A Migratory Life-Cycle Release-Recapture Model for Salmonid PIT-Tag Investigations

Rebecca A. BUCHANAN and John R. SKALSKI

Since 1987, millions of juvenile salmonids (smolts; *Oncorhynchus* species) in the Snake and upper Columbia rivers have been tagged with Passive Integrated Transponder (PIT) tags, and detected at hydroelectric projects as they migrate downriver to the Pacific Ocean. Since the late 1990s, detection of PIT-tagged adults has been possible at some dams. Existing release-recapture models are designed for either juvenile data or adult data, but not both. We present a migratory life-cycle release-recapture model that follows tagged individuals from their release as juveniles through their return migration as adults, accounting for downstream barge transportation of juveniles, right-censoring due to known removals at dams, and adult age at maturity. This branching model estimates river survival, age-specific probabilities of adult return, and relative effects of smolt transportation on survival. Performance measures are defined using model parameters. We analyze a dataset of 58,447 PIT-tagged summer Chinook salmon released in 2000 in the Snake River. For nontransported fish, juvenile survival from passage at Lower Granite Dam to Bonneville Dam was estimated at 60.3% ($\widehat{\mathrm{SE}} = 8.1\%$), and the ocean return probability to Bonneville was estimated at 4.5% ($\widehat{\mathrm{SE}} = 0.7\%$). The smolt-to-adult ratio (SAR) for the entire release group was estimated at 2.0% ($\widehat{\mathrm{SE}} = 0.09\%$), and perceived inriver adult survival was estimated at 87.1% ($\widehat{\mathrm{SE}} = 1.7\%$).

Key Words: Age-class model; Chinook salmon; Columbia River; Mark-recapture; Smolt-to-adult ratio; Smolt transportation.

1. INTRODUCTION

Pacific salmonids (*Oncorhynchus* spp.) make two migrations in their life cycle. The juvenile (smolt) outmigration is from freshwater rearing grounds to the Pacific Ocean; the adult upriver migration is from the Pacific Ocean back to the spawning grounds. Salmonids from the lower Snake River Basin pass eight large hydroelectric dams on the Snake and Columbia Rivers during both their migrations (Figure 1); upper Columbia River salmonids pass up to nine dams on their migrations. At three Snake River dams and one Columbia River dam, smolts are collected for transportation downriver by barge or truck, and returned to the river downstream of Bonneville Dam (river kilometer [RKM] 234), the dam closest to

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the mouth of the Columbia River. Because several Snake River and Upper Columbia River salmon populations are listed under the Endangered Species Act (16 USC 1531-1544), fishery managers monitor the salmon migrations, estimating adult return rates as well as both juvenile and adult survival probabilities over particular reaches and past individual dams. They must also determine the effect of transporting smolts downriver on adult return rates.

Tagging studies using Passive Integrated Transponder (PIT) tags have been conducted on these rivers since 1987. From 1995 to 2006, an average of 1.4 million juvenile salmonids were PIT-tagged annually. Juveniles are marked with PIT tags at the beginning of, or during, their outmigration, and are detected in the juvenile bypass systems located at most downstream dams. Tagged adults are detected in fish ladders located at several dams during their upriver migration. The resulting release-recapture data combine both juvenile and adult detections. Because the age at maturity varies, a single juvenile cohort provides adult returns to the spawning grounds over several years. Estimation of ocean survival, maturation rates, and the effect of smolt transportation on adult returns is tied to estimation of both juvenile and adult inriver survival. Current estimation methods address these problems separately. Cormack-Jolly-Seber (CJS; Cormack 1964; Jolly 1965; Seber 1965) release-recapture models are used to estimate juvenile survival (Skalski et al. 1998) and adult survival separately, while variations of the Ricker (1975) paired-release model (Burnham et al. 1987, pp. 78–99) are used to estimate smolt transportation effects. If the purpose is to estimate performance measures related to both juvenile and adult migrations, then the disjoint analysis of the life-history information contained in the juvenile-adult PIT-tag detections can result in model misspecification, bias, and information loss. The purpose of this article is to present a comprehensive likelihood model capable of extracting maximum information from the salmonid life history data contained in PIT-tag detection records routinely collected in the Columbia River Basin.

Migrating adults may be classified by age at maturity, or equivalently by year of adult return to freshwater. Thus, there are similarities between the salmon life history and the age-dependent "accession to breeding" models of Clobert et al. (1994), Pradel and Lebreton (1999), and Lebreton et al. (2003), in which adults are detected on their migration to breeding grounds. Two key differences between the salmon life history and the age-dependent breeding models are that salmon other than steelhead (*O. mykiss*) are semelparous (no repeat breeders), and that differing environmental conditions in different years prevent pooling all breeders (returning adults) across years. Differing environmental conditions also prevent us from assuming a common survival for breeders (returning salmon) and nonbreeders (nonmature individuals in the ocean), as assumed in the models of Clobert et al. (1994), Pradel and Lebreton (1999), and Lebreton et al. (2003). The available age-dependent breeding models are inappropriate for a semelparous, migratory species with varying age at reproduction. Instead, the necessary release-recapture model for these juvenile and adult salmonid data combines aspects of CJS models, age-dependent models, and the treatment-control models of Burnham et al. (1987).

In this article, we model the migratory life stages of Pacific salmon using both juvenile and adult release-recapture data, and allow for both smolt transportation and separation of adults into multiple age classes. We extract estimators of ocean survival and maturation, transportation effects, adult age distribution, and inriver survival. We demonstrate the model with a dataset from summer Chinook salmon (*O. tshawytscha*) tagged and released as smolts in 2000.

2. EXAMPLE: 2000 SUMMER CHINOOK SALMON RELEASED IN THE SNAKE RIVER

To illustrate the release-recapture model presented in this article, PIT-tag release and recapture data from summer Chinook salmon (*O. tshawytscha*) released in the Snake River upstream of Lower Granite Dam (RKM 695) in 2000 are used. Tagging data for $N = 58{,}477$ hatchery summer Chinook salmon released from traps, Knox Bridge, or Johnson Creek in Idaho in 2000 were obtained from the PTAGIS database maintained by the Pacific States Marine Fisheries Commission. We used the University of Washington software PitPro to convert the raw tagging data into detection (capture) histories and to perform quality control based on PTAGIS records. Juvenile detections were available from Lower Granite (LGR), Little Goose (LGO; RKM 635), and Lower Monumental (LMO; RKM 589) dams on the Snake River, and from McNary (MCN; RKM 470), John Day (JD; RKM 347), and Bonneville (BON) dams on the Columbia River (Figure 1). Returning migrants ("adults") were

