Estimating Salmon Spawning Escapement Using Capture–Recapture Methods

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We describe a method of estimating the spawning escapement of coho salmon (*Oncorhynchus kisutch*) from capture–recapture data. Traditional capture–recapture analyses do not directly provide estimates of escapements; however, we show how simple modifications to the Jolly–Seber method can estimate the total number of fish returning to a river including those that enter and die between sampling occasions. Spawning runs of Pacific salmon were simulated and their escapements estimated using capture–recapture. The performance of the maximum likelihood estimators (MLEs), the censored MLEs, the constrained MLEs, and less-biased estimators in estimating the run sizes and providing estimates of precision were evaluated. Simulation results indicated that constrained MLEs provided the most appropriate estimates of escapement and that standard errors be computed using the large-sample variance formulae evaluated at these estimates. These methods were used to estimate the escapements of coho salmon to a small river on Vancouver Island in 1989 and 1990.

Nous décrivons une méthode permettant d'estimer les échappées de géniteurs de saumons coho (*Oncorhynchus kisutch*) à partir de données sur les prises et recaptures. Les analyses traditionnelles de ce type ne donnent pas des estimations directes des échappées; nous montrons toutefois comment des modifications simples apportées à la méthode de Jolly–Seber peuvent permettre d'estimer le nombre total de poissons remontant dans un cours d'eau, y compris ceux qui entrent et meurent entre les échantillonnages. Les remontes de saumon du Pacifique ont été simulées, et leurs échappées estimées par prises et recaptures. Nous avons évalué la performance des estimateurs de vraisemblance maximale (MLE), des MLE tronqués, des MLE contraints et d'autres estimateurs moins biaisés pour calculer la taille des remontes et donner des estimations de la précision. Les résultats de la simulation indiquent que les MLE contraints ont donné les estimations les plus appropriées des échappées, les erreurs types étant calculées à l'aide des formules de variance de grand échantillon déduites de ces estimations. Ces méthodes ont servi à estimer les échappées de saumon coho dans une petite rivière de l'île de Vancouver en 1989 et 1990.

1. Introduction

The need for better salmon spawning escapement estimates, and the standardization of estimation procedures, has been well documented (Walters and Ludwig 1981; Pearse 1982; Symons and Waldichuk 1984). Accurate estimates of spawning stocks are required to assess whether stock sizes and harvest rates are at an optimum, and precise estimates of escapement are required if fishery managers are to have confidence in management strategies. These objectives may be achieved in various ways. A counting fence or weir has traditionally been the most reliable method of escapement enumeration, although fences are prone to flood damage and costly to operate. Recent developments in visual survey techniques (Tschaplinski and Hyatt 1990; Irvine et al. 1992) have also resulted in acceptable estimates of escapement. In this paper, we describe a method to estimate the total number of coho salmon (*Oncorhynchus kisutch*) returning to a stream to spawn using capture–recapture methods.

Previous capture–recapture studies on Pacific salmon have focused on the use of closed models or the Petersen estimator. Closed models are appropriate for populations that have no recruitment or losses during the study. The Petersen estimate has been employed for many salmon stocks, and its use for escapement was reviewed by Cousens et al. (1982) and Simpson (1984). Because recruitment and losses can occur during the course of a study, attention has moved to models for open populations, and Labelle (1990) developed an iterative approach "open model" for estimating salmon escapements.

The Jolly–Seber model (Pollock et al. 1990) is an appropriate tool for estimating abundances of open populations in capture–recapture studies. However, it has rarely been used for Pacific salmon, perhaps in part because the analysis of capture–recapture data using the Jolly–Seber model does not provide a

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direct estimate of escapement. The Jolly–Seber model does provide estimates of the probability of survival between sampling occasions, of abundance at sampling occasions, and of the net number of new animals that enter between sampling occasions and survive to the next sampling occasion. For escapement estimation, these parameters are of secondary importance. Interest lies in estimating the number of fish present at any time between the first and last sampling occasion including those fish that enter the system and die between consecutive sampling occasions. In addition, the population size of interest includes those fish that entered before the first sampling occasion and those that entered after the last sampling occasion. In a well-designed study, these numbers should be small enough that they can be ignored.

Previous authors have estimated the equivalent of escapement using capture–recapture methods. Crosbie and Manly (1985) modeled the recruitment and survival processes by probability distributions requiring fewer parameters than required by the Jolly–Seber model. Furthermore, they showed that when uniform recruitment and mortality rates are assumed between sampling occasions, the estimates of escapement are simple functions of the Jolly–Seber estimates, and they determined analytic large-sample estimates of precision. McKay and Bradley (1988) followed a similar approach using a different set of distributions than Crosby and Manly for recruitment and survival and used numerical methods to estimate recruitment and survival parameters and their standard errors. Sykes and Botsford (1986) examined the problem of estimating the spawning escapement of chinook salmon (*O. tshawytscha*) by tagging and recovering carcasses. They also modified the Jolly–Seber estimates by assuming that all recruitment took place halfway between sampling occasions and used a parametric bootstrap to estimate the precision of the estimates.

However, several issues that may greatly affect estimates of escapement and their precision remain unresolved. The objectives of this paper are to explore the consequences of these issues and to make recommendations for their resolution. In particular:

(1) What are the effects of different assumptions about recruitment upon estimates of the escapement?

(2) How should recruitment be estimated at the start and at the end of an experiment, when the parameters of interest are confounded?

(3) Should maximum likelihood estimates, which are known to be biased, or less-biased estimators (Pollock et al. 1990) be used? It may occur that the closed-form estimates are outside the parameter space (e.g., estimated births less than zero). How should these be adjusted?

(4) How are estimates of precision obtained? How closely do the asymptotic formulae for the variances and covariances approximate the true sampling error? Is the distribution of the estimates sufficiently close to a normal distribution that the usual large sample confidence intervals may be used with assurance that they are valid?

(5) What are the effects of violations of the assumptions of homogeneous survival and recapture?

Because the Jolly–Seber model forms the basis for our method, we begin by briefly reviewing it and its shortcomings for escapement estimation. Next we propose an estimator for the escapement and then discuss the resolution of objectives 1–4. A simulation example is presented to illustrate the properties of our estimator and to investigate violations of assump-

TABLE 1. Notation.

Fundamental Jolly–Seber parameters

s Number of sampling occasions

p_i Probability of capture at sampling occasion i, $i = 1, \ldots, s$

ϕ_i Probability that an animal alive at sampling occasion i will be alive at sampling occasion $i + 1$, $i = 1, \ldots, s - 1$

B_i Number of animals that enter the river system after sampling occasion i and *are still alive* at sampling occasion $i + 1$, $i = 0, \ldots, s - 1$. These are subsequently referred to as "births." B_0 is defined as the number of animals that enter before the first sampling occasion and are alive at the first sampling occasion

Derived Jolly–Seber parameters

N_i Number of animals alive in the system at sampling occasion i, i.e., the abundance at occasion i, $i = 1, \ldots, s$. $N_1 = B_0$; $N_{i+1} = (N_i - n_i + R_i) \phi_i + B_i$, $i = 1, \ldots, s - 1$

M_i Number of marked animals alive in the system at sampling occasion i, $i = 1, \ldots, s$

New parameters

B_i^* Number of animals that enter the system after sampling occasion i but before sampling occasion $i + 1$, $i = 0, \ldots, s - 1$. $B_i^* \geq B_i$ because it includes those animals that enter after sampling occasion i but die before sampling occasion $i + 1$

N Total number of animals that enter the system before the last sampling occasion, i.e., the escapement. $N = B_0^* + B_1^* + \ldots + B_{s-1}^*$

Statistics

m_i Number of marked animals captured in the ith sample, $i = 1, \ldots, s$

u_i Number of unmarked animals captured in the ith sample, $i = 1, \ldots, s$

n_i Number of animals captured in the ith sample, $i = 1, \ldots, s$. $n_i = m_i + u_i$

R_i Number of the n_i that are released after the ith sample, $i = 1, \ldots, s - 1$. $R_i \leq n_i$ because of losses on capture

r_i Number of R_i released at i that are captured again, $i = 1, \ldots, s - 1$

z_i Number of animals captured before i, not captured at i, and captured later, $i = 1, \ldots, s - 1$

tions (objective 5). Finally, 2 yr of experimental data are analyzed.

2. Jolly–Seber Analysis

Details of the design, required assumptions, and subsequent analysis of capture–recapture experiments using the Jolly–Seber model are presented in Seber (1982) and Pollock et al. (1990). The notation used is shown in Table 1. At each of s sampling occasions, animals are captured. Unmarked animals are individually marked and subsequently released. Tag numbers of previously marked animals are recorded and the animals are also released. The number of releases may be less than the number of captures due to losses on capture or, less commonly, more than the number of captures due to additions by the researcher. There are a total of $3s - 1$ parameters: $p_1, \ldots, p_s$, $\phi_1, \ldots, \phi_{s-1}$, and $B_0, \ldots, B_{s-1}$. The parameters $\{N_i\}$ and $\{M_i\}$ can be derived from these parameters.

A likelihood equation can be constructed that gives the probability of observing the statistics $\{m_i\}$, $\{u_i\}$, $\{R_i\}$, $\{r_i\}$, and $\{z_i\}$

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TABLE 2. Closed-form MLEs and less-biased estimators for the Jolly–Seber model.

