A Multinomial Likelihood Model for Estimating Survival Probabilities and Overwintering for Fall Chinook Salmon Using Release: Recapture Methods

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A Multinomial Likelihood Model for Estimating Survival Probabilities and Overwintering for Fall Chinook Salmon Using Release–Recapture Methods

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Standard release–recapture analysis, using Cormack–Jolly–Seber (CJS) models to estimate survival probabilities between hydroelectric facilities for juvenile Snake River fall chinook salmon (*Oncorhynchus tschawytscha*), ignore the possibility of individual fish overwintering and completing their migration in the year following tagging. These models do not utilize available capture history data from this second year and produce negatively biased estimates of survival probabilities. A new multinomial likelihood model was developed that results in biologically relevant, unbiased estimates of joint survival and overwintering probabilities using the full two years of capture history data. This model was applied to 1995 Snake River fall chinook hatchery releases to estimate the survival probability between a release site at Asotin, Washington (U.S.) and Lower Granite Dam. In the example presented here, overwintering is not a common physiological response and thus the use of CJS models (estimate of the survival probability = .4235; SE = .0162) did not result in an appreciably lower estimate for the survival probability than that calculated considering overwintering (estimate of the survival probability = .4360; SE = .0164) and obtained using the new multinomial model. However, analysis of releases in subsequent years may show greater impacts of overwintering on the estimates of survival probabilities.

Key Words: Estimable parameters; Fall chinook salmon; Overwintering; Release–recapture; Sufficient statistics; Survival estimation.

1. INTRODUCTION

The wild population of Snake River fall chinook salmon (*Oncorhynchus tschawytscha*) has been classified as a threatened or endangered species since 1992. The population is anadromous and returns to the portion of the Snake River below Hell's Canyon Dam along the Idaho and Washington border for spawning. Unlike yearling spring chinook salmon smolts that are active migrants with relatively fast travel times, subyearling fall chinook may overwinter, or residualize, somewhere downstream, completing their

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migration the following year. The degree to which this overwintering occurs is poorly known and probably depends on several factors, including flow and flooding patterns. One report (Connor et al. 1996) estimated the percentage of overwintering migrants to be above 3% for one group of Snake River hatchery subyearling fall chinook salmon tagged and released in 1994.

The single release–recapture model first presented by Cormack (1964), Jolly (1965), and Seber (1965), a special case of the paired-release models introduced by Burnham et al. (1987), has been used successfully to estimate survival and capture probabilities for a wide variety of species and in varied ecological settings. Recent citations include work on the effects of habitat loss on gray-tailed voles (Wolff et al. 1997) and studies of sexual dimorphism among marine iguanas (Wikelski and Trillmich 1997). Often, applications of Cormack–Jolly–Seber (CJS) models have required a modification or extension of the basic model because of assumptions that are not met, a desire to estimate different parameters, or the particular biology or behavior of the species under study. For example, Burnham, et al. (1996) adjusted survival rates to account for emigration of juvenile northern spotted owls from a study area. Lebreton et al. (1992) synthesized many of the extensions of CJS models in a unified modeling framework.

CJS models have been used to estimate survival and detection probabilities for juvenile spring chinook salmon migrants on the Snake River (Muir et al. 1996; Skalski et al. in press). However, the versions of the Cormack–Jolly–Seber (CJS) models currently in use on the Snake River are not appropriate with the type of behavior exhibited by fall subyearling smolts. These models do not account for the possibility of overwintering, nor do they utilize available release–recapture data from the second year of migration. We have developed a multinomial likelihood model for use with release–recapture data that allows the calculation of the survival probability in river reaches, taking into account the probability of overwintering. This new model uses the two years of capture history information to more realistically reflect the biology of fall chinook smolts so that survival may be more accurately estimated. The improvement in survival estimates will provide more complete information for better management of this endangered species.

