

Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers

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Abstract: Single-release and modified single-release statistical models were evaluated as means to generate reliable survival estimates from release–recapture studies of migrant salmonid smolts in the Snake and Columbia rivers of the northwestern United States. Monte Carlo simulation studies were used to assess robustness of estimation methods to violations of model assumptions. To field test model assumptions, passive integrated transponder tagged chinook salmon (*Oncorhynchus tshawytscha*) smolts were released on seven consecutive days in 1993 above Lower Granite Dam on the Snake River. These releases were used to estimate sampling variability of survival estimates for comparison with model-based variance estimates and to assess mixing of detected and nondetected individuals. Field results satisfied model assumptions. The average survival estimate from point of release to the tailrace of Lower Granite Dam (31 km) was 0.902 ± 0.004 (mean \pm SE). From the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam (60 km) the average survival estimate was 0.859 ± 0.013 .

Résumé : On a évalué l'efficacité de modèles statistiques de lâcher simple et de lâcher simple modifié pour produire des estimations fiables de la survie à partir d'études de lâcher–recapture de smolts en migration dans la rivière Snake et le fleuve Columbia, dans le nord-ouest des États-Unis. On s'est servi de la méthode de Monte Carlo pour évaluer la robustesse des méthodes d'estimation dans les cas où les hypothèses du modèle ne sont pas respectées. Afin de mettre ces hypothèses à l'essai sur le terrain, des saumons quinnats (*Oncorhynchus tshawytscha*) étiquetés à l'aide d'une marque transpondeur intégré passif ont été libérés pendant 7 jours consécutifs en 1993 en amont du barrage Lower Granite, sur la rivière Snake. On s'est servi de ces lâchers pour estimer la variabilité due à l'échantillonnage dans les estimations de la survie afin de les comparer aux estimations de la variance fondées sur le modèle et d'évaluer le mélange des individus détectés et non détectés. Les résultats obtenus sur le terrain correspondaient aux hypothèses du modèle. L'estimation de la survie moyenne entre le point de lâcher et le canal de fuite du barrage Lower Granite (31 km) était $0,902 \pm 0,004$ (moyenne \pm ET). Entre le canal de fuite du barrage Lower Granite et celui du barrage Little Goose (60 km), l'estimation de la survie moyenne était $0,859 \pm 0,013$.
[Traduit par la Rédaction]

Introduction

In the middle to late 1980s, the National Marine Fisheries Service (NMFS) developed a miniature passive integrated transponder (PIT) tag that, when implanted in the body cavity of juvenile fish, allows for unique identification of individuals (Prentice et al. 1990a, 1990b, 1990c). For migrant juvenile salmonids PIT-tagged in the Snake River Basin, detectors automatically decode the tags as fish pass through juvenile fish collection facilities at selected hydroelectric dams (Fig. 1).

In 1988, the University of Washington (UW) began to develop statistical theory and software to estimate survival

probabilities and assess survival relationships from data generated by release and detection of PIT-tagged fish in the Snake and Columbia rivers. From this work was developed the statistical software SURPH.1 (Smith et al. 1994) used in the studies described herein. In 1993, these technologies came together in a joint NMFS–UW pilot study of smolt survival in the Snake River (Iwamoto et al. 1994). This collaboration of electronic technology, statistical theory, and fisheries biology to devise an effective system for information gathering and analysis is a first in the science of animal-tagging studies.

This paper describes the statistical models used to analyze survival studies with PIT-tagged fish, their assumptions, sampling precision, and robustness to model violations. Further, we describe the field methods used in 1993 to collect, PIT-tag, and release migrant juvenile salmonids in the Snake River to gather data for the models. Monte Carlo simulation results are presented, along with the results of seven replicate releases in 1993, to determine the validity of the estimation procedures. The PIT-tag studies in 1993 also provided some of the first survival estimates for juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River since a summary of survival estimates in the 1970s was made by Sims and Ossiander (1981). We discuss extension of these technologies to the investigation, mitigation, and recovery of salmonid stocks in the Snake–Columbia River Basin.

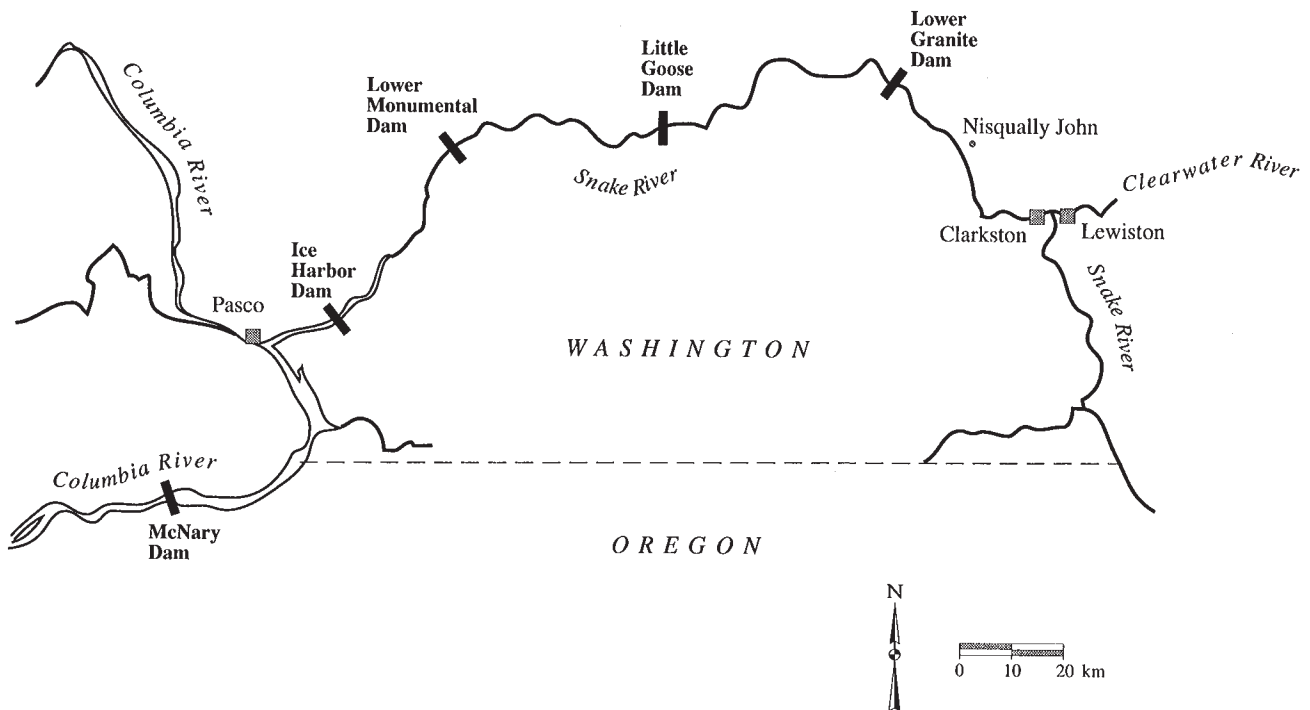
Received September 5, 1996. Accepted December 5, 1997.
J13638

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Fig. 1. Study area showing release and detection sites.