Parameter	Closed-form MLE	Less-biased estimator	Range
	Unconfounded parameters		
M_i	$\hat{M}_i = m_i + \dfrac{R_i z_i}{r_i}$	$\tilde{M}_i = m_i + \dfrac{(R_{i+1})z_i}{(r_{i+1})}$	$2, \ldots, s-1$
N_i	$\hat{N}_i = \dfrac{n_i \hat{M}_i}{m_i}$	$\tilde{N}_i = \dfrac{(n_i + 1)\tilde{M}_i}{(m_i + 1)}$	$2, \ldots, s-1$
p_i	$\hat{p}_i = \dfrac{m_i}{\hat{M}_i}$	$\tilde{p}_i = \dfrac{m_i}{\tilde{M}_i}$	$2, \ldots, s-1$
ϕ_i	$\hat{\phi}_i = \dfrac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i}$	$\tilde{\phi}_i = \dfrac{\tilde{M}_{i+1}}{\tilde{M}_i - m_i + R_i}$	$1, \ldots, s-2$
B_i	$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i - n_i + R_i)$	$\tilde{B}_i = \tilde{N}_{i+1} - \tilde{\phi}_i(\tilde{N}_i - n_i + R_i)$	$2, \ldots, s-2$
	Confounded parameters		
$\phi_{s-1}p_s$	$\widehat{\phi_{s-1}p_s} = \dfrac{r_{s-1}}{R_{s-1}}$	Same as MLE	
$B_0 p_1$	$\widehat{B_0 p_1} = n_1$	Same as MLE	
$B_1 + B_0(1 - p_1)\phi_1$	$\hat{N}_2 - \hat{\phi}_1 R_1$	$\tilde{N}_2 - \tilde{\phi}_1 R_1$	
B_{s-1}/ϕ_{s-1}	$\dfrac{n_s}{\widehat{\phi_{s-1}p_s}} - (\hat{N}_{s-1} - n_{s-1} + R_{s-1})$	$\dfrac{n_s}{\widetilde{\phi_{s-1}p_s}} - (\tilde{N}_{s-1} - n_{s-1} + R_{s-1})$	

given these parameters (Seber 1982, p. 198). Closed-form maximum likelihood estimators (MLEs) can be found (Pollock et al. 1990) and are shown in Table 2.

Because escapement is defined as the number of fish that escape marine fisheries and return to a river to spawn, one possible estimator for the escapement could be formed as $\hat{B}_0 + \hat{B}_1 + \ldots + \hat{B}_{s-1}$ which is the sum of the net number of fish that enter the river system between sampling occasions. However, there are several problems with this approach that will be outlined in the remainder of this section and resolved in the next section.

First, the Jolly–Seber estimators of birth estimate the number of animals that enter the population after a sampling occasion *and are alive at the next sampling occasion*. Such estimates exclude those animals that enter the system but die *before* the next sampling occasion which also form part of the escapement. Consequently, Jolly–Seber estimates of birth underestimate the true number of new animals, except when all animals are guaranteed to survive from their entry to the next sampling occasion.

Second, not all of the parameters can be estimated. Only $3s - 7$ parameters of the $3s - 1$ parameters are individually estimable as shown in Table 2. The parameters p_1, p_s, ϕ_{s-1}, B_0, B_1, and B_{s-1} cannot be individually estimated; they are confounded. Four estimable functions of these parameters are shown in Table 2. Consequently, it is impossible to estimate the number of recruits at the start and end of the experiment.

Third, despite the optimal large-sample properties of the MLEs, they are biased when used with small samples (Pollock et al. 1990). This bias occurs in small samples because there is an appreciable chance that m_i will equal zero at some sampling occasion and then the MLE for the number of births will take the value of infinity. The less-biased estimators (Table 2) do

not suffer from this defect, but are still biased for small values of the sample statistics. Pollock et al. (1990, p. 21) recommend that m_i and r_i should be at least 10 to obtain satisfactory performance from the less-biased estimators. This may be unobtainable in many studies.

Lastly, it is possible that the estimators in Table 2 may produce estimates that are out of range, e.g., estimates of survival greater than 1 or estimates of births less than zero. Simply censoring the estimates to the boundary value, e.g., setting negative estimates of birth to zero, will result in bias. It is not clear how to modify the likelihood equations to impose the constraints to keep all estimates in bounds.
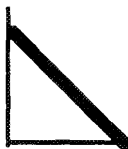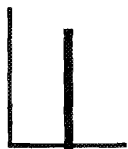
3. Estimating Escapement

3.1. Accounting for Deaths before the Next Sampling Occasion

Two approaches have been proposed to account for deaths of newly recruited fish between sampling occasions.

In the first approach, the recruitment process over the entire experiment is modeled by a probability distribution. Because, by definition, probability distributions must integrate to one over the entire experiment, the fate of all animals will be modeled. Crosbie and Manly (1985) assumed that time of recruitment followed a beta distribution and McKay and Bradley (1988) assumed an Erlangian distribution. An additional advantage of using a probability distribution is that estimates of recruitment at the start and the end of the study are no longer confounded. The disadvantages of this approach are the mathematical complexity and, more seriously, the substantial bias introduced if the mathematical model chosen is inappropriate. Additionally, it may be difficult to find an appropriate probability distribution for bi- or trimodal

TABLE 3. Comparison of the adjustment factors under various distributions of recruitment between sampling occasions (uniform survival rate assumed). Each graph depicts recruitment versus time. The formula under the graph is the adjustment factor as derived in Appendix A.

	Distribution of recruitment between sampling occasions and derived adjustment factors					
Survival rate between sampling occasions ϕ	All take place after previous sample time	Declining over time	All take place at midpoint (Sykes and Botsford 1986)	Uniform (Crosbie and Manly 1985)	Increasing over time	All take place at just before next sample time
	$1/\phi$	$\dfrac{\log(\phi)^2}{2 + 2\phi\log(\phi) - 2\phi}$	$\dfrac{1}{\sqrt{\phi}}$	$\dfrac{\log(\phi)}{\phi - 1}$	$\dfrac{\log(\phi)^2}{2\phi - 2\log(\phi) - 2}$	1
1.00	1.00	1.00	1.00	1.00	1.00	1.00
0.90	1.11	1.07	1.05	1.05	1.04	1.00
0.80	1.25	1.16	1.12	1.12	1.08	1.00
0.70	1.43	1.26	1.20	1.19	1.12	1.00
0.60	1.67	1.40	1.29	1.28	1.18	1.00
0.50	2.00	1.57	1.41	1.39	1.24	1.00
0.40	2.50	1.80	1.58	1.53	1.33	1.00
0.30	3.33	2.14	1.83	1.72	1.44	1.00
0.20	5.00	2.71	2.24	2.01	1.60	1.00
0.10	10.00	3.96	3.16	2.56	1.89	1.00
0.05	20.00	5.61	4.47	3.15	2.19	1.00

distributions of recruitment such as those that occurred in the examples later in this paper.

In the second approach which we prefer, assumptions are made to describe the recruitment process between individual sampling occasions. The likelihood function of the Jolly–Seber model is then modified to incorporate a description of the recruitment process, e.g., Crosbie and Manly (1985) derived a likelihood equation (their equation (6)) suitable when recruitment and mortality are assumed to occur uniformly between sampling occasions. The solution of their likelihood equations yielded identical MLEs for $\{\phi_i\}$, $\{p_i\}$, and $\{B_i\}$ as shown in Table 2. The MLE for the total recruitment between sampling occasions (including those that die before the next sampling time) is

$$(1) \quad \hat{B}_i^* = \hat{B}_i \frac{\log\hat{\phi}_i}{\hat{\phi}_i - 1},$$

i.e., the total number of new recruits is a simple function of the net number of recruits and the survival rate for that period. Crosbie and Manly (1985) ignored losses on capture, but modifications to their results to account for such losses are straightforward (Appendix C).

The assumption of uniform recruitment and mortality rates between sampling occasions cannot be verified with the data collected in a capture–recapture experiment. However, the sensitivity of the adjustment process to the choice of recruitment distributions can be investigated by choosing different patterns for recruitment (Appendix A). The adjustment factors corresponding to various recruitment distributions and mortality rates to be used with the Jolly–Seber estimates of birth (e.g., equation (1)) are shown in Table 3. The adjustment factors are similar when survival rates are high, since most animals that enter between sampling occasions survive to the next sampling

occasion. However, the adjustment factors differ considerably for mid- to low survival rates. In such cases, careful consideration must be given to the assumptions about the recruitment process to avoid extreme over- or underestimation of the total recruitment. The adjustment factors in Table 3 can be estimated by replacing the parameters in the formulae by estimators from the Jolly–Seber analysis.

3.2. Accounting for Confounding at the Start and End of the Run

If all recruitment parameters were estimable, then the escapement could be estimated as

$$\hat{N} = \hat{B}_0^* + \ldots + \hat{B}_{s-2}^* + \hat{B}_{s-1}^*$$

where $\hat{B}_i^*$ are obtained from the Jolly–Seber estimates and the appropriate adjustment factor as in equation (1). Because B_0, B_1, and B_{s-1} are not identifiable without further assumptions, Seber (1982, p. 201) suggested on one hand that p_1 and p_s be estimated in an ad hoc fashion from the pattern of recapture rates found in the data. Then the confounded parameters may be individually resolved and the recruitment in the first and last sampling periods estimated. However, any assumptions about p_1 and p_s cannot be tested using information in the model. On the other hand, it may be reasonable on biological and logistical grounds to assume that the capture rates at all sampling occasions are equal, i.e., $p_1 = p_2 = \ldots = p_s$. Under this assumption, all recruitment parameters may be estimated, but closed-form estimators do not exist and numerical methods must be used (Jolly 1982; Pollock et al. 1990, section 5.3.3).

Because it is relatively easy to extend capture–recapture escapement studies until recruitment has virtually ended, we propose to ignore the problem of estimating B_{s-1} and will set it to zero. However, it may be more difficult to start an escape-

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ment enumeration study before much escapement occurs. We propose to resolve the problem of confounded parameters at the start of the experiment by applying an adjustment factor to $N_2 = B_0\phi_1 + B_1$, the number of animals alive at the second sampling occasion. Then, for example, under the assumption of uniform recruitment between all sampling occasions, our proposed estimator for the escapement is

$$(2) \quad \hat{N} = \hat{N}_2 \frac{\log\hat{\phi}_1}{\hat{\phi}_1 - 1} + \hat{B}_2 \frac{\log\hat{\phi}_2}{\hat{\phi}_2 - 1} + \ldots + \hat{B}_{s-2} \frac{\log\hat{\phi}_{s-2}}{\hat{\phi}_{s-1} - 1}.$$

Our estimator is slightly biased if all assumptions are valid, since it estimates

$$B_0\phi_1 \frac{\log\phi_1}{\phi_1 - 1} + B_i^* + B_2^* + \ldots B_{s-2}^*$$

which is less than the escapement (ϕ_1 ($\log\phi_1/(\phi_1 - 1)$) is less than 1 and B_{s-1}^* is missing). However, in a well-designed study, there should be little recruitment before the start of sampling or near the end of sampling and the bias is expected to be small.