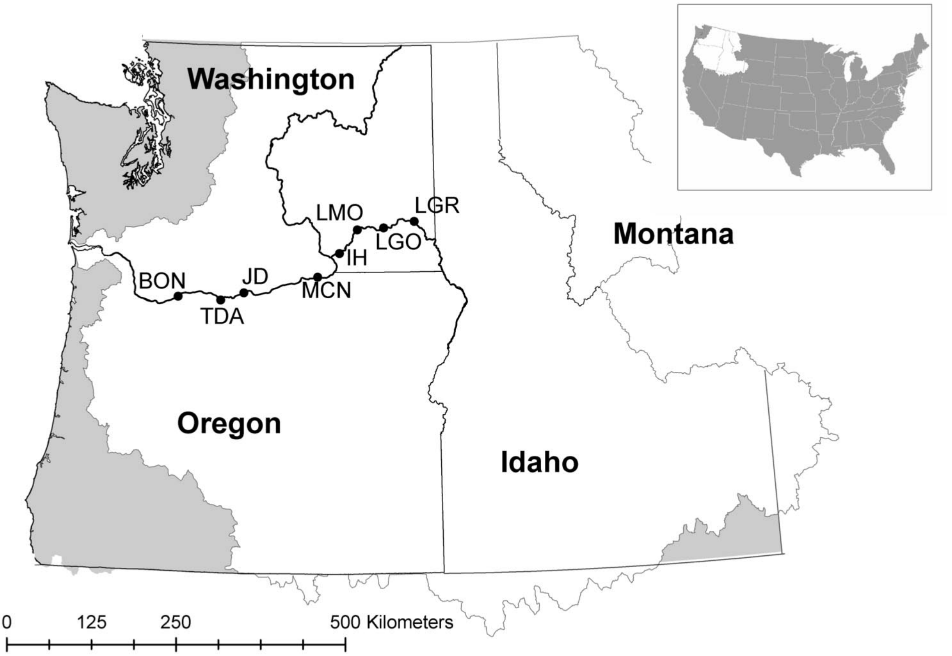

Figure 1. Columbia and Snake river basins, with hydroelectric dams passed by migrating summer Chinook salmon from the Snake River. Regions outside the basins are shaded. Abbreviations of dam names are as follows: BON = Bonneville, TDA = The Dalles, JD = John Day, MCN = McNary, IH = Ice Harbor, LMO = Lower Monumental, LGO = Little Goose, and LGR = Lower Granite.

detected in the adult fish ladders at BON and LGR from 2001 to 2004. Only a single age-4 (or “4-ocean”) adult was detected (in 2004), so this fish was censored at its last juvenile detection. Adult detections were also available from MCN in 2002 and 2003, and from Ice Harbor Dam on the Snake River (RKM 538) in 2003, but we omitted these extra data because they were not available in all return years, and added little to the demonstration of the model. Juvenile fish were collected and transported during their outmigration from LGR, LGO, LMO, and MCN. Because informative transportation effects cannot be estimated from small transport groups, we right-censored records of transport groups smaller than 1,000. Thus, the 862 fish transported at LMO and the 17 fish transported at MCN were right-censored at those sites. All further statements about the dataset pertain to the modified dataset after this censoring was performed.

3. STATISTICAL MODEL

The processes represented in this release-recapture model include inriver survival between successive detection sites for both juveniles and adults, ocean survival and maturation, and site-specific detection probabilities. At the juvenile detection sites, some detected fish are diverted to sampling rooms for study purposes or otherwise known to be removed from the migrating population; the records of these individuals are right-censored at these dams. Smolts labeled as “transported” at a transport dam but subsequently detected downstream as juveniles are right-censored at the transport dam. Adults may be removed from the migrating population (e.g., harvested or otherwise recovered) or recaptured and used in another study; thus, censoring of adults is also allowed, with records of removed adults right-censored at the last dam where they were detected. Censoring probabilities are estimated but considered nuisance parameters. Transportation probabilities at juvenile detection sites and the effect of transportation on age-specific adult return probabilities are also represented in the model. Ocean survival and maturation parameters, transportation effect parameters, and upriver adult survival, detection, and censoring parameters are distinguished by age class (i.e., year of adult return).

3.1 ASSUMPTIONS

The assumptions underlying the model are the usual assumptions of single-release, multiple recapture models (Cormack 1964; Skalski et al. 1998) as follows.

(A1) All nontransported smolts have equal probabilities of survival, detection, censoring, and transportation at juvenile sites.

(A2) All nontransported smolts have common ocean survival and maturation proclivities, and common age-specific adult survival, detection, and censoring probabilities, regardless of detection at previous juvenile sites.

(A3) All smolts transported at a given site have common probabilities of subsequent survival, maturation, and age-specific adult detection and censoring.

(A4) All adults at a given site in a given year have a common probability of upstream survival, detection, and censoring that may be dependent on juvenile transportation history.

(A5) Detection at an adult site has no effect on subsequent survival, detection, or censoring.

(A6) The fate of each tagged individual is independent of the fate of all other tagged individuals.

(A7) Interrogation for PIT tags occurs over a negligible distance relative to the lengths of the river reaches between sampling events.

(A8) Individuals selected for PIT-tagging are representative of the population of interest.

(A9) Tagging and release have no effect on subsequent survival, detection, censoring, or transportation probabilities.

(A10) All tags are correctly identified, and the detection histories (e.g., censored, transported) are correctly assigned.

(A11) There is no tag loss after release.

Assumptions (A1) and (A2) imply no effect of juvenile detection on survival. Because juvenile detection occurs only in the juvenile bypass systems, this implies no post-detection bypass mortality. Muir et al. (2001) found no significant effect of upstream detection (bypass) on downstream survival and detection for migrating yearling Chinook salmon and steelhead (*O. mykiss*) from 1993 through 1998. Assumptions (A1) and (A2) also imply mixing of nonbypassed smolts and smolts that are bypassed and returned to the river, immediately upon entering the tailrace of a dam. Smith et al. (1998) found violations of this assumption during periods of high spill, when detected (bypassed) fish arrived at downstream dams later than nondetected fish. However, there was no significant effect on downstream survival and detection.

There is some evidence that multiply-detected (bypassed) smolts have different survival than singly- or nondetected smolts (e.g., Sandford and Smith 2002). It is unclear whether this phenomenon is caused by inherent (e.g., size-related) heterogeneous detection and survival probabilities among the release group, or reflects an effect of passing through a bypass system (Smith et al. 2006). It is a violation of either Assumption (A1) or Assumption (A2). The focus of the model on estimation of survival, however, minimizes the effects of this violation, because survival estimators are known to be robust to heterogeneity in detection and survival parameters (Carothers 1973, 1979; Zabel et al. 2005).

Assumptions (A1) and (A2) also imply that release groups including significant numbers of fish that delay their migration to overwinter (e.g., fall Chinook salmon) should not be analyzed with this model. Because migration parameters vary with species, run type or race, and migration year, Assumptions (A1), (A2), (A3), and (A4) imply that combining release groups over these factors should be avoided. However, some pooling of release groups may be necessary to achieve required sample sizes. Pooling within species and races but across daily or weekly release groups within a migration season should be acceptable, because reach survival estimates for juveniles show little temporal variation within a season (Skalski 1998; Skalski et al. 1998; Muir et al. 2001).

