Cumulative Effects of Colonial Waterbird Predation on the Survival of Juvenile Upriver Bright Fall Chinook Salmon: A Retrospective Analysis

Prepared for: Pacific Salmon Commission Chinook Technical Committee

Prepared by: Quinn Payton and Allen Evans
Real Time Research, Inc.
1000 SW Emkay Dr., Bend, OR 97702

Jeffrey Fryer and Tommy Garrison
Columbia River Inter-Tribal Fish Commission
700 NE Multnomah St, Suite 1200
Portland, OR 97232

Citation: Q. Payton, A. Evans, J. Fryer, and T. Garrison. 2020. Cumulative effects of colonial waterbird predation on the survival of juvenile Upriver Bright fall Chinook salmon: A Retrospective Analysis. Draft Technical Report submitted to the Pacific Salmon Commission Chinook Technical Committee in partial fulfillment of Agreement No. C19-10. Once finalized, available on-line at: www.birdresearchnw.org

Table of Contents

Summary

To investigate the cumulative effects of avian predation on fish mortality and to determine what proportion of all sources of fish mortality were due to avian predation, we conducted a mark–recapture–recovery analysis on juvenile (smolt) Upriver Bright (URB) fall Chinook Salmon *Oncorhynchus tshawytscha* that were PIT-tagged and released in the Hanford Reach of the Columbia River, USA. We used a state–space Bayesian model that incorporated live detections of tagged fish during out-migration and recoveries of dead tagged fish on up to 13 different piscivorous avian colonies to jointly estimate predation and survival probabilities over an 11-year study period (2008-2018). Results indicated that avian predation probabilities (proportion of available fish consumed) on URB fall Chinook smolts were highly variable depending on the predator species (Caspian tern *Hydroprogne caspia*, double-crested cormorant *Phalacrocorax auritus*, California gull *Larus californicus*, ring-billed gull *L. delawarensis*, or American white pelican *Pelecanus erythrorhynchos*), the location of the colony, and the rearing-type (hatchery, wild) of the fish. Estimates of cumulative predation (predation by all colonies combined) indicated birds annually consumed 0.064 (95% credible interval = 0.055 – 0.076) to 0.413 (0.353 – 0.474) of available tagged fish during out-migration from the Hanford Reach to the Pacific Ocean, with predation probabilities often higher on wild Chinook smolts compared to hatchery Chinook smolts. Results indicated that avian predation annually accounted for 8.6% (6.7 – 11.8) to 42.8% (34.3 – 52.6) of all sources of smolt mortality (1-survival) during out-migration to Bonneville Dam, the furthest downstream dam URB fall Chinook smolts encountered during seaward migration. Collectively, results indicated that the cumulative effects of avian predation on URB fall Chinook smolts were substantial in some, but not all, river reaches and years.

Recoveries of fish PIT tags on bird colonies, coupled with mark-recapture-recovery models, may increase the accuracy and precision of survival estimates in juvenile salmonids. To investigate, we conducted a simulation study that compared URB fall Chinook smolt survival estimates from a standard, Cormack-Jolly-Seber (CJS) model to the joint mortality and survival (JMS) model that was used to estimate predation and survival as part of this study. Results indicated that the JMS model provided survival estimates with less absolute and maximum bias and more precise uncertainty intervals, with better parameter coverage, than CJS model estimates. By using recoveries of PIT tags on bird colonies, the JMS model was also able to estimate survival during smolt out-migration throughout the entire Columbia River Power System to the lower Columbia River estuary. Collectively, results indicated that the JMS model increased the precision of survival estimates, reduced the magnitude of bias, and allowed for the generation of survival estimates across larger spatial-scales compared with the CJS model.

Several data gaps and critical uncertainties were identified as part of this study. More specifically, additional research is needed to investigate which biological and environmental factors were associated with the high levels of variation observed in hatchery and wild URB Chinook smolt predation probabilities. Additional research is also needed to estimate what proportion of consumed PIT tags by American white pelicans are subsequently deposited on breeding colonies. Without this information, predation estimates by pelicans could be biased to an unknown degree. Finally, efforts to scan all piscivorous avian breeding sites for fish tags each year are needed to generate accurate estimates of the cumulative effects of avian predation on smolt mortality in the Columbia River basin.

Introduction

Identifying factors that affect the survival of juvenile salmonids *Oncorhynchus spp.* is necessary to develop effective management plans. Recent research suggests that avian predation is a factor limiting the survival of some salmonid populations in the Columbia River basin (Evans et al. 2016; Evans et al. 2019; Payton et al. 2019). Multiple colonial waterbird species nest in the region and previous research indicates that Caspian terns *Hydroprogne caspia*, double-crested cormorants *Phalacrocorax auritus*, California gulls *Larus californicus*, ring-billed gulls *L. delawarensis,* and American white pelicans *Pelecanus erythrothynchos* are the principal avian predators of juvenile salmonids during seaward migration (Evans et al. 2012; Evans et al. 2016). Avian breeding colonies are located on numerous nesting sites (generally islands) spread throughout the Columbia River, with colony sizes ranging from less than a 100 breeding pairs to well over 10,000 pairs per colony, depending on the avian species and year (Collis et al. 2002; Adkins et al. 2014). The timing of the breeding season (April to September) also coincides with the peak salmonid smolt outmigration period (April to August), making most anadromous salmonids in the Columbia River susceptible to predation by colonial waterbirds (Adkins et al. 2014; Evans et al. 2016).

Previous studies indicate that individual bird colonies can consume a large number and proportion of available juvenile (smolt) salmonids. For instance, Roby et al. (2003) estimated that Caspian terns nesting on Rice Island in Columbia River estuary consumed between 8.1 – 12.4 million smolts (Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka* and Steelhead Trout *O. mykiss* combined) annually, while Lyons (2010) estimated that double-crested cormorants nesting on East Sand Island, also located in the estuary, consumed between 2.4 – 15.0 million smolts annually. In a study of avian predation probabilities (proportion of available fish consumed), Evans et al. (2016) estimates that California and ring-billed gulls nesting on Miller Rocks Island, located in The Dalles Reservoir on the lower Columbia River, consumed between 2 – 10% of available smolts, depending on the salmonid species and year. Evans et al. (2019) estimated that Caspian terns nesting on Goose Island in Potholes Reservoir, located adjacent to the Columbia River, consumed more than 20% of the available smolts in some years. Previous research has largely focused on the impacts of piscivorous birds from specific breeding colonies on fish mortality, but some salmonid populations must migrate through the foraging ranges of breeding birds from multiple colonies during seaward migration. The system-wide, cumulative impact of multiple piscivorous colonial waterbirds on smolt survival, however, is largely unknown, but may be substantial given the high impacts documented by individual colonies (Evans et al. 2019).

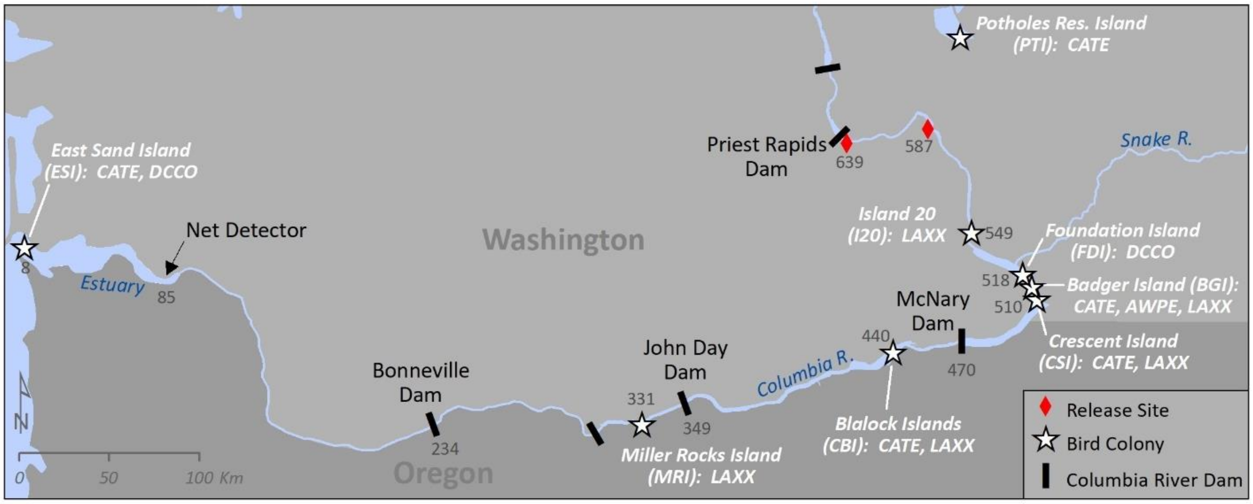
Studies involving Upriver Bright (URB) fall Chinook Salmon from the Hanford Reach of the Columbia River have been on-going since 1987 (Fryer 2019). Upriver Bright fall Chinook are one of the most productive Chinook Salmon stocks in the Pacific Northwest (Langness and Reidinger 2003, Harnish et al. 2013). The stock is important to both regional and international commercial ocean fisheries and local sport and tribal fisheries. The stock is also an integral part of the culture of Columbia River Tribes that rely on salmon for ceremonial, subsistence, and economic reasons. Tagging studies involving URB fall Chinook rely on releasing fish and then using subsequent recapture and recovery events to estimate fish behavior and survival (Fryer 2019; FPC 2019). Although results of these studies provide critical information, the specific causes of URB fall Chinook mortality, particularly mortality of juveniles, remain largely unknown (Harnish et al. 2014). As such, having a better understanding of the effects of avian predation on URB fall Chinook mortality may be important for identifying and developing effective management plans. In addition to avian predation, salmonid smolts are subject to numerous other non-avian sources of mortality during out-migration (e.g., hydroelectric dam passage, predation by piscivorous fish, disease, and other factors; Ward et al. 1995; Muir et al. 2001; Dietrich et al. 2011; Harnish et al. 2014) and determining to what degree avian predation limits smolt survival relative to these other sources of mortality is also critical for prioritizing management actions for URB fall Chinook Salmon and other salmonid species and populations in the Columbia River basin (Evans e al. 2016; Evans et al. 2019).

