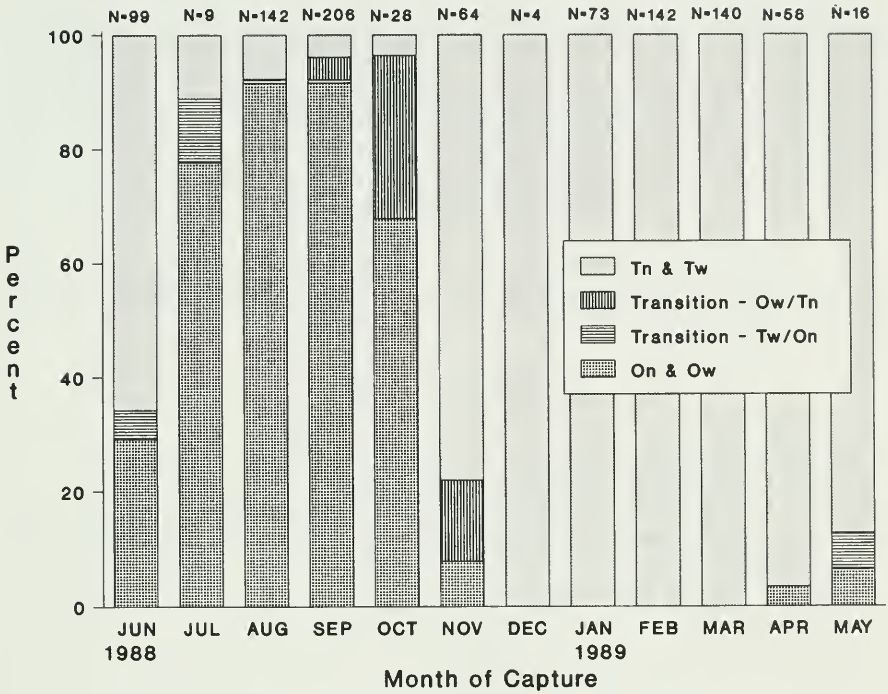

Figure 2. Seasonal changes in the otolith outer margin of age 2 (1986 year class) sardines.

by examining changes in the otolith margin over time. Individuals from the 1986 year class were used, and ranged in size from 163 mm SL to 247 mm SL during the collection period, with a grand monthly mean of 217 mm SL. Deposition of new material on the outer margin of the otoliths followed a seasonal pattern. We found most opaque growth to occur during July-October, and most translucent growth during the remainder of the year (Fig. 2), which coincides with the timing of annulus formation found in younger fish (Fig. 1). Generally, the seasonality of annulus formation can vary a month or two within fish populations. Blacker (1974) noted changes in time of annulus formation on the order of about two months in North Sea cod (*Gadus sp.*) that may be linked with change in feeding habits, distributions, or the onset of maturity.

CONCLUSIONS

Annual periodicity of major growth increments is demonstrated for young sardines in the Southern California Bight. When using annuli to assign sardines to a year class, an aging error can occur for fish that hatch after the onset of the formation of the first translucent growth increment. In recent years, this source of error has been minor because the formation of the first translucent growth increment occurred later in the season and was separated in time from the dominant spawning period.

Seasonal variability in peak spawning activity and variability in the relationship between hatch date and the timing of annulus formation should be monitored annually. If environmental conditions change and cause the spawning peak to closely coincide with the time of annulus formation, the potential for aging errors could become significant.

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AN EFFICIENT TECHNIQUE FOR CAPTURING SWIMMING DEER

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We developed a technique to capture Columbian black-tailed deer (*Odocoileus hemionus columbianus*) swimming in Clair Engle Reservoir in Trinity County, California. The materials required were inexpensive and readily available. Construction can be accomplished within 30 minutes, and three people can execute the technique. Pursuit time was less than 2 minutes and handling time of deer captured to attach radio-collars averaged 5.5 minutes (n = 8, SE = 0.6). The probability of pseudoreplicated data sets was reduced by capturing deer from groups moving independently of one another. The technique is an efficient method for capturing deer to attach radio-collars or ear-tags in areas where deer swim waterways.

