

May 2000

**THE DESIGN AND ANALYSIS OF SALMONID TAGGING  
TAGGING STUDIES IN THE COLUMBIA BASIN  
VOLUME XIII**

Appraisal of System-Wide Survival Estimation of Snake River  
Yearling Chinook Salmon Released in 1997-98, using PIT-Tags  
Recovered from Caspian Tern and Double-Crested  
Cormorant Breeding Colonies on Rice Island

Technical Report 2000



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Appraisal of System-Wide Survival Estimation of Snake River Yearling Chinook  
Salmon Released in 1997-98, using PIT-Tags Recovered from Caspian Tern and  
Double-Crested Cormorant Breeding Colonies on Rice Island

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## **PREFACE**

Project 8910700, Epidemiological Survival Methods, was developed to provide statistical guidance on design and analysis of PIT-tag (Passive Integrated Transponder) survival studies to the Northwest fisheries community. Studies under this project have determined the statistical feasibility of conducting PIT-tag smolt survival studies, assessed analytical capabilities for analyzing the tagging experiments, and made recommendations on study design. As PIT-tag capabilities developed and research interests increased, the project has been instrumental in maintaining the statistical capabilities for designing and analyzing tagging studies to meet these expanded objectives.

In this report, PIT-tags recovered from tern and cormorant breeding colonies on Rice Island were incorporated to survival analyses to allow the appraisal of project-wide survivals of PIT-tagged chinook yearlings released in 1997 and 1998. Previous analyses of PIT-tagged juvenile salmonids, performed by the National Marine Fisheries Service (NMFS) and the University of Washington, have provided consistent estimates of yearling survival between Lower Granite and McNary Dams since 1993. Yet the estimate of survival at the lower reaches of the Columbia River was never attempted because of the inefficient interrogation systems at John Day and Bonneville Dams, as well as the lack of a final collection or detection site beyond Bonneville Dam. The increase in detection efficiency at John Day and Bonneville of the past two years, and the collection and identification of PIT-tags from Rice Island have removed these two obstacles. Thus, attempts to satisfy the managerial need for survival estimates from Lower Granite Dam to Bonneville Dam can be undertaken for the first time.

This report provides a detailed examination of the smolt survival estimates at Bonneville and John Day reaches and the possible effects of model violations from using the PIT-tag returns from Rice Island.

## ABSTRACT

PIT-tags recovered from tern and cormorant breeding colonies at Rice Island and observations from the interrogation systems at John Day and Bonneville Dams were incorporated into survival analyses. Whether the estimates for the upper reaches of the system, between Lower Granite and McNary Dams were as expected (with weighted averages  $\overline{\hat{S}_{LGR-LGS}} = 0.996$ ,  $\overline{\hat{S}_{LGS-LMN}} = 0.837$ , and  $\overline{\hat{S}_{LMN-McN}} = 0.941$ ), those for the lower reaches, between John Day and Bonneville Dams, appeared positively biased with survival estimates typically greater than 1. Their weighted averages were  $\overline{\hat{S}_{McN-JDA}} = 0.707$  and  $\overline{\hat{S}_{JDA-BON}} = 1.792$  for 1997 releases. For the 1998 releases, they were  $\overline{\hat{S}_{McN-JDA}} = 0.795$  and  $\overline{\hat{S}_{JDA-BON}} = 1.312$ . If the estimates for the lower reaches were biased, the estimates for the whole project would also be biased ( $\overline{\hat{S}_{LGR-BON}} = 0.819$ ).

We determined that bias could have arisen if the terns and cormorants of Rice Island fished for salmon yearlings in waters of the BON-Rice reach at low rates ( $M_{BON-Rice} \leq 0.2$ ), and the rates of tag-deposition and tag-detection were low ( $R_D \times R_R \leq 0.4$ ). Moreover, unknown levels of uncensored post-detection mortality and scavenging of previously dead salmon yearlings may have also added to the bias.

## EXECUTIVE SUMMARY

### Objectives

- 1) To evaluate the efficacy of using PIT-tags recovered from Rice Island to obtain survival estimates for the lower reaches of the Columbia River.
- 2) To estimate survival of hatchery chinook salmon yearlings from the Snake River Basin between McNary Dam (McN) and John Day Dam (JDA), and between John Day Dam and Bonneville Dam (BON).
- 3) To assess system-wide (i.e., Lower Granite to Bonneville Dam) survival for the 1997 and 1998 outmigrations of yearling chinook salmon.
- 4) To assess the robustness of the PIT-tag models to possible assumption violations associated with using Rice Island PIT-tag recoveries.

### Results

PIT-tags from two 1997, and four 1998 releases of hatchery-reared spring chinook yearlings, and from two 1997 releases and one 1998 release of hatchery-reared summer chinook yearlings that had been recovered from the nesting bird colonies on Rice Island were included in smolt survival analyses. This inclusion allowed for a sampling site beyond Bonneville Dam, thus enabling the Cormack/Jolly-Seber (CJS) capture-recapture model to estimate survival at the JDA-BON reach. However, the low number of detections at JDA in 1997 (Fig. 1*b* and 2*b*, Table 1) led to extremely variable estimates of survival for the 1997 releases, and even prevented estimation in one occasion. The McN-JDA and JDA-BON reach survival estimates for that year were often greater than 1, with extremely large associated standard errors (Table 4). The estimates for the 1998 releases, particularly those for the McN-JDA reach, were somewhat more realistic than those for 1997. They ranged from 0.72 to 0.84, with considerably smaller standard errors (Table 5). However, the estimates of smolt survival for JDA-BON were greater than 1.

The survival estimates for the Snake River reaches, Lower Granite Dam-Little Goose Dam (LGR-LGS), LGS-Lower Monumental Dam (LMN) and LMN-McN, were reasonable for both the 1997 and 1998 releases. The estimates ranged from 0.77 to 1, with moderate to small variances, and were consistent with those of previous years and studies.

The system-wide (LGR-BON) survival estimates ranged from 0.51 to 1.31, and possessed large variances that appear to increase with the survival estimates (Table 6). The weighted average of the LGR-BON annual survival estimates was 0.819, with an estimated standard error of 0.095. The decomposition of the hydrosystem-wide survival estimates into two survival estimates (one for the LGR-McN reach, and the other for the McN-BON reach) showed that the average estimates for LGR-McN were slightly larger than 0.78, with relatively tight 95% confidence intervals (Table 6). On the other hand, estimates for McN-BON were larger than 1 with broader confidence intervals.

The fact that the estimates of  $S_{JDA-BON}$  and, to a lesser extent, of  $S_{McN-JDA}$  were typically greater than 1 (Table 4 and 5) suggested the existence of a positive bias in the estimates. To assess the possible source of bias in our estimates, we performed 18 simulations. These simulations were based on a seven-reach system depicted in Figure 5. In simulations 1-8 (Table 2), we attempted to evaluate the bias that bird predation level and location, and the rate at which PIT-tags were deposited on and recovered from Rice Island could introduce into the CJS estimation of reach survivals, and detection and terminal probabilities. We limited our analysis to three cases: *a*) Bird predation occurs only at the last reach, at low, moderate and high rates with low tag-deposition and recovery rates, *b*) Bird predation occurs at the last two reaches, at low, moderate and high rates with low tag-deposition and recovery rates, and *c*) Bird predation occurs only at the last reach, at a low rate with low to high tag-deposition and recovery rates. In each case, we also analyzed the bias added by the consumption of previously dead fish. In simulations 9-12 (Table 2) we also analyzed the added effects of scavenging of previously dead fish and of uncensored post-detection mortality. By means of simulations 13-18 (Table 3), we attempted to evaluate the additional bias generated by uncensored transported fish.

Our simulations suggested that a positively biased survival estimate for the lower Columbia reaches could have arisen under at least three situations:

- 1) If bird predation occurs not only nearby Rice Island, but also in reaches upstream BON.
- 2) Whenever bird predation rates nearby Rice Island are low.
- 3) Whenever the tag-deposition rate at Rice Island and the tag recovery rates are low.
- 4) If terns and cormorants eat tagged fish that have died from causes other than bird predation.
- 5) Whenever there is uncensored post-detection mortality at Bonneville or other detection sites.

6) Whenever transported fish have not been correctly censored.

Only when predation occurred exclusively in the last reach (i.e., between BON and Rice Island), accompanied by high tag-deposition and detection rates, in the absence of uncensored post-detection mortality, scavenging and uncensored fish transportation, would the reach survival estimate  $\hat{S}_{\text{JDA-BON}}$  be unbiased (Fig. 6 and 10a).

## **Management implications**

The recent availability of PIT-tag recoveries from Rice Island, together with the installation of PIT-tag interrogation systems at John Day and Bonneville Dams, allowed the estimation of survival for salmonid yearlings through the Snake-Columbia hydrosystem. To properly mitigate for hydrosystem losses, unbiased smolt survival estimates are necessary. However, the pattern of inflated survival estimates in the lower river, along with the results of the simulation studies, suggest that the 1997-1998 data need to be used cautiously. There is the possibility that the system-wide survival estimates may be positively biased by model violations from using the Rice Island PIT-tag recoveries.

## **Recommendations**

Little can be done at present to correct for possible bias introduced by the Rice Island PIT-tag data. Radiotelemetry studies of the tern colony may be used to assess model violations. Detailed radiotelemetry studies on the feeding radius of the Rice Island bird breeding colonies and the incidence of feeding on live and dead smolt would resolve some uncertainties. On the other hand, PIT-tag recovery efforts at Rice Island and the reporting of all facility and raceway mortality in all Lower Columbia and Snake River dams should be improved to eradicate bias introduced by small recovery rates and uncensored post-detection mortality. Until the assumptions can be better verified, the Rice Island recoveries may not be an adequate substitute for proper downriver PIT-tag detections. Currently only the towed array is providing some limited information on below Bonneville Dam detections of PIT-tagged smolt. However, the numbers of smolt detected by the towed array is often inadequate for survival estimation.

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# 1. INTRODUCTION

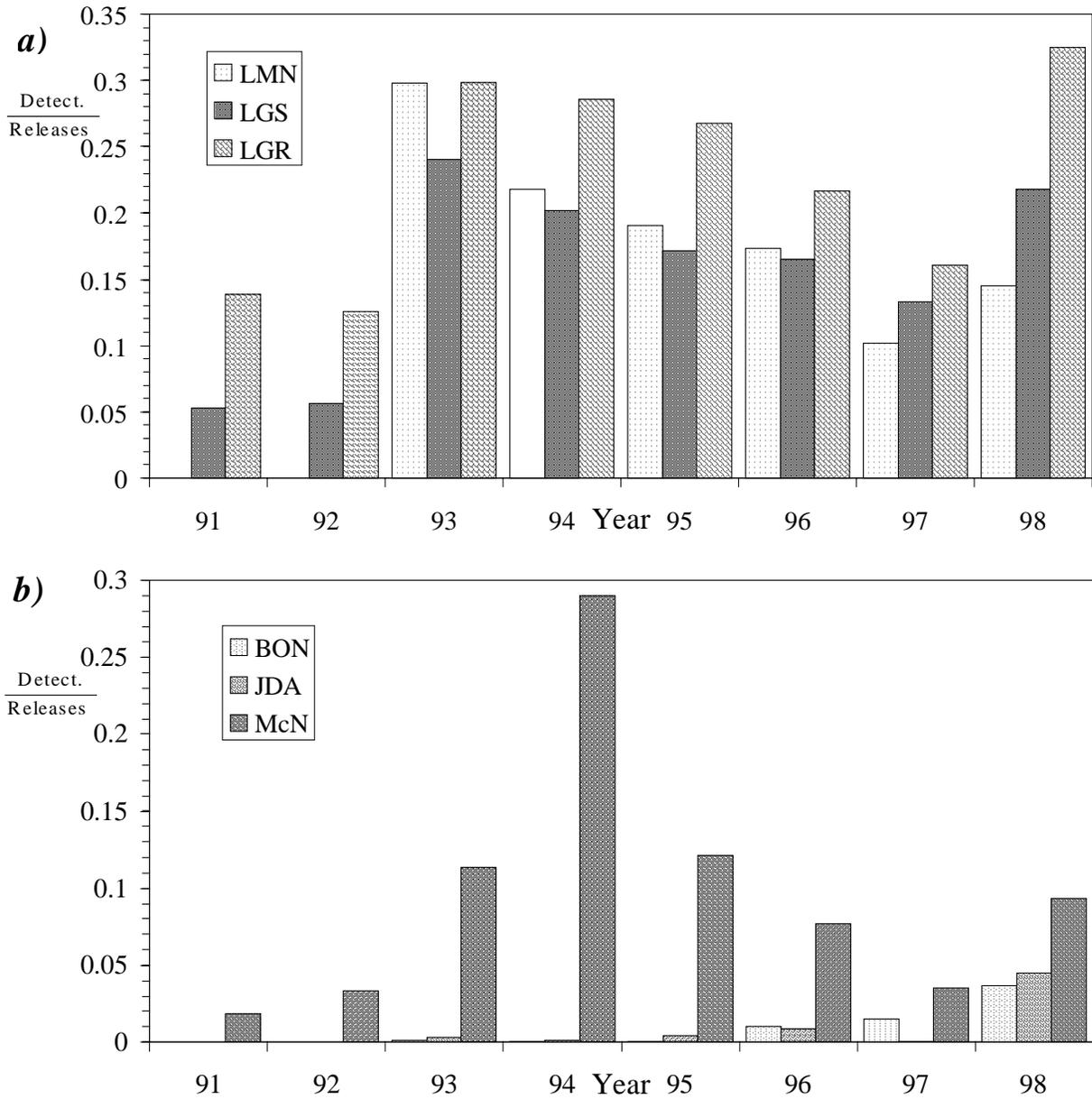
Since the late 1980s PIT (Passive Integrated Transponder) tags (Prentice et al. 1990a, b, c) have been released in ever increasing numbers to estimate survival and investigate the dynamics of smolt migration. However, it was not until 1993 that the National Marine Fisheries Service (NMFS) and the University of Washington were able to apply a single-release model (Cormack 1964, Jolly 1965, Seber 1965) to produce reliable survival estimates for specific groups of PIT-tagged yearlings (Iwamoto et al. 1994). Through 1997 (Figs. 1 and 2), NMFS studies (Muir et al. 1995, 1996; Smith et al. 1997; Hockersmith et al. 1998) presented yearling survival estimates only for reaches on the Snake River basin, between Lower Granite (LGR) and McNary (McN) Dams. Moreover, lack of a detection site downstream at BON hindered any survival estimation for the JDA-BON reach, because the single-release capture-recapture model requires at least one detection site below the last reach of interest.

Last year, the results of the Columbia River Inter-Tribal Fish Commission (CRITFC), Oregon State University (OSU), and NMFS surveys for PIT-tags found at the Caspian tern (*Sterna caspia*) and double-crested cormorant (*Phalacrocorax auritus*) breeding colonies at Rice Island were available in PTAGIS (PIT Tag Information System) files. These lists of recovered PIT-tags encouraged the possible use of Rice Island as a final detection/recovery site in the single-release capture-recapture models to attempt the estimation of survival for salmonid yearlings migrating down the Snake and Lower Columbia between JDA-BON and hence, complete the survival estimation for that entire hydrosystem.

