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Accounting for Tag Loss and Its Uncertainty in a Mark-Recapture Study with a Mixture of Single and Double Tags

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Abstract

Unless accounted for in the estimation, tag loss will cause mark–recapture methods to overestimate the true abundance of a closed population and to underestimate the associated uncertainty. Current methods of accounting for tag loss require all marked individuals to be double-tagged. We present a new model that fully accounts for tag loss and allows for the use of a mixture of single- and double-tagged individuals, thus simplifying implementation in the field. Treating abundance, tag loss rate, and capture probabilities as free parameters, we estimated those parameters and their uncertainty by using maximum likelihood. Whereas existing methods assume that a double-tagged animal does not lose both tags, the new model allows the animal to lose both tags. The new model's performance was assessed and compared with that of other estimators (modified Petersen and Seber–Felton) via simulation. As expected, estimates from the new model were less biased and more precise than estimates from the other models. The model was used to estimate the abundance of the kokanee *Oncorhynchus nerka* population in the Metolius River, Oregon, during 2007. Abundance was estimated at 102,970 fish ($\widehat{SE} = 8,930$), tag loss rate was estimated at 0.27 ($\widehat{SE} = 0.05$), the capture probability for the first sample (tagging) was 0.03 ($\widehat{SE} = 0.00$), and the capture probability for the second sample (recovery) was 0.11 ($\widehat{SE} = 0.01$). The new model uses all of the information from single- and double-tag data, provides unbiased abundance estimates in the presence of tag loss for a closed population, and has less-stringent field requirements that make it easier to employ than other methods.

Mark–recapture is often used to estimate the abundance of fish populations. In the single-recapture design, a random sample is taken in which the individuals are marked and then returned to the population. Later, the second sample is taken. When the population is closed to emigration and immigration during the period of the study, the proportion of marked animals recaptured in the second sample and the number of animals orig-inally marked can be used to estimate the population abundance by methods such as Petersen estimators (Seber 1982; Everhart et al. 1975; Otis et al. 1978; Seber and Felton 1981). If marks are lost between sampling events and this loss is not accounted for in the estimation, the resulting estimates of abundance and its uncertainty will be biased, and the magnitude of the biases will be proportional to the rate of tag or mark loss (Robson

and Regier 1966; Seber 1982; Arnason and Mills 1981; Seber and Felton 1981; McDonald et al. 2003; Cowen and Schwarz 2006).

Fisheries research employs a wide variety of marking or tagging systems (see reviews by Parker et al. 1990 and Nielsen 1992), most of which are susceptible to some level of non-detection or loss. The rate of tag loss can be substantial even over relatively short time periods (Carline and Brynildson 1972; Ebener and Copes 1982; Parker et al. 1990; McAllister et al. 1992; Muoneke 1992; Nielsen 1992; Guy et al. 1996). Plastic T-bar anchor tags, commonly used because of their low cost and ease of application, have had documented tag loss rates of 11.1–18.9% per year for lake whitefish *Coregonus clupeaformis* (Ebener and Copes 1982) and 24.8% per year for white bass *Morone chrysops* (Muoneke 1992).

Early work showed how tag loss rate could be estimated by using a double-tagging design; however, this method assumed that a double-tagged fish would not lose both tags, and the method did not account for uncertainty in the estimated rate of tag loss (Gulland 1963). The Petersen estimators of abundance (N) and its variance ($\text{var}[\hat{N}]$) have been modified to partially account for tag loss under the condition that all marked fish receive two independent marks (Seber 1982; Seber and Felton 1981). However, the modified estimators do not account for how the uncertainty from estimating tag loss rate affects the uncertainty of the abundance estimate. Furthermore, the abundance estimate can suffer large bias at moderate rates of tag loss (Seber and Felton 1981; Seber 1982). Subsequently, these estimators have not been widely employed, especially since double-tagging is commonly only applied to a subset of the marked fish.

More importantly, it should be noted that these estimators (Chapman 1951; Gulland 1963; Seber 1982; Seber and Felton 1981) cannot be applied to a mixture of single- and double-tagged fish. Cowen and Schwarz (2006) developed a model to account for tag loss and its uncertainty, but those authors discounted the possibility that a double-tagged animal could lose both tags. Cowen and Schwarz (2006) also assumed an open population subjected to multiple recapture periods, and thus their model is not applicable to analysis of common closed-population studies, such as those used to estimate spawning abundance of anadromous stocks.

Since the work of Seber and Felton (1981), computational and software advances have greatly increased the researcher's ability to fit nonlinear statistical models. Specifically, modern numerical optimization methods allow maximum likelihood estimation to be conducted on a closed-population model that explicitly incorporates tag loss. As we demonstrate, this approach allows for a direct estimate of tag loss rate while also accounting for its estimation not only in abundance and capture probabilities but also in their associated uncertainty, thereby overcoming all of the constraints associated with the modified Peterson estimators developed by Seber and Felton (1981).

We present a closed-population mark–recapture model for a two-sample design (i.e., one tagging event and one recapture event) incorporating the use of both single- and double-tagged fish and accounting for the random loss of one or both tags in the abundance estimation. Simulation was used to assess bias and precision in the resulting estimates and to compare the model's performance with that of the modified Peterson (Chapman 1951) and Seber–Felton (Seber and Felton 1981; Seber 1982) estimators. By way of actual example, the model was applied to estimate tag loss, abundance, and capture probabilities from a 2007 study of adult kokanee *Oncorhynchus nerka* in the Metolius River, Oregon, where a mixture of single and double tags was used.

METHODS

Our model assumes that a subset of the marked fish receive two tags (i.e., are double-tagged). We consider two scenarios for the double-tagged fish: (1) tagging scenario 1, in which the double-tagged fish receive two tags of a type that is identical to but differentiable (e.g., by color) from the tag used on the single-tagged fish; and (2) tagging scenario 2, in which the second tag is a permanent tag or mark (e.g., a fin clip or opercular punch). The model assumes that all nonpermanent tags are susceptible to loss, that the probability of a tag being lost is constant across all tags and all tagged fish, and that the loss of a specific tag on a fish occurs independently of the loss of any other tag on that fish.

Fish are randomly caught in the first sample for purposes of tagging and then are released. Later, the second random sample of fish is caught for the recovery of tagged fish (Figures 1, 2). The model is a product of independent binomial and multinomial functions but with different multinomial cell probabilities depending on tag type.

Tagging Scenario 1: Two Identical and Independent Nonpermanent Tags

Binomial likelihood.—The number of fish in the first sample (n_1) is assumed to follow a binomial distribution with parameters N and p_1 (Figure 1; i.e., $n_1 \sim \text{Bin}[N, p_1]$) according to the expression

$$\Pr(n_1) = \frac{N!}{(N - n_1)! n_1!} \cdot p_1^{n_1} \cdot (1 - p_1)^{(N - n_1)}. \qquad (1)$$

Thus, the likelihood function of parameters N and p_1 is

$$L_B(N, p_1) \propto \frac{\Gamma(N + 1)}{\Gamma(N - n_1 + 1)} \cdot p_1^{n_1} \cdot (1 - p_1)^{(N - n_1)}. \qquad (2)$$

The binomial likelihood is denoted by L_B. A proportion of the fish that are randomly caught in the first sample are randomly selected to receive a single, nonpermanent tag of color A ($n_A = n_1 S$ in Figure 1), whereas the other fish are double-marked with similar tags of color B ($n_{BB} = n_1[1 - S]$ in Figure 1).
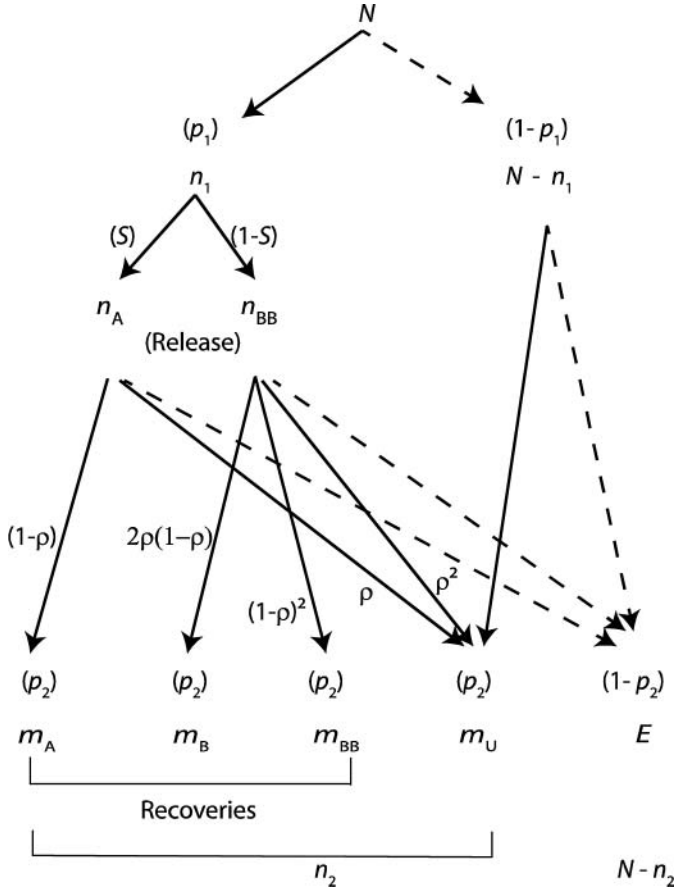
FIGURE 1. Diagram of binomial and multinomial cell probabilities for the full likelihood model under tagging scenario 1 for a closed population (i.e., double-tagged fish receive two identical, independent nonpermanent tags). Notation is defined in Table 1. The first capture event is modeled with a binomial probability mass function (PMF), $n_1 \sim \mathrm{Bin}(N, p_1)$, while the second capture event is modeled with a multinomial PMF, $(m_A, m_B, m_{BB}, m_U, E) \sim \mathrm{Multin}(N, \theta)$, where θ is a vector of cell probabilities (equation 4). The multinomial model incorporates unknown value $E\ (= N - n_2)$, associated with the dashed lines. Unknown parameters are N, p_1, p_2, and ρ, whereas known values are n_1, S, n_A, n_{BB}, m_A, m_B, m_{BB}, and m_U.

FIGURE 2. Diagram of binomial and multinomial cell probabilities for the full likelihood model under tagging scenario 2 for a closed population (i.e., double-tagged fish receive one nonpermanent tag and one permanent tag or mark). Notation is defined in Table 1. The first capture event is modeled with a binomial probability mass function (PMF), $n_1 \sim \mathrm{Bin}(N, p_1)$, while the second capture event is modeled with a multinomial PMF, $(m_A, m_F, m_{AF}, m_U, E) \sim \mathrm{Multin}(N, \theta)$, where θ is a vector of cell probabilities (equation 8). The multinomial model incorporates unknown value $E\ (= N - n_2)$, associated with the dashed lines. Unknown parameters are N, p_1, p_2, and ρ, whereas known values are n_1, S, n_A, n_{AF}, m_A, m_F, m_{AF}, and m_U.

Multinomial likelihood.—Each fish in the second random sample falls into one of four possible categories determined by tag presence, color, and number (Table 1; m_A, m_B, m_{BB}, and m_U in Figure 1) based on the assumption that all fish share an equal probability of capture in the second sample, independent of tag category. However, we additionally consider another category—fish that are caught in the first sample but are not caught in the second sample (i.e., escapement E in Figure 1). We apply a multinomial probability mass function (PMF) with five categories, including the E category, as follows:

$$\Pr(m_A, m_B, m_{BB}, m_U, E)$$
$$= \frac{N!}{m_A! m_B!\, m_{BB}! m_U! E!} \cdot \theta_A^{m_A} \cdot \theta_B^{m_B} \cdot \theta_{BB}^{m_{BB}} \cdot \theta_U^{m_U} \cdot \theta_E^{E} \quad (3)$$

with cell probabilities of

$$\theta_A = p_1 S(1 - \rho)p_2;$$
$$\theta_B = p_1(1 - S)2\rho(1 - \rho)p_2;$$
$$\theta_{BB} = p_1(1 - S)(1 - \rho)^2 p_2;$$
$$\theta_U = p_1 S\rho p_2 + p_1(1 - S)\rho^2 p_2 + (1 - p_1)p_2;$$
$$\theta_E = p_1 S(1 - p_2) + p_1(1 - S)(1 - p_2) + (1 - p_1)(1 - p_2)$$
$$= 1 - (\theta_A + \theta_B + \theta_{BB} + \theta_U + \theta_E). \quad (4)$$

Note that S, the proportion of single tags in a mixture of tags (Table 1), is known and under the control of the researcher. Thus, the likelihood function of parameters N, p_1, p_2,

TABLE 1.   Model notation for tagging scenarios 1 and 2, and observed values from the 2007 mark–recapture survey for kokanee in the Metolius River, Oregon (an example of tagging scenario 1).

Notation	Description	2007 data
n_A	Number of fish marked with a single tag of color A	2,807
n_{BB}	Number of fish marked with two tags of color B	491
n_{AF}	Number of fish marked with a nonpermanent tag of color A and a permanent mark F	
n_1	Number of fish captured in the first sample: for tagging scenario 1, $n_1 = n_A + n_{BB}$; for tagging scenario 2, $n_1 = n_A + n_{AF}$.	3,298
S	Proportion of single-tagged animals in a mixture of single- and double-tagged animals: $S = n_A/n_1$.	0.85
n_2	Number of fish captured (or sighted) in the second sample	11,444
m_A	Number of captured (or sighted) fish with one tag of color A in the second sample	218
m_B	Number of captured (or sighted) fish with only one tag of color B in the second sample	24
m_{BB}	Number of captured (or sighted) fish with two tags of color B in the second sample	35
m_F	Number of captured (or sighted) fish with one permanent mark F in the second sample	
m_{AF}	Number of captured (or sighted) fish with one tag of color A and one permanent mark F in the second sample	
m_U	Number of captured (or sighted) fish without any tag in the second sample: for tagging scenario 1, $m_U = n_2 - (m_A + m_B + m_{BB})$; for tagging scenario 2, $m_U = n_2 - (m_A + m_F + m_{AF})$.	11,167
p_1	A fish's probability of capture in the first (tagging) sample	
p_2	A fish's probability of capture in the second (recovery) sample	
ρ	Tag loss rate, $0 \leq \rho \leq 1$. Thus, the tag retention rate is $(1 - \rho)$.	
N	Population abundance	
E	Escapement from the second capture; number of fish that were not caught in the second sample	
π	Vector of parameters: when capture probabilities differ between the two samples, $\pi = (N, p_1, p_2, \rho)$; when capture probability is the same for the two samples, $\pi = (N, p, \rho)$.	

and ρ is

$$L_M(N, p_1, p_2, \rho) \propto \frac{\Gamma(N + 1)}{\Gamma(N - n_2 + 1)} \cdot \theta_A^{m_A} \cdot \theta_B^{m_B} \cdot \theta_{BB}^{m_{BB}} \cdot \theta_U^{m_U} \cdot \theta_E^{(N-n_2)}, \quad (5)$$

where L_M denotes the multinomial likelihood.