To investigate the cumulative effects of avian predation and, in turn, determine what proportion of total mortality (1-survival) was due to avian predation, we conducted a mark-recapture-recovery analysis on hatchery and wild (i.e., naturally produced) URB fall Chinook that were tagged with passive integrated transponder (PIT) tags and released on the Columbia River. Data were from an historical dataset of tag detection histories of live fish and recoveries of tags from dead fish on bird colonies. Survival and predation probabilities were estimated in multiple river reaches, with predation from Caspian terns, double-crested cormorants, American white pelicans, California and ring-billed gulls nesting at up to 13 individual breeding colonies. Collectively, results provide a comprehensive, system-wide evaluation of the cumulative effects of avian predation on the survival of UCR fall Chinook at different spatial- and temporal-scales across an 11-year study period (2008-2018).

Finally, recently developed state-space Bayesian models allows for the incorporation of recoveries of fish tags from bird colonies to generate more accurate and precise estimates of juvenile salmonid survival in the Columbia River basin (Hostetter et al. 2018; Payton et al. 2019). For instance, recoveries of smolt PIT-tags on bird colonies can be used to increase detection rates of fish following release, detections that provide additional information to evaluate spatially-explicit survival during smolt out-migration. These models may be especially important in cases where sample sizes of tagged fish are small and/or where recapture probabilities are low (Hostetter et al. 2018). To assess the effectiveness and quantify the informational value provided by the incorporation of tag recoveries in URB fall Chinook, we conducted a statistical simulation study comparing and contrasting estimates of survival as generated from a standard CJS capture-recapture model (based on live detections of tagged fish) to those of a capture-recapture-recovery model (based on live and dead detections of tagged fish). Comparisons involved several measures of accuracy and precision of survival estimates for out-migrating wild URB fall Chinook smolts, the rear-type with smallest average annual sample sizes of PIT-tagged fish included in the study.

Methods

Study Area – We investigated predation and survival of both hatchery and wild URB fall Chinook smolts marked with PIT tags during 2008-2018. Hatchery fish were released at the Priest Rapids Hatchery downstream of Priest Rapids Dam (Map 1). Wild fish were captured and in the Hanford Reach between River kilometer (Rkm) 557 and 639 and released at Rkm 576 or 587 downstream of Priest Rapids Dam (Map 1). Following release, survival and predation were evaluated through four river reaches or sections of the Columbia River: (1) release to McNary Dam, (2) McNary Dam to John Day Dam, (3) John Day Dam to Bonneville Dam, and (4) Bonneville Dam to the Pacific Ocean (Map 1). River reaches were defined by the location of PIT tag detection sites and the location of bird colonies capable of foraging on tagged fish within each river reach (see also Evans et al. 2019). Smolt survival and predation through Reaches 1 - 3 were estimated based on detections of live fish passing in-river PIT tag arrays and recoveries of tags from dead fish on bird colonies. Smolt predation in Reach 4 was also based on recoveries of dead fish on bird colonies on East Sand Island in the Columbia River estuary, however, survival could not be estimated in Reach 4 due to a lack of PIT tag detection sites downstream of East Sand Island at the mouth of the Columbia River (Map 1). Smolt survival to adulthood (i.e., smolt-to-adult returns) were estimated based on detections of tagged URB fall Chinook that returned to Bonneville Dam fishways one to five years following release as a smolt.



Map 1. Mark-recapture-recovery locations of PIT-tagged hatchery and wild fall Chinook released downstream of Priest Rapids Dam during 2008-2018. Release sites included the Priest Rapids Hatchery and the Hanford Reach section of the Columbia River. Recapture locations include McNary Dam, John Day Dam, Bonneville Dam, plus a net detection system in the lower Columbia River. Recovery locations include Caspian tern (CATE), double-crested cormorant (DCCO), California and ring-billed gull (LAXX), and American white pelican (AWPE) bird colonies. Distances represents river kilometers from the Pacific Ocean.

Mark-Recapture-Recovery – Hatchery URB fall Chinook from Priest Rapids Hatchery (PRH) and wild fish captured in the Hanford Reach (HR) were PIT-tagged and released annually during 2008-2018. Following tagging, fish were measured (fork-length, mm) and allowed to recover from handling before being released (see also Fryer 2019). Release dates varied based on rear-type and year. In most years (2009-2016), hatchery fish were released during a two-week period in the latter half of June, except for 2017-2018, when fish were released during a four-week period from mid-May to mid-June. Wild fish were released during a one-week period in early June in all years.

Following release, a proportion of tagged URB Chinook were detected (volitionally recaptured) at downstream detection sites equipped with PIT tag arrays (a series of antennas). Arrays were located at the McNary Dam (Rkm 470), John Day Dam (Rkm 349), and Bonneville Dam (Rkm 234) juvenile bypass fish facilities and at a vessel towed pair-trawl net detection system in the lower Columbia River (Rkm 75; Map 1). Adult Chinook returning to the Columbia River following ocean residency were detected at arrays located in fishways at Bonneville Dam one to five years following release as a smolt (Map 1). Recapture records were retrieved from the PIT Tag Information System (PTAGIS), a regional mark, recapture, recovery database maintained by Pacific States Marine Fisheries Commission.

Following release, a proportion of tags implanted in URB fall Chinook were also recovered on bird colonies (i.e., dead fish). Colonies included in the study were those previously identified as posing a potential threat to juvenile salmonids during out-migration (Evans et al. 2012; Evans et al. 2016). Bird species and colonies included Caspian terns (CATE) nesting on (1) Potholes Reservoir Islands, (2) Badger Island, (3) Crescent Island, (4) Central Blalock Islands, and (5) East Sand Island; California and ring-billed gulls (LAXX) nesting on (6) Island 20, (7) Badger Island, (8) Crescent Island, (9) Central Blalock Islands, and (10) Miller Rocks Island; double-crested cormorants (DCCO) nesting on (11) Foundation Island and (12)

East Sand Island; American white pelicans nesting on (13) Badger Island (Map 1). The methods of Evans et al. (2012) were used to recover PIT tags from each bird colony. In brief, portable PIT tag antennas were used to detect tags after birds dispersed from their breeding colonies in August–October. The entire land area occupied by nesting birds were scanned for tags following each breeding season, with a minimum of two complete sweeps or passes of each colony site conducted each year. The land area occupied by birds during each breeding season was determined based on aerial images and/or ground surveys of the colony taken during the peak nesting season (see also Adkins et al. 2014).

Not all PIT tags ingested by avian predators were deposited on the bird's nesting colony (i.e., deposition probabilities were less than 1.0) and not all deposited tags were detected by researchers after the breeding season (i.e., detection probabilities were less than 1.0). For instance, some proportion of consumed tags were regurgitated or defecated at off-colony loafing or roasting sites, deposited tags were removed or damaged by wind or water erosion, or deposited tags were missed (not detected) by researchers during the scanning process (see also Hostetter et al. 2015). Given these known sources of tag loss, an accurate estimate of the total number of fish consumed by birds required an adjustment or correction for PIT-tag deposition and detection probabilities on bird colonies (collectively referred to as "recovery probabilities"). The methods and data of Hostetter et al. (2015) were used to estimate colony-specific recovery probabilities. In brief, juvenile salmonids implanted with PIT tags of known codes were fed to nesting CATE, DCCO, and LAXX throughout the peak breeding season (April - June) at multiple colonies and years. The numbers of ingested tags subsequently found by researchers at each colony at the end of the breeding season were used to estimate tag deposition probabilities by predator species and colony. To estimate detection probabilities, PIT tags with known tag codes were intentionally sown on each bird colony by researchers prior to, during (when possible), and following the nesting season (see also Evans et al. 2012). Recoveries of these tags during scanning efforts after the breeding season were then used to model the probability of detecting a tag that was deposited during the breeding season (see Survival and Predation Estimation for additional details). Colony-specific PIT tag recovery probabilities for CATE, DCCO, and LAXX colonies included in the study were those previously reported by Evans et al. (2019) and are provided in Appendix A, Table A1.

Estimated deposition probabilities from American white pelicans (AWPE) nesting on Badger Island (the sole pelican colony included in the study) were not available as there have been no studies conducted to directly estimate PIT tag deposition probabilities for this species and colony to-date. Results from CATE, DCCO, and LAXX deposition studies indicate that deposition probabilities can substantially influence predation probabilities (Hostetter et al. 2015) and so without a correction for deposition probabilities, estimates of predation could be grossly underestimated. Thus, to provide informed approximations of AWPE predation probabilities on tagged URB fall Chinook smolts, we used the data of Teuscher et al. (2015) to develop "speculative" deposition probabilities for AWPE nesting on Badger Island. Similar to Hostetter et al. (2015), Teuscher et al. (2015) intentionally fed fish with known tag codes to AWPE to investigate recovery probabilities in PIT-tagged Yellowstone cutthroat trout *O. clarkii* in the Blackfoot Reservoir, ID. Unlike Hostetter et al. (2015), however, the recovery probabilities from Teuscher et al. (2015) did not identify deposition and detection probabilities separately (independently). We therefore used the average annual detection rates observed on the Badger Island AWPE colony to infer approximate rates of deposition from Teuscher et al. (2015) study. The detection and deposition rates from that study area and colony, however, may differ considerably from those of AWPE on Badger Island and therefore could bias predation rate estimates in URB fall Chinook smolts to an unknown degree and direction. As such, estimated Badger Island AWPE predation probabilities presented herein should be considered best-guess estimates (see *Discussion* for additional details).

Not all active bird colonies were scanned for fish PIT tags in all years during 2008-2018. Two notable examples were that of the Badger Island pelican colony in 2013 and the Foundation Island cormorant during 2013 and 2015-2018, where large numbers of birds nested, but there were no efforts to recovery fish tags following the breeding season. To address this data gap, we assumed the average annual predation probabilities observed from years (when the colony was scanned) to be similar to those in years where the colony was not scanned. Estimates of colony size (number of breeding adults) by BRNW (2019) indicated that the Foundation Island cormorant colony has remained relatively stable in size since 2008, ranging from 308 to 390 breeding pairs. The Badger Island pelican colony, however, has rapidly increased in size from 1,349 breeding pairs in 2008 to 3,330 pairs in 2018 (BRNW 2019). Because PIT tag scanning data were lacking in several years, estimates again represent best-guess estimates of predation (see *Discussion* for additional details). All best-guess estimates are explicitly labelled as such in tables and figures (see *Results* below).