3.3. Adjusting the Estimates for Small Sample Biases

As noted earlier, the individual MLEs of births are biased upwards (Pollock et al. 1990, p. 20). The less-biased estimators (Table 2) can be used, but Seber (1982, p. 204) indicated that both m_i and r_i should be at least 10 for satisfactory improvements. In studies where m_i and r_i are less than 10, we recommend that adjacent sample occasions be pooled. Arnason and Baniuk (1978, section 5.3) and Hargrove and Borland (1993) indicated that pooling leads to nearly unbiased estimates of the net number of births and survival rates for the pooled period if the mortality rate is low (less than 50%) for each of the pooled intervals. However, pooling may introduce additional bias if the patterns of recruitment are very different in the two intervals, i.e., bias will be introduced if the assumption of uniform recruitment over the pooled intervals is imposed on two nonuniform recruitment patterns in each interval. If pooling is performed, the choice of recruitment distribution for the pooled interval should be given careful consideration.

3.4. Adjusting Out-of-Range Estimates

It is possible that some of the closed-form estimators produce estimates that are out of range, e.g., survival estimates greater than 1 or birth estimates less than zero. This is not unusual and does not indicate that the model is wrong. For example, estimates of net births are essentially found as $\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i\hat{N}_i$. Both $\hat{N}_{i+1}$ and $\hat{N}_i$ are highly variable when the capture rate is small (Pollock et al. 1990, p. 72), and consequently, negative estimates of net births can easily occur if the actual number of net births is small. One common solution is to censor the out-of-range estimators to the boundary values, e.g., estimates of survival greater than 1 are set to 1 or estimates of births less than zero are set to zero. However, this can introduce substantial positive bias into the birth estimates (Appendix B). We recommend either the use of numerical methods that constrain all estimates in bounds (constrained MLEs, Appendix C) or the use of the negative estimates as is. The first solution may involve difficult numerical computations. However, when numerical methods force the negative estimate to zero, they simultaneously reduce neighboring estimates so that the sum and therefore the estimated escapement is little changed. The latter option

works well because estimates of recruitment in neighboring occasions are highly correlated.

3.5. Estimates of Precision

Two methods used to obtain estimates of the precision of estimators are large-sample asymptotic formulae and bootstrap methods.

Asymptotic large sample variances and covariances were derived for the net recruitment estimates (Appendix D). These are similar to those of Crosbie and Manly (1985) except Crosbie and Manly used a different subscript notation, they did not allow for losses on capture, and they did not use our suggested estimator for the recruitment at the start of the experiment. Our formulae were found conditional upon the escapement rather than upon the actual (unknown) number of births in each interval which explains the differences from the formulae presented in Pollock et al. (1990). Our formulae can than be used in a Taylor-series expansion with the particular recruitment adjustment factor employed and the expansions summed to obtain the variance of the escapement estimate.

Problems can occur in evaluating the asymptotic formulae when estimates are outside the parameter space, e.g., negative estimates of birth. Simply evaluating the formulae using these invalid estimates may lead to nonsensical estimates, e.g., estimated variances less than zero. In this case, numerical methods should first be used to find estimates that are within the parameter space. Then the asymptotic formulae can be evaluated at these constrained estimates after using the constrained estimates to evaluate $E[m_i]$ and other expected statistics that appear in the asymptotic formulae rather than using m_i and other statistics from the experiment. Alternatively, estimated variances can be obtained directly by inverting the information matrix at the last iteration of the constrained numerical optimization. However, the numerical methods used to constrain estimates cannot distinguish between a constraint necessary to keep an estimate within a parameter space and a constraint that represents real knowledge about a parameter and may report estimated variances of zero for such estimates. For example, estimates of births that are constrained to be zero are reported with an estimated variance of zero even though the constraint does not imply that we know that births are zero. Consequently, the standard errors (SEs) obtained from using the inverse of the information matrix following a constrained maximum likelihood estimation may be underestimates of the true SE, particularly if many parameters were constrained.

A confidence interval for the escapement formed by multiplying the estimated SE by a confidence factor and bracketing the estimate (e.g., estimate ± 1.96 SE) is expected to perform well even though the usual Jolly–Seber estimates of the births between each sampling occasion are skewed (Buckland and Garthwaite 1991). This is as a result of the Central Limit Theorem that applies when the individual estimates of recruitment are added.

In the bootstrap approach, the observed experimental data are either simulated (parametric bootstrap) or resampled (nonparametric bootstrap) to create a series of "pseudo-experiments" (Buckland 1980; Buckland and Garthwaite 1991). Each of these "pseudo-experiments" is analyzed to obtain an estimate. The resulting distribution of the estimates may provide good information on the bias and precision of the estimator. Sykes and Botsford (1986) used a parametric bootstrap to obtain an estimated sampling distribution of the escapement and

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TABLE 4. Parameter values used in the baseline simulation and expected statistics.

Sample occasion	New entrants (B_i^*)	Survival rate (ϕ_i)	Capture rate (p_i)	Average sample size $E(n_i)$	Average marked of n_i $E(m_i)$	Average recoveries $E(r_i)$
0	100					
1	150	0.60	0.25	25.0	0.0	6.8
2	250	0.60	0.25	44.4	3.8	12.1
3	200	0.60	0.25	75.6	8.3	20.5
4	0	0.60	0.25	84.5	15.1	22.9
5	0	0.60	0.25	50.7	19.5	13.6
6	350	0.60	0.25	30.4	16.4	8.0
7	100	0.60	0.25	86.9	11.9	21.5
8	50	0.60	0.25	71.6	18.4	15.6
9	0	0.60	0.25	52.8	19.0	7.9
10		0.60	0.25	31.7	16.5	
Total	1200					

TABLE 5. Summary of the point estimates from the baseline simulation. Column numbers (at top) are cited in the text (ne = nonestimable).

1	2	3	4	5	6	7
		Closed-form MLEs		Less-biased closed-form estimators		
Sample occasion	B_i^*	Uncensored	Censored	Uncensored	Censored	Constrained MLE
0 + 1	250	282	282	209	209	260
2	250	260	271	252	254	250
3	200	200	212	205	209	169
4	0	−4	33	3	32	22
5	0	−5	14	−4	12	12
6	350	387	387	343	343	363
7	100	104	115	108	114	104
8	50	41	52	41	48	40
9	0	ne	ne	ne	ne	ne
Total	1200	1266	1366	1157	1219	1221

formed confidence intervals based upon percentiles of this bootstrap sampling distribution as suggested by Buckland (1980). A problem with the parametric bootstrap approach occurs when some estimates are invalid, e.g., how is a population simulated that has a survival rate greater than 1 or negative births? Simply setting the out-of-range estimates to the boundary points will result in bias as previously shown. Buckland and Garthwaite (1991) demonstrated that a nonparametric bootstrap method, conditional upon the number of animals actually caught, may be used to find confidence intervals with good coverage. This method has the advantage that it is not necessary to simulate the birth and death processes between sampling occasions, nor is it necessary to simulate the animals never caught, which is necessary in a parametric bootstrap approach. The major impediment to using bootstrap procedures is the amount of computing required.

4. Simulation Experiment

Two sets of simulation experiments were performed. The first set compared the properties of five estimators of escapement under ideal conditions; the second set compared the constrained MLE in situations where the underlying assumptions were violated.

4.1. Comparing Estimators when the Assumptions are Satisfied

In the first set of simulations, recruitment to the population and the mortality rate were assumed to be uniform between sampling occasions. No losses on capture were modeled. The number of new entrants to the population, the capture rates, and the survival rates were chosen based upon the results from the 1989 data analyses. These and the expected number of marked animals and subsequent recoveries are presented in Table 4.

Parameters were estimated five different ways (Table 5) in each of the 200 simulations: the closed-form MLEs (Table 2), with and without censoring of negative estimates of births; the less-biased closed-form estimators (Table 2), with and without censoring of negative estimates of birth; and the MLEs when the estimates are constrained to lie in the parameter space (Appendix C). For each method, the escapement was estimated using equation (2). The average values of the point estimates of recruitment between sample occasions and the estimates of the escapement over the simulations are shown in Table 5.

As expected, simply censoring negative estimates increased the average value of the estimator (column 4 versus column 3; column 6 versus column 5), particularly if the number of births was close to zero (sample occasions 4 and 5). Censoring increased the estimates of escapement by about 100 fish for the
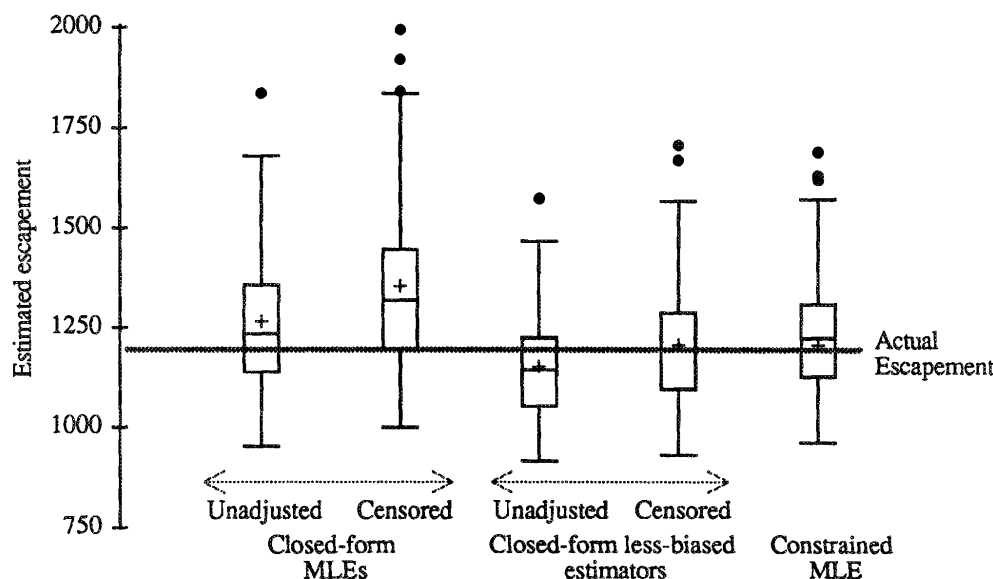
FIG. 1. Box plots of the distribution of the estimated escapement from the baseline simulation using the five methods described in the text.

closed-form MLE and by about 60 fish for the less-biased estimator. The uncensored closed-form MLEs are positively biased (column 3 versus column 2). The uncensored less-biased estimators are nearly unbiased (column 5 versus column 2) at all sample occasions except, as noted following equation (2), the initial population size (B_0^*) was underestimated. This accounted for the underestimation of the escapement.