Total likelihood.—The binomial and multinomial events are independent; thus, the total likelihood function is their product:

$$L(N, p_1, p_2, \rho) = L_B \cdot L_M. \quad (6)$$

Tagging Scenario 2: a Nonpermanent Tag and a Permanent Tag or Mark

The binomial likelihood term (equation 2) used for tagging scenario 1 is also applied under tagging scenario 2, but the multinomial likelihood is modified because different tag types are used. All fish that are caught in the first sample are marked with a single, nonpermanent tag of color A; a randomly selected proportion of these fish also receive a permanent second mark denoted as F. Each fish in the second random sample falls into one of four possible categories determined by tag presence and types (Table 1; Figure 2), again under the assumption that all fish share an equal probability of capture in the second sam-

ple, independent of tag category. As in tagging scenario 1, we additionally consider category E, representing fish that are not caught in the second sample (Figure 2). Thus, we have the following multinomial PMF:

$$\Pr(m_A, m_F, m_{AF}, m_U, E) = \frac{N!}{m_A! m_F! m_{AF}! m_U! E!} \cdot \theta_A^{m_A} \cdot \theta_F^{m_F} \cdot \theta_{AF}^{m_{AF}} \cdot \theta_U^{m_U} \cdot \theta_E^{E} \quad (7)$$

with cell probabilities of

$$\theta_A = p_1 S(1 - \rho)p_2;$$
$$\theta_F = p_1(1 - S)\rho p_2;$$
$$\theta_{AF} = p_1(1 - S)(1 - \rho)p_2;$$
$$\theta_U = p_1 S\rho p_2 + (1 - p_1)p_2;$$
$$\theta_E = p_1 S(1 - p_2) + p_1(1 - S)(1 - p_2) + (1 - p_1)(1 - p_2)$$
$$= 1 - (\theta_A + \theta_F + \theta_{AF} + \theta_U + \theta_E). \quad (8)$$

The likelihood function of parameters N, p_1, p_2, and ρ is

$$L_M(N, p_1, p_2, \rho) \propto \frac{\Gamma(N + 1)}{\Gamma(N - n_2 + 1)} \theta_A^{m_A} \cdot \theta_F^{m_F} \cdot \theta_{AF}^{m_{AF}} \cdot \theta_U^{m_U} \cdot \theta_E^{(N-n_2)}. \quad (9)$$

The total likelihood is $L(N, p_1, p_2, \rho) = L_B \cdot L_M$, where L_M is from equation (9) and L_B is from equation (2) (the same as in tagging scenario 1).

Equal Capture Probabilities

If capture probabilities at the first and second samples are considered to be equal, then the above model equations are modified by replacing p_1 and p_2 with the common capture probability p (i.e., $p_1 = p_2 = p$).

Estimation

Parameters are estimated by minimizing the logarithm of the total likelihood function, $L(\boldsymbol{\pi})$, where $\boldsymbol{\pi}$ is equal to (N, p_1, p_2, ρ) when capture probabilities differ between the two samples or is equal to (N, p, ρ) when the capture probabilities are the same. We used Automatic Differentiation Model Builder (ADMB) software (Fournier 2007) for differentiation of the total likelihood. The variance–covariance matrix of the parameter estimates is estimated from the observed information matrix (Casella and Berger 1990).

Assessment of Bias and Precision

Bias in the estimates of parameters and in the estimates of uncertainty was assessed by simulating observations under various scenarios representing realistic situations. We considered four levels of tag loss: no tag loss ($\rho = 0$), low ($\rho = 0.05$), medium ($\rho = 0.30$), and high ($\rho = 0.55$). The effect of each level of tag loss was assessed under seven expected sample sizes for the initial marked sample at the common capture probability: $n_1 = pN$, where p is 0.005, 0.01, 0.02, 0.03, 0.04, 0.05, or 0.10. We considered two pairs of differing capture probabilities ($p_1 = 0.03$, $p_2 = 0.10$; and $p_1 = 0.10$, $p_2 = 0.03$). In the 2007 data describing Metolius River kokanee, estimates of p_1 and p_2 were about 0.03 and 0.11. We also considered two levels for the proportions of single and double tags in the mixture: an S equal to 0.15 (i.e., 15% of fish have single tags and 85% of fish have double tags) and an S equal to 0.85 (i.e., 85% of fish have single tags and 15% of fish have double tags). For Metolius River kokanee, S was about 0.85. Finally, we considered combinations under tagging scenarios 1 and 2, which yielded a total of 144 scenarios (i.e., [2 tagging scenarios × 2 S-values × 7 p-values × 4 ρ values] + [2 tagging scenarios × 2 S-values × 2 pairs of p_1 and p_2 × 4 ρ values]). In all simulations, the true population abundance N was fixed at 100,000. The values of n_A, n_{BB} (or n_{AF}), cell probabilities in the multinomial PMF (equation 4 or 8), and the multinomial random values (m_A, m_B [or m_F], m_{BB} [or m_{AF}], and m_U) were determined by the stochastic simulations.

We generated the multinomial random values by using the rmultinom function in R software (Ihaka and Gentleman 1996), and we then applied the Monte Carlo samples to the full likelihood model's estimation in ADMB (Fournier 2007). The repetition of generating the Monte Carlo samples, estimating parameters, and saving the results was accomplished with PBSadmb software (Schnute and Haigh 2009).

For each of the 144 scenarios, 3,000 mark–recapture samples were independently simulated, thereby producing 3,000 observation vectors, which were then used to fit the relevant total likelihood for that scenario. The resulting Monte Carlo estimate of the sampling distribution of each estimator ($\hat{\boldsymbol{\pi}}$ and $\widehat{\text{var}}[\hat{\boldsymbol{\pi}}]$, where $\boldsymbol{\pi} = [N, p, \rho]$ or $[N, p_1, p_2, \rho]$) was used to assess the estimator's bias and precision. For example, the bias of the tag loss estimator $\hat{\rho}$ was calculated as Bias $(\hat{\rho}) = E(\hat{\rho}) - \rho \cong \sum \hat{\rho}/3,000 - \rho$. For the sampling variances, bias was calculated similarly but with true sampling variance set to the variance of the 3,000 Monte Carlo estimates of a parameter, as appropriate (Reynolds et al. 2007). Relative bias (%) was calculated as $100 \times$ (bias/true value). The 95% coverage probability for a parameter was calculated as the frequency with which 95% confidence intervals (CIs) of parameter estimates actually contained the true parameter. We used the standard normal theory for CIs; for example, the estimated 95% CI for N was equal to $\hat{N} \pm |z_{0.025}| \cdot \widehat{\text{SE}}(\hat{N})$, where $z_{0.025}$ is the 0.025th quantile of the standard normal (Gaussian) variable. We also checked for correlations between parameter estimates.

Comparison with Other Estimators

The cost of using the full likelihood model when there is no tag loss was investigated by comparing the estimation bias and uncertainty of the full model with those of the modified Petersen estimators (Chapman 1951; equations 10 and 11, given below) for the simulations in which ρ was set at zero. For comparison purposes, the simulation data were also applied to the modified Petersen and Seber–Felton estimators (Seber and Felton 1981; equations 12 and 13, given below). Note the incompatibility in tag composition between our full likelihood model and the other models: the full likelihood model uses a mixture of single and double tags, whereas the other estimators do not.

The following equations are the modified Petersen estimators (Chapman 1951):

$$\hat{N}_P = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1 \qquad (10)$$

and

$$\widehat{\text{var}}(\hat{N}_P) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}, \qquad (11)$$

where $n_1 = n_A + n_{BB}$ and $m_2 = m_A + m_B + m_{BB}$ because the modified Petersen estimators were originally designed for single-tagged animals. For tag-loss-adjusted Petersen estimators, we modified n_1 with the analytical estimator based on double tags (i.e., $\hat{\rho}_D = m_B/[m_B + 2 \cdot m_{BB}]$; Gulland 1963; Seber and Felton 1981; Seber 1982); the new n_A was equal to $n_A(1 - \hat{\rho}_D)$, and the new n_{BB} was equal to $n_{BB}(1 - \hat{\rho}_D)^2$. Instead of adjusting n_1, we could adjust m_A, m_B, and m_{BB}; for example, the new m_{BB} was equal to $m_{BB}/(1 - \hat{\rho}_D)$. Most published studies adopt the latter, but the latter idea loses information about a fish that has lost a tag and is caught in the second sample (i.e.,

TABLE 2. Summary of simulation results for relative bias (to the nearest 1%) of parameter estimates and 95% coverage probability (%) for parameters under tagging scenario 1 (identical, independent double tags) and a common capture probability ($p_1 = p_2 = p$). The tagging scenario 1 model (equations 2, 5, and 6) was applied to data simulated under scenarios of differing values of tag composition (S = proportion of fish with single tags; $1 − S$ = proportion of fish with double tags), true p (i.e., the number of marked animals differs: $n_1 = Np$), and true tag loss rate (ρ). Relative bias (%) was estimated as $100 \times$ (mean of 3,000 simulation estimates − true value)/true value. True abundance (N) was fixed at 100,000; NA = not applicable.