Materials and methods

Field methods

Study area

PIT-tagged fish were released in Lower Granite Reservoir near Nisqually John boat landing (river kilometer (Rkm) 726), at Lower Granite Dam (Rkm 695), and at Little Goose Dam (Rkm 635) on the Snake River in Washington State. PIT-tagged fish were detected at Lower Granite Dam, Little Goose Dam, and Lower Monumental Dam (Rkm 589) on the Snake River and at McNary Dam (Rkm 470) on the Columbia River (Fig. 1). Lower Granite and Little Goose dams also had facilities to return PIT-tagged fish detected in the bypass systems back into the river in the tailrace (Fig. 2).

Survey design

The primary objective of the field study was to estimate smolt survival from Nisqually John boat landing to the tailrace of Lower Granite Dam (S_1) and survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam (S_2). A secondary objective was to estimate survival from the point of detection in the bypass system to the point in the tailrace at each dam where detected fish remixed with nondetected fish ($\hat{\tau}_2, \hat{\tau}_3$) (Fig. 2). Primary release groups (R_1) consisted of hatchery-reared yearling chinook salmon captured by purse seine in Lower Granite Reservoir and PIT-tagged near the Nisqually John boat landing (Fig. 2). There was one primary release per day for seven consecutive days. Daily releases ranged from 797 to 1405 tagged fish, depending on availability. Capture histories from each group were the basis for estimating survival in the river sections above Little Goose Dam (Table 1).

Secondary, paired releases of PIT-tagged fish were made at Lower Granite (R_{B2}, C_{B2}) and Little Goose Dams (R_{B3}, C_{B3}) to investigate potential mortality of fish returned to the river after detection. If such mortality occurs in the bypass system, it could bias estimates of reach survival obtained from the primary releases. Test groups were released in the bypass system at the juvenile collection facilities, just downstream from the PIT-tag detector. Control groups were released

in the river below the dam at a point where bypassed fish remixed with fish that passed via turbines or spillways. Each paired release was replicated three times at each dam (Table 2).

Release and detection data were transmitted to the PIT-tag information system (PTAGIS) for later retrieval and analysis. PTAGIS is a computer database developed for the Columbia River Basin and managed by the Pacific States Marine Fisheries Commission (PIT Tag Operations Center, 45 SE 82nd Drive, Suite 100, Gladstone, OR 97207, U.S.A.).

Fish collection and handling

For the primary release groups in Lower Granite Reservoir, fish were collected using two purse-seine vessels (Durkin and Park 1967). Purse seines were approximately 229 m long and 11 m deep with 1- to 2-cm webbing (stretch measure). Effective fishing depth was about 6 m. Seines were towed upstream in a U shape for 10–30 min prior to pursuing. For the secondary releases, fish were obtained from the juvenile collection facilities at the respective dams.

Only hatchery-reared yearling chinook salmon, determined by the absence of either adipose or ventral fins (clipped at hatchery), were used in this study. Fish with extreme injuries, excessive descaling, or obvious bacterial kidney disease (BKD) symptoms were excluded, as were previously PIT-tagged fish (identified by scanning with a PIT-tag detector). During sorting and marking, fish were kept anesthetized with tricaine methanesulfonate (MS-222) in a recirculating anesthetic system at a dosage of approximately 50 ppm.

Fish were PIT-tagged using modified hypodermic syringes containing a push rod, terminal air hole, and 12-gauge needle (Prentice et al. 1990c; Nielsen 1992). The PIT-tag needle was inserted alongside the midventral line between the ventral and pelvic fins, and the tag was placed into the body cavity posterior to the pyloric caeca (Prentice et al. 1990c). Studies that have looked at the effects of PIT-tagging on salmon smolt growth or survival have found no significant effects (Prentice et al. 1987, 1990a; Prentice 1990). The small entry wound tends to heal quickly.

Smolts used in the primary releases (i.e., R_1) were kept in net-pens (1.8 × 0.9 × 0.7 m) for 32–54 h prior to release. Mortalities were

removed, scanned, and recorded prior to release. Smolts used to estimate post-detection bypass mortality were held in aluminum tanks with flow-through water at the dams. These smolts were generally held for at least 24 h prior to release with all mortalities recorded and counts adjusted accordingly.

Detection of PIT-tagged fish

At each dam, a variety of passage routes were available for migrating smolt. Fish could either pass over the spillway or enter the powerhouse (passage through navigation locks is negligible). The powerhouses of each dam were equipped with screening devices to guide fish away from turbine intakes and into "juvenile bypass systems," that have historically been used to collect fish to be transported downstream in barges or trucks. Not all fish were successfully guided and consequently some passed through turbines. PIT-tag detectors were installed only in the juvenile bypass systems. As a PIT-tagged fish passed through a detector, the tag code was recorded automatically (the fish was not handled). At Lower Granite and Little Goose Dams, the PIT-tag detector triggered a "slide gate" to divert the fish away from the transportation collection facilities and back into the river. However, not all detected fish were successfully diverted back to the river. Nondiverted fish were transported, and their capture histories were subsequently censored at that point.

