Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies

John R. Skalski, Richard Townsend, James Lady, Albert E. Giorgi, John R. Stevenson, and Robert D. McDonald

Abstract: A tag–release study is illustrated using radio-tagged chinook (*Oncorhynchus tshawytscha*) smolts to concurrently estimate passage rates and survival probabilities through the spillway and turbines of a hydroelectric project. The radio antennas at the forebays of the dam were arranged in double arrays allowing the estimation of route-specific detection probabilities and converting smolt detections to estimates of absolute passage. A maximum likelihood model is presented using the downstream detection histories to jointly estimate the route-specific passage and survival probabilities. In turn, these estimates were combined to estimate smolt survival through the dam, pool, and the entire hydroelectric project. The detailed migration information derived by these techniques can be used to evaluate mitigation programs focused on improving downstream passage of migrating salmonid smolts. At a mid-Columbia River hydroproject, the average spillbay survival calculated across replicate releases of hatchery and run-of-river yearling chinook salmon smolts was 1.000 (estimated standard error, $\widehat{SE} = 0.0144$). Average survivals through the two different powerhouses at the hydroproject were estimated to be 0.9409 ($\widehat{SE} = 0.0294$) and 0.9841 ($\widehat{SE} = 0.0119$). Project survival after combining the route-specific survival and passage probabilities was estimated across stocks to be 0.9461 ($\widehat{SE} = 0.0016$).

Résumé : Des saumoneaux du saumon quinnat (*Oncorhynchus tshawytscha*) ont été munis de radio-émetteurs et relâchés dans le but d'estimer leur taux de passage et leur probabilité de survie à travers le canal de fuite et les turbines d'un complexe hydroélectrique. Les antennes radio dans les biefs d'aval du barrage étaient placées en rangées doubles pour permettre l'estimation de probabilités de détection spécifiques à la route choisie et la conversion des détections de saumoneaux en estimations de passage absolues. On trouvera ici un modèle de vraisemblance maximale qui utilise les données de détection d'aval pour estimer à la fois le passage en fonction de la route et les probabilités de survie. Ensuite, ces estimations ont été combinées pour évaluer la survie des saumoneaux à travers le barrage, le bassin et tout le complexe hydroélectrique. L'information détaillée sur la migration fournie par ces techniques peut servir à évaluer les programmes de mitigation qui visent à améliorer le passage vers l'aval des saumoneaux migrateurs. À une installation hydroélectrique du cours moyen du Columbia, la survie moyenne dans le canal de fuite calculée d'après une remise à l'eau combinée de saumoneaux de 1 an du saumon quinnat provenant de piscicultures et de la rivière même était de 1,000 (erreur type estimée, $\widehat{SE} = 0{,}0144$). Les survies moyennes à travers deux centrales différentes du complexe hydroélectrique étaient respectivement de 0,9409 ($\widehat{SE} = 0{,}0294$) et de 0,9841 ($\widehat{SE} = 0{,}0119$). La survie à travers le complexe, qui combine la survie spécifique à la route choisie et les probabilités de passage pour tous les stocks, a été évaluée à 0,9461 ($\widehat{SE} = 0{,}0016$).

[Traduit par la Rédaction]

Introduction

Smolt survival studies have been a cornerstone of salmonid research in the Snake–Columbia River basin for more than three decades (Bickford and Skalski 2000). These survival studies have either attempted to estimate smolt survival through an entire project (i.e., dam and reservoir) or through a specific passage route at a dam such as a spillway or turbine (Bickford and Skalski 2000). However, mitigation projects such as surface bypass collectors, extended-length bar screens, spillway deflectors, and biological guidance systems used in the Snake–Columbia River system require precise information on both route-specific passage rates and subsequent smolt survival. The information also needs to be

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of sufficient detail to reconstruct survival of the migrating smolts through the entire dam and project to evaluate the overall benefits of the mitigation efforts.

The prevailing PIT tag (passive integrated transponder tag) release–recapture techniques (Skalski et al. 1998) used in the Snake–Columbia River basin are well suited to providing estimates of smolt survival through river reaches and entire hydroprojects (Muir et al. 2001). However, these same techniques are ill suited for providing the fine-scaled information needed to guide and evaluate mitigation efforts at powerhouses or spillways so central to the recovery efforts of salmonids listed under the U.S. Endangered Species Act (ESA 1973). Only the PIT-tagged smolts that go through the juvenile bypass system at hydroprojects can currently be detected. Smolts that pass through spillways, turbines, and surface bypass systems go unnoticed.

Radiotelemetry, on the other hand, can be used to monitor the passage of radio-tagged smolts through the entire array of passage routes at a hydroproject. The use of radiotelemetry in salmonid smolt survival studies has become feasible with the advent of small, relatively long-life radiotelemetry tags, and the ability to monitor smolt detections across the face of the dam with extensive radio antenna arrays (Skalski et al. 2001*a*). The higher detection rates of radio-tagged smolts also means fewer smolts need to be tagged than required for PIT-tag studies for comparable precision. The purpose of this paper is to describe the adaptation of radiotelemetry techniques and statistical models for the specific purpose of providing detailed information on route-specific passage and survival probabilities of salmonid smolts through hydroprojects. Skalski et al. (2001*a*) describe the analysis of radiotelemetry data for the simpler purpose of estimating pool, dam, and project survival of smolt through hydroprojects.