Assumption (A5) is reasonable because of the high detection rates at most adult detection sites, and Assumption (A6) is reasonable due to the large numbers of individuals migrating. Violations of Assumption (A6) may negatively bias standard errors, but should not affect point estimates. Assumption (A7) allows us to attribute estimated mortality to the river reaches being studied, rather than to the detection process. This assumption is reasonable because detection occurs only in dam bypass systems (juvenile or adult), which are passed relatively quickly compared to the time spent migrating. In addition, Skalski et al. (1998) found that predetection bypass mortality has no effect on point estimates or standard error estimates for survival parameters, and Muir et al. (2001) found no significant post-detection bypass mortality for hatchery yearling Chinook salmon and steelhead. The model developed here accounts for known removals from the bypass systems through the censoring parameters.

The results of the tagging study are directly applicable only to the tagged release group. Assumptions (A8) and (A9) are necessary to make inferences to a broader, untagged population. Assumption (A8) implies that individuals should not be chosen for tagging based on size or condition. Drawing conclusions for wild fish is a concern if only hatchery fish were tagged. One obvious violation of Assumption (A9) occurs when only some tagged smolts in the bypass system are transported but all untagged smolts are transported. This violation requires adjustment of certain performance measures derived for tagged fish in order to apply them to the release group, had they been untagged (Buchanan et al. 2006).

3.2 LIKELIHOOD

The model accommodates v juvenile detection sites, u adult detection sites, and w adult age classes. Detection sites are numbered consecutively, so site $v + 1$ is the first adult site and site $v + u$ is the final adult site. Site 0 is the initial release. Detection sites after the release are generally dams, and each dam included has either juvenile or adult detection capability, or both. Alternatively, the final adult detection site may be a hatchery, trap, or spawning grounds. Estimable parameters (Table 1) include survival, detection, censoring, and transportation parameters.

Release-recapture data for a tagged individual are often presented as a detection history, a sequence of codes indicating when or where the individual was detected and its treatment on those occasions. To illustrate the parameterization of detection histories for this model, consider a study design with $v = 3$ juvenile detection sites, $u = 3$ adult detection sites, and $w = 2$ adult age classes, with transportation available at the first two juvenile sites (Figure 2). Detection history codes for each juvenile site are: 0 = not detected; 1 = detected and returned to the river; 2 = detected and censored (known removal or diverted to sampling room); 3 = detected and transported. Detection history codes for adult sites are: 0 = not detected; A = detected as age-1 adult and returned to the river; B = detected as age-2 adult and returned to the river; a = detected as age-1 adult and censored (known removal); b =

Table 1. Model parameters. Detection sites are numbered consecutively. Site 0 is the initial release location. If present, the subscript y represents the juvenile migration method: $y = C$ represents the nontransported group, and $y = T_k$ represents the site-k transport group, for $k = 1, \ldots, v$. In all cases, $j = 1, \ldots, w$.

Parameter	Definition
S_i	Probability of juvenile inriver survival from site $i-1$ to site i; $i = 1, \ldots, v$
p_i	Probability of juvenile detection at site i, given survival to site i; $i = 1, \ldots, v$
q_i	$= 1 - p_i$; $i = 1, \ldots, v$
c_i	Censoring probability of detected juveniles at site i; $i = 1, \ldots, v$
t_i	Probability that a juvenile is transported at site i, given that it is detected and not censored there; $i = 1, \ldots, v$
$S_{v+1,jC}$	Joint probability of ocean survival and age-j maturation; Conditional probability of returning to site $v+1$ as an age-j adult, given reaching last juvenile detection site (v) inriver (nontransported)
S_{ijy}	Probability of age-j adult survival from site $i-1$ to site i for fish with juvenile migration method y; $i = v+2, \ldots, v+u-1$
p_{ijy}	Probability of age-j adult detection at site i, given survival to site i for fish with juvenile migration method y; $i = v+1, \ldots, v+u-1$
q_{ijy}	$= 1 - p_{ijy}$; $i = v+1, \ldots, v+u-1$
c_{ijy}	Age-j censoring probability of detected adults at site i for fish with juvenile migration method y; $i = v+1, \ldots, v+u-1$
λ_{jy}	Joint probability of surviving from site $v+u-1$ to site $v+u$ and detection at site $v+u$ for age-j adults with juvenile migration method y
R_{ij}	Multiplicative effect of transportation on age-j return probability to first adult site for juveniles transported at site i; $i = 1, \ldots, v$
χ_i	Probability of a nontransported, noncensored juvenile not being detected after site i, conditional upon reaching site i; $i = 0, \ldots, v$
χ_{iT}	Probability of a juvenile transported at site i not being detected after site i; $i = 1, \ldots, v$
χ_{ijy}	Probability of a noncensored age-j adult not being detected after site i, conditional upon reaching site i for fish with juvenile migration method y; $i = v+1, \ldots, v+u-1$

detected as age-2 adult and censored (known removal).

For example, a fish detected at the first and third juvenile sites, not transported, and detected as an age-1 adult at each adult site has detection history $101AAA$. The probability of this detection history is

$$\begin{aligned} P(101AAA) &= S_1 p_1 (1-c_1)(1-t_1) S_2 q_2 S_3 p_3 (1-c_3) \\ &\quad \times S_{41C} p_{41C} (1-c_{41C}) S_{51C} p_{51C} (1-c_{51C}) \lambda_{1C}. \end{aligned}$$

Detection at site 1 occurs after release of the tagged smolts, so p_1 is the detection probability at the first post-release detection site. In this case, S_{41C} is the probability of returning from the last juvenile site ($i = 3$) to the first adult site ($i = 4$) as an age-1 adult, conditional on reaching the last juvenile site as an inriver migrant (i.e., nontransported fish). The S_{41C} parameter includes ocean survival, as well as the proclivity to mature as an age-1 adult and