The constrained MLEs (column 7) exhibit features from columns 3 to 6. Because the estimator constrains all estimates of births to be positive, the estimates at sampling occasions with small numbers of births are positively biased. However, the numerical optimization then forces estimates of births at neighboring occasions (sampling occasions 3 and 6) to be reduced compared with the unconstrained MLEs. Consequently, the overall estimate of escapement lies between that of the closed-form MLE and that of the less-biased estimator.

Box plots of the escapement estimates (Fig. 1) indicate that the closed-form MLEs are more variable than the other estimators. The plots show the positive bias introduced by censoring and that the distributions of the less-biased estimators and the constrained MLE are nearly symmetric. The distribution of the constrained MLE appears to be intermediate between the closed-form MLE and the less-biased estimator.

SEs were computed for the estimates of the recruitment between sample occasions and for the escapement (Table 6) by using the closed-form asymptotic expressions of Appendix C, and using the true parameter values (these of course are never known in practice); finding the standard deviation of the estimates among the simulations (this is an estimate of the correct SE for an estimator, since, by definition, it measures the changes in the estimates over repeated experiments with the same parameter values); using the closed form expressions of Appendix C, and using estimates in place of the true value of the parameters as is usually done in practice (this was done using the closed form MLEs, the closed-form less-biased estimators, and the constrained MLEs; in the latter, the parameter estimates were used to estimate the $E[m_i]$ and other expected sample statistics that appear in the asymptotic formulae); and using the inverse of the information matrix found at the final

step of the numerical optimization of the likelihood. These were then averaged over all the simulations.

The closed-form MLEs are more variable than the asymptotic results predicted early in the experiment when there are few marked animals in the population (column 3 versus column 2). This leads to an over dispersion of the escapement estimates as seen in Fig. 1. The estimated SEs appear to reflect this increased variability (column 4 versus column 3). The actual variation of less-biased estimators matches the asymptotic results well (column 5 versus column 2), and the estimated SEs appear to be consistent (column 6 versus column 5). The constrained MLE also performs well (column 7 versus column 2; columns 8 and 9 versus column 7). For all methods, it is important that the estimated SE be a good estimate of the actual variation in the estimator (column 4 versus column 3; column 6 versus column 5; columns 8 and 9 versus column 7) rather than matching the asymptotic results (column 2). Consequently, Table 7 indicates that the estimated SE are reliable for the less-biased estimators and the constrained MLEs.

A normal probability plot of the constrained MLEs of escapement (Fig. 2) shows that the estimator is approximately normally distributed between normal scores of -2 and $+2$ as a consequence of the Central Limit Theorem. This implies that confidence intervals should perform well. The coverage of a nominal 95% confidence interval for the escapement was also estimated (Table 6). Because the closed-form MLEs and the less-biased estimators were positively and negatively biased, respectively, the coverage failed to achieve the nominal level despite the estimated SE being a good estimate of the actual variability. The constrained MLE has an estimated coverage close to the nominal level.

The simulations confirmed the properties of our proposed estimator as outlined in Section 3. In particular, the closed-form MLEs are positively biased; the unconstrained less-biased estimators perform well except as noted at the start of the experiment; the constrained MLE is intermediate between the closed form MLE or the less-biased estimator; censoring negative estimates of birth leads to a positive bias; the closed-form MLEs are more variable than expected at the beginning of the sam-
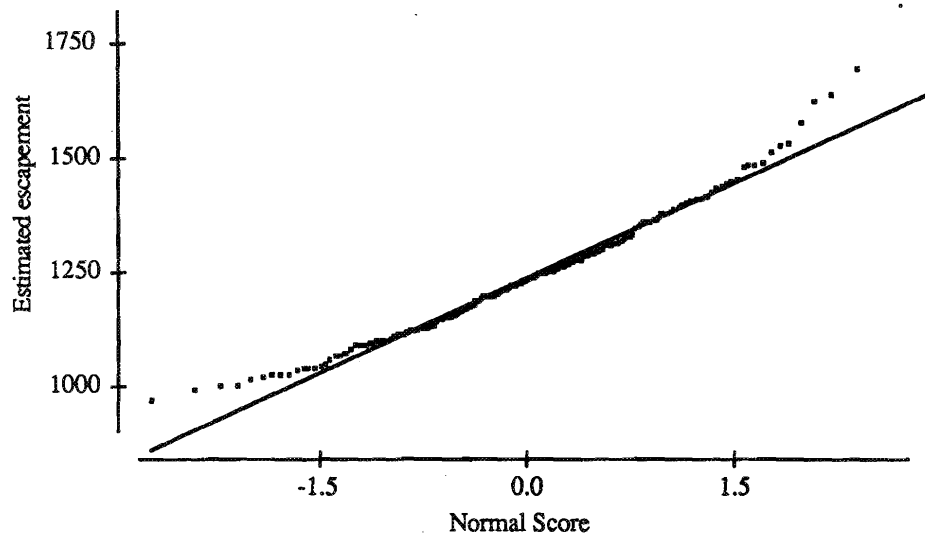
FIG. 2. Normal probability plot of constrained MLE of the escapement. The straight line represents the expected values of the estimated escapements if the sampling distribution was actually normally distributed. Distributions of the uncensored estimates were similar and are not shown here.

TABLE 6. Comparison of the SEs of the estimates and of the coverage of a 95% confidence interval from the baseline simulation. Column numbers (at top) are cited in the text.

1	2	3	4	5	6	7	8	9
		Uncensored closed-form MLEs		Uncensored less-biased closed-form estimators		Constrained MLE		
Sample occasion	Asymptotic SE from formula	Actual SD from simulations	Average estimated SE from formula	Actual SD from simulations	Average estimated SE from formula	Actual SD from simulations	Average estimated SE from inv. of info. matrix	Average estimated SE from formula
0 + 1	118	176	177	91	119	134	135	139
2	125	263	217	154	160	155	148	136
3	120	140	156	129	134	92	100	95
4	74	54	90	82	80	37	33	55
5	36	25	44	36	38	23	19	62
6	123	150	147	117	129	122	124	130
7	100	94	120	97	107	89	85	92
8	63	65	73	61	64	43	45	37
Escapement	125	197	170	132	153	139	142	147
coverage			0.92		0.91		0.96	

pling experiment; the closed-form, large-sample estimates of the variance work reasonably well; and the estimates of the SE obtained by inverting the information matrix give good estimates of precision except when the number of births is small, when they underestimate the true SE.

4.2. Effects of Violations of the Assumptions

The preceding section indicated that the constrained MLE performed well when the assumptions of the model were satisfied. However, assumptions are never completely satisfied in real experiments. In this section, we investigate, through simulation, the likely effects of violations of the key assumptions of the Jolly–Seber model, i.e., the assumptions of homogeneity in the survival and capture rates among fish.

Five simulations were conducted as described in Table 7. The extent and types of violations were chosen to be realistic biologically. Two hundred replications of each simulation were generated and the constrained MLEs were computed for each

replicate of each simulation. Box plots of the estimated escapements are given in Fig. 3.

Pollock et al. (1990, section 4.6) indicated that pure heterogeneity in survival rates that is independent of capture rates (simulation 2) leads to a positive bias in survival rate and population size estimates. Since net births are essentially estimated as $\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i \hat{N}_i$, a positive bias in $\hat{\phi}_i$ will lead to a negative bias in $\hat{B}_i$. The positive bias in $\hat{\phi}_i$ will also lead to a negative bias in the adjustment factor (Table 3), which implies that estimates of gross births will be negatively biased. This is confirmed by comparing the results of simulation 2 to the baseline simulation (Fig. 3); estimates of escapement have been reduced. The amount of bias caused by this degree of heterogeneity is only about 0.50 of a SE of the baseline estimates.

When "newer" fish have higher survival rates than "older" fish (simulation 3), survival rates will be biased downwards. Survival rates are essentially estimated by the ratio of recoveries from previously marked ("older") fish to those of newly

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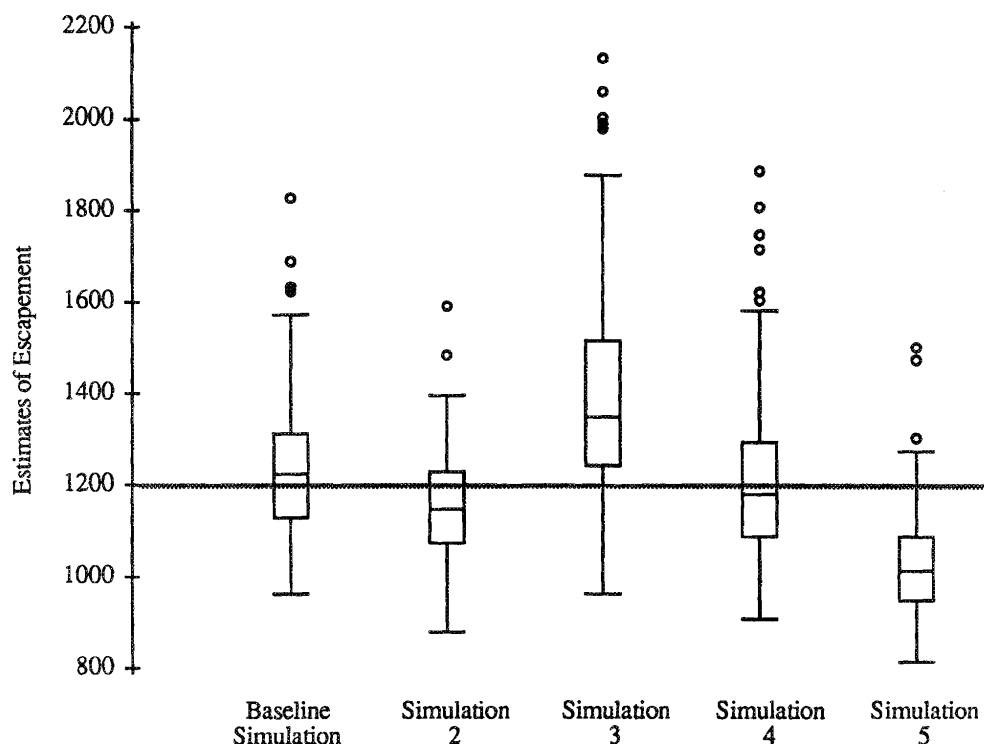Can. J. Fish. Aquat. Sci., Vol. 50, 1993

FIG. 3. Box plots of the estimates of escapement from the five simulations (see text for description of simulations). The horizontal line is the actual escapement.