Materials and methods

Study area

During spring 2000, smolt passage and survival were estimated during outmigration at the Rock Island Dam project in the mid-Columbia River (Fig. 1) operated by Public Utility District (PUD) No. 1 of Chelan County. This study area extends from the tailrace of Rocky Reach Dam (river kilometre (RK) 762.3), through Rock Island Dam (RK 729.7), and beyond to the three antenna arrays in the pool of Wanapum Dam (RK 694.1, 698.8, and 702.8).

Rock Island Dam is located approximately 21 km downstream of Wenatchee, Washington. The dam has two powerhouses. The original powerhouse 1, built in 1933, has 10 vertical-axis turbine units, each with three intakes. Powerhouse 2, built in 1979, has eight horizontal-axis turbine units, each with two intakes. The spillway consists of 32 spillbays separated between bays 14 and 16 by an adult fish ladder. The reservoir extends 32 km upstream to Rocky Reach Dam.

Radio transmitters

The radiotelemetry tags used in this study were pulse-coded transmitters developed by Lotek Wireless, Inc., (Newmarket, Ont.) The tag (model MCFT-3G) including the battery was 8.2 mm in diameter and 18.9 mm in length, and weighed 1.75 g in air and 1.4 g in water. The in-water weight of the tags is a more important measure, for it best characterizes the added burden of the tag on the fish. Stainless steel 40-cm-long antennas were used on the tags. The tags were powered by a 3.0 V battery that provided a minimum tag life of 22 days at the prescribed transmission rate of 1 pulse every 2.5 s. The radio tags operated over a range of radio frequencies of 149.320–149.780 MHz. The detection range of the tags depended on reception by underwater or aerial antennas. For underwater antennas, the range was approximately 14 m. For aerial antennas, the range was approximately 25 m and 110 m for tags at a water depth of 6 m and 1 m, respectively. All range calculations were based on a water salinity of 30–40 $\mu S \cdot cm^{-1}$.

System antenna configuration

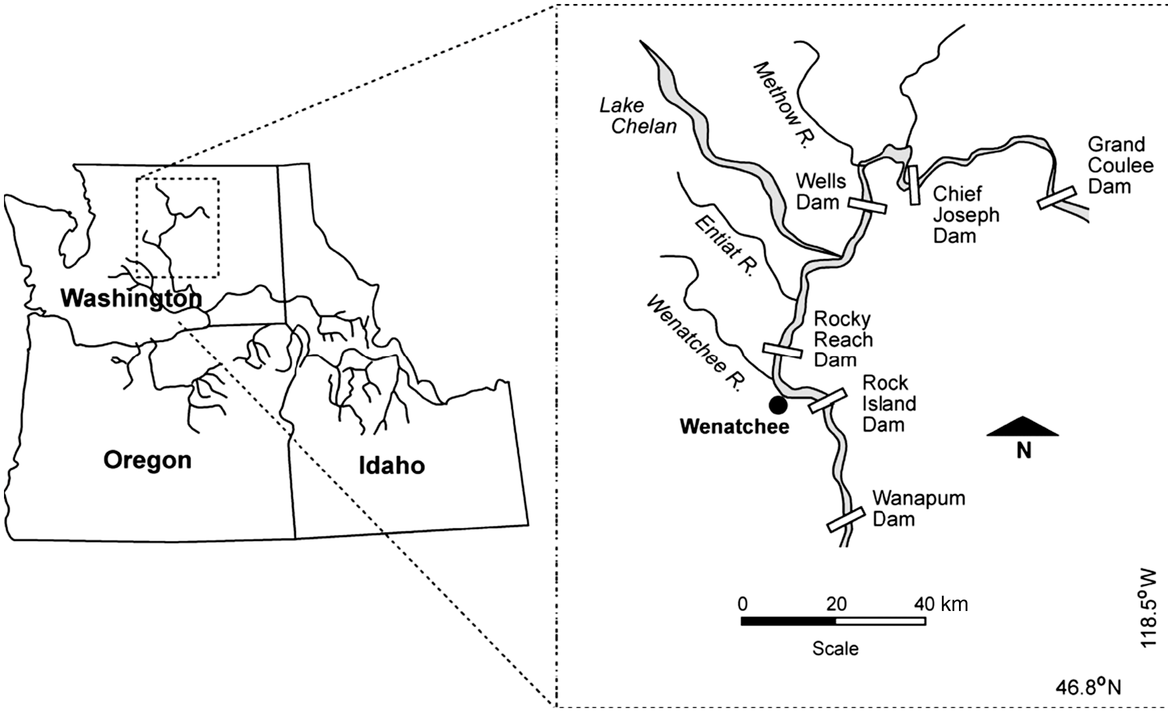
Radio-tagged smolts were monitored at Rock Island Dam and at the three Wanapum Dam pool arrays during the downstream migration. The primary antenna system at Rock Island Dam consisted of four-element aerial antennas distributed across the upstream face of the structure along the deck. Eight aerial antennas were evenly spaced (30.5 m) across the upstream face of powerhouse 1. Similarly, five aerial antennas were spaced 30.5 m apart across the upstream face of powerhouse 2. Another 12 aerial antennas were evenly spaced (30.5 m) across the breadth of the Rock Island spillway.