INTRODUCTION

Deer can be effectively captured using a variety of techniques. Mechanical techniques such as clover traps (Clover 1954), drive nets (Beasom et al. 1980, Thomas and Novak 1991), drop nets (Jessup et al. 1989), net guns (Krausman et al. 1985, Potvin and Breton 1988), tree guns (Walton 1986), and snares (Ashcraft and Reese 1957) are more efficient than chemical immobilization when many animals are sought for capture (Jessup et al. 1989). However, site characteristics such as topographic and vegetative features, weather conditions, season, and available forage affect their efficiency. Consequently, to capture deer efficiently, biologists select and adapt proven techniques or develop new techniques based on site characteristics.

Columbian black-tailed deer (*Odocoileus hemionus columbianus*) swim across Clair Engle Reservoir (Trinity County, California) during spring and fall migrations (Loft et al. 1984). A new, efficient mechanical technique for capturing these swimming deer to attach radio-collars was used in April 1992. The technique should prove useful in areas where deer swim across waterways large enough to allow pursuit and capture by boat.

Table 1. List of materials required for mechanically capturing swimming deer from a boat.[a]

Item	Description	Approximate Cost
Canvas Pack Cinch	Length 76.5 cm, Width 7.5 cm	$ 24.50
Leather Latigo Strap	Length 187 cm, Width 3 cm	$ 12.95
Nylon Piggin String	Diameter 0.79 cm, Length 203 cm, Hardness level - Hard	$ 11.95
Diver's Weight	1.4 kg weight for weight belt #8,	$ 4.00
Nylon Cord	Length 110 cm	$ 0.65
Foam Pipe Insulation	Diameter 2 cm, Length 8 cm	$ 4.30
Self-locking Cable Tie	Length 37 cm, Width 0.8 cm	$ 0.10
Pants Leg Bottom	Length 41 cm, Regular cut	$ 0.0[b]

[a]Construction requires needle and thread, tape, and a knife.
[b]Assumes use of spare old pants.

CONSTRUCTION

Little expense and construction is required (Table 1). First, construct a floatable "head bag" (Fig 1). Cut the bottom 41 cm off one leg of a pair of pants. Split the seam on the upper half of this pants leg, and sew along each side of the split seam, to reinforce it. Sew a 12.8-cm hem in the bottom of the pants leg, leaving a hole so that you can insert pipe insulation (Table 1) into the hem for floatation. Cut the pipe insulation to match the circumference of the pants leg, and sew the hem shut.

Second, make the "piggin" string (Table 1) floatable. Tape the remaining pipe insulation (Table 1) to the string just before the looped end (Fig 1).

Buckle the latigo strap to the pack cinch (Table 1) at the first hole in the strap. About 26 cm of strap should extend past the buckle. Slide the diver's weight (Table 1) onto this portion of the strap, and loop the strap back into the first side of the buckle. Securely fasten the cable tie across this side of the buckle on top of the latigo strap. Loop the latigo strap over the cable tie and back through the buckle again (Fig 1). Tighten the latigo strap, and cut the excess portion of the cable tie and latigo strap.

METHODS

Capture was determined to be most efficient with three people in the boat: one boat operator and two deer handlers. A boat with a shallow freeboard worked well. A model 16 Big Jon (Lowe Industries)[1] was stable during capture activities. Use the nylon cord (Table 1) to attach the cinch assembly to the boat. Locate the cinch aft, a distance one third the length of the boat, on the side on which deer will be captured. Right-handed

[1] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

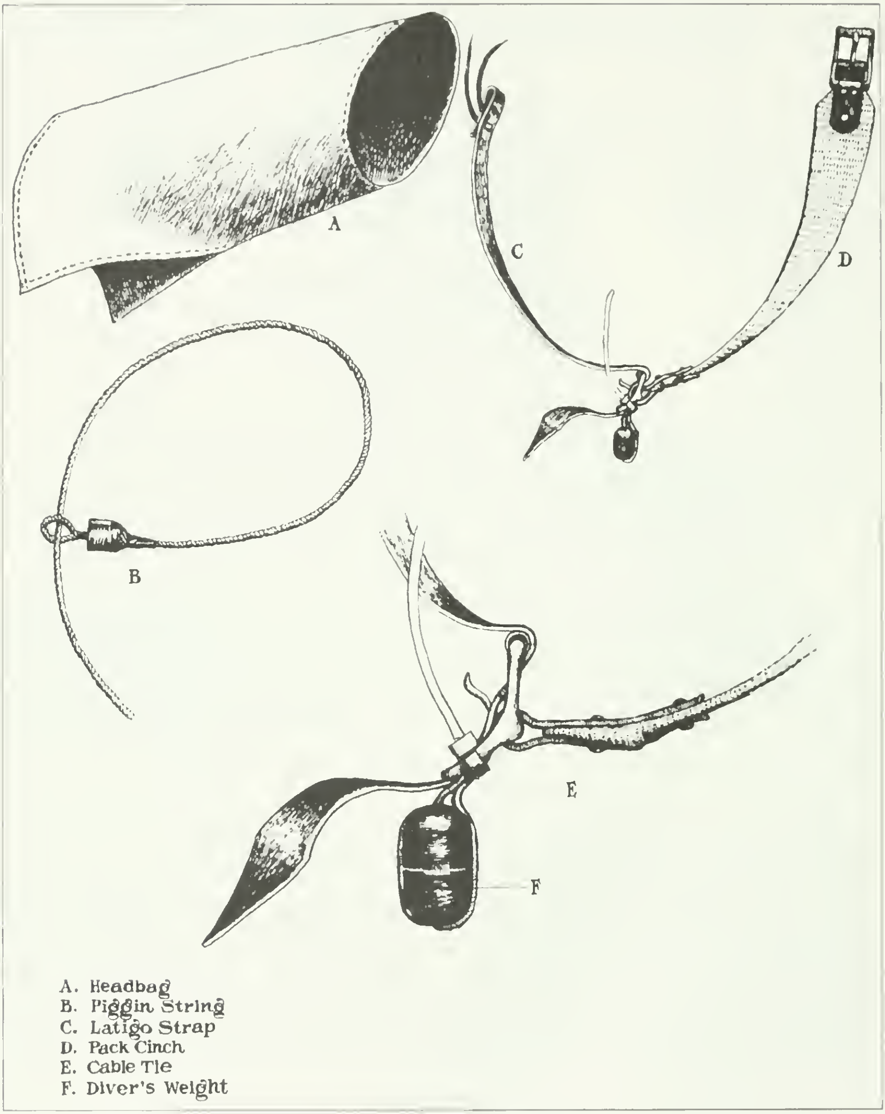

Figure 1. Materials used in capturing and restraining swimming deer.

people preferred capturing deer on the right side. Tie the cinch to position the center under the abdomen of a deer when it is alongside the boat (Fig 2). Place the side of the cinch with the diver's weight down away from the deer.

We located swimming deer by traversing the reservoir and searching from vantage points on shore. Vantage points on the shore deer were swimming toward proved more efficient than traversing the reservoir. The type of waterway, behavior of the animals, and objective of the capture effort will affect search technique efficiency and,

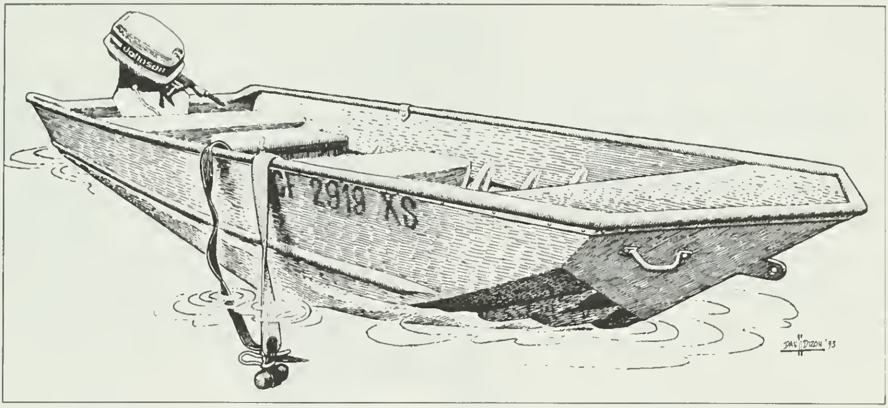

Figure 2. Position of cinch assembly in a mechanical technique for capturing swimming deer.

consequently, selection of a search technique.

Approach the swimming deer when they are about halfway between shores to reduce the probability of their reaching either shore before capture. Approach directly from behind the swimming animals regardless of group size. Front and side approaches cause deer to circle, increasing pursuit time and their fatigue level.