2. EXAMPLE: SNAKE RIVER FALL CHINOOK SALMON

Beginning in the spring of 1995, the U.S. National Marine Fisheries Service (NMFS) has conducted release–recapture studies of subyearling chinook salmon smolts on the Snake River to estimate survival rates between hydroelectric projects during the juvenile migration. Typically, these survival rates have been calculated using standard CJS models without regard for overwintering or consideration of second-year capture histories. Due to the low numbers of wild fall chinook tagged, the use of the new overwintering model is demonstrated using Snake River hatchery releases of fall chinook salmon. The three tag groups selected for analysis were released in the Snake River above Lower Granite Dam at Asotin, Washington (river km 235 above the confluence with the Columbia River). The subyearling fall chinook salmon in these releases were the progeny of stray adult fall chinook salmon collected at Lower Granite Dam in 1994 and spawned at Lyons Ferry Hatchery (Smith et al. 1996). Capture histories of these migrating juvenile fall

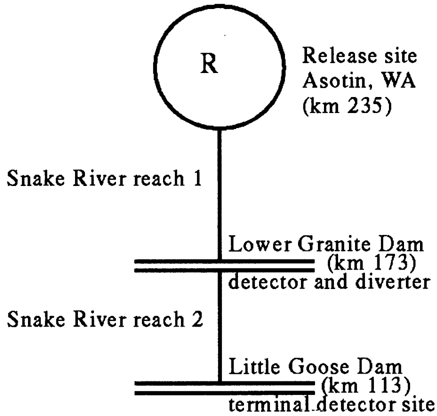

Figure 1. Tagging and Detection Scenario for Fall Chinook Salmon PIT-Tag Survival Study on the Snake River. Initial releases took place near Asotin, Washington above Lower Granite Dam and subsequent detections occurred at Lower Granite Dam and Little Goose Dam.

chinook salmon for 1995 and 1996 were retrieved from the PIT Tag Information System (PTAGIS; Mead and Stein 1996). Estimates of survival obtained with the overwintering model are compared to those obtained using the standard CJS model.

The scenario modeled consists of a PIT-tag (passive integrated transponder) study with an initial release of R fall chinook subyearlings above Lower Granite Dam (river km 173) and subsequent downstream detection opportunities at Lower Granite Dam and at Little Goose Dam (river km 113) (Fig. 1). The PIT-tag is implanted in the body cavity of juvenile fish and allows for unique identification of individuals (Prentice et al. 1990a, b, c). For juvenile fish in the Snake River, detectors automatically decode the identification information as the fish pass through the juvenile fish collection facilities at equipped hydroelectric dams, including Lower Granite Dam and Little Goose Dam. Studies have indicated that the tagging process has no significant effect on the survival of the fish (Prentice et al. 1990a).

Under current dam operations, the PIT-tag detectors at the Snake River dams are shut down at the end of the primary migration season (usually around November 1) for up to four months. This results in the possibility of missed detections among late migrants and subsequently may underestimate survival. The likelihood model developed here assumes that the shut down time for the Snake River PIT-tag detection facilities is relatively short and that missed detections are not appreciable. Also, a clear demarcation between the two years of the study is assumed. The model developed here considers only the first two river reaches below the release site, but it can be readily extended to any number of reaches.

In release–recapture studies, a capture history for each tagged individual is recorded. Let a "1" denote a period in which the animal was seen alive at a resampling opportunity and a "0" denote that the animal was not recaptured or resighted at a resampling opportunity. In the current context, a "recapture" means that the fish was detected at the juvenile collection facility at the dam. A fish not detected may have passed the dam over the spillway, may have passed through the turbines, or may not have survived. An initial "1" was recorded in the capture history for each fish, representing its initial release.

Table 1. The Ten Possible Capture Histories for a Two Period Fall Chinook Salmon Release–Recapture Study With the Possibility of Overwintering and Removal for Transportation

Capture history	*Description*	*Count*
1 0 0	Individual is released, then is not detected again:	6,487
1 0 1	Released, detected at Little Goose Dam in the first year:	449
1 1 0	Released, detected at Lower Granite Dam in the first year, not detected at Little Goose Dam in either the first or the second year:	808
1 1 1	Released, detected at both dams in the first year:	246
1 0 2	Released, not detected at Lower Granite Dam in either year, detected at Little Goose Dam in the second year:	50
1 1 2	Released, detected at Lower Granite Dam in the first year, detected at Little Goose Dam in the second year:	5
1 2 2	Released, detected at both dams in the second year:	6
1 2 0	Released, detected at Lower Granite Dam in the second year, not detected at Little Goose Dam in the second year:	8
1 3 0	Released, detected at Lower Granite Dam in the first year and removed for transportation:	731
1 4 0	Released, detected at Lower Granite Dam in the second year and removed for transportation:	0

NOTE: Capture history counts are given for the combined Asotin releases (n = 8,790).

