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[Article]

Comparison of Two Alternative Approaches for Estimating Dam Passage Survival of Salmon Smolts

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Abstract.—Traditional single and paired release–recapture models are incapable of providing unbiased estimates of dam passage survival because their assumptions can never be met. Nevertheless, regulatory requirements mandate the estimation of this important performance measure for migratory fish species passing through hydroprojects. We present a new release–recapture model that uses a virtual release of in-river migrants known to have arrived at the dam, combined with a paired release below the dam, to estimate dam passage survival. Analytical comparisons of the sampling precision of the proposed virtual–paired-release model and an established route-specific model found that the new approach was always more precise for equal release numbers of tagged fish. In a field trial at Rocky Reach Dam, Washington, using smolts of sockeye salmon *Oncorhynchus nerka*, the new approach estimated dam passage survival with more than twice the precision of the alternative method. The proposed virtual–paired-release design has the potential to provide robust and precise estimates of dam passage survival under a variety of hydroproject scenarios.

The migration of fish through hydroprojects is commonplace in many regulated rivers. In the Pacific Northwest, survival of anadromous smolts through dams is of major concern (Skalski et al. 1998; Muir et al. 2001). Survival standards have been established for many of the major Columbia and Snake River dams. In the North Atlantic, the survival of catadromous stocks such as eels of the genus *Anguilla* is perhaps of even more concern because they are large adults when they pass through turbines on their way to the ocean (Winter et al. 2006; Bruijs et al. 2009).

Regulatory requirements to estimate dam passage survival have often been established without consideration of study design and statistical sampling approaches. Early attempts to estimate dam passage survival using single or paired release–recapture methods have resulted in biased estimates because one or more model assumptions have been systematically violated. Skalski et al. (2009) developed a model that reconstructs dam passage survival via route-specific passage proportions and survival probabilities. The approach was developed to not only estimate passage survival but also examine the contributions of various routes (e.g., spillways, turbines, sluiceways, etc.) to overall passage success. Although the method can provide valid estimates and insights into the roles various passage routes play in overall dam passage survival, it can also be relatively inefficient because of the need to estimate multiple survival and passage parameters.

Over the last 2 decades, much has been learned about estimating smolt passage survival with active tags (acoustic, radio), and these lessons can be used to avoid problems and design more efficient studies. These lessons include (1) smolts released in the immediate vicinity of the forebay do not pass through a dam in the same spatial distribution as run-of-river fish, (2) paired releases are an excellent way to isolate survival estimates to a specific river reach and account for any postrelease handling effects, (3) fish used in the paired releases must be similar in all aspects, including origin and handling experience, and (4) a hydrophone array too close to the dam tailrace may result in false-positive detections of fish that died during dam passage and were washed downstream with still active tags. These considerations preclude many of the common

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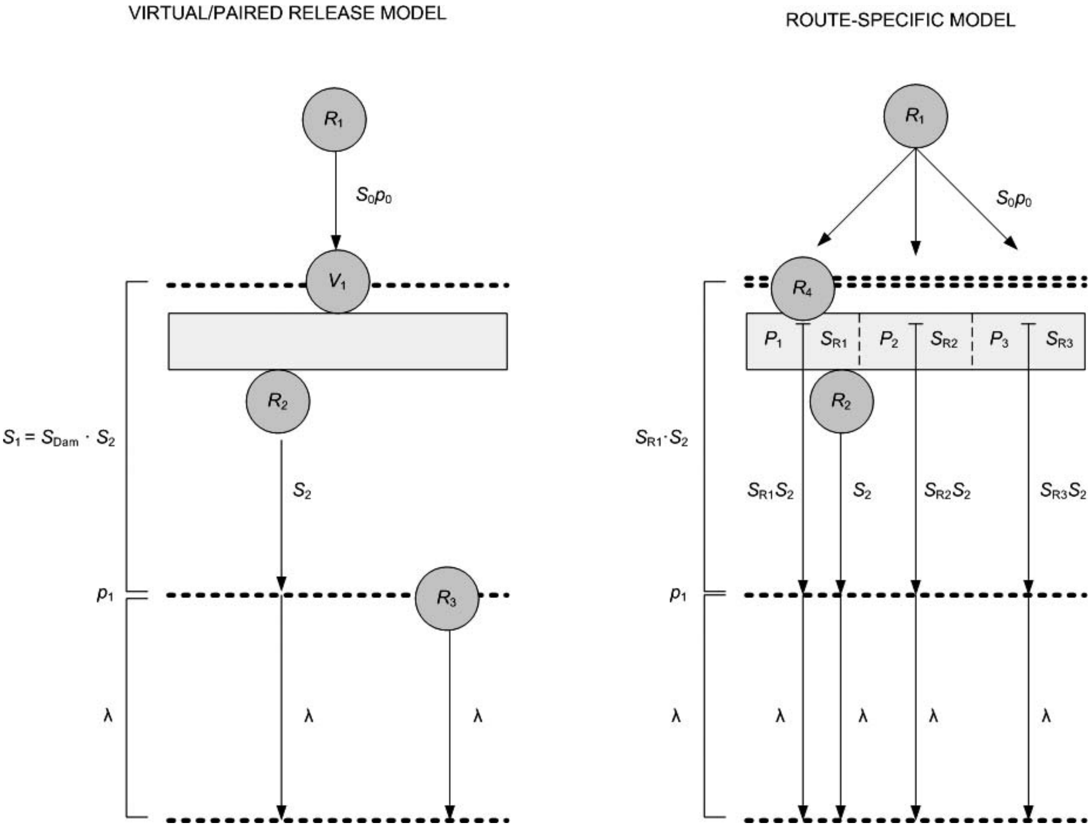