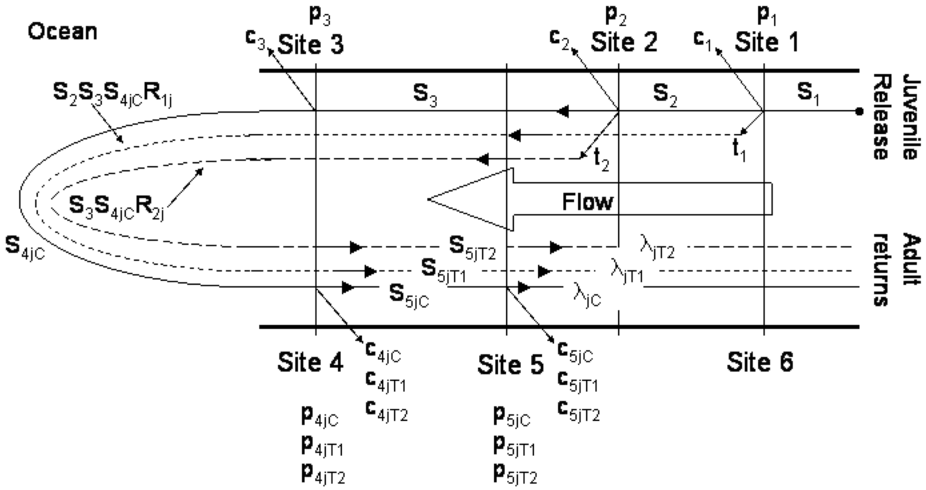

Figure 2. Schematic of processes estimated by the release-recapture PIT-tag model for the study design with three juvenile detection sites (sites 1, 2, and 3) and three adult detection sites (sites 4, 5, and 6). Transportation is possible at the first two juvenile sites, and censoring is possible at all but the final adult site. Directed lines indicate migration paths. Vertical bars indicate detection sites. Juvenile and adult detection may occur at different detection sites. Estimable processes are: juvenile inriver survival probabilities (S_i); age-j-specific ocean survival/return probabilities for nontransported fish (S_{4jC}); age-j adult inriver survival probabilities for nontransported (S_{5jC}) and transported (S_{5jT_1}, S_{5jT_2}) fish; age-j last reach parameters for nontransported and transported fish ($\lambda_{jC} = S_{6jC}p_{6jC}$, and similarly for λ_{jT_1} and λ_{jT_2}); juvenile detection probabilities (p_i); age-j adult detection probabilities for nontransported and transported fish (p_{ijC}, p_{ijT_1}, p_{ijT_2}); juvenile censoring probabilities (c_i); age-j adult censoring probabilities for nontransported and transported fish (c_{ijC}, c_{ijT_1}, c_{ijT_2}); juvenile transportation probabilities (t_i); and age- and site-specific transportation effects (R_{ij}).

inriver survival between the ocean and the nearest juvenile and adult sites. In the Columbia River, these sites are typically both Bonneville Dam (BON). Thus, the $S_{v+1,jC}$ parameters in general are joint ocean survival, maturation, and adult return parameters that are specific to a particular age class. The sum of the $S_{v+1,jC}$ parameters (here, S_{41C} and S_{42C}) is the ocean return probability for nontransported fish.

Another example of a detection history is $3000B0$ for a fish transported from site 1 and detected as an age-2 adult at the second adult site, with probability of occurrence

$$P(3000B0) = S_1 p_1 (1 - c_1) t_1 S_2 S_3 S_{42C} R_{12} q_{42T_1} S_{52T_1} p_{52T_1} (1 - c_{52T_1})(1 - \lambda_{2T_1}).$$

We parameterize the survival of transported fish to the first adult site using the inriver and ocean survival parameters of nontransported fish (i.e., S_2, S_3, and S_{42C}) along with a multiplier (R_{12}). Historically, transportation effects have been measured on a relative basis (e.g., Ricker 1975), and this parameterization allows us to incorporate relative transportation effect parameters (R_{ij}) directly into the model. The R_{ij} parameters modify the survival and age-j ocean return probabilities of nontransported fish to give the joint survival and age-j ocean return probabilities for site-i transport fish. If $R_{ij} > 1$, then transportation from site i increases the probability of returning (to the first adult site) after j years in the ocean. The R_{ij} parameters are commonly referred to as transport-inriver ratios or T/I (Buchanan et al.

2006).

The possible fates that could befall a fish are indicated by the "final detection" parameters χ_i, χ_{iT}, χ_{ijC}, and χ_{ijT_k}. If a juvenile salmon reaches site i and is neither censored nor transported there, then the probability of its not being detected after site i is

$$\chi_i = \begin{cases} 1 - S_{i+1} + S_{i+1} q_{i+1} \chi_{i+1} & \text{for} \quad i = 0, \dots, v-1, \\ 1 - \sum_{j=1}^{w} S_{v+1,jC} + \sum_{j=1}^{w} S_{v+1,jC} q_{v+1,jC} \chi_{v+1,jC} & \text{for} \quad i = v, \end{cases} \tag{3.1}$$

where $i = 0$ represents the initial release. The sum $\sum_{j=1}^{w} S_{v+1,jC}$ is the overall probability of returning to the first adult site, conditional upon reaching the final juvenile site inriver (i.e., nontransported). For a fish transported from site i, the probability of not being detected thereafter is (for $i = 1, \dots, v$)

$$\chi_{iT} = 1 - \prod_{k=i+1}^{v} S_k \sum_{j=1}^{w} S_{v+1,jC} R_{ij} + \prod_{k=i+1}^{v} S_k \sum_{j=1}^{w} S_{v+1,jC} R_{ij} q_{v+1,jT_i} \chi_{v+1,jT_i}. \tag{3.2}$$

A tagged fish may be detected for the last time as an age-j adult. The probability of not being detected after site i, conditional upon reaching site i as an age-j adult via juvenile migration method y ($y = C$ for nontransported fish, or $y = T_k$ for site-k transported fish), is

$$\chi_{ijy} = \begin{cases} 1 - S_{i+1,jy} + S_{i+1,jy} q_{i+1,jy} \chi_{i+1,jy} & \text{for} \quad i = v+1, \dots, v+u-2, \\ 1 - \lambda_{jy} & \text{for} \quad i = v+u-1. \end{cases} \tag{3.3}$$

For any combination of v, u, and w parameters, all possible detection histories and their probabilities can be listed to construct the multinomial likelihood. It is more convenient to express the likelihood using summary statistics (Table 2). The release-recapture data can be organized using a modification of the m-array from Burnham et al. (1987) (Tables 3 and 4). This age-structured m-array is similar to the multiple-strata m-array in Brownie et al. (1993). The likelihood can be expressed using the summary statistics from the m-array as follows:

$$\begin{aligned} L \propto{}& \chi_0^{N-b_0} \prod_{i=1}^{v} \Bigg\{ S_i^{g_{i-1} + \sum_{k=1}^{i-1} b_{kT}} p_i^{a_i} q_i^{g_{i-1}-a_i} c_i^{d_i} (1-c_i)^{a_i-d_i} t_i^{h_i} (1-t_i)^{a_i-d_i-h_i} \chi_i^{a_i-d_i-h_i-b_i} \\ & \times \chi_{iT}^{h_i-b_{iT}} \prod_{j=1}^{w} \Bigg[R_{ij}^{b_{ijT}} \lambda_{jT_i}^{g_{v+u-1,jT_i}} \prod_{k=v+2}^{v+u-1} S_{kjT_i}^{g_{k-1,jT_i}} \prod_{k=v+1}^{v+u-1} \Big(p_{kjT_i}^{a_{kjT_i}} q_{kjT_i}^{g_{k-1,jT_i}-a_{kjT_i}} c_{kjT_i}^{d_{kjT_i}} \\ & \times \left(1 - c_{kjT_i}\right)^{a_{kjT_i}-d_{kjT_i}} \chi_{kjT_i}^{a_{kjT_i}-d_{kjT_i}-b_{kjT_i}} \Big) \Bigg] \Bigg\} \\ & \times \prod_{j=1}^{w} \Bigg\{ \lambda_{jC}^{g_{v+u-1,jC}} S_{v+1,jC}^{g_{vjC} + \sum_{k=1}^{v} b_{kjT}} \prod_{i=v+2}^{v+u-1} S_{ijC}^{g_{i-1,jC}} \prod_{i=v+1}^{v+u-1} \Big[p_{ijC}^{a_{ijC}} q_{ijC}^{g_{i-1,jC}-a_{ijC}} c_{ijC}^{d_{ijC}} \\ & \times \left(1 - c_{ijC}\right)^{a_{ijC}-d_{ijC}} \chi_{ijC}^{a_{ijC}-d_{ijC}-b_{ijC}} \Big] \Bigg\}. \end{aligned} \tag{3.4}$$

Table 2. Summary statistics. Detection sites are numbered consecutively. Site 0 is the initial release location. If present, the subscript y represents the juvenile migration method: $y = C$ represents the nontransported group, and $y = T_k$ represents the site-k transport group, for $k = 1, \dots, v$. In all cases, $j = 1, \dots, w$.