A secondary antenna system at Rock Island Dam consisted of underwater antennas deployed throughout each of the passage locations (i.e., turbine intakes and spillbays). Two underwater antennas were mounted within the individual headgate slots of each turbine intake. At the spillways, two underwater antennas were mounted to the pier-nose of each spillbay. At Rock Island, some of the spillbays were capable of spilling water near the surface and from the bottom simultaneously. In which case, four antennas were deployed per spillbay. In the tailrace of Rock Island Dam, directional aerial antennas were also aimed downriver to provide auxiliary passage information. These tailrace detections were used only in a confirmatory role to help identify passage and were not used as part of the formal survival analysis.

Within the Wanapum pool, three transects were deployed (Wanapum 1, 2, and 3). At each transect, two telemetry systems were deployed, one on each side of the river. Wanapum 3 was located near the south end of Quilomene Island, so the system for monitoring the eastern portion of the river was placed on this island. At each receiver, two antenna arrays were deployed with a total of three antennas per array; one antenna pointed upstream, one across the river, and the third downstream. Therefore, each transect consisted of a total of 12 antennas and two receivers, except for transect 3, which had 18 antennas and two receivers, with the six additional antennas monitoring the east channel at Quilomene Island. For the purpose of the survival analysis at Rock Island Dam, the detections at the three Wanapum arrays were pooled.

For all aerial systems, radio receivers (SRX 400 manufactured by Lotek Wireless, Inc.) were used with a scan period of 3 s. Multiple receivers were used to minimize the number of channels monitored by each receiver. Underwater antenna arrays were monitored by SRX and Digital Spectrum Processor (DSP) systems. These DSP systems allowed all antennas and frequencies to be monitored simultaneously.

Fig. 1. Study area for the survival study conducted in mid-Columbia River, Wash., U.S.A., in 2000.



Details of the antenna arrays and receiver configuration can be found in Stevenson et al. (2000).

Fish tagging and release

To estimate passage and survival probabilities at Rock Island Dam, a total of approximately 350 run-of-river chinook (*Oncorhynchus tshawytscha*) smolts and 350 hatchery chinook salmon smolts were tagged and released in the tailraces of Rocky Reach and Rock Island dams (10 replicate releases of 35 fish at each release site) over a 36-day period. The run-of-river smolts were composed of yearling hatchery chinook salmon smolts that were released from a variety of hatcheries upriver and that had migrated and were subsequently collected at the hydroproject. The hatchery smolts came from the Turtle Rock facility operated at Chelan PUD. Instead of one large release, numerous small replicate release groups were used to extend the study over the course of the migration period. Because the sizes of the individual release groups were small, the data from the replicate releases were pooled for the subsequent survival analysis.

At the time of tagging, smolts were placed in a holding tank containing a 100 mg·L^{-1} solution of MS-222 (tricaine methanesulfonate). Once anesthetized, fish were inspected and fish with obvious injuries, excessive descaling, an adipose fin (because ESA precluded use of wild smolts, hatchery smolts were identified from adipose fin clips), or that were less than 150 mm in fork length were excluded. Radio tags were surgically implanted within the peritoneal cavity of the host fish using procedures described in English et al. (1999). Following implantation, individual fish were held in separate compartments (approximately 9.5 L) in a flow-through water delivery system to prevent tangling of the external antennas. The smolts were allowed to recover in ambient river water for 40–48 h prior to release.

Releases at Rocky Reach and Rock Island tailraces occurred sequentially in time. There was a one-day delay in releases between Rocky Reach Dam and Rock Island Dam tailraces to promote downstream mixing of the release groups. At each project, the fish were ferried to the release sites, which were mid-channel, within 0.5 km downstream of each dam.

Converting radio signals into detection histories

The numerous radio antennas and associated receivers recorded vast numbers (i.e., approximately 1.5 million records) of radio signals that had to be interpreted and converted into useful detection histories. These radio signals included multiple detections from tagged fish along with spurious radio signals. The role of signal processing was to differentiate true detections of radio-tagged smolt from spurious radio signals. In general, three sets of criteria were used to identify valid detections. These criteria included (*i*) the power level of the received signal, (*ii*) the number of signals received per unit of time above a minimum power threshold, and (*iii*) the geographic distribution of the radio signals within the antenna arrays at a site.

For each antenna, a minimum power threshold (MPH) was specified, above which a signal was considered a valid tag transmission. In establishing the MPH, a distribution of observed power levels was constructed based on signals known not to have come from tagged fish. These false signals, which are typically of relatively low power levels, were collected either before the tagged fish were released or after the tagged fish had left the area. A MPH was then uniquely established for each antenna that excluded most false signals while recognizing higher power levels as possible valid tag signals. Signal frequency was the minimum number of consecutive signal transmissions above the MPH required for a detection to be considered valid. The third criterion took into account the geography of the antennas receiving the signal transmissions. It was not uncommon for two or more antennas to receive signals from the same tagged fish. Multiple signals received over time and locations were evaluated to determine their consistency with possible smolt movement patterns.