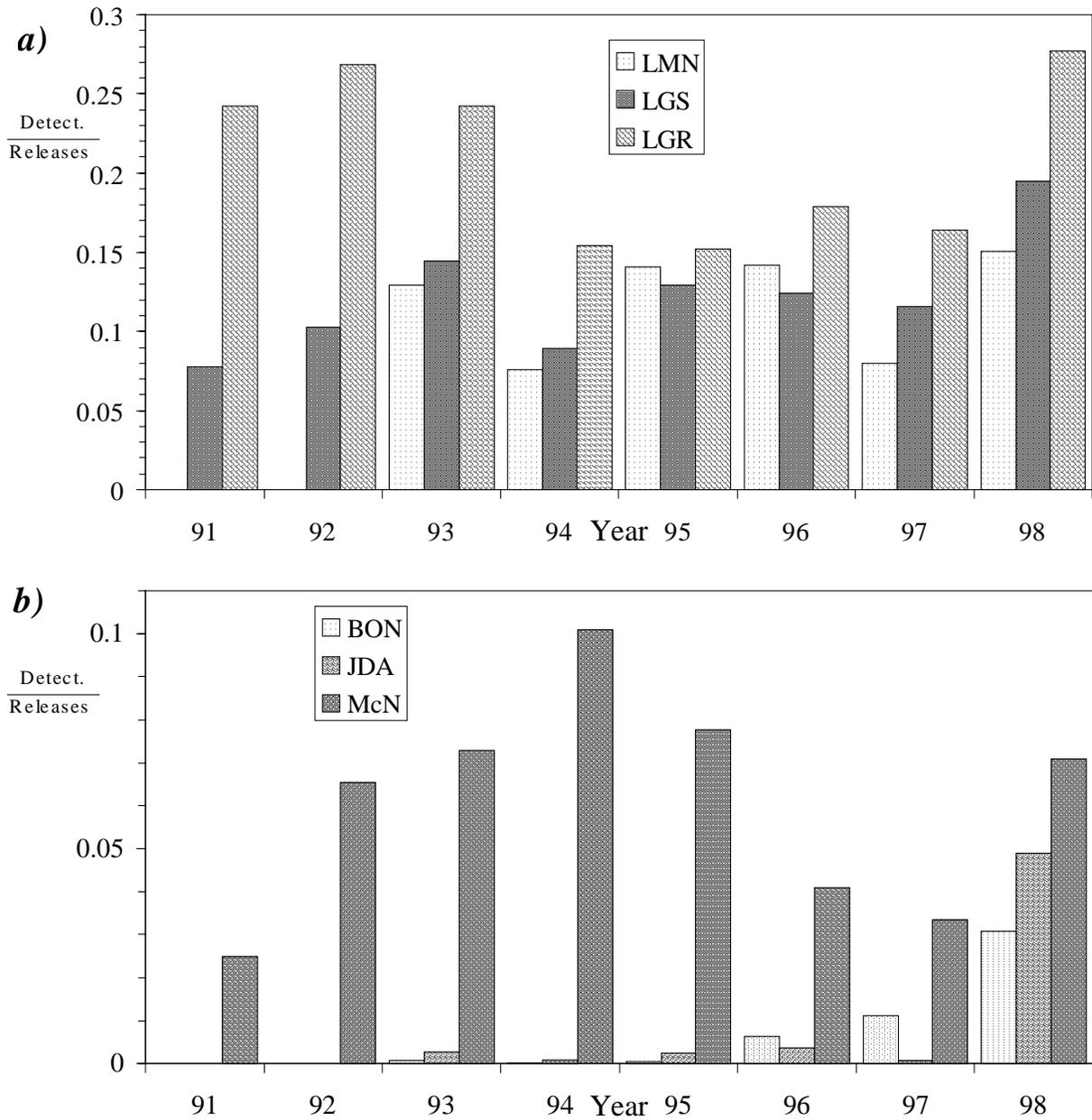
The objectives of the present study are:

1. To evaluate the efficacy of using PIT-tags recovered from Rice Island to obtain survival estimates for the lower reaches of the Columbia River, and discuss possible sources of bias.
2. To estimate survival of hatchery chinook salmon yearlings from the Snake River Basin between McNary and John Day Dam, and between John Day and Bonneville Dam.
3. To assess system-wide (LGR-BON) survival for the 1997 and 1998 outmigrations of yearling chinook salmon.
4. To assess the robustness of the PIT-tag models to possible assumption violations associated with using Rice Island PIT-tag recoveries.

**Figure 1:** Proportion of detected PIT-tagged hatchery spring chinook yearlings at dam interrogation sites on the **(a)** Snake River Basin, and **(b)** Lower Columbia River Basin, from 1991 to 1998.



**Figure 2:** Proportion of detected PIT-tagged hatchery summer chinook yearlings at dam interrogation sites on the **(a)** Snake River Basin, and **(b)** Lower Columbia River Basin, from 1991 to 1998.



## 2. MATERIALS AND METHODS

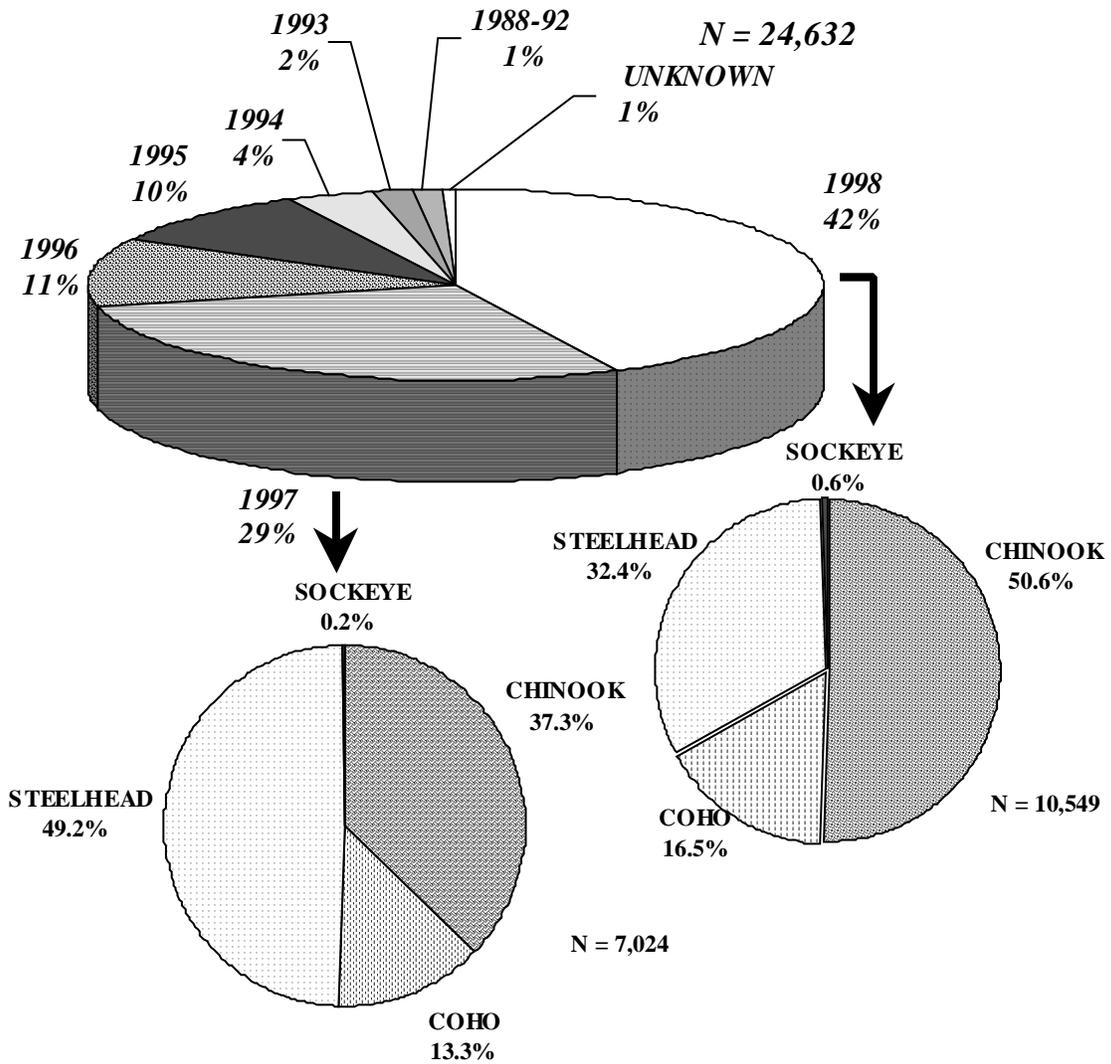
### 2.1 PIT-tag recoveries from Rice Island

Rice Island, a dredge material disposal island, is located in the Columbia River estuary (34 Rkm) on the north side of the shipping channel above Tongue Point. The island has a large population of Caspian terns (approximately 8,000 breeding pairs) that nest on a rather short strip of bare sand. Besides the tern colony, there is also a 30-m<sup>2</sup> nesting site for double-crested cormorants. Both terns and cormorants are strictly piscivorous birds that are expected to be one of the more important predators on juvenile salmonids in the Columbia River basin (PTAGIS Newsletter, 1997, Volume 2, Issue 8). When the birds eat PIT-tagged salmonids, they deposit the glass-encapsulated tags in and around their breeding colonies on Rice Island.

In 1996 and 1997, the Columbia River Inter-Tribal Fish Commission (CRITFC), in cooperation with the Oregon State University (OSU), conducted a study to recover the PIT-tags from Rice Island, using stratified systematic sampling involving meter square plots located along a grid covering areas both inside and outside the nesting ground. A nonsystematic visual search through areas of high tag density was also applied. Based on the stratified sampling of 1997, CRITFC and OSU estimated 33,801 PIT-tags on the tern colony (PTAGIS Newsletter, 1997, Volume 2, Issue 8). In 1998, NMFS personnel from the Hammond Research Station surveyed the southwest tip of Rice Island for PIT-tags using a "Sand Flea," a mechanical sifting device capable of sieving and retrieving tag-sized material from the top 15 cm of substrate (PTAGIS Technical Topic #98-02.1 and #98-02.2). NMFS also used a mobile flat-plate detector along 1-m wide transects in mixed terrain such as the cormorant stick nests.

In 1998, PTAGIS personnel generated the tagging, recapture, and interrogation data files from lists of PIT-tags recovered from the tern and cormorant breeding colonies at Rice Island by CRITFC, OSU, and NMFS in 1996, 1987, and 1998 (PTAGIS Technical Topic #98-02.1). These data consist of 24,632 PIT tags from juvenile salmonids released as far back as 1988 (Fig. 3). Most of the tags correspond to salmon and steelhead released in 1998 (42%) and 1997 (29%). The rather large numbers of tag recoveries belonging to marked chinook and steelhead (37.3% and 50.6% for tagged chinook, and 49.2% and 32.4% for tagged steelhead released in 1997 and 1998, respectively) represent only small portions of the total annual releases of marked fish in the Snake-Columbia River Basin. Thus, 0.59% and 0.70% of the chinook releases of 1997 and 1998, and 2.71% and 3.97% of the steelhead releases of 1997 and 1998 ended up in Rice Island.

**Figure 3:** PIT-tags collected at Rice Island by year of release. For the 1997 and 1998 releases, recoveries are summarized by species.



## 2.2 Data

To evaluate the efficacy of using PIT-tags recovered from Rice Island to obtain survival estimates for the lower reaches of the Columbia River, we first identified the 1997 and 1998 releases of PIT-tagged chinook yearlings that were well-represented in the Rice Island database (Table 1). These consisted of four 1997 (Fig. 4a) and five 1998 (Fig. 4b) releases of hatchery-reared chinook yearlings. All the release sites were located on tributaries of the Snake River, more than 100 km upstream the first interrogation site at LGR (Fig. 4c). Six releases were comprised of spring chinook (those released from Dworshak, Rapid River, and Lookingglass hatcheries and from Imnaha River Weir and Clearwater River North Fork). The remaining three groups were summer chinook, released from Pahsimeroi Pond and Knox Bridge. All the releases were larger than 10,000 fish, and they were efficiently detected at five of the six detection sites, the only exception being John Day Dam in 1997 (Table 1). The recoveries from Rice Island were all in the order of hundreds of fish, and ranged between 1.12% (1997 DWOR) and 0.44% (1997 KNOXB) of the original releases.

In the Snake-Columbia River Basin, barges or trucks often transport PIT-tagged yearlings from LGR, LGS, LMN, or McN to the BON reservoir. Transported fish must be censored because transported fish do not contribute any information on inriver survival below the point of transport. Unfortunately, transported fish are rarely directly identified as transferred fish in the PTAGIS database. Instead, in most survival studies PIT-tag data are censored after tracking the passage of tagged fish through the various coils of each dam. In general, fish that are detected at holding tanks, sampling rooms, or raceways and exits to barges, and those detected only at the separator gates of a detection facility are censored (Table 1). This censoring procedure certainly accounts for all truly transported fish, but it may also censor some fish that were not transported.

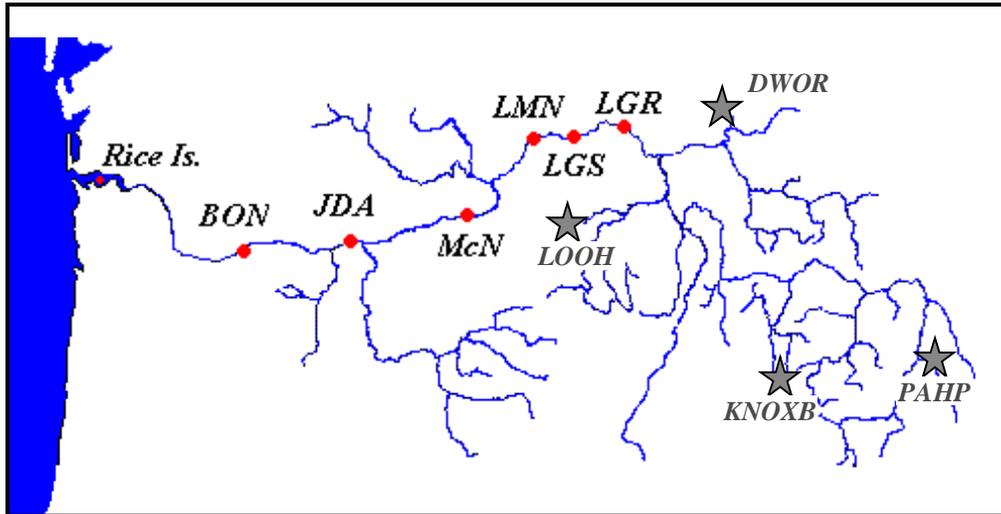
In a similar way, fish that died immediately after detection because of damage suffered during its passage through the detection facility do not contribute any information on inriver survival below the last point of detection. If they are not censored, they can alter the relative proportions of downstream detected and undetected fish leading to bias in the survival estimates. The data in Table 1 was censored for post-detection mortality by using the deaths reported in PTAGIS mortality tables.

**Table 1:** PIT-tagged hatchery chinook yearlings released in 1997 and 1998, and subsequently recovered at Rice Island in substantial numbers (i.e.,  $\geq 100$  tags) at Rice Island. Censored observations are indicated in parentheses.

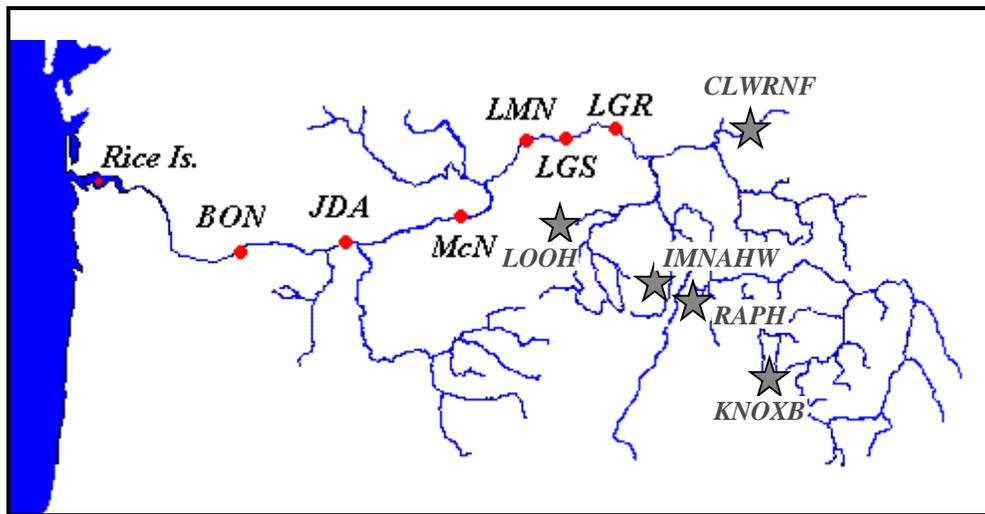
Release Date	Release Site	Released Numbers	Detections at						
			LGR	LGS	LMN	McN	JDA	BON	Rice Is.
4/7/97	<b>PAHP</b>	33,326	6,523 (5,335)	4,290 (379)	2,903 (64)	1,220 (9)	23	395 (4)	165
4/7/97	<b>DWOR</b>	14,080	2,388 (1,916)	2,355 (125)	1,659 (31)	492 (1)	5	220 (3)	157
4/7/97	<b>LOOH</b>	40,401	7,747 (6,247)	6,270 (467)	5,068 (91)	2,045 (2)	22	667 (17)	230
3/20/97	<b>KNOXB</b>	52,734	7,548 (6,147)	5,506 (250)	3,758 (61)	1,117 (6)	31	640 (11)	233
4/13/98	<b>RAPH</b>	48,348	16,283 (11,870)	9,875 (1,972)	7,206 (528)	3,589 (225)	1,965	1,372 (1)	334
3/25-3/26/98	<b>CLWRNF</b>	48,575	16,273 (12,648)	10,928 (4,293)	6,321 (403)	6,408 (445)	1,674	1,624 (1)	330
3/30/98	<b>KNOXB</b>	47,474	13,100 (9,639)	8,750 (1,294)	6,911 (412)	2,868 (139)	1,932	1,331 (2)	351
4/6/98	<b>IMNAHW</b>	19,174	5,848 (4,235)	4,495 (808)	3,136 (232)	1,622 (118)	940	703 (699)	176
4/6/98	<b>LOOH</b>	45,122	15,532 (11,522)	9,115 (2,441)	5,871 (383)	3,115 (245)	1,596	941 (3)	333

**Figure 4:** Selected release sites of PIT-tagged chinook yearlings (stars) in relation to the dam observation sites and final collection site at Rice Island in (a) 1997 and (b) 1998. (c) Distance from release sites and dams to the mouth of the Columbia River, in river kilometers (Rkm).