Statistic	Definition
a_i	Number of juveniles detected at site i; $i = 1, \dots, v$
a_{ijy}	Number of age-j adults with juvenile migration method y detected at site i; $i = v+1, \dots, v+u$
b_i	Number of juveniles detected at site i, re-released to the river, and detected at a later site; $i = 0, \dots, v$
b_{iT}	Number of juveniles detected and transported from site i and detected at an adult site; $i = 1, \dots, v$
b_{ijT}	Number of juveniles transported from site i and detected as an age-j adult; $i = 1, \dots, v$
b_{ijy}	Number of age-j adults with juvenile migration method y detected and re-released to the river at site i and detected at a later site; $i = v+1, \dots, v+u-1$
d_i	Number of juveniles censored at site i; $i = 1, \dots, v$
d_{ijy}	Number of age-j adults with juvenile migration method y censored at site i; $i = v+1, \dots, v+u-1$
h_i	Number of juveniles transported from site i; $i = 1, \dots, v$
g_i	Number detected after site i; $i = 0, \dots, v-1$
g_{ijy}	Number of age-j adults with juvenile migration method y detected after site i; $i = v, \dots, v+u-1$

We interpret any product whose initial index is greater than its final index as equal to 1. For example, $\prod_{i=v+1}^{v} \theta_i = 1$ for any set of parameters θ_i.

This model is a branching version of the CJS model, and can be fit using program ROSTER (River-Ocean Survival and Transportation Effects Routine), available online at *http://www.cbr.washington.edu/paramest/roster*. Program ROSTER requires input of the parameters v, u, and w, and provides maximum likelihood estimates and standard errors for the model parameters and the performance measures defined in Section 3.3.

3.3 Performance Measures for Tagged Fish

Beyond the model parameters, there are numerous performance measures of interest to fisheries managers that can be extracted from the likelihood. Maximum likelihood estimates (MLEs) of these quantities are found using the invariance property of MLEs, that is, by replacing the model parameters in the following formulas with their maximum likelihood estimates. Variance estimates may be found using the Delta Method (Seber 1982, pp. 7-9). They were also presented by Buchanan (2005).

Several estimators use the parameter $S_{v+u,jC}$, survival over the final adult reach for age-j fish that were not transported as juveniles. This parameter is not estimated by the model, per se. However, if detection at the final adult site is considered to be 100% (often the case), then $\lambda_{jC} = S_{v+u,jC}$. Otherwise, the parameter $S_{v+u,jC}$ should be removed from the following estimators, and those estimators should be noted as reflecting adult survival

Table 3. The modified m-array (nontransported releases) for the study design with three juvenile detection sites (sites 1, 2, and 3), three adult detection sites (sites 4, 5, and 6), two adult age classes (1 and 2), and censoring possible at all but the final adult site. The first column identifies the release site for the row. The statistic N is the size of the initial release. Row totals (b_i, b_{ijC}) and column totals (a_i, a_{ijC}) are of the m_{ik} and $m_{ik,jC}$ statistics. The statistic m_{ik} is the number of fish released to the river at juvenile site i that are next detected at juvenile site k; $m_{ik,jC}$ is the number of nontransported fish released to the river at site i (in age class j if site i is an adult site) that are next detected as age-j fish at adult site k. The statistics d_i and d_{ijC} are the numbers of nontransported fish censored at juvenile site i and at adult site i in age class j, respectively. The statistic h_i is the number transported from juvenile site i.

Site		Juvenile Sites			Adult Sites (and age class)						Number
					Site 4		Site 5		Site 6		
(age class)	Release	Site 1	Site 2	Site 3	(1	2)	(1	2)	(1	2)	recaptured
Initial	N	m_{01}	m_{02}	m_{03}	$m_{04,1C}$	$m_{04,2C}$	$m_{05,1C}$	$m_{05,2C}$	$m_{06,1C}$	$m_{06,2C}$	b_0
Site 1	$a_1 - d_1 - h_1$		m_{12}	m_{13}	$m_{14,1C}$	$m_{14,2C}$	$m_{15,1C}$	$m_{15,2C}$	$m_{16,1C}$	$m_{16,2C}$	b_1
Site 2	$a_2 - d_2 - h_2$			m_{23}	$m_{24,1C}$	$m_{24,2C}$	$m_{25,1C}$	$m_{25,2C}$	$m_{26,1C}$	$m_{26,2C}$	b_2
Site 3	$a_3 - d_3 - h_3$				$m_{34,1C}$	$m_{34,2C}$	$m_{35,1C}$	$m_{35,2C}$	$m_{36,1C}$	$m_{36,2C}$	b_3
Site 4 (1)	$a_{41C} - d_{41C}$						$m_{45,1C}$		$m_{46,1C}$		b_{41C}
Site 4 (2)	$a_{42C} - d_{42C}$							$m_{45,2C}$		$m_{46,2C}$	b_{42C}
Site 5 (1)	$a_{51C} - d_{51C}$								$m_{56,1C}$		b_{51C}
Site 5 (2)	$a_{52C} - d_{52C}$									$m_{56,2C}$	b_{52C}
Number detected		a_1	a_2	a_3	a_{41C}	a_{42C}	a_{51C}	a_{52C}	a_{61C}	a_{62C}	
Number censored		d_1	d_2	d_3	d_{41C}	d_{42C}	d_{51C}	d_{52C}			
Number transported		h_1	h_2	h_3							

Table 4. The modified m-array (site-s transport group) for the study design with three juvenile detection sites (sites 1, 2, and 3), three adult detection sites (sites 4, 5, and 6), two adult age classes (1 and 2), and censoring possible at all but the final adult site. The first column identifies the release site for the row. The statistic h_s is the size of the transport group from juvenile site s ($s = 1, 2, 3$). Row totals (b_{sT}, b_{ijT_s}) and column totals (a_{ijT_s}) are of the m_{ik,jT_s} statistics, where m_{sk,jT_s} is the number of fish transported at juvenile site s that are next detected at adult site k in age class j, and m_{ik,jT_s} is the number of site-s transport fish that are detected as age-j adults at site i and next detected at adult site k. The statistics d_{ijT_s} are the numbers of site s-transport fish censored at adult site i in age class j.