The data were repeatedly processed using alternative thresholds for the frequency and signal power level criteria. Signals identified as valid detections under all sets of alternative processing criteria were considered reliable. When detections were designated as valid using some criteria but not all, the signal data were manually reinspected. Manual inspection involved examining the times and locations of all received signals to determine whether the observed pattern was consistent or not with a valid detection. If the manual inspection was inconclusive, the detection history was right-censored (Elandt-Johnson and Johnson 1980; Lee 1992) to the last location where the smolt was known to be alive. Details of the data processing techniques used to convert the radio signals to detection histories can be found in Skalski et al. (2001*a*).

In Skalski et al. (2001*a*), radio signals were analyzed to simply identify the presence or absence of a tagged smolt at a location. In this study, the signal processing included the additional task of differentiating smolt passage at Rock Island Dam through powerhouses 1 and 2 (i.e., turbines) and the spillway. Once a smolt was identified as arriving at the dam, the subsequent step was to determine the route of passage. Passage determination was often facilitated by the underwater antenna arrays. When smolts were detected by the underwater secondary arrays, they were generally already entrained by the water flow through the turbines or spillbays, making passage determination straightforward. Less obvious were cases when the smolts were detected by the aerial forebay antennas but not the underwater antennas. In these cases, detections in the tailrace in conjunction with the forebay detection locations typically identified the passage route. When the passage routes could not be determined with certainty, the detection histories of the smolts were right-censored at the last known location where the smolt were found alive (i.e., the forebay). As a final step in the signal processing, the radiotelemetry data were independently reviewed by staff at LGL Limited of Sidney, B.C., to provide an independent peer review of the signal processing results.

Statistical methods

Parameter estimation

The classical release–recapture (Cormack 1964; Jolly 1965; Seber 1965) and the paired release–recapture (Burnham et al. 1987) models (PRRM) used in estimating smolt survival do not use all of the available information on smolt passage generated by the radiotelemetry studies. Detection histories that indicate the exact routes of smolt passage through the hydroprojects contain information on both route-specific survival and passage probabilities. These route-specific detections can be formally incorporated in statistical analyses to extract route-specific passage rates and survival.

The ability to extract route-specific passage rates and survival was possible because of the double-antenna arrays deployed at Rock Island Dam in 2000. The double-array system within each passage route permits the estimation of route-specific detection probabilities. In turn, these detection probabilities can be used to convert detection frequencies into absolute counts of smolt passage numbers at each route.

In constructing the route-specific survival model (RSSM), the following parameters were defined: S_{pool}, Rock Island pool survival probability; E, probability that smolts will travel over the spillway at Rock Island Dam, i.e., spill efficiency at Rock Island Dam; G, conditional probability of guidance to powerhouse 2, given that smolts were going to a powerhouse; p_{T1}, powerhouse (turbine) 1 primary array detection probability ($q_{\text{T1}} = 1 - p_{\text{T1}}$); p'_{T1}, powerhouse 1 secondary array detection probability ($q'_{\text{T1}} = 1 - p'_{\text{T1}}$); p_{T2}, powerhouse 2 primary array detection probability ($q'_{\text{T2}} = 1 - p'_{\text{T2}}$); P'_{T2}, powerhouse 2 secondary array detection probability ($q'_{\text{T2}} = 1 - p'_{\text{T2}}$); p_s, spillway primary array detection probability ($q_s = 1 - p_s$); p'_s, spillway secondary array detection probability ($q'_s = 1 - p'_s$); S_{T1}, powerhouse 1 survival probability at Rock Island Dam; S_{T2}, powerhouse 2 survival probability at Rock Island Dam; S_{SP}, spillway survival probability at Rock Island Dam; λ, joint probability of surviving and being detected at the three Wanapum pool arrays; δ, probability that a smolt is censored at Rock Island Dam.

The Rocky Reach tailrace release (R_1) and Rock Island tailrace release (R_2) were radio-tracked to the Wanapum pool arrays. A branching process was used to model the migration and survival of releases R_1 and R_2 (Fig. 2).

The joint likelihood for the RSSM used to estimate the passage and survival probabilities at Rock Island Dam can be written as

$$(1)\qquad L(\underset{\sim}{\theta}\,|\,\underset{\sim}{n}_1, \underset{\sim}{n}_2) = \binom{R_1}{\underset{\sim}{n}_1}\prod_{i=1}^{9} p_i^{n_{1i}} \binom{R_2}{n_2}\lambda^{n_2}(1-\lambda)^{R_2-n_2}$$