(a)



(b)



(c)

Release Sites			Observation Sites		
		Rkm			Rkm
<i>PAHP</i>	Pahsimeroi Pond	1325	<i>LGR</i>	Lower Granite Dam	695
<i>KNOXB</i>	Knox Bridge	1152	<i>LGS</i>	Little Goose Dam	635
<i>RAPH</i>	Rapid River Hatchery	978	<i>LMN</i>	Lower Monumental Dam	589
<i>LOOH</i>	Lookingglass Hatchery	933	<i>McN</i>	Mc Nary Dam	470
<i>IMNAHW</i>	Imnaha River Weir	904	<i>JDA</i>	John Day Dam	347
<i>DWOR</i>	Dworshak Hatchery	811	<i>BON</i>	Bonneville Dam	234
<i>CLWRNF</i>	Clearwater River, North Fork	811	<i>Rice Is.</i>	Rice Island	34

## 2.3 Reach and project-wide survival estimates

To obtain survival estimates for the nine releases we used the Cormack-Jolly-Seber (CJS) capture-recapture model (Cormack 1964, Jolly 1965, Seber 1965) as implemented in the statistical computer program SURPH.1 (Smith et al. 1994, Skalski et al. 1998). The CJS model has been also used in all previous NMFS PIT-tag studies (Iwamoto et al. 1994; Muir et al. 1995, 1996; Smith et al. 1997; Hockersmith et al. 1998). In this model, the counts of the capture histories<sup>1</sup> in a given release group are treated as a multinomial sample, where the multinomial cells are the capture histories, and the cell probabilities depend on the survival between sample sites and the capture/detection probabilities at the sampling sites.

For the present analyses, besides the nine release sites, there were seven observation sites (Fig 4). These observation sites were the three Snake River dams (LGR, LGS, LMN), the three lower Columbia River dams (McN, JDA, BON) and finally, Rice Island. Rice Island was treated as another detection site, although the detection process at the island is radically different from the coil detection at the dams. Coil detections at the dams were based on live fish. On the contrary, the detections at Rice Island involved the deposition of PIT-tags from smolts consumed by terns or cormorants and recovered by CRITFC, OSU, or NMFS.

For each release group, the CJS model estimates six reach survivals,  $\hat{S}_{\text{Rel-LGR}}$ ,  $\hat{S}_{\text{LGR-LGS}}$ ,  $\hat{S}_{\text{LGS-LMN}}$ ,  $\hat{S}_{\text{LMN-McN}}$ ,  $\hat{S}_{\text{McN-JDA}}$  and  $\hat{S}_{\text{JDA-BON}}$ , as well as six capture probabilities,  $\hat{p}_{\text{LGR}}$ ,  $\hat{p}_{\text{LGS}}$ ,  $\hat{p}_{\text{LMN}}$ ,  $\hat{p}_{\text{McN}}$ ,  $\hat{p}_{\text{JDA}}$  and  $\hat{p}_{\text{BON}}$ , and a terminal probability  $\hat{\lambda}$ . This terminal probability is the product between the survival at the last reach and the capture probability at Rice Island (i.e.,  $\lambda = S_{\text{BON-Rice Is.}} \times p_{\text{Rice Is.}}$ ). Thus, it is the result of a tag being retrieved by birds and deposited on the island.

For the first time, the incorporation of JDA, BON, and Rice Island as observation sites allowed the estimation of a system-wide survival probability:

$$\hat{S}_{\text{LGR-BON}} = \hat{S}_{\text{Rel-LGR}} \times \hat{S}_{\text{LGR-LGS}} \times \hat{S}_{\text{LGS-LMN}} \times \hat{S}_{\text{LMN-McN}} \times \hat{S}_{\text{McN-JDA}} \times \hat{S}_{\text{McN-BON}}, \quad (1)$$

---

<sup>1</sup> The capture history of a marked fish is a collection of “0’s”, “1’s” or “2”, one number for each observation site. The number “1” is used for the release site, and for each observation site where the fish was detected. The “0” is used each time that the fish was not detected at a particular detection site. Finally, a “2” at a particular observation site indicates a known removal, that is the fish was detected and removed at that site. Removals may be due to transportation or handling mortality.

in addition to the six individual reach-survival estimates.

Annual average estimates were calculated using weights:

$$w_i = \frac{\hat{\theta}_i^2}{\text{Var}(\hat{\theta}_i | \theta_i)}, \quad (2)$$

where  $\hat{\theta}_i$  are either the reach or system-wide survival estimates. These particular weights were

used instead of the more traditional  $w'_i = \frac{1}{\text{Var}(\hat{\theta}_i | \theta_i)}$ , because the variance estimates are a

function of  $\hat{\theta}_i^2$ . By using weights that are inversely proportional to the coefficient of variation squared, the relative precision of the estimate is accounted for without being correlated with the survival estimates.

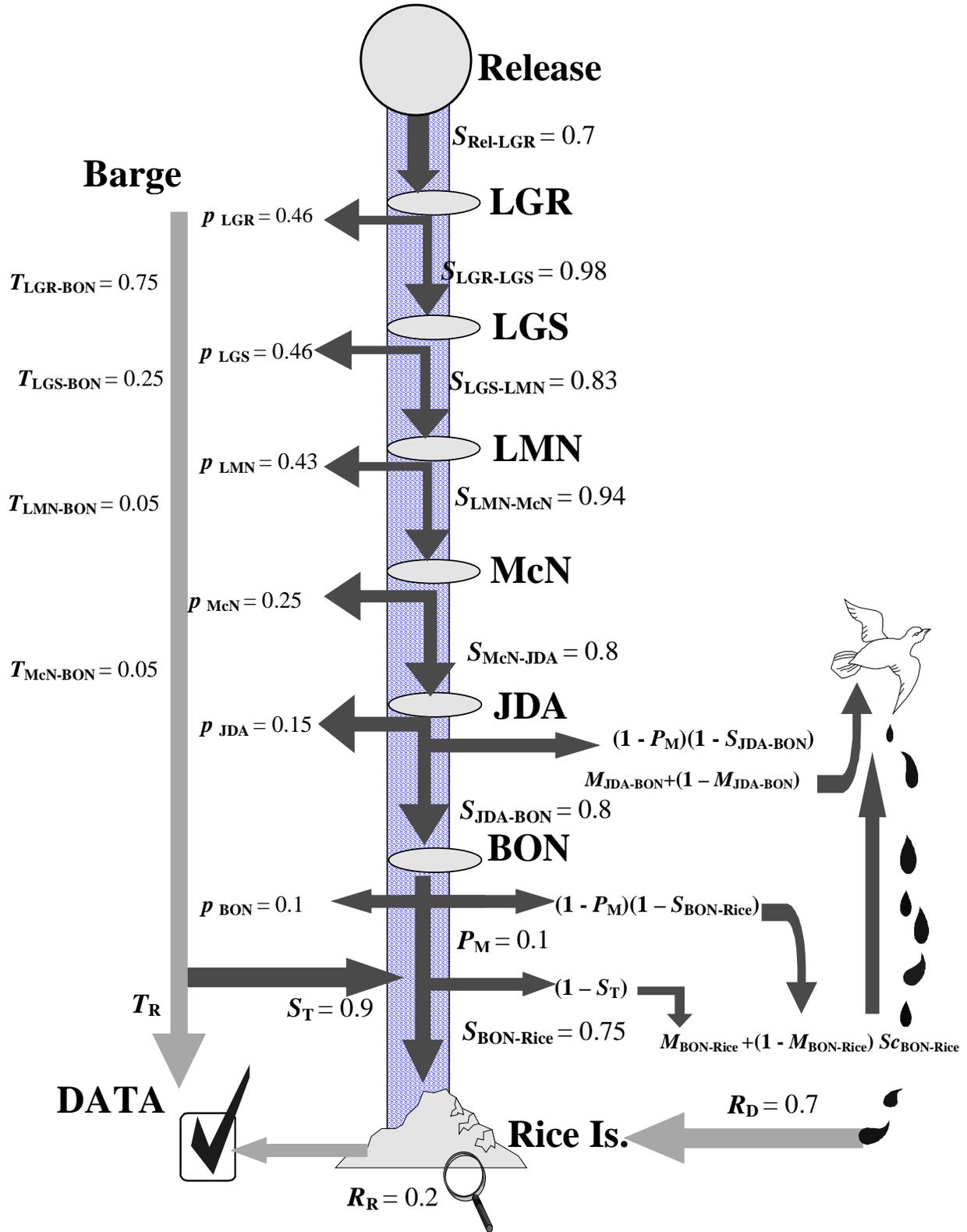
## 2.4 Assessment of bias

Given the complexity of the detection process at Rice Island and its difference from coil detection in juvenile bypass systems, a series of assumptions must be met to avoid bias in the CJS model estimates:

1. Tagged fish have the same probability of being detected and eaten as untagged fish.
2. All PIT tags of fish eaten by terns or cormorants have an equal probability of being deposited on Rice Island.
3. Tern and cormorant predation of PIT-tagged fish occurs only in the last reach (BON-Rice Island).
4. Terns and cormorants eat only PIT-tagged fish that are alive.
5. All transported PIT-tagged fish are known and correctly censored at the site of transportation.
6. All bypassed-detected fish that died after detection (i.e., post-detection mortality) are known and correctly censored at the site of detection.
7. All tags deposited on Rice Island have the same probability of being recovered or detected.

To assess the type of bias caused by departures from some of the above six assumptions, we performed 18 simulation studies. These simulations were based on the seven-reach system depicted in Figure 5 using the parameter values in Tables 2 and 3. For each of the 18 scenarios, we simulated 100 release groups of 50,000 tagged fish each, and simulated the observed frequencies for the 191 unique capture histories that are possible ( $2^7 + 2^{(7-1)} - 1 = 191$ ). For each

**Figure 5:** Schematic of processes in the seven-reach system used in simulations. (See text for details).



**Table 2:** Parameters used in 12 simulations of a seven-reach system used to assess possible bias induced by bird predation ( $M_{\text{JDA-BON}}$ ,  $M_{\text{BON-Rice}}$ ), rates tag deposition ( $R_{\text{D}}$ ) and recovery ( $R_{\text{R}}$ ), consumption of dead fish ( $S_{\text{CBON-Rice}}$ ) and post-detection mortality ( $PM_{\text{BON}}$ ).

Common Parameters						
<u>Survivals:</u>		$S_{\text{Rel-LGR}} = 0.7$ , $S_{\text{LGR-LGS}} = 0.98$ , $S_{\text{LGS-LMN}} = 0.83$ , $S_{\text{LMN-McN}} = 0.94$ ,				
		$S_{\text{McN-JDA}} = 0.8$ , $S_{\text{JDA-BON}} = 0.8$ , $S_{\text{BON-Rice}} = 0.75$				
<u>Capture Probabilities:</u>		$p_{\text{LGR}} = 0.46$ , $p_{\text{LGS}} = 0.46$ , $p_{\text{LMN}} = 0.43$ , $p_{\text{McN}} = 0.25$ ,				
		$p_{\text{JDA}} = 0.15$ , $p_{\text{BON}} = 0.1$				
Specific Conditional Probabilities						
Scenario	$M_{\text{JDA-BON}}$	$M_{\text{BON-Rice}}$	$S_{\text{CBON-Rice}}$	$PM_{\text{BON}}$	$R_{\text{D}}$	$R_{\text{R}}$
1	0	0.25	0	0	0.7	0.2
2	0	0.5	0	0	0.7	0.2
3	0	0.8	0	0	0.7	0.2
4	0.175	0.25	0	0	0.7	0.2
5	0.25	0.5	0	0	0.7	0.2
6	0.4	0.8	0	0	0.7	0.2
7	0	0.25	0	0	0.8	0.4
8	0	0.25	0	0	0.95	0.7
9	0	0.5	0.05	0	0.7	0.2
10	0	0.8	0.05	0	0.7	0.2
11	0	0.5	0.05	0.1	0.7	0.2
12	0	0.8	0.05	0.1	0.7	0.2

**Table 3:** Parameters used in 6 simulations of a seven-reach system used to assess possible bias induced by fish transportation.

<b>Common Parameters</b>									
<u>Survivals:</u> $S_{\text{Rel-LGR}} = 0.7$ , $S_{\text{LGR-LGS}} = 0.98$ , $S_{\text{LGS-LMN}} = 0.83$ , $S_{\text{LMN-McN}} = 0.94$ , $S_{\text{McN-JDA}} = 0.8$ , $S_{\text{JDA-BON}} = 0.8$ , $S_{\text{BON-Rice}} = 0.75$									
<u>Capture Probabilities:</u> $p_{\text{LGR}} = 0.46$ , $p_{\text{LGS}} = 0.46$ , $p_{\text{LMN}} = 0.43$ , $p_{\text{McN}} = 0.25$ , $p_{\text{JDA}} = 0.15$ , $p_{\text{BON}} = 0.1$									
<u>Tag Deposition Probability:</u> $R_{\text{D}} = 0.7$					<u>Tag Recovery Probability:</u> $R_{\text{R}} = 0.2$				
<b>Specific Conditional Probabilities</b>									
Scenario	$M_{\text{BON-Rice}}$	$S_{\text{CBON-Rice}}$	$P_{\text{MBON}}$	$T_{\text{LGR-BON}}$	$T_{\text{LGS-BON}}$	$T_{\text{LMN-BON}}$	$T_{\text{McN-BON}}$	$T_{\text{R}}$	$S_{\text{T}}$
13	0.5	0.05	0.1	0.75	0.25	0.05	0.05	1	0.9
14	0.8	0.05	0.1	0.75	0.25	0.05	0.05	1	0.9
15	0.5	0.05	0.1	0.75	0.25	0.05	0.05	0.9	0.9
16	0.8	0.05	0.1	0.75	0.25	0.05	0.05	0.9	0.9
17	0.5	0.05	0.1	0.75	0.25	0.05	0.05	0.5	0.9
18	0.8	0.05	0.1	0.75	0.25	0.05	0.05	0.5	0.9

release group, we estimated reach survivals and capture-probabilities using the CJS model. The observed frequencies of the 191 capture histories were simulated using the same set of survivals ( $S$ ) and capture probabilities ( $p$ ) in the 18 scenarios:

$S_{\text{Rel-LGR}} = 0.7$ ,  $p_{\text{LGR}} = 0.46$ ,  $S_{\text{LGR-LGS}} = 0.98$ ,  $p_{\text{LGS}} = 0.46$ ,  $S_{\text{LGS-LMN}} = 0.83$ ,  $p_{\text{LMN}} = 0.43$ ,  
 $S_{\text{LMN-McN}} = 0.94$ ,  $p_{\text{McN}} = 0.25$ ,  $S_{\text{McN-JDA}} = 0.8$ ,  $p_{\text{JDA}} = 0.15$ ,  $S_{\text{JDA-BON}} = 0.8$ ,  $p_{\text{BON}} = 0.1$ ,  
 $S_{\text{BON-Rice}} = 0.75$ . With the exception of those for BON, the survivals and capture probabilities used in the simulations were derived from average estimates from the five release groups in 1998. Fish transportation was assumed at the first four detection dams, with respective probabilities:  $T_{\text{LGR-BON}} = 0.75$ ,  $T_{\text{LGS-BON}} = 0.25$ ,  $T_{\text{LMN-BON}} = 0.05$ ,  $T_{\text{McN-BON}} = 0.05$ .

In all the simulations, we assumed that predation by tern and cormorant always occurred at the BON-Rice reach. Bird predation was modeled as a conditional probability at three predation levels: low ( $M_{\text{BON-Rice}} = 0.25$ ), medium ( $M_{\text{BON-Rice}} = 0.5$ ) and high ( $M_{\text{BON-Rice}} = 0.8$ ). In simulations 4-6, we postulated that bird predation also occurred at the JDA-BON reach, with probability  $M_{\text{JDA-BON}} = 0.5 \times M_{\text{BON-Rice}}$ . Scavenging by terns and cormorants was added in simulations 9-18. It was modeled as the probability  $S_{\text{cBON-Rice}} = 0.05$ , affecting the fate of fish that died in the last reach from causes other than bird predation. Finally, in simulations 11-18, an uncensored post-detection mortality was assumed for Bonneville dam ( $P_{\text{MBON}} = 0.1$ ). Thus, the probability that a PIT-tag would end up in the guts of tern and cormorant was:

- 1)  $(1 - S_{\text{JDA-BON}}) \times M_{\text{JDA-BON}}$ , at JDA-BON reach, and
- 2)  $(1 - P_{\text{MBON}}) \times (1 - S_{\text{BON-Rice}}) \times (M_{\text{BON-Rice}} + (1 - M_{\text{BON-Rice}}) \times S_{\text{cBON-Rice}})$ , at BON-Rice reach.

After consumption, the glass-encapsulated tags were excreted and deposited in Rice Island with a tag-deposition probability  $R_{\text{D}}$  and finally recovered and incorporated into the data with probability  $R_{\text{R}}$  (Fig. 5). We considered three levels of tag deposition and recovery: low ( $R_{\text{D}} = 0.7$  and  $R_{\text{R}} = 0.2$ , simulations 1-6 and 9-18), medium ( $R_{\text{D}} = 0.8$  and  $R_{\text{R}} = 0.4$ , simulation 7) and high ( $R_{\text{D}} = 0.95$  and  $R_{\text{R}} = 0.7$ , simulation 8). In simulations 13-18 (Table 3), we modeled fish transport as a conditional probability  $T$ , whose value was the proportion of detected fish that were censored at each dam facility for the five 1998 release groups (Table 1). Transported fish were reported and censored with probability  $T_{\text{R}}$ . In simulations 13 and 14, all transported fish were censored ( $T_{\text{R}} = 1$ ). In simulations 15 and 16, one-tenth the transported fish were not censored ( $T_{\text{R}}$

= 0.9). Finally, half the transported fish were censored in simulations 17 and 18 ( $T_R = 0.5$ ). We assumed that all transported fish survived transportation downstream BON, but after transportation they were subject to survival probability  $S_T = 0.9$ . In the BON-Rice reach, tern and cormorant could kill transported fish with probability  $M_{\text{BON-Rice}}$ . Those fish that were killed by causes other than predation could still be scavenged with probability  $Sc_{\text{BON-Rice}}$ . Thus, tags from transported fish would end up in Rice Island with probability:

$$T_i \times (1 - T_R) \times (1 - S_T) \times (M_{\text{BON-Rice}} + (1 - M_{\text{BON-Rice}}) \times Sc_{\text{BON-Rice}}) \times R_D \times R_R,$$

where  $i = \text{LGR, LGS, LMN, McN}$  (Fig. 5).