Predation and Survival Estimation – The joint mortality and survival (JMS) estimation methods of Payton et al. (2019) were used to estimate reach-specific and cumulative URB fall Chinook smolt predation and survival rates. This hierarchical state-space Bayesian model incorporated both live and dead detections of PIT-tagged fish in space and time to simultaneously estimate predation and survival rates. In brief, the model used two vectors, $\boldsymbol{y}$ and $\mathbf{r}$, to describe each fish's recapture history following tagging and release at each of the five (5) downstream recapture sites and each of the 14 avian recovery sites under consideration. Each vector $\mathbf{y}$ was a 5-length vector, where y_j was an indicator variable of a fish's recapture at recapture opportunity j, and $\mathbf{r}$ was a 15-length vector, where, for $d \in \{1,2,\dots,14\}$, r_d was an indicator variable of recovery from colony *d* and r_{15} indicated a fish was unrecovered. Implicitly, the model provided inference about each fish's state, represented by an unobserved 5-length vector $\mathbf{z}$, where z_j was an indicator variable of whether the fish was still alive at recapture opportunity j.

Parameters used in the model were:

> $\boldsymbol{\Theta}$**,** a 15x5 matrix where $\Theta_{k,d}$ represented the probability a fish released survived to recapture opportunity k and then subsequently succumbed to mortality cause *d* prior to arrival at recapture opportunity $k+1$
>
> **p,** a 5-length vector where p_k represented the probability that a fish alive at recapture opportunity *k* was successfully recaptured
>
> $\boldsymbol{\gamma}$, a 15-length vector where, for $d \in \{1,2,\dots,14\}$, γ_d represented the probability of recovering a fish which died due to mortality cause *d,* and γ_{15} = 0 represented the lack of recoveries of fish which died from all other unspecified causes.

Low recapture rates inhibit precision in partitioning the morality impacts of colony d among the river reaches where that colony was assumed to forage. Previous research indicates that predation impacts by individual colonies were spatially proportionate amongst river reaches and years (Evans et al. 2016;

Hostetter et al. 2018). Therefore, we implemented a hierarchical “informed partitioning” method to share information among years based on the assumption that the odds of being consumed by a colony foraging among multiple river segments were similar among years. Specifically, informed partitioning involved first defining $\boldsymbol{\theta}_{\mathbf{y}}^{cumulative}$ to be a 15-sized vector where ${\theta_y}_d^{cumulative}$ represented the probability a released fish succumbed to mortality cause d, in year y. Then, for each colony d in year y, 5-length vector ${\boldsymbol{\rho}_y}_d$ defined the partitioning of ${\theta_y}_d^{cumulative}$ into $[{\Theta_y}_{\mathbf{1},d}, {\Theta_y}_{\mathbf{2},d}, \dots, {\Theta_y}_{\mathbf{5},d}]$. That is,

$$[{\Theta_y}_{\mathbf{1},d}, {\Theta_y}_{\mathbf{2},d}, \dots, {\Theta_y}_{\mathbf{5},d}] = {\theta_y}_d^{cumulative} {\boldsymbol{\rho}_{\mathbf{y}}}_d$$

where

$$\boldsymbol{\rho}_d \sim dirichlet(\boldsymbol{\alpha}^d).$$

From the spatially explicit rates of $\boldsymbol{\Theta}$, the survival rates across river reaches could be derived. Explicitly $\boldsymbol{\Phi}$ was defined to be a 5-length vector where Φ_k represented the probability a fish released at Priest Rapids Hatchery or in the Hanford Reach survives through river reach *k* (i.e., $\Phi_{\mathrm{k}} = 1 - \sum_{i \le k} \sum_d \Theta_{k,d}$).

It follows that an individual fish’s life can be expressed with the following state-space interpretation:

$$z_j \sim bernoulli(z_{(j-1)} * \Phi_j),$$
$$y_j \sim bernoulli(z_j * p_j),$$

and

$$r_d \sim bernoulli(\sum_{j=1}^{M-1} (z_{j+1} - z_j) * \Theta_{j,d} * \gamma_d).$$

Temporal variation was assumed to be inherent to rates of mortality (Evans et al. 2014, Hostetter et al. 2015), recapture (Sandford and Smith 2002), and recovery (Ryan et al. 2003; Evans et al. 2012). Under the assumption that fish released within the same week experienced similar rates of mortality/survival, recapture, and recovery; URB fall Chinook were grouped into weekly release cohorts. The week specific rates were accordingly denoted $\boldsymbol{\Theta}_{\mathrm{y,w}}$, $\mathbf{p}_{y,w}$, and $\boldsymbol{\gamma}_{y,w}$. Rates of mortality, recapture, and recovery from weeks closer in time were assumed to be more alike than those temporally further apart. Serial correlation in survival/mortality and recapture rates were assumed and accounted for with life path simplexes as described by Payton et al. (2019). Temporal variation in detection rates were estimated more directly by intentionally sown PIT tags with known tag codes on each colony before, after, and, in some instances, within each breeding season (see Hostetter et al. 2015). Estimated detection probabilities at each colony were then interpolated from the logistic curve estimated from the intentionally sown tags. In some uncommon instances, researchers were unable to sow PIT tags prior to the nesting season. In these cases, the methods of Payton et al. (2019) were used to infer an estimation of inner-seasonal variation in recovery rates using information from similar colonies in the same year or using information from the same colony in different years. These instances are denoted in Appendix A, Table A1.

Weakly informative priors (as suggested by Gelman et al. [2017]) were assigned to most of the parameters of the model. The prior for the initial week’s detection probability in each year was defined to be $uniform(0,1)$. Analogously, the prior distribution assigned for the life paths simplexes in the initial week of each year was assumed to be $Dirichlet(\mathbf{1})$, where $\mathbf{1}$ was an appropriately sized vector of ones. Weakly-informative priors of $half\ normal(0, 5)$ were also implemented for all variance parameters.

All models were implemented using the software STAN accessed through R version 3.1.2 (R Development Core Team 2014) using the rstan package (version 2.8.0; Stan Development Team 2015). To simulate random draws from the joint posterior distribution we ran four Hamiltonian Monte Carlo (HMC) Markov Chain processes. Each chain contained 4,000 adaptation iterations, followed by 4,000 posterior iterations. Posterior iterations were then thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2013) and all accepted chains reported zero divergent transitions. Reported estimates represent simulated posterior medians along with 95% highest (posterior) density intervals (95% credible interval {CRI}).

Survival Model Comparisons

Previous research indicates that survival models that incorporate recoveries of fish tags on bird colonies can improve the accuracy and precision of survival estimates, particularly in cases where recapture probabilities of live fish following tagging and release were low (Hostetter et al. 2018; Payton et al. 2019). To investigate if recoveries of URB fall Chinook PIT tags on bird colonies increased the accuracy and precision of survival estimates in the current study, we compared JMS model estimates to those of a standard, frequentist CJS model developed from a series of simulated datasets. Specifically, we simulated datasets that were constructed to resemble seasonal runs of wild Chinook smolts with average annual samples of 9,040 PIT-tagged fish (range = 4,183 to 16,651). In order to represent a broad array of relevant survival, recapture, and recovery rates, prescribed probabilities for simulations were based on estimates from four years of data (2008, 2013, 2015, and 2017). Five hundred simulated datasets were developed from each set of prescribed rates. Estimates of cumulative survival were then developed for each simulated dataset using both the CJS and JMS models. Survival was estimated at a weekly level with annual rates defined as a weighted average. for by the JMS Standard metrics of bias, the difference between the point estimate and the prescribed parameter value, were examined to assess the relative fitness of each model in estimating survival. These metrics included: average bias, average absolute bias, maximum bias, coverage, and average uncertainty. Coverage was defined as the proportion of uncertainty intervals which contained the prescribed parameter value. Average uncertainty was defined as the average width of the estimated uncertainty intervals.

Results

Mark-recapture-recovery – In total, 411,350 URB fall Chinook smolts were PIT-tagged and released during 2008 - 2018 (Table 1). Of these, 311,902 were hatchery fish released from the Priest Rapid Hatchery (PRH) into the tailrace of Priest Rapids Dam and 99,448 were wild fish captured and released into the Hanford Reach (HR) of the Columbia River downstream of Priest Rapids Dam (HR; Map 1). Release numbers varied considerably by year (range = 7,807 – 52,886 per year) and rear-type (range = 2,994 – 42,955 per year, per rear-type). Numbers of tagged Chinook detected alive at downstream recapture sites also varied by river reach and year, as did the number of tags recovered dead on bird colonies (Table 1). The largest numbers of tags were recovered dead on bird colonies at breeding sites upstream of McNary Dam in Reach 1 (n=4,810; Table 1). Conversely, the smallest number of smolts were recaptured alive at the pair-trawl net detector in the Columbia River estuary in Reach 3 (n=714; Table 1).

Only a small number and proportion of smolts released at PRH and HR returned to BON as adults, with adult returns ranging from 56 – 945 adults, per release year (Table 1). Numbers of tags recovered on each bird colony are provided in Appendix A, Table A1. Recapture and recovery probabilities are provided in Appendix A, Table A2.

Table 1. Numbers of PIT-tagged Upriver Bright fall Chinook that were subsequently detected alive at PIT-tag arrays or recovered dead on bird colonies (see Map 1 for release, recapture, and recovery locations). The number of smolts returning as adults to Bonneville Dam were also provided. Dashed-line denotes that complete adult returns were not available.