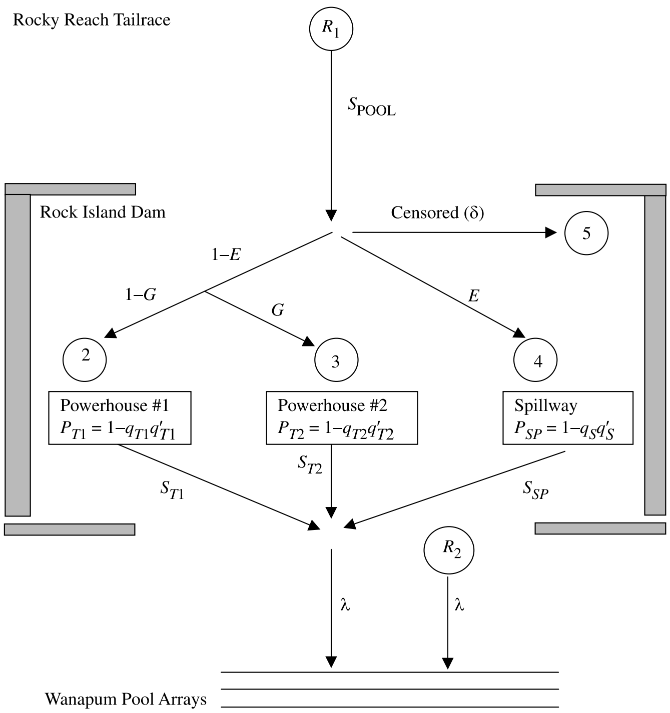
R_1 has nine possible unique downstream detection histories (i.e., four possible outcomes at Rock Island × two possible outcomes at Wanapum pool arrays + censored at Rock Island). Only two detection histories (i.e., detected or not detected) are possible for the Rock Island tailrace release (R_2) to the Wanapum pool arrays. The data used in the analyses (i.e., $\underset{\sim}{n}_1$ and $\underset{\sim}{n}_2$) are the vectors of smolt counts associated with the mutually exclusive and exhaustive detection histories for each release group (i.e., R_1 and R_2). The values of p_i in eq. 1 are the probabilities of occurrence of each of the unique downstream detection histories possible for a release group. For example, the probability of a smolt released at R_1 being detected at Rock Island powerhouse 1, followed by detection at the Wanapum pool arrays can be expressed as

$$S_{\text{pool}}(1-E)(1-G)(1-\delta)P_{\text{T1}}S_{\text{T1}}\lambda$$

In a similar way, the probabilities of occurrence for the other detection histories for releases R_1 and R_2 can be modeled using the branching processes in Fig. 2.

As currently expressed, the number of parameters in likelihood eq. 1 is greater than the dimension of the minimum sufficient statistics, making parameter estimation using this likelihood impossible. However, additional information from the primary and secondary arrays can be used to support the likelihood equation. At each passage route, the numbers of

Fig. 2. Schematic of route-specific passage and survival through the Rock Island project based on Rocky Reach (R_1) and Rock Island (R_2) tailrace releases.



smolts detected at only the primary array (m_1), at only the secondary array (m_2), and at both arrays ($m_{1,2}$) can be used to estimate the route-specific detection probabilities. For example, the auxiliary likelihood model for the detection process at powerhouse 1 can be written in the form

$$(2)\qquad L(p_{T1}, p'_{T1}|\underset{\sim}{m}) \propto \left(\frac{p_{T1}(1-p'_{T1})}{1-q_{T1}q'_{T1}}\right)^{m_1}\left(\frac{p'_{T1}(1-p_{T1})}{1-q_{T1}q'_{T1}}\right)^{m_2}\left(\frac{p_{T1}p'_{T1}}{1-q_{T1}q'_{T1}}\right)^{m_{1,2}}$$

and where the overall probability of detection within powerhouse 1 is expressed as

$$P_{T1} = 1-(1-p_{T1})(1-p'_{T1}) = 1-q_{T1}q'_{T1}$$

The detection probabilities were estimated independently for the three routes at Rock Island Dam (depicted in Fig. 2). With the inclusion of the three auxiliary likelihoods of the form of eq. 2 along with eq. 1, all parameters were estimable. The maximum likelihood estimates (MLE) were solved numerically using the program FLETCH (Fletcher 1970), and the standard errors for the parameters calculated based on the inverse Hessian matrix.

Model assumptions

The assumptions (A) of the RSSM are essentially the same as those of the paired release–recapture models of Burnham et al. (1987) with the exception of two additional assumptions (A10–A11).

Assumptions associated with the RSSM are as follows:

(A1) Individuals marked for the study are a representative sample from the population of interest.

Table 1. Counts of radio-tagged chinook hatchery smolts for the releases from Rocky Reach tailrace (R_1) and Rock Island tailrace (R_2) used in the route-specific survival model (RSSM).

Release	Detection history[a]	Counts	Within-route histories at Rock Island[b] 11	01	10
R_1 = 349	100	16			
	101	70			
	120	3 }	19	3	2
	121	21 }			
	130	10 }	38	56	58
	131	142 }			
	140	2 }	49	6	23
	141	76 }			
	15	9			
R_2 = 349	010	14			
	011	335			

[a]Detection history recorded at Rocky Reach tailrace, Rock Island Dam, and the Wanapum pool arrays, respectively: 1, detected; 0, not detected; 2–5, specific passage routes (see Fig. 2 for code designations).
[b]Detection history at primary and secondary antenna routes within a route: 1, detected; 0, not detected.

Table 2. Counts of radio-tagged chinook run-of-river smolts for the releases from Rocky Reach tailrace (R_1) and Rock Island tailrace (R_2) used in the route-specific survival model (RSSM).