Simulation setting		Relative bias (%)						95% coverage probability (%)		
p	ρ	$\hat{\rho}$	$\hat{N}$	$\hat{p}$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p})$	ρ	N	p
Tagging scenario 1; $S = 0.15$ ($1 − S = 0.85$)										
0.005	0.00	NA	52	2	NA	5	5	NA	83	93
	0.05	101	30	369	−60	131	−63	17	85	95
	0.30	43	22	2,729	−55	535	−56	41	65	80
	0.55	25	32	5,661	−61	−44	−47	25	40	58
0.01	0.00	NA	13	1	NA	4	0	NA	94	93
	0.05	9	13	5	−8	6	−74	56	93	92
	0.30	7	8	108	−13	11	−62	88	92	93
	0.55	6	−1	1,038	−21	2	−57	77	78	83
0.02	0.00	NA	3	0	NA	1	0	NA	95	94
	0.05	3	2	0	−1	−1	1	88	96	94
	0.30	2	2	2	−2	−1	2	94	94	95
	0.55	2	1	9	−2	2	18	93	94	95
0.03	0.00	NA	1	0	NA	−1	−2	NA	94	94
	0.05	1	1	0	2	0	0	93	95	95
	0.30	1	1	1	0	1	2	94	95	95
	0.55	1	0	3	−2	1	2	94	95	95
0.04	0.00	NA	0	0	NA	1	0	NA	95	95
	0.05	0	0	0	−2	−2	−2	92	94	94
	0.30	1	0	0	0	−1	0	95	95	95
	0.55	1	0	2	−3	−2	−1	94	94	95
0.05	0.00	NA	1	0	NA	−1	−1	NA	96	95
	0.05	0	1	0	1	0	0	94	95	95
	0.30	0	0	0	1	0	−1	95	95	95
	0.55	0	0	1	−1	−2	−1	94	94	95
0.10	0.00	NA	0	0	NA	−2	−1	NA	95	95
	0.05	0	0	0	−1	−2	−1	95	94	94
	0.30	0	0	0	−1	0	1	95	95	95
	0.55	0	0	0	0	0	0	95	95	95
Tagging scenario 1; $S = 0.85$ ($1 − S = 0.15$)										
0.005	0.00	NA	48	5	NA	4	4	NA	83	93
	0.05	41	39	278	−84	76	−54	1	84	95
	0.30	−15	72	1,618	−85	14	−56	3	72	80
	0.55	−20	143	2,124	−90	−21	−57	2	55	62
0.01	0.00	NA	14	−1	NA	8	0	NA	94	92
	0.05	14	13	136	−31	−3	−59	12	93	90
	0.30	5	22	1,391	−52	−11	−53	27	78	68
	0.55	−19	78	2,339	−70	−21	−48	16	65	42
0.02	0.00	NA	3	0	NA	−2	−1	NA	95	94
	0.05	6	2	2	−2	0	−75	45	95	94
	0.30	4	1	94	−14	−6	−58	84	92	89
	0.55	4	−2	695	−20	−17	−57	71	74	74

TABLE 2. Continued.

Simulation setting		Relative bias (%)						95% coverage probability (%)		
p	ρ	$\hat{\rho}$	$\hat{N}$	$\hat{p}$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p})$	ρ	N	p
0.03	0.00	NA	1	0	NA	1	2	NA	95	95
	0.05	0	1	0	−4	0	1	70	95	95
	0.30	1	1	5	−3	−1	−57	91	95	93
	0.55	3	−2	142	−11	−10	−61	86	89	87
0.04	0.00	NA	1	0	NA	−1	−1	NA	95	95
	0.05	−1	1	0	0	0	0	89	95	95
	0.30	1	0	2	2	−1	3	94	95	94
	0.55	1	−1	27	−6	−5	−54	92	93	92
0.05	0.00	NA	0	0	NA	1	1	NA	95	95
	0.05	−2	1	0	−2	1	1	85	96	95
	0.30	1	0	1	−2	0	3	93	95	95
	0.55	1	−1	9	−4	−2	−4	92	93	93
0.10	0.00	NA	0	0	NA	−1	−1	NA	95	95
	0.05	0	0	0	0	1	2	94	95	95
	0.30	0	0	0	0	1	1	95	95	95
	0.55	0	0	1	−3	−2	−1	94	95	94

TABLE 3. Summary of simulation results for relative bias (to the nearest 1%; defined in Table 2) of parameter estimates and 95% coverage probability (%) for parameters under tagging scenario 1 (identical, independent double tags) and different capture probabilities ($p_1 \neq p_2$). The tagging scenario 1 model (equations 2, 5, and 6) was applied to data simulated under scenarios of differing values of tag composition (S = proportion of fish with single tags; $1 - S$ = proportion of fish with double tags), true p_1 and p_2 (i.e., the number of marked animals differs: $n_1 = Np_1$; the catch in the second sample differs: $n_2 = Np_2$), and true tag loss rate (ρ). True abundance (N) was fixed at 100,000; NA = not applicable.

Simulation setting		Relative bias (%)								95% coverage probability (%)			
(p_1, p_2)	ρ	$\hat{\rho}$	$\hat{N}$	$\hat{p}_1$	$\hat{p}_2$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p}_1)$	$\widehat{SE}(\hat{p}_2)$	ρ	N	p_1	p_2
Tagging scenario 1; $S = 0.15$ ($1 - S = 0.85$)													
(0.03, 0.10)	0.00	NA	0	0	0	NA	0	−1	0	NA	95	95	95
	0.05	0	0	0	0	−1	−1	0	−1	94	95	95	95
	0.30	0	0	0	0	3	0	0	0	95	95	95	95
	0.55	0	0	1	1	0	1	1	1	95	95	95	95
(0.10, 0.03)	0.00	NA	0	0	0	NA	1	1	0	NA	95	95	95
	0.05	0	0	0	0	−1	0	−1	−1	94	94	95	94
	0.30	0	0	0	0	−1	0	0	0	95	95	95	95
	0.55	0	0	1	1	−2	0	1	1	94	95	95	95
Tagging scenario 1; $S = 0.85$ ($1 - S = 0.15$)													
(0.03, 0.10)	0.00	NA	0	0	0	NA	−2	−2	−2	NA	94	94	95
	0.05	0	0	0	0	1	1	2	2	91	96	96	95
	0.30	0	0	1	1	1	1	3	3	94	95	95	95
	0.55	1	−1	7	7	−3	−1	−27	−28	93	94	93	93
(0.10, 0.03)	0.00	NA	0	0	0	NA	−2	−2	−2	NA	95	95	95
	0.05	1	0	0	0	−3	−1	−1	−1	91	95	94	94
	0.30	0	1	1	1	−3	−3	−2	−2	93	94	94	94
	0.55	0	0	6	6	0	1	−31	−32	94	95	94	94

TABLE 4. Summary of simulation results for relative bias (to the nearest 1%; defined in Table 2) of parameter estimates and 95% coverage probability (%) for parameters under tagging scenario 2 (double-tagged fish receive one permanent tag and one nonpermanent tag) and a common capture probability ($p_1 = p_2 = p$). The tagging scenario 2 model (equations 2, 6, and 9) was applied to data simulated under scenarios of differing values of tag composition (S = proportion of fish with single tags; $1 - S$ = proportion of fish with double tags), true p (i.e., the number of marked animals differs: $n_1 = Np$), and true tag loss rate (ρ). True abundance (N) was fixed at 100,000; NA = not applicable.

