**September 1997**

# THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

## VOLUME VIII: A NEW MODEL FOR ESTIMATING SURVIVAL PROBABILITIES & RESIDUALIZATION FROM A RELEASE RECAPTURE STUDY OF FALL CHINOOK SALMON (ONCORHYNCHUS TSCHAWYTSCHA) SMOLTS IN THE SNAKE RIVER

Technical Report

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# THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

## VOLUME VIII

A New Model for Estimating Survival Probabilities and Residualization
from a Release-Recapture Study of Fall Chinook Salmon
(*Oncorhynchus tschawytscha*) Smolts in the Snake River

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## PREFACE

Project 89-107, Epidemiological Survival Methods, was developed to provide statistical guidance on the design and analysis of PIT-tag survival studies to the Northwest fisheries community. Studies under this project have determined the statistical feasibility of conducting PIT-tag smolt survival studies, assessed analytical capabilities for analyzing the tagging experiments, and made recommendations on study design. As PIT-tag capabilities developed and research interests increased, the project has been instrumental in maintaining the statistical capabilities for designing and analyzing tagging studies to meet these expanded objectives. This report describes the extension of release-recapture theory to the analysis of fall subyearling chinook salmon with a new model that includes not only spring survival but also the probabilities of smolt residualizing and surviving over winter.

The statistical analysis was motivated by the continuing need for better and more realistic analytic tools and models for assessing the status of threatened and endangered salmon runs in the Snake and Columbia River system. Because some subyearling fall chinook salmon tend to overwinter before continuing their outmigration, it may not be appropriate to analyze their survival with models that consider only first-year capture history data. In years in which a substantial percentage of migrants overwinter, the effect of ignoring residualization behavior on the estimates of survival would be profound. This project compares methods for estimating survival and assesses the value of incorporating second-year yearling PIT-tag detections into overall smolt survival estimates. This analysis was conducted in cooperation with the National Marine Fisheries Service (NMFS) to assist in finding the most appropriate statistical methods for estimating in-river survival rates of fall chinook salmon smolt.

# ABSTRACT

## Objectives

Standard release-recapture analysis using Cormack-Jolly-Seber (CJS) models to estimate survival probabilities between hydroelectric facilities for Snake River fall chinook salmon (*Oncorhynchus tschawytscha*) ignore the possibility of individual fish residualizing and completing their migration in the year following tagging. These models do not utilize available capture history data from this second year and, thus, produce negatively biased estimates of survival probabilities. A new multinomial likelihood model was developed that results in biologically relevant, unbiased estimates of survival probabilities using the full two years of capture history data.

## Results

This model was applied to 1995 Snake River fall chinook hatchery releases to estimate the true survival probability from one of three upstream release points (Asotin, Billy Creek, and Pittsburgh Landing) to Lower Granite Dam. In the data analyzed here, residualization is not a common physiological response and thus the use of CJS models (e.g. S=0.4235, s.e. = 0.0162 for the combined Asotin releases) did not result in appreciably different results than the true survival probability (S=0.4360, s.e.=0.0164 for the combined Asotin releases) obtained using the new multinomial likelihood model.

## Recommendations

The differences between the models were not substantial for the release groups examined here due to a very small percentage of fish that residualized and were detected in the second year. However, because the behavior and migration timing of fall chinook salmon is not well understood, we can not assume that the degree of residualization will continue to be as low in future migrations or in other locations. Considering the overwintering response of subyearling fall chinook salmon results in more realistic models and more accurate estimates of the crucial survival rates for this threatened 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.

# ACKNOWLEDGMENTS

This study was funded by the Bonneville Power Administration under contract DE-BI79-90BP02341. The fall chinook analyzed were provided by the Lyons Ferry Hatchery of the Washington Department of Fish and Wildlife and were released and monitored by the staff of the Coastal Zone and Estuarine Studies Division of the Northwest Fisheries Science Center, National Marine Fisheries Service. Capture history information was obtained from the PTAGIS database maintained by the Pacific States Marine Fisheries Commission.

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## Introduction

The wild population of Snake River fall chinook salmon (*Oncorhynchus tschawytscha*) has been classified as a threatened or an 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 migration the following year. The degree to which this residualization 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 residualization to be above 3% for one group of Snake River hatchery sub-yearling fall chinook salmon tagged and released in 1994.