Release	Detection history[a]	Counts	Within-route histories at Rock Island[b] 11	01	10
R_1 = 345	100	20			
	101	79			
	120	2 }	22	3	3
	121	26 }			
	130	7 }	45	63	37
	131	138 }			
	140	4 }	34	8	29
	141	67 }			
	15	2			
R_2 = 350	010	15			
	011	335			

[a]Detection history recorded at Rocky Reach tailrace, Rock Island Dam, and the Wanapum pool arrays, respectively: 1, detected; 0, not detected; 2–5, specific passage routes (see Fig. 2 for code designations).
[b]Detection history at primary and secondary antenna routes within a route: 1, detected; 0, not detected.

(A2) Survival and capture probabilities are not affected by tagging or sampling. That is, tagged animals have the same survival probabilities as untagged animals.

(A3) All sampling events are “instantaneous”. That is, sampling occurs over a negligible distance relative to the length of the intervals between sampling events.

(A4) The fate of each tagged individual is independent of the fate of all others.

(A5) All tagged individuals alive at a sampling location have the same probability of downstream survival.

(A6) All tagged individuals alive at a sampling location have the same probability of being detected.

Fig. 3. Schematic of estimated route-specific passage and survival probabilities for hatchery chinook salmon (*Oncorhynchus tshawytscha*) through the Rock Island project in 2000. Estimated standard errors are in parentheses.

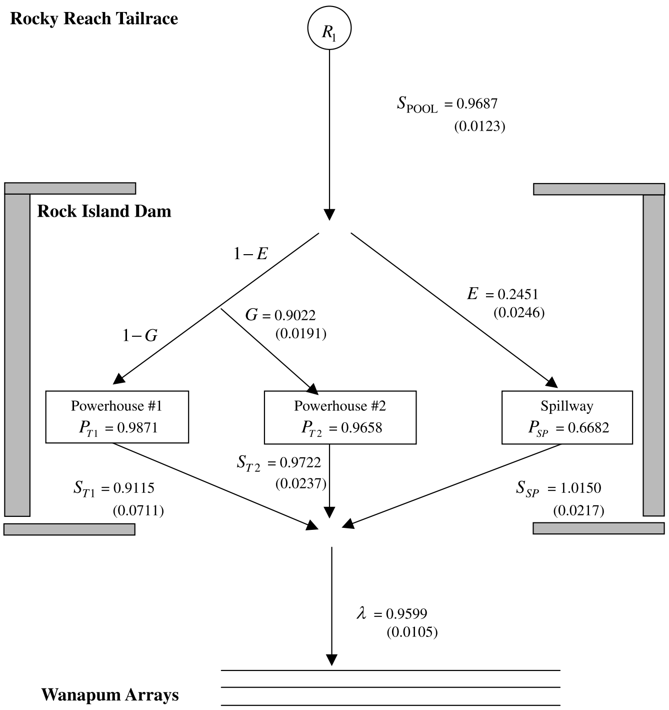
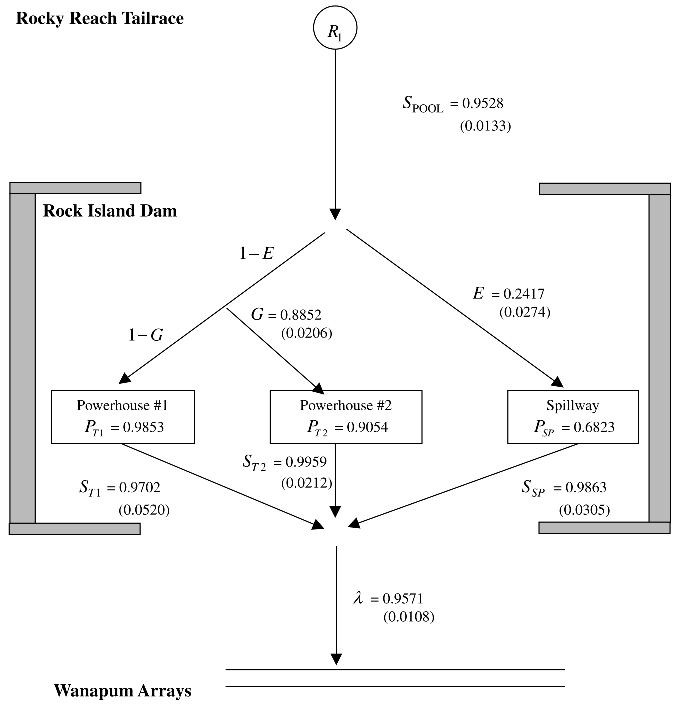


Fig. 4. Schematic of estimated route-specific passage and survival probabilities for run-of-river chinook salmon (*Oncorhynchus tshawytscha*) through the Rock Island project in 2000. Estimated standard errors are in parentheses.



(A7) All tags are correctly identified and the status of smolt (i.e., alive or dead) is correctly assessed.
(A8) Survival in the lower river segments is conditionally independent of survival in the upper river segments.
(A9) Both the upstream and downstream release groups within a paired release experience the same survival probability in the segment of the river that they travel together.
(A10) Routes taken by the radio-tagged smolts through the project are known without error.
(A11) Detection in the primary and secondary antenna arrays within a passage route are independent.

Skalski et al. (2001*a*) discussed the fulfillment of A1–A9 in a radiotelemetry survival study. A10 can be qualitatively assessed by examining the radiotelemetry detection histories to determine whether inconsistencies in individual smolt detection histories might exist. For example, a smolt detected in the upstream array at one route but found in the downstream array of another route would suggest a violation of A10. In a few instances, passage routes for smolts arriving at Rock Island Dam could not be confirmed, in which case, the data were right-censored at the last known upstream location to avoid violations of A10.