		--- Reach 1 --- Release to McNary Dam		--- Reach 2 --- McNary Dam to John Day Dam		--- Reach 3 --- John Day Dam to Bonneville Dam		--- Reach 4 --- Bonneville Dam to Pacific Ocean		Adult Returns
Year	Number Released	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live
2008	19,645	1,202	335	698	1	465	16	47	83	164
2009	16,722	1,370	358	546	1	396	5	44	72	56
2010	7,807	698	184	296	1	285	5	31	25	75
2011	13,331	861	346	628	0	363	0	3	21	250
2012	47,735	3,214	690	4,317	0	1,707	21	74	267	811
2013	47,089	5,161	90	2,741	10	974	57	115	434	945
2014	52,843	7,311	574	3,163	68	2,509	81	226	253	193
2015	47,586	2,798	254	2,106	299	687	101	14	249	-
2016	52,881	4,458	362	2,080	323	1,587	97	71	81	-
2017	52,829	3,377	654	2,412	127	3,374	118	50	134	-
2018	52,882	2,659	963	2,139	71	1,817	104	39	182	-

Avian Predation – Of the colonies foraging in Reach 1 (Release to McNary Dam), the highest predation probabilities were those of the mixed AWPE and LAXX colony on Badger Island (BGI) and the DCCO colony on Foundation Island (FDI), with annual predation probabilities ranging from 0.014 (95% CRI = 0.008 – 0.025) to 0.099 (0.076 – 0.129) depending on the colony, year, and smolt rear-type (hatchery, wild; Figure 1). Predation probabilities by all other colonies foraging in Reach 1 were generally less than 0.010 per colony, per year. Cumulative estimates of predation (predation by all colonies foraging in Reach 1 combined) ranged from a low 0.033 (0.027 – 0.040) on hatchery smolts in 2013 to a high 0.183 (0.136 – 0.247) on wild smolts in 2017 (Figure 1). In Reach 2 (McNary Dam to John Day Dam), predation probabilities were again generally low (< 0.010) in most years, with the exception of predation by the mixed colony on BGI and the CATE and LAXX colonies on Central Blalock Islands (CBI), where predation probabilities as high as 0.049 (0.015 – 0.099), 0.052 (0.019 – 0.105), 0.032(0.009 – 0.079), respectively, were observed on wild smolts (Figure 1). Predation probabilities in Reach 3 (John Day Dam to Bonneville Dam) were again low for most colonies in most years prior to 2014, but increased starting in 2015, with predation as high 0.067 (0.011 – 0.237), 0.102 (0.029 – 0.245), and 0.068 (0.022 – 0.172) on wild smolts by the BGI mixed colony and the CBI and Miller Rocks Island (MRI) gull colonies, respectively (Figure 1). Predation probabilities in Reach 3 were especially high on wild smolts in 2015 and 2016, with cumulative estimates of 0.199 (0.098 – 0.353) and 0.355 (0.184 – 0.577), respectively. Results indicate that despite the location of the BGI colony in McNary Reservoir, birds were commuting to forage on smolts downstream of John Day Dam, over 150 Rkm from their nesting site. Cumulative estimates of avian predation on wild smolts in 2016 were the highest reach-specific estimates observed during the 11-year study period. Estimates in Reach 3, however, were based on small sample sizes of wild fish (those surviving passage to below John Day and Bonneville dams), which resulted in imprecise estimates of predation. Of the colonies foraging in Reach 4 (Bonneville Dam to the Pacific Ocean), predation probabilities were often the highest by DCCO nesting on East Sand Island (ESI), with probabilities ranging annually from 0.012 (0.004 – 0.030) to 0.097 (0.012 – 0.338) depending on the year and rear-type (Figure 1). Cumulative estimates of predation by both DCCO and CATE in Reach 4 ranged annually from 0.030 (0.018 – 0.052) to 0.059 (0.044 – 0.083) on hatchery smolts and from 0.013 (0.006 – 0.025) to 0.227 (0.057 – 0.532) on wild smolts (Figure 1). Analogous to results in Reach 2 and 3, small sample sizes of surviving fish to below Bonneville Dam resulted in imprecise estimates of predation in Reach 4, particularly estimates on wild fish.

Cumulative, system-wide predation probabilities, measured as the impact of all 13 bird colonies on URB fall Chinook mortality from Release to the Pacific Ocean, ranged annually from 0.064 (0.055 – 0.076) to 0.413 (0.353 – 0.474) depending on the rear-type (Figure 2). Of the bird species evaluated (CATE, DCCO, LAXX, AWPE), aggregated (species-specific) predation probabilities on were often, but not always, the highest by American white pelicans and double-crested cormorants (Figure 2). The aggregate effects of predation by all LAXX colonies were also appreciable in some years, with predation probabilities as high as 0.115 (0.007 – 0.164) observed on wild smolts in some years. In general, the aggregate effects of predation by all CATE colonies was the lowest of four predator species evaluated, although impacts as high as 0.094 (0.052 – 0.145) were observed on wild smolts in some years.

Relative comparisons of predation between hatchery and wild URB fall Chinook smolts indicated that wild fish were often, but not always, more likely to be predated than hatchery fish, with significant differences in predation probabilities observed in multiple river-reaches and years (Figure 1 and Figure 2). There was some evidence that predation, particularly predation on wild smolts, increased during the study period, with cumulative, average annual predation estimates increasing from 0.088 (0.074 – 0.107) during 2008 - 2012 to 0.205 (0.178 – 0.234) during 2013 - 2018. Increases in predation during the latter part of the study period were largely associated with the BGI mixed-species colony. Increases in predation at the BGI colony site were also coincident with increase in the size of these colonies. For instance, the AWPE colony on BGI increased over the course of the study period, with the number of breeding birds observed in 2018 (ca. 3,330 birds) more than twice the number observed in 2008 (ca. 1,349 birds; BRNW 2019). The LAXX colony on BGI formed in 2015 when large numbers (several thousand adults) of birds were documented breeding on the island for the first time since monitoring began in 2000 (BRNW 2019).

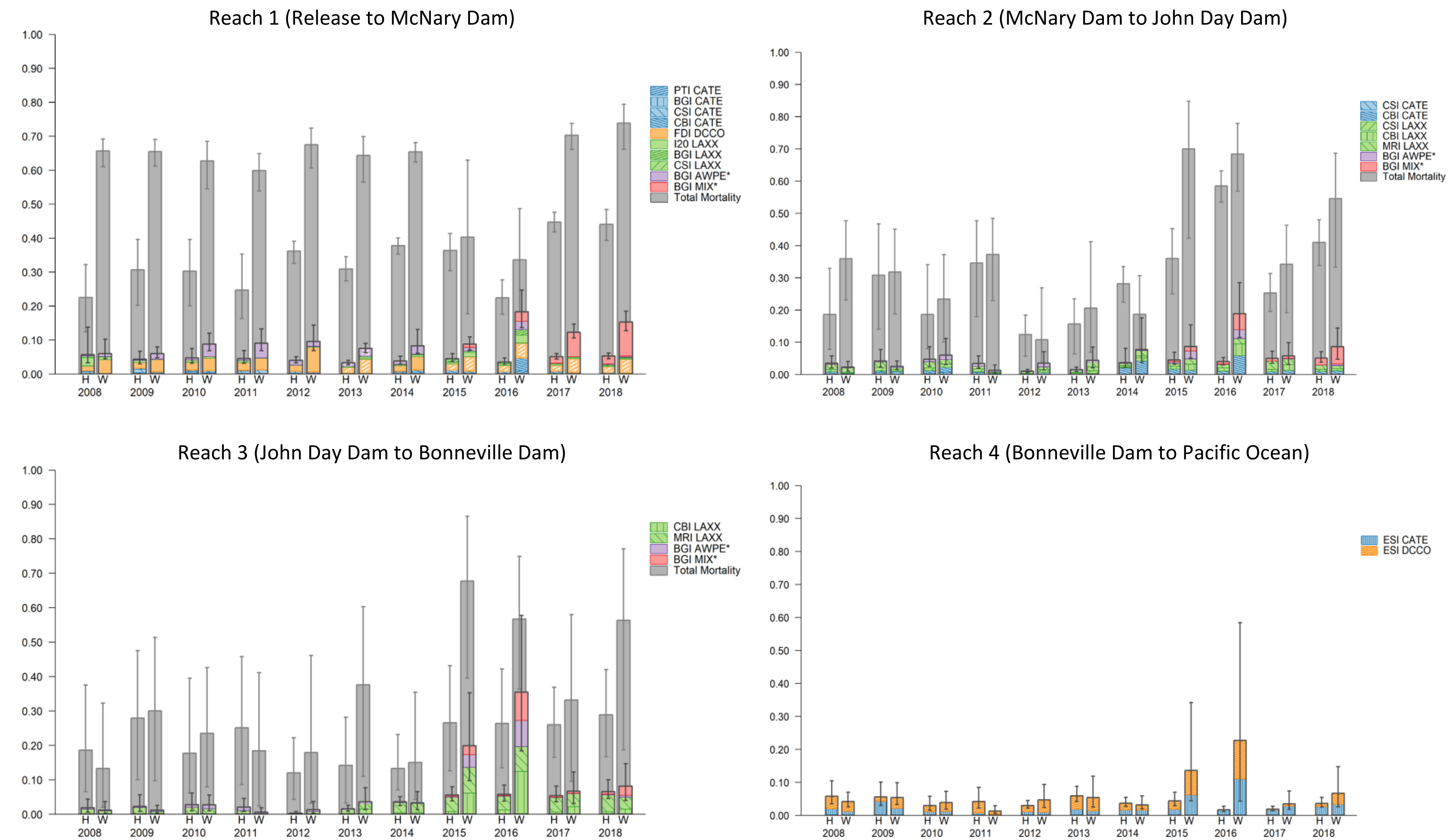


Figure 1. Estimated reach-specific total mortality (grey bars) and mortality due to avian predation (colored bars) of PIT-tagged hatchery (H) and wild (W) Chinook smolts during 2008-2018. Estimates represent the proportion of available fish by rear-type and year. Predator species include Caspian terns (CATE), double-crested cormorants (DCCO), California and ring-billed gulls (LAXX), and American white pelicans (AWPE; see Map 1 for colony names). Mixed colonies (MIX) are those of AWPE and LAXX. Error bars represent 95% credible intervals. Asterisks for BGI AWPE or MIX colonies denote that estimates were based on deposition data from an out-of-basin colony and may be biased to an unknown degree (see Methods). White cross hatching represents best-guess estimates based on cases where empirical data for that colony, in that year, were lacking and where the average rate from years past was used instead (see Methods).