FIGURE 1.—Schematic of two alternative release–recapture designs, each with three release groups (R), comparable dam survival (S_{Dam}), the same probability of tagged fish reaching the dam (S_0p_0), and the same downstream survival and detection probabilities (S_2, p_1, and λ, where S = survival probability, p = capture probability, λ = the joint probability of survival and detection in the last reach). These two simplified scenarios were used to compare the relative precision of the route-specific and virtual–paired-release models. Detection arrays are denoted by dashed lines.

single- and paired-release options for estimating dam passage survival and suggest an alternative.

Using an upstream release (R_1; Figure 1) and a detection array at the dam face, a virtual release can be constructed of fish known to have arrived alive and nominally distributed at the dam (V_1; Figure 1). This tag group can then be used to estimate survival through the dam and downriver sufficiently far enough to avoid false positive detections due to dead, tagged fish. However, that reach includes the opportunity for additional mortality beyond dam passage. To account for the extra mortality, a paired release of freshly tagged fish is performed at the dam tailrace and at the first downstream detection site (R_2 and R_3; Figure 1). Dam passage survival is then estimated as the quotient of the reach survival estimate derived from the virtual release group divided by the paired release estimate of survival below the tailrace. Only two parameter estimates go into this virtual–paired-release model for dam passage survival, making it more efficient than the existing route-specific model of Skalski et al. (2009).

The purpose of this paper is to compare the statistical performance of this virtual–paired-release model with the established route-specific model (Skalski et al. 2009) for estimating dam passage survival. This comparison will be based on analytical calculations of sampling error and a field trial using acoustically tagged sockeye salmon *Oncorhynchus nerka* smolts at Rocky Reach Dam, Washington. The goal is to identify a tagging model that can be efficiently and effectively used to comply with regulatory requirements to validly and precisely estimate dam passage survival.

Methods

Precision Evaluation

The two competing study designs and release–recapture models to estimate dam passage survival were compared in terms of relative precision. Compa-

TABLE 1.—Relative precision (RP) of the route-specific model (RS) to that of the virtual–paired-release model (V) under alternative field conditions of release size ($R_1 = R_2 = R_3 = R_4$), route-specific passage proportions (P_1, P_2, and P_3) and survivals probabilities (S_{R1}, S_{R2}, and S_{R3}), and downstream detection and survival probabilities (p_1, S_1, and λ) and $S_0 p_0 = 0.95$ (see Figure 1).

			Route-specific survivals				Downstream parameters			
Scenario	Release size	Passage proportions	S_{R1}	S_{R2}	S_{R3}	S_{Dam}	p_1	S_2	λ	$\text{RP} = \frac{\text{SE}(\hat{S}_{\text{Dam}-\text{RS}})}{\text{SE}(\hat{S}_{\text{Dam}-\text{V}})}$
1	300	0.33:0.33:0.33	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1.46
2	400									1.46
3	500									1.46
4	400	0.4:0.4:0.2	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1.35
5		0.45:0.45:0.10								1.28
6	400	0.33:0.33:0.33	0.98	0.98	0.90	0.9533	0.95	0.95	0.95	1.36
7			0.98	0.98	0.80	0.92				1.30
8	400	0.33:0.33:0.33	0.95	0.95	0.95	0.95	0.80	0.80	0.80	1.34
9							0.70	0.70	0.70	1.28
10	400	0.33:0.33:0.33	0.90	0.90	0.90	0.90	0.95	0.95	0.95	1.49
11			0.80	0.80	0.80	0.80				1.49

rable scenarios for the two designs were constructed to allow a direct comparison of statistical precision (Figure 1). The dam was conceptualized as having three alternative passage routes in this comparative evaluation (e.g., powerhouse, spillway, and sluiceway). In the scenario investigated, the virtual–paired-release–recapture design estimated dam passage survival by the equation

$$\hat{S}_{\text{Dam}} = \frac{\hat{S}_1}{\hat{S}_2} \tag{1}$$

(see Figure 1). The route-specific model (Skalski et al. 2009) estimated dam passage survival by the expression

$$\hat{S}_{\text{Dam}} = \hat{S}_{R1}[\hat{P}_1 + \widehat{\text{RS}}_{2/1}\hat{P}_2 + \widehat{\text{RS}}_{3/1}(1 - \hat{P}_1 - \hat{P}_2)], \tag{2}$$

$\hat{S}_{R1}$ = estimated survival through the first route at the dam,
$\hat{P}_1$ = estimated proportion of fish through the first route,
$\hat{P}_2$ = estimated proportion of fish through the second route,
$\widehat{\text{RS}}_{2/1}$ = estimated relative survival of fish through route 2 compared to route 1 (i.e., $\text{RS}_{2/1} = S_{R2}/S_{R1}$),
$\widehat{\text{RS}}_{3/1}$ = estimated relative survival of fish through route 3 compared to route 1 (i.e., $\text{RS}_{3/1} = S_{R3}/S_{R1}$).