TABLE 7. Description of the five simulations used to investigate the effects of violations of the assumptions.

Simulation	Description
Baseline	As performed in Section 4.1 using the parameter values given in Table 4.
2	Pure heterogeneity in survival rates among fish. As each fish enters the experiment, its survival rate was selected from a uniform distribution on the interval [0.40, 0.80]·wk^{-1} and remained at this level until death. Capture rates were homogeneous for all fish as given in Table 4
3	Heterogeneity in survival rates among fish caused by increasing mortality after entering the stream. When fish enter the experiment, they have initial survival rates of 0.60·wk^{-1}. This declines by 20%·wk^{-1}, e.g., fish that entered in week 1 would have a survival rate of 0.48 in week 2; fish that first entered in week 2 would have a survival rate of 0.60
4	Declining survival rate after entry with increased recapture rates for "older" fish. Survival rates decline as in (3), but recapture rates increase as survival decreases, since "weaker" fish are more easily recaptured. The product of survival and recapture was set to 0.25, e.g., a fish with a survival rate of 0.48 would have a recapture rate of 0.52
5	Pure heterogeneity in recapture rates. As in the baseline simulation but each fish is assigned a recapture rate from a uniform distribution on the interval [0.05, 0.45], which remain fixed for the entire experiment

marked fish. The recoveries of the previously marked fish will be reduced because their survival rates are lower leading to the negative bias. Consequently, the adjustment factors will be biased upwards (Table 3) leading to a positive bias relative to the baseline simulation (Fig. 3). The size of the bias for this simulation was on the order of 1 SE.

When "older" fish are also more prone to recapture (simulation 4), two opposing effects are active. Heterogeneity in survival rates related to the "age" of the fish causes a positive bias; heterogeneity in capture rates causes a negative bias (Pollock et al. 1990, section 4.6). In this simulation, the two forces fortuitously nearly cancel leading to almost a zero bias (Fig. 3).

Lastly, pure heterogeneity in capture rates (simulation 5) leads to negative bias. In practice, the bias is small when the average capture rate is high, say >0.50 (Pollock et al. 1990, section 4.6). As well, the practice of pooling several closely spaced sampling occasions into one reduces the heterogeneity because the multiple captures of the more catchable fish are treated as a single capture. In this simulation, the heterogeneity is large relative to the average capture rate (0.25) which leads to a large negative bias (Fig. 3).

These simulations suggest that our proposed estimator is robust to moderate violations of assumptions. They also demonstrate how simulations may be used to assess the consequences of likely violations in real experiments.

5. Application of the Method to Estimate Coho Salmon Escapements to the Chase River in 1989 and 1990

5.1. Methods and Suitability of the Jolly–Seber Model

A capture–recapture study to estimate coho salmon escapements to the Chase River, British Columbia, was performed in 1989 and 1990. The Chase River is a small stream, flowing northeast out of the Colliery Park Dams in south Nanaimo for approximately 4.5 km, entering the Strait of Georgia in the Nanaimo River estuary. Discharge ranges from

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less than 0.2 m$^3 \cdot$s^{-1} at summer low flows to greater than 30 m$^3 \cdot$s^{-1} during winter floods.

During each week of the fall salmon run, water conditions permitting, the entire river was sampled, usually over 2 d, and the entire week's sampling effort was considered to be a single pass. Early in the run, prior to the salmon dispersing to the spawning areas, large pools in the lower 2 km of river were tangle-netted weekly. Tangle-netting was performed using 25 m $\times$ 3 m $\times$ 3 cm mesh gill nets. These nets, when operated as seines, tangled both adult and jack (precocious male) coho, although fish did not become trapped by the opercula as would happen in conventional gillnetting. After the first fall freshet event, flows were often too high for netting to be practical, the fish moved into shallower areas of the river, and consequently, electrofishing was used to capture most fish. Electrofishing was performed by crews of three, two people carrying large-frame (1.25 m hoop), fine-meshed (1 cm) landing nets and the third person operating the electrofisher. Electrofishing was carried out using Smith Root Mk. 11A and 12A shockers, operating at $200-300$ V pulsed DC at 30 Hz. Near the end of each field season, when no live fish were observed, several walks of the entire stream were conducted over a 3-wk period to recover carcasses (dead pitch).

Individually numbered Ketchum No. 1 operculum tags (Ketchum Manufacturing Sales Ltd., 396 Berkley Ave., Ottawa, Ont., Canada K2A 2G6 were applied to the operculum of each live fish captured, and the sex, degree of sexual maturity, date, and location of capture were recorded. The tag number of each recaptured fish was recorded. Multiple recaptures within a week were treated as a single capture, and carcass recoveries were recorded as losses-on-capture. Once counted, carcasses were cut in half to prevent recounting. Data from the dead-pitch stream walks at the end of the experiment were pooled to form one final sampling "week."

In this study, sampling was not instantaneous, but took place over 2–3 d for most of the study and over 3 wk for the final dead pitch. The former instance is small enough that the violation of the assumption of instantaneous sampling is not judged to be serious. Since the latter occurs at the end of the experiment, and involves carcass recoveries only, its extended period has little effect on the estimates.

Catchability was presumably unequal among fish. This was due in part to the location of the fish, the type of capture method, variability in size and maturity of the fish, and any previous encounters with a capture method. The pools in the lower river were more intensively sampled by net than those in the upper river early in the study. During electrofishing, those few fish that were under cover in runs but not in deep pools were very susceptible to capture. Fish in shallow runs during and after spawning were more visible and less timid, and again were easier to catch by electrofishing. The skin of silver-bright fish is more conductive than that of darker, more mature fish, which makes them easier to catch using electrofishing. However, any multiple captures within a week were recorded as a single capture within the week. Consequently, the bias caused by heterogeneity among animals within any week are expected to be slight (refer to Section 4.2).

Little tagging mortality occurred. Natural survival rates likely differed among animals within any week because the animals were at differing stages of maturity. Survival rates were likely highly correlated with maturity; bright, early fish have been recorded alive some 50 d after first capture, but fish that were actively spawning were commonly found as carcasses within

1 wk (R.E. Bailey, unpublished data). As shown in Section 4.2, pure heterogeneity in survival rates will have a negative bias on the estimates of escapement. This type of heterogeneity occurs if a mixture of fish at different stages of maturity enter each week. If, however, fish enter the stream at a relatively fixed maturity level, this corresponds to heterogeneity as explored in simulation 3 of Section 4.2, and the resultant estimate of escapement will have a positive bias. Heterogeneity in capture rates will lead to a negative bias. In practice, a mixture of different types of heterogeneity occur, some with negative and some with positive biases.

Based upon 3 yr of experimental data, tag loss was less than 1%. It is not likely that tags were overlooked, since all crews were experienced.

The use of carcass recoveries and normal recoveries will not lead to serious bias if the number of carcass recoveries is small, or if carcasses do not remain in the stream long after death. If carcasses can remain in the stream for long periods after death, estimates of survival will be inflated because carcass recoveries will be treated as if the fish had survived to the time of carcass recovery. In this experiment, the number of carcass recoveries was small at all sampling occasions except the last. The last 3 wk of dead pitch when no live fish were observed were pooled into one last sampling occasion where parameters of survival and capture are confounded, not estimated in any case, and the number of entries was assumed to be zero.

We assumed that recruitment between sampling occasions occurred uniformly. Since the weekly survival rates were over 50%, the choice of distribution for the recruitment was not critical (Table 3) and we used equation (2) to estimate the escapement.

5.2. 1989 Escapement Estimates

The run to the Chase River in 1989 consisted of two pulses of fish. The first pulse began to arrive around the last week of September (week 1) and peaked with the first heavy rains in mid-October. A second smaller pulse arrived in mid-November.

The summary statistics for this experiment (in Jolly–Seber notation) are as follows. Only carcasses were recovered in weeks 10, 11, and 12; data for these have been grouped together.

Week	Number of captures n_i	Number of marks m_i	Losses on capture	Released after marking R_i	Subsequently recaptured r_i	Seen before i, not at i, and after i z_i
1	5	0	0	5	1	0
2	80	0	0	80	27	1
3	35	12	1	34	19	16
4	97	14	25	72	31	21
5	84	25	6	78	34	27
6	67	39	11	56	14	22
7	51	28	14	37	5	8
8	9	6	9	0	0	7
9	30	0	1	29	7	7
10+	18	14	18	0	0	0

Goodness-of-fit tests (Pollock et al. 1990) failed to detect any serious evidence of failure of the assumptions of equal catchability or survival, except for some evidence of differential mortality between previously marked and newly marked fish. Previously marked animals may have entered the river earlier, and hence were more likely to be spawning or have finished spawning.

More serious problems exist, however. In weeks 2 and 9, no previously marked fish were captured. This implies that the MLEs of abundance (and consequently of births) are infinite.

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TABLE 8. Estimates and estimated SEs computed using three methods for the 1989 Chase River study (ne = nonestimable).