During pursuit, the primary handler (person using the "piggin" string) instructs the boat operator on the pursuit of the deer targeted for capture. The secondary handler supports the primary handler by holding onto the back of the primary handler's personal floatation device.

As the primary handler places the "piggin" string around the deer's neck, the boat operator reverses the engine and the secondary handler drops the cinch assembly over the side of the boat. The primary handler pulls the deer alongside of the boat, reaches over the back of the deer, and supports the animal by the abdomen with his arm. Concurrently, the secondary handler places the "head bag" on the deer to calm the animal. Position the bag so the hemmed end is near the mouth and the split seam is under the jaw.

The secondary handler then raises the posterior end of the deer by grabbing the loose skin on the top of the rump and lifting. Raising the rump of the deer and lowering the shoulders will reduce kicking. Move the animal until the cinch is positioned in front of its rear legs. Moving the cinch too far forward on the deer fails to support the rump and encourages kicking. The secondary handler then reaches under the deer and grabs the loose end of the latigo strap floating under the abdomen. Pull the strap over the deer until the cinch is snug on the lower abdomen. Only enough lift to prevent the rump of the deer from sinking is required. When the procedure is done correctly, the deer will float alongside the boat or attempt to continue swimming. Excessive lift will cause the deer to struggle. Place the end of the strap under the knee of the primary handler. The strap could also be held by the boat operator serving as a counter weight on the opposite side of the boat (Fig 3). The secondary handler is now able to attach a radio-collar to the deer. After the radio-

Figure 3. Restraint and radio-collaring of a deer captured while swimming.

collar is attached, remove the "piggin" string. Simultaneously remove the "head bag" and release the latigo strap, allowing the animal to swim freely. Assisting the animal to shore is not usually necessary. If the animal is energetic, release in the direction the animal was swimming before capture and remain near the capture site until the deer reaches shore. However, if handling time is extended and the deer displays signs of fatigue, it may be prudent to assist the animal. Moving the restrained deer through the water increases its struggling and is recommended only when absolutely necessary.

In the unlikely event that a deer inhales water and becomes unconscious, secure the animal to the outside of the boat, move the animal to shore and administer cardiopulmonary resuscitation. We do not recommend bringing a conscious or semi-conscious deer into the boat under any circumstances. Drugging an unconscious animal before transport to shore is not recommended because it reduces the animal's heart rate and respiration, thereby reducing the likelihood of resuscitation.

Radio-Collaring

If deer are to be captured for attaching radio-collars, cut the collars to the appropriate length in advance to reduce handling time. A collar length of 46 cm works well for adult female black-tailed deer. Secure a thin string from the boat to the radio-collar to prevent it from sinking if dropped. When the collar is attached to the deer, cut the string with shears instead of a knife to reduce the chance of injuring handler and animal. Tape pipe insulation around the handle of the nut driver to make it floatable, and have spare nuts and bolts readily available.

RESULTS

Deer swimming across Clair Engle Reservoir were captured to attach radio-collars. Of 40 deer seen swimming, 10 were captured during 58.25 hours of trapping. About 30 percent of the capture hours occurred during periods of rain. Capture rate decreased from 0.22 deer/hour when clear to 0.06 deer/hour when raining. Deer were captured throughout the day (0600 - 1600 hours). Group size of swimming deer ranged from one to five and averaged 3.1 (n = 13 groups, SE = 0.4). Only one deer was captured per group. Pursuit time was less than two minutes, and handling time of captured deer averaged 5.5 minutes (n = 8, SE = 0.6).

DISCUSSION

Advantages: Capturing swimming deer can be an efficient technique with several advantages. First, the technique is inexpensive provided a boat is already owned or can be borrowed. The materials used cost less than $60 and are readily available. The expense may be further reduced by substituting other materials already owned for those recommended. For instance, sewn canvas or wide nylon straps may be used in place of the cinch strap. Construction can be accomplished by one person within 30 minutes, and three people can execute the technique.

Handling time is short, and restraining the legs of deer is not required. Consequently, we found this technique the least physically demanding mechanical capture technique for deer.