Release-recapture models (Cormack 1964) have been used successfully to estimate survival and detection probabilities for juvenile spring chinook salmon migrants on the Snake River (Muir et al. 1996). However, the versions of the Cormack (1964) model 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 residualization. This new model uses the two years of capture history information to more realistically reflect the biology of fall chinook smolts in order to more accurately estimate survival. The improvement in survival estimates will provide more complete information for better management of this threatened species.

## Example: Snake River fall chinook salmon

Beginning in the spring of 1995, the 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 the standard Cormack (1964) model without regard for residualization or consideration of second-year capture histories. Due to the low numbers of wild fall chinook tagged, the use of the new residualization model is demonstrated using Snake River hatchery releases of fall chinook salmon. The nine tag groups selected for analysis were released in the Snake River above Lower Granite Dam at three sites, Asotin (river km 235 above the confluence with the Columbia River), Billy Creek (river km 265), and Pittsburgh Landing (km 346). 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 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 residualization model are compared to those obtained using the standard Cormack (1964) 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, and subsequent downstream detection opportunities at Lower Granite Dam (river km 173) and at Little Goose Dam (river km 113) (Fig. 1). 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 fish that may be late migrants and a resulting underestimation of survival. The likelihood model developed here assumes 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 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. To account for the possibility of individuals overwintering in the river, the notation must be expanded. A “2” is 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 has been 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

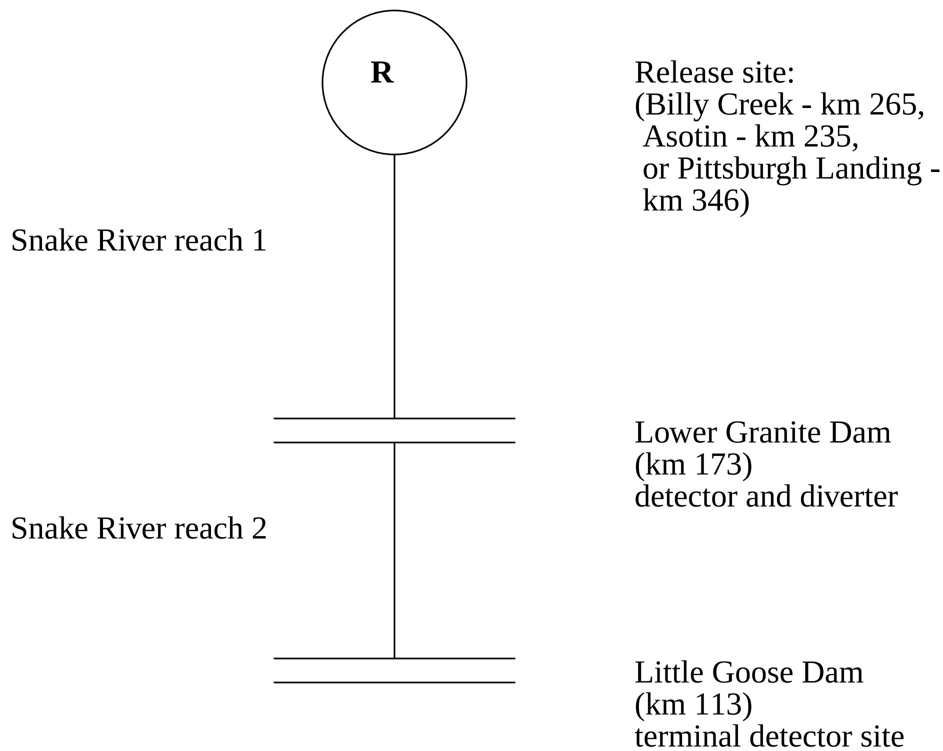


**Fig. 1.** Tagging and detection scenario for fall chinook PIT-tag survival study on the Snake River. Initial releases took place above Lower Granite Dam and subsequent detections occurred at Lower Granite Dam and Little Goose Dam.

depicted in Fig. 1, there are ten 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 residualized 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 ten 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 ($R$ = 8790) 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.