Analytical variance formulas were derived using the delta method (Seber 1982:7–9) for each estimator. The variance functions were derived under the ideal conditions of perfect downstream mixing to allow passage proportions (P_i), relative survivals (i.e., $\text{RS}_{i/1}$), and paired release–recapture estimates of survival based on binomial sampling models. This approach was selected to minimize the parameter space of the alternative scenarios examined. Nevertheless, we do not recommend investigators design studies with these expectations. In practice, additional downstream detection arrays should be employed to assure that absolute survivals can be estimated if necessary.

The relative precision (RP) for the competing models was expressed as the ratio

$$\text{RP} = \frac{\text{SE}(\hat{S}_{\text{Dam-RS}})}{\text{SE}(\hat{S}_{\text{Dam-V}})},$$

where $\hat{S}_{\text{Dam-RS}}$ = estimate of dam passage survival using the route-specific (RS) model, and $\hat{S}_{\text{Dam-V}}$ = estimate of dam passage survival using the virtual/paired-release (V) model.

The RP ratio was calculated for varying release sizes ($R_1 = R_2 = R_3 = R_4$), passage proportions through three routes at a dam (P_1, P_2, and P_3), route-specific survival probabilities (S_{R1}, S_{R2}, and S_{R3}), downstream detection (p_1), survival (S_2), and joint detection and survival ($\lambda = p_2 S_3$) parameters (Figure 1; Table 1). The purpose of the analysis was to assess under which field conditions the virtual–paired-release model might be more precise than the route-specific model.

Field Trial

Study site.—Rocky Reach Dam is a hydroelectric project on the middle Columbia River (river kilometer [rkm] 762.3 measured from the mouth of the Columbia River) operated by Public Utility District No. 1 of Chelan County (Chelan PUD) in north-central Washington State. Rocky Reach has 11 hydraulic turbines, for a combined hydraulic capacity through the powerhouse of 6,229.7 m^3/s. There are 12 spillway gates through which smolts may pass during spill