Simulation setting		Relative bias (%)						95% coverage probability (%)		
p	ρ	$\hat{\rho}$	$\hat{N}$	$\hat{p}$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p})$	ρ	N	p
Tagging scenario 2; $S = 0.15$ ($1 - S = 0.85$)										
0.005	0.00	NA	51	3	NA	0	6	NA	83	92
	0.05	142	51	3	−71	3	4	9	82	92
	0.30	14	59	2	−54	−4	2	37	81	90
	0.55	5	63	0	−50	−12	5	45	81	89
0.01	0.00	NA	13	1	NA	7	−1	NA	93	91
	0.05	−3	12	0	−7	8	1	34	93	93
	0.30	−2	15	0	−9	7	0	86	94	92
	0.55	−1	15	0	−7	−6	0	88	94	93
0.02	0.00	NA	2	0	NA	1	0	NA	95	94
	0.05	−1	3	0	−1	−3	−2	81	95	94
	0.30	0	3	0	−2	2	2	93	96	95
	0.55	0	3	0	−1	−2	−2	94	95	94
0.03	0.00	NA	1	0	NA	1	0	NA	96	95
	0.05	1	1	0	1	1	1	90	95	95
	0.30	0	1	0	−3	−2	−2	93	94	95
	0.55	0	1	0	−2	−1	−2	94	96	94
0.04	0.00	NA	1	0	NA	0	1	NA	96	95
	0.05	−1	1	0	0	0	1	92	95	95
	0.30	0	0	0	0	2	3	95	96	95
	0.55	0	1	0	1	4	4	95	96	95
0.05	0.00	NA	1	0	NA	1	1	NA	96	95
	0.05	0	0	0	0	0	0	93	95	95
	0.30	0	0	0	1	2	2	95	95	95
	0.55	0	0	0	0	1	0	95	96	95
0.10	0.00	NA	0	0	NA	2	2	NA	95	96
	0.05	0	0	0	2	1	1	95	95	95
	0.30	0	0	0	0	1	0	94	96	95
	0.55	0	0	0	2	1	0	95	95	95
Tagging scenario 2; $S = 0.85$ ($1 - S = 0.15$)										
0.005	0.00	NA	48	4	NA	2	6	NA	82	93
	0.05	132	65	1	−91	−8	3	0	79	89
	0.30	−15	93	7	−85	−13	4	3	71	84
	0.55	−23	137	8	−86	−18	2	6	60	74
0.01	0.00	NA	12	1	NA	6	0	NA	93	93
	0.05	−42	15	0	−45	6	2	6	95	92
	0.30	−33	35	0	−45	−4	1	31	94	81
	0.55	−31	77	0	−53	−10	1	47	92	69
0.02	0.00	NA	2	1	NA	1	0	NA	94	94
	0.05	−11	3	0	−13	−2	−1	26	95	94
	0.30	−11	7	0	−14	−6	0	80	92	88
	0.55	−8	14	−1	−16	−11	−3	89	90	89

TABLE 4. Continued.

Simulation setting		Relative bias (%)						95% coverage probability (%)		
p	ρ	$\hat{\rho}$	$\hat{N}$	$\hat{p}$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p})$	ρ	N	p
0.03	0.00	NA	1	0	NA	−2	−1	NA	94	95
	0.05	−6	2	0	−7	−1	0	48	95	94
	0.30	−4	3	0	−5	−3	1	90	94	93
	0.55	−3	5	0	−2	−2	2	94	95	93
0.04	0.00	NA	0	0	NA	−2	−3	NA	94	94
	0.05	−5	1	0	−5	−1	−1	69	94	94
	0.30	−3	2	0	−3	0	2	93	95	94
	0.55	−2	2	0	−2	2	3	94	95	95
0.05	0.00	NA	0	0	NA	0	0	NA	95	94
	0.05	−1	0	0	−2	−2	−2	84	94	94
	0.30	−2	1	0	0	−1	0	94	95	95
	0.55	−1	2	0	−3	−2	−1	94	94	94
0.10	0.00	NA	0	0	NA	2	1	NA	96	95
	0.05	−1	0	0	−2	−1	0	92	95	95
	0.30	0	0	0	−1	1	1	94	95	95
	0.55	0	0	0	−1	−2	−2	95	94	94

m_0 or m_{00}; of course, we do not know whether the fish has never been tagged or has actually lost a tag or tags). Only under the assumption that a double-tagged fish does not lose both tags will the latter idea be valid.

The Seber–Felton tag loss correction model (Seber and Felton 1981) for tagging scenario 1 is

$$\hat{N}_{SF} = \frac{(n_1 + 1)(n_2 + 1)}{(m_T + 1)} \cdot \left[1 - \frac{m_B(m_B - 1)}{4m_T(m_{BB} + 1)} \right] - 1 \quad (12)$$

and

$$\widehat{\mathrm{var}}(\hat{N}_{SF})$$
$$= (\hat{N}_{SF} + 1)^2 - \frac{(n_1 + 1)(n_1 + 2)(n_2 + 1)(n_2 + 2)}{(m_T + 1)(m_T + 2)}$$
$$\times \left[1 - \frac{m_B(m_B - 1)}{2m_T(m_{BB} + 1)} \right.$$
$$\left. + \frac{m_B(m_B - 1)(m_B - 2)(m_B - 3)}{16m_T(m_T - 1)(m_{BB} + 1)(m_{BB} + 2)} \right]$$
$$+ (\hat{N}_{SF} + 1), \quad (13)$$

where $m_T = m_B + m_{BB}$ because Seber–Felton estimators assume that all animals are double-tagged. Seber and Felton's original notations are modified here because in the present paper tag A represents single-tagged fish (different color from double tags) whereas in the paper by Seber and Felton (1981) it represents double-tagged fish.

Analysis of Metolius River Data

Development of the full likelihood model was initiated from questions regarding the analysis of mark–recapture data obtained during a 2007 study to estimate the abundance of an adfluvial population of kokanee that rear in Lake Billy Chinook (Jefferson County, Oregon) and then migrate into the Metolius River for spawning. In 2007, managers began double-tagging a portion of the tagged fish to obtain an estimate of tag loss. In August and September 2007, the period just before the spawning run, adult kokanee were collected by beach seining in the upper arm of the lake near the confluence with the Metolius River (J. Lovtang and coworkers, unpublished). The fish were generally larger than 250 mm, and all were considered to be prespawning adults. Fish were tagged with nonpermanent, plastic T-bar anchor tags (Dell 1968; tagging scenario 1) and then were released back into the lake. Randomly selected fish received single tags of one color, while the other fish received two tags of a second color (tagging scenario 1; i.e., the double tags were identical in color). During late September through October, spawning ground surveys were conducted by 2–3 people walking abreast in a downstream direction (or floating, in sections where the water depth and flow were too great to allow walking). Instead of being physically recaptured, the fish were resighted as they swam freely in the clear, relatively shallow water within the spawning areas of the river. The total number of fish observed with or without a tag (or tags) was recorded for each section, and information on the number and color of tags for each marked fish was also noted. After completion of the surveys, the data were first analyzed with a two-way analysis of variance to test the effects of survey time (week) and area (section).

The proportion of tagged fish did not significantly differ by week or by section, so the data were pooled (Galbreath and Hyun 2008). The number of marked and unmarked kokanee observed and the number and color of tags on each marked fish are summarized in Table 1. Kokanee population abundance and its uncertainty were estimated by the tagging scenario 1 likelihood model given in equations (2), (5), and (6). For comparison, abundances and uncertainties were also estimated with the modified Petersen estimators (Chapman 1951; equations 10 and 11) and the Seber–Felton estimators (Seber and Felton 1981; equations 12 and 13).

RESULTS

Estimator Bias and Precision

Overall, the full likelihood model's estimates were effectively unbiased. There was a clear pattern in the model performance under tagging scenarios 1 and 2 (Tables 2–5). Generally, the model's estimation performance improved with increases in the proportion of double tags $(1 - S)$ in the mixture of tags, increases in the value of p (or p_1, p_2), or decreases in the value of ρ.

Under the double-tag proportion of 0.85 (i.e., $S = 0.15$) in tagging scenario 1, relative biases in point estimates of all parameters were under 2% unless p was very low (≤ 0.01) and

ρ was very high (i.e., $\rho = 0.55$; $\hat{\rho}$, $\hat{N}$, and $\hat{p}$ in Table 2). At $p \geq 0.03$ those point estimates were effectively unbiased even when ρ was 0.55 (Table 2). Sampling variances tended to be underestimated ($\widehat{SE}[\hat{\pi}]$ in Table 2), but like the point estimates, the magnitude of the relative bias in $\widehat{SE}(\hat{\pi})$ did not exceed 2% except for the cases of low p (≤ 0.01) and very high ρ (0.55). At $p \geq 0.03$ the 95% coverage probability for π was satisfactory overall. The 95% coverage probability for N, the parameter of primary interest, was most satisfactory even when $\rho = 0.55$ and $p \geq 0.02$ (Table 2). As would be expected, when the proportion of double-tagged fish was 0.15 (i.e., $S = 0.85$) in tagging scenario 1, the model's performance was not as good, but the pattern of the model performance remained the same (Table 2).