Statistical methods

Single-release (SR) model

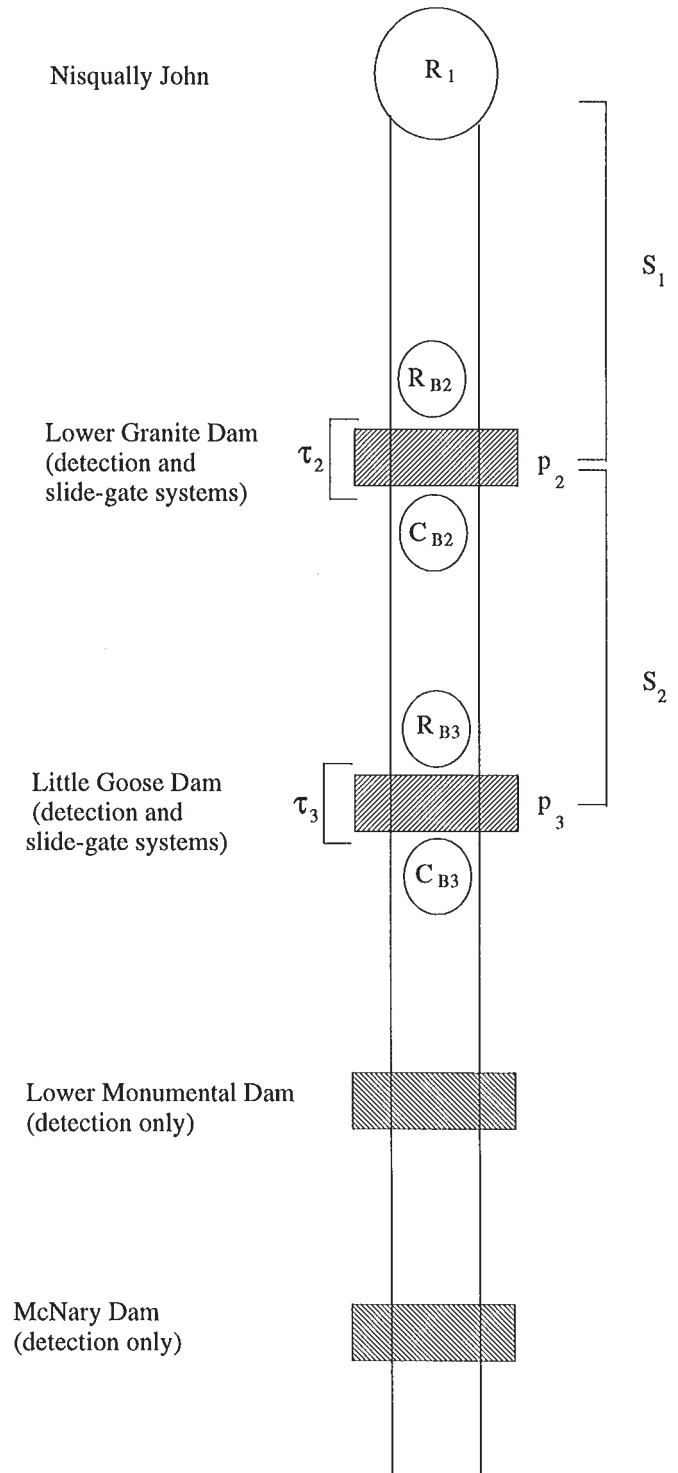
Survival probabilities through a section of a river or reservoir can be estimated using a single release of tagged fish upstream with multiple detection sites downstream. The minimal design configuration is an upstream release site and two downstream detection sites with the uppermost detection facility capable of returning detected fish to the river. In 1993, the Snake-Columbia River study used four detection sites. The two uppermost sites (Lower Granite and Little Goose dams) had both detection and rerelease capabilities and the two lower sites (Lower Monumental and McNary dams) had only detection and removal capabilities. For purposes of data analysis, detections at Lower Monumental and McNary Dams were not differentiated. The single release-recapture (SR) model was first presented by Cormack (1964), Jolly (1965), and Seber (1965). This model is also a special case of paired-release models using complete capture histories introduced, but not fully developed in its own right, by Burnham et al. (1987). The single release-recapture design is a special case of designs that can readily be analyzed using the interactive computer program SURPH.1 (Smith et al. 1994).

The likelihood model (SR model) for each single release of the 1993 Snake River survival study can be written as follows:

$$\begin{aligned}
 (1) \quad L(\underline{S}, \underline{p}, \lambda | \underline{R}, \underline{m}_1, \underline{m}_2, \underline{m}_3) = & \\
 & \binom{R_1}{m_{12}, m_{13}, m_{14}} (S_1 p_2)^{m_{12}} (S_1 (1 - p_2) S_2 p_3)^{m_{13}} \\
 & \times (S_1 (1 - p_2) S_2 (1 - p_3) \lambda)^{m_{14}} \\
 & \times (1 - S_1 (p_2 + (1 - p_2) \lambda + (1 - p_2) S_2 (1 - p_3) \lambda))^{R_1 - r_1} \\
 & \times \binom{R_2}{m_{23}, m_{24}} (S_2 p_3)^{m_{23}} (S_2 (1 - p_3) \lambda)^{m_{24}} \\
 & \times (1 - S_2 (p_3 + (1 - p_3) \lambda))^{R_2 - r_2} \binom{R_3}{m_{34}} \lambda^{m_{34}} (1 - \lambda)^{R_3 - r_3}
 \end{aligned}$$

where R_1 is the number of PIT-tagged fish released above Lower Granite Dam; R_2 is the number of PIT-tagged fish detected and rereleased at Lower Granite Dam; R_3 is the number of PIT-tagged fish detected and rereleased at Little Goose Dam; m_{ij} is the number of fish released at the i th site ($i = 1, 2, 3$) first detected at the j th detection site ($j = i+1, \dots, 4$); $r_i = \sum_{j=i+1}^4 m_{ij}$, for $i = 1, 2, 3$; S_1 is the survival probability

Fig. 2. Schematic of release locations, detection, and slide-gate rerelease facilities used to estimate survival (S), capture rates (p), and post-detection survival (τ).



from point of release to tailrace of Lower Granite Dam; S_2 is the survival probability from Lower Granite tailrace to tailrace of Little Goose Dam; p_1 is the detection probability at Lower Granite Dam; p_2 is the detection probability at Little Goose Dam; and λ is the joint probability of surviving from tailrace of Little Goose Dam and being detected at either Lower Monumental Dam or McNary Dam.

Table 1. Number of fish in each primary release group and their associated capture histories (0, not detected; 1, detected and released; 2, detected and removed).

Capture history	Release group and date						
	R_{11} 15 April	R_{12} 16 April	R_{13} 17 April	R_{14} 18 April	R_{15} 19 April	R_{16} 20 April	R_{17} 21 April
1 1 1	66	118	91	74	75	52	96
0 1 1	111	146	128	120	86	69	97
1 0 1	81	119	100	106	107	82	130
0 0 1	129	142	132	160	136	109	171
1 1 0	46	52	33	42	33	28	53
0 1 0	70	93	66	48	50	36	80
1 0 0	87	110	103	114	115	67	156
0 0 0	223	280	259	296	260	177	351
2 0 0	148	174	171	182	204	133	226
0 2 0	54	71	69	66	47	44	45
1 2 0	30	44	36	27	29	23	43
Total	1015	1305	1152	1208	1113	797	1405

Table 2. Number of fish released (i.e., R_{B2} and C_{B2} or R_{B3} and C_{B3}) and subsequent capture histories for each pair of replicate releases (0, not detected; 1, detected and released; 2, detected and removed).