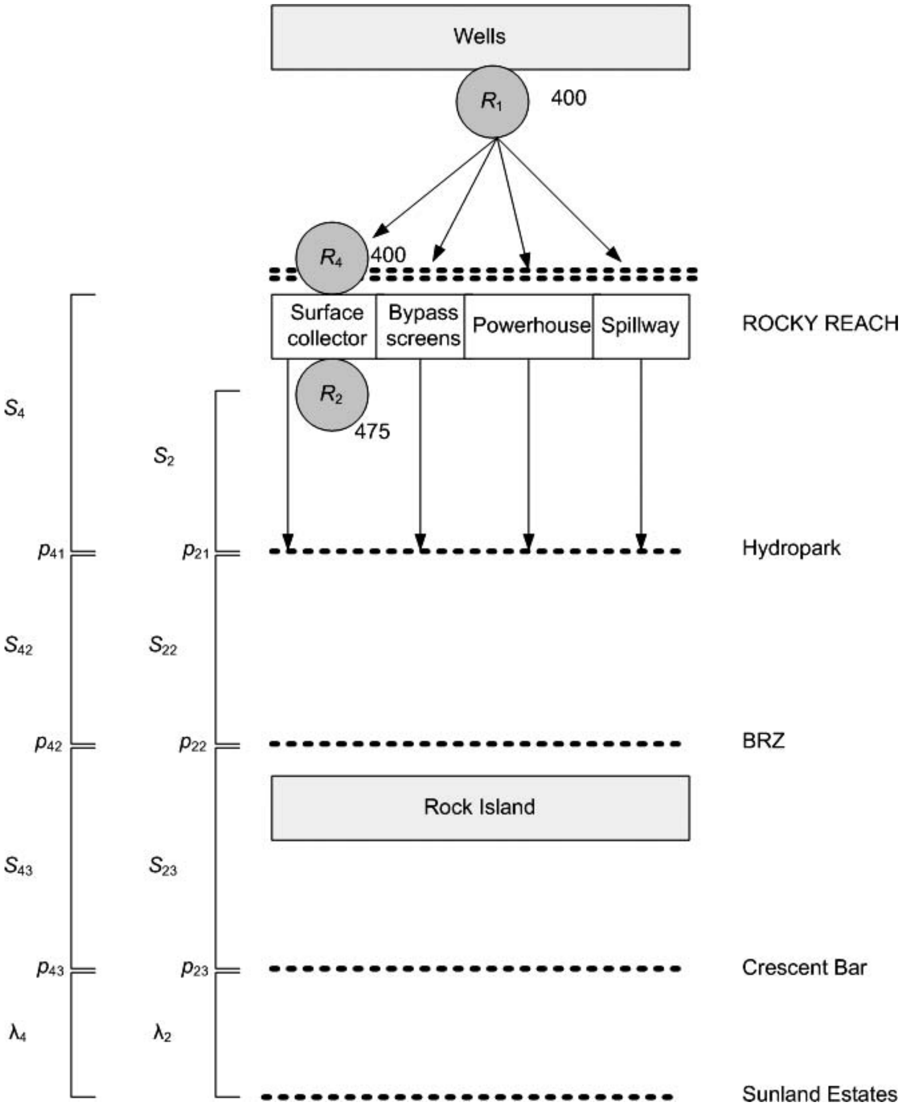

FIGURE 2.—Schematic of the route-specific release–recapture design used to estimate dam passage survival at Rocky Reach Dam in 2008. See Figure 1 for definition of terms. Where there are two numerical subscripts, the first indicates the release group, the second the reach (e.g., S_{22} is the survival of R_2 through reach 2). Numbers released are given to the right of each release group (circles). Passage survival through the surface collector is estimated by $\hat{S}_{SC} = \hat{S}_4/\hat{S}_2$. The abbreviation BRZ stands for boat restriction zone.

operations. Alternatively, smolts may pass through a surface collector, the bypass screens, or the powerhouse (turbines). Both the surface collector and the bypass screens divert smolts around the dam to the tailrace through a system of tubes. Rocky Reach's reservoir, Lake Entiat, extends upriver 66.7 rkm to the tailrace of Wells Dam.

Smolt tagging.—Run-of-river sockeye salmon smolts were collected from the bypass collector at Rocky Reach Dam. Acoustic transmitter tags were surgically implanted in each smolt at least 95 mm in length. Fish were first anesthetized in tricaine methanesulfonate (MS-222) at 100 mg/L of water and inspected for injuries, deformations, and extreme scale loss before tagging. Fish were held for 48 h after tagging to allow for recovery and identification of posttagging mortality, tag loss, or premature tag failure.

Tags used were the HTI Model 795m acoustic tags. These tags were approximately 6.8 mm in diameter by 16.5 mm long and had an average weight of 0.75 g in

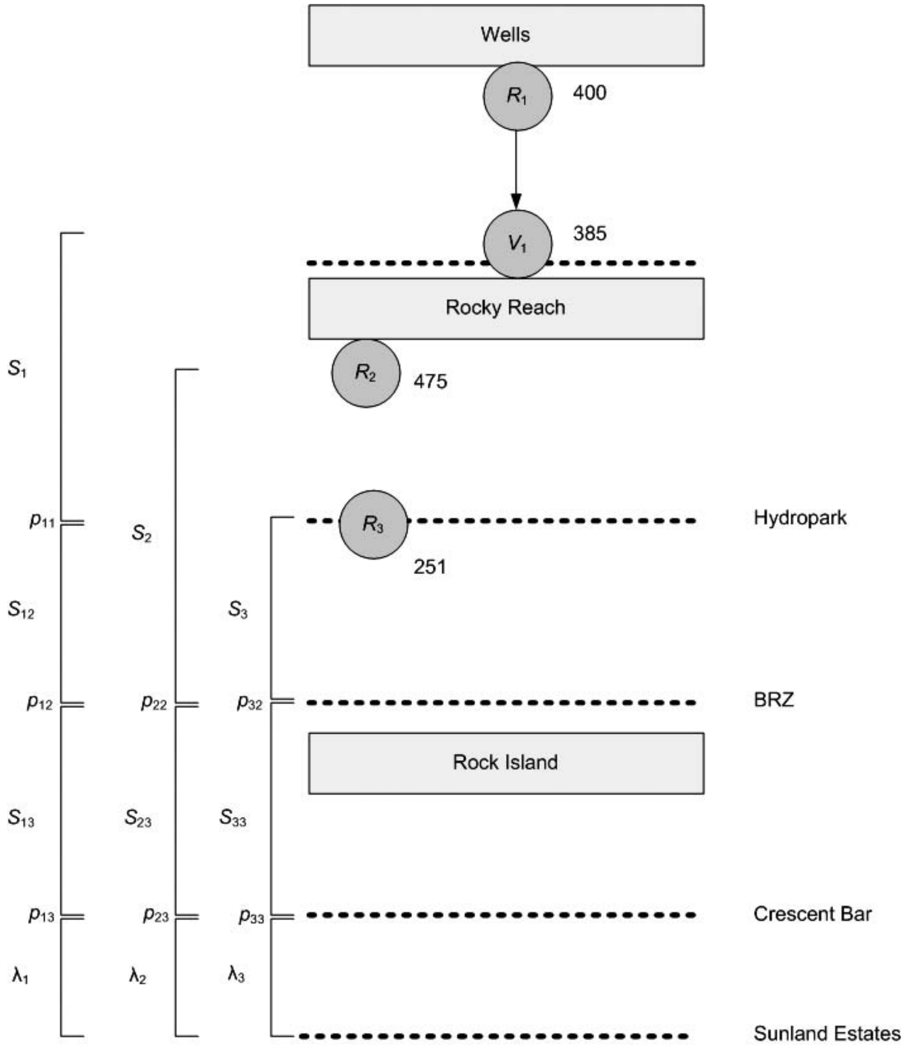

FIGURE 3.—Schematic of the virtual–paired release design to estimate dam passage survival at Rocky Reach Dam in 2008. Dam passage survival is estimated by $\hat{S}_{\text{Dam}} = \hat{S}_1 \cdot \hat{S}_3/\hat{S}_2$. See Figures 1 and 2 for additional information.

air and an average operating life of 15–21 d. The tags were approximately 2.7–8.4% of fish body weight. The HTI Model 290 acoustic tag receiver (ATR) system was used to detect tagged fish at various downriver sites. The ATR system supports up to 16 hydrophones and operates at 307 kHz. For more information on the acoustic-tag methods used, see Steig et al. (2005) .