When capture probabilities differed at the time of marking and recapture for tagging scenario 1 ($p_1 = 0.03$, $p_2 = 0.10$; or $p_1 = 0.10$, $p_2 = 0.03$), there was little difference in model performance between the two pairs (Table 3). The overall pattern remained the same as the above results relative to the effects of tag composition (S), capture probabilities (p_1, p_2), and ρ.

The model performance under tagging scenario 2 was marginally better than under tagging scenario 1, but its general pattern was the same between the two scenarios (Tables 4, 5). The slightly improved performance under tagging scenario 2 was due to the permanence of the second tag.

TABLE 5. Summary of simulation results for relative bias (to the nearest 1%; defined in Table 2) of parameter estimates and 95% coverage probability (%) for parameters under tagging scenario 2 (double-tagged fish receive one permanent tag and one nonpermanent tag) and different capture probabilities ($p_1 \neq p_2$). The tagging scenario 2 model (equations 2, 6, and 9) was applied to data simulated under scenarios of differing values of tag composition (S = proportion of fish with single tags; $1 - S$ = proportion of fish with double tags), true p_1 and p_2 (i.e., the number of marked animals differs: $n_1 = Np_1$; the catch in the second sample differs: $n_2 = Np_2$), and true tag loss rate (ρ). True abundance (N) was fixed at 100,000; NA = not applicable.

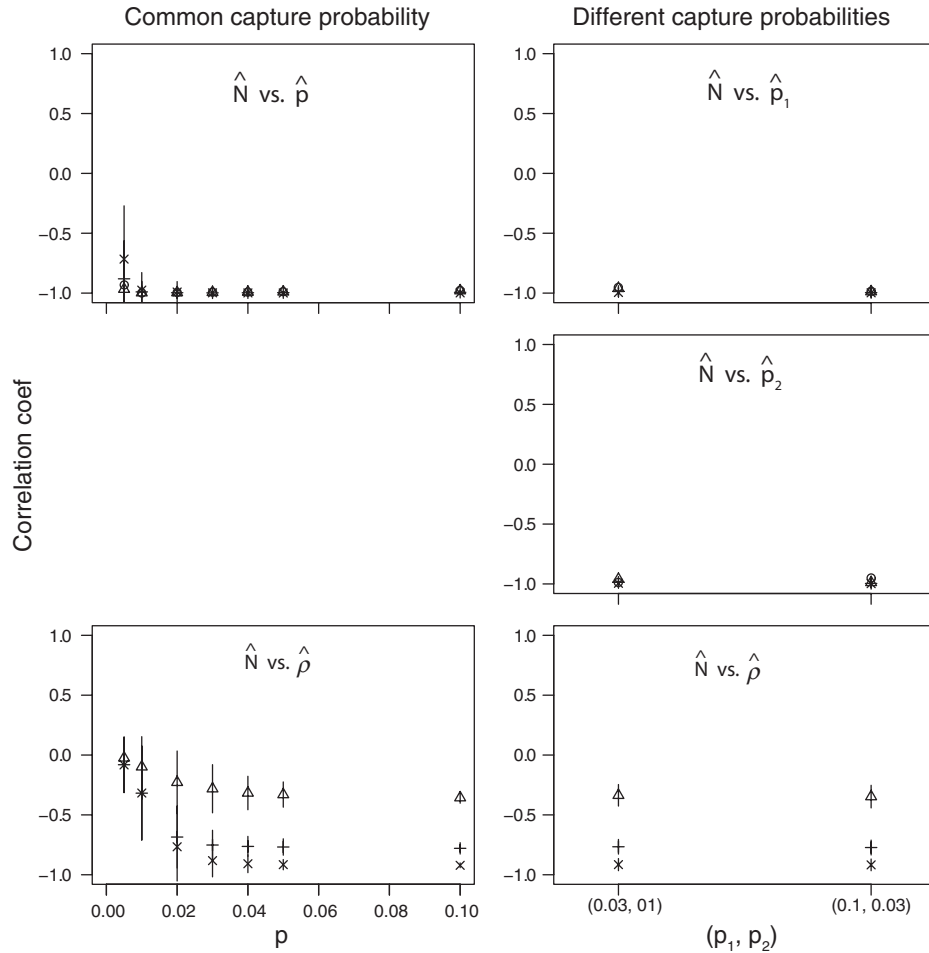| Simulation setting		Relative bias (%)								95% coverage probability (%)			
(p_1, p_2)	ρ	$\hat{\rho}$	$\hat{N}$	$\hat{p}_1$	$\hat{p}_2$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p}_1)$	$\widehat{SE}(\hat{p}_2)$	ρ	N	p_1	p_2
Tagging scenario 2; $S = 0.15$ ($1 - S = 0.85$)													
(0.03, 0.10)	0.00	NA	0	0	0	NA	2	1	1	NA	95	95	95
	0.05	−1	0	0	0	0	1	2	1	93	95	95	95
	0.30	0	0	0	0	0	−1	0	−1	95	94	95	94
	0.55	0	1	0	0	1	1	0	1	95	96	95	95
(0.10, 0.03)	0.00	NA	0	0	0	NA	4	3	2	NA	96	95	95
	0.05	0	0	0	0	−3	−1	−1	−1	92	95	95	94
	0.30	0	0	0	0	1	−3	−3	−3	95	94	94	94
	0.55	0	0	0	0	0	−1	−1	0	95	95	95	95
Tagging scenario 2; $S = 0.85$ ($1 - S = 0.15$)													
(0.03, 0.10)	0.00	NA	0	0	0	NA	1	1	1	NA	95	95	95
	0.05	−1	0	0	0	−4	1	1	1	89	95	95	95
	0.30	0	0	0	0	0	2	3	3	94	95	95	95
	0.55	−1	1	0	0	−1	−1	−1	−1	94	95	94	94
(0.10, 0.03)	0.00	NA	0	0	0	NA	1	1	1	NA	95	95	95
	0.05	−2	0	0	0	−2	0	0	0	88	95	95	95
	0.30	−2	1	0	0	−2	0	0	0	94	95	94	94
	0.55	−1	2	0	0	−3	−2	−2	−2	94	95	93	94

FIGURE 3.   Correlation coefficients between parameter estimates for an S-value of 0.85 (i.e., $1 - S = 0.15$) and four tag loss rates (ρ) under tagging scenario 1 (notation is defined in Table 1). Symbols represent the mean correlation coefficients (based on 3,000 Monte Carlo estimates) between parameter estimates for each value of ρ (open circles: $\rho = 0$; open triangles: $\rho = 0.05$; plus symbols: $\rho = 0.30$; $\times$ symbols: $\rho = 0.55$). The vertical line through each symbol represents ± 1 SD of the correlation coefficient. For the scenario of no tag loss ($\rho = 0$), $\hat{\rho}$ was not calculated.

Correlation coefficients between parameter estimates were examined. Under tagging scenarios 1 and 2, there were strong negative correlations between $\hat{N}$ and capture probability estimates (common probability $\hat{p}$; or differing probabilities $\hat{p}_1$ and $\hat{p}_2$) at all values of ρ (i.e., 0.00, 0.05, 0.30, and 0.55; Figure 3). As ρ increased, correlations between $\hat{N}$ and $\hat{\rho}$ turned negative. Regardless of the level of ρ, correlations between $\hat{p}_1$ and $\hat{p}_2$ were strongly positive. Correlations between $\hat{p}$ (or $\hat{p}_1$, $\hat{p}_2$) and $\hat{\rho}$ were not significant. The variability of correlation coefficients was smaller at $S = 0.15$ than at $S = 0.85$. These relationships were self-explanatory. As an example, we show the correlation pattern in Figure 3 under tagging scenario 1 and an $S = 0.85$, similar to the 2007 Metolius River kokanee data.