## Statistical Model

### 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 insuring 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 tags on the fish remain attached 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 residualize may have a different survival

**Table 1: The ten possible capture histories for a two period fall chinook salmon release-recapture study with the possibility of residualization and removal for transportation. Capture history counts are given for the combined Asotin releases (n=8790).**

| Capture history | Description | Count |
|---|---|---|
| 1 0 0 | Individual is released, then is not detected again | 6487 |
| 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 |

probability than those that do not residualize.

(4) The history of survival, capture, and residualization 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 residualizes in a reach is the same for all tagged fish alive at the beginning of the reach.

(8) The probability that a fish residualizes in a reach is not affected by its previous history of captures.

(9) Fish that residualize 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 residualize between Lower Granite Dam and Little Goose Dam may experience quite different river conditions depending on the exact location of residualization 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 residualizing 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.

## Model parameters

The fall chinook salmon residualization 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 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 residualize, a parameter is included representing the conditional probability of survival from release to Lower Granite Dam the following year, given that the fish residualized 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 residualized somewhere in the second reach. Parameters $r_1$ and $r_2$ are defined as the probability that a smolt will residualize in the first or second reach, respectively. The parameters of the general model are detailed below and their function illustrated in Fig. 2

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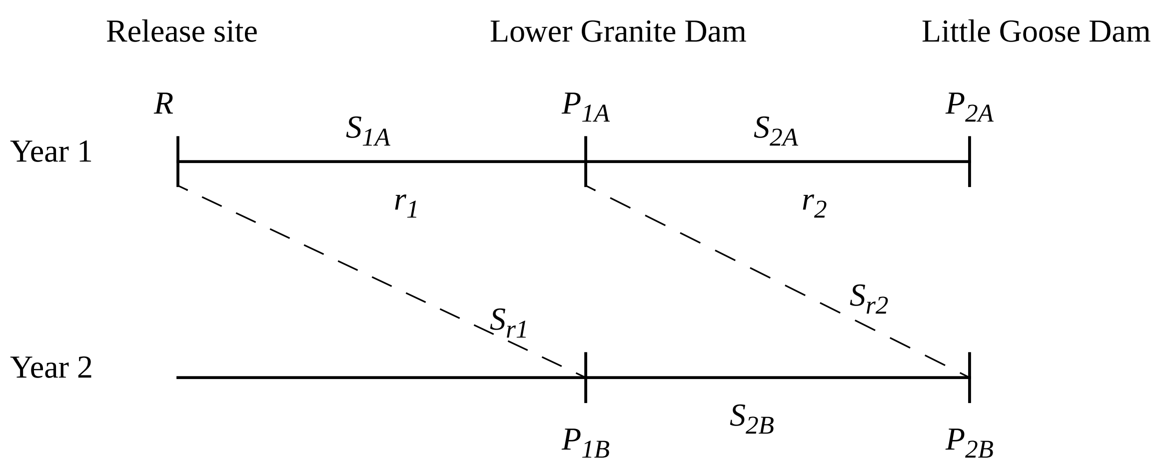


**Fig. 2.** Schematic of the parameters used to define the multinomial likelihood model. The subscripts 1 and 2 refer to the reach of the river, while the subscripts A and B refer to the first and second years, respectively.

$S_{1A}$ = 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 residualize 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,

$S_{2A}$ = 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 residualize in reach 2 (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,

$P_{1B}$ = probability of detection of a live individual at Lower Granite Dam in year 2,

$S_{2B}$ = 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 residualized in 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,

$r_1$ = probability of 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 residualization for an individual in the reach from Lower Granite Dam to Little Goose Dam, given that the individual enters the reach in the first year of study - this parameter does not imply survival,

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

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

This set of eleven parameters is the minimum set required to realistically model the scenario presented in Fig. 2.