To account for the possibility of individuals overwintering in the river, the notation was expanded. A "2" was used in the capture history to represent a fish being detected in the second year. In the Snake River juvenile salmon survival studies there may be a sizable number of fish that are detected at a hydroelectric facility that are not returned to the river because they are diverted to barges or trucks and transported downriver. The capture history notation was further expanded to include a "3" to indicate this type of "known-removal" at Lower Granite Dam in the first year, and a "4" to indicate a known-removal at Lower Granite Dam in the second year. For the two-period study depicted in Figure 1, there are 10 possible mutually exclusive and exhaustive capture histories that are listed in Table 1 along with a brief description of what each represents.

Some of these capture histories reveal all the information about the migration of an individual smolt (e.g., 1 1 2), while others are quite ambiguous. For example, from an individual with a capture history 1 0 2, it can be inferred that the fish overwintered somewhere in the river between the release site and Little Goose Dam, but we can not extract in which reach of the river this occurred. The R fish in the release group can be categorized by the 10 capture histories. The counts for these capture histories will be denoted by n with a subscript containing the particular capture history (i.e., n_{100}, n_{101}, n_{111}, n_{110}, n_{112}, n_{102}, n_{122}, n_{120}, n_{130}, n_{140}; $\Sigma n_{ijk} = R$). The counts for the combined releases at Asotin are given in Table 1. Note that even in a large ($R = 8,790$) release of fish, there is sparseness in the data as shown by the low counts for several capture histories: $n_{120} = 8$, $n_{122} = 6$, $n_{112} = 5$, $n_{140} = 0$.

3. STATISTICAL MODEL

3.1 ASSUMPTIONS

Release–recapture models are based on a series of assumptions that justify the use of the multinomial likelihood and the nature of the parameterization (Burnham et al. 1987; Smith 1991). Some of these assumptions relate to the necessity of treating the animals as independent and identically distributed and ensuring that the initial release R is typical of the population as a whole. Other assumptions characterize the migratory processes of the fish. The assumptions of the fall chinook salmon smolt survival model are as follows:

1. The PIT-tags remain in the body cavity of the fish and are read correctly.
2. The space of the resampling (i.e., a dam) is small relative to the interval (i.e., a river reach) of the study.
3. All previously tagged fish alive in the population at the beginning of a given period (river reach) have the same probability of surviving until the end of that period (river reach). However, within a reach, fish that overwinter may have a different survival probability than those that do not overwinter.
4. The history of survival, capture, and overwintering of each tagged fish is independent of all others.
5. All tagged fish alive at a particular sampling location have the same probability of being captured.
6. The probability of capture or survival of any individual is not affected by its previous history of captures.
7. The probability that a fish overwinters in a reach is the same for all tagged fish alive at the beginning of the reach.
8. The probability that a fish overwinters in a reach is not affected by its previous history of captures.
9. Fish that overwinter either migrate in the second year or die.
10. The test fish are representative of the population of interest.
11. Test conditions are representative of the conditions of interest.

Fish that overwinter between Lower Granite Dam and Little Goose Dam may experience quite different river conditions depending on the exact location of overwintering and the timing of the resumption of migration. However, this does not violate the assumptions (2, 3, and 5) of the model, as they assert that overwintering fish experience the same conditions in expectation, not that conditions experienced by each fish must be identical. The first nine assumptions are necessary for the construction of the multinomial likelihood model, while the final two assumptions allow statistical inference from the release group to the population of fall chinook salmon.