Release–recapture methods.—A release–recapture design was used that would generate data that could be used for both the route-specific (Skalski et al. 2009) and virtual–paired-release models. Multiple releases totaling 400 acoustically tagged sockeye salmon smolts were performed in the Wells tailrace (R_1 in Figures 2, 3) over 24 d to provide smolts arriving at Rocky Reach Dam over the course of the emigration. A total of 385 fish from these upstream releases were detected at the boat restriction zone (BRZ) located approximately 1 rkm above the dam. Upon arrival at the BRZ, these fish formed a "virtual" release group that was then used to estimate dam passage survival based on the virtual–paired-release design. At a double hydrophone array immediately in front of Rocky Reach Dam, 375 fish of the original 400 tagged smolts released were detected and assigned a route of passage (i.e., surface collector, bypass screens, powerhouse, or spillbay). These 375 fish were the basis for estimating dam passage survival using the route-specific model.

In addition, three other groups of fish were released at Rocky Reach Dam. A total of 400 tagged sockeye salmon smolts were released into the surface collector (R_4; Figure 2) and paired with 475 fish in the tailrace (R_2; Figure 2) to estimate absolute survival through the surface collector as part of the route-specific model. A final release of 251 fish downstream at the Rock Island Hydropark (R_3; Figure 3) was performed to pair with the tailrace release as part of the virtual–paired-release model.

Downstream detection sites at Rock Island Hydropark (rkm 742), BRZ (rkm 765), Crescent Bar (rkm 711), and Sunland Estates (rkm 692) completed the design. For the virtual–paired-release design, a minimum of two downstream detection sites below release R_3 was required to estimate dam passage survival. For the route-specific model, a minimum of two detections arrays below the tailrace release was needed to estimate dam passage survival, in the case of imperfect downstream mixing when absolute survival techniques must be used (Cormack 1964).

Statistical methods.—Skalski et al. (2009) provide detailed description of the maximum likelihood model, estimator of dam passage survival, and associated sampling variance for the route-specific model. Double-detection arrays in front of the dam permitted estimation (via a Lincoln/Petersen Index; Seber 1982:59–61) of the number of tagged fish going through each route. These passage abundance estimates, in turn, were used to estimate the passage proportions (e.g., $\hat{P}_{\mathrm{SC},}$ $\hat{P}_{\mathrm{BS}}$, etc), where SC is surface collector and BS is bypass screens.

Rather than directly estimating absolute survival through each route, survival through the surface collector was estimated ($\hat{S}_{\mathrm{SC}}$) based on a paired release–recapture model (Burnham et al. 1987) using releases R_2 and R_4 (Figure 2). At the same time, fish known to have passed through the various routes were tracked downstream. The downstream recovery rates of these route-specific fish were then used to estimate the relative survival of fish going through an alternative route compared with the surface collector (e.g., $\mathrm{RS}_{\mathrm{BS/SC}}$, $\mathrm{RS}_{\mathrm{PH/SC}}$, and $\mathrm{RS}_{\mathrm{SP/SC}}$), where PH is powerhouse and SP is spillway. Estimates of absolute passage survival through the alternative routes were calculated as the product of the surface collector survival ($\hat{S}_{\mathrm{SC}}$) and the relative survival rates ($\hat{S}_{i/\mathrm{SC}}$). In this manner, the expense and effort of conducting paired releases through each passage route at a dam was avoided. At Rocky Reach Dam, seven parameters had to be estimated to reconstruct dam passage survival:

$$\hat{S}_{\mathrm{Dam}} = \hat{S}_{\mathrm{SC}}[\hat{P}_{\mathrm{SC}} + \mathrm{RS}_{\mathrm{BS/SC}}\hat{P}_{\mathrm{BS}} + \mathrm{RS}_{\mathrm{PH/SC}}\hat{P}_{\mathrm{PH}} + \mathrm{RS}_{\mathrm{SP/SC}}(1 - \hat{P}_{\mathrm{SC}} - \hat{P}_{\mathrm{BS}} - \hat{P}_{\mathrm{PH}})]. \tag{3}$$

Skalski et al. (2009) provide a variance estimator for equation (3), as well as a maximum likelihood model that can be used to directly estimate S_{Dam}.

In the case of the virtual–paired release design, the fish known to have arrived alive at the BRZ (V_1) were used to estimate survival from the BRZ in front of Rocky Reach Dam to a hydrophone array 22 rkm downstream of the dam (Figure 3). While the array 22 rkm below the dam was sufficiently far to avoid false positive detections due to dead tagged fish, it also included the opportunity for additional mortality beyond that caused by dam passage effects. To account for this extra mortality, releases of freshly tagged fish were performed at the dam tailrace (R_2; Figure 3) and at the first hydrophone array (R_3; Figure 3) to estimate survival through that reach. In the last reach of any release–recapture study, only the joint probability of a fish surviving and being detected can be estimated (i.e., λ) because mortality in the last reach cannot be differentiated from nondetection. Therefore, at least two more hydrophone arrays (i.e., a total of three) are needed below the downstream release site to estimate reach survival using the fully parameterized release–recapture methods (Cormack 1964).