In summary, by comparing the results of our 18 simulations, we attempted to appraise the potential biases that the use of the PIT-tags recovered from Rice Island can introduce in the CJS estimation of reach survivals, when:

- a)** Bird predation occurred only within the last reach at low, medium and high predation rates with low tag deposition and recovery rates, in the absence of transportation, post-detection mortality and scavenging (simulations 1-3);
- b)** Bird predation occurred in the last two reaches at low, medium and high predation rates with low tag deposition and recovery rates, in the absence of transportation, post-detection mortality and scavenging (simulations 4-6);
- c)** A low bird predation rates occurred only within the last reach, with low, medium and high tag deposition and recovery rates, in the absence of transportation, post-detection mortality and scavenging (simulations 1, 7 and 8);
- d)** Scavenging, and medium and high bird predation rates occurred only within the last reach, with low tag deposition and recovery rates, in the absence of transportation and post-detection mortality (simulations 9 and 10);
- e)** Post-detection mortality, scavenging, and medium and high bird predation rates occurred only within the last reach, with low tag deposition and recovery rates, in the absence of transportation (simulations 11 and 12);
- f)** Fish transported from LGR, LGS, LMN and McN dams were fully or partially censored and post-detection mortality, scavenging, and medium and high bird predation rates occurred only within the last reach, with low tag deposition and recovery rates (simulations 13-18).

### 3. RESULTS

#### 3.1 Reach and project-wide estimates for 1997 and 1998

Tables 4 and 5 display the CJS estimates of reach survivals for the 1997 and 1998 releases of PIT-tagged hatchery chinook yearlings. Although the inclusion of the PIT tags recovered from Rice Island allowed for the estimation of survival for the Lower Columbia reaches, the survival estimates for JDA-BON had a preponderance of values larger than one, with large standard errors. The low detection numbers at JDA during 1997 (Fig. 1*b* and 2*b*, Table 1) prevented the estimation of  $S_{\text{McN-JDA}}$  and  $S_{\text{JDA-BON}}$  for the DWOR release. Consequently, this release was dropped from the analysis.

The McN-JDA and JDA-BON reach survival estimates of the remaining three releases of 1997 were often larger than one with large associated variances (Table 4). On the other hand, the  $S_{\text{McN-JDA}}$  estimates for the releases of 1998 were less variable than the estimates for the releases of 1997 (Table 5). While in 1997 the values ranged between 0.45 and 2.2, in 1998  $S_{\text{McN-JDA}}$  estimates ranged between 0.72 and 0.84. Moreover, the standard errors estimated for the 1998 releases were smaller than the standard errors estimated for the 1997 survival estimates. Nonetheless, the survival estimates for JDA-BON also showed a preponderance of values larger than one. Only the estimates for the 1998 LOOH release and for the 1997 KNOXB release were smaller than one ( $S_{\text{JDA-BON}} = 0.99$  and  $S_{\text{JDA-BON}} = 0.78$ , respectively). This preponderance of survival estimates larger than one suggests the possible presence of bias in the CJS estimation.

The survival estimates for the Snake River reaches, LGR-LGS, LGS-LMN and LMN-McN, ranged from 0.77 to 1, with moderate to small variances (Tables 4 and 5). These estimates for the releases of 1997 and 1998 were consistent with estimates of previous years (e.g., Table 4 in Hockersmith et al., 1998). The estimates of capture probability for the Snake River dams (LGR, LGS and LMN) were almost twice those for McN dam and more than four times the estimates for JDA and BON (Tables 4-5).

System-wide survivals, calculated by applying Equation (1) to the CJS survival estimates for reaches between LGR and BON, varied from 0.51 to 1.31 (Table 6). Their variances ranged from 0.007 to 5.7, with the larger values corresponding to the releases of 1997. Annual averages for 1997 were smaller, though not significantly smaller ( $P > 0.05$ ), than the averages for 1998. The corresponding 95% confidence intervals were (0.493 - 0.969) for 1997, and (0.614 - 1.028) for

**Table 4:** Cormack-Jolly-Seber estimates of survivals, capture probabilities and terminal probability ( $\lambda$ ) for 1997 releases of PIT-tagged hatchery chinook yearlings. Estimated standard errors are given in parentheses. Weighted averages were based on equation 2.

Release Sites	Reach Survivals					
	Release-LGR	LGR-LGS	LGS-LMN	LMN-McN	McN-JDA	JDA-BON
<b>PAHP</b>	0.508 (0.008)	0.957 (0.026)	0.876 (0.032)	1.125 (0.132)	0.604 (0.413)	1.132 (0.845)
<b>LOOH</b>	0.599 (0.009)	0.922 (0.022)	0.837 (0.021)	0.816 (0.057)	0.446 (0.203)	2.369 (1.241)
<b>KNOXB</b>	0.426 (0.008)	0.927 (0.026)	0.888 (0.033)	0.946 (0.102)	2.157 (2.133)	0.780 (0.820)
Average	0.523 (0.049)	0.934 (0.011)	0.859 (0.016)	0.908 (0.085)	0.707 (0.396)	1.792 (0.480)

Release Sites	Capture Probabilities						$\lambda$ BON-RICE Is.
	LGR	LGS	LMN	McN	JDA	BON	
<b>PAHP</b>	0.385 (0.007)	0.386 (0.008)	0.309 (0.011)	0.116 (0.013)	0.004 (0.003)	0.055 (0.018)	0.023 (0.008)
<b>LOOH</b>	0.32 (0.006)	0.379 (0.006)	0.377 (0.009)	0.188 (0.013)	0.005 (0.002)	0.058 (0.016)	0.02 (0.005)
<b>KNOXB</b>	0.336 (0.007)	0.364 (0.007)	0.284 (0.010)	0.090 (0.010)	0.001 (0.001)	0.031 (0.011)	0.011 (0.004)
Average	0.349 (0.020)	0.376 (0.006)	0.339 (0.029)	0.151 (0.030)	0.004 (0.001)	0.050 (0.008)	0.019 (0.003)

**Table 5:** Cormack-Jolly-Seber estimates of survivals, capture probabilities and terminal probability ( $\lambda$ ) for 1998 releases of PIT-tagged hatchery chinook yearlings. Estimated standard errors are given in parentheses. Weighted averages were based on equation 2.

Release sites	Reach Survivals					
	Release-LGR	LGR-LGS	LGS-LMN	LMN-McN	McN-JDA	JDA-BON
<b>RAPH</b>	0.66 (0.004)	1.013 (0.009)	0.853 (0.011)	0.977 (0.029)	0.824 (0.048)	1.824 (0.393)
<b>CLWRNF</b>	0.843 (0.006)	1.075 (0.015)	0.766 (0.013)	0.937 (0.023)	0.763 (0.046)	1.4 (0.263)
<b>KNOXB</b>	0.587 (0.004)	0.984 (0.010)	0.850 (0.011)	0.966 (0.030)	0.837 (0.048)	1.413 (0.253)
<b>IMNAHW</b>	0.682 (0.006)	0.982 (0.014)	0.848 (0.016)	0.948 (0.037)	0.831 (0.062)	1.125 (0.232)
<b>LOOH</b>	0.698 (0.004)	0.972 (0.011)	0.829 (0.014)	0.882 (0.029)	0.719 (0.045)	0.992 (0.160)
Average	0.691 (0.040)	1.002 (0.016)	0.834 (0.015)	0.943 (0.016)	0.795 (0.023)	1.312 (0.138)

Release sites	Capture Probabilities						$\lambda$ BON-RICE Is.
	LGR	LGS	LMN	McN	JDA	BON	
<b>RAPH</b>	0.511 (0.004)	0.487 (0.005)	0.462 (0.006)	0.244 (0.007)	0.164 (0.009)	0.063 (0.013)	0.015 (0.003)
<b>CLWRNF</b>	0.397 (0.004)	0.359 (0.004)	0.316 (0.005)	0.349 (0.008)	0.123 (0.007)	0.085 (0.015)	0.017 (0.003)
<b>KNOXB</b>	0.470 (0.004)	0.487 (0.005)	0.488 (0.007)	0.216 (0.007)	0.176 (0.009)	0.086 (0.015)	0.023 (0.004)
<b>IMNAHW</b>	0.447 (0.006)	0.518 (0.007)	0.47 (0.009)	0.266 (0.011)	0.189 (0.013)	0.126 (0.025)	0.031 (0.007)
<b>LOOH</b>	0.493 (0.004)	0.470 (0.005)	0.417 (0.007)	0.258 (0.009)	0.188 (0.011)	0.111 (0.017)	0.039 (0.006)
Average	0.473 (0.019)	0.463 (0.026)	0.434 (0.031)	0.280 (0.026)	0.167 (0.012)	0.096 (0.010)	0.026 (0.005)

**Table 6:** Estimates of project survival (product of reach survivals from LGR to BON), Snake-Middle Columbia reach survival (product of reach survivals from LGR to McN), Lower Columbia reach survival (product of reach survivals from McN to BON) and associated standard errors, for 1998 and 1997 releases of PIT-tagged hatchery chinook yearlings. Annual weighted averages were based on equation 2.

YEAR	Release Site	LGR-BON		LGR-McN		McN-BON	
		Survival	SE	Survival	SE	Survival	SE
1997	<b>PAHP</b>	0.645	0.730	0.943	0.119	0.684	0.773
1997	<b>LOOH</b>	0.665	0.519	0.630	0.048	1.057	0.814
1997	<b>KNOXB</b>	1.310	2.387	0.779	0.089	1.682	3.066
1997	Weighted Average	0.731	0.145	0.729	0.087	1.019	0.201
1998	<b>RAPH</b>	1.269	0.287	0.844	0.028	1.503	0.336
1998	<b>CLWRNF</b>	0.824	0.169	0.772	0.025	1.068	0.215
1998	<b>KNOXB</b>	0.956	0.181	0.808	0.030	1.183	0.219
1998	<b>IMNAHW</b>	0.738	0.164	0.789	0.035	0.935	0.205
1998	<b>LOOH</b>	0.507	0.086	0.711	0.027	0.713	0.119
1998	Weighted Average	0.821	0.126	0.787	0.022	1.041	0.131
	Weighted Average	0.819	0.095	0.783	0.022	1.041	0.099

1998. The weighted average for the eight LGR-McN survival estimates was 0.819, with an estimated standard error of 0.095.

The decomposition of the system-wide survival estimates into two survival estimates (one for the LGR-McN reach, and the other for the McN-BON reach) showed that the average estimates for LGR-McN were slightly larger than 0.78 (Table 6). The 95% confidence intervals were relatively tight: (0.585 – 0.872) for 1997, (0.75 – 0.824) for 1998. On the other hand, the average estimates for McN-BON were larger than one with extremely broad confidence intervals (0.689 – 1.349 for 1997 and 0.826 – 1.257 for 1998).

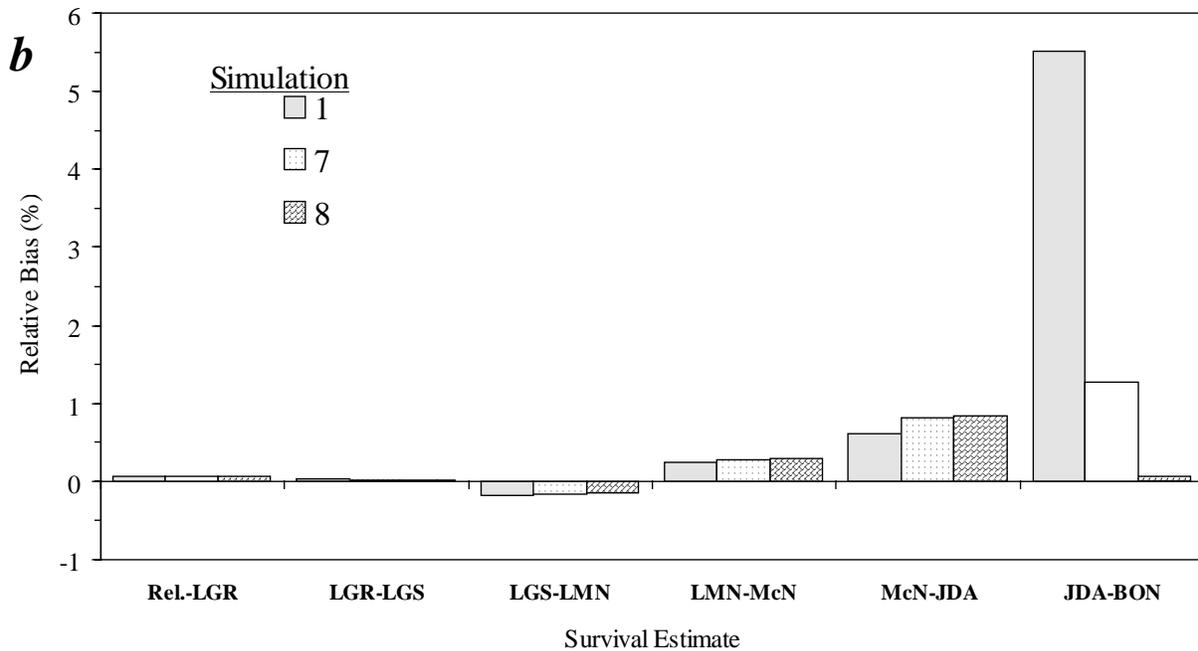
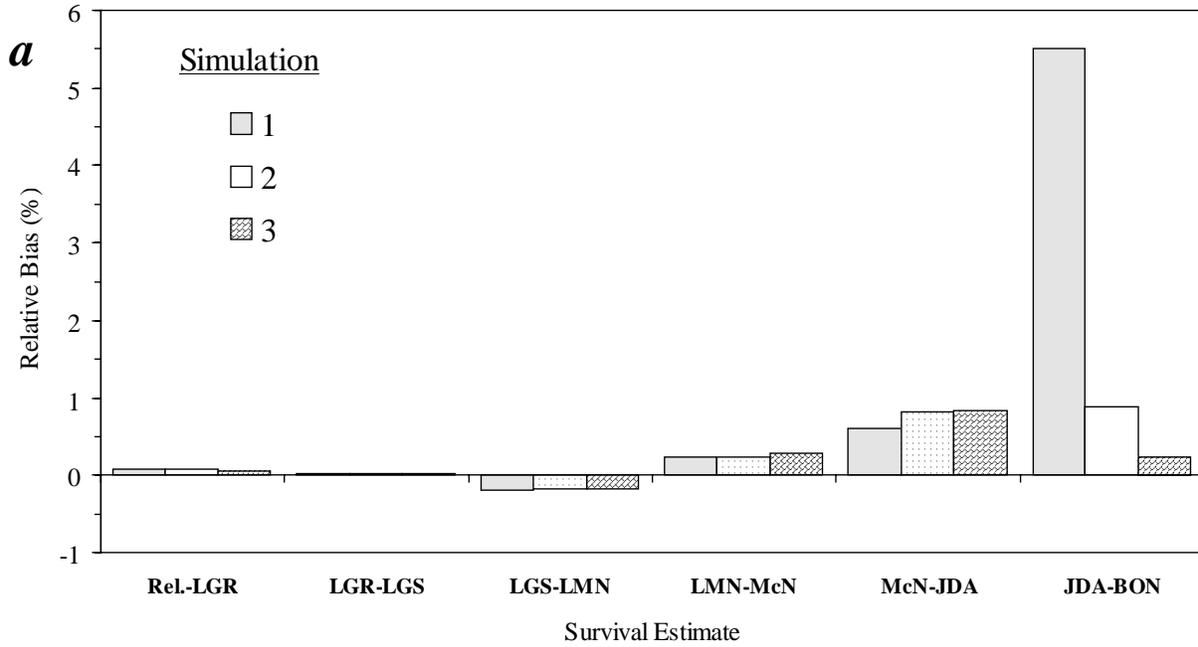
### 3.2 Possible sources of bias

The fact that the estimates of  $S_{\text{JDA-BON}}$ , and to a lesser extent of  $S_{\text{McN-JDA}}$ , were greater than one (Table 4 and 5) determined the large annual averages of  $S_{\text{McN-BON}}$  (Table 6), and hints about the existence of positive bias due to departures from assumptions 1-7.

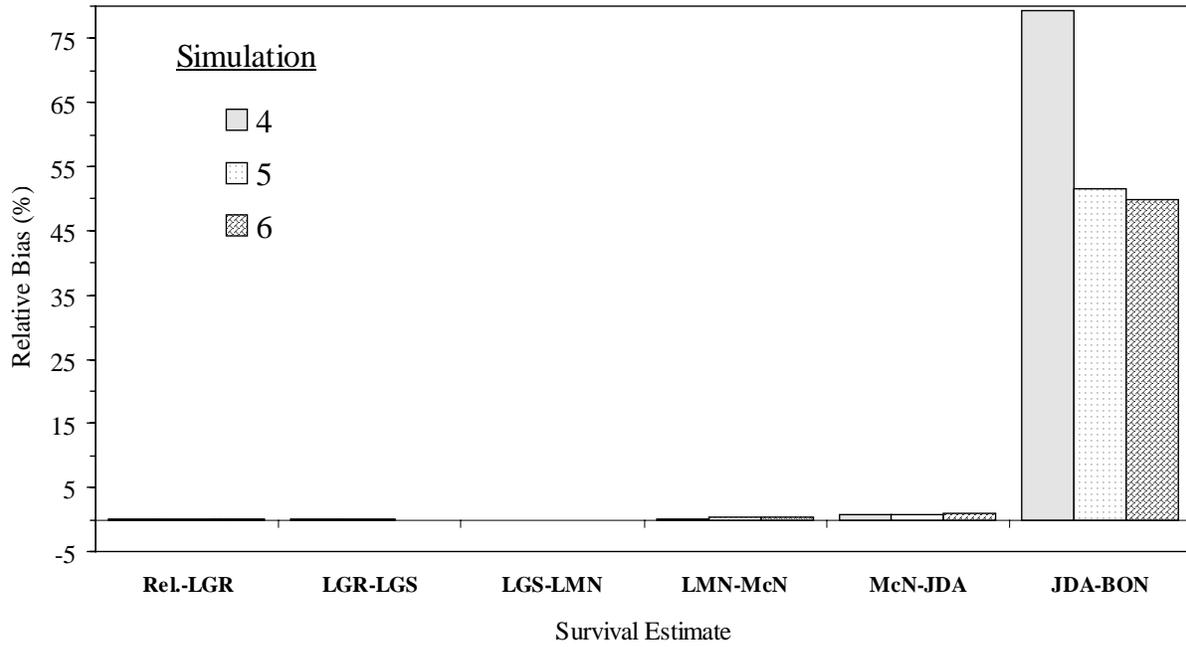
Our simulation results for Scenarios 1-3 indicated that when predation by terns and cormorants occurred only in the last reach and there was neither scavenging, post-detection mortality or transportation, reach survival estimates for the upper reaches (i.e., LGR-LGS, LGS-LMN and LMN-McN) were practically unbiased (Fig. 6a, Tables A.1-A.3). Survival estimates for McN-JDA presented only a very small positive bias ( $\%B \leq 0.81\%$ ). This bias was the probable result of the low rates used to model detection at JDA and BON ( $p_{\text{JDA}} = 0.15$ ,  $p_{\text{BON}} = 0.1$ ). On the other hand, survival estimates for JDA-BON could be as high as 5.5%, whenever bird predation, tag-deposition and tag-recovery rates were low (Table A.I.1). Moderate tag-deposition and tag-recovery rates reduced the relative percent bias to 1.3%, and higher rates made it almost undetectable (Fig. 6b, Tables A.I.7-A.I.8). The addition of bird predation to the BON-McN reach increased the relative percent bias of the survival estimates for JDA-BON considerably ( $\%B \approx 50 - 79\%$ ), but did not affect the estimates for other reaches (Fig. 7, Tables A.I.4-A.I.6).

The addition of scavenging to moderate and high bird predation rates produced a minor increase (e.g., 0.55% for  $M_{\text{BON-Rice}} = 0.5$ ) in the relative percent positive bias of JDA-BON survival estimates (Fig. 8, Tables A.I.9-A.I.10). On the other hand, the addition of an uncensored post-detection mortality of 0.1 at Bonneville dam produced increases of 11.6-10.1% in the

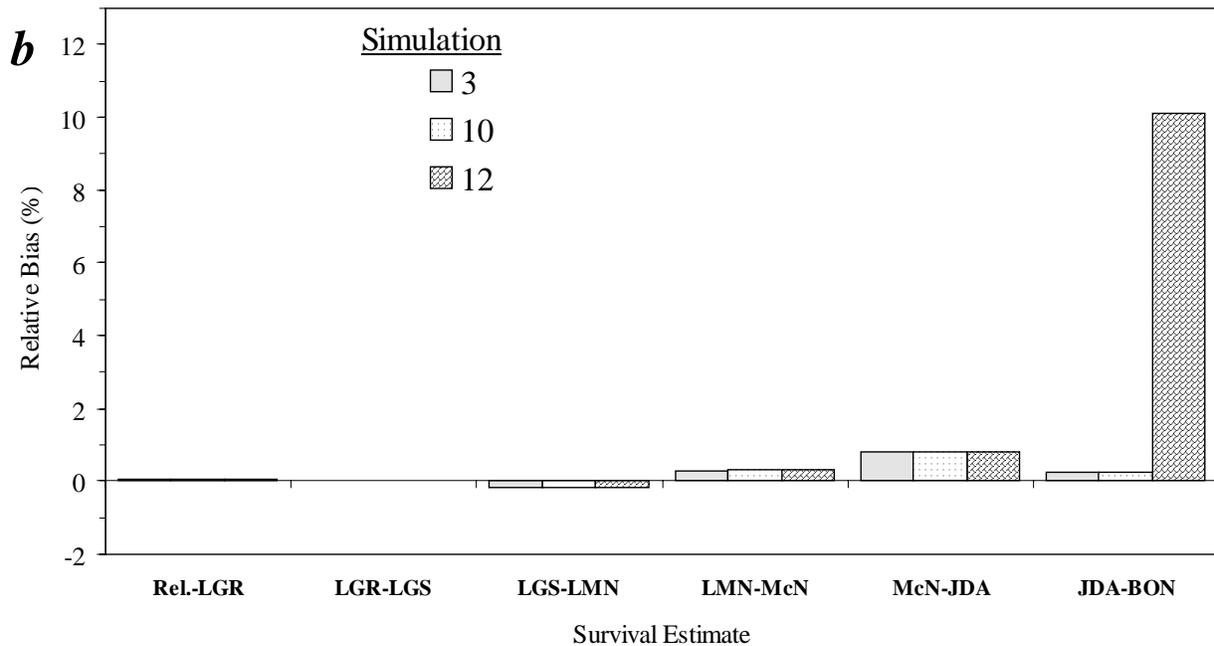
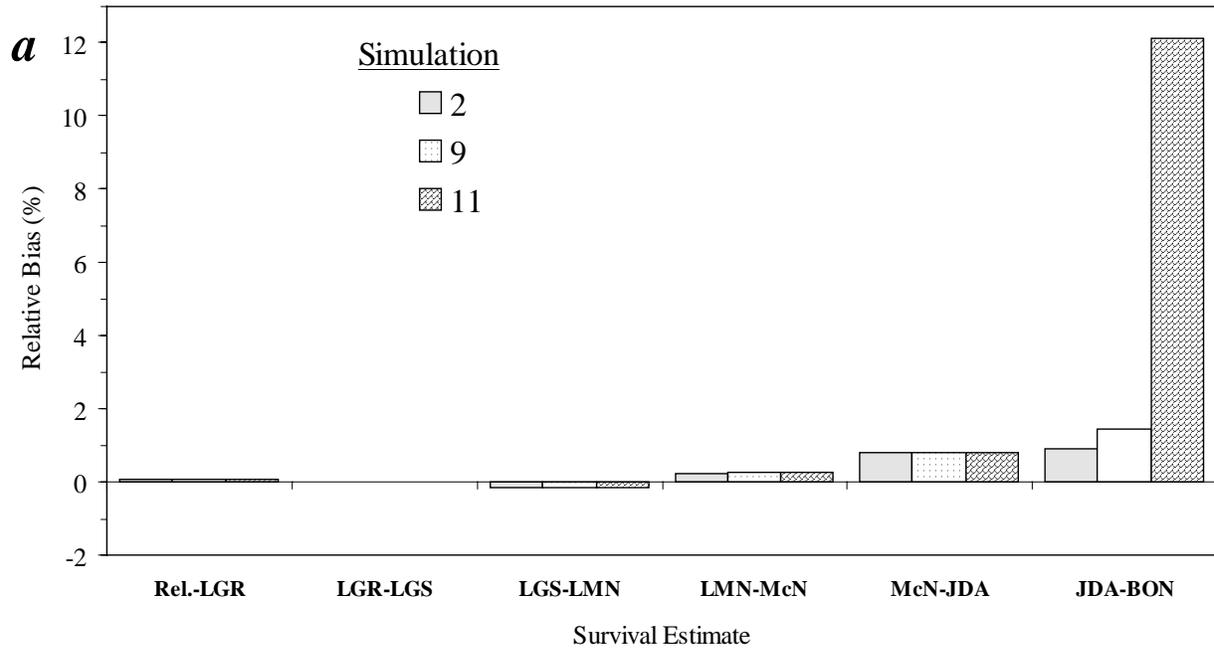
**Figure 6:** Bias in the survival estimates for a seven-reach system with predation by terns and cormorants in the last reach. **a)** Effect of different predation rates ( $M_{\text{BON-Rice}} = 0.25, 0.5$  and  $0.8$ ) with low tag-deposition ( $R_D = 0.7$ ) and recovery rates ( $R_R = 0.2$ ; see Appendix, Simulations 1-3). **b)** Effect of different tag-deposition ( $R_D = 0.7, 0.8$  and  $0.95$ ) and tag-recovery rates ( $R_R = 0.2, 0.4$  and  $0.7$ ) with a low predation rate ( $M_{\text{BON-Rice}} = 0.25$ , see Appendix, Simulations 1, 7 and 8). In all cases, fish were not transported, and there was no scavenging or post-detection mortality.



**Figure 7:** Bias in the survival estimates for a seven-reach system with predation by terns and cormorants in the last two reaches (Appendix, Simulations 4-6;  $M_{\text{BON-Rice}} = 0.25, 0.5$  and  $0.8$ ;  $M_{\text{JDA-BON}} = 0.5 M_{\text{BON-Rice}}$ ). In all cases, fish were not transported, and there was no scavenging or post-detection mortality. Tag-deposition and recovery rates were low.



**Figure 8:** Bias induced by tern scavenging and post-detection mortality, in the survival estimates for a seven-reach system, when: **(a)** the mortality due to terns was  $M_{\text{BON-Rice}} = 0.5$  (Appendix, Simulations 2, 9 and 11), and **(b)** the mortality due to terns was  $M_{\text{BON-Rice}} = 0.8$  (Appendix, Simulations 3, 10 and 12). In all cases, fish were not transported.



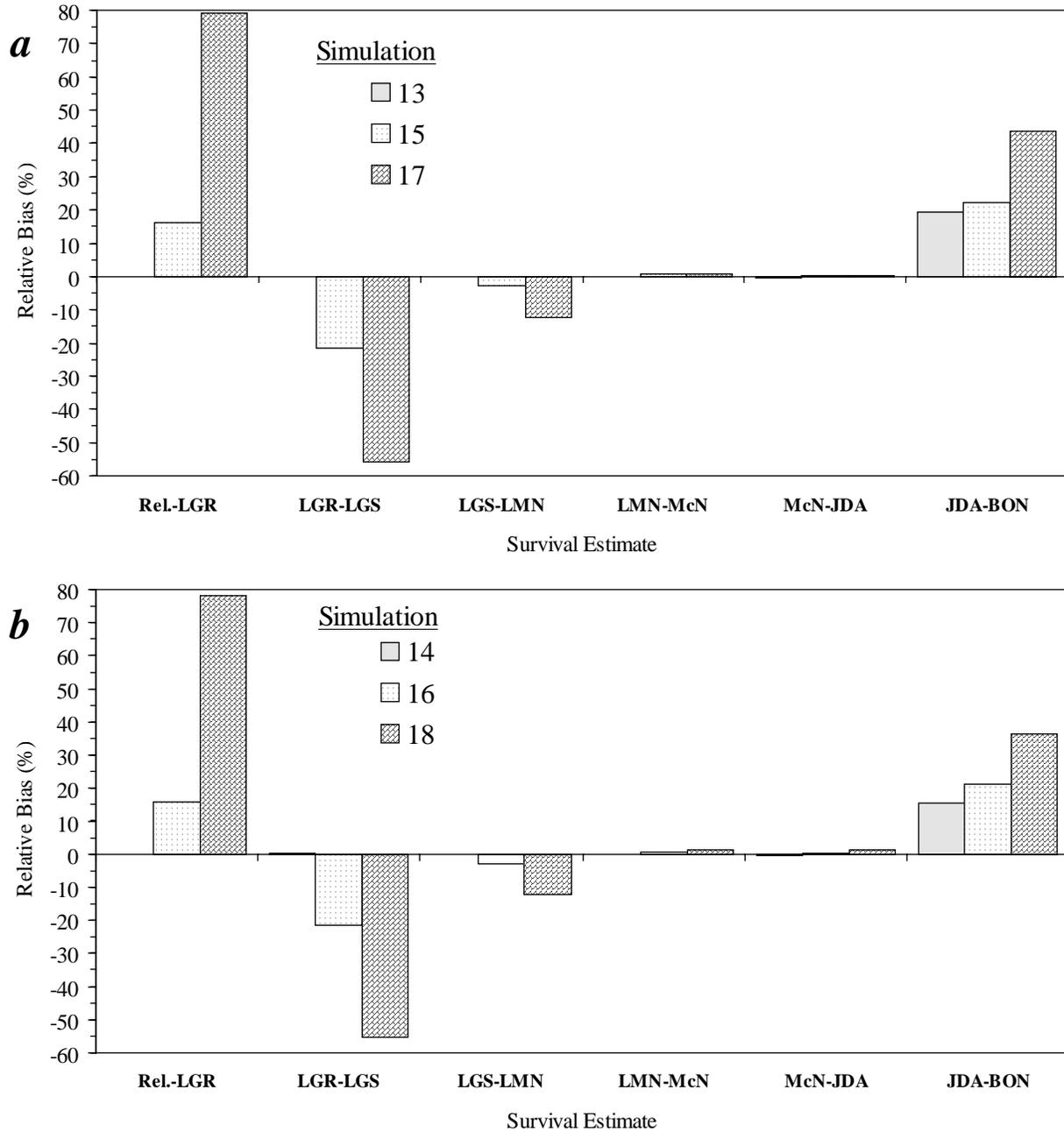
relative percent bias of JDA-BON survival estimates (Fig. 8, Tables A.11-A.12). In both situations, the estimates for other reaches remained practically unchanged.

The location where bird predation took place, the scavenging of previously dead PIT-tagged fish and the presence of uncensored post-detection mortality were not the only sources of bias detected. Our results from Scenarios 13-18 suggested that any failure to correctly censor transported fish (i.e.,  $T_R < 1$ ) could also produce biased survival estimates (Fig. 9, Tables A.13-A.18). Not only the survival estimates for the Lower Columbia reaches would be positively biased, but also the estimates for the upper reaches would be biased. Those for Rel.-LGR would be positively biased while those for LGR-LGS and LGS-LMN would be negatively biased. For example, if 10% of the fish transported from LGR, LGS, LMN and McN were not censored, the relative percent bias of the JDA-BON, McN-JDA, LMN-McN and Rel.-LGR survival estimates would increase by 5.5%, 0.7%, 0.7% and 16%, respectively, over those of a fully censored system (scenario 14). The relative percent bias of the LGR-LGS and LGS-LMN survival estimates, on the other hand, would decrease by 21% and 3%, respectively (Fig. 9b).