3.2 MODEL PARAMETERS

The fall chinook salmon overwintering model is developed generally, without consideration of removal of individuals for transportation. The scenario accounting for barging of individuals is developed subsequently. To construct a valid multinomial likelihood

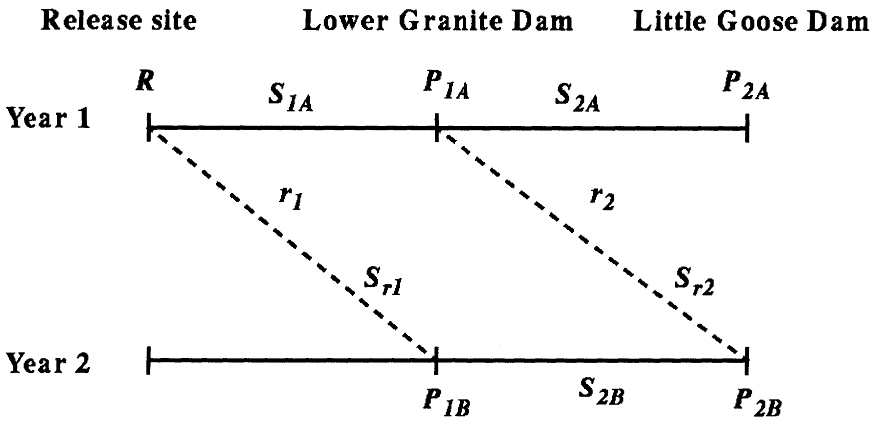

Figure 2. Schematic of the Parameters Used to Define the Multinomial Likelihood Model. The subscripts 1 and 2 refer to the reach of the river, while the subscripts A and B refer to the first and second years, respectively.

model for the general release–recapture scenario, it is necessary to calculate the probability for each multinomial cell (each possible capture history) in terms of the parameters of the model. Parameters are included for first and second year survival probabilities (s) in each of the two reaches and detection probabilities (p) at each of the two dams. For those fish that migrate the first year, the parameters s_{1A} and s_{2A} represent the survival probabilities in the first and second reaches, respectively. In addition, for fish that overwinter, a parameter is included representing the conditional probability of survival from release to Lower Granite Dam the following year, given that the fish overwintered somewhere in the first reach (s_{r1}). Similarly, the parameter (s_{r2}) represents the conditional probability of survival from Lower Granite Dam to Little Goose Dam the following year, given that the fish overwintered somewhere in the second reach. Parameters r_1 and r_2 are defined as the probability that a smolt will overwinter in the first or second reach, respectively. The parameters of the general model (their function illustrated in Figure 2) are

$s_{1A} =$ survival probability for an individual in reach 1 (i.e., from the release site to the tailrace of Lower Granite Dam) for the first year given that the fish does not overwinter in reach 1 (the subscript 1 refers to reach 1 and the A refers to year 1);

$p_{1A} =$ probability of detection of a live individual at Lower Granite Dam in year 1, given that the fish has survived to Lower Granite Dam and did not overwinter in reach 1;

$s_{2A} =$ survival probability for an individual in reach 2 (i.e., from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam) for the first year given that the fish does not overwinter in either reach and given that the fish survived the first reach (the subscript 2 refers to reach 2 and the A refers to year 1);

$p_{2A} =$ probability of detection of a live individual at Little Goose Dam in year 1, given that the fish survived to Little Goose Dam and did not overwinter in either reach;

$p_{1B} =$ probability of detection of a live individual at Lower Granite Dam in year 2, given that the fish overwintered in the first reach and survived to Lower Granite Dam;

$s_{2B} =$ survival probability for an individual in reach 2 (i.e., from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam) for the second year given that the fish overwintered in and survived the first reach during the first year (the subscript 2 refers to reach 2 and the B refers to year 2);

$p_{2B} =$ probability of detection of a live individual at Little Goose Dam in year 2, given that the fish survived to Little Goose Dam and overwintered in either of the two reaches;

$r_1 =$ probability of overwintering (r for "residualization") for an individual in the reach from the release site to Lower Granite Dam, given that the individual enters the reach in the first year of study—this parameter does not imply survival;

$r_2 =$ probability of overwintering for an individual in the reach from Lower Granite Dam to Little Goose Dam, given that the individual survives the first reach and enters this reach in the first year of study—this parameter does not imply survival of the second reach;

$s_{r1} =$ probability of survival from the release site to the tailrace of Lower Granite Dam the following year, given that the fish overwintered somewhere in reach 1 during the first year; and

$s_{r2} =$ probability of survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam the following year, given that the fish survived to Lower Granite Dam during the first year and subsequently overwintered somewhere in reach 2.