A11 is necessary for valid estimation of in-route detection probabilities, but cannot be empirically assessed with the detection data collected by a study. Instead, the detection fields for the primary and secondary arrays need to be located in such a way that a smolt detected in one array does not have a higher or lower probability of detection in the secondary array than a smolt not detected in the first array. This is best accomplished by having independent receivers for each antenna array and having the detection field for at least one array encompass the entire passage route.

Estimating dam and project survival and passage proportions

The proportions of smolts passing through the various routes at Rock Island Dam can be calculated from the estimated movement parameters. The proportion passing through the spillway is simply $\hat{E}$, whereas the proportion passing through powerhouse 1 is estimated by

$$(3) \qquad (1-\hat{E})(1-\hat{G})$$

and the proportion passing through powerhouse 2 is estimated by

$$(4) \qquad (1-\hat{E})\hat{G}.$$

The individual route-specific survival and passage probabilities can also be combined following maximum likelihood estimation to estimate survival through the dam. The survival through the Rock Island Dam was estimated from the expression

$$(5) \qquad \hat{S}_{\mathrm{dam}} = (1-\hat{E})(1-\hat{G})\hat{S}_{\mathrm{T1}} + (1-\hat{E})\hat{G}\hat{S}_{\mathrm{T2}} + \hat{E}\hat{S}_{\mathrm{SP}}.$$

Total project survival was then estimated from the general expression

$$(6) \qquad \hat{S}_{\mathrm{project}} = \hat{S}_{\mathrm{dam}} \times \hat{S}_{\mathrm{pool}}.$$

Variances for expressions (eqs.) 3–6 were estimated using the delta method (Seber 1982, pp. 7–9).

Table 3. Comparison of estimates from the route-specific survival model (RSSM) for both hatchery and run-of-river chinook salmon smolts and the estimates from the paired release–recapture model (PRRM) (Skalski et al. 2001*b*).

	Hatchery chinook		Run-of-river chinook	
Parameter	RSSM	PRRM	RSSM	PRRM
Proportion through spillway ($\hat{E}$)	0.2451	—	0.2417	—
	(0.0246)		(0.0274)	
Proportion through powerhouse 1 (eq. 3)	0.0739	—	0.0871	—
	(0.0141)		(0.0140)	
Proportion through powerhouse 2 (eq. 4)	0.6810	—	0.6712	—
	(0.0267)		(0.0298)	
Spillway survival ($\hat{S}_{SP}$)	1.0150	—	0.9863	—
	(0.0217)		(0.0305)	
Powerhouse 1 survival ($\hat{S}_{T1}$)	0.9115	—	0.9702	—
	(0.0711)		(0.0520)	
Powerhouse 2 survival ($\hat{S}_{T2}$)	0.9722	—	0.9959	—
	(0.0237)		(0.0212)	
Pool survival ($\hat{S}_{pool}$)	0.9687	0.9621	0.9528	0.9551
	(0.0123)	(0.0122)	(0.0133)	(0.0131)
Dam survival (eq. 5)	0.9782	0.9848	0.9913	0.9833
	(0.0208)	(0.0187)	(0.0202)	(0.0190)
Project survival (eq. 6)	0.9476	0.9475	0.9445	0.9391
	(0.0186)	(0.0192)	(0.0190)	(0.0156)

Note: Standard errors are in parentheses.

Results

Detection histories

For the 2000 study, 343 and 350 radio-tagged hatchery chinook smolts were released at Rocky Reach and Rock Island tailraces, respectively. Concurrently, 349 radio-tagged run-of-river chinook salmon smolts were released at each of the Rocky Reach and Rock Island tailraces, respectively. Downstream detection histories were recorded separately for the hatchery (Table 1) and run-of-river (Table 2) releases of chinook salmon smolts.

Route-specific passage and survival probabilities

Maximum likelihood estimates of the route-specific passage and survival probabilities were calculated for the hatchery (Fig. 3) and run-of-river (Fig. 4) smolts along with associated standard errors. The diversion probabilities generated by the RSSM estimated 24.51% of the hatchery smolts and 24.17% of the run-of-river smolts passed through the Rocky Island spillway during the 2000 study. During that same time in spring 2000 (i.e., 15 April – 15 June), spill constituted 16.8% of the total flow volume going through Rock Island Dam.

Spillway survival ($\hat{S}_{SP}$) at Rock Island Dam for the hatchery chinook was indistinguishable from 100% (i.e., $\hat{S}_{SP}$ = 1.0150). Although survival cannot exceed 100% for a passage route, the point estimates can. A constrained maximization could be used to restrict all estimated probabilities within the admissible range (i.e., 0–1), but the resulting point estimates would no longer be unbiased (White 1983). The $\hat{S}_{SP}$ for the run-of-river chinook was estimated at 0.9863. Survival through powerhouse 1 was estimated to be 0.9115 and 0.9702 (average 0.9409, $\widehat{SE}$ = 0.0294) for the hatchery and the run-of-river chinook salmon smolts, respectively. The survival estimates through powerhouse 2 were 0.9722 and 0.9959 (average 0.9841, $\widehat{SE}$ = 0.0119) for the hatchery and the run-of-river chinook salmon smolts, respectively. Powerhouse operations are purposefully geared to pass more smolts through powerhouse 2, where survival is generally greater. Of the smolts passing through the powerhouses and not passing through the spillway, 90.22% ($\widehat{SE}(\hat{G})$ = 1.91) of the hatchery chinook and 88.52% ($\widehat{SE}(\hat{G})$ = 2.06) of the run-of river chinook went through powerhouse 2 during the 2000 study.