For the virtual–paired-release model, dam passage survival was estimated as the quotient of the reach survival estimate (S_1) derived from the virtual-release group divided by a paired-release estimate of survival in the lower part of that river reach (i.e., S_2/S_3; Figure 3), where

$$\hat{S}_{\mathrm{Dam}} \frac{\hat{S}_1}{\left(\dfrac{\hat{S}_2}{\hat{S}_3}\right)} = \frac{\hat{S}_1\hat{S}_3}{\hat{S}_2}. \tag{4}$$

The variance of the estimate of dam passage survival can be expressed as

$$\begin{aligned}\mathrm{Var}(\hat{S}_{\mathrm{Dam}}) = {} & \left(\frac{1}{S_2^2} + \frac{\mathrm{Var}(\hat{S}_2)}{S_2^4}\right)[S_1^2\mathrm{Var}(\hat{S}_3) \\ & + S_3^2\mathrm{Var}(\hat{S}_1) + \mathrm{Var}(\hat{S}_1)\cdot\mathrm{Var}(\hat{S}_3)] \\ & + \left(\frac{S_1^2S_3^2}{S_2^4}\right)\mathrm{Var}(\hat{S}_2)\end{aligned} \tag{5}$$

and the estimated variance as

$$\begin{aligned}\widehat{\mathrm{Var}}(\hat{S}_{\mathrm{Dam}}) = {} & \left(\frac{1}{\hat{S}_2^2} - \frac{\widehat{\mathrm{Var}}(\hat{S}_2)}{\hat{S}_2^4}\right)[\hat{S}_1^2\widehat{\mathrm{Var}}(\hat{S}_3) \\ & + \hat{S}_3^2\widehat{\mathrm{Var}}(\hat{S}_1) - \widehat{\mathrm{Var}}(\hat{S}_1)\cdot\widehat{\mathrm{Var}}(\hat{S}_3)] \\ & + \left(\frac{\hat{S}_1^2\hat{S}_3^2}{\hat{S}_2^4}\right)\widehat{\mathrm{Var}}(\hat{S}_2),\end{aligned} \tag{6}$$

TABLE 2.—Detection histories (1 = detected, 0 = not detected) at each passage route at Rocky Reach Dam, estimated passage abundance of acoustically tagged sockeye salmon, route-specific passage proportions, and downstream detections used to estimate relative survival by route compared with surface collector.

Route	Detection histories at route 1, 1	1, 0	0, 1	Total detected	Estimated passage abundance (SE)	Route-specific passage proportion (SE)	Downstream recoveries	Relative survival to surface collector (SE)
Surface collector	155	0	0	155	155 (0)	0.4128 (0.0254)	154	
Bypass screens	16	1	0	17	17 (0)	0.0453 (0.0107)	17	1.0065 (0.0065)
Powerhouse	183	5	6	194	194.163 (0.415)	0.5171 (0.0258)	178	0.9235 (0.0208)
Spillway	6	1	2	9	9.286 (0.606)	0.0247 (0.0082)	9	1.0065 (0.0065)

according to Goodman (1960). A joint likelihood model describing the three releases can be written by reparameterizing $S_1 = S_{\text{Dam}} \cdot S_{11}$ and $S_2 = S_{11} \cdot S_3$ (Figure 3).

Results

Comparison of Relative Precision

The relative precision (RP) of the route-specific model compared with that of the virtual–paired-release model was calculated and compared under 11 alternative sampling conditions (Table 1). The various scenarios examined alternative release sizes (scenarios 1, 2, and 3), passage proportions (scenarios 2, 4, and 5), route-specific survivals (scenarios 1, 6, 7, 10, and 11), and downstream survival and detection probabilities (scenarios 2, 8, and 9). Changes in the downstream detection rates were found to have a major influence on study performance (see scenarios 2, 8, and 9; Table 1). Another important factor in study performance was the proportions of fish through the various routes at a dam. As the passage proportions became more disparate and one route had increasingly fewer fish, the relative performance of the virtual–paired-release model declined (see scenarios 2, 4, and 5; Table 1). Nevertheless, in all cases, the standard errors for the route-specific model were greater than that for the virtual–paired-release design (RP $>$ 1). The values of RP ranged from 1.28 to 1.49 (Table 1). A value of 1.49 indicates the subsequent confidence interval for S_{Dam} would be approximately 50% wider for the route-specific model than that of the virtual–paired-release design under comparable test conditions. Under those circumstances, the release sizes of the route-specific model would need to be approximately twice the size of those of the virtual–paired-release design for comparable precision (i.e., equal SEs).

These precision calculations were performed under ideal circumstances where relative recovery methods, such as the Ricker (1975) model, and binomial sampling can be used to estimate survival and passage proportions at a dam. Should route-specific detections rates vary such that passage proportions need to be estimated by absolute abundance procedures rather than relative abundance, the standard errors of the route-specific model will be larger and the RP values greater than those reported in the analytical comparisons.