Sample occasion	Unconstrained MLE		Less biased estimators		Constrained MLE	
	Estimate	Estimated SE	Estimate	Estimated SE	Estimate	Estimated SE[a]
Recapture rates (p_i)						
1 & 2	ne		ne		ne	
3	0.30	0.086	0.30	0.086	0.30	0.086
4	0.22	0.064	0.23	0.065	0.25	0.037
5	0.29	0.063	0.29	0.063	0.33	0.050
6	0.31	0.075	0.32	0.077	0.29	0.071
7	0.32	0.126	0.36	0.132	0.32	0.126
8 & 9	0.17	0.092	0.19	0.098	0.46	0.118
10+	ne		ne		ne	
Survival rates (ϕ_i)						
1 & 2	0.48	0.093	0.47	0.092	0.48	0.093
3	1.00	0.195	1.00	0.195	0.98	0.181
4	0.72	0.124	0.72	0.123	0.69	0.114
5	0.91	0.203	0.88	0.197	0.93	0.211
6	0.61	0.247	0.56	0.227	0.61	0.247
7	0.36	0.190	0.37	0.191	0.23	0.106
8 & 9						
Population size (N_i) *with SE conditional upon N, not* N_i						
1 & 2	ne		ne		ne	
3	118.5	31.6	110.8	29.0	118.5	29.9
4	434.9	119.8	404.5	110.1	392.3	47.4
5	292.1	59.3	281.0	56.4	254.1	30.7
6	218.2	50.1	208.4	47.5	231.5	51.8
7	158.8	60.6	141.1	52.5	158.8	59.5
8 & 9	227.5	117.9	184.3	93.7	84.6	19.2
10+	ne		ne		ne	
Net births (B_i) *with SE conditional upon N, not* B_i						
1 & 2	ne		ne		ne	
3	317.2	121.3	294.9	102.8	277.3	43.7
4	−3.0	88.0	9.0	78.6	0.0	0.0
5	−41.5	45.7	−34.2	41.5	0.0	0.0
6	33.4	26.1	29.8	21.8	25.3	23.1
7	174.8	108.9	137.5	81.9	51.5	13.9
8 & 9	ne		ne		ne	
Gross births (B_i^*)						
0 & 1 & 2	167.6	43.7	157.7	40.5	167.6	41.6
3	316.8	102.4	295.1	94.3	280.4	43.0
4	−3.5	100.0	10.6	92.2	0.0	0.0
5	−43.5	46.9	−36.4	44.2	0.0	0.0
6	42.4	29.1	39.2	26.3	32.2	28.0
7	277.8	145.9	217.6	114.8	98.5	29.4
8 & 9	ne		ne		ne	
Escapement	757.6	162.4	683.7	131.4	578.7	49.7 64.7[b]

[a]When estimates of the parameters are constrained to lie on the bounds of the parameter space, the estimated SE is reported as 0.00
[b]This estimate of the SE is obtained by evaluating the asymptotic formula using the constrained MLE.

The bias-adjusted estimates are not much better. Consequently, sample occasions 1 and 2 and 8 and 9 were pooled. Animals seen at least once in a pooled period were recorded as being seen once. This led to the revised summary statistics:

Week	Number of captures n_i	Number of marks m_i	Losses on capture	Released after marking R_i	Subsequently recaptured r_i	Seen before i, not at i, and after i z_i
1 and 2	85	0	0	85	28	0
3	35	12	1	34	19	16
4	97	14	25	72	31	21
5	84	25	6	78	34	27
6	67	39	11	56	14	22
7	51	28	14	37	5	8
8 and 9	39	6	10	29	7	7
10+	18	14	18	0	0	0

These summary statistics were used to compute the unconstrained MLEs, the unconstrained less-biased estimates, and the constrained MLEs. The estimates (Table 8) confirmed the two pulses of fish, one early and the second late in the season. The fish had a survival rate over $70\% \cdot wk^{-1}$. Note that the pooled estimates for weeks 1 and 2, and 8 and 9 refer to the 2-wk periods. The high survival rate implies that estimates of total recruitment between sampling occasions are not very sensitive to the assumed distribution of recruitment within the interval (Table 3). The estimated recapture rate (Table 8) appears to have been roughly constant at about $30\% \cdot wk^{-1}$ except at the end of the season when mainly carcasses were recovered. The three estimates of the escapement have a wide range, the unconstrained MLE of 758 being the highest and the constrained MLE of 579 being the lowest. These differences are largely artifacts of this particular data set caused by differences in confounded parameters at the end of the experiment. For example, using the estimators from Table 2, we find that

$$\phi_{8\&9}\tilde{p}_{10} = r_{8\&9}/R_{8\&9} = 7/29 = 0.24$$

$$B_{8\&9}\tilde{}/\phi_{8\&9} = \frac{n_{10}}{\phi_{8\&9}p_{10}} - (\tilde{N}_{8\&9} - n_{8\&9} + R_{8\&9})$$

$$= \frac{18}{0.24} - (184.3 - 39 + 29) = -99.3.$$

This estimate is out-of-range. If this out-of-range estimate is added to the escapement estimate, the result is now much closer to the estimate using the constrained MLEs. The contrained MLE ensures that all estimates are within the range of the parameter space, i.e., constrains the last term to be nonnegative. The high negative sampling correlation between neighboring estimates of births implies that raising the estimate of the last "confounded parameter" to zero must decrease neighboring estimates. Consequently, we believe that the constrained MLE is a more realistic estimate of the escapement. If no correction for mortality of entering fish is made, the estimate of escapement found by adding estimates of $N_2, B_2, \ldots,$ and B_{s-2} is about 470 fish, a presumed undercount of almost 20%.

The estimated SEs of the unconstrained MLE and unconstrained less-biased estimator are similar and both are much larger than the estimated SE for the constrained MLE. A large part of the difference is again an artifact of the data and is caused by the out-of-range confounded parameter estimate. A small part of the difference is due to the numerical method used to constrain parameter estimates which reports the estimated SEs of those constrained estimates as zero. This is seen when

the SE of the constrained MLE is evaluated using the asymptotic formulae; this leads to a slight increase in the estimated SE. A 95% confidence interval for the escapement is estimated to be $578.7 \pm 1.96 (64.7)$ or from 452 to 705 fish.

The constrained MLE was also computed ignoring carcass recoveries. We obtained an estimated escapement of 638 with an estimated SE of 70. A nonparametric bootstrap of the constrained MLE gave an estimated mean escapement of 630 with an estimated SE of 47. The estimated 95% confidence interval was found to be from 559 to 727. The nonsymmetric bootstrap confidence interval would seem to indicate that the distribution of the constrained MLE is skewed, a likely result of the problems identified in the data. Both estimates are similar to our result.

Finally, a pooled Petersen estimate was computed by treating the initial tagging of a fish over all sampling occasions as the "first" sample and carcass recoveries over all weeks as the "second" sample. We obtained an estimated escapement of 524 with an estimated SE of 43. However, as discussed by Seber (1982, p. 437), this "pooled" estimate will be consistent if a constant proportion of the carcasses is sampled and/or if a constant proportion of the population is marked. After the fact, this may have occurred because the estimates of p_i (Table 8) are very similar.

These data had numerous problems that made their analysis difficult. First, there were no marks recovered in two of the sample periods which led to infinite estimates of escapement. This problem was resolved by pooling adjacent sample periods. The recruitment in the last sample period was still not estimable, but the negative estimate of the confounded parameter had a serious effect on the closed-form MLE and less-biased estimator. For this data set, the constrained MLE was the most appropriate estimate. Similar effects were seen on the estimated precisions. Again, the asymptotic formula evaluated at the constrained MLEs was the most appropriate. Despite these problems, the estimate of escapement was quite precise with a CV of about 11%.

5.3. 1990 Escapement Estimates

The approach was repeated in the fall of 1990 and gave data with fewer problems than the 1989 experiment. This example will illustrate that under these conditions, all methods will give similar results.

The returning run of coho salmon in 1990 consisted of three pulses of fish. The first group arrived in late September (week 1), and numbers of fish entering the river peaked by mid-October. A second pulse arrived in early November, and a smaller, late pulse arrived at the end of the first week of December. The field data gave rise to the following summary statistics:

Week	Number of captures n_i	Number of marks m_i	Losses on capture	Released after marking R_i	Subsequently recaptured r_i	Seen before i, not at i, and after i z_i
1	3	0	0	3	1	0
2	10	1	0	10	4	0
3	16	3	0	16	5	1
4	124	3	3	121	36	3
5	82	30	3	79	13	9
6	125	12	20	105	22	10
7	117	18	36	81	16	14
8	51	16	12	39	7	14
9	63	18	31	32	1	3
10+	14	4	14	0	0	0

Goodness of fit tests (Pollock et al. 1990) failed to detect

TABLE 9. Population estimates and estimated SEs computed using three methods for 1990 Chase River study (ne = nonestimable).

Sample occasion	Unconstrained MLE		Less biased estimators		Constrained MLE	
	Estimate	Estimated SE	Estimate	Estimated SE	Estimate	Estimated SE[a]
Recapture rates (p_i)						
1	ne		ne		ne	
2	1.00	0.000	1.00	0.000	1.000	0.001
3	0.48	0.303	0.51	0.303	0.48	0.303
4	0.23	0.146	0.23	0.148	0.34	0.052
5	0.35	0.105	0.37	0.106	0.35	0.103
6	0.20	0.075	0.21	0.077	0.20	0.075
7	0.20	0.068	0.21	0.070	0.22	0.053
8	0.17	0.071	0.19	0.076	0.16	0.066
9	0.16	0.155	0.27	0.228	0.16	0.155
10+	ne		ne		ne	
Survival rates (ϕ_i)						
1	0.33	0.272	0.33	0.272	0.33	0.272
2	0.62	0.329	0.58	0.313	0.62	0.329
3	0.68	0.303	0.68	0.304	0.58	0.225
4	0.65	0.172	0.62	0.166	0.65	0.175
5	0.48	0.147	0.44	0.147	0.45	0.147
6	0.58	0.169	0.57	0.165	0.56	0.151
7	0.62	0.239	0.58	0.223	0.63	0.242
8	0.97	0.972	0.62	0.600	0.97	0.971
9	ne		ne		ne	
Population size (N_i) with SE conditional upon N, not N_i						
1	ne		ne		ne	
2	10.0	3.2	5.5	est < 0	10.0	0.0
3	33.1	20.6	24.8	13.3	33.1	19.8
4	540.8	343.1	402.9	242.5	363.6	48.5
5	231.5	66.6	218.0	62.1	235.6	66.9
6	622.2	228.3	563.0	204.5	622.2	227.4
7	577.7	188.9	531.2	172.5	532.2	120.6
8	299.6	119.6	263.1	104.2	312.9	119.8
9	399.0	389.2	227.4	213.0	398.9	388.7
10+	ne		ne		ne	
Net births (B_i) with SE conditional on N, not B_i						
1	ne		ne		ne	
2	26.9	21.3	21.6	13.0	26.9	17.6
3	518.2	368.2	385.9	243.4	344.4	47.6
4	−116.0	218.3	−30.7	150.1	0.0	0.0
5	520.1	221.6	467.2	187.6	518.2	208.1
6	227.3	176.0	223.8	151.9	194.8	128.6
7	−35.6	103.3	−23.7	86.4	0.0	0.0
8	118.8	150.5	71.9	84.4	105.8	135.6
9	ne		ne		ne	
Gross births (B_i^*)						
+1	16.5	7.5	9.1	est < 0	16.5	3.7
2	33.8	19.3	27.9	15.5	33.8	19.3
3	624.0	356.0	463.6	258.6	446.0	89.7
4	−143.1	271.9	−38.6	189.6	0.0	0.0
5	757.4	259.4	681.4	233.3	754.8	258.3
6	294.3	201.8	293.5	183.3	256.6	164.8
7	−44.9	128.2	−30.7	112.6	0.0	0.0
8	120.3	113.4	90.5	80.8	107.2	102.8
9	ne		ne		ne	
Escapement	1658.3	273.0	1496.7	236.7	1614.8	193.0 238.1[b]

[a]When estimates of the parameters are constrained to lie on the bounds of the parameters space, the estimated SE is reported as 0.00
[b]This estimate of the SE is obtained by evaluating the asymptotic formula using the constrained MLE.

any violation of assumptions. The numbers of recoveries were marginally adequate at the start and end of the experiment, but no pooling was done, since the number of births at the start and end was small and any bias resulting from the small counts was felt to be acceptable.

