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Estