Correcting Bias in Survival Estimation Resulting From Tag Failure in Acoustic and Radiotelemetry Studies

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The high detection rates of acoustic- and radio-tagged fish greatly improve the ability of an investigator to obtain information on survival and movement of fish with fewer tags. The trade-off, though, is a greater dependence on the individual tag performance, as each tagged fish in a smaller study represents a greater proportion of the outcome. This reduction in release size, due to the increase in detection capability, places a greater emphasis on the need to accurately gauge the status of the tagged fish. Should a tag fail while a smolt is migrating through the study area, the release–recapture model cannot discern the difference between smolt death and tag failure. If the release-recapture models are not adjusted for the probability of tag failure, the estimates of smolt survival will therefore be negatively biased. This article presents a semiparametric approach for adjusting survival estimates from release-recapture studies for tag failure, and provides subsequent estimation of sampling variance and its contributing components.

Key Words: Bootstrap; Cormack-Jolly-Seber; Gompertz distribution; Mark–recapture; Maximum likelihood; Release–recapture.

1. INTRODUCTION

In the late 1990s, radio-tags and acoustic tags began to be used in salmonid smolt investigations in the Columbia River Basin as the result of improvements in tag miniaturization and battery operation. Smolt tagging studies in the Basin will always be dominated by PIT-tags, but the trend is toward greater use of active tags. Today, tens of thousands of radio-tags and thousands of acoustic tags are used each year for smolt survival studies in the Columbia River Basin and the numbers are increasing annually. There are several reasons for the shift in tagging methods. First, the higher detection probabilities of acoustic- and radio-tags

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allow fewer fish to be marked for the same level of precision. A 1,000 acoustic-tag smolt survival study can have the same precision as a 104,000 smolt PIT-tag investigation (Skalski et al. 2004). Second, the smaller sample size requirements permit the study of threatened or endangered fish stocks that could not accommodate the large PIT-tag release numbers. Third, the active tags can provide more detailed information on movements and survival of salmonid smolts through the hydroprojects. Stevenson et al. (2000) demonstrated the use of a radio-tag study to estimate route-specific as well as project-wide estimates of passage survival. Although field investigations indicated the feasibility of using either acoustic- or radio-tags to estimate survival, tag failure has the potential to bias survival results.

The possibility of nondetection due to tag failure violates an assumption of release-recapture models, that all tagged individuals alive at a sampling location have the same probability of being detected. When tag failure is present in a tag release-recapture study, the analysis will underestimate survival, attributing nondetections to mortality (Arnason and Mills 1981). The purpose of this article is to describe the statistical nature of tag failure data, and to provide bias-corrected estimates of survival for release-recapture studies.

Tag failure data will be illustrated using four different acoustic- or radio-tag studies conducted from 2000–2004. The replicate studies illustrate the general nature of the data and the cross-study applicability of our analysis approach. To demonstrate the bias corrections for tag failure, a paired release-recapture study (Burnham et al. 1987) is presented. General recommendations on likelihood model construction for survival estimation and the design of release-recapture studies in the presence of tag failure are provided.

2. DATA

Survival studies with active tags (tags that send out a signal) generally set aside tags during the study to monitor their operation and tag life. Radio-tags were used in 2000 (19 tags) and 2001 (30 tags) tag-life studies (Skalski et al. 2001; English et al. 2001), and acoustic tags were used in the 2002 (25 tags), 2003 (50 tags), and 2004 (50 tags, two tag types) tag-life studies (Skalski et al. 2003, 2004, 2005). In each case, tags were randomly selected from those intended for the survival study, activated, and monitored until failure. The Appendix details more specific tag information and their set-up for each study. The technical reports containing the original analyses can be found at *http://www.chelanpud.org/rr_relicense/existing/hcp/index.htm*.

An example of incorporating the estimated tag life into the survival estimates uses results from a Chelan County (WA) Public Utility District (PUD) study. In 2003, an acoustic-tag study was conducted to estimate smolt survival through the Rock Island project. Yearling hatchery Chinook salmon smolts were tagged and grouped into 20 replicate paired releases. Each paired-release consisted of approximately 25 smolts into each of the Rocky Reach [river kilometer (RK) 762.3] and Rock Island (RK 729.7) tailraces (i.e., $2 \times 25 \times 20 \approx 2,000$). Tagging and release occurred in the Rocky Reach and Rock Island tailraces. Tagged fish were detected at downstream hydrophone arrays located at Crescent Bar (RK 710.2) and Sunland Estates (RK 694.1). Capture histories were pooled across replicates in estimating project survival. The 2003 acoustic-tag lifetime data mentioned earlier were a part of this experiment. Approximately every 40th tag to be used in the smolt survival study was systematically withheld and used in the concurrent tag-life study. This systematic sample assured the tags used in the tag-life study were representative of the tags in the smolt survival study.

3. STATISTICAL METHODS

The model for the release-recapture study has two components; one element describing the observed capture histories, the other describing the operating life of the radio or acoustic tag. Together, these two components permit estimation of the survival parameters of interest.

3.1 RELEASE-RECAPTURE MODEL

The probability of detecting a smolt after release is a function of survival of the fish, operational survival of its tag, and detection probabilities at downstream detection arrays. The paired-release design (Figure 1) provides for detections at two downstream detection arrays for a total of $4(=2^2)$ possible capture histories per release.

The joint likelihood for the paired-release is therefore the product of two multinomial distributions describing the likelihood of the observed capture histories for each release group. Define the following parameters:

$R_1 =$ number of tagged fish released at the upstream release location;
$R_2 =$ number of tagged fish released at the downstream release location;
$n_{ij} =$ number of individuals from release R_1 with capture history $ij (i = 0, 1), (j = 0, 1)$, where 1 denotes detection, 0 otherwise;
$m_{ij} =$ number of individuals from release R_2 with capture history $ij (i = 0, 1), (j = 0, 1)$, where 1 denotes detection, 0 otherwise;
$S_{k1} =$ survival probability to the first detection array by the kth release group ($k = 1, 2$);
$p_k =$ probability of detection at the first downstream array for the kth release group;
$\lambda_k =$ joint probability of surviving from the first detection array to the second detection array and being detected at the last array for the kth release group.

In the absence of tag loss concerns, the paired-release design is an example of the full capture history protocol of Burnham et al. (1987). In the case of tag failure, additional parameters are required [Model (3.1)]. Table 1 presents the expected probabilities of occurrence for each of the possible capture histories in the presence of possible tag failure. The following probabilities for tags being operational at a downstream detection array must be defined:

$P(L_{11}) =$ probability a tag from release R_1 is operational at the first detection array;

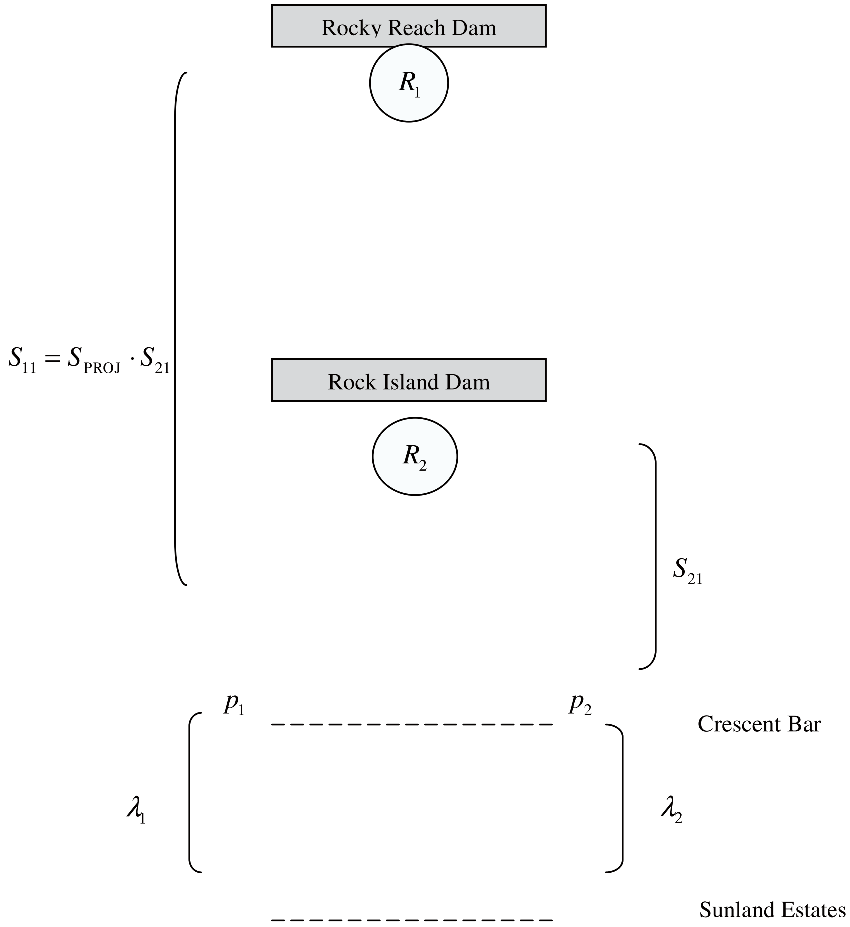


Figure 1. Schematic of release-detection design for estimating project survival. Release sites denoted by R_1 and R_2, and detection arrays by dashed lines. Estimable parameters are presented.

$P(L_{12} \mid L_{11}) =$ conditional probability a tag from release R_1 is operational at the second detection array, given it is active at the first detection array;
$P(L_{12}) =$ probability a tag from release R_1 is operational through both detection arrays 1 and 2;
$P(L_{21}) =$ probability a tag from release R_2 is operational at the first detection array;
$P(L_{22} \mid L_{21}) =$ conditional probability a tag from release R_2 is operational at the second detection array, given it is active at the first detection array;
$P(L_{22}) =$ probability a tag from release R_2 is operational through both detection arrays 1 and 2.

The joint likelihood, L, of the release-recapture model is then the product of the multi-

Table 1. Detection Histories, Expected Probabilities of Occurrences, and Recapture Numbers for Releases R_1 and R_2. For detection history, a "1" indicates a detection, "0" nondetection.

Release	*Detection history*	*Expected probabilities*	*Number fish with history*
$R_1 =$	11	$S_{11}P(L_{11})p_1\ P\left(L_{12}\vert L_{11}\right)\lambda_1 = S_{11}p_1P(L_{12})\lambda_1$	396
500	01	$S_{11}P(L_{11})\left(1-p_1\right)P\left(L_{12}\mid L_{11}\right)\lambda_1 = S_{11}\left(1-p_1\right)P(L_{12})\lambda_1$	25
	10	$S_{11}P(L_{11})p_1\left[1-P\left(L_{12}\vert L_{11}\right)\lambda_1\right] = S_{11}p_1\left(P(L_{11})-P(L_{12})\lambda_1\right)$	31
	00	$\left(1-S_{11}\right)+S_{11}\left[\left(1-P(L_{11})\right)+P(L_{11})(1-p_1)-P(L_{12})(1-p_1)\lambda_1\right]$	48
$R_2 =$	11	$S_{21}P(L_{21})p_2P\left(L_{22}\vert L_{21}\right)\lambda_2 = S_{21}p_2P(L_{22})\lambda_2$	444
499	01	$S_{21}P(L_{21})\left(1-p_2\right)P\left(L_{22}\vert L\ {}_{21}\right)\lambda_2 = S_{21}\left(1-p_2\right)P(L_{22})\lambda_2$	22
	10	$S_{21}P(L_{21})p_2\left[1-P\left(L_{22}\vert L_{21}\right)\lambda_2\right] = S_{21}p_2\left(P(L_{21})-P(L_{22})\lambda_2\right)$	17
	00	$\left(1-S_{21}\right)+S_{21}\left[\left(1-P(L_{21})\right)+P(L_{21})(1-p_2)-P(L_{22})(1-p_2)\lambda_2\right]$	16

nomial likelihoods as follows:

$$L = L\left(\mathbf{S}_{11}, \mathbf{p}_1, \lambda_1, P\left(\mathbf{L}_1\right)\vert R_1, \mathbf{n}\right) \cdot L\left(\mathbf{S}_{21}, \mathbf{p}_2, \lambda_2, P\left(\mathbf{L}_2\right)\vert R_2, \mathbf{m}\right). \tag{3.1}$$

From release R_1, the probability of being detected at both downstream arrays (history 11) can be written as $S_{11}P(L_{11})p_1P(L_{12}|L_{11})\lambda_1$, which reduces to $S_{11}p_1P(L_{12})\lambda_1$. Table 1 provides the expected probabilities for the remaining capture histories of the paired-release design, along with the observed counts from the 2003 Chelan acoustic-tag survival study (Skalski et al. 2004).

3.2 TAG-LIFE MODEL

The probability a tag is active at a detection array is dependent on the travel time to the array. The failure-time data from the four tag-life studies were found to fit the Gompertz distribution (Elandt-Johnson and Johnson 1980) of the form

$$f(t_i) = \beta \exp\left[\left(\beta/\alpha\right)\left(1-\exp(\alpha t_i)\right)+\alpha t_i\right],$$

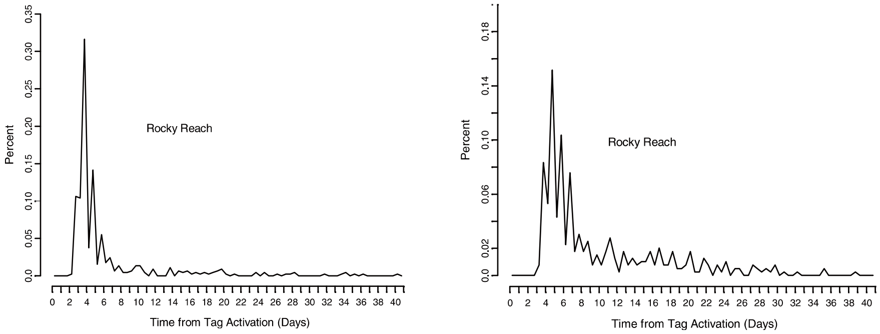
where $t_i =$ the lifetime of the ith tag. The joint likelihood for a sample of Q tags is then

$$L = \prod_{i=1}^{Q} \beta \exp\left[(\beta/\alpha)(1-\exp(\alpha t_i))+\alpha t_i\right]. \tag{3.2}$$

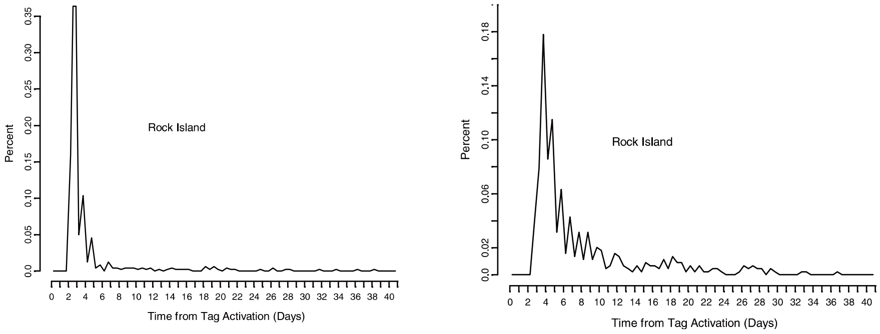
The probability of a tag surviving to time t_i is then expressed by the survival function

$$S(t) = \exp(\beta/\alpha)(1-\exp(\alpha t)). \tag{3.3}$$

The probability a tag is operational at a downstream detection array is a function of the travel time (h_{ij}) of the fish to the detection array, where $h_{ij} =$ duration of time from tag activation to arrival at the jth location $(j = 1, 2)$ for the ith tagged fish. Arrival smolt distributions $(f(h_{ij}))$ are dependent on numerous factors including ambient river conditions, hydroproject operations, and degree of smoltification of the individual fish. These factors


a. Travel time distribution to Crescent Bar

b. Travel time to Sunland Estates


c. Travel time distribution to Crescent Bar

d. Travel time to Sunland Estates

Figure 2. Arrival distributions for releases from Rocky Reach and Rock Island tailraces to detection arrays at Crescent Bar and Sunland Estates, Chelan County PUD 2003 acoustic-tag study.

can act in unison or singularly to produce irregular and multimodal distributions that are difficult to characterize parametrically. As an example, the observed arrival distributions at Crescent Bar and Sunland Estates detection arrays for the 2003 acoustic-tag study bear this out (Figure 2). A multimodal distribution is apparent in the fish released from Rocky Reach tailrace arriving at Sunland Estates. Consequently, the empirical distribution of arrival times was used nonparametrically to estimate the probabilities of tag operation at downstream detection arrays. An estimate of the probability a tag was operational at the jth detection array was therefore estimated by the average probability from the ith release

$$\hat{P}\left(L_{ij}\right) = \left(1/k_{ij}\right) \sum_{x=1}^{k_{ij}} \hat{S}\left(h_{ijx}\right), \tag{3.4}$$

where $\hat{S}(h_{ijx})$ = estimated probability a tag is operational at time h_{ijx} for the xth fish arriving at the jth location $(j = 1, 2)$ from the ith release group $(i = 1, 2)$; k_{ij} = number of fish that were detected at the jth location $(j = 1, 2)$ from the ith release group $(i = 1, 2)$. The estimates of $\hat{P}\left(L_{ij}\right)$ were incorporated into the likelihood (3.1) as constants while deriving the maximum likelihood estimates for survival. In variance calculations, the uncertainty in $\hat{P}\left(L_{ij}\right)$ was incorporated into the error variance of $\hat{S}$ through bootstrap resampling techniques (Efron and Tibshirani 1993).

This tag-life correction model is based on the following assumptions:

1. The underlying release-recapture model is valid.
2. The empirical fish travel time distribution does not reflect or is affected by tag loss.
3. The distribution of tag-failure times is the same for tags monitored in ambient river conditions and in marked fish.
4. The tag failure times follow a Gompertz distribution.

Assumptions of single-release and paired release-recapture studies were reviewed by Skalski et al. (1998) and Burnham et al. (1987), respectively. The violation of assumptions 2 and 3, in particular, will tend to bias subsequent survival estimates downward. Implications of these assumptions to study design will be found in Section 5.

3.3 VARIANCE CALCULATIONS

Project survival, S_{PROJ}, between release locations R_1 and R_2 (Figure 1) is estimated by the equation

$$S_{\text{PROJ}} = \hat{S}_{11}/\hat{S}_{21}, \tag{3.5}$$

based on the paired release-recapture model of Burnham et. al. (1987), with the associated variance estimate based on the delta method (Seber 1982, pp. 7–9)

$$\begin{aligned} \widehat{\text{var}}\left(\hat{S}_{\text{PROJ}}\right) &\doteq \left(\hat{S}_{11}/\hat{S}_{21}\right)^2 \left[\left(\text{var}\left(\hat{S}_{11}\right)/\hat{S}_{11}^2\right) + \left(\text{var}\left(\hat{S}_{21}\right)/\hat{S}_{21}^2\right)\right] \\ &\doteq \hat{S}_{\text{PROJ}}^2 \left[\widehat{\text{CV}}\left(\hat{S}_{11}\right)^2 + \widehat{\text{CV}}\left(\hat{S}_{21}\right)^2\right], \end{aligned} \tag{3.6}$$

where $\widehat{\text{CV}}(\hat{\theta}) = \sqrt{\text{var}(\hat{\theta})}/\hat{\theta}$.

The estimates of the survival and capture parameters in likelihood model (3.1) were calculated, treating the estimates of tag-operational probabilities [i.e., $\hat{P}(L_{12})$, $\hat{P}(L_{11})$, $\hat{P}(L_{21})$, and $\hat{P}(L_{22})$] as known constants. However, to calculate a realistic variance estimate for the survival parameters, the error in the estimation of the tag-operational probabilities must be incorporated into an overall variance calculation. The variance of the survival estimate can be calculated using the total variance formula

$$\text{var}\left(\hat{S}_{\text{PROJ}}\right) = \text{var}_{\hat{\mathbf{L}}}\left[E\left(\hat{S}_{\text{PROJ}}|\hat{\mathbf{L}}\right)\right] + E_{\hat{\mathbf{L}}}\left[\text{var}\left(\hat{S}_{\text{PROJ}}|\hat{\mathbf{L}}\right)\right].$$

The above variance can therefore be estimated in stages using the expression

$$\widehat{\text{var}}\left(\hat{S}_{\text{PROJ}}\right) = s^2_{\hat{S}_{\text{PROJ}}|\hat{L}} + \widehat{\text{var}}\left(\hat{S}_{\text{PROJ}} \mid \hat{\mathbf{L}}\right). \tag{3.7}$$

The second term in Equation (3.7) was derived from the maximum likelihood model (3.1) conditioning on the tag-life probabilities [i.e., $\hat{P}(\mathbf{L})$]. The first variance component was calculated using bootstrap resampling techniques (Efron and Tibshirani 1993). Alternative estimates of $\hat{P}(L)$ are computed by bootstrapping both the observed tag-life data and travel-time data. For each estimated vector of tag-operational parameters, survival was estimated using likelihood model (3.1). One thousand bootstrap estimates of the tag-operational parameters are calculated along with the corresponding conditional maximum likelihood estimates of survival. The first variance component in Equation (3.7) is then estimated by the quantity

$$s^2_{\hat{S}_{\text{PROJ}}|\hat{L}} = \sum_{b=1}^{1,000} \left(\hat{S}_b - \hat{\bar{S}}\right)^2 \Big/ (1{,}000 - 1),$$

where $\hat{S}_b =$ the bth bootstrap estimate of survival $(b = 1, \ldots, 1{,}000)$;

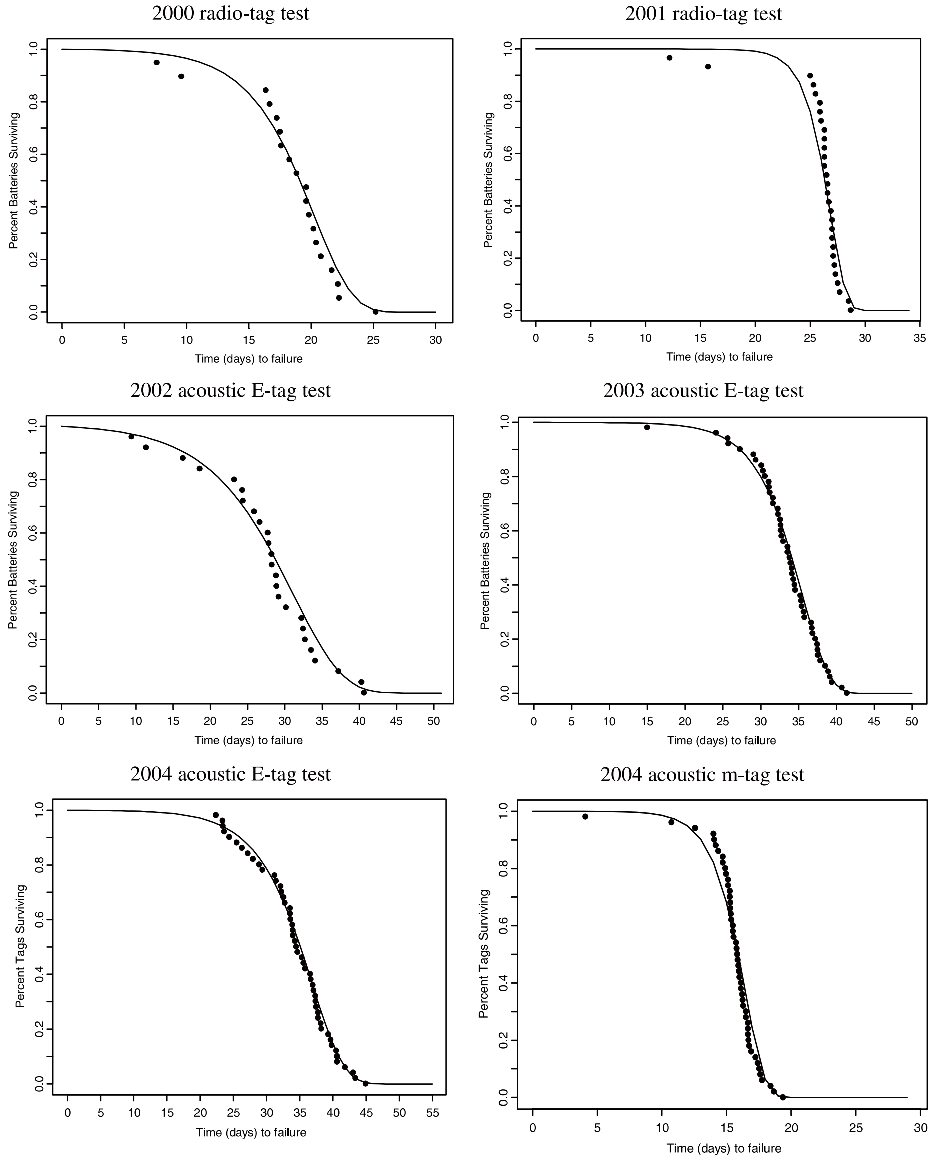


Figure 3. *Tag-life data and fitted Gompertz survivorship curves for acoustic- and radio-tags, 2000–2004.*

Table 2. Results of Parameter Estimation for Time to Tag Failure Using the Gompertz Model. Data are from tag studies conducted by Chelan County Public Utility District and Grant County Public Utility District, 2000–2004. Standard errors are in parentheses.

Tag-life study	*Number tags used*	α	β	*Estimated mean tag life (days)*
Radio-tags (Chelan 2000)	19	0.32 (0.06)	4.75×10^{-4} (5.16×10^{-4})	18.48
Radio-tags (Grant 2001)	29	0.70 (0.11)	4.70×10^{-9} (13.22×10^{-9})	26.03
Acoustic E-tags (Chelan 2002)	25	0.15 (0.02)	1.41×10^{-3} (1.00×10^{-3})	27.58
Acoustic E-tags (Chelan 2003)	50	0.27 (0.03)	1.62×10^{-5} (1.63×10^{-5})	33.38
Acoustic E-tags (Chelan 2004)	50	0.21 (0.02)	9.84×10^{-5} (7.74×10^{-5})	34.14
Acoustic m-tags (Chelan 2004)	50	0.66 (0.07)	1.29×10^{-5} (1.39×10^{-5})	15.68

$$\hat{\hat{S}} = \sum_{b=1}^{1,000} \hat{S}_b \bigg/ 1,000.$$

This approach permits examining the contributions of the mark-recapture process and the sampling error in the tag-operational parameters to the overall variance in survival estimates. Appropriate sample sizes can then be calculated to help reduce the overall variance of the survival estimate. The increase in the number of tags used in the tag-life studies from 19 in 2000 to 50 in 2003 was due in large part to examination of these variance components.

4. RESULTS

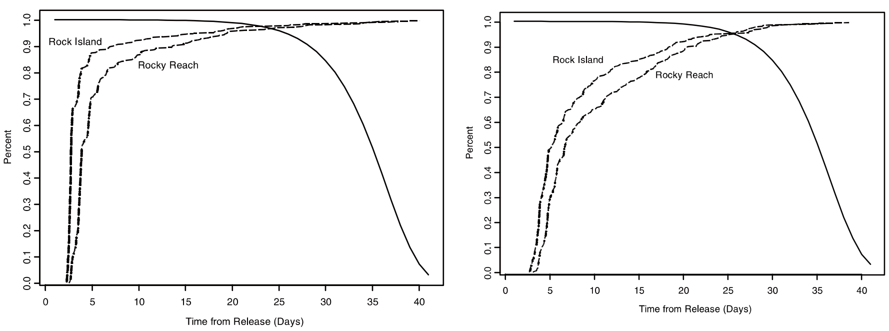
4.1 TAG-LIFE DISTRIBUTIONS

Each of the four tag-life studies was analyzed separately to estimate the parameters of the Gompertz distribution (3.2). In each case, the model appeared to characterize the failure-time data well, with better fits as more data became available (Figure 3). Expected tag life ranged from 18.5 to 34.14 days (Table 2).

In the case of the 2003 acoustic-tag life study, expected tag life was estimated to be 33.4 days. The fitted parameters were used to estimate the probabilities of tag operation at the downstream detection arrays during the 2003 smolt survival study (Table 3). The cumulative arrival distributions of the smolts plotted against the Gompertz tag survival curves indicate that the majority of the fish passed through the detection arrays before tag failure became substantial (Figure 4). Tag-operational probabilities for the 2003 smolt survival study ranged from 0.9855 to 0.9938.

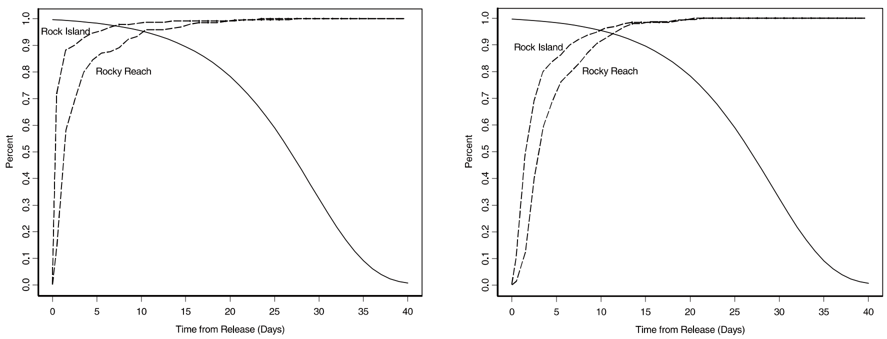
Table 3. Estimated Probabilities an Acoustic-Tag was Operational at a Detection Array as a Function of Release Location from the 2003 Chelan County PUD Acoustic-Tag Study. Standard errors are in parentheses.

Release site	*Crescent Bar*	*Sunland Estates*
Rocky Reach tailrace	$\hat{P}(L_{11}) = 0.9888$ (0.0015)	$\hat{P}(L_{12}) = 0.9855$ (0.0032)
Rock Island tailrace	$\hat{P}(L_{21}) = 0.9938$ (0.0009)	$\hat{P}(L_{22}) = 0.9909$ (0.0023)



a. Travel time to Crescent Bar (2003)

b. Travel time to Sunland Estates (2003)



c. Travel time to Crescent Bar (2002)

d. Travel time to Sunland Estates (2002)

Figure 4. Cumulative arrival distributions (dashed lines) versus tag survivorship curves for releases from Rocky Reach and Rock Island tailraces to detection arrays at Crescent Bar and Sunland Estates, Chelan County, WA, PUD 2002 and 2003 acoustic-tag study. Acoustic-tags were operational 48 hours prior to release of smolts in the survival study.

4.2 SURVIVAL ESTIMATES

Model selection procedures (i.e., AIC, likelihood-ratio tests) found a parsimonious model for the paired-release study could be used to estimate Rock Island Project survival. The selected model assumed common capture (i.e., $p_1 = p_2$) and survival processes (i.e., $\lambda_1 = \lambda_2$) at and below the first acoustic detection array at Crescent Bar. Project survival was estimated to be $\hat{S}_{\text{PROJ}} = 0.9387(\widehat{\text{SE}} = 0.0157)$, with corresponding downstream detection probabilities of $\hat{p} = 0.9470(\widehat{\text{SE}} = 0.0075)$, and $\hat{\lambda} = 0.9490\left(\widehat{\text{SE}} = 0.0076\right)$. The uncorrected survival estimate was $\hat{S}_{\text{PROJ}} = 0.9339\left(\widehat{\text{SE}} = 0.0156\right)$. The first variance component of Equation (3.7) associated with estimating tag-operational probabilities had a value of 0.00000036; the second variance component associated with the release-recapture process had a value of 0.00024649. Hence, the estimation of tag operation contributed only 0.15% to the overall variance of the project survival estimate.

5. DISCUSSION

The importance of tag-life corrections in survival studies is proportional to the anticipated tag failure rate prior to the smolts exiting the study. In the case of the 2003 Rock Island study, the vast majority of tags (>98%) were still operational when the smolt exited the last hydrophone detection array. Consequently, the adjusted survival estimate of 0.9387 differed little from the unadjusted estimate of 0.9339. On the other hand, in 2002 when the acoustic-tags were first used, tag life was shorter, 27.6 days versus 33.4 days (Table 2). In that year, the uncorrected estimate of project passage survival was 0.9397 ($\widehat{\mathrm{SE}} = 0.0250$), compared to 0.9520 ($\widehat{\mathrm{SE}} = 0.0263$) after bias adjustment. The shorter tag life was, fortunately, mitigated by shorter travel times (Figure 4) that year. Flow volumes and water temperatures change from year to year, and can have an impact on smolt travel times. Studies on smaller smolts, such as subyearling Chinook and sockeye, must use micro-acoustic tags (i.e., acoustic m-tag, Table 2), with roughly half the battery life expectancy of the larger tags. For these species, with often longer travel times, bias correction may be appreciable. Adjustments as little as 1–2% can be the difference between hydroprojects being in compliance with survival guidelines or not. Furthermore, many of the mitigation actions to improve smolt survival through hydroprojects are in this same range. Hence, even small bias corrections can have important management implications.