(A) Lower Granite Dam.

Capture history	28 April		30 April		12 May	
	R_{B2}	C_{B2}	R_{B2}	C_{B2}	R_{B2}	C_{B2}
1 1	132	155	107	152	15	20
0 1	155	189	193	189	137	129
1 0	79	85	99	82	65	81
0 0	287	263	250	260	525	501
2 0	75	68	47	59	6	12
Total	728	760	696	742	748	743

(B) Little Goose Dam.

Capture history	7 May		8 May		13 May	
	R_{B3}	C_{B3}	R_{B3}	C_{B3}	R_{B3}	C_{B3}
1	273	413	452	423	117	98
0	186	279	285	307	634	637
Total	459	692	737	730	751	735

When all fish detected at a dam are rereleased (i.e., $R_2 = m_{12}$, $R_3 = m_{13} + m_{23}$), the statistical model can be simplified.

Formulae for the parameter estimates are simplified by defining the following variables:

$$m_j = \sum_{i=1}^{j-1} m_{ij}, \quad \text{for } j = 2 \text{ and } 3$$

$$z_j = \sum_{i=1}^{j-1} \sum_{k=j+1}^4 m_{ik}, \quad \text{for } j = 2 \text{ and } 3$$

$$T_j = m_j + z_j, \quad \text{for } j = 2 \text{ and } 3$$

The parameter estimates and associated variances can be written as follows:

$$(2) \quad \hat{S}_1 = \frac{r_1}{R_1} \left(\frac{m_2}{T_2} + \frac{z_2 R_2}{T_2 r_2} \right)$$

with

$$(3) \quad \widehat{\text{Var}}(\hat{S}_1 | S_1) = (\hat{S}_1)^2 \left[\frac{1}{r_1} - \frac{1}{R_1} + (1 - p_2)^2 \left(\frac{1}{r_2} - \frac{1}{R_2} \right) \right] + (\hat{S}_1)^2 (1 - p_2)^2 \left(1 - \frac{r_2}{R_2} \right)^2 \frac{m_2}{z_2 T_2}$$

$$(4) \quad \hat{S}_2 = \frac{r_2}{R_2} \left(\frac{m_3}{T_3} + \frac{z_3 R_3}{T_3 r_3} \right)$$

with

$$(5) \quad \widehat{\text{Var}}(\hat{S}_2 | S_2) = (\hat{S}_2)^2 \left[\frac{1}{r_2} - \frac{1}{R_2} + (1 - p_3)^2 \left(\frac{1}{r_3} - \frac{1}{R_3} \right) \right] + (\hat{S}_2)^2 (1 - p_3)^2 \left(1 - \frac{r_3}{R_3} \right)^2 \frac{m_3}{z_3 T_3}$$

while

$$(6) \quad \hat{p}_2 = \frac{m_2}{m_2 + z_2 R_2 / r_2}$$

$$(7) \quad \hat{p}_3 = \frac{m_3}{m_3 + z_3 R_3 / r_3}$$

and

$$(8) \quad \hat{\lambda} = \frac{r_3}{R_3}$$

These estimators were first derived by Cormack (1964) and later by Burnham et al. (1987, pp. 112–116). Approximate 95% confidence interval estimates for survival probabilities (S_k) can be calculated according to the formula:

$$(9) \quad 95\% \text{ CI} = \hat{S}_k \pm 1.96 (\widehat{\text{Var}}(\hat{S}_k | S_k))^{1/2}$$

Although we used the standard formula (eq. 9), normality assumptions could be avoided by using profile likelihood methods (Hudson 1971).

Assumptions associated with the SR model are as follows:

- (A1) The test fish are representative of the population of inference.
- (A2) Test conditions are representative of the conditions of interest.
- (A3) The number of fish released is exactly known.
- (A4) PIT-tag codes are accurately recorded at the time of tagging and at all detection sites.
- (A5) For replicated studies, data from different releases are statistically independent.

- (A6) The fate of each individual fish is independent of the fates of all other fish.
- (A7) All fish in a release group have equal survival and detection probabilities.
- (A8) Prior detection history has no effect on subsequent survival and detection probabilities.

Assumptions A1–A5 are pertinent for the validity of statistical inferences to the population of interest and to the proper conduct of the study. These assumptions (i.e., A1–A5) are largely satisfied by appropriate capture, handling, marking, and release procedures of the study protocol. Postrelease handling mortality could violate assumption A1 and tend to underestimate actual survival probabilities. Careful handling is therefore needed to avoid such bias and was the reason fish were held at least 24 h prior to release.

The key assumptions in constructing the multinomial likelihood (eq. 1) are A6–A8, which imply that the fates (i.e., capture histories) of all PIT-tagged fish in a release group are independent, identically distributed, multiple Bernoulli trials. Assumptions A6–A8 are mathematical constraints in the formulation of likelihood (eq. 1), and investigators have less direct control over them than assumptions A1–A5. For this reason, these assumptions warrant closer scrutiny. In the sections that follow, we first describe the effects of various violations of assumptions A6–A8 on survival estimates and associated variance estimates from the SR model. We then present a series of data analyses that were performed to test whether the assumptions were satisfied in the 1993 Snake River survival study.

Monte Carlo simulations

Heterogeneity in survival probabilities among the fish within a release group can violate assumption A7. Monte Carlo simulation studies were used to evaluate the robustness of the SR model to three forms of survival heterogeneity. The first potential violation of assumption A7 can be stated as follows:

- (V7a) Survival probabilities for individual smolts are heterogeneous because of inherent differences in viability of fish.