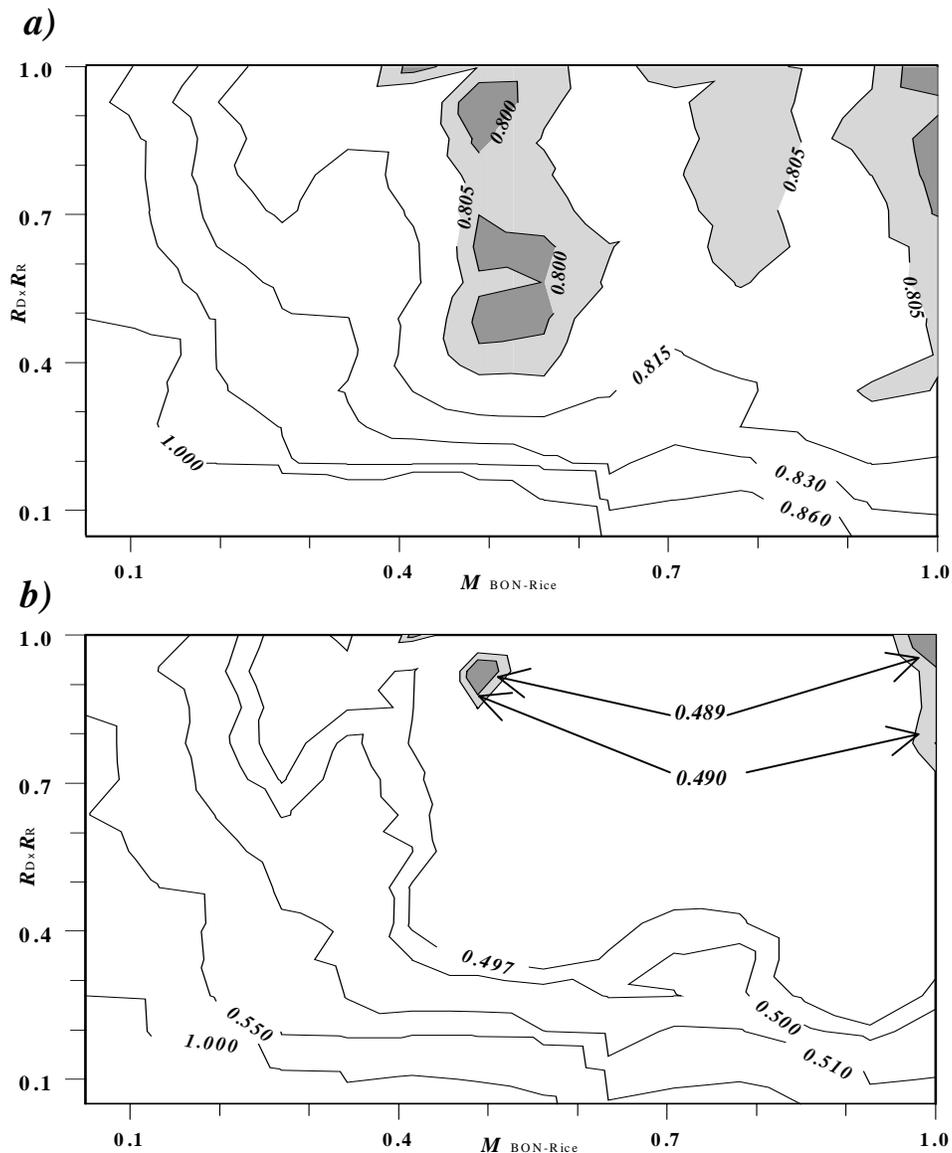
Consequently, only when the predation by terns and cormorants occurs at the last reach, at moderate to high rates ( $M_{\text{BON-Rice}} \geq 0.4$ ;  $M_{\text{Rel.-BON}} = 0$ ), with moderate to high tag-deposition and tag-recovery rates ( $R_D \times R_R \geq 0.4$ ), and absence of scavenging, uncensored post-detection mortality, and uncensored transported fish ( $T_R = 1$ ), will the reach and system survival estimates be relatively unbiased (Fig. 10).

Our simulations indicate that only high tag-deposition and recovery rates ( $R_D \times R_R$ ), together with high levels of bird predation nearby Rice Island ( $M_{\text{BON-Rice}}$ ) could produce a relatively unbiased  $\hat{S}_{\text{JDA-BON}}$  (Fig. 6b and 10a). However achieving high levels of  $R_D \times R_R$  and  $M_{\text{BON-Rice}}$  in a near future may be unfeasible. Whether the recovery rate  $R_R$  could eventually be increased by improving PIT-tag recovery efforts at Rice Island, the tag-deposition rate  $R_D$  and avian predation rate  $M_{\text{BON-Rice}}$  are likely to be reduced if the methods to discourage nesting by terns on Rice Island are successful (Collis et al., 1999). Recent studies on avian predation on Lower Columbia juvenile salmonids (Roby et al., 1998; Collis et al., 1999) provided maximum and minimum estimates for the number of chinook smolts consumed by the Caspian tern colony of Rice Island ( $\hat{C}$ ) in 1997 and 1998 (2,194,259-6,636,981 and 8,593,004-4,303,054, respectively). These preliminary estimates allowed us to get

**Figure 9:** Transport-induced bias in the survival estimates for a seven-reach system, when: **(a)** the mortality due to terns was  $M_{\text{BON-Rice}} = 0.5$  (Appendix, Simulations 13, 15 and 17), and **(b)** the mortality due to terns was  $M_{\text{BON-Rice}} = 0.8$  (Appendix, Simulations 14, 16 and 18). In all cases, the probabilities that a detected fish is transported were  $T_{\text{LGR-BON}} = 0.75$ ,  $T_{\text{LGS-BON}} = 0.25$ ,  $T_{\text{LMN-BON}} = 0.05$ ,  $T_{\text{McN-BON}} = 0.05$ , and transported fish were reported with probabilities  $T_{\text{R}} = 1$ ,  $T_{\text{R}} = 0.9$  and  $T_{\text{R}} = 0.5$ .



**Figure 10:** Contour plots of survival estimates for a seven-reach system as function of bird predation  $M_{\text{BON-Rice}}$  and the product of tag deposition ( $R_D$ ) and recovery ( $R_R$ ) rates. **(a)** Average reach survival estimates ( $\bar{S}_{\text{JDA-BON}}$ ). **(b)** Average hydro-system survival estimates ( $\bar{S}_{\text{LGR-BON}}$ ). In both cases, data correspond to the averages of 100 simulations of releases of 50,000 PIT-tagged fish for a hydro-system with the reach survivals, detection and transport probabilities of Table 3. The simulations assumed bird predation bellow Bonneville Dam with no post-detection mortality or scavenging by birds, and all transported fish censored. The shadowed areas in the plots indicate proximity to the true survival values ( $S_{\text{JDA-BON}} = 0.8$  and  $S_{\text{LGR-BON}} = 0.489$ ).



**Table 7:** Rough estimates of Caspian tern predation rates on chinook smolts ( $M_{\text{BON-Rice}}$ ).

$\hat{N}_{\text{R}_{\text{aBON}}}$  and  $\hat{N}_{\text{R}_{\text{bBON}}}$  are the estimated number of chinook smolts released on Columbia river tributaries above and bellow Bonneville Dam;  $\hat{N}_{\text{T}}$  is the estimated number of transported chinook smolts;  $\hat{S}_{\text{T}}$  is the estimated survival of transported chinook smolts;  $\hat{S}_{\text{Rel-LGR}}$  and  $\hat{S}_{\text{LGR-BON}}$  are the average survival estimates from Tables 4-6 and  $\hat{S}_{\text{Rel-Rice}}$  is a guessed value for the survival of the fish released bellow Bonneville Dam between its release site and some 21 km off Rice Island.  $\hat{C}$  is the estimated number of chinook smolts consumed by the Caspian tern colony of Rice Island in 1997 and 1998 (Roby et al., 1998; Collis et al., 1999).  $\hat{N}_{\text{R}_{\text{aBON}}}$  and  $\hat{N}_{\text{R}_{\text{bBON}}}$  were obtained from RMIS (Regional Mark Information System), and  $\hat{N}_{\text{T}}$  and  $\hat{S}_{\text{T}}$  were obtained from FPC (Fish Passage Center).

YEAR	1997		1998	
	<i>Low</i>	<i>Upper</i>	<i>Low</i>	<i>Upper</i>
$\hat{C}$	2,194,259	6,636,981	4,303,054	8,539,004
$\hat{N}_{\text{R}_{\text{aBON}}}$	44,229,094	44,229,094	65,774,779	65,774,779
$\hat{N}_{\text{R}_{\text{bBON}}}$	35,984,649	35,984,649	22,020,631	22,020,631
$\hat{N}_{\text{T}}$	5,764,029	5,764,029	10,788,779	10,788,779
$\hat{S}_{\text{T}}$	0.9994	0.9994	0.9994	0.9994
$\hat{S}_{\text{Rel-Rice}}$	0.523	0.523	0.691	0.691
$\hat{S}_{\text{LGR-BON}}$	0.729	0.729	0.821	0.821
$\hat{S}_{\text{Rel-Rice}}$	0.800	0.500	0.800	0.500
$\hat{M}_{\text{BON-Rice}}$	0.046	0.182	0.076	0.170

rough estimates of the rates of Caspian tern predation ( $M_{\text{BON-Rice}}$ ) for 1997 and 1998. To this end, we utilized the formula:

$$\hat{M}_{\text{BON-Rice}} = \frac{\hat{C}}{(\hat{N}_{\text{R}_{\text{aBON}}} \times \hat{S}_{\text{Rel-LGR}} - \hat{N}_{\text{T}}) \times \hat{S}_{\text{LGR-BON}} + (\hat{N}_{\text{T}} \times \hat{S}_{\text{T}}) + \hat{N}_{\text{R}_{\text{bBON}}} \times \hat{S}_{\text{Rel-Rice}}}, \quad (3)$$

where  $\hat{N}_{\text{R}_{\text{aBON}}}$  and  $\hat{N}_{\text{R}_{\text{bBON}}}$  are the estimated number of chinook smolts released on Columbia river tributaries above and bellow Bonneville Dam;  $\hat{N}_{\text{T}}$  is the estimated number of transported chinook smolts;  $\hat{S}_{\text{T}}$  is the estimated survival of transported chinook smolts;  $\hat{S}_{\text{Rel-LGR}}$  and  $\hat{S}_{\text{LGR-BON}}$  are the average survival estimates from Tables 4-6 and  $\hat{S}_{\text{Rel-Rice}}$  is a guessed value for the survival of the fish released bellow Bonneville Dam between its release site and some 21 km off Rice Island. The results of these rough calculations (Table 7) suggest that, at least for Caspian terns and chinook smolts,  $M_{\text{BON-Rice}}$  might have been smaller than  $0.20^2$ . If this was actually the case, PIT-tag recovery efforts at Rice Island should be increased considerably in order to attain levels of  $R_{\text{D}} \times R_{\text{R}}$  that could provide a considerable reduction in bias of  $\hat{S}_{\text{JDA-BON}}$  (Fig. 10a).

## 4. DISCUSSION

The recent availability of PIT tags recoveries from Rice Island, together with the also recent installation of PIT-tag interrogation systems at John Day and Bonneville Dams raised the prospect of obtaining survival estimates for the Lower Columbia reaches, as well as system-wide survival estimates. However, our results (Tables 4-6) suggest that these estimates should be handled cautiously because they might be biased. The use of tags recovered from Rice Island in survival estimation imposes a series of extra assumptions, and our simulations suggest that the CJS model may not be robust to departures from these assumptions.

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<sup>2</sup> The actual level of bird predation on chinook smolts nearby Rice Island may be larger than 0.2, because the piscivorous colonies of double-crested cormorant and Californian, glaucous-winged and western gulls (*Larus californicus*, *L. glaucescens* and *L. occidentalis*) that breed on Rice Island were not included in Table 7.

When compared to previous estimates (e.g., Table 4 in Hockersmith et al., 1998), our survival estimates for the reaches of the Snake River, with values ranging from 0.77 to 1 and overall weighted average  $\overline{\hat{S}}_{\text{LGR-McN}} = 0.785$ , appear reliable enough. Nonetheless, the estimates for the Lower Columbia River reaches, with values ranging from 0.45 to 2.2 and overall average  $\overline{\hat{S}}_{\text{McN-BON}} = 1.267$ , look less reliable. The preponderance of values larger than one among the survival estimates for JDA-BON, and to a lesser extent McN-BON, suggests the possible presence of bias in the CJS estimation (Tables 4 and 5).

Our simulations suggest that positively biased survival estimates may arise in the JDA-BON and McN-BON reaches at least under six situations:

- 7) If bird predation occurs not only nearby Rice Island, but also in reaches upstream BON.
- 8) Whenever bird predation rates nearby Rice Island are low.
- 9) Whenever the tag-deposition rate at Rice Island and the tag recovery rates are low.
- 10) If terns and cormorants eat tagged fish that have died from causes other than bird predation.
- 11) Whenever there is uncensored post-detection mortality at Bonneville or other detection sites.
- 12) Whenever transported fish have not been correctly censored.

Only when the predation by terns and cormorants occurred bellow Bonneville Dam at moderately to high rates, without scavenging of previously dead fish, and when post-detection mortality and all transported fish were correctly censored, will reach survival estimates be relatively unbiased, depending on the rates at which tags were deposited on and recovered from Rice Island (Fig. 10).

Of the six possible sources of bias investigated in our simulations, the bias caused by transported fish going uncensored is less likely to have affected our JDA-BON and McN-BON reach survival estimates. Although transported fish are rarely reported as such in the PTAGIS database, the PIT-tag data used in our estimations (Tables 4 and 5) was carefully censored after tracking the passage of tagged fish through the various PIT-tag detector coils of each dam (Table 1).

It is also improbable that the bias suggested by the preponderance of reach survival estimates larger than one was due to bird predation occurring in reaches upstream BON, scenario depicted in simulations 4-6. For a Rice Island tern to feed in a reach upstream BON it would have to fly too long a distance in each foraging trip. For example, a tern nesting at Rice Island

need to fly at least 244 km to reach JDA dam, and 350 km to reach McN dam. Despite the scant information on the foraging radius of breeding terns, these distances appeared too extreme. The only published radio-telemetry study on Caspian terns suggest that adult terns do not forage in predictable patterns, and that at least the breeding terns of Lake Ontario may fish at least 2.5 km offshore (Sirdevan and Quinn, 1997). On the other hand, pairs of common (*Sterna hirundo*) and Aleutian tern (*Sterna aleutica*) are known to occupy and defend feeding territories that may be more than 20 and 56 km away from their respective breeding colonies (Ehrlich et al., 1988). Moreover, radio-tracked common tern may have feeding trips lasting on average 115 min that cover about 30 km each, with a mean radius of 6.3 km (Becker et al., 1993). In Oklahoma, least terns (*Sterna antillarum*) were observed to fish 12 km away from their salt-flat colonies (Schweitzer and Leslie, 1996), while South African little terns (*Sterna albifrons*) seem to prefer feeding in the vicinity of turbid plumes of estuarine water, some 5 km offshore (Cyrus, 1991). The only, and recently completed, study on avian predation on Lower Columbia juvenile salmonids (Collis et al., 1999) reported that aerial surveys indicated that the foraging activity of Caspian terns was mostly centered around the Rice Island colony site, with 90% of all terns seen off-colony within 21 km of Rice Island. Consequently, the breeding terns and cormorants of Rice Island are unlikely to have fed in the Bonneville pool or above. Instead, the high survival estimates in the JDA-BON reach appear consistent with variation in the level of avian predation nearby Rice Island, and in tag-deposition and recovery rates. Also but to a lesser extent, scavenging of smolts that died from causes other than bird predation, and uncensored post-detection mortality at the interrogation sites may have contributed to the perceived bias.

Preliminary calculations of the predation rate of chinook smolts by the Caspian terns of Rice Island suggest low predation levels ( $M_{\text{BON-Rice}} \leq 0.2$ ) for both 1997 and 1998 (Table 7). Then, if we assume the absence of scavenging and uncensored post-detection mortality, it is likely that most of the bias in  $\hat{S}_{\text{JDA-BON}}$  and  $\hat{S}_{\text{LGR-BON}}$  may have been due to low values of tag-deposition ( $R_D$ ) and tag-recovery ( $R_R$ ) rates (Fig. 10). That  $R_D \times R_R$  may have been low both in 1997 and 1998 appeared corroborated by the low percentages of chinook smolt PIT tags detected at Bonneville Dam and subsequently found on the tern and cormorant colonies on Rice Island (see Fig.15 in Collis et al., 1999).

Our simulations (scenarios 9 and 10) suggest that scavenging of smolts that died from causes other than bird predation may have contributed, albeit meagerly, to the bias in  $\hat{S}_{\text{JDA-BON}}$  (Fig. 8). This scarce contribution to bias, and the present lack of evidence for scavenging behavior among the Lower Columbia piscivorous waterfowl (Roby et al., 1998; Collis et al., 1999), suggest that scavenging may not have been an important source of bias in the CJS estimates of Tables 4-5. On the other hand, the relative contribution of uncensored post-detection mortality ( $P_{M_{\text{BON}}}$ ) to the bias in  $\hat{S}_{\text{JDA-BON}}$  appears more serious.

The addition of an uncensored post-detection mortality of 0.1 at Bonneville Dam may increase the relative percent bias of  $\hat{S}_{\text{JDA-BON}}$  some 12-10%. Our survival estimates (Tables 4-5) might have been partially affected by uncensored post-detection mortality. Although the data (Table 1) was censored by using the mortality tables reported by PTAGIS, these reported mortalities do not necessarily account for all facility and raceway mortality in the customarily monitored Snake River dams (Verhey et al., 1998, page 43). Moreover, Bonneville Dam was rarely monitored for facility and raceway mortality in 1997 and 1998. For example, only 1.4% of all dead chinook smolts reported in 1997-98 came from Bonneville Dam, a relatively small proportion when contrasted to the 44.3% and 35.9% reported at LGR and LGS. Currently, there is no available estimate for  $P_{M_{\text{BON}}}$ . However, studies using paired PIT-tagged release groups and balloon-tagged groups have been conducted to measure post-detection bypass survivals at the three Snake River dams LGR, LGS and LMN (Muir et al., 1995, 1996 and Normandeau et al., 1996). Using the weighted average<sup>3</sup> of all available post-detection bypass survival estimates, we estimated the 95% confidence interval for post-detection mortality as 0.072-0.019. Thus, if the post-detection mortality at Bonneville Dam was similar to that encountered at the Snake River dams, our simulation scenarios that used  $P_{M_{\text{BON}}} = 0.1$  may have been rather extreme, and the expected added bias may have been smaller than the one generated by simulations 11 and 12.