Site		Adult Sites (and age class)						Number
		Site 4		Site 5		Site 6		
(Age Class)	Release	(1	2)	(1	2)	(1	2)	recaptured
Site s	h_s	$m_{s4,1T_s}$	$m_{s4,2T_s}$	$m_{s5,1T_s}$	$m_{s5,2T_s}$	$m_{s6,1T_s}$	$m_{s6,2T_s}$	b_{sT}
Site 4 (1)	$a_{41T_s} - d_{41T_s}$			$m_{45,1T_s}$		$m_{46,1T_s}$		b_{41T_s}
Site 4 (2)	$a_{42T_s} - d_{42T_s}$				$m_{45,2T_s}$		$m_{46,2T_s}$	b_{42T_s}
Site 5 (1)	$a_{51T_s} - d_{51T_s}$					$m_{56,1T_s}$		b_{51T_s}
Site 5 (2)	$a_{52T_s} - d_{52T_s}$						$m_{56,2T_s}$	b_{52T_s}
Number detected		a_{41T_s}	a_{42T_s}	a_{51T_s}	a_{52T_s}	a_{61T_s}	a_{62T_s}	
Number censored		d_{41T_s}	d_{42T_s}	d_{51T_s}	d_{52T_s}			

only to site $v + u - 1$. The same consideration applies to the parameters S_{v+u,jT_i}.

For most release-recapture models, it is assumed that the results from a tagged release group apply to untagged animals as well. In the case of tagged salmonids migrating through the Columbia River hydrosystem, however, we know that tagged and untagged individuals are transported from dams at different rates, due to the operations of the transportation collection system. Thus, certain performance measures are developed separately for tagged and untagged individuals. The direct inference for the measures for untagged fish is to fish in the release group, had they been treated as untagged.

3.3.1 Ocean Return Probability for Nontransported Fish (O_{NT}).

The age-specific ocean return parameters, $S_{v+1,jC}$, include both survival in the ocean and the propensity to mature in a given adult age class for nontransported fish. Thus, the sum of the $S_{v+1,jC}$ parameters is the overall probability of adult return from the final juvenile site to the first adult site, regardless of age at return. This measure is O_{NT}, the ocean return probability of nontransported fish:

$$O_{\mathrm{NT}} = \sum_{j=1}^{w} S_{v+1,jC}. \tag{3.5}$$

3.3.2 Site-Specific Transport-Inriver Ratio (R_i).

Transportation effects are incorporated into the likelihood model via the transport-inriver ratio (T/I) parameters, R_{ij}. The model parameters R_{ij} are specific to transport site i and returning adult age class j, and represent the relative (i.e., multiplicative) effect of transportation from site i on the probability of returning to the first adult detection site in adult age class j. The age-specific T/I parameters for site i may be combined with ocean and adult survival parameters to give a site-specific T/I value R_i, reflecting returns to the final adult site $(v + u)$ and pooled over all adult age classes, as follows:

$$R_i = \frac{P(\text{ Adult return to site } v+u \mid \text{ Transported from site } i)}{P(\text{Adult return to site } v+u \mid \text{Pass site } i \text{ inriver, no other transportation})}$$
$$= \left[\sum_{j=1}^{w}\left(R_{ij}S_{v+1,jC}S_{v+2,jT_i}\cdots S_{v+u,jT_i}\right)\right] \Big/ \left[\sum_{j=1}^{w}\left(S_{v+1,jC}\cdots S_{v+u,jC}\right)\right]. \quad (3.6)$$

Both R_{ij} and R_i isolate the effect of transportation at site i from the rest of the transportation program, which generally includes more than one transportation site. The parameters R_{ij} reflect transportation effects only in the ocean, while R_i reflects effects in both the ocean and the upriver adult migration.

3.3.3 Smolt-to-Adult Ratios for Tagged Fish (SAR).

The probability of a smolt returning to the final detection site (typically LGR) as an adult is the smolt-to-adult ratio (SAR). The SAR for all tagged fish, regardless of migration method (i.e., inriver or transportation), is defined as follows:

$$\text{SAR} = S_1 \cdots S_v \Psi \sum_{j=1}^{w}\left[S_{v+1,jC}\cdots S_{v+u,jC}\right], \quad (3.7)$$

where

$$\Psi = \sum_{i=1}^{v}\left[p_i t_i R_i \prod_{k=1}^{i-1}(1-p_k t_k)\right] + \prod_{k=1}^{v}(1-p_k t_k) \quad (3.8)$$

and where $1 - p_k t_k$ is the probability of passing site k without being transported, conditional on surviving inriver to site k. The sum Ψ is the weighted average of the site-specific T/I measures (R_i), with weights equal to the probabilities of the different passage histories and using $R_{ij} = 1$ (and so $R_i = 1$) for the nontransportation path.

3.3.4 Adult Upriver Survival for Tagged Fish (S_A).

The overall upriver survival of adults from a given juvenile release group, regardless of age at maturity or juvenile transportation history, is S_A:

$$S_A = P(\text{Survive from } v+1 \text{ to } v+u \mid \text{Reach } v+1)$$
$$= \frac{\Psi \sum_{j=1}^{w}\left[S_{v+1,jC}\cdots S_{v+u,jC}\right]}{\sum_{i=1}^{v}\left\{p_i t_i \sum_{j=1}^{w} S_{v+1,jC}R_{ij}\prod_{k=1}^{i-1}(1-p_k t_k)\right\} + \sum_{j=1}^{w} S_{v+1,jC}\prod_{i=1}^{v}(1-p_i t_i)}, \quad (3.9)$$

where Ψ is as defined in Equation (3.8).

3.4 PERFORMANCE MEASURES FOR UNTAGGED FISH

The measures SAR and S_A depend on the conditional transportation probability for tagged fish, t_i. However, tagged and untagged fish are transported at different rates. Typically, all untagged fish in the bypass system are transported, but some tagged fish may be diverted back to the river for study purposes. Thus, Equations (3.7) and (3.9) are valid only for tagged fish; for untagged fish, parameter t_i is replaced with the appropriate conditional transportation probability for untagged fish, t_i^U. If all untagged fish entrained in the bypass system are transported, then $t_i^U = 1$. In general, t_i^U cannot be estimated from tagging data, but must be determined from records of transportation operations at site i. The direct inference for these untagged estimators is to fish in the release group, had they been treated as untagged.

4. ANALYSIS OF THE 2000 SUMMER CHINOOK SALMON EXAMPLE

A total of 24,489 of the 58,477 summer Chinook salmon tagged and released in 2000 were detected during outmigration at 1 or more of the 6 juvenile detector dams (Table 5). Of these detected smolts, 11,723 were transported, 10,450 were returned to the river after each detection, and 2,316 were censored due to rehandling in the sampling rooms at the dams, transportation in a small transport group, or being labeled "transport" followed by a downstream juvenile detection. A total of 1,239 unique adults were detected during upmigration at either Bonneville or Lower Granite dams; of these detected adults, 663 had been transported as juveniles (Tables 5–7).

After censoring the small transport groups ($<$ 1,000), there was no transportation at sites 3 (LMO) through 6 (BON), so the nuisance parameters for these events (i.e., t_3, t_4, t_5, and t_6) are all zero, and factors involving these parameters were removed from the likelihood in Equation (3.4). For the purpose of estimating performance measures for untagged fish, the parameters t_i^U were fixed to 1 for $i = 1, 2$, and to 0 for $i = 3, 4, 5, 6$.