A parametric approach to modeling failure-time data for tags was used because failures should be a function of relatively simple mechanical processes. The Gompertz (1825) distribution has been widely used in actuarial studies. Other parametric models, as well as the nonparametric Kaplan and Meier (1958) and Nelson (1972) and Aalen (1978) models, may be used to characterize the tag-life distribution. The advantage of the parametric model is most evident in the bootstrap variance calculations.

A nonparametric approach to characterizing the travel-time distributions was used in this article because numerous factors can influence travel times, resulting in irregular and multimodal distributions not easily modeled parametrically. Flow pulsing, changes in hydroproject operations, and heterogeneity among the individuals are the most likely causes for irregular travel-time distributions. Should a parametric model properly fit the data, then bootstrap variance calculations can also benefit from the simplicity of its form.

The detected fish arriving at downstream arrays are a function of both travel times and tag-failure rates. Fish with longer travel times are less likely to show up downstream because of a greater likelihood of tag failure by the time they arrive. As such, any observed arrival distribution may have extreme travel times truncated by prior tag failure. Hence, any bias correction to survival estimates based on the observed arrival times may be conservative. This problem can be minimized by not using travel times measured directly at the array of interest, but instead, by using travel-time information from smolts detected at the next array downstream. For example, (Figure 1), smolts known to have arrived at Sunland Estates are known to have passed through Crescent Bar with their tags operational. These smolts could be used to characterize the arrival distribution at that array. In this way, observed travel-time distributions are less affected by tag failure. In the same way Manly and Parr (1968) used upstream and downstream detections to estimate capture probabilities at intermediate locations, upstream and downstream detections can be used to estimate arrival distributions. The implication is that one detection array beyond the geographic frame of reference is needed in the study design in order to obtain nearly unbiased arrival distributions.

Estimation bias can also arise if the conditions in which tag life are monitored are not typical of the environment tagged fish will experience. In general, battery life of the tags decreases with increased water temperature. For this reason, the tags are monitored in ambient river water. In addition, tags are monitored at an average water depth that salmonid smolts travel. However, other fish behavior and the passage through hydroprojects could put stress on tags implanted in fish that the monitored tags do not experience. Thus, the tag-life correction may be an incomplete adjustment providing bias reduction rather than complete bias elimination.

The use of radio- and acoustic-tags to estimate smolt passage survival has permitted greater sampling precision with substantially fewer fish than required with passive tagging methods. The freedom to use fewer fish has opened up the possibility of studying threatened and endangered species previously prohibited by restrictions on incidental take. Providing model corrections for tag failure provides the opportunity to obtain reliable survival information for these critical species of interest.

Cowen and Schwarz (2005) addressed the problem of correcting release-recapture studies of survival for tag-life using a slightly different approach. They assumed travel times could be parametrically modeled using a half-normal distribution. Changing river flows and hydro operations, however, can have a disparate effect on smolt outmigration, producing multimodal and skewed distributions, which we felt would be better modeled nonparametrically. Alternatively, Cowen and Schwartz (2005) used a nonparametric method of characterizing tag-failure times, which we found could be successfully modeled using either a Gompertz or Weibull distribution in over ten studies to date.

Finally, Cowen and Schwarz (2005) used bootstrap techniques to estimate the entire sampling variances, while we expressed the variance of the survival estimates in terms of variance components, estimating one via likelihood and the other through bootstrapping. Separating the variance components permits examination of the contributions of the tag-life sample to the overall error variance, which is useful in designing investigations.

APPENDIX: ACTIVE TAG TYPES AND SETTINGS USED IN ANALYSES

Radio-tags, Lotek model MCFT-36M, were used in the 2000 (19 tags) and 2001 (30 tags) tag-life studies (Skalski et al. 2001; English et al. 2001). The radio-tags were approximately 8.2 mm in diameter by 18.9 mm long, and averaged 1.75 grams in air. The burst rate was set at 1 pulse every 2.5 seconds. Acoustic tags, HTI Model 795E, were used in the 2002 (25 tags), 2003 (50 tags), and 2004 (50 tags) tag-life studies (Skalski et al. 2003, 2004, 2005). The tags were approximately 7 mm in diameter by 16 mm long, and averaged 1.5 grams in air. The ping rate was set at 1 ping every 4–6 seconds, with a pulse width of 0.5

millisecond in 2002 and 2003. In 2004, an additional 50 model 795m micro-acoustic tags were used, approximately 7 mm in diameter by 16.5 mm long, averaging 0.75 gm in air. Ping rates in 2004 were set at 1 every 4–8 seconds, with a pulse width of 1.0 millisecond.

In all studies, tags were submerged in ambient river water and monitored continuously until failure. For each tag, failure time and duration of operation were recorded.

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