To evaluate the robustness of the model in eq. 1 to violation V7a, Monte Carlo simulations were conducted, each consisting of 1000 fish released above Lower Granite Dam. A total of 1000 simulations were conducted for each scenario investigated. Detection probabilities were 0.50, 0.55, and 0.60 at Lower Granite, Little Goose, and McNary dams, respectively. The distribution of survival probabilities among individual smolts depended on the distribution of a condition index. Each fish was assigned a standardized condition index from a normal distribution with mean (μ) = 0 and standard deviation (σ) = 0.1 for convenience. Heterogeneous survival probabilities among individual smolts were created by assuming a proportional hazards relationship based on the condition index. In terms of survival probabilities, a smolt with condition index x was assigned survival probabilities $S_1 = S_{10}^{e^{-2x}}$, $S_2 = S_{20}^{e^{-2x}}$, and $S_3 = S_{30}^{e^{-2x}}$ from release to Lower Granite, Lower Granite to Little Goose, and Little Goose to Lower Monumental, respectively. Two scenarios were investigated. In scenario V7a.1, the baseline survival (i.e., S_{k0}) probability was 0.88 for all three reaches. In scenario V7a.2, the baseline survival probabilities were $S_{10} = 0.6$, $S_{20} = 0.9$, and $S_{30} = 0.5$. In both scenarios, 20% of detected fish were removed for barging downstream at each dam. Program SURPH.1 (Smith et al. 1994) can relax assumption A7 by permitting the survival and detection probabilities of individual fish to be modeled as functions of individual-based covariates. Individual-based models will not be explored in this analysis (see Skalski et al. 1993; Smith et al. 1994).

The second potential violation of A7 can be stated as follows:

(V7b) Survival probabilities for individual smolts are heterogeneous because survival rates differ among the various routes through the hydroelectric projects (i.e., spill, bypass, turbines).

Risks of mortality are not the same in each of the passage routes through a dam. For the simulated scenarios, survival probabilities were calculated as the product of two independent probabilities. The

Table 3. Passage route-specific survival rates for scenarios simulated under violation V7b.

Scenario	Probability through spill	Survival probabilities		
		S_{spill}	S_{bypass}	S_{turbine}
V7b.1	0.2	0.90	0.90	0.90
V7b.2	0.6	0.90	0.90	0.90
V7b.3	0.2	0.97	0.98	0.85
V7b.4	0.6	0.97	0.98	0.85
V7b.5	0.2	0.80	0.50	0.30
V7b.6	0.6	0.80	0.50	0.30

Note: Release sizes of 1000 PIT-tagged fish were simulated 1000 times under each scenario.

first component was survival from the top of the reach to the forebay of the next downstream dam (i.e., the “pool”). This survival probability was set at 0.95. The second component of survival was the probability of surviving dam passage. Survival through the dam depended on whether passage occurred through the spillways (S_{spill}), turbines (S_{turbine}), or bypass system (S_{bypass}). In this set of simulations, mortality in the bypass system occurred before detection. The proportion of fish going through the alternative routes was allowed to vary (Table 3). In all V7b scenarios, of those fish entering the powerhouse (not the spill), the proportion passing through the bypass system (i.e., fish guidance efficiency (FGE)) was 0.45, 0.50, and 0.55 at Lower Granite, Little Goose, and McNary dams, respectively. In all scenarios, 20% of detected fish at each dam were removed for barging downstream (i.e., right censored).

A potential violation of assumption A8 can be stated as follows:

- (V8) Survival probabilities for individual smolts are heterogeneous because the route taken through a hydroelectric project affects downstream survival (or detection) probabilities.

Currently, PIT-tagged fish can be detected only in the juvenile bypass facilities of the dams. Consequently, detected fish traverse a different part of the tailrace than fish that pass via turbines or spillway. Assumption A8 would be violated if the subsequent level of mortality experienced by detected fish differs from that experienced by nondetected fish. For example, such a difference could be caused by differential predation mortality in the tailrace between fish passing through the bypass system and those using other passage routes, prior to remixing below the dam. The parameters for scenarios under violation V8 were identical to those under V7b (Table 3), except that mortality in the bypass system occurred after detection and before remixing with nondetected fish at Lower Granite and Little Goose Dams.

Tests of assumptions based on field trials

The validity of assumption A8 was evaluated using three distinct approaches. If two or more groups of tagged fish are mixed as they travel down the river, they will experience the same river and dam passage conditions. Thus, mixing of distinct groups is a sufficient, but not necessary, condition for equal capture and survival probabilities. The hypothesis that groups are mixed can be tested by comparing distributions of daily detections at downstream dams, using Pearson χ^2 tests of homogeneity based on contingency tables (Snedecor and Cochran 1989, pp. 210 and 211). The first test of assumption A8 was a comparison of the distributions of daily detections at downstream sites for subgroups of primary releases defined by their upstream capture history. Contingency table entries for Little Goose Dam distributions were the number of fish detected each day from two subgroups of each release: those detected at Lower Granite Dam, and those not detected at Lower Granite Dam. Similar tests of homogeneity were based on daily tag detections at Lower Monumental Dam for four subgroups defined by capture histories at Lower Granite and Little Goose dams.

The second method for testing assumption A8 was presented by

Burnham et al. (1987) and called TEST 3. This test checked the internal consistency of survival and capture probabilities by dividing a single release group into subgroups based on their capture histories up to a specified location. The two detection and diversion sites followed by two detection-only sites provided sufficient data to construct one contingency table analysis under TEST 3.

Each series of contingency table tests (one test for each of seven primary releases) was considered to be a single experiment, and significance levels were selected to control the experimentwise type I error rate at $\alpha_{EX} = 0.05$. With seven tests in each experiment, the testwise significance level was $\alpha_T = 0.0073$.

A third approach to testing assumption A8 was based on data from the secondary paired releases and is presented in the next section.

If the fates of individual fish are not independent (i.e., assumption A6 violated), point estimates of survival and detection probabilities for a release group remain valid and unbiased. However, model-based variance estimates tend to underestimate true variability under nonindependence. To determine whether the likelihood model (eq. 1) provided an accurate estimate of the variance of the survival estimates (eqs. 3 and 5), the seven primary releases in Lower Granite Reservoir were clustered in time as closely as possible. As such, the variability in the respective point estimates of survival should be almost exclusively the result of sampling variability and not because of changing survival probabilities associated with varying river conditions. The empirical variance among the seven point estimates (i.e., $s_{\hat{S}_i}^2$) was compared with the average variance estimated from the model (i.e., $\widehat{\text{Var}}(\hat{S}_i|S_i)$). There was no formal test of significance. However, if the empirical variance was much greater than the average variance predicted by the model, this would imply that the model was not accounting for a substantial source of variability.

Modified single-release (MSR) model

Assumption A8 is violated if fish detected in the juvenile fish bypass facility experience differential mortality before remixing with fish that passed through turbines or spillways. Data from the secondary paired releases at Lower Granite and Little Goose Dams, in conjunction with a modification of the SR model (eq. 1), can be used to estimate post-detection bypass mortality and provide valid estimates of smolt survival in the river reaches. The MSR model provides a robust alternative to the traditional SR model (Dauble et al. 1993).