## The multinomial likelihood function

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

$$L(n_{100}, n_{101}, n_{110}, n_{111}, n_{112}, n_{102}, n_{120}, n_{122} | R, \underset{\sim}{r_i}, \underset{\sim}{P_{ij}}, \underset{\sim}{S_{ij}}, \underset{\sim}{S_{ri}}) =$$

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

$$\bullet\ (p_{102})^{n_{102}} (p_{120})^{n_{120}} (p_{122})^{n_{122}} (p_{100})^{n_{100}}$$

where $n_{100} = R - (n_{101} + n_{110} + n_{111} + n_{112} + n_{102} + n_{120} + n_{122})$ and the $p_{ijk}$ 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, $p_{102}$. 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 may have residualized in either of the two reaches. Suppose, first that the fish residualized 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 residualized in reach 2. Thus, the fish did not residualize 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 ($1-P_{1A}$), residualized 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 $p_{102}$ is found by summing these two terms. The other cell probabilities can be found similarly.

In this formulation, the model contains eleven parameters but only seven minimum sufficient statistics (MSS). With more parameters than MSS, it is impossible to separately estimate all eleven parameters. However, there are certain groupings of parameters in the cell probabilities

**Table 2: Expected values for the cell (capture history) probabilities under the full parameterization (center column) and under the reduced parameterization (right column). Here $p_{ijk}$ is used to represent the probability than an individual fish has capture history i j k.**

| Probability of capture history | Expected value given the original parameterization | Expected value with reduced parameterization |
|---|---|---|
| $p_{111}$ | $(1-r_1)S_{1A}P_{1A}(1-r_2)S_{2A}P_{2A}$ | $\delta_1 P_{1A}\gamma_1$ |
| $p_{101}$ | $(1-r_1)S_{1A}(1-P_{1A})(1-r_2)S_{2A}P_{2A}$ | $\delta_1(1-P_{1A})\gamma_1$ |
| $p_{112}$ | $(1-r_1)S_{1A}P_{1A}r_2S_{r2}P_{2B}$ | $\delta_1 P_{1A}\gamma_2$ |
| $p_{102}$ | $(1-r_1)S_{1A}(1-P_{1A})r_2S_{r2}P_{2B} +$ $r_1S_{r1}(1-P_{1B})S_{2B}P_{2B}$ | $\delta_1(1-P_{1A})\gamma_2 + \delta_2(1-P_{1B})\theta$ |
| $p_{120}$ | $r_1S_{r1}P_{1B}(1-S_{2B}P_{2B})$ | $\delta_2 P_{1B}(1-\theta)$ |
| $p_{122}$ | $r_1S_{r1}P_{1B}S_{2B}P_{2B}$ | $\delta_2 P_{1B}\theta$ |
| $p_{110}$ | $(1-r_1)S_{1A}P_{1A}\bullet$ $(1-S_{2A}P_{2A}(1-r_2)-r_2S_{r2}P_{2B})$ | $\delta_1 P_{1A}(1-\gamma_1-\gamma_2)$ |
| $p_{100}$ | $1-\sum_{above} p_{ijk}$ | $1-\sum_{above} p_{ijk}$ |

that always appear together and can be replaced with a smaller number of new parameters to reduce the dimensionality. Overall, the eleven parameters can be condensed into seven such parameter groupings ( $\delta_1 = (1-r_1)S_{1A}$ , $\delta_2 = r_1S_{r1}$ , $\theta = S_{2B}P_{2B}$, $\gamma_1 = (1-r_2)S_{2A}P_{2A}$ , $\gamma_2 = r_2S_{r2}P_{2B}$, 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 given below (Eq. 1):

$$\hat{\delta}_1 = \frac{(n_{101} + n_{111})(n_{110} + n_{111} + n_{112})}{Rn_{111}} \quad \text{(Eq. 1a)}$$

$$\hat{\delta}_2 = \frac{(n_{120} + n_{122})(n_{111}n_{102} + n_{111}n_{122} - n_{101}n_{112})}{Rn_{111}n_{122}} \quad \text{(Eq. 1b)}$$

$$\hat{\gamma}_1 = \frac{n_{111}}{n_{110} + n_{111} + n_{112}} \quad \text{(Eq. 1c)}$$

$$\hat{\gamma}_2 = \frac{n_{112}}{n_{110} + n_{111} + n_{112}} \quad \text{(Eq. 1d)}$$

$$\hat{\theta} = \frac{n_{122}}{n_{120} + n_{122}} \quad \text{(Eq. 1e)}$$

$$\hat{P}_{1A} = \frac{n_{111}}{n_{101} + n_{111}} \quad \text{(Eq. 1f)}$$

$$\hat{P}_{1B} = \frac{n_{111}n_{122}}{n_{111}n_{102} + n_{111}n_{122} - n_{101}n_{112}}. \quad \text{(Eq. 1g)}$$

## Interpretation and comparison of parameters

The parameters $\delta_1$ and $\delta_2$ 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 residualize) and survives to the tailrace of Lower Granite Dam. Second, $\delta_2$ (= $r_1S_{r1}$) is the probability that an individual fish residualizes 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:

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

When some smolts residualize, but only first-year detection data are used to construct capture histories, the survival probability reported from the standard Cormack (1964) model is actually the joint probability of migrating in the first year (not overwintering) and surviving in the river reach, referred to as $\delta_1$ 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 Cormack estimate of the survival probability, $\hat{S}_1$, is equal to the estimate, $\hat{\delta}_2$. That is, in the presence of residualization, the bias incurred through the use of the Cormack (1964) model in estimating the overall reach survival is $-\delta_2$. As would be expected, this bias increases as the degree of residualization increases. Note that the residualization rate can not be separately estimated by this approach.

The three other grouped parameters, $\gamma_1$, $\gamma_2$, and $\theta$, 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 Cormack (1964) likelihood model.

## Allowing for known-removals in the capture history

The expansion of the residualization 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 given below (Eq. 2):

$$\hat{T}_1 = \frac{n_{130}}{n_{130} + n_{110} + n_{111} + n_{112}} \qquad \text{(Eq. 2a)}$$

$$\hat{T}_2 = \frac{n_{140}}{n_{140} + n_{120} + n_{122}} \qquad \text{(Eq. 2b)}$$

$$\hat{\gamma}_1 = \frac{n_{111}}{n_{110} + n_{111} + n_{112}} \qquad \text{(no change from general model)} \qquad \text{(Eq. 2c)}$$

$$\hat{\gamma}_2 = \frac{n_{112}}{n_{110} + n_{111} + n_{112}} \qquad \text{(no change from general model)} \qquad \text{(Eq. 2d)}$$

$$\hat{\theta} = \frac{n_{122}}{n_{120} + n_{122}} \qquad \text{(no change from general model)} \qquad \text{(Eq. 2e)}$$

$$\hat{P}_{1A} = \frac{(n_{130} + n_{110} + n_{111} + n_{112})n_{111}}{(n_{101} + n_{111})(n_{130} + n_{110} + n_{111} + n_{112}) - n_{130}n_{101}} \qquad \text{(Eq. 2f)}$$

$$\hat{\delta}_1 = \frac{(n_{101} + n_{111})(n_{110} + n_{111} + n_{112} + n_{130}) - n_{101}n_{130}}{Rn_{111}} \qquad \text{(Eq. 2g)}$$

$$\hat{P}_{1B} = \frac{(n_{120} + n_{122} + n_{140})\hat{\theta}}{n_{102} + (n_{120} + n_{122} + n_{140})\hat{\theta} - R\hat{\delta}_2(1 - \hat{P}_{1A})\hat{\gamma}_2} \qquad \text{(Eq. 2h)}$$

$$\hat{\delta}_2 = \frac{n_{120} + n_{122} + n_{140}}{R\hat{P}_{1B}}. \qquad \text{(Eq. 2i)}$$

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. However, due to the complicated nature of the closed-form estimators, these computations would be lengthy, and their expressions awkward. Alternatively, use of a numerical optimization procedure to find the parameter estimates also provides an estimate of the Hessian matrix of second derivatives of the parameters at the final iteration (Seber and Wild 1989). This estimate of the Hessian is then inverted to obtain the approximate variance-covariance matrix. The optimization routine FLETCH (Fletcher 1970) was used in the models developed here to estimate the parameters and to numerically calculate variance estimates for the parameters.