Comparison with Other Estimators

Under a scenario of no tag loss ($\rho = 0$), estimates of N were less biased from the modified Petersen estimators (Table 6) than from the full likelihood model, although the bias from the full likelihood's estimator was serious only at the small values of p and approached 0 as p increased (Table 2). The negligible bias in estimates of N at $p \geq 0.03$ was common regardless of the values of S and $(1 - S)$ (Table 2). However, regardless of S and $(1 - S)$, the values of SE($\hat{N}$) from the modified Petersen estimators were consistently underestimated even for large values of p (there was a -5% relative bias in $\widehat{SE}[\hat{N}]$ even at $p = 0.10$; Table 6). In contrast, those from the full likelihood model were much less biased: relative bias in $\widehat{SE}(\hat{N})$ decreased as p increased (i.e., from 4% at $p = 0.005$ to -1% at $p = 0.10$; Table 2).

Performance of the other methods was poor when tag loss was incorporated (modified Petersen method at $\rho > 0$; and Seber–Felton method; see Table 6). The poor performance was due to incompatibility rather than to the nature of these estimators per se. Neither the tag-loss-adjusted Petersen estimators nor the Seber–Felton estimators were directly applicable to data from a mixture of single- and double-tagged individuals.

TABLE 6.   Relative bias (to the nearest 1%) in estimates of abundance (N) and $\widehat{SE}(\hat{N})$ and 95% coverage probability (%) for N from (1) the modified Petersen estimators (Chapman 1951; equations 10 and 11) under a tag loss rate (ρ) of zero and adjusted for tag loss (i.e., $\rho > 0$); and (2) the Seber–Felton estimators (equations 12 and 13). The estimators were applied to data simulated under tagging scenario 1 with $S = 0.85$, similar to the Metolius River kokanee data; these results are intended for comparison with performance of the full likelihood model under the same scenarios in Table 2. NA = not applicable.

Simulation setting		Modified Petersen			Seber–Felton		
		Relative bias (%)		95% coverage probability (%)	Relative bias (%)		95% coverage probability (%)
p	ρ	$\hat{N}$	$\widehat{SE}(\hat{N})$	N	$\hat{N}$	$\widehat{SE}(\hat{N})$	N
0.005	0.00	−10	20	76	NA	NA	5
	0.05	−41	NA	17	NA	NA	6
	0.30	−62	NA	10	NA	NA	5
	0.55	−73	NA	6	NA	NA	2
0.01	0.00	1	−2	88	NA	NA	44
	0.05	−10	NA	62	NA	NA	45
	0.30	−27	NA	41	NA	NA	41
	0.55	−44	NA	23	NA	NA	30
0.02	0.00	1	−2	94	NA	NA	10
	0.05	−3	NA	86	NA	NA	10
	0.30	−12	NA	63	NA	NA	27
	0.55	−24	NA	44	NA	NA	56
0.03	0.00	0	−3	94	563	−2	0
	0.05	−1	−14	88	567	−1	0
	0.30	−11	−49	63	NA	NA	4
	0.55	−19	NA	44	NA	NA	40
0.04	0.00	0	−3	95	561	−1	0
	0.05	−1	−15	88	566	−1	0
	0.30	−9	−49	59	560	−3	1
	0.55	−17	−67	42	NA	NA	40
0.05	0.00	0	−2	95	563	−1	0
	0.05	−2	−12	89	567	−1	0
	0.30	−9	−48	57	560	0	0
	0.55	−16	−68	39	NA	NA	37
0.10	0.00	0	−5	93	566	−2	0
	0.05	−2	−16	86	566	−3	0
	0.30	−9	−51	33	561	2	0
	0.55	−15	−69	24	NA	NA	12

Analysis of Metolius River Kokanee Survey Data

The Metolius River kokanee mark–recapture data were analyzed with the full likelihood model for tagging scenario 1 (Table 7): $\hat{N}$ was 102,970 fish ($\widehat{SE}[\hat{N}] = 8{,}930$), $\hat{\rho}$ was 0.27 ($\widehat{SE}[\hat{\rho}] = 0.05$), $\hat{p}_1$ was 0.03 ($\widehat{SE}[\hat{p}_1] = 0.00$), and $\hat{p}_2$ was 0.11 ($\widehat{SE}[\hat{p}_2] = 0.01$). For comparison, the data were also analyzed with the other estimators. Failing to account for tag loss resulted in an $\hat{N}$ of 135,816 fish ($\widehat{SE}[\hat{N}] = 7{,}686$) under the modified Petersen method (Table 7). While accounting for an estimated tag loss rate of 0.26 ($\hat{\rho}_D = m_B/[m_B + 2 \cdot m_{BB}]$), the tag-loss

adjusted Petersen method (Gulland 1963; Seber and Felton 1981; Seber 1982) resulted in $\hat{N} = 97{,}306$ (Table 7), which was closer to that provided by the full likelihood model; however, the $\widehat{SE}(\hat{N})$ of 5,405 was substantially underestimated. As expected, estimates from the tag-loss-adjusted Petersen and Seber–Felton models were not comparable. It should be noted that our full likelihood model provided not only point estimates of all parameters but also their respective levels of uncertainty, including $\widehat{SE}(\hat{\rho})$, $\widehat{SE}(\hat{p}_1)$, and $\widehat{SE}(\hat{p}_2)$, whereas the other estimators did not (Table 7).

TABLE 7. Parameter estimates (notation is defined in Table 1) from analysis of the 2007 Metolius River kokanee data by using the full likelihood model (tagging scenario 1) and, for comparison, the modified Petersen estimators assuming a tag loss rate (ρ) of zero (Chapman 1951; equations 10 and 11), the modified Petersen estimators adjusted for tag loss ($\rho > 0$), and the Seber–Felton model (Seber and Felton 1981; Seber 1982; equations 12 and 13). In the tag-loss-adjusted Petersen and Seber–Felton models, the ρ value of 0.26 (indicated by asterisk) is calculated by the analytical estimator for double tags ($\hat{\rho}_D = m_B/[m_B + 2 \cdot m_{BB}]$; Gulland 1963; Seber and Felton 1981; Seber 1982). The Seber–Felton estimate of var($\hat{N}$) was negative because the model's requirement that all fish be double-tagged was incompatible with the use of single and double tags in the kokanee study. In the modified Petersen, tag-loss-adjusted Petersen, and Seber–Felton models, $\hat{p}_1 = n_1/\hat{N}$ and $\hat{p}_2 = n_2/\hat{N}$. NA = not applicable.

Model	$\hat{\rho}$	$\hat{N}$	$\hat{p}_1$	$\hat{p}_2$	$\widehat{SE}(\hat{\rho})$	$\widehat{SE}(\hat{N})$	$\widehat{SE}(\hat{p}_1)$	$\widehat{SE}(\hat{p}_2)$
Full likelihood	0.27	102,970	0.03	0.11	0.05	8,930	0.00	0.01
Modified Petersen	NA	135,816	0.02	0.08	NA	7,686	NA	NA
Tag-loss-adjusted Petersen	0.26*	97,306	0.03	0.12	NA	5,405	NA	NA
Seber–Felton	0.26*	588,398	0.01	0.02	NA	NA	NA	NA

DISCUSSION

Performance of our full likelihood model was impressive (Tables 2–5). Except in cases where the proportion of double-tagged fish ($1 - S$) was small, the capture probabilities (p or [p_1, p_2]) were small, and the value of ρ was high, bias in parameter estimates was negligible and the coverage probability was satisfactory for each of the parameter estimates. These quantities of S, p (or p_1, p_2), and ρ control random errors in the full model composed of binomial and multinomial likelihood functions. That is, there are two sources of random error: binomial and multinomial. The term p (or p_1) involves binomial error, while S, p (or p_1, p_2), and ρ involve multinomial error because binomial data on $n_1 = Np$ (or Np_1; equation 1) and multinomial data on m_A, m_B (or m_F), m_{BB} (or m_{AF}), m_U, and E are a function of S, p (or p_1, p_2), and ρ (equations 4 and 8). The binomial and multinomial random errors are revealed more clearly in the difficult cases. In other words, the two sources of random error are better controlled as S and p (or p_1, p_2) increase and as ρ decreases.