The upriver adult parameters in the likelihood presented in Equation (3.4) are classified by juvenile migration method (nontransport versus transport), and by transport group. We used likelihood ratio tests (LRTs) to select the most parsimonious characterization of upriver adult parameters for this dataset. There was no significant difference in upriver adult parameters among transport groups from different dams (LRT $= 1.948$, df $= 7$, $P = 0.9627$), but there was a significant difference in upriver performance between transported and nontransported fish (LRT $= 22.618$, df $= 7$, $P = 0.0020$). Thus, we used a model that characterized adult detection and censoring at BON and the final reach parameter (λ) by age class and juvenile migration method but not by transport dam.

We parameterized the probability parameters in Equation (3.4) on the logistic scale in order to avoid probability estimates that are greater than one. Maximum likelihood estimates (MLEs) of the model parameters (Table 8) were found by numerically maximizing Equation (3.4); standard errors are based on the inverse of the estimated Hessian. In cases where the constrained MLE falls on the boundary ($\widehat{S_4}$, $\widehat{S_5}$), no standard error is given.

Table 5. Modified m-array (nontransported releases) for hatchery summer Chinook salmon released in the Snake River above LGR in 2000. Adult age classes are: 1 = 2001 adults (jacks); 2 = 2002 adults; 3 = 2003 adults. The first column identifies the release site for the row.

								Adult Detection Sites (age class)						
	Juvenile	Juvenile Detection Sites						BON			LGR			Number
Site	Release	LGR	LGO	LMO	MCN	JD	BON	(1	2	3)	(1	2	3)	recaptured
Initial	58,477	13,837	5,060	1,585	2,220	208	1,579	18	161	74	21	3	1	24,767
LGR	4,667		1,041	337	466	26	315	2	30	18	4	0	0	2,239
LGO	2,789			385	411	41	238	6	19	10	3	1	0	1,114
LMO	1,177				288	22	111	0	9	5	1	0	0	436
MCN	3,233					62	508	15	37	15	3	0	0	640
JD	222						34	0	1	2	1	0	0	38
BON	2,647							5	66	34	9	1	1	116
BON (1)	41										38			38
BON (2)	322											299		299
BON (3)	153												127	127
Number detected		13,837	6,101	2,307	3,385	359	2,785	46	323	158	80	304	129	
Number censored		613	146	1,130	152	137	138	5	1	5				
Number transported		8,557	3,166	0	0	0	0							

Table 6. Modified m-array (LGR-transport group) for hatchery summer Chinook salmon released in the Snake River above LGR in 2000. Adult age classes are: 1 = 2001 adults (jacks); 2 = 2002 adults; 3 = 2003 adults. The first column identifies the release site for the row.

Site		Adult Detection Sites						Number
		BON			LGR			
(Age Class)	Release	(1	2	3)	(1	2	3)	recaptured
LGR	8,557	44	327	123	22	8	2	526
BON (1)	41				36			36
BON (2)	327					283		283
BON (3)	123						92	92
Number detected		44	327	123	58	291	94	
Number censored		3	0	0				

Goodness-of-fit was assessed with tests based on Test 2 and Test 3 of Burnham et al. (1987), and standard errors were expanded to account for overdispersion using a resultant inflation factor of 1.677 (Lebreton et al. 1992). Survival of nontransported juveniles from LGR to BON was estimated at 0.6028 ($\widehat{SE} = 0.0813$). In general, standard errors on survival estimates increased going downriver, because of effectively smaller sample sizes as fish were lost due to mortality or removal: $\widehat{\mathrm{SE}}\big(\widehat{S}_1\big) = 0.0114$, $\widehat{\mathrm{SE}}\big(\widehat{S}_3\big) = 0.0479$, and $\widehat{\mathrm{SE}}\big(\widehat{S}_6\big) = 0.1045$. Although adult detections allow for estimation of smolt survival in the lowest reach (ending at BON), they provide little information on inriver survival of smolts in the upper reaches because so few smolts return as adults. Thus, improved adult detection cannot replace downriver juvenile detection requirements.

The estimated ocean return probability (i.e., BON to BON) for nontransported fish was $\widehat{O}_{\mathrm{NT}} = 0.0445$ ($\widehat{\mathrm{SE}} = 0.0067$), meaning that approximately 4.5% of the nontransported fish who survived to BON returned to BON as adults. Because O_{NT} includes survival of juveniles from BON to the ocean (234 km) and survival of adults from the ocean back to BON, actual ocean survival is higher than the 4.5% estimated.

Table 7. Modified m-array (LGO-transport group) for hatchery summer Chinook salmon released in the Snake River above LGR in 2000. Adult age classes are: 1 = 2001 adults (jacks); 2 = 2002 adults; 3 = 2003 adults. The first column identifies the release site for the row.

Site		Adult Detection Sites						Number
		BON			LGR			
(Age Class)	Release	(1	2	3)	(1	2	3)	recaptured
LGO	3,166	10	87	28	9	2	1	137
BON (1)	9				8			8
BON (2)	87					76		76
BON (3)	28						22	22
Number detected		10	87	28	17	78	23	
Number censored		1	0	0				

Table 8. Maximum likelihood estimates for hatchery summer Chinook salmon released in the Snake River above LGR in 2000. The first or only subscript is the index of the detection site: 1 = LGR (juvenile), 2 = LGO, 3 = LMO, 4 = MCN, 5 = JD, 6 = BON (juvenile), 7 = BON (adult), 8 = LGR (adult). A second subscript denotes the adult age class: 1 = 2001 adults (jacks); 2 = 2002 adults; 3 = 2003 adults. The subscript C denotes the nontransported group, and T denotes a transport group.

Category	Parameter	Estimate	S.E.
Juvenile Survival	S_1	0.6262	0.0114
	S_2	0.8677	0.0339
	S_3	0.9203	0.0479
	S_4	1.0000	–NA–
	S_5	1.0000	–NA–
	S_6	0.7549	0.1045
Juvenile Detection	p_1	0.3779	0.0078
	p_2	0.2562	0.0093
	p_3	0.1223	0.0061
	p_4	0.1908	0.0091
	p_5	0.0204	0.0020
	p_6	0.2114	0.0286
Conditional Juvenile Censoring	c_1	0.0443	0.0029
	c_2	0.0239	0.0033
	c_3	0.4898	0.0175
	c_4	0.0449	0.0060
	c_5	0.3816	0.0430
	c_6	0.0496	0.0069
Conditional Transportation	t_1	0.6471	0.0070
	t_2	0.5317	0.0108
Age-Specific Joint Ocean Survival and Maturation	S_{71C}	0.0070	0.0016
	S_{72C}	0.0252	0.0041
	S_{73C}	0.0123	0.0023
Conditional Adult Detection	p_{71C}	0.5039	0.0913
	p_{72C}	0.9837	0.0122
	p_{73C}	0.9849	0.0177
	p_{71T}	0.6055	0.0926
	p_{72T}	0.9729	0.0142
	p_{73T}	0.9746	0.0244
Conditional Adult Censoring	c_{71C}	0.1094	0.0772
	c_{72C}	0.0031	0.0052
	c_{73C}	0.0317	0.0234
	c_{71T}	0.0743	0.0598
Final Reach	λ_{1C}	0.9272	0.0681
	λ_{2C}	0.9286	0.0241
	λ_{3C}	0.8302	0.0509
	λ_{1T}	0.8807	0.0769
	λ_{2T}	0.8671	0.0280
	λ_{3T}	0.7552	0.0587
Age- and Site-Specific T/I	R_{11}	1.9165	0.5330
	R_{12}	2.5863	0.3380
	R_{13}	1.9819	0.3976
	R_{21}	1.2969	0.5549
	R_{22}	1.6130	0.3244
	R_{23}	1.0790	0.3657