Note that the tailrace of the dams was used as the endpoint for the river reaches in question. Because the fish had various routes past the dam, this is the point where the detected fish remixed with the undetected fish. Essentially, this results in the additional assumption that there is no mortality between the detection site and the tailrace. This assumption was experimentally verified in previous Snake River salmonid releases (Skalski et al. in press). The preceding set of 11 parameters is the minimum set required to realistically model the scenario presented in Figure 2.

3.3 THE MULTINOMIAL LIKELIHOOD FUNCTION

The multinomial likelihood model for the fall chinook outmigration can be written as:

$$L(n_{100}, n_{101}, n_{111}, n_{110}, n_{112}, n_{102}, n_{120}, n_{122} | R, \mathbf{r_i}, \mathbf{p_{ij}}, \mathbf{s_{ij}}, \mathbf{s_{ri}})$$

$$= \binom{R}{n_{100}, n_{101}, n_{111}, n_{110}, n_{112}, n_{102}, n_{120}, n_{122}} (\pi_{101})^{n_{101}} (\pi_{110})^{n_{110}} (\pi_{111})^{n_{111}}$$
$$\times (\pi_{112})^{n_{112}} (\pi_{102})^{n_{102}} (\pi_{120})^{n_{120}} (\pi_{122})^{n_{122}},$$

where $n_{100} = R - (n_{101} + n_{111} + n_{110} + n_{112} + n_{102} + n_{120} + n_{122})$ and the π_{ijk} are as defined in Table 2.

As an example, it may be helpful to elaborate on the calculation of one of the cell probabilities, say, π_{102}. A capture history of 102 implies that the animal was not detected at Lower Granite Dam but survived and was detected the year after release at Little Goose Dam. Thus, this fish overwintered in one of the two reaches. Suppose first that

Table 2. Expected Values for the Cell (Capture History) Probabilities Under the Full Parameterization (center column) and Under the Reduced Parameterization (right column)

Probability of capture history	*Expected value given the original parameterization*	*Expected value with reduced parameterization*
π_{111}	$(1-r_1)\ s_{1A}\ p_{1A}\ (1-r_2)\ s_{2A}\ p_{2A}$	$\delta_1 p_{1A} \gamma_1$
π_{101}	$(1-r_1)\ s_{1A}\ (1-p_{1A})\ (1-r_2)\ s_{2A}\ p_{2A}$	$\delta_1 (1-p_{1A}) \gamma_1$
π_{112}	$(1-r_1)\ s_{1A}\ p_{1A}\ r_2\ s_{r2}\ p_{2B}$	$\delta_1 p_{1A} \gamma_1$
π_{102}	$(1-r_1)\ s_{1A}\ (1-p_{1A})\ r_2\ s_{r2}\ p_{2B}$ $+r_1\ s_{r1}\ (1-p_{1B})\ s_{2B}\ p_{2B}$	$\delta_1 (1-p_{1A}) \gamma_2 + \delta_2\ (1-p_{1B})\,\theta$
π_{120}	$r_1\ s_{r1}\ p_{1B}\ (1-s_{2B}\ p_{2B})$	$\delta_2 p_{1B} (1-\theta)$
π_{122}	$r_1\ s_{r1}\ p_{1B}\ s_{2B}\ p_{2B}$	$\delta_2 p_{1B}\,\theta$
π_{110}	$(1-r_1)\ s_{1A}\ p_{1A}$ $\times[1-s_{2A}\ p_{2A}\ (1-r_2)-r_2\ s_{r2}\ p_{2B}]$	$\delta_1\ p_{1A}\ (1-\gamma_1-\gamma_2)$
π_{100}	$1-\sum_{\text{above}} \pi_{ijk}$	$1-\sum_{\text{above}} \pi_{ijk}$

NOTE: Here π_{ijk} is used to represent the probability than an individual fish has capture history *ijk*.

the fish overwintered in reach 1 (r_1), survived to Lower Granite Dam (s_{r1}), was not detected at Lower Granite Dam in the second year ($1 - p_{1B}$), migrated and survived from Lower Granite Dam to Little Goose Dam in the second year (s_{2B}), and finally was detected at Little Goose Dam (p_{2B}). The probability of this event can be expressed as $r_1 s_{r1}(1 - p_{1B})(s_{2B})(p_{2B})$. Now, suppose that the fish overwintered in reach 2. Thus, the fish did not overwinter in reach 1 ($1 - r_1$), survived in year 1 to Lower Granite Dam (s_{1A}), was not detected at Lower Granite Dam in year 1 ($1 - p_{1A}$), overwintered in reach 2 (r_2), survived from Lower Granite Dam to Little Goose Dam (s_{r2}), and finally was detected at Little Goose Dam (p_{2B}). The probability of this event can be expressed as $(1 - r_1)s_{1A}(1 - p_{1A})r_2 s_{r2} p_{2B}$. Then π_{102} is found by summing these two terms. The other cell probabilities can be found similarly (Table 2).

In this formulation, the model contains 11 parameters but only 7 minimum sufficient statistics (MSS). With more parameters than MSS, it is impossible to separately estimate all 11 parameters. However, there are certain groupings of parameters in the cell probabilities that always appear together and can be replaced with a smaller number of new parameters to reduce the dimensionality. Overall, the 11 parameters can be condensed into 7 such parameter groupings [$\delta_1 = (1 - r_1)s_{1A}$, $\delta_2 = r_1 s_{r1}$, $\theta = s_{2B} p_{2B}$, $\gamma_1 = (1 - r_2)s_{2A} p_{2A}$, $\gamma_2 = r_2 s_{r2} p_{2B}$, and p_{1A} and p_{1B}]. These seven parameters result in a revised parameterization for the cell probabilities (Table 2) and can be estimated using maximum likelihood estimation. Because the number of parameters equals the dimension of the MSS, closed forms solutions for the estimators can be found using the method of moments (Arnold 1990). These closed form solutions for the seven parameters are

$$\hat{\delta}_1 = \frac{(n_{101} + n_{111})(n_{110} + n_{111} + n_{112})}{R n_{111}},$$

$$\hat{\delta}_2 = \frac{(n_{120} + n_{122})(n_{111} n_{102} + n_{111} n_{122} - n_{101} n_{112})}{R n_{111} n_{122}},$$

$$\hat{\gamma}_1 = \frac{n_{111}}{n_{110} + n_{111} + n_{112}},$$

$$\hat{\gamma}_2 = \frac{n_{112}}{n_{110} + n_{111} + n_{112}},$$

$$\hat{\theta} = \frac{n_{122}}{n_{120} + n_{122}},$$

$$\hat{p}_{1A} = \frac{n_{111}}{n_{101} + n_{111}},$$

and

$$\hat{p}_{1B} = \frac{n_{111}n_{122}}{n_{111}n_{102} + n_{111}n_{122} - n_{101}n_{112}}.$$

3.4 Interpretation and Comparison of Parameters

The parameters δ_1 and δ_2 are easily interpreted in terms of the original model. First, $\delta_1 = (1 - r_1)s_{1A}$ gives the probability that an individual migrates the first year (i.e., does not overwinter) and survives to the tailrace of Lower Granite Dam. Second, $\delta_2 = r_1 s_{r1}$ is the probability that an individual fish overwinters between the release point and Lower Granite Dam and survives to Lower Granite Dam the following year. Thus, the total survival probability from the release site to the tailrace of Lower Granite Dam over the two years of study is given by

$$\text{total survival probability } = \delta_1 + \delta_2 = (1 - r_1)s_{1A} + r_1 s_{r1}.$$

When some smolts overwinter, but only first-year detection data are used to construct capture histories, the survival probability reported from the standard CJS model is actually the joint probability of migrating in the first year (not overwintering) and surviving in the river reach, referred to as δ_1 in the new model. Thus, the difference between the overall survival probability estimated by the new model ($\hat{\delta}_1 + \hat{\delta}_2$) and the CJS estimate of the survival probability, $\hat{s}_1$, is equal to the estimate, $\hat{\delta}_2$. That is, in the presence of overwintering, the bias incurred through the use of the CJS model in estimating the overall reach survival is $-\hat{\delta}_2$. As would be expected, this bias increases as the prevalence of overwintering increases. Note that the overwintering rate can not be separately estimated by this approach.

The three other grouped parameters, γ_1, γ_2, and θ, combine elements of the survival process and the capture process in the second (and last) reach in much the same way that the last period survival probability and the final detection probability can not be separately estimated in the standard CJS likelihood models.