It should be reiterated that p (or p_1) affects both binomial and multinomial random errors. As can be expected, an increase in the accuracy and precision of parameter estimates can be achieved by increasing p (or p_1; i.e., tagging a larger number of fish; $n_1 = Np$ [or Np_1]). Assuming that the levels of S and p are reasonable, the tag loss rate will be of less concern. In the simulations, only the very high ρ (0.55) yielded substantial error levels. From a practical standpoint, a $\rho = 0.55$ is unreasonable. If such a high propensity for tag loss is recognized, managers will necessarily seek an alternative type of tag for field use in their particular circumstances. If logistical constraints preclude the tagging of a greater number of fish, then increasing the proportion of double-tagged fish will increase the accuracy and precision for the given number tagged.

The derivation of tag loss rate and its incorporation into abundance estimation in our likelihood model are distinct relative to methods employed in the more commonly studied models (i.e., Gulland 1963; Seber 1982; Seber and Felton 1981). These previous papers describe analytical estimators of tag loss rate: for example, their notations for two identical independent tags are

$_1N/(_1N + _2{}_2N)$ (Gulland 1963) and $m_C/(m_C + 2m_{AB})$ (Seber 1982; Seber and Felton 1982), where $_1N$ or m_C in the numerator is the number of fish recovered with only one tag and $_2N$ or m_{AB} in the denominator is the number of fish recovered with two tags. In the Seber and Felton (1982) paper, $\tilde{\theta}$ denotes the tag retention rate, and thus the tag loss rate is $(1 - \tilde{\theta}) = m_C/(m_C + 2m_{AB})$. It is extremely important to recognize that the analytical forms of tag loss rate are based on the assumption that an individual cannot lose both of its tags, although the previous papers do not explicitly state this assumption. Because these models show that the probability of losing both tags is the product of two independent tag rates ($= \rho \cdot \rho$), many people incorrectly assume that tag loss has been appropriately derived in the models.

To clarify the problem associated with this assumption, consider a simple mark–recapture experiment. Fish from the first sample are tagged with identical double tags and are then released. In the second (recovery) sample, the researcher will observe three categories of fish: those with one tag, those with two tags, and those with no tag. However, there is no way to identify whether fish without tags in the second sample had lost both tags or had never been tagged before. Thus, the previous models apply the binomial model by considering only two categories in the second sample: recoveries with only one tag and recoveries with two tags. Thus, the third category (fish without a tag) in the second sample is ignored. This model is described as:

$$L(\rho|D_1) = \binom{D}{D_1} \cdot \theta^{D_1} \cdot (1 - \theta)^{(D - D_1)}$$

$$\propto \left[\frac{2(1 - \rho)\rho}{2(1 - \rho)\rho + (1 - \rho)^2} \right]^{D_1}$$

$$\cdot \left[1 - \frac{2(1 - \rho)\rho}{2(1 - \rho)\rho + (1 - \rho)^2} \right]^{D_2}, \quad (14)$$

where D is the total number of fish that are recovered with one or two tags ($D_1 + D_2$); D_1 is the number of fish that are recovered with only one tag; D_2 is the number of fish that are recovered with two tags; and ρ is the tag loss rate. The numerator in the cell probability indicates that a fish loses one tag either from one

side or the other (i.e., it loses one and retains the other, or vice versa: $\rho[1-\rho] + [1-\rho]\rho = 2[1-\rho]\rho$). The denominator in the cell probability shows that a fish either (1) loses one tag from one side or the other or (2) retains both tags (i.e., $\rho[1-\rho] + [1-\rho]\rho + [1-\rho]^2 = 2[1-\rho]\rho + [1-\rho]^2$). In this simple example, it is easy to analytically differentiate the binomial likelihood with respect to ρ. Thus, we have the following analytical maximum likelihood estimator of ρ: $\hat{\rho} = D_1/(D_1 + 2D_2)$. This form is exactly the same as that presented by Gulland (1963), Seber (1982), and Seber and Felton (1982).

In contrast, the full likelihood model accounts for the possibility that double-tagged fish could lose both tags. Furthermore, the full likelihood model does not require double-tagging of all marked fish, contrary to the models described by Gulland (1963), Seber (1982), and Seber and Felton (1982); relative to the existing methods, our full likelihood model is unbiased in all but the most difficult cases (Tables 2–5). The full likelihood model simultaneously uses all information in the data, incorporating a combination of both single-tagged and double-tagged fish into the likelihood estimation.

Employing the full likelihood model in double-tagging studies will provide managers with more accurate information and hopefully will avoid the consequences of conducting stock assessment with greatly underestimated uncertainty. Although previous studies partially accounted for tag loss in double-tagging studies, they provided no estimate of the uncertainty associated with the estimated ρ. Furthermore, there is no existing model that systematically provides a method of estimating the uncertainty associated with the estimated capture probability. The full likelihood model here provides estimates of $SE(\hat{\rho})$ and $SE(\hat{p})$ (or $SE[\hat{p}_1]$, $SE[\hat{p}_2]$) as well as estimates of ρ, N, p (or p_1, p_2), and $SE(\hat{N})$. This allows managers to effectively compare tag types and tagging methods with regard to their associated loss rates.

In situations involving tag loss, there are obvious gains in accuracy and precision from using the full likelihood model. However, even under a scenario of no tag loss ($\rho = 0$), the performance of the full model was comparable to that of the modified Petersen estimators (Table 6). For example, performance of the modified Petersen estimators at $\rho = 0$ under tagging scenario 1 and $S = 0.85$ (Table 6) can be compared with the results under the same scenarios at $\rho = 0$ for the full likelihood model (Table 2). Relative bias in $\hat{N}$ and $\widehat{SE}(\hat{N})$ from use of the full likelihood model was negligible at $p \geq 0.02$, compared with improvement in $\widehat{SE}(\hat{N})$ (at $\rho = 0$ in Table 2). Relative bias in $\hat{N}$ from the full likelihood model was only 3% at $P = 0.02$, and relative bias was 0–1% at $p > 0.02$ (at $\rho = 0$ in Table 2). Importantly, relative bias in $\widehat{SE}(\hat{N})$ from the full likelihood model was smaller (at $\rho = 0$ in Table 2) than those from the modified Petersen estimators (relative bias as high as 20%; at $\rho = 0$ in Table 6). Thus, the 95% coverage probability for N (at $\rho = 0$) was better for the full likelihood model (Table 2) than for the modified Petersen estimators (Table 6). The serious bias in $\widehat{SE}(\hat{N})$ is unsurprising when we recall the condition for the unbiased estimator of

variance from the modified Petersen method, $\widehat{var}(\hat{N}_P)$ (equation 11). It is known that $\widehat{var}(\hat{N}_P)$ is unbiased only when $n_1 + n_2 \geq N$ (Seber 1982: 60). Because the largest n_1 and n_2 values were both 10,000 in the simulation setting (Table 6), the sum (20,000) is still much less than N (100,000) and thus we see the obvious bias. However, it is unrealistic to meet the condition of $n_1 + n_2 \geq N$ in the field. Our full likelihood model is therefore more appropriate in practice compared with other models as well as being logically coherent.

Finally, note that the full likelihood model was developed to accommodate tag loss in a mixture of single- and double-tagged fish within a study design that uses a single marking event and a single recapture event. The methodologies permit modification of the model to accommodate a multiple mark–recapture design.

Conclusions

The model we have presented fully incorporates tag loss in a closed-population mark–recapture study with a mixture of single- and double-tagged animals and accounts for tag loss in the estimation of abundance and its uncertainty. Unlike the classical, more frequently used models, the full likelihood model does not require the assumption that double-tagged animals cannot lose both tags. In addition, the full likelihood model provides simultaneous estimates of the following free parameters and their uncertainty: ρ, N, p (or p_1 and p_2), $SE(\hat{\rho})$, $SE(\hat{N})$, and $SE(\hat{p})$ (or $SE[\hat{p}_1]$, $SE[\hat{p}_2]$). Estimates of these parameters exhibit negligible bias relative to that arising from the use of existing methods. Application of the present model will provide much-improved estimates of stock status and uncertainty, which can be used to address fisheries management needs.

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