In conclusion, low bird predation rates nearby Rice Island ( $M_{\text{BON-Rice}} \leq 0.2$ ), accompanied by low tag-deposition and detection rates ( $R_{\text{D}} \times R_{\text{R}} \leq 0.4$ ) and unknown levels of uncensored post-detection mortality were the most likely causes for bias in  $\hat{S}_{\text{JDA-BON}}$ , and to a

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<sup>3</sup> Weights were inversely proportional to the estimated variances.

lesser extent in  $\hat{S}_{\text{McN-JDA}}$  (Table 4 and 5). Little can be done at present to correct for these sources of bias, unless more detailed studies on bird predation by Rice Island bird breeding colonies is undertaken. These studies might employ radio-telemetry to determine the feeding radius of the birds, and should provide detailed estimates of the consumption of the various salmonid species by the different bird species breeding on and feeding nearby Rice Island. The studies could also assess the incidence with which terns, cormorants and Californian, glaucous-winged and western gulls feed upon fish previously dead. Moreover, PIT-tag recovery efforts at Rice Island and the reporting of all facility and raceway mortality in all Lower Columbia and Snake River dams should also be improved. Until such studies and tasks are implemented, the use of Rice Island PIT-tag recoveries must be treated cautiously in order not to inflate estimates of system-wide survival, and prematurely conclude that the hydrosystem mitigation activities have been completely successful.

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## 6. APPENDIX I: Bias assessment by means of simulations

**Table A.I.1:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 1. Simulation 1 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last reach ( $M_{\text{BON-Rice}} = 0.25$ ), and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0003	0.03	$p_{\text{LGS}}$	0.460	0.004	-0.0005	-0.10
$S_{\text{LGS-LMN}}$	0.828	0.011	-0.0015	-0.18	$p_{\text{LMN}}$	0.431	0.005	0.0011	0.25
$S_{\text{LMN-McN}}$	0.942	0.020	0.0022	0.23	$p_{\text{McN}}$	0.250	0.006	-0.0001	-0.04
$S_{\text{McN-JDA}}$	0.805	0.047	0.0048	0.61	$p_{\text{JDA}}$	0.150	0.009	-0.0005	-0.33
$S_{\text{JDA-BON}}$	0.844	0.234	0.0441	5.51	$p_{\text{BON}}$	0.101	0.025	0.0010	1.02
					$\lambda$	0.009	0.002	0.0001	1.64

**Table A.I.2:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

estimates for simulation 2. Simulation 2 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last reach ( $M_{\text{BON-Rice}} = 0.5$ ), and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.17	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.942	0.021	0.0023	0.24	$p_{\text{McN}}$	0.250	0.006	-0.0001	-0.05
$S_{\text{McN-JDA}}$	0.807	0.047	0.0065	0.81	$p_{\text{JDA}}$	0.149	0.009	-0.0008	-0.55
$S_{\text{JDA-BON}}$	0.807	0.155	0.0071	0.89	$p_{\text{BON}}$	0.102	0.017	0.0019	1.85
					$\lambda$	0.018	0.003	0.0004	2.01

**Table A.I.3:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 3. Simulation 3 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last reach ( $M_{\text{BON-Rice}} = 0.8$ ), and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.17	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.943	0.020	0.0028	0.29	$p_{\text{McN}}$	0.250	0.006	-0.0003	-0.10
$S_{\text{McN-JDA}}$	0.807	0.046	0.0066	0.83	$p_{\text{JDA}}$	0.149	0.009	-0.0009	-0.62
$S_{\text{JDA-BON}}$	0.802	0.107	0.0019	0.23	$p_{\text{BON}}$	0.101	0.013	0.0010	0.96
					$\lambda$	0.028	0.004	0.0004	1.33

**Table A.I.4:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 4. Simulation 4 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last two reaches ( $M_{\text{BON-Rice}} = 0.25$ ,  $M_{\text{JDA-BON}} = 0.175$ ), and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.17	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.942	0.021	0.0022	0.23	$p_{\text{McN}}$	0.250	0.006	-0.0001	-0.04
$S_{\text{McN-JDA}}$	0.806	0.047	0.0064	0.80	$p_{\text{JDA}}$	0.149	0.009	-0.0008	-0.54
$S_{\text{JDA-BON}}$	1.434	0.420	0.6342	79.27	$p_{\text{BON}}$	0.060	0.015	-0.0403	-40.28
					$\lambda$	0.009	0.002	-0.0048	-34.84

**Table A.I.5:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 5. Simulation 5 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last two reaches ( $M_{\text{BON-Rice}} = 0.5$ ,  $M_{\text{JDA-BON}} = 0.25$ ), and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.17	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.943	0.020	0.0027	0.28	$p_{\text{McN}}$	0.250	0.006	-0.0002	-0.09
$S_{\text{McN-JDA}}$	0.806	0.046	0.0064	0.80	$p_{\text{JDA}}$	0.149	0.009	-0.0009	-0.59
$S_{\text{JDA-BON}}$	1.214	0.235	0.4135	51.69	$p_{\text{BON}}$	0.068	0.011	-0.0322	-32.25
					$\lambda$	0.018	0.003	-0.0066	-27.14

**Table A.I.6:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 6. Simulation 6 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last two reaches ( $M_{\text{BON-Rice}} = 0.8$ ,  $M_{\text{JDA-BON}} = 0.4$ ), and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.010	-0.0012	-0.15	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.22
$S_{\text{LMN-McN}}$	0.943	0.020	0.0030	0.32	$p_{\text{McN}}$	0.250	0.006	-0.0004	-0.14
$S_{\text{McN-JDA}}$	0.807	0.043	0.0071	0.89	$p_{\text{JDA}}$	0.149	0.008	-0.0011	-0.76
$S_{\text{JDA-BON}}$	1.200	0.164	0.3998	49.98	$p_{\text{BON}}$	0.067	0.009	-0.0326	-32.56
					$\lambda$	0.028	0.004	-0.0108	-27.62

**Table A.I.7:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 7. Simulation 7 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last reach ( $M_{\text{BON-Rice}} = 0.25$ ), moderate tag deposition and recovery rates ( $R_D = 0.8$ ,  $R_R = 0.4$ ) and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.16	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.943	0.021	0.0025	0.27	$p_{\text{McN}}$	0.250	0.006	-0.0002	-0.08
$S_{\text{McN-JDA}}$	0.807	0.047	0.0066	0.82	$p_{\text{JDA}}$	0.149	0.009	-0.0009	-0.58
$S_{\text{JDA-BON}}$	0.810	0.146	0.0102	1.28	$p_{\text{BON}}$	0.101	0.017	0.0012	1.21
					$\lambda$	0.020	0.003	0.0003	1.34

**Table A.I.8:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 8. Simulation 8 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish by terns and cormorants at the last reach ( $M_{\text{BON-Rice}} = 0.25$ ), high tag deposition and recovery rates ( $R_D = 0.95$ ,  $R_R = 0.7$ ) and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.010	-0.0012	-0.15	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.22
$S_{\text{LMN-McN}}$	0.943	0.019	0.0028	0.30	$p_{\text{McN}}$	0.250	0.006	-0.0003	-0.13
$S_{\text{McN-JDA}}$	0.807	0.043	0.0068	0.85	$p_{\text{JDA}}$	0.149	0.008	-0.0011	-0.70
$S_{\text{JDA-BON}}$	0.801	0.100	0.0006	0.07	$p_{\text{BON}}$	0.101	0.011	0.0007	0.69
					$\lambda$	0.042	0.005	0.0004	0.91

**Table A.I.9:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 9. Simulation 9 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish ( $M_{\text{BON-Rice}} = 0.5$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0013	-0.16	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.942	0.021	0.0024	0.26	$p_{\text{McN}}$	0.250	0.006	-0.0002	-0.07
$S_{\text{McN-JDA}}$	0.806	0.047	0.0065	0.81	$p_{\text{JDA}}$	0.149	0.009	-0.0008	-0.56
$S_{\text{JDA-BON}}$	0.812	0.156	0.0115	1.44	$p_{\text{BON}}$	0.101	0.017	0.0013	1.27
					$\lambda$	0.019	0.003	0.0003	1.41

**Table A.I.10:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

estimates for simulation 10. Simulation 10 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish ( $M_{\text{BON-Rice}} = 0.8$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.17	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.943	0.020	0.0028	0.30	$p_{\text{McN}}$	0.250	0.006	-0.0003	-0.11
$S_{\text{McN-JDA}}$	0.806	0.046	0.0064	0.80	$p_{\text{JDA}}$	0.149	0.009	-0.0009	-0.60
$S_{\text{JDA-BON}}$	0.802	0.109	0.0020	0.25	$p_{\text{BON}}$	0.101	0.013	0.0010	1.01
					$\lambda$	0.029	0.004	0.0004	1.35

**Table A.I.11:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 11. Simulation 11 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish ( $M_{\text{BON-Rice}} = 0.5$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants, post-detection mortality ( $P_{\text{MBON}} = 0.1$ ) and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0013	-0.16	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.942	0.021	0.0024	0.26	$p_{\text{McN}}$	0.250	0.006	-0.0002	-0.07
$S_{\text{McN-JDA}}$	0.806	0.047	0.0065	0.81	$p_{\text{JDA}}$	0.149	0.009	-0.0008	-0.56
$S_{\text{JDA-BON}}$	0.897	0.189	0.0972	12.15	$p_{\text{BON}}$	0.092	0.017	-0.0078	-7.84
					$\lambda$	0.017	0.003	-0.0016	-8.71

**Table A.I.12:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 12. Simulation 12 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with predation of live fish ( $M_{\text{BON-Rice}} = 0.8$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants, post-detection mortality ( $P_{\text{MBON}} = 0.1$ ) and no fish transport. See Table 2 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.003	0.0005	0.07	$p_{\text{LGR}}$	0.460	0.003	0.0002	0.05
$S_{\text{LGR-LGS}}$	0.980	0.007	0.0002	0.02	$p_{\text{LGS}}$	0.460	0.004	-0.0004	-0.09
$S_{\text{LGS-LMN}}$	0.829	0.011	-0.0014	-0.17	$p_{\text{LMN}}$	0.431	0.005	0.0010	0.24
$S_{\text{LMN-McN}}$	0.943	0.020	0.0028	0.30	$p_{\text{McN}}$	0.250	0.006	-0.0003	-0.11
$S_{\text{McN-JDA}}$	0.806	0.046	0.0064	0.80	$p_{\text{JDA}}$	0.149	0.009	-0.0009	-0.60
$S_{\text{JDA-BON}}$	0.881	0.124	0.0809	10.11	$p_{\text{BON}}$	0.092	0.012	-0.0079	-7.91
					$\lambda$	0.026	0.004	-0.0024	-8.50

**Table A.I.13:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 13. Simulation 13 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with fish transport, predation of live fish ( $M_{\text{BON-Rice}} = 0.5$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and post-detection mortality ( $P_{\text{MBON}} = 0.1$ ). All transported fish were censored. See Table 3 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.004	0.0000	0.00	$p_{\text{LGR}}$	0.460	0.004	-0.0001	-0.02
$S_{\text{LGR-LGS}}$	0.981	0.011	0.0012	0.12	$p_{\text{LGS}}$	0.460	0.005	0.0001	0.02
$S_{\text{LGS-LMN}}$	0.828	0.012	-0.0017	-0.21	$p_{\text{LMN}}$	0.430	0.006	-0.0002	-0.04
$S_{\text{LMN-McN}}$	0.939	0.031	-0.0010	-0.11	$p_{\text{McN}}$	0.251	0.008	0.0008	0.33
$S_{\text{McN-JDA}}$	0.796	0.058	-0.0043	-0.53	$p_{\text{JDA}}$	0.152	0.011	0.0017	1.17
$S_{\text{JDA-BON}}$	0.955	0.311	0.1545	19.31	$p_{\text{BON}}$	0.091	0.022	-0.0093	-9.32
					$\lambda$	0.017	0.004	-0.0018	-9.87

**Table A.I.14:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

estimates for simulation 14. Simulation 14 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with fish transport, predation of live fish ( $M_{\text{BON-Rice}} = 0.8$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and post-detection mortality ( $P_{\text{MBON}} = 0.1$ ). All transported fish were censored. See Table 3 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.700	0.004	-0.0001	-0.01	$p_{\text{LGR}}$	0.460	0.004	-0.0001	-0.01
$S_{\text{LGR-LGS}}$	0.981	0.011	0.0012	0.13	$p_{\text{LGS}}$	0.460	0.005	0.0001	0.02
$S_{\text{LGS-LMN}}$	0.828	0.012	-0.0017	-0.20	$p_{\text{LMN}}$	0.430	0.006	-0.0002	-0.04
$S_{\text{LMN-McN}}$	0.939	0.031	-0.0009	-0.10	$p_{\text{McN}}$	0.251	0.008	0.0008	0.31
$S_{\text{McN-JDA}}$	0.798	0.060	-0.0024	-0.30	$p_{\text{JDA}}$	0.151	0.011	0.0014	0.95
$S_{\text{JDA-BON}}$	0.925	0.204	0.1248	15.60	$p_{\text{BON}}$	0.091	0.019	-0.0090	-9.01
					$\lambda$	0.026	0.005	-0.0027	-9.43

**Table A.I.15:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 15. Simulation 15 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with fish transport, predation of live fish ( $M_{\text{BON-Rice}} = 0.5$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and post-detection mortality ( $P_{\text{MBON}} = 0.1$ ). Ninety percent of the transported fish were censored. See Table 3 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.812	0.007	0.1121	16.01	$p_{\text{LGR}}$	0.396	0.004	-0.0638	-13.86
$S_{\text{LGR-LGS}}$	0.770	0.010	-0.2099	-21.42	$p_{\text{LGS}}$	0.452	0.005	-0.0083	-1.81
$S_{\text{LGS-LMN}}$	0.806	0.012	-0.0239	-2.88	$p_{\text{LMN}}$	0.428	0.007	-0.0025	-0.57
$S_{\text{LMN-McN}}$	0.945	0.036	0.0052	0.55	$p_{\text{McN}}$	0.247	0.010	-0.0026	-1.03
$S_{\text{McN-JDA}}$	0.802	0.064	0.0016	0.20	$p_{\text{JDA}}$	0.149	0.011	-0.0009	-0.59
$S_{\text{JDA-BON}}$	0.977	0.259	0.1771	22.13	$p_{\text{BON}}$	0.086	0.021	-0.0139	-13.88
					$\lambda$	0.017	0.004	-0.0026	-13.56

**Table A.I.16:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 16. Simulation 16 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with fish transport, predation of live fish ( $M_{\text{BON-Rice}} = 0.8$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and post-detection mortality ( $P_{\text{MBON}} = 0.1$ ). Ninety percent of the transported fish were censored. See Table 3 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	0.811	0.007	0.1113	15.91	$p_{\text{LGR}}$	0.397	0.004	-0.0634	-13.78
$S_{\text{LGR-LGS}}$	0.771	0.010	-0.2087	-21.30	$p_{\text{LGS}}$	0.451	0.005	-0.0085	-1.85
$S_{\text{LGS-LMN}}$	0.807	0.012	-0.0231	-2.78	$p_{\text{LMN}}$	0.427	0.007	-0.0031	-0.71
$S_{\text{LMN-McN}}$	0.946	0.035	0.0058	0.62	$p_{\text{McN}}$	0.247	0.009	-0.0031	-1.22
$S_{\text{McN-JDA}}$	0.803	0.061	0.0029	0.37	$p_{\text{JDA}}$	0.149	0.010	-0.0015	-1.00
$S_{\text{JDA-BON}}$	0.969	0.229	0.1691	21.14	$p_{\text{BON}}$	0.085	0.018	-0.0146	-14.59
					$\lambda$	0.025	0.006	-0.0043	-14.47

**Table A.I.17:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 17. Simulation 17 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with fish transport, predation of live fish ( $M_{\text{BON-Rice}} = 0.5$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and post-detection mortality ( $P_{\text{MBON}} = 0.1$ ). Fifty percent of the transported fish were censored. See Table 3 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	1.254	0.015	0.5543	79.19	$p_{\text{LGR}}$	0.257	0.003	-0.2030	-44.14
$S_{\text{LGR-LGS}}$	0.434	0.008	-0.5465	-55.76	$p_{\text{LGS}}$	0.420	0.005	-0.0396	-8.61
$S_{\text{LGS-LMN}}$	0.727	0.012	-0.1032	-12.43	$p_{\text{LMN}}$	0.419	0.006	-0.0113	-2.62
$S_{\text{LMN-McN}}$	0.946	0.028	0.0062	0.66	$p_{\text{McN}}$	0.240	0.007	-0.0095	-3.82
$S_{\text{McN-JDA}}$	0.802	0.060	0.0019	0.23	$p_{\text{JDA}}$	0.144	0.011	-0.0062	-4.13
$S_{\text{JDA-BON}}$	1.148	0.344	0.3481	43.51	$p_{\text{BON}}$	0.071	0.017	-0.0291	-29.13
					$\lambda$	0.017	0.004	-0.0059	-26.35

**Table A.I.18:** Average (Avg.), standard error (s.e.), bias (B.) and relative percent bias (i.e.,

$$\%B. = \frac{\hat{\theta} - \theta}{\theta} \times 100)$$

of survival ( $S$ ), capture-probability ( $p$ ), and terminal-probability ( $\lambda$ ) estimates for simulation 18. Simulation 18 consisted of 100 groups of 50,000 tagged fish released in a seven-reach system with fish transport, predation of live fish ( $M_{\text{BON-Rice}} = 0.8$ ) and scavenging of dead fish ( $S_{\text{CBON-Rice}} = 0.05$ ) by terns and cormorants and post-detection mortality ( $P_{\text{MBON}} = 0.1$ ). Fifty percent of the transported fish were censored. See Table 3 for parameter values.