The modification to the design for the SR model consists of concurrent releases of PIT-tagged fish in the bypass system just downstream from the PIT-tag detector and control fish in the zone of the tailrace where detected and nondetected fish remix. The MSR model explicitly estimates mortality between the detector and the remixing zone at Lower Granite and Little Goose Dams, and adjusts the reach survival estimates (\hat{S}_1 and \hat{S}_2).

Additional terms for the MSR model (Fig. 2) are defined as follows:

R_{B2} is the number of fish released in the bypass system at Lower Granite Dam; C_{B2} is the number of fish released in the tailrace at Lower Granite Dam; R_{B3} is the number of fish released in the bypass system at Little Goose Dam; C_{B3} is the number of fish released in the tailrace at Little Goose Dam; n_{R2} is the number of fish recovered downstream from the treatment release (R_{B2}); n_{C2} is the number of fish recovered downstream from the control release (C_{B2}); n_{R3} is the number of fish recovered downstream from the treatment release (R_{B3}); n_{C3} is the number of fish recovered downstream from the control release (C_{B3}); τ_2 is the survival probability between detector and remixing zone at Lower Granite Dam; τ_3 is the survival probability between detector and remixing zone at Little Goose Dam; λ_2 is the joint probability of secondary release fish from Lower Granite Dam surviving and being detected downriver; and λ_3 is the joint probability of secondary release fish from Little Goose Dam surviving and being detected downriver.

The likelihood model for the MSR design can be written as the joint likelihood for the primary and secondary releases:

$$(10) \quad L(S, p, \tau, \lambda | R, C, m, n) = \binom{R_1}{m_{12}, m_{13}, m_{14}} (S_1 p_2)^{m_{12}} (S_1 (1 - p_2) S_2 p_3)^{m_{13}} \times (S_1 (1 - p_2) S_2 (1 - p_3) \lambda)^{m_{14}} \times (1 - S_1 (p_2 + (1 - p_2) S_2 p_3 + (1 - p_2) S_2 (1 - p_3) \lambda))^{R_1 - \tau_1} \times \binom{R_2}{m_{23}, m_{24}} (\tau_2 S_2 p_3)^{m_{23}} (\tau_2 S_2 (1 - p_3) \lambda)^{m_{24}} \times (1 - \tau_2 S_2 (p_3 + (1 - p_3) \lambda))^{R_2 - \tau_2} \times \binom{R_3}{m_{34}} (\tau_3 \lambda)^{m_{34}} (1 - \tau_3 \lambda)^{R_3 - m_{34}} \times \binom{R_{B2}}{n_{R2}} (\tau_2 \lambda_2)^{n_{R2}} (1 - \tau_2 \lambda_2)^{R_{B2} - n_{R2}} \binom{C_{B2}}{n_{C2}} (\lambda_2)^{n_{C2}} (1 - \lambda_2)^{C_{B2} - n_{C2}} \times \binom{R_{B3}}{n_{R3}} (\tau_3 \lambda_3)^{n_{R3}} (1 - \tau_3 \lambda_3)^{R_{B3} - n_{R3}} \binom{C_{B3}}{n_{C3}} (\lambda_3)^{n_{C3}} (1 - \lambda_3)^{C_{B3} - n_{C3}}$$

Iterative numerical methods were used to estimate reach survival and post-detection bypass survival simultaneously. However, the following formula (the “relative-recovery” estimate) can be given for estimates of post-detection bypass survival:

$$(11) \quad \hat{\tau}_i = \frac{(n_{Ri} / R_{Bi})}{(n_{Ci} / C_{Bi})}, \text{ for } i = 2 \text{ and } 3.$$

The null hypotheses $H_0: \tau_2 = 1$ and $H_0: \tau_3 = 1$ were tested using likelihood ratio tests (LRT). Fish from the secondary releases were pooled in performing the LRTs.

A critical assumption of the MSR likelihood model (eq. 10) model is that the treatment fish of the paired release have the same survival and capture probabilities as the control fish downstream from the remixing zone (i.e., the difference between the downstream detection rates for the two groups is entirely due to mortality in the bypass system). For paired groups that pass two or more detection and diversion sites, an alternative formulation of the MSR model is available, based on survival probabilities from the point of release to the next site downstream. Post-detection bypass survival probability is then based on relative survival for the two groups, rather than on relative recovery rates.

Results

Assessment of the validity of using PIT-tag data in single release–recapture analysis was first evaluated using Monte Carlo methods to identify nonrobust properties of the model and then by empirical results from replicated field trials.

Monte Carlo simulations

Effect of heterogeneity of individuals on estimates of survival probabilities

Under conditions of heterogeneity of survival probabilities among individuals (violation V7a), the estimates of survival were unbiased, while theoretical variance estimates were slightly inflated (Table 4). Consequently, nominal 95% confidence intervals (eq. 9) covered the true survival probability (S_1 and S_2) slightly more than 95% of the time. These results are consistent with properties of independent but nonidentical Bernoulli trials used to estimate binomial proportions (Feller 1968, pp. 230–231).

Effect of route-specific dam passage mortality on estimates of survival probabilities

When bypass mortality occurred before detection (violation

Table 4. Results from 1000 Monte Carlo simulations for scenarios with heterogeneous survival rates due to individual differences (violation V7a).

Scenario	Reach	True \bar{S}_k	\bar{S}_k	$\widehat{\text{Var}}(\hat{S}_k S_k)$	$s_{\hat{S}_k}^2$	95% CI coverage
V7a.1	Rel-LGR	0.878	0.878	0.000 564	0.000 563	95.0
	LGR-LGO	0.878	0.880	0.001 651	0.001 565	95.4
V7a.2	Rel-LGR	0.598	0.598	0.000 679	0.000 663	94.9
	LGR-LGO	0.898	0.904	0.005 343	0.005 100	95.7

Note: True mean survival probability (\bar{S}_k), average survival estimate (\bar{S}_k), average variance estimate ($\widehat{\text{Var}}(\hat{S}_k|S_k)$), empirical variance among survival estimates ($s_{\hat{S}_k}^2$), and 95% confidence interval coverage are given. Survival probabilities were estimated for release to Lower Granite Dam (Rel-LGR) and Lower Granite to Little Goose Dam (LGR-LGO) reaches.

V7b) and the dead fish went undetected, there was no bias in overall reach survival estimates (\hat{S}) or associated variance estimates ($\widehat{\text{Var}}(\hat{S}_k|S_k)$) (Table 5). Confidence interval coverage for \hat{S} was nominal.