Combining spillway and powerhouse survivals (eq. 15), survival through the Rock Island Dam was estimated to be 0.9782 for the hatchery smolts and 0.9913 for the run-of-river smolts (Table 3). The total project survival (eq. 6) at Rock Island, taking into account both dam and pool survival, was estimated to be 0.9476 for the hatchery smolts and 0.9445 (Table 3) for the run-of-river smolts (average 0.9461, $\widehat{SE}$ = 0.0016).

Discussion

Study design considerations

Traditionally, tagging studies to characterize animal movements have focused on the analysis of release–recovery data (Hilborn 1990; Schwarz et al. 1993; Anganazzi et al. 1994). Estimating is often difficult in these studies because of the convolution of the parameters, or worse, the overparameterization of the likelihood models. At best, the estimates of survival and recovery probabilities are highly and inversely correlated. On the other hand, capture–recapture studies have traditionally focused on movement rates between two or more populations (Chapman and Junge 1956; Darroch 1961; Nichols et al. 1993). Again, for the model parameters to be estimable, simplified assumptions concerning movement patterns or common survival must be imposed.

The key to the effectiveness of the RSSM is the double-array system in each passage route that permits independent estimation of route-specific detection probabilities. These detection probabilities can then be combined with the observed smolt counts to estimate the spatial distribution of the fish through the hydroprojects. For these estimates of detection probabilities to be reliably estimated by likelihood eq. (2), the probabilities that smolts are detected in the primary (e.g., aerial) and secondary (e.g., underwater) need to be independent. Smolts detected in the primary array should be no more or less likely to be detected in the secondary antenna array than those smolts not detected in the primary antenna array. The physical layout of the primary and secondary antenna arrays is crucial in fulfilling this key requirement. In this study, the underwater antennas were deployed such that the reception fields of the underwater antennas covered all or most of the turbine intake slots or spillbays. Hence, regardless of whether the smolts were high enough in the water column to be detected by the aerial primary arrays, all smolts were susceptible to detection by the underwater secondary antenna arrays.

Successful use of the RSSM also depends on the accurate classification of detected smolts to specific passage routes at a dam. To do so, great care must be taken in deploying the antenna array systems to limit or shield environmental noise that can generate false signals. In addition, aerial antennas need to be adjusted to minimize the reception of radio signals from unintended areas that might lead to misclassification of the passage routes. When route-specific passage cannot be accurately classified for a smolt, that detection history should be censored at the last location where the smolt was known to be alive. In this study, some tagged fish known to have arrived at Rock Island Dam but with uncertain passage histories were right-censored. In so doing, estimation bias was avoided.

Comparison of survival estimates

In this study, we also compared the estimates of smolt survival through the Rock Island Dam, pool, and project from the RSSM for both the hatchery smolts and the run-of-river smolts with the estimates from a simple PRRM (Skalski et al. 2001*b*) that directly estimates these values (Table 3). The consistency of the estimates for the hatchery smolts with those for the run-of-river smolts, as well as their consistency with the PRRM estimates, suggests that detailed passage and survival information can be reliably generated from the RSSM. Estimates of pool, dam, and project survival from the RSSM and PRRM were within 0.01 of each other for both hatchery and run-of-river chinook salmon smolts. However, precision for some of the route-specific survival estimates is limited by the numbers of smolts taking a specific route. For example, pool survival was estimated with high precision ($\widehat{SE}(\hat{S}_{\text{pool}}) = 0.0123$) because large numbers of smolt went through that passage. On the other hand, for example, only 7.4% of the hatchery smolts reaching Rock Island Dam went through powerhouse 1. As such, the survival estimate through powerhouse 1 had the largest estimated standard error (i.e., $\widehat{SE}\ \hat{S}_{\text{T1}} = 0.0711$). The variation in precision between passage routes is an inherent limitation of this type of study.

Typically, smolt radio-tag studies have been used to provide only descriptive information on migration behavior and relative passage counts at hydroelectric projects. This paper has shown that by modifying the antenna receiver system at the dams, relative passage counts can be converted to passage probabilities and provide information on smolt salmon survival. This estimation capability is important because of the detailed information that can be generated and because it can be applied to a variety of riverine sites. In this paper, the RSSM has been shown to be capable of generating smolt survival estimates simultaneously through multiple passage routes at hydroelectric projects. The radiotelemetry methods can also be applied at hydrosites that cannot be readily studied by the more conventional PIT-tag methods currently used in the Columbia Basin (Skalski et al. 1998). We hope this paper will increase interest among fisheries biologists to develop the quantitative potential radiotelemetry techniques have in addressing resource management issues.

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