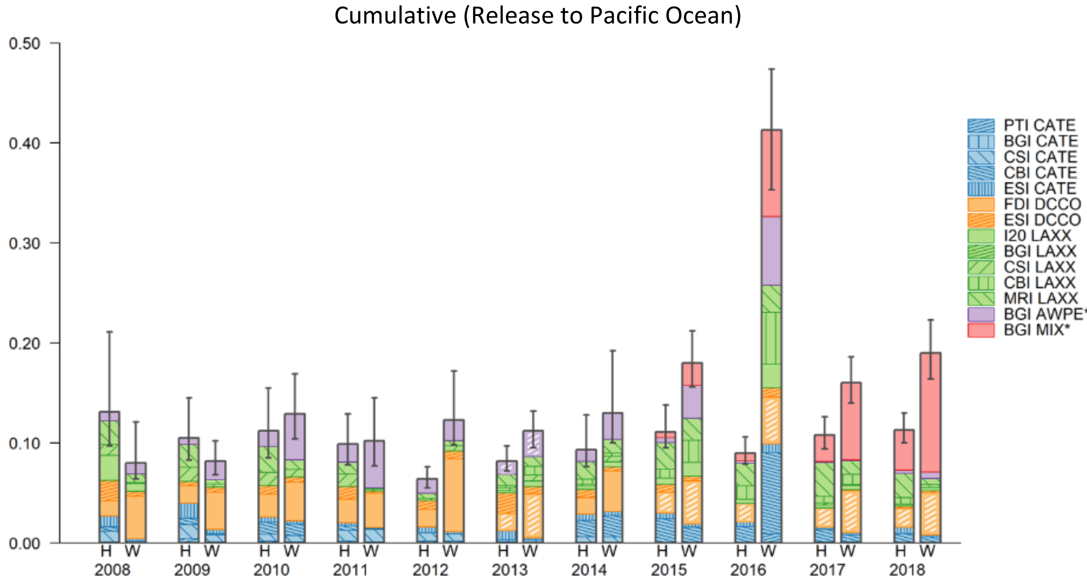


Figure 2. Estimated cumulative mortality due to avian predation (proportion of available fish consumed) of PIT-tagged hatchery (H) and wild (W) juvenile Upriver Bright fall Chinook during 2008 - 2018. Estimates represent the proportion of available fish consumed by rear-type and year. Predator species include Caspian terns (CATE), double-crested cormorants (DCCO), California and ring-billed gulls (LAXX), and American white pelicans (AWPE; see Map 1 for colony names). Mixed colonies are those of AWPE and LAXX combined. Error bars represent 95% credible intervals. Asterisks for BGI AWPE or MIX colonies denote that estimates were based on deposition data from an out-of-basin colony (see Methods). White cross hatching represents best-guess estimates based on cases where empirical data for that colony, in that year, were lacking and where the average rate from years past was used instead (see Methods).

Total Mortality – Estimated total mortality (1-survival) of URB fall Chinook smolts was highly variable depending on the river reach, year, and smolt rear-type (hatchery, wild; Figure 1). Total mortality was consistently the highest in Reach 1 (Release to McNary Dam), ranging annually from 0.224 (0.176 – 0.277) to 0.447 (0.418 – 0.478) in hatchery smolts and 0.336 (0.169 – 0.487) to 0.739 (0.662 – 0.794) in wild smolts. Results indicated more than 50% of all wild smolts died prior to reaching McNary Dam in 9 of the 11 study years evaluated. Total mortality was often, but not always, lower in Reach 2 and 3, with the majority of hatchery and wild smolts surviving passage in most years. Cumulative total mortality estimates indicated that the majority of Chinook smolts died prior to reaching Bonneville Dam, with estimates ranging from 0.499 (0.376 – 0.618) to 0.767 (0.725 – 0.807) in hatchery smolts and 0.764 (0.717 – 0.822) to 0.949 (0.906 – 0.970) in wild smolts. The was some evidence that total mortality of URB fall Chinook, particularly wild smolts, increased during the study period, with estimates from 2015 - 2018 significantly higher than those during 2008 – 2014 in Reach 2 and 3 (Figure 1). An estimate of smolt mortality through Reach 4 could not be calculated because there were no PIT tag detection sites downstream of the bird colonies on ESI in the lower Columbia River estuary (Map 1). Estimated total mortality to adulthood, based on the proportion of smolts released that die prior to returned to Bonneville Dam as adult, ranged annually from 0.964 (0.958 – 0.969) to 0.996 (0.996 – 0.997) in hatchery fish and 0.986 (0.984 – 0.988) to 0.997 (0.996 – 0.998) in wild fish during 2008 - 2014 (the last year with complete adult returns data available; Table 1). These translate into smolt-to-adult survival percentages of just 0.3% to 3.6%, depending on the out-migration year and the fish's rear-type.

Comparisons of total mortality based on a fish's rear-type indicated that wild fish were significantly more likely to die than hatchery fish during out-migration in most, but not all, river reaches and years (Figure 1). For instance, in Reach 1, wild fish were significantly more likely to die than hatchery fish in 10 of the 11 study years evaluated. Similar levels of total mortality between hatchery and wild fish, however, were observed in Reaches 2 and 3 during 2008 - 2014, but during 2015 - 2018 wild fish were again more likely to die relative to their hatchery counterparts. Collectively (all reaches and years), results indicated that hatchery URB smolts were more likely to survive out-migration to Bonneville Dam and were more likely to return as adults compared to wild URB Chinook smolts.

Annual comparisons of total URB fall Chinook smolt mortality (1 - survival) and mortality due to bird predation indicated that avian predation accounted for 11.2% (95% CRI = 9.2 – 13.2) to 19.8% (11.0 – 47.6) of hatchery fish mortality and 8.6% (6.7 – 11.8) to 42.8% (34.3 – 52.6) of wild fish mortality during smolt out-migration from the release to Bonneville Dam. The relative effects of avian predation were often the greatest on wild smolts in Reach 1, with bird predation accounting for 9.1% (7.3 – 14.7) to 54.5% (50.7 – 80.4) of total mortality per year. In Reach 2 and 3, avian predation accounted for less than 20% of total mortality in most years, with the exception of 2015 and 2016 where increases in predation probabilities were coincide with increase in total mortality (Figure 1). Results indicate that although the cumulative effects of bird predation were a substantial source of URB Chinook mortality in some river reaches and years, it was not the dominate source of mortality, with most fish dying from non-avian causes during out-migration to Bonneville Dam.

Survival Model Comparisons – On average, the CJS model tended to produce less biased estimates of survival across all years compared to the JMS model (Table 2). This bias was generally small in magnitude (< 0.03) with the notable exception of the 2015 datasets. The JMS model generally produced more biased estimates on average but not grossly greater in magnitude than those of the CJS model. However, the average absolute bias of the JMS model estimates was less than that of the CJS model estimates in 9 out of the 12 comparable year-reach estimate combinations (Table 2). Together these metrics suggest that, the CJS estimates were less biased on average to the prescribed parameter values, but the estimates of the JMS model were less biased individually (i.e. displayed less absolute bias). Furthermore, the maximum level of bias in any given river reach and year, however, was often greater with the CJS estimates compared with the JMS estimates (Table 2 and Figure 3). The estimates produced by the JMS model were more consistent, with the most egregious bias measuring 0.19. In contrast, estimates produced by the CJS model could be significantly different from the prescribed estimate, overestimating survival to JDA by up to 0.82 in the 2015 simulations (Table 2).

The uncertainty intervals for the JMS model were also consistently more compact (i.e. precise) than those of the CJS model (Figure 3). For all 12 comparable year-reach estimate combinations, the average uncertainty interval widths produced by the JMS model was less than those produced by the CJS model with some year-reach combinations generating uncertainty intervals on average 2 to 4 times the size of the intervals produced by the JMS model for the same dataset (Table 2). The CJS model often produced very wide confidence intervals, which in many cases were uninformative (Figure 3). This was especially true for estimates of survival to Bonneville Dam, where CJS estimates ranged from zero survival to over

100% survival in the same year. The generally greater precision of the JMS model's estimates did not tend to result in reduced coverage, with the estimated uncertainty interval coverage associated with the JMS model was generally greater than that of the CJS model. The annual estimates for which the JMS coverage probabilities were reduced were associated with the widest CJS intervals in which many overlapped on, or both, the limits of the unit interval (Figure 3). The JMS model consistently produced compact credible intervals throughout the system, including for estimates of survival to the net trawl in the Columbia River estuary. Estimates of survival to net trawl, however, could not be generated using the CJS model due to a lack of live detection sites downstream of the net trawl in the lower Columbia River estuary.

Table 2. Summary statistics of cumulative survival estimates for simulated datasets produced from Cormack-Jolly-Seber (CJS) and Joint Mortality and Survival (JMS) models. Model performance was evaluated using average bias, average absolute bias, maximum absolute bias, coverage, and uncertainty. Values depicted in blue (for JMS) and green (for CJS) represent the best fitting model for each simulation by river reach and year. NA denotes that no estimate of survival could be generated by that model in that river reach and year. Survival is of tagged wild Upriver Bright Chinook smolts during outmigration from Hanford Reach of the Columbia River to McNary Dam (MCJ), John Day Dam (JDA), Bonneville Dam (BON), and a pair trawl net detector in the Columbia River Estuary (EST; see also Map 1).