The resulting estimates (Table 9) confirm three pulses of recruitment. Survival rates in all weeks except the first were approximately $60\% \cdot wk^{-1}$, which implies that the choice for the assumed distribution of recruitment between sampling occasions was relatively unimportant (Table 3). The small number of new fish in week 1 implies that any biases from using an incorrect recruitment distribution will be small. Note that the high survival rate in week 8 resulted from treating carcass recoveries in week 9 as losses on capture. Recapture rates appeared to be roughly constant over time. Escapement estimates are more similar than those calculated from the 1989 results, since there were fewer problems with out-or-range estimates of either the identifiable or confounded parameters. The 1990 estimated escapement ranged from 1497 from the less-biased estimator to 1658 for the unconstrained MLE. The estimate of the SE of the constrained MLE is slightly smaller than the estimated SEs of the other methods due to the constraints of the recapture rate at time 2, and the constraints to keep the estimated number of births admissible. For these data, either the unconstrained less-biased estimate or the constrained MLE could be used as a good estimate of the escapement, and it is felt that the estimates of SE are reliable. Using the constrained MLEs, a 95% confidence interval for the escapement is found to be 1615 ± 1.96 (238.1) or between 1148 and 2081 fish. In 1990, more fish were marked than in 1989, but fewer recaptures occurred giving less precise estimates than the previous year (CV of about 15%).

The constrained MLE of escapement, ignoring carcass recoveries, was 1611 with an estimated SE of 312, very similar to the above results. The increase in the estimated SE is expected because information is lost by ignoring carcass recoveries. A nonparametric bootstrap applied to the constrained MLE gave an estimate for the escapement of 1650 fish with an estimated SE of 188 fish and a 95% confidence interval of 1359–2132 fish. The results are consistent with the initial analysis. Finally, a Petersen estimate computed as for the 1989 data gave an estimated escapement of 1738 fish with an estimated SE of 260 fish. Given the imprecise estimates of the capture rates (Table 9), it again may be possible that initial capture rates are constant over time.

6. Summary

A reluctance by fishery workers to use open-population capture–recapture methods to estimate escapement is due, in part, to uncertainty of how to account for fish that enter and die before a sampling occasion and how to estimate recruitment at the start and end of the experiment. In this paper, we demonstrated that simple modifications to the Jolly–Seber estimates can yield useful estimates of escapement (equation (2)). These modifications depend upon the assumed distribution of recruitment between sampling occasions. If survival between sampling occasions is low, the adjustment factors vary considerably; if the survival rates are high ($\geq 50\%$), then the choice of recruitment distribution is not critical. This implies that an experiment should be designed to ensure high survival between sampling occasions. The study should also be planned so that few entries occur outside their temporal bounds.

As well, uncertainty existed about a number of technical problems that often occur in a particular dataset (e.g., the 1989 Chase data). The closed-form MLEs are biased and the bias is greatest when the sample sizes are small. The less-biased estimators are an improvement but only work well when m_i and r_i are at least 10. Consequently, when data are sparse, we recommend the pooling of adjacent sample occasions. The practice of simply censoring out-of-range estimates is to be avoided because this leads to a positive bias in the estimates of recruitment and of the escapement. Either negative estimates of births should be used as given or numerical methods should be used to maximize the likelihood subject to the boundary constraints (Appendix C). The latter is particularly important if estimates of the confounded parameters at the end of the experiment are out of range. The large-sample closed-form estimates of SE provide good estimates of the precision of the escapement when the sample sizes are reasonably large. They are suspect when some estimates are out of range regardless of sample size. Numerical optimization methods typically report SEs of constrained parameters as zero which leads to under-estimates of the SEs when the inverse of the information matrix is used to estimate precision. We recommend that the asymptotic formulae be evaluated at the constrained MLE. Finally, the estimates of the escapement are approximately normally distributed due to an application of the Central Limit Theorem and the large sample confidence intervals are expected to perform well.

It is important that the usual assumptions for capture–recapture studies be valid for a particular experiment, in particular, the assumptions of homogeneity of survival and capture rates. Good discussions of the effects of violations of the assumptions of capture–recapture experiments and of planning capture–recapture experiments can be found in Sykes and Botsford (1986) and Pollock et al. (1990, sections 4.6 and 8.7).

The precision of the escapement estimates depends upon several aspects of the study. In general, precision will increase as the number of marked animals recovered increases. Higher recoveries of marked animals may be obtained by increasing the capture rates at each sampling occasion (not necessarily possible) or by increasing the number of sampling occasions relative to the age of the animal (e.g., more frequent sampling). Because of the complexity of the estimation process, it is not possible to give rules of thumb for sample sizes. We recommend that the experimenter use simulations to generate sets of "dummy data" and then analyze these "data" to determine if precision is adequate. This method may also be used to investigate the effects of varying effort and other aspects of the study upon precision.

7. Software

Computer software to find the constrained MLE is available from the first author. It is written in FORTRAN 77 and requires subroutines to invert matrices commonly found in numerical libraries. It is also integrated into POPAN (Arnason and Baniuk 1978).

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Appendix A. Obtaining Adjustment Factors

Let B_i^* be the total recruitment and ϕ_i be the survival rate between two sampling periods. Without loss of generality, we may take the time interval between the two sampling points as being [0,1].

A uniform mortality rate in the interval implies that the probability that an animal that enters the population at a time t will survive to the next sampling period at time 1 is $\phi^{(1-t)}$.

Suppose that recruitment follows a probability distribution $f(t)$. Then the net recruitment can be computed as

$$B_i = \int_0^1 B_i^* f(t) \, \phi^{(1-t)} \, dt.$$

This equation is then inverted to solve for B_i^* in terms of B_i.

For a uniform recruitment, $f(t) = 1$. For the left triangular distribution, $f(t) = 2(1 - t)$. For the right triangular distribution, $f(t) = 2t$.

Appendix B. Approximating the Bias Caused by Censoring Negative Estimates

Suppose that an estimator $\hat{\theta}$ has an approximate normal distribution with a mean of θ and a standard deviation of σ and let $\hat{\theta}' = \max(\hat{\theta},0)$ be the censored estimator where estimates below 0 are replaced by 0. Then the expected value $E[\hat{\theta}'] = \sigma/\sqrt{2\pi} \exp(-0.5(\theta/\sigma)^2) + \theta(1-\Phi-\theta/\sigma))$ where $\Phi(\cdot)$ is the standard normal cumulative distribution. The extent of the potential bias is shown in the following table:

θ/σ	$E[\hat{\theta}']/\theta$
0.10	4.51
0.20	2.53
0.40	1.58
0.60	1.28
0.80	1.15
1.00	1.08

For example, suppose that the true number of recruits is around 40 and that the SE of the estimate is about 100. Now, $\theta/\sigma = 0.40$ and the mean of the censored estimate of births will be $1.58 \cdot 40 = 63.2$ for a positive bias of $63.2 - 40 = 23.2$ animals.

Appendix C. Likelihood Equation

Under the usual assumptions for capture–recapture studies (Pollock et al. 1990), the likelihood function can be partitioned into two components:

$$L = L_1 \times L_2$$

$$= P(\{u_i\}) \times P(\text{subsequent recaptures or losses} \mid \{u_i\}).$$

Seber (1982, p. 198) modeled L_1 conditional upon the number of animals alive in the population at sampling occasion i. The actual recruitment process between sampling occasion is not modeled. Consequently, it is difficult to impose a probability model that describes the recruitment process or to impose constraints to force all estimates of births to be nonnegative.