## Analysis of Snake River fall chinook salmon data

For each release group the combined survival and residualization 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, simply given by $\hat{\delta}_1 + \hat{\delta}_2$. These results are compared with the estimates obtained using the Cormack (1964) 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 3, as well as the counts for the Asotin releases in Table 1) that residualization was not a common response for the fish in these release groups. Out of over 16,000 fish released only 102 (0.62%) were detected in the second year. In many cases, the parameter $\hat{\delta}_1$ could not be calculated (see Table 3) due to $n_{122}$ being equal to zero resulting in division by zero (see Eqs. 1b, 2i, 2h, and 2e). For the three Pittsburgh landing releases, there were

**Table 3: Combined survival and residualization parameters for Snake River fall chinook, 1995 releases. Survival refers to the river reach from the release site to Lower Granite Dam. The abbreviations for the release sites are BC = Billy Creek, PL = Pittsburgh Landing, and AS = Asotin. The parameters $\hat{\delta}_1$ and $\hat{\delta}_2$ were obtained using the new multinomial model developed in this chapter. The estimate $\hat{S}_1$ was obtained using the Cormack (1964) model over two river reaches.**

| Release site | Release date | Number released | $\hat{\delta}_1$ | $\hat{\delta}_2$ | $\hat{\delta}_1 + \hat{\delta}_2$ | $\hat{S}_1$ |
|---|---|---|---|---|---|---|
| BC1 | June 1 | 1220 | 0 | 0.6687 | 0.6687 | 0.6687 |
| BC2 | June 8 | 1317 | No estimate | 0.5862 | 0.5862 | 0.5862 |
| BC3 | June 15 | 1124 | 0.00284 | 0.5892 | 0.5921 | 0.5892 |
| all BC | | 3661 | 0.00442 | 0.6135 | 0.6180 | 0.6135 |
| | | | | | | |
| PL1 | May 31 | 1353 | No estimate | 0.6515 | 0.6515 | 0.6515 |
| PL2 | June 7 | 1341 | 0 | 0.6918 | 0.6918 | 0.6918 |
| PL3 | June 14 | 1326 | No estimate | 0.6403 | 0.6403 | 0.6403 |
| all PL | | 4020 | 0 | 0.6585 | 0.6585 | 0.6585 |
| | | | | | | |
| AS1 | June 19 | 2778 | 0 | 0.4927 | 0.4927 | 0.4927 |
| AS2 | June 27 | 2489 | 0.0174 | 0.4293 | 0.4467 | 0.4293 |
| AS3 | July 5 | 3523 | 0.00949 | 0.4056 | 0.4151 | 0.4056 |
| all AS | | 8790 | 0.0124 | 0.4235 | 0.4360 | 0.4235 |
| all releases | | 16471 | 0.0110 | 0.5219 | 0.5329 | 0.5219 |

only two detections at Lower Granite Dam in the second year and neither of these fish was subsequently detected at Little Goose Dam, thus not allowing for the calculation of $\hat{\delta}_1$. Even though the combined residualization and survival parameter can not be calculated mathematically, we see that it is essentially zero - that is, very few fish are residualizing. This degree of residualization does not appreciably alter the estimates of the reach survival probability.

The counts of the individual capture histories and all the parameter estimates and associated standard errors for the combined Asotin releases are provided for illustrative purposes in Table 4.

**Table 4: Summary of the combined Asotin releases. The counts of the ten possible capture histories comprise the data used in the analysis. Estimates of all nine parameters and their standard errors are also given.**

| Capture history | Count | Parameter | Estimate | S.E.(estimate) |
|---|---|---|---|---|
| 1 1 1 | 246 | $\delta_1$ | 0.0124 | 0.0040 |
| 1 1 0 | 808 | $\delta_2$ | 0.4235 | 0.0162 |
| 1 0 1 | 449 | $P_{1A}$ | 0.4808 | 0.0192 |
| 1 0 0 | 6487 | $P_{1B}$ | 0.1280 | 0.0509 |
| 1 0 2 | 50 | $\gamma_1$ | 0.2323 | 0.0130 |
| 1 2 0 | 8 | $\gamma_2$ | 0.0047 | 0.0021 |
| 1 2 2 | 6 | $\theta$ | 0.4286 | 0.1327 |
| 112 | 5 | $B_1$ | 0.4084 | 0.0116 |
| 1 5 | 731 | $B_2$ | 0 | 0 |
| 1 6 | 0 | | | |