	<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>		<b>Avg.</b>	<b>s.e.</b>	<b>B.</b>	<b>%B.</b>
$S_{\text{Rel-LGR}}$	1.247	0.015	0.5465	78.07	$p_{\text{LGR}}$	0.259	0.003	-0.2014	-43.79
$S_{\text{LGR-LGS}}$	0.437	0.008	-0.5426	-55.37	$p_{\text{LGS}}$	0.419	0.005	-0.0409	-8.88
$S_{\text{LGS-LMN}}$	0.730	0.012	-0.1005	-12.10	$p_{\text{LMN}}$	0.416	0.006	-0.0138	-3.21
$S_{\text{LMN-McN}}$	0.952	0.028	0.0121	1.28	$p_{\text{McN}}$	0.238	0.007	-0.0122	-4.88
$S_{\text{McN-JDA}}$	0.810	0.059	0.0098	1.22	$p_{\text{JDA}}$	0.141	0.010	-0.0090	-6.03
$S_{\text{JDA-BON}}$	1.091	0.220	0.2912	36.40	$p_{\text{BON}}$	0.071	0.013	-0.0288	-28.83
					$\lambda$	0.026	0.005	-0.0090	-26.00

## **7. APPENDIX II: Review comments and authors' reply**

### **7.1 Comments by Steve G. Smith (Northwest Fisheries Science Center), 11 Jan. 2000**

Here are some more detailed comments on your report "Appraisal of System-wide survival estimation of Snake River yearling chinook salmon using PIT-tags recovered from Caspian tern and double-crested cormorant breeding colonies on Rice Island" (November 1999 draft).

#### **General comments**

The report correctly identifies a problem arising when using data from PIT tags recovered on Rice Island in 1998 to estimate survival to Bonneville Dam using the Cormack Model for Snake River yearling chinook salmon that migrated in 1997 and 1998. We were aware of the high incidence of survival estimates greater than 100% from John Day Dam to Bonneville Dam, and the problem was also discovered by one PATH participant who independently worked with the data. Because of the problem we have not used the data (have not presented survival estimates below John Day Dam based on bird-colony data) for yearling chinook salmon for 1997 and 1998 in any report, memo, or paper.

The report details efforts to determine a systematic cause of the estimates in excess of 100%, using Monte Carlo simulation of three situations:

- 1) Tags recovered from islands in the estuary represent live fish taken by birds upstream of Bonneville Dam.
- 2) Tags recovered on islands represent fish that died from causes other than bird predation (i.e., dead fish were scavenged by birds).
- 3) Tagged fish transported from collector dams are not properly censored (i.e., identified as detected and returned to the river at the collector dam, rather than removed from further analysis.

I have concerns with the handling of all three situations.

Situation (1) and (3) would certainly cause problems with the Cormack Model, if they occurred, and the simulation results demonstrate the problems. However, as the report states in the discussion, it is clear that neither situation occurs in actuality (Rice Island birds don't fly

above Bonneville Dam and analysts take care not to incorrectly leave transported fish in the analysis). This conclusion could be made at the beginning of the report, and there would be no need to go through with the simulations of the two situations. (I also note that failing to censor transported fish at Lower Granite Dam, say, would bias Cormack estimates regardless of what piscivorous birds were doing 400 km downstream in the estuary).

Situation (2) bears investigation, and I agree that it merits the simulation study to see if it is a plausible cause of bias. The report concludes that bird scavenging on smolts that died from other causes is sufficient to cause the apparent observed bias, and it seems to imply that it is the most likely (only?) possible cause. I have attempted to replicate the results, writing my own version of a simulation program, and have been unable to repeat the result. In my simulations with parameters that replicate those in the report, survival estimates to Bonneville Dam remain unbiased whenever a PIT-tag recovery on Rice Island means that the fish that carried the tag survived to the tailrace Bonneville Dam. It made no difference if the recovered tag came from a fish that was taken live or from a fish that died from some other cause between Bonneville Dam and Rice Island and was then scavenged. (Actually, scavenging increased the precision of the estimates by increasing the sampling rate below Bonneville Dam).

Other scenarios that I simulated that were not considered for the report, lead me to believe the observed estimates in excess of 100% were far more likely due to some combination of two causes:

- 1) post-detection mortality at Bonneville Dam (i.e., mortality that occurred to bypassed/detected fish but not to non-bypassed fish; and
- 2) a mathematical consequence of low sampling rates at Bonneville Dam (i.e., low detection rates) and at Rice Island (i.e., low predation/scavenging/deposit/recovery rates).

You didn't consider either of these possibilities in your report, so I'll explain my reasoning in detail.

The effect of post-detection mortality on the data is the same as failure to properly censor transported fish. Fish that ought to be removed at the dam of transport/bypass mortality (traditional capture history "2") are left in the analysis as if they were returned alive to the tailrace (capture history "1"). Consequently, the proportion of "1"s that are detected again

downstream is incorrectly decreased relative to the proportion of “0'S” that are detected downstream. This leads to detection probability estimates that are too low, which in turn leads to survival estimates that are too high.

After the 1998 migration season and before the 1999, a new \$16 million juvenile bypass system for the 2<sup>nd</sup> powerhouse was completed. I have been told (personal communication with NMFS biologists on site) that gulls were thick at the outfall of the old system, and nearly absent from the outfall of the new system in 1999, suggesting the possibility of post-detection mortality problems in 1997 and 1998 data.

To complete the task relatively quickly, I used a considerably simpler simulation scenario than in your report: releases in the tailrace of The Dalles Dam, with only two detection sites downstream; Bonneville Dam and the bird colonies. By simplifying, I focused attention on the reach in which problems occurred in real data, and made the investigation easier to manage. (I also simulated releases in the tailrace of McNary Dam to verify that the same patterns occurred for John Day-to-Bonneville survival when upstream reaches were added).

My second proposed cause of estimates that are too high results from the asymmetry of the distribution of estimated survival probabilities. The cause of the asymmetry is easily seen in my simplified 2-reach simulations. In that scenario, estimated survival from release to Bonneville Dam is:

$$\hat{S} = \frac{P_{\text{det}}}{\hat{P}}, \text{ where } P_{\text{det}} \text{ is the proportion of fish detected at Bonneville Dam (product}$$

survival probability and conditional detection probability) and  $\hat{P}$  is the estimated detection probability at Bonneville Dam. The detection probability is estimated using tags that are recovered in the bird colonies. If sampling rates in the estuary are low, then the detection probability estimate is relatively imprecise. Though the distribution of estimated detection probability from the simulations might be symmetric around its mean, the distribution of estimated survival probability would not be. For example, if the mean detection probability is 0.10, then estimates of 0.05 and 0.15 are symmetric about the mean. However, their reciprocals are not symmetric about the reciprocal of the mean (numbers are 6.7, 10, 20). The effect on the survival estimate is that errors on the positive side of the true parameter value tend to be greater

than errors on the negative side.

If I am correct, the implication is that the median value of the distribution of survival estimates should be reported along with the mean. (In my simulations with no post-detection mortality but low sampling rates, the median was always near the true parameter value of 0.8, even when the mean of the distribution was as high as 1.00 solely because of this mathematical phenomenon.)

Finally, I note that none of the parameter combinations used in the reported simulations resulted in recovery rates at the bird colonies as low as those observed in the actual data. Tables 4 and 5 show that all estimates of  $\lambda$  were on the order of 1% to 4%. Yet the mean estimates in the appendix tables indicate that the effective simulated value was around 10% (the lowest mean estimate of  $\lambda$  was 8.1%). With recovery rates that low, you start getting into the situation where you can't estimate every parameter every time. However, I think parameter estimates are pretty sensitive in the low end of the range of sampling rates, and I would have liked to see at least a few simulations in that range.

### **Specific and editorial comments**

- 1) Title – I suggest indicating the years 1997 and 1998.
- 2) Page v. paragraph 1 line 3 – I believe LGR-BON is meant here, not LGR-McN.
- 3) Page vi. Management implications, last sentence. – Perhaps the apparent innuendo could be removed by using a sentence more like “If Rice Island recoveries are used to estimate system-wide survival for migrant yearling chinook salmon in 1997 and 1998, the resulting estimates are likely positively biased.” To the best of my knowledge, nobody has presented such estimates. NMFS has, however, presented estimates based on bird island recoveries for steelhead in 1997, 1998, and 1999 and for yearling chinook salmon in 1999. If the intention is to cast doubt on all estimates derived from bird island recoveries, I suggest adding a second sentence to that effect to the one suggested above.
- 4) Page vi. Recommendations, line 1 – “possibly” should be “possible”.
- 5) Page 6 paragraph 2, -second sentence – Censoring is necessary more because transported fish do not contribute any information on in-river survival below the point of transport than because they have different survival probabilities. I guess that the concern here is that the

tag from an incorrectly censored transported fish could end up in the bird colony. A clearer statement of this possibility and the effect it would have on data would help. However, given the low sampling rate by the predacious birds, I think the effect of failing to censor would be much greater on survival estimates in reaches immediately below the transport dam than on the JDA-BON estimate.

- 6) Page 6, paragraph 2 -third sentence – Should be more explicit here. Certainly, transported fish are identified as such because detectors, installed on the lines that lead to barges directly detect them. Do you mean that fish aren't detected on the barge?
- 7) Page 6, paragraph 2 – Here you've stated that "many" survival studies (including all of ours) correctly censor all transported fish, and then to be cautious about it, censor some that probably don't need to be. Is there really a reason to simulate a scenario that doesn't occur in actual analyses? Or if you want to caution people about censoring transported fish, is a report on PIT-tag recoveries from bird colonies the right forum for the message?
- 8) Page 10, assumption 1 – this is more an issue of representativeness than of bias. For estimation of survival for the group of tagged fish, it matters not one bit what happens to untagged fish.
- 9) Page 10 assumption 5 – again, this is always critically important, and it is not made clear why it is more than routinely important in the case of using Rice Island recoveries.
- 10) Bottom page 10 – the  $T_R$  parameters should be defined and valued here, so that they appear in the text before Figure 5 and Tables 2 and 3.
- 11) Page 14 last paragraph – Now that  $T_R$  is defined, I'm wondering what a non-zero value for  $T_{BON}$  means.
- 12) Tables 5 and 6 – For some of the estimates greater than 1.0 the standard errors look very suspicious to me. I don't think I've ever seen an estimate greater than 1.0 with such small standard errors – 95% confidence intervals in almost every case I've seen have included 1.0. Certainly the standard errors on my own estimates for the 1998 hatchery releases are not close to what is reported (e.g., 1998 Rapid River S(JDA-BON) is reported as 1.824 with s.e. 0.060; my calculations gave 1.445 with s.e. 0.241).
- 13) Page 18, paragraph 1 – Methods for confidence intervals should be given – the interval cited for 1998 does not include the point estimate!

## 7.2 Authors' response to Steve G. Smith's comments

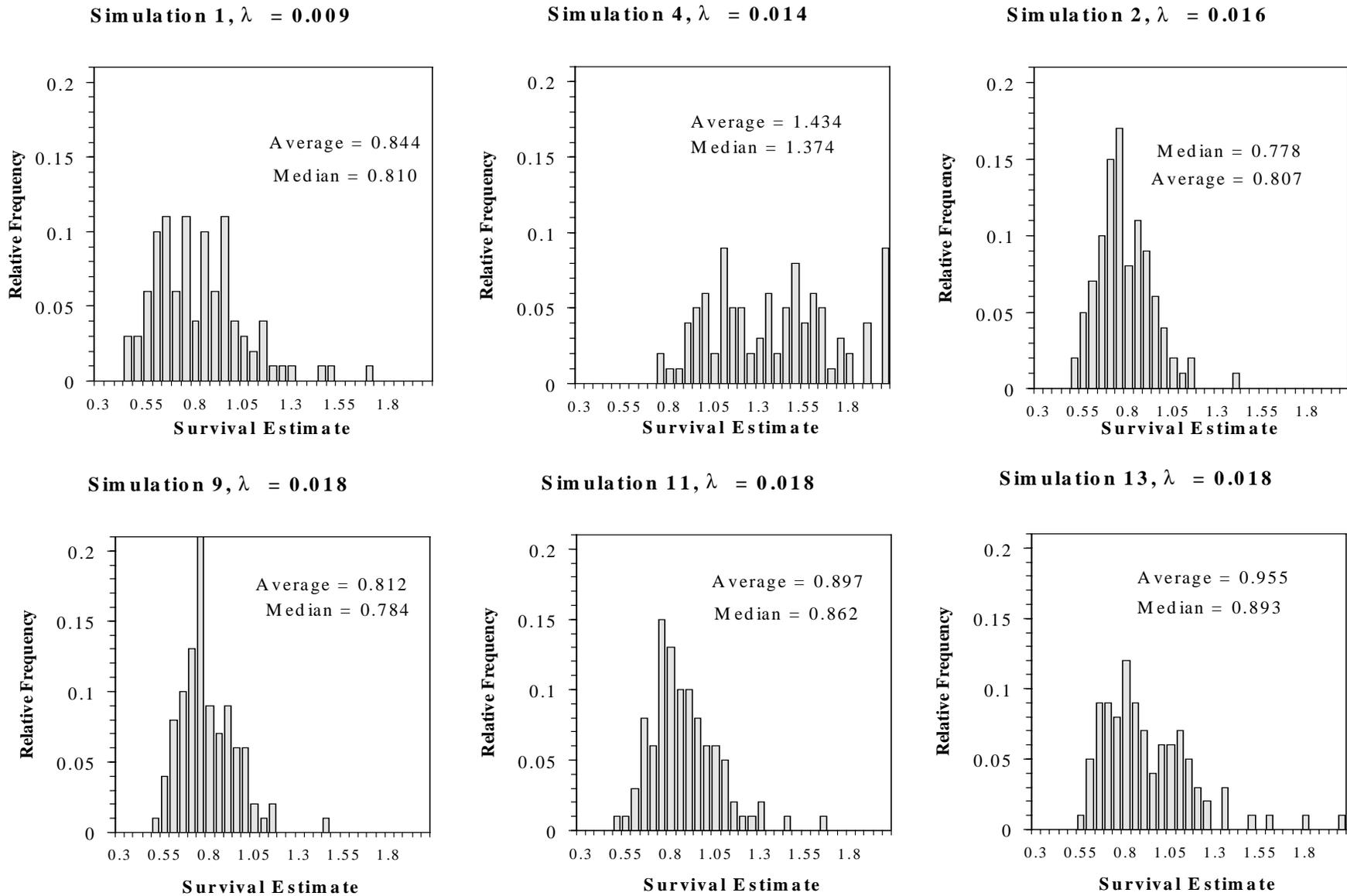
We thank Steve G. Smith for his very detailed review of our manuscript. We have produced a new manuscript where all his specific and editorial comments have been accounted for.

With respect to his general comments on the causes for survival estimates greater than 1, we redid our simulations and modify the original program to specifically incorporate post-detection mortality as well as the effect of different predation rates and tag-deposition and tag-recovery rates. In particular, we tried to mimic the  $\lambda$  values obtained in the analysis of the 1997-98 data. In our new simulations, we still kept some scenarios showing the effects of bird predation on reaches upstream Bonneville dam, and of uncensored transported fish for the sake of generalization.

The results of our new simulations that allowed for a separation of post-detection mortality and scavenging suggested a considerably reduced contribution of scavenging to the bias in reach survival estimates, and a more important contribution of uncensored post-detection mortality. Finally, the trial of various levels of predation, tag-deposition and tag-recovery rates showed the very important role of these rates in biasing Cormack's survival estimates.

Finally, with respect to the mathematical consequences of low sampling rates at Bonneville Dam, we agree that the distribution of the estimated P's was symmetric around the mean but the distribution of the estimated JDA-BON reach survivals was not. However, the use of the median instead of the average did not appear to reduce the estimated bias in the degree suggested by S.G. Smith. As an example, the Figure A.II.1 shows the distributions of the estimated JDA-BON reach survivals for the six scenarios with the lowest terminal-probabilities ( $\lambda$ ). Granted, in the six cases the median was smaller than the average but in none of them was so close to the true value ( $S_{\text{JDA-BON}} = 0.8$ ) as to require a modification in the definition of estimated bias. Figure A.II.2 shows the detection probability estimates at Bonneville Dam for the reach survival estimates of Fig. A.II.1. The distributions of  $\hat{P}_{\text{BON}}$  are considerably more symmetric than those of  $\hat{S}_{\text{JDA-BON}}$ , with both average and median very close to the true value  $P_{\text{BON}} = 0.1$ .

**Figure A.II.1:** Distributions of 100 survival estimates ( $\hat{S}_{\text{JDA-BON}}$ ) from the six scenarios with lowest terminal-probability ( $\lambda$ ).



**Figure A.II.2:** Distributions of 100 detection probability estimates ( $\hat{P}_{\text{BON}}$ ) from the six scenarios with lowest terminal-probability ( $\lambda$ ).