		2008 Simulations				2013 Simulations				2015 Simulations				2017 Simulations			
		To MCJ	To JDA	To BON	To EST	To MCJ	To JDA	To BON	To EST	To MCJ	To JDA	To BON	To EST	To MCJ	To JDA	To BON	To EST
Average Bias	CJS	-0.01	-0.01	-0.01	NA	0.00	-0.01	0.01	NA	0.11	0.03	0.08	NA	0.00	0.00	0.02	NA
	JMS	0.00	0.01	-0.02	-0.04	0.06	-0.01	-0.03	-0.04	0.04	0.10	0.00	0.01	0.02	0.01	-0.03	0.00
Absolute Bias	CJS	0.02	0.02	0.04	NA	0.03	0.04	0.06	NA	0.20	0.06	0.08	NA	0.01	0.01	0.06	NA
	JMS	0.02	0.02	0.02	0.04	0.06	0.02	0.03	0.04	0.04	0.10	0.01	0.01	0.02	0.01	0.03	0.01
Max Bias	CJS	0.08	0.10	0.12	NA	0.26	0.19	0.24	NA	0.41	0.82	0.79	NA	0.09	0.08	0.13	NA
	JMS	0.09	0.07	0.08	0.10	0.18	0.09	0.08	0.08	0.14	0.19	0.06	0.03	0.08	0.05	0.06	0.04
Coverage	CJS	0.88	0.91	0.80	NA	0.90	0.83	0.69	NA	0.55	0.84	0.70	NA	0.90	0.91	0.40	NA
	JMS	0.95	0.95	0.89	0.85	0.69	0.96	0.76	0.85	1.00	0.43	0.99	0.99	0.83	0.94	0.52	0.99
Average Uncertainty	CJS	0.09	0.09	0.15	NA	0.16	0.17	0.21	NA	0.51	0.29	0.23	NA	0.07	0.07	0.08	NA
	JMS	0.09	0.09	0.09	0.12	0.15	0.13	0.10	0.11	0.26	0.19	0.06	0.04	0.06	0.07	0.05	0.08

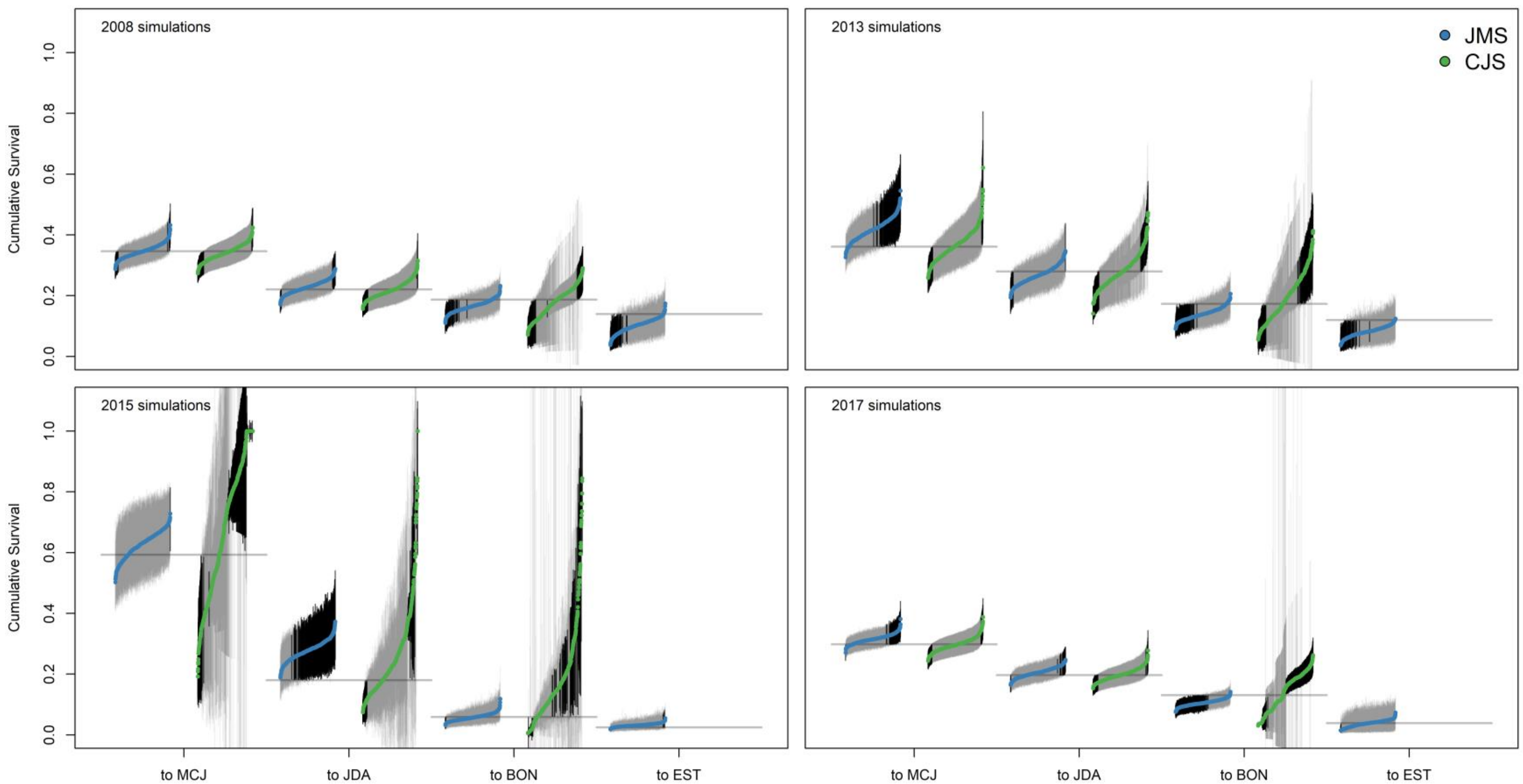


Figure 3. Graphical representations of the 500 simulated wild Upriver Bright fall Chinook smolt survival estimates and associated uncertainty intervals produced according to the CJS and JMS models for each reach and year combination. Comparisons are ordered by magnitude of the point estimates. Horizontal grey line segments represent the prescribed parameter values, dots represent the estimates produced by each model (blue for JMS estimates, green for CJS estimates), vertical line segments represent the associated uncertainty intervals; grey indicating successful coverage of the prescribed parameter value and black indicating unsuccessful coverage. Survival is of tagged wild Chinook smolts during outmigration from the Hanford Reach of the Columbia River to McNary Dam (MCJ), John Day Dam (JDA), Bonneville Dam (BON), and a pair trawl net detector in the Columbia River estuary (EST; see also Map 1).

Discussion

Predation Impacts – Numerous factors have been linked to URB fall Chinook mortality in the Columbia River basin, including harvest (Hyun et al. 2012), ocean conditions (Hyun et al. 2007), predation by piscivorous fish (Harnish et al. 2014), and passage restrictions and mortality associated with hydroelectric dams (Harnish et al. 2013). Results from this study indicate that predation from piscivorous colonial waterbirds, a previously unquantified source of mortality in URB fall Chinook, were substantial in some river-reaches and years. Predation probabilities were highly variable, however, with cumulative estimates ranging from just 0.064 to upwards of 0.413, indicating birds consumed as few as 6.4% to as many as 41.3% of available smolts each year. Comparisons of total mortality (1 - survival) to mortality due to colonial waterbird predation indicated that avian predation accounted for 8.6% to 42.8% of all sources of URB fall Chinook smolt mortality annually during out-migration from the Hanford Reach to Bonneville Dam. Collectively, results indicated that the cumulative effects of avian predation were an important factor regulating the survival of URB fall Chinook smolts to Bonneville Dam in some, but not all, river reaches and years.

A system-wide evaluation of colonial waterbird predation across multiple river reaches provided data to identify which bird species (Caspian terns, double-crested cormorants, American white pelican, or California and ring-billed gulls) and individual colonies posed the greatest risk to URB fall Chinook smolts. Comparisons of Chinook smolt losses by predator species indicated that the mixed American white pelican and gull colonies on Badger Island and the double-crested cormorant colony on Foundation Island often consumed the largest proportion of available smolts compared with other predator species and colonies. Most of the other individual colonies posed little threat to UBR fall Chinook, with predation probabilities often less than 0.03 per colony, per year, despite the finding that total mortality was consistently greater than 0.50 or 50% of all available smolts each year. Predation by the gull colonies included in the study were generally the lowest of the predator species evaluated, with the exception of gull colonies on Miller Rocks Island and Central Blalock Islands, colonies that were in close proximity to hydroelectric dams. Unlike pelicans, terns, and cormorants, gulls are omnivorous, and previous research indicated that juvenile salmonids comprised less than 10% of the diet (by mass) of gull colonies in the Columbia River basin (Collis et al. 2002). Despite this, predation probabilities on URB fall Chinook smolts by the Miller Rocks Island and Central Blalock Islands colonies were similar to those of nearby pelican, tern, and cormorant colonies in some years. Hostetter et al. (2015) attributed high levels of gull predation on juvenile salmonids to the large size (tens of thousands of breeding adults) of gull colonies, coupled with behavior flexibility to exploit temporarily available food sources (Winkler 1996). Evans et al. (2016) observed that gulls nesting on Miller Rocks Island disproportionately consumed juvenile salmonids near John Day Dam, located just 18 Rkm upstream of the colony site. Studies have hypothesized that smolts may be more vulnerable to gull predation near dams due to delays in travel times associated with forebay passage, mortality and injury associated with turbine passage, or smolts temporarily being stunned or disoriented by hydraulic conditions in the tailrace of dams (Ruggurone 1996; Evans et al. 2016).

There was evidence that wild URB fall Chinook smolts were more susceptible to avian predation than their hatchery counterparts. This finding was surprising, as other studies of avian predation have generally found that hatchery fish are either more susceptible to avian predation than wild fish (Hostetter et al. 2012) or that hatchery and wild fish are equally susceptible to avian predation (Evans et al. 2016; Evans et al. 2019). Differences in the relative susceptibility between hatchery and wild Chinook were especially pronounced at the Badger Island breeding site, with predation probabilities on wild fish often 2 – 5 times greater than those on hatchery fish. Higher predation on wild smolts by birds nesting on Badger Island could be due to the close proximity of the breeding site to the Hanford Reach (where wild fish were capture, tagged, and released), due to differences in the size of wild and hatchery smolts (with wild fish, on average, smaller), and/or due to differences in the behavior of wild and hatchery smolts. For instance, longer residence times of wild fish compared with hatchery fish likely make wild fish more susceptible to predation. Furthermore, wild smolts were captured and released in shallow water habitats in the Hanford Reach, areas where fish are more susceptible to predation by pelicans, cooperative foragers that corral fish in shallow water (Knopf and Evans 2004). Pelicans are also capable of commuting long distances from their breeding sites to forage (over 300 km; Scoppettone et al. 2006), so pelicans nesting on Badger Island were able to consume smolts in multiple river-reaches, including downstream of John Day Dam in The Dalles Reservoir, over 150 km downstream of Badger Island. Evidence that wild URB fall Chinook smolts were more susceptible to avian predation than their hatchery counterparts also has important implications from a population enhancement perspective. For instance, unlike many other Chinook stocks in the Columbia River basin, natural spawning URB fall Chinook outnumber hatchery returning adults, with approximately 60 – 70% of adult returns from wild origin fish (Stuart Ellis, CRITFC, personal communication). Given higher avian predation rates on wild URB fall Chinook, efforts to reduce avian predation would have a greater benefit to the wild population, benefits that could result in substantially adult returns in the future.