When mortality occurred in the bypass system after detection but before remixing with nondetected survivors, the PIT-tagged fish are counted as survivors. This type of route-specific mortality (violation 8) resulted in biased point estimates and variance estimates of survival and poor confidence interval coverage (Table 5). These simulation results motivated the development of the MSR model and the paired post-detection bypass releases in 1993.

Field trials

Effect of upstream detection on the probability of downstream detection

Daily distributions of detections at Little Goose Dam for the two subgroups of each primary release that passed Lower Granite Dam (i.e., detected or not detected) differed significantly ($P = 0.007$) only for the fifth release. Among the detection distributions at Lower Monumental Dam for four subgroups of each primary release defined by capture histories at Lower Granite and Little Goose Dams, again only the fifth release had significant differences ($P = 0.004$).

Differences in detection distributions at Little Goose Dam may have been the result of a 1- or 2-day delay for fish detected at Lower Granite Dam. However, river conditions over the peak days of passage for both groups were sufficiently stable and unlikely to cause a significant difference in survival or detection probability at Little Goose Dam. Furthermore, the test of homogeneity (TEST 3) proposed by Burnham et al. (1987) did not indicate significantly different survival and capture probabilities for detected and nondetected fish at Lower Granite Dam. The distribution of capture histories at Lower Monumental and McNary Dams did not depend on the capture history at Lower Granite and Little Goose dams for any of the seven primary releases.

Effect of upstream detection on the probability of downstream survival

Estimates (eq. 11) of post-detection bypass survival using relative recovery numbers from paired releases at Lower Granite Dam (τ_2) ranged from 0.915 to 0.986 with a weighted average (weights inversely proportional to respective estimated variances) of 0.950 ± 0.022 (mean \pm SE). Based on the weighted average, an approximate 95% confidence interval for post-

detection bypass survival at Lower Granite Dam of 0.907–0.993 does not include 1.0, suggesting that significant mortality may have occurred. Likelihood ratio tests based on the model in eq. 10 also indicated significant mortality at Lower Granite Dam ($\chi_1^2 = 4.774$, $P = 0.029$). However, there is some indication that the assumption of equal detection probabilities for the paired releases was violated at Little Goose Dam for the second paired release. Applying the SR model independently to the two groups, the estimated detection probabilities were 0.405 ± 0.028 and 0.502 ± 0.026 for the second treatment and control groups, respectively. The weighted average of post-detection bypass survival at Lower Granite Dam based on the relative survival method was 1.001 ± 0.070 . Consequently, conclusions regarding post-detection bypass mortality depend on whether the relative recovery or the relative survival method is used in the analysis of the paired releases. Differential detection probabilities within the paired releases suggest the better estimate of post-detection bypass mortality is provided by the relative survival method. Therefore, survival estimates for the primary releases were calculated using both the SR and MSR models.

Accuracy of model-based estimates of measurement error

For the seven survival estimates in the reach from release to Lower Granite Dam (Table 6), the average estimated sampling variance was 0.000 49 (SD = 0.022 1), while the empirical variance among the seven point estimates of survival was 0.000 12 (SD = 0.010 9). The two variance estimates are of the same order of magnitude, and the model-based variance is greater than the empirical variance. For survival estimates in the Lower Granite Dam to Little Goose Dam reach (Table 7), the average estimate of sampling variance was 0.000 13 (SD = 0.011 4), while the empirical variance among the seven point estimates was 0.000 12 (SD = 0.010 7), almost identical. There was no evidence that the model failed to adequately measure any significant source of variability.

Survival estimates for Snake River reaches

The primary releases, besides testing model assumptions, also provide an opportunity to examine survival of run-of-the-river hatchery-reared yearling chinook salmon during their out-migration to the ocean. However, when examining the resulting survival estimates, it must be remembered that these estimates represent only 1 week in the seasonal and interseasonal history of the river.

The following reach survival estimates are based on the SR model (i.e., assumption of 0% post-detection bypass

Table 5. Results from 1000 Monte Carlo simulations for scenarios with passage route-specific mortality.

Scenario	Reach	True \bar{S}_k	\bar{S}_k	$\widehat{\text{Var}}(\hat{S}_k S_k)$	$s_{\hat{S}_k}^2$	95% CI coverage
V7b.1	Rel-LGR	0.855	0.858	0.001 71	0.001 62	95.9
	LGR-LGO	0.855	0.860	0.005 27	0.005 26	95.3
V8.1	Rel-LGR	0.889	0.954	0.002 20	0.002 16	75.3
	LGR-LGO	0.893	0.862	0.005 67	0.005 60	90.3
V7b.2	Rel-LGR	0.855	0.868	0.012 85	0.013 70	95.9
	LGR-LGO	0.855	0.888	0.043 06	0.043 17	94.2
V8.2	Rel-LGR	0.872	0.972	0.018 00	0.017 57	97.0
	LGR-LGO	0.874	0.883	0.048 58	0.052 37	91.4
V7b.3	Rel-LGR	0.875	0.878	0.001 59	0.001 69	94.9
	LGR-LGO	0.880	0.883	0.004 92	0.005 10	95.0
V8.3	Rel-LGR	0.882	0.897	0.001 67	0.001 68	95.2
	LGR-LGO	0.887	0.881	0.004 98	0.004 91	94.2
V7b.4	Rel-LGR	0.894	0.904	0.011 84	0.012 77	94.3
	LGR-LGO	0.898	0.922	0.037 79	0.034 58	94.3
V8.4	Rel-LGR	0.902	0.940	0.013 16	0.013 79	95.8
	LGR-LGO	0.904	0.913	0.037 58	0.035 57	93.2
V7b.5	Rel-LGR	0.448	0.456	0.003 71	0.003 32	95.7
	LGR-LGO	0.456	0.484	0.017 87	0.015 83	94.6
V8.5	Rel-LGR	0.619	1.044	0.022 92	0.022 91	2.3
	LGR-LGO	0.646	0.538	0.023 63	0.022 38	72.1
V7b.6	Rel-LGR	0.604	0.624	0.021 18	0.020 30	93.2
	LGR-LGO	0.608	0.696	0.132 30	0.100 98	92.5
V8.6	Rel-LGR	0.690	1.371	0.214 11	0.198 25	92.4
	LGR-LGO	0.703	0.774	0.472 80	0.287 62	87.3