3.5 Allowing for Known-Removals in the Capture History

The expansion of the overwintering model to account for known-removals due to transportation required the inclusion of two additional parameters, T_1 and T_2, and the inclusion of two more capture histories (n_{130} and n_{140}) in the multinomial likelihood. The first parameter, T_1, gives the probability that a fish recaptured at Lower Granite Dam in the first year will not be returned to the river (i.e., will be transported). The second,

T_2, gives the probability that a fish recaptured at Lower Granite Dam in the second year will not be returned to the river. Analytic solutions for these transportation parameters were easily obtained as they are simply the ratio of the number of fish removed for transportation at the site to the number of fish detected at the site in the given year. Analytic solutions for the nine parameters are

$$\hat{T}_1 = \frac{n_{130}}{n_{130} + n_{110} + n_{111} + n_{112}},$$

$$\hat{T}_2 = \frac{n_{140}}{n_{140} + n_{120} + n_{122}},$$

$$\hat{\gamma}_1 = \frac{n_{111}}{n_{110} + n_{111} + n_{112}} \text{(no change from general model)},$$

$$\hat{\gamma}_2 = \frac{n_{112}}{n_{110} + n_{111} + n_{112}} \text{(no change from general model)},$$

$$\hat{\theta} = \frac{n_{122}}{n_{120} + n_{122}} \text{(no change from general model)},$$

$$\hat{p}_{1A} = \frac{(n_{130} + n_{110} + n_{111} + n_{112})n_{111}}{(n_{101} + n_{111})(n_{130} + n_{110} + n_{111} + n_{112}) - n_{130}n_{101}},$$

$$\hat{\delta}_1 = \frac{(n_{101} + n_{111})(n_{130} + n_{110} + n_{111} + n_{112}) - n_{130}n_{101}}{Rn_{111}},$$

$$\hat{p}_{1B} = \frac{(n_{120} + n_{122} + n_{140})\hat{\theta}}{n_{102} + (n_{120} + n_{122} + n_{140})\hat{\theta} - R\hat{\delta}_2(1 - \hat{p}_{1A})\hat{\gamma}_2},$$

and

$$\hat{\delta}_2 = \frac{n_{120} + n_{122} + n_{140}}{R\hat{p}_{1B}}.$$

In a release–recapture study design, there is no need to account for known removals at the terminal detection site. Thus, in the two-period study described here, it was not necessary to account for known removals at Little Goose Dam.

In theory, approximations to the variances of these parameter estimates could be calculated using the delta method (Seber 1982). However, due to the complicated nature of the closed-form estimators, these computations would be lengthy and their expressions awkward. Alternatively, we implemented a numerical optimization procedure to find the values for the parameters that maximized the likelihood function. Such optimization procedures usually produce an estimate of the variance-covariance matrix as a byproduct at the final iteration (Seber and Wild 1989). The optimization routine FLETCH [Fletcher 1970; Vaessen 1984 (available from the first author)] was used with the models developed here to estimate the parameters and to numerically calculate variance estimates for the parameters. In addition, most statistical software packages (e.g., S-Plus) include nonlinear optimization procedures for maximum likelihood estimation that provide standard errors of the parameter estimates.

Table 3. Combined Survival and Overwintering Parameters for Snake River Fall Chinook Salmon, 1995 Asotin Releases

Release group	*Release group*	*Number released*	$\hat{\delta}_1$	$\hat{\delta}_2$	$\hat{\delta}_1 + \hat{\delta}_2$	$\hat{s}_1$
AS1	June 19	2,778	.4927	0	.4927	.4927
			(.0262)	(0)	(.0262)	(.0262)
AS2	June 27	2,489	.4293	.0174	.4467	.4293
			(.0272)	(.0096)	(.0285)	(.0272)
AS3	July 5	3,523	.4056	.00949	.4151	.4056
			(.0413)	(.0033)	(.0412)	(.0413)
Combined		8,790	.4235	.0124	.4360	.4235
			(.0162)	(.0040)	(.0164)	(.0162)

NOTES: Survival refers to the river reach from the Asotin release site to the tailrace of Lower Granite Dam. The parameters and were obtained using the new multinomial model developed in this article. The estimate was obtained using the CJS model over two river reaches. Standard errors are given in parentheses below the estimates.