In addition to biotic factors (i.e., a fish's rear-type, size, and behavior), abiotic conditions experienced by smolts during out-migration may also be related to their susceptibility to avian predation. For instance, Hostetter et al. (2012) observed that increased river flows were related to a decrease in Caspian tern predation probabilities on smolts originating from the Snake River. Payton et al. (2017) observed that faster water transient times (a measure of flow in relation to reservoir levels) were associated with lower predation by terns on smolts passing through the Wanapum and Priest Rapids reservoirs in the Columbia River. Although not the focus of this study, the JMS modelling approach used to jointly estimate predation and survival could also be used to identify and test the strength of interactions between various biotic and abiotic factors and predation rates, potential providing important insight to the suite of factors that influence URB fall Chinook smolt susceptible to avian predation in the Columbia River basin.

Several data gaps and critical uncertainties were identified as part of this study. First, as detailed above, information regarding to what degree biotic and abiotic factors explain variation in Chinook smolt predation probabilities are needed to better understand predator-prey interactions and, possibly, to predict survival in any given year. Secondly, not all avian colonies were scanned for smolt PIT-tags in all years (see Methods), nor were all piscivorous avian predator species included in the study. For instance, we did not investigate smolt predation probabilities for non-colonial or semi-colonial piscivorous waterbirds, such as the common merganser *Mergus merganser*, Forster's tern *Sterna forsteri*, great blue heron *Ardea herodias*, black-crowned nightheron *Nycticorax nycticorax*, and grebes *Aechmophorus spp*. Although these piscivorous species are known to consume juvenile salmonids in the Columbia River, their predation impacts on smolts have generally been shown to be less than the impacts of colonial nesting piscivorous waterbirds (Wiese et al. 2008), primarily because the non-colonial and semi-colonial nesting species have smaller regional populations. Finally, due to a lack of empirical estimates regarding PIT tag deposition probabilities for American white pelicans on Badger Island, predation probabilities presented herein were based on data from a different pelican colony (see *Methods*). As such, predation probabilities could be biased to unknown degree. Hostetter et al. (2015) noted that deposition estimates for Caspian terns, double-crested cormorants, and California and ring-billed gulls in the Columbia River varied significantly by predator species. Thus, although field studies for terns, cormorants, and gulls have previously been conducted, studies aimed at quantifying PIT tag deposition probabilities in Badger Island pelicans are needed, and maybe paramount to generating more accurate estimates of predation in the future.

Several other studies have documented that avian predation probabilities vary substantially based on the species of salmonid. For instance, Roby et al. (2015) and Evans et al. (2016) documented significantly higher rates of predation on Steelhead Trout *O. mykiss* compared to Chinook Salmon in the Columbia River. Evans et al. (2019) reported alarmingly high rates of avian predation on Upper Columbia River steelhead, with more fish succumbing to predation by colonial waterbirds than from all other sources of mortality combined during out-migration from Rock Island Dam (Rkm 729) to Bonneville Dam. In the present study, avian predation on URB fall Chinook smolts was often, but not always, low and constituted a minor component of total mortality in some river-reaches and years. One possible component of unaccounted-for mortality in the present study is predation by piscivorous fishes (Harnish et al. 2014; McMichael 2018), such as the Northern Pikeminnow Ptychocheilus oregonensis, Smallmouth Bass Micropterus dolomieu, Walleye *Sander vitreus*, and Channel Catfish *Ictalurus punctatus*. Rieman et al. (1991) estimated that approximately 14% of juvenile salmonids passing through John Day Reservoir were consumed by Northern Pikeminnow, Smallmouth Bass, and Walleye combined and that mortality rates were highest for subyearling Chinook relative to other salmonid species and age-classes. Harnish et al. (2014) estimated there were large numbers of pikeminnow in the Hanford Reach of the Columbia River, with an estimated 37,392 predatory fish annually. In addition to piscivorous fish and birds, other sources of mortality on URB fall Chinook smolts occur, but data to quantify these impacts are generally lacking in published literature.

Survival Models – The inclusion of tag recoveries on bird colonies resulted in more precise estimates of survival in wild URB fall Chinook smolts compared with CJS model estimates that relied solely on detections of live fish. The JMS model generally provided narrower uncertainty intervals, of relatively similar size, across all simulations. Conversely, by relying solely on detections of live fish, the CJS model had difficulty consistently producing informative confidence intervals and estimates near the prescribed parameter value. Our results are similar to those of Hostetter et al. (2018) and Payton et al. (2019), which found that the information provided by the recovery of tags of bird colonies significantly increased the level of precision and the overall reliability of statistical estimates of fish survival. The most prevalent argument for using the standard, frequentist CJS model is that the estimates produced are unbiased given a large enough sample size. Although the results of our simulation study confirmed that CJS estimates were on average (across all years) unbiased, they also demonstrated that this criterion, although statistically elegant, was of little practical value because the magnitude of the biases associated with individual CJS estimates were large and often resulted in uninformative estimates of survival. Collectively, results indicated that recoveries of fish tags on bird colonies increased parameter precision and were able to generate survival estimates across larger spatial scales.

ACKNOWLEDGEMENTS

This project was supported by the Pacific Salmon Commission Chinook Technical Committee with funding from U.S. Chinook Salmon Agreement Fund. We thank Brad Cramer of Real Time Research (RTR) for assistance compiling PIT tag capture-recapture-recovery records and Aaron Turecek for providing study maps.

REFERENCES

Adkins, J. Y., D. E. Lyons, P. J. Loschl, D. D. Roby, K. Collis, A. F. Evans, and N. J. Hostetter. 2014. Demographics of piscivorous colonial waterbirds and management implications for ESA-listed Salmonids on the Columbia Plateau. Northwest Science 88(4):344–359.

BRNW (Bird Research Northwest). 2019. Avian predation on juvenile salmonids in the Lower Columbia River, Annual Reports submitted to the Bonneville Power Administration, U.S. Army Corps of Engineers, Grant County Public Utility District, and Priest Rapid Coordinating Committee. Available on-line: www.birdresearchnw.org.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the Lower Columbia River: implications for loses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537–550.

Dietrich, J.P., D.A. Boylen, D.E. Thompson, E.J. Loboschefsky, C.F. Bravo, D.K. Spangenberg, G.M. Ylitalo, T.K. Collier, D.S. Fryer, M.R. Arkoosh, and F.J. Loge. 2011. An evaluation of the influence of stock origin and out-migration history on the disease susceptibility and survival of juvenile Chinook salmon. Journal of Aquatic Animal Health 23:35-47.

Evans, A.F., N.J. Hostetter, D.D. Roby, K. Collis, D.E. Lyons, B.P. Sandford, and R.D. Ledgerwood. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of Passive Integrated Transponder tags. Transactions of the American Fisheries Society 141:975-989.

Evans, A.F., Q. Payton, A. Turecek, B.M. Cramer, K. Collis, D.D. Roby, P.J. Loschl, L. Sullivan, J. Skalski, M. Weiland, and C. Dotson. 2016. Avian predation on juvenile salmonids: Spatial and temporal analysis based on acoustic and Passive Integrated Transponder tags. Transactions of the American Fisheries Society 145:860-877.

Evans, A. F., Q. Payton, B. M. Cramer, K. Collis, N. J. Hostetter, D. D. Roby, and C. Dotson. 2019a. Cumulative effects of avian predation on Upper Columbia River steelhead. Transactions of the American Fisheries Society 148(5):896–913.

Fish Passage Center (FPC). 2019. Juvenile passage timing, juvenile travel times, juvenile survival, and smolt-to adult returns of Hanford Reach wild subyearling fall Chinook (1993-2019). Memorandum to Jeff Fryer (CRITFC).

Fryer, J.K. 2019. Expansion of the 2018 Hanford Reach fall Chinook salmon juvenile coded-wire tagging and PIT tagging project. Report to Pacific Salmon Commission Chinook Technical Committee. Available from the Columbia River Inter-Tribal Fish Commission, Portland, OR, USA.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. Bayesian Data Analysis (3rd ed.). Chapman and Hall/CRC, Boca Raton, Florida, USA.

Harnish, R.A., R. Sharma, G.A. McMichael, R.B. Langshaw, and T.N. Pearsons. 2013. Effect of hydroelectric dam operations on the freshwater productivity of a Columbia River fall Chinook salmon population. Canadian Journal of Fisheries and Aquatic Sciences 71:602–615.

Harnish. R. A., E. D. Green, K. A. Deters, K. D. Ham, Z. Deng, H. Li, B. Rayamajhi, K. W. Jung, and G. A. McMichael. 2014. Survival of wild Hanford Reach and Priest Rapids Hatchery fall Chinook Salmon juveniles in the Columbia River: Predation Implications. Report PNNL-23719 to the Pacific Salmon Commission. Pacific Northwest National Laboratory, Richland, Washington.

Hostetter, N.J., A.F. Evans, D.D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. Transactions of the American Fisheries Society 141:1586–1599.

Hostetter, N.J., A.F. Evans, B.M. Cramer, K. Collis, D.E. Lyons, and D.D. Roby. 2015. Quantifying avian predation on fish populations: Integrating predator-specific deposition probabilities in tag–recovery studies. Transactions of the American Fisheries Society 144:410-422.

Hostetter, N. J., B. Gardner, A. F. Evans, B. M. Cramer, Q. Payton, K. Collis, and D. D. Roby. 2018. Wanted dead or alive: a state-space mark–recapture–recovery model incorporating multiple recovery types and state uncertainty. Canadian Journal of Fisheries and Aquatic Sciences 75(7):1117–1127.