Field Trial

The route-specific model estimated survival from the face of the Rocky Reach Dam to the tailrace release location approximately 0.30 rkm downstream of the dam. From the double hydrophone array in front of the dam, we estimated that 0.4128 ($\widehat{\text{SE}} = 0.0254$) of the sockeye salmon smolts passed through the surface collector, 0.5171 ($\widehat{\text{SE}} = 0.0252$) through the powerhouse, 0.0453 ($\widehat{\text{SE}} = 0.0107$) through the bypass screens, and 0.0247 ($\widehat{\text{SE}} = 0.0082$) through the spillway. Survival through the surface collector (i.e., $\hat{S}_{\text{SC}}$) was estimated by the paired-release to be $\hat{S}_{\text{SC}} =$ 1.0091 ($\widehat{\text{SE}} = 0.0082$). Using the fish known to have passed through the dam, relative survival rates compared with the surface collector were estimated to be $\widehat{\text{RS}}_{\text{BS/SC}} = 1.0065$ ($\widehat{\text{SE}} = 0.0065$), $\widehat{\text{RS}}_{\text{PH/SC}} = 0.9235$ ($\widehat{\text{SE}} = 0.0208$), and $\widehat{\text{RS}}_{\text{SP/SC}} = 1.0065$ ($\widehat{\text{SE}} = 0.0065$; Table 2). Combining the results of the passage proportions, relative survivals, and survival estimates through the surface collector produced an estimate of dam passage survival (equation 3) of $\hat{S}_{\text{Dam}} = 0.9608$ ($\widehat{\text{SE}} = 0.0396$) when adjusting for survival through the surface collector at $S_{\text{SC}} = 1.0$.

The virtual–paired-release model estimated dam passage survival from a point 1.0 rkm above the dam to 0.30 rkm below the dam in the tailrace. The virtual release group estimated survival from the Rocky Reach BRZ to the Rock Island Hydropark hydrophone array 22 rkm downstream of the dam to be 0.9487 ($\widehat{\text{SE}} =$ 0.0135; Table 3). The paired-release method estimated survival between the tailrace and the hydropark hydrophone array to be 0.9882 ($\widehat{\text{SE}} = 0.0069$; Table 4). Their quotient produced an estimate of dam passage survival of $\hat{S}_{\text{Dam}} = 0.9600$ ($\widehat{\text{SE}} = 0.0152$).

In this field trial, the RP of the route-specific model to the virtual–paired-release model was 2.60, which

TABLE 3.—Capture histories (1 = detected, 0 = not detected) for the 385 sockeye salmon smolts detected at the Rocky Reach boat restriction zone (BRZ) that formed the virtual release in the virtual–paired-release design in 2008. The four detection sites were Rock Island Hydropark, BRZ, Crescent Bar, and Sunland Estates.

Detection history	Number of fish
1, 1, 1, 1	325
0, 1, 1, 1	4
1, 0, 1, 1	8
0, 0, 1, 1	2
1, 1, 0, 1	1
0, 1, 0, 1	0
1, 0, 0, 1	0
0, 0, 0, 1	0
1, 1, 1, 0	7
0, 1, 1, 0	0
1, 0, 1, 0	1
0, 1, 0, 0	1
1, 0, 0, 0	0
0, 0, 0, 0	24

was much higher than those reported in Table 1 because there were more routes (four versus three) and, hence, more parameters to estimate at Rocky Reach Dam. In addition, passage proportions were more disparate between routes, and passage proportions were estimated using absolute rather than relative abundance procedures in this application. All of these factors contributed to the greater precision of the virtual–paired-release design.

Discussion

Assumptions and Robustness

The virtual–paired-release design is composed of a single release (V_1, Figure 3) and a paired release (R_2 and R_3, Figure 3) and, consequently, has the model assumptions for both (Burnham et al. 1987; Skalski et al. 1998). In addition, this new approach to estimating dam passage survival has the following added requirements:

(1) The virtual release (V_1) is composed of fish known to have arrived alive and passed through the dam.
(2) The virtual release (V_1) has a dam passage distribution representative of run-of-river fish.
(3) The paired releases (R_2, R_3) provide an unbiased estimate of survival between the tailrace and the first downstream detection site (Figure 3).
(4) The first downstream detection site is sufficiently far below the dam to avoid false-positive detections of tagged fish that died during dam passage.

Assumptions 1 and 4 can be achieved logistically by appropriate spacing of release and detection sites. A prudent investigator would, nevertheless, want to verify these assumptions by releasing fish from various distances upriver to examine the arrival distributions at the dam and by releasing dead, tagged fish into the tailrace to confirm they do not arrive at the downstream detection sites.

Should mortality occur between the time a fish is assigned to the forebay virtual release (V_1) and entry into the dam, the estimate S_1 will be negatively biased, as will the estimate of dam passage survival (i.e., violation of assumption 1). The estimate of S_1 would also be negatively biased if there is postrelease handling mortality among the fish assigned to the virtual release (V_1). The resulting estimate of dam passage survival will therefore be either valid or conservative, depending on fulfillment of assumptions. This is a desirable property of a performance measure used in assessing regulatory compliance.