Note: True survival probability (\bar{S}_k), average survival estimate (\hat{S}_k), average variance estimate ($\widehat{\text{Var}}(\hat{S}_k|S_k)$), empirical variance among survival estimates ($s_{\hat{S}_k}^2$), and 95% confidence interval coverage are given. Survival probabilities were estimated for release to Lower Granite Dam (Rel-LGR) and Lower Granite to Little Goose Dam (LGR-LGO) reaches. Mortality in the bypass system occurs either before detection (violation V7b) or after detection (violation V8) at Lower Granite and Little Goose dams.

mortality). For the river section between Nisqually John and the tailrace of Lower Granite Dam (Table 6), smolt survival estimates (\hat{S}_1) ranged between 0.886 ± 0.020 and 0.920 ± 0.024 with a weighted average (\hat{S}_2) of 0.902 ± 0.004 . The \hat{S}_2 values between the tailrace of Lower Granite Dam and the tailrace of Little Goose Dam (Table 7) ranged from 0.818 ± 0.034 to 0.902 ± 0.044 with a \hat{S}_2 of 0.859 ± 0.013 . These estimates correspond well with other survival estimates of wild and hatchery-released yearling chinook over the wider range of the 1993 outmigration season reported by Iwamoto et al. (1994), and over the 1994 and 1995 seasons reported by Muir et al. (1995, 1996). Under the SR model, the estimated survival from Nisqually John to the tailrace of Little Goose Dam is 0.775 ($= 0.902 \times 0.859$).

Using the relative recovery method, post-detection bypass mortalities at Lower Granite and Little Goose dams are estimated to be 6% and 0%, respectively. If these survival figures are correct, the pooled estimates of survival for the primary releases are 0.875 ± 0.014 from Nisqually John to Lower Granite Dam tailrace and 0.913 ± 0.021 from Lower Granite Dam tailrace to Little Goose Dam tailrace. The effect of post-detection mortality is to lower the estimated survival rate in the subsequent reach. Essentially, the MSR model redistributes this “extra” dam mortality to the proper reach. Under the MSR model, the estimated survival from Nisqually John to the tailrace of Little Goose Dam is 0.799 ($= 0.875 \times 0.913$) compared with 0.775 under the SR model.

Discussion

By establishing the validity of the statistical and field methodology, we have shown that reliable survival estimates can be obtained from release–recapture models of detection data from PIT-tagged migrant juvenile salmonids in the Snake–Columbia River Basin. The ability to obtain reliable survival estimates is a powerful tool for the investigation, mitigation, and recovery of threatened and endangered salmonid stocks.

Our Monte Carlo simulation studies showed that heterogeneity of survival and detection probabilities among animals had no effects on estimates of mean survival probabilities but resulted in overestimation of the sampling variance and produced confidence intervals that were too wide. Conversely, the fates of fish within a release group are not independent; model-based variance estimates will tend to underestimate the true variance. While it is intuitive that there is heterogeneity among animals, there is no empirical evidence that fates of fish within a group are not independent. The empirical variance estimates from seven replicate releases estimated very near the model-based error variances estimated from the likelihood model. Hence, not only do the point estimates generated by this pilot study appear to be accurate and robust, but the standard errors of the estimates appear to be reliable measures of the uncertainty of the survival estimates. These results indicate the use of PIT-tags and release–recapture models can provide valid estimates of survival probabilities. Since 1993, diversion

Table 6. Estimated survival probabilities, estimated sampling variances, and average estimated variance from release to Lower Granite Dam tailrace based on primary releases.

Release	Point estimate of survival (\hat{S}_{1i})	Estimated variance ($\widehat{\text{Var}}(\hat{S}_{1i} S_{1i})$)
R_{11}	0.920	0.000 576
R_{12}	0.900	0.000 361
R_{13}	0.911	0.000 484
R_{14}	0.903	0.000 529
R_{15}	0.901	0.000 484
R_{16}	0.895	0.000 576
R_{17}	0.886	0.000 400
Overall estimated variance		0.000 487 (0.022 1)
Empirical variance (s_{1i}^2)		0.000 119 (0.010 9)

Note: Values for average estimated variance and empirical variance are variance and standard deviation.

systems have been completed at Lower Monumental and McNary dams extending the capability to perform survival studies much further downriver.

The assumption that survival and detection probabilities were not affected by upstream capture histories was evaluated by comparing temporal passage distributions for detected and nondetected smolts. Coincident downstream migrations were evident in six of seven cases. In one case, the timing was delayed 1 or 2 days for detected fish. Coincident passage is a sufficient condition for assuring that all fish are exposed to similar survival and detection conditions. However, coincident passage is not necessary for equal probabilities if river conditions vary little over a 1- or 2-day period. Indeed, for the group with apparent noncoincident passage, the Burnham et al. (1987) test of homogeneity (TEST 3) found no significant difference in downstream capture histories for groups of fish with differing upstream detection histories.

Our smallest release group of only 797 PIT-tagged fish on 20 April 1993 resulted in standard errors of 0.024 and 0.044 on survival estimates from the release to Lower Granite Dam and Lower Granite Dam to Little Goose Dam reaches, respectively. The largest release of 1405 fish resulted in standard errors of 0.020 and 0.036 for the two reaches, respectively. These levels of precision for survival estimates have not been attainable using more conventional marking techniques in the past (e.g., freeze-brand, fin-clipping), even with tens of thousands of marked fish. Hence, the PIT-tag has the capability of providing accurate and precise estimates of survival using a minimum number of fish at a time when the need for information is the greatest and the opportunity to handle large numbers of fish is low because of listings of salmonids stocks under the Endangered Species Act.

Acknowledgments

This research was supported by Bonneville Power Administration under contracts DE-AI79-93BP10891 (Project No. 93-29) and DE-AI79-90BP62611 (Project No. 86-118).

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Table 7. Estimated survival probabilities, estimated sampling variances, and average estimated variance from Lower Granite Dam tailrace to Little Goose Dam tailrace based on primary releases.

Release	Point estimate of survival (\hat{S}_{2i})	Estimated variance ($\widehat{\text{Var}}(\hat{S}_{2i} S_{2i})$)
R_{11}	0.888	0.001 52
R_{12}	0.889	0.000 84
R_{13}	0.831	0.000 96
R_{14}	0.818	0.001 16
R_{15}	0.831	0.001 37
R_{16}	0.902	0.001 94
R_{17}	0.869	0.001 30
Overall estimated variance		0.000 130 (0.011 4)
Empirical variance (s_{2i}^2)		0.000 115 (0.010 7)

Note: Values for average estimated variance and empirical variance are variance and standard deviation.

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