The estimated transportation effects were $\widehat{R}_1 = 2.1629$ ($\widehat{\mathrm{SE}} = 0.2330$) at LGR, and $\widehat{R}_2 = 1.3282$ ($\widehat{\mathrm{SE}} = 0.2182$) at LGO. This implies that fish transported at LGR had approximately twice the adult return probability of fish that migrated wholly inriver. Thus, the estimated R_i values indicate that transportation at LGR and LGO was beneficial, with LGR-transportation more beneficial than LGO-transportation. This is reasonable, because LGO-transported fish experienced inriver mortality risks over a greater stretch of river than LGR-transported fish.

The probability of returning from the release site to LGR as an adult, assuming 100% adult detection at LGR, was estimated to be $\widehat{\mathrm{SAR}} = 0.0200$ ($\widehat{\mathrm{SE}} = 0.0009$) for tagged fish and extrapolated to be $\widehat{\mathrm{SAR}}^U = 0.0251$ ($\widehat{\mathrm{SE}} = 0.0012$) for the release group, had they been untagged. The value for untagged fish is higher due to the assumption that, unlike tagged smolts, all untagged smolts in the bypass system were transported. If transportation were detrimental, then SAR^U would be less than SAR.

Overall upriver adult survival from BON to LGR, assuming 100% adult detection at LGR, was estimated at $\widehat{S}_A = 0.8708$ ($\widehat{\mathrm{SE}} = 0.0169$) for tagged fish. This survival applies to both transported and nontransported fish, but can be partitioned into survivals for the two groups separately, with 0.8430 upriver adult survival ($\widehat{\mathrm{SE}} = 0.0342$) for transported fish and 0.9011 survival ($\widehat{\mathrm{SE}} = 0.0225$) for nontransported fish. Because we estimated lower upriver adult survival for transported fish and assumed that a higher proportion of untagged than tagged fish were transported, we estimated a lower overall upriver adult survival for untagged fish than for tagged fish: $\widehat{S}_A^U = 0.8602$ ($\widehat{\mathrm{SE}} = 0.0187$). These estimates of "upriver adult survival" are actually estimates of perceived survival, whose complement includes straying to non-natal tributaries below LGR and fallback over BON, in addition to mortality. Mortality includes both natural mortality and that due to harvest.

5. DISCUSSION

The release-recapture model presented here represents the migratory portion of the life cycle of semelparous Pacific salmonids in the Columbia River Basin. The life-cycle approach to modeling survival and recapture has multiple benefits. It connects the juvenile and adult data in a biologically reasonable way, and avoids model misspecification that may result from separate single life-stage models. The life-cycle approach also provides estimation of quantities that are not directly estimable if juvenile and adult stages are modeled separately. For example, the ocean return probability (survival from BON as a juvenile to BON as an adult) cannot be estimated from separate analyses of juvenile and adult data, but is estimable from our joint analysis. Finally, the migratory life-cycle model and its parameters provide a basis for defining performance measures such as SAR and transport-inriver ratios, along with easily computed maximum likelihood estimates and variance estimates.

The focus of much mark-recapture literature has shifted from parameter estimation to model selection (Lebreton et al. 1992; Burnham and Anderson 2002). Model selection is inherently tied to research hypotheses, and certain hypotheses of interest to the fisheries community can be explored with this model. For example, an important issue is the extent of transportation effects on upriver adult survival. Some researchers (e.g., Chapman et al. 1997) have suggested that transportation may affect adult homing ability, with increased straying rates among adults transported as smolts. This would result in perceived upriver survival estimates that are smaller for transported fish than for nontransported fish. This was observed for the 2000 dataset highlighted in this article, where the final reach parameters were smaller for previously transported fish than for nontransported fish ($\widehat{\lambda}_{jT_i} < \widehat{\lambda}_{jC}$). A LRT showed these differences to be significant ($P = 0.0138$).

A second useful hypothesis might be a particular functional form relating the R_{ij} parameters to river kilometer or date of transport. For example, if it is expected that the R_{ij} parameters monotonically decrease for downriver transport sites, this could be incorporated via a log-linear model for R_{ij}. River kilometer and other environmental variables are not incorporated into the model presented here, but could be introduced easily, with model selection among functional forms done via LRTs or Akaike's information criterion (Burnham and Anderson 2002). Similarly, survival or detection probabilities could be modeled explicitly on environmental variables such as flow, water temperature, or release date.

Current analysis of adult tagging data to estimate SARs and transportation effects pools adult recapture and recovery data over age classes. If only a single adult detection site is used, this practice is mathematically reasonable although it does not allow separate estimation of ocean and adult survival. If multiple adult detection sites are used in a release-recapture framework, however, pooling over age classes is inappropriate unless adult parameters are constant over age class. This hypothesis can easily be explored using this model.

The model presented here is restricted to a single release group, but the approach may be extended to allow for multiple releases made over several years. With multiple brood years, the year of adult return is no longer confounded with the age of adult return, and it may be possible to determine whether it is the calendar year or the age of adult return that affects ocean return probabilities and upriver adult survival probabilities. Extending the model to multiple brood years may allow for yet more ambitious explorations.

Model selection and hypothesis testing can produce useful biological information. Nevertheless, the primary use of release-recapture models is still parameter estimation. Both model parameters and functions of them are useful performance measures for fishery and hydrosystem managers, and can shed light on the effects of treatments and conservation efforts. A question of increasing interest is the relative contribution to SAR of survival through the hydrosystem and river environment versus survival in the ocean. The survival parameters and SAR estimated from this model can address this question. For example, for the 2000 dataset highlighted here, decreasing juvenile inriver mortality by 50% would increase SAR by 82%, but decreasing ocean mortality by 50% would increase SAR by more than 1,000%. This type of observation is possible only with estimates of parameters that tie together the juvenile, ocean, and adult life stages. Thus, parameter estimation remains an important application of this model, both to evaluate current performance and to identify the focus of future conservation efforts.

Modeling both juvenile and adult migrations concurrently is a departure from previous salmon migration models (e.g., Skalski et al. 1998), and is made possible by reliable detections of PIT-tagged adults. The migratory life-cycle model presented here provides a rich framework for estimating important performance measures such as transportation effect ratios and SARs. As more dams are equipped for adult detection, such life-cycle release-recapture models will become increasingly important in understanding hydrosystem operations and in managing fish resources in the Columbia River.

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