In the past, attempts to estimate dam passage survival have been based on pairing the forebay virtual release (V_1) with a tailrace release (R_2) of freshly tagged fish (Skalski et al. 2002). That approach has generally produced positively biased estimates of dam passage survival because of differential expression of postrelease handling mortality. The virtual–paired-release design attempts to avoid that problem by using comparable releases of freshly tagged fish (R_2 and R_3) to more accurately estimate survival between the tailrace and the first downstream detection site (assumption 3).

The virtual–paired-release model can be adapted to alternative definitions of dam passage survival. In some contexts, the immediate forebay is included in the definition of dam passage, and in other contexts, dam passage survival begins at the dam face. By strategi-

TABLE 4.—Capture histories (1 = detected, 0 = not detected) for the sockeye salmon smolt releases at Rocky Reach tailrace (R_2) and Rock Island Hydropark (R_3) used in the virtual–paired-release design. The three detection sites were the Rock Island boat restriction zone, Crescent Bar, and Sunland Estates.

	Number of fish by detection history								
Release	1, 1, 1	0, 1, 1	1, 0, 1	0, 0, 1	1, 1, 0	0, 1, 0	1, 0, 0	0, 0, 0	Total
R_2	432	4	0	0	3	0	27	9	475
R_3	243	0	0	0	0	0	8	0	251

cally locating the upstream detection array either at the dam face or at the BRZ, as in this sockeye salmon example, these alternative definitions of dam passage survival can be accommodated. With careful attention to detail and verification of model assumptions whenever possible, the virtual–paired release design should be compatible with both acoustic and radio tag technologies.

Design Efficiency

The sockeye salmon example illustrated and the analytical calculations (Table 1) confirmed the virtual–paired-release design for equal tag–release numbers is more precise than the route-specific model. It can be expected that the relative efficiency of the virtual–paired-release design will increase as the number of passage routes (and parameters) at a dam also increases. The analytical calculations showed relative precision values of $\mathrm{RP} = 1.28–1.49$ under ideal conditions, where relative recovery and relative abundance procedures could be employed in the route-specific estimation. However, in practical cases like the sockeye salmon example, where absolute passage abundance and survivals were estimated, the precision gains may be much greater. The RP value in the field trial was greater than 2. As a general rule, to reduce the standard error by 50%, sample sizes must increase by a factor of 4 (i.e., $\mathrm{SE}[\hat{S}] \propto 1/\sqrt{R}$); Cormack 1964).

The tradeoffs between the precision of the virtual–paired-release design with the fine-scaled information of the route-specific model need not be as stark as a first glance might suggest. By using a double-detection array at the dam face, where the virtual release is formed, an estimate of dam passage survival can be obtained with the virtual–paired-release design, along with estimates of route-specific passage abundance, proportions, and relative survivals. The resulting relative survival estimates ($\widehat{\mathrm{RS}}$) can provide almost as much information as absolute passage survival estimates, if the baseline route used in estimating the ratios has high passage survival, such as a spillway or sluiceway. This melding of approaches illustrates that release–recapture models and tag–release designs are not static. Instead, by tailoring tagging models to the ever-changing needs of scientists and regulators, both detailed and precise information can be obtained for the management of aquatic resources.

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References

Bruijs, M. C. M., R. H. Hadderingh, U. Schwevers, B. Adams, U. Dumont, and H. V. Winter. 2009. Managing human impact on downstream migrating European eel in the River Meuse. Pages 381–390 *in* J. M. Casselman and D. K. Cairns, editors. Eels at the edge: Science, status, and conservation concerns. American Fisheries Society, Symposium 58, Bethesda, Maryland.

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

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51(3/4):429–438.

Goodman, L. A. 1960. On the exact variance of products. Journal of the American Statistical Association 55:708–713.

Muir, W. D., S. G. Smith, J. G. Williams, and E. E. Hockersmith. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers. North American Journal of Fisheries Management 21:269–282.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Seber, G. A. F. 1982. The estimation of animal abundance. MacMillan, New York.

Skalski, J. R., R. A. Buchanan, R. L. Townsend, T. W. Steig, and S. Hemstrom. 2009. A multiple-release model to estimate route-specific and dam passage survival at a hydroelectric project. North American Journal of Fisheries Management 29:670–679.

Skalski, J. R., S. G. Smith, R. N. Iwamoto, J. G. Williams, and A. Hoffmann. 1998. Use of PIT tags to estimate survival of migrating juvenile salmonids in the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 55:1484–1493.

Skalski, J. R., R. Townsend, J. Lady, A. E. Giorgi, J. R. Stevenson, and R. D. McDonald. 2002. Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. Canadian Journal of Fisheries and Aquatic Sciences 59:1385–1393.

Steig, T. W., J. R. Skalski, and B. H. Ransom. 2005. Comparison of acoustic and PIT-tagged juvenile Chinook, steelhead, and sockeye salmon (*Oncorhynchus* spp.) passing dams on the Columbia River, USA. Pages 275–286 *in* M. T. Spedicato, G. Lembo, and G. Marmulla, editors. Aquatic telemetry: advances and applications. Food and Agriculture Organization of the United Nations, Rome.

Winter, H. V., H. M. Jansen, and M. C. M. Bruijs. 2006. Assessing the impact of hydropower and fisheries on downstream-migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. Ecology of Freshwater Fish 15:221–228.