Hyun, S., Myers, K.W., Talbot, A., 2007. Year-to-year variability in ocean recovery rate of Columbia River Upriver Bright fall Chinook salmon (Oncorhynchus tshawytscha). Fisheries Oceanography. 16, 350–362.

Hyun, S., Sharma, R., Carlile, J.K., Norris, J.G., Brown, G., Briscoe, R.J., Dobson, D., 2012. Integrated forecasts of fall Chinook salmon returns to the Pacific Northwest. Fisheries Research. 125–126, 306–317.

Langness, O.P., and K.F. Reidinger. 2003. Escapement goals for upriver bright (URB) fall Chinook salmon stocks of the Columbia River. Washington Department of Fish and Wildlife, Olympia.

Lyons, D.E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Unpublished Ph.D. dissertation, Oregon State University, Corvallis, Oregon.

McMichael, G. 2018. Upriver Bright Predator Abundance Estimation. FINAL Report to the Letter of Agreement- U. S. Chinook Technical Committee, Pacific Salmon Commission, under contract CTC-2017-1.

Muir, W.D., S.G. Smith, J.G. Williams, and B.P. Sandford. 2001. Survival of juvenile salmonids passing through bypass systems, turbines, and spillways with and without flow deflectors at Snake River dams. North American Journal of Fisheries Management 21:135-146.

Payton, Q., A.F. Evans, and B. Cramer. 2017. Effects of biotic and abiotic factors on juvenile steelhead survival in the Middle Columbia River, 2008-2015. Final Report submitted to the Grant County Public Utility District and the Priest Rapids Coordinating Committee. Available on-line at: www.birdresearchnw.org.

Payton, Q., N.J. Hostetter, and A.F. Evans. 2019. Jointly estimating survival and mortality: Integrating recapture and recovery data from complex multiple predator systems. Environmental and Ecological Statistics 26:107-125.

R Development Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.

Rieman, B. E., R. C. Beamesderfer, S. Viggs, and T. P. Poe. 1991. Estimated loss of juvenile salmonids by Northern Squawfish, Walleyes, and Smallmouth Bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:44–458.

Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. Canadian Journal of Zoology 81(2):250–265.

Ryan, B.A., S.G. Smith, J.M. Butzerin, and J.W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with Passive Integrated Transponders in the Columbia River estuary, 1998–2000. Transactions of the American Fisheries Society 132:275–288.

Ruggerone, G. T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Transactions of the American Fisheries Society 115:736–742.

Scoppettone, G.G., P.H. Rissler, D. Withers, and M.C. Fabes. 2006. Fish tag recovery from the American white pelican nesting colony on Anaho Island, Pyramid Lake, Nevada. Great Basin Birds 8:6–10.

Stan Development Team. 2015. Stan: A C++ Library for Probability and Sampling, Version 2.8.0. URL http://mc-stan.org/.

Teuscher, D. M., M. T. Green, D. J. Schill, A. F. Brimmer, and R. W. Hillyard. 2015. Predation by American white pelicans on Yellowstone cutthroat trout in the Blackfoot River drainage, Idaho. North American Journal of Fisheries Management 35(3):454–463.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27.5:1413-1432.

Ward, D.L, J.H. Petersen, and J.J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. Transactions of the American Fisheries Society 124:321-334.

Wiese, F. K, J. K. Parrish, C. W. Thompson, and C. Maranto. 2008. Ecosystem based management of predator–prey relationships: piscivorous birds and salmonids. Ecological Applications 18:681–700.

Winkler, D.W. 1996. California gull (*Larus californicus*), version 2.0. *In* The Birds of North America. *Edited by* A. Poole. Cornell Lab of Ornithology, Ithaca, New York.

APPENDICES

Table A1. Numbers of PIT-tagged fall Chinook released into the Columbia River that were subsequently recovered dead on bird colonies. Bird colonies include Caspian terns (CATE), American white pelicans (AWPE), double-crested cormorants (DCCO), and California and ring-billed gulls (LAXX; see Figure 1 for map of colony locations). NC denotes there was no colony at the site and year. Green dashed-lined denote that the colony was active but was not scanned and predation rate estimates were imputed based on data from other years at that colony site. Red dashed-line denotes that colony was active but was not scanned and no estimate of predation was included in study results.

Colony	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Potholes Reservoir, CATE	1	5	1	4	32	11	0	NC	0	NC	NC
Badger Island, CATE	NC	NC	NC	-	-	NC	NC	NC	NC	18	NC
Crescent Island, CATE	23	54	16	75	166	53	152	NC	NC	NC	NC
Central Blalock Islands, CATE	0	0	1	0	-	2	54	271	277	110	56
East Sand Island, CATE	40	52	12	5	129	160	134	136	81	54	143
BGI AWPE	69	136	105	174	290	-	315	114	85	-	47
BGI Mix (AWPE/LAXX)	NC	NC	NC	NC	NC	NC	NC	111	245	623	902
Island 20, LAXX	-	-	-	-	-	12	15	29	32	13	14
Crescent Island, LAXX	1	0	0	0	5	14	7	NC	NC	NC	NC
Central Blalock Islands, LAXX	-	-	-	-	-	8	14	28	46	17	15
Miller Rock Island, LAXX	16	5	5	0	21	57	81	101	97	118	104
Foundation Island, DCCO	236	163	62	90	182	-	85	-	-	-	-
East Sand Island, DCCO	43	20	13	16	138	274	119	113	0 [1]	2 [1]	39

[1] DCCO temporarily abandoned the nesting site at times during the breeding season; this atypical behavior likely resulted in fewer tags being deposited.

Table A2. Average annual recovery probabilities (95% credible intervals) of PIT tags on colonial waterbird breeding sites. Recovery probabilities are from Caspian tern (CATE), California and ring-billed gull (LAXX), double-crested cormorant (DCCO), and American white pelican (AWPE) colonies (see Map 1 for map of colony locations and names). Recovery probability is shown as the deposition probability multiplied by the detection probability. Data are those previously reported by Evans et al. (2019), with the exception of BGI AWPE colony, where estimates of deposition were imputed from Teuscher et al. (2015). Blanks cells indicate the colony sites was either inactive or was not scanned for PIT tags (see Table A1 above).

Recovery	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
PTI CATE	0.38 (0.25-0.51)	0.25 (0.18-0.34)	0.34 (0.23-0.45)	0.35 (0.25-0.45)	0.22 (0.13-0.3)	0.33 (0.22-0.45)					
I20 LAXX						0.12 (0.08-0.16)	0.12 (0.08-0.16) [1]	0.12 (0.08-0.17)	0.12 (0.08-0.16)	0.12 (0.09-0.17)	0.14 (0.1-0.19)
FDI DCCO [2]	0.37 (0.24-0.50)	0.36 (0.23-0.48)	0.31 (0.20-0.43)	0.23 (0.13-0.33)	0.18 (0.11-0.26)		0.10 (0.05-0.14)				
BGI AWPE [3]	0.66 (0.59-0.72)	0.84 (0.78-0.89)	0.73 (0.65-0.79)	0.56 (0.26-0.82)	0.67 (0.51-0.78)		0.71 (0.61-0.79)	0.61 (0.50-0.69)	0.58 (0.47-0.69)	0.54 (0.44-0.65)	0.52 (0.42-0.64)
BGI MIX (AWPE/LAXX)								0.12 (0.08-0.17) [1]	0.07 (0.04-0.11) [1]	0.11 (0.07-0.14)	0.08 (0.05-0.1)
BGI CATE										0.62 (0.45-0.79)[1]	
CSI LAXX	0.12 (0.08-0.16)	0.10 (0.07-0.14)	0.12 (0.08-0.16)	0.11 (0.07-0.15)	0.11 (0.07-0.15)	0.10 (0.07-0.14)	0.13 (0.09-0.17)				
CSI CATE	0.41 (0.29-0.52)	0.49 (0.34-0.63)	0.5 (0.36-0.63)	0.56 (0.39-0.71)	0.43 (0.29-0.56)	0.54 (0.38-0.67)	0.57 (0.4-0.73)				
CBI LAXX						0.12 (0.09-0.17)	0.14 (0.11-0.18)	0.14 (0.1-0.19)	0.14 (0.1-0.18)	0.14 (0.1-0.18) [1]	0.14 (0.1-0.18) [1]
CBI CATE	0.67 (0.49-0.84)	0.64 (0.45-0.8)	0.56 (0.3-0.79) [1]	0.58 (0.42-0.74)		0.62 (0.45-0.78) [1]	0.47 (0.26-0.67) [1]	0.46 (0.27-0.63)	0.46 (0.32-0.59)	0.32 (0.21-0.41)	0.23 (0.16-0.31)
MRI LAXX	0.12 (0.09-0.17)	0.12 (0.08-0.15)	0.11 (0.08-0.15)	0.12 (0.08-0.16)	0.12 (0.08-0.16)	0.12 (0.08-0.16)	0.13 (0.09-0.17)	0.13 (0.09-0.18)	0.12 (0.08-0.16)	0.11 (0.07-0.15)	0.12 (0.08-0.16)
ESI CATE	0.65 (0.48-0.81)	0.63 (0.45-0.79)	0.55 (0.39-0.69)	0.54 (0.39-0.67)	0.49 (0.35-0.63)	0.38 (0.26-0.49)	0.42 (0.31-0.54)	0.58 (0.41-0.72)	0.50 (0.36-0.65)	0.46 (0.32-0.58)	0.47 (0.32-0.6)
ESI DCCO	0.32 (0.21-0.43)	0.31 (0.19-0.44)	0.35 (0.22-0.48)	0.35 (0.23-0.49)	0.33 (0.2-0.45)	0.33 (0.21-0.45)	0.35 (0.22-0.48)	0.34 (0.19-0.48)	0.30 (0.19-0.4)	0.33 (0.21-0.45)	0.44 (0.28-0.6)

[1] Variation in detection probability partially inferred from other years (see also Payton et al. 2019)

[2] Colony was not scanned in 2013 and 2015-2018 but average annual estimates of recovery probabilities from other years were used to impute estimates of predation in those years (see Methods)

[3] Deposition was inferred using data from a different pelican colony