4. ANALYSIS OF SNAKE RIVER FALL CHINOOK SALMON DATA

For each release group, the combined survival and overwintering parameters for the first reach, $\hat{\delta}_1$ and $\hat{\delta}_2$, were calculated (Table 3), as well as the estimate of the overall survival probability, given simply by $\hat{\delta}_1 + \hat{\delta}_2$. These results are compared with the estimates obtained using the CJS model over the two reaches, $\hat{s}_1$. The models used in the analysis allowed for known-removals of fish in the smolt transportation program.

It is clear from the data (Table 1) that overwintering was not a common response for the fish in these three releases. Out of 8,790 fish released, only 69 (.78%) were detected in the second year, with 14 second-year detections at Lower Granite Dam and 61 second year detections at Little Goose Dam. This degree of overwintering does not appreciably alter the estimates of the reach survival probability. The estimate of the total reach survival for the combined Asotin releases is given by $\hat{\delta}_1 + \hat{\delta}_2 = .4360$ (SE=.0164), whereas the estimate based on only first-year capture histories is given by $\hat{\delta}_1 = .4235$ (SE=.0162). The discrepancy between the two methods (.0125) falls within one standard error (.0162) of the estimate of the survival probability found using the CJS method on the first-year capture histories only.

Alternatively, the two years of capture history data could be collapsed into a single "year" and then basic CJS estimates obtained. This approach resulted in a point estimate for $\hat{s}_1$ of .4423 (SE=.0167). The disadvantage of this approach is that it assumes a constant detection probability for the two years of study. The new model developed here separately estimates the detection probability at Lower Granite Dam for each year of the study. For the Asotin releases, the first year detection probability was estimated as .4808 (SE=.0192), and the second year estimate of the detection probability was .1280 (SE=.0509). Collapsing the data into single-year capture histories gave an estimate of .4641 (SE=.0185) for the constant detection rate at Lower Granite Dam. Given the potential for greatly varying river conditions from year to year, it seems most reasonable not to assume a common detection probability across years.

In 1995 and 1996, the seasonal shutdown of the PIT-tag detection system may have resulted in an underestimation of survival and provided insight into the potential for a greater degree of future overwintering. In late November of 1995, a large flood pushed many fish down the river that might otherwise have overwintered. This flood occurred after the detection facilities at Lower Granite Dam and Little Goose Dam had been shut down for the season, so these fish were not detected for this study. However, the PIT-tag detection system at McNary Dam (Columbia River km 470), three dams and 165 km downstream from Little Goose Dam, remained in operation until December 13, with the flood resulting in a pulse of detections of migrating subyearling fall chinook salmon (Smith et al. 1996). If not for this flood, more subyearling migrants may have overwintered in the river reaches under study.

5. DISCUSSION

The new model developed here for assessing survival probabilities in the presence of overwintering represents an important theoretical improvement over the current release–recapture models for estimating survival of subyearling fall chinook salmon. The consideration of overwintering increases the biological realism of the model. In particular, the degree of this improvement increases with the degree of overwintering that occurs.

In the example of 1995 releases of hatchery fall chinook salmon presented here, the use of the new model and the inclusion of second-year capture histories did not produce substantially different results than were obtained using the standard CJS model and ignoring the second-year capture histories. This was due to the small percentage (.16% detected) of juveniles that overwintered between the release site and the first PIT-tag detection site at Lower Granite Dam. This confirms that CJS models provide a good approximation to total survival when the degree of overwintering is low.

This formal analysis confirms that the joint overwintering and second-year survival rate is very low (.0124) for the 1995 fall brood stock. However, this analysis does not assure that the percent of juveniles outmigrating the second year will always be so small. The November 1995 flood may have prevented subyearling fall chinook migrants from overwintering. Because the behavior and migration timing of fall chinook salmon is not well understood, we can not assume that the degree of overwintering will continue to be as low in future migrations. The overwintering tendency of juveniles probably depends on a combination of environmental conditions and particular river operations regulating flow and influencing temperature conditions, as well as habitat availability and suitability. Considering the overwintering response of subyearling fall chinook salmon can only result in more realistic models and more accurate estimates of the crucial survival rates for this endangered species. With stocks as small as they currently are, even the small percentage of second year migrants can not be ignored in attempts to protect this endangered salmon run.

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