We follow, instead, the approach of Crosbie and Manly (1985) who conditioned upon the escapement and model L_1, the number of animals that enter the system between sampling occasions, as a multinomial distribution drawn from the escapement. Additionally, we follow the approach of Burnham (1991) who showed that L_2 can be written as the product of binomial distributions. The likelihood function is then the product of the following terms:

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	Term	Distribution
(C.1)	$P(\{u_i; i = 1,\ldots,s\}\|N)$	Multinomial$(N; \{\psi_i^* p_i; i = 1,\ldots,s\})$
	$P(R_1\|n_1)$	Binomial$(n_1; \nu_1)$
	$P(r_1\|R_1)$	Binomial$(R_1; \lambda_1)$
	$P(m_2\|T_2)$	Binomial$(T_2; \tau_2)$
	$P(R_2\|n_1)$	Binomial$(n_2; \nu_2)$
	$P(r_2\|R_2)$	Binomial$(R_2; \lambda_2)$
(C.2)	$P(m_3\|T_3)$	Binomial$(T_3; \tau_3)$
	$\cdot$	$\cdot$
	$\cdot$	$\cdot$
	$\cdot$	$\cdot$
	$P(m_{s-1}\|T_{s-1})$	Binomial$(T_{s-1}; \tau_{s-1})$
	$P(R_{s-1}\|n_{s-1})$	Binomial$(n_{s-1}; \nu_{s-1})$
	$P(r_{s-1}\|R_{s-1})$	Binomial$(R_{s-1}; \lambda_{s-1})$

where b_i^* is the probability than an animal enters the system between sampling occasion i and $i + 1$, b_0^* refers to entrance before the first sampling occasion, $\psi_1 = b_0^*$, $\psi_{i+1} = \psi_i(1 - p_i)\phi_i + b_i^* h(\phi_{i-1})$, $h(\phi_{i-1})$ is the probability that an animal that enters between sampling occasion $i - 1$ and i survives to the next sampling occasion (for the case of uniform entry and constant mortality, $h(\phi_{i-1}) = (\phi_{i-1} - 1)/\log(\phi_{i-1})$), ν_i is the probability of a loss of capture at sampling time i, $i = 1,\ldots,s$, $\lambda_i = \phi_i(p_{i+1} + (1 - p_{i+1})\lambda_{i+1})$, $i = 1,\ldots, s - 1$, $\lambda_s = 0$, $\tau_i = p_i/(p_i + (1 - p_i)\lambda_i)$, $i = 1,\ldots,s$, $T_1 = R_1$, and $T_{i+1} = T_i - m_i + r_i = m_{i+1} + z_{i+1}$, $i = 2,\ldots,s$. There are $3s$ parameters, $\{\phi_i; i = 1,\ldots,s - 1\}$, $\{p_i; i = 1,\ldots,s\}$, and $\{b_i^*; i = 0,\ldots,s - 1\}$, and N subject to the constraint that $\Sigma b_i^* = 1$. This likelihood differs from Crosbie and Manly (1985) in that we allow losses on capture and express the second component, L_2 in a more convenient form. Losses on capture are assumed to be at random from animals captured and so are noninformative about $\{\phi_i\}$, $\{p_i\}$, $\{b_i^*\}$, or N. As in the Jolly–Seber model, not all parameters are individually identifiable. As in Crosbie and Manly (1985), MLEs obtained from this likelihood are identical to those from the Jolly–Seber model presented in Table 2 and also give rise to our equation (1). As shown by Burnham (1991), this representation is particularly convenient for deriving large-sample covariances. The large-sample variances and covariances for $\{\hat{\phi}_i\}$ and $\{\hat{p}_i\}$ are also the same as from the Jolly–Seber model, but the covariance formulae for $\{\hat{B}_i\}$ differ slightly, since we condition upon the escapement (N) rather than on the actual births ($\{B_i\}$). However, by using the formulae on conditional variances presented in Seber (1982, p. 9), identical covariances to those presented in Pollock et al. (1990) can be obtained from our results if suitable conditioning is performed.

This likelihood is not fully convenient for numerical optimization, since the parameter N appears in a factorial term. We further partition the component (C.1) of the likelihood into two parts:

(C.1a) $= P(u_.\|N)$ which is binomial$(N; \Sigma \psi_i^* p_i)$

(C.1b) $\times P(\{u_i\} \| u_.)$ which is multinomial$(u_.; \psi_i^* p_i / \Sigma \psi_i^* p_i)$

where $u_. = \Sigma u_i$ is the total number of unmarked animals seen. Now, the parameter N appears only in (C.1a). As shown by Sanathanan (1977), the conditional maximum likelihood estimates found by maximizing (C.1b) $\times$ (C.2) to find conditional MLEs for $\{\phi_i\}$, $\{p_i\}$, and $\{b_i^*\}$ and then using these conditional

MLEs in (C.1a) to estimate N are asymptotically equivalent to the unconditional MLEs obtained by maximizing (C.1a) $\times$ (C.1b) $\times$ (C.2). Numerical optimization of the conditional MLE is relatively straightforward because no parameters appear in factorial term, the score functions (the first partial derivatives) are equivalent to those obtained from weighted least squares, and the expected information matrix can be obtained from the score functions. Good, stable, numerical methods to solve these type of equations are available (e.g., Press et al. 1989). By using the log-odds of the parameters, i.e., $\log(\theta/(1 - \theta))$, and the method of Lagrange multipliers, it is not difficult to constrain the estimates within the bounds of the parameter space, i.e., $0 \leqslant \{\hat{\phi}_i\}$, $\{\hat{p}_i\}$, and $\{b_i^*\} \leqslant 1$.

Appendix D. Asymptotic Variances and Covariances of Birth and Survival Terms

These formulae appear to differ from Crosbie and Manly (1985) because they used a different notation and did not consider losses on capture, and they differ from Pollock et al. (1990) because these are conditional upon the escapement rather than the actual number of births between the sampling occasions. All formulae are evaluated at the expected value of the statistics. When estimating the variances and covariances the actual value of the statistics is used unless constrained MLEs are used, in which case the expected value of the statistics should be estimated using the estimated parameters rather than from the observed values in the experiment.

$$\text{cov}\{\hat{N}_2, \hat{N}_2\} = N_2(N_2 - n_2)\frac{M_2 - m_2 + R_2}{M_2}\left(\frac{1}{r_1} - \frac{1}{R_2}\right)$$
$$+ \frac{N_2 - M_2}{N_2 m_2} + N_2\frac{N - N_2}{N}$$

$$\text{cov}\{\hat{N}_2, \hat{B}_2\} = N_2\phi_2(1 - p_2)\left(\frac{1}{r_2} - \frac{1}{R_2}\right)(N_2 - n_2 + R_2)$$
$$+ N_2\phi_2 - \frac{N_2 N_3}{N} - \text{cov}\{\hat{N}_2, \hat{N}_2\}\phi_2$$

$$\text{cov}\{\hat{N}_2, \hat{B}_j\} = \frac{-N_2 N_{j+1}}{N} + \frac{N_2 N_j \phi_j}{N} \quad j = 3,\ldots, s - 2$$

$$\text{cov}\{\hat{B}_i, \hat{B}_i\} = B_i^2(M_{i+1} - m_{i+1})\frac{M_{i+1} - m_{i+1} + R_{i+1}}{M_{i+1}^2}$$
$$\times \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}}\right)$$
$$+ \frac{(M_i - m_i)}{(M_i - m_i + R_i)}\frac{[\phi_i R_i(N_i - M_i)]^2}{M_i^2}$$
$$\times \left(\frac{1}{r_i} - \frac{1}{R_i}\right)$$
$$+ \frac{(N_i - n_i)(N_{i+1} - B_i)(N_i - M_i)(1 - \phi_i)}{N_i(M_i - m_i + R_i)}$$

$$+ \frac{(N_{i+1} - n_{i+1})(N_{i+1} - M_{i+1})}{m_{i+1}}$$

$$+ \frac{\phi_i^2 (N_i - n_i)(N_i - M_i)}{m_i}$$

$$+ \frac{B_i(N - B_i)}{N} \qquad i = 2, \ldots, s - 2$$

$$\text{cov}\{\hat{B}_i, \hat{B}_{i+1}\} = \frac{-\phi_{i+1}(N_{i+1} - n_{i+1})(N_{i+1} - M_{i+1})}{N_{i+1}}$$

$$\times \left\{ \frac{B_i R_{i+1}}{M_{i+1}} \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right) + \frac{N_{i+1}}{m_{i+1}} \right\} - \frac{B_i B_{i+1}}{N}$$

$$i = 2, \ldots, s - 3$$

$$\text{cov}\{\hat{B}_i, \hat{B}_j\} = \frac{-B_i B_j}{N} \qquad i = 2, \ldots, s = 4, j > i + 1$$

$$\text{cov}\{\hat{\phi}_i, \hat{\phi}_i\}$$

$$= \phi_i^2 \left[\frac{(M_{i+1} - m_{i+1})(M_{i+1} - m_{i+1} + R_{i+1})}{M_{i+1}^2} \right.$$

$$\times \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right) + \frac{(M_i - m_i)}{(M_i - m_i + R_i)} \left(\frac{1}{r_i} - \frac{1}{R_i} \right)$$

$$\left. + \frac{(1 - \phi_i)}{M_{i+1}} \right] i = 1, \ldots, s - 2$$

$$\text{cov}\{\hat{\phi}_i, \hat{\phi}_{i+1}\} = -\phi_i \phi_{i+1} \frac{(M_{i+1} - m_{i+1})}{M_{i+1}} \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right)$$

$$i = 1, \ldots, s - 3$$

$$\text{cov}\{\hat{N}_2, \hat{\phi}_1\} = N_2 \phi_1 (1 - p_2)^2$$

$$\times \left[\frac{1}{r_2} - \frac{1}{R_2} + \frac{\left(1 - \frac{r_2}{R_2} \right)}{(r_1 - m_2)} \left(1 - \frac{1}{N_2} \right) \right]$$

$$\text{cov}\{\hat{N}_2, \hat{\phi}_2\} = -N_2 \phi_2 (1 - p_2) \left(\frac{1}{r_2} - \frac{1}{R_2} \right)$$

$$\text{cov}\{\hat{B}_i, \hat{\phi}_{i-1}\} = -\phi_{i-1} \phi_i (N_i - n_i) \left(1 - \frac{m_i}{n_i} \right)$$

$$\times \frac{(M_i - m_i + R_i)}{M_i} \left(\frac{1}{r_i} - \frac{1}{R_i} \right) \qquad i = 2, \ldots, s - 2$$

$$\text{cov}\{\hat{B}_i, \hat{\phi}_i\} = \phi_i \frac{(N_{i+1} - n_{i+1})}{N_{i+1}} \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right)$$

$$\times \left[B_i \frac{(M_{i+1} - m_{i+1} + R_{i+1})}{M_{i+1}} + \phi_{i+2}(N_i - n_i) \right.$$

$$\left. \times \left(1 - \frac{m_i}{n_i} \right) \frac{r_{i+1}}{(z_{i+1} + m_{i+1})} \right] \qquad i = 2, \ldots, s - 2$$

$$\text{cov}\{\hat{B}_i, \hat{\phi}_{i+1}\} = -\phi_{i+1}(N_{i+1} - n_{i+1})$$

$$\times \left(1 - \frac{m_{i+1}}{n_{i+1}} \right) \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right) \qquad i = 2, \ldots, s - 3.$$

The variances and covariances of the estimated adjusted number of births are obtained by a Taylor-series expansion of the net births times the adjustment factor chosen. The variance of the estimated escapement is then the sum of the variances and covariances of the adjusted estimates.

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