Lastly, based on the capture rate, individual deer captured were likely from groups moving independently of one another. Attaching a radio-collar to one deer from each group reduces the probability of having pseudoreplicated (Hurlbert 1984) deer locations.

Disadvantages: The technique does have some limitations. It is not recommended in water shallow enough for deer to stand because their capability to struggle is increased. Without modification, the technique is not suitable for animal relocation.

Use of this technique during frigid weather might cause hypothermia in deer. The fur of captured deer appeared to absorb more water than that of uncaptured deer. Captured deer left a distinct water trail upon exiting the water, whereas uncaptured deer left none.

The technique does not facilitate the extraction of blood from deer or assessment of ectoparasite infestation. This technique provides an efficient method for capturing deer to attach radio-collars or ear-tags in areas where deer swim waterways.

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WATERFOWL KILLED BY LIGHTNING

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On the morning of 19 February 1993, between 0400-0545 hours, an intense electrical storm passed over Beale Air Force Base and surrounding areas of Butte County, California. Beale AFB is located about 50 miles north of Sacramento at the eastern edge of the Central Valley. The base is 23,000 acres in size and is dominated by rolling foothills of annual grassland and oak (*Quercus* sp.) savanna. Later that day, base personnel collected the following dead waterfowl:

205	Lesser snow geese (*Anser caerulescens caeurlescens*)
82	Ross geese (*Anser rossii*)
17	Pintail (*Anas acuta*)
9	Wigeon (*Anas americana*)
4	White-fronted geese (*Anser albifrons*)
2	Green-winged teal (*Anas carolinensis*)
1	Cackling Canada goose (*Branta canadensis minima*)
1	Gadwall (*Anas strepera*)
1	Mallard (*Anas platyrhynchos*)
1	Female common merganser (*Mergus merganser*)

An additional estimated 300 lesser snow and Ross geese were observed but not collected. Dead waterfowl were observed over a 5,000-10,000 acre area on the base, and on approximately 10,000 acres both north and south of the base. About 25 percent of the total estimated affected area was surveyed by base personnel. The 600+ waterfowl collected or observed represented a minimum number of dead waterfowl as a result of this storm.

Five freshly killed birds were taken to the Department of Fish and Game's Wildlife Investigations Laboratory to be necropsied. The following descriptions are from the necropsy report:

Bird #1: Male northern pintail - featherless streak approximately three centimeters in width, running from base of skull along dorsal neck caudally to tip of left wing (feathers were singed at the edge of streak). Internal gross lesions consist of massive hemorrhaging throughout body; hemorrhagic lungs; liver macerated; trachea contains clotted blood; gizzard and crops full of barley, etc.

Bird #2: Adult female snow goose - large laceration and hemorrhaging at left abdominal wall; the feathers adjacent to the cloaca were burned; fractured left humerus; internal gross lesions consist of hemorrhaging and macerated organs.

Bird #3: Adult male snow goose - featherless; burn streak that runs along the ventral cranial wing (bilat); internal massive hemorrhages; macerated liver.

Bird #4: Adult female Ross goose - large burn area at dorsal wing and dorsum; massive internal hemorrhage.

Bird #5: Adult snow goose - Severe head and beak trauma; multiple large lacerated areas on body; no necropsy done due to the extensive external injuries.

Specimens taken: Smear of heart; blood taken; and culture of liver. All smears and cultures were negative for bacteria.

Diagnosis: These birds appear to have been struck by lightning. This was supported by the gross lesions, the histology, and the lack of evidence of an infectious process.

The Beale AFB newspaper, *The Space Sentinel* reported that about 4:00 a.m. on 19 February Mr. Robert Wilkey was emptying trash dumpsters at the base landfill. He heard a whistling sound, looked up, and was struck in the chest by a dead white goose. Mr. Wilkey was surprised but not injured.

On a historical note, the spring 1991 issue of *California Waterfowl* reported that during the early 1970's, the Paul Crapuchette family was staying in a motel in the town of Live Oak during a lightning storm. Live Oak is located 20 miles northwest of Beale AFB. Immediately following a lightning flash, a dull "thud" was heard on the carport and a pintail was retrieved. Ten pintail were reportedly found dead in the motel parking lot. All of the birds except one were virtually unmarked. The one bird had a thumb-size hole burned completely through it.

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INSTRUCTIONS FOR CONTRIBUTORS

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