The Asotin releases contained the highest proportion of residualizing fish with 14 second year detections at Lower Granite Dam and 61 second year detections at Little Goose Dam. Even here, however, this degree of residualization does not significantly alter the estimates of the reach survival probability. The estimate of the true reach survival for the combined Asotin releases is given by $\hat{\delta}_1 + \hat{\delta}_2 = 0.4360$ (s.e. 0.0164), whereas the estimate based on only first year capture histories is given by $\hat{\delta}_2 = 0.4235$ (s.e. 0.0162). Even this largest discrepancy between the two methods falls within one standard error (0.0162) of the estimate of the survival probability found using the Cormack 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. For the combined Asotin releases, this approach resulted in a point estimate for $\hat{S}_1$ of 0.4423 (s.e. 0.0167). 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 0.4808 (s.e. 0.0192), and the second year estimate of the detection probability was 0.1280 (s.e. 0.0509). Collapsing the data into single year capture histories gave an estimate of 0.4641 (s.e. 0.0185) 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 residualization. In late November of 1995, a large flood pushed many fish down the river that may have overwintered. This flood occurred after the detection facilities at Lower Granite Dam and Little Goose Dam had been shut down for the season and thus 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.

## Discussion

The new model developed here for assessing survival probabilities in the presence of residualization 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 residualization 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 Cormack (1964) model and ignoring the second-year capture histories. This was due to the small percentage (0.16% detected) of juveniles that overwintered between the release site and the first PIT-tag detection site at Lower Granite Dam. This confirms that the Cormack model provides a good approximation to total survival when the degree of residualization is low.

This formal analysis confirms that the joint residualization and second year survival rate is very low (0.0124) for the 1995 fall brood stock. However, this analysis does not assure 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 residualization 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.

## Literature cited


Arnold, S.F. 1990. Mathematical Statistics. Prentice-Hall, Inc, Englewood Cliffs, NJ. 636 p.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., and Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. Bethesda, MD. 437 p.

Connor, W.P., Burge, H.L., Nelle, R.D., Eaton, C., and Waitt, R. 1996. Rearing and emigration of naturally produced juvenile Snake River fall chinook salmon. *In* D.W. Rondorf and K.F. Tiffan [ed.] Identification of the spawning, rearing, and migratory requirements of fall chinook salmon in the Columbia River basin. Annual report 1994 to Bonneville Power Administration, contract DE-AI79-91BP21708. (Available from Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.)

Cormack, R.M. 1964. Estimates of survival from the sightings of marked animals. Biometrika 51:429-438.

Fletcher, R. 1970. A new approach to variable metric algorithms. Computer Journal 13:317-322.

Mead, J., and Stein, C., eds. 1996. PTAGIS3 user manual. Pacific States Marine Fisheries Commission. Gladstone, OR 97027.

Muir, W.D., Smith, S.G., Hockersmith, E.E., Achord, S., Absolon, R.F., Ocker, P.A., Eppard, M.B., Ruehle, T.E., Williams, J.G., Iwamoto, R.N., and Skalski, J.R. Survival estimates for the passage of yearling chinook salmon and steelhead through Snake River dams and reservoirs. Annual report to Bonneville Power Administration, Portland, OR, and U.S. Army Corps of Engineers, Walla Walla, WA, Project E86940119. (Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112-2097.)

Seber, G.A.F. and Wild, C.J. 1979. Nonlinear regression. Wiley, New York, NY.

Smith, S.G. 1991. Assessing hazards in wild populations using auxiliary variables in tag-release models. Ph.D. dissertation. University of Washington. Seattle, WA. 351 p.

Smith, S.G., Muir, W.D., Hockersmith, E.E., Eppard, M.B., and Connor, W.P. 1996. Passage survival of natural and hatchery subyearling fall chinook salmon to Lower Granite, Little Goose, and Lower Monumental Dams. *In* J.G. Williams and T.C. Bjornn [ed.] Fall chinook salmon survival and supplementation studies in the Snake River and lower Snake River reservoirs.

Annual report to Bonneville Power Administration, Portland, OR, and U.S. Army Corps of Engineers, Walla Walla, WA, Project E86950141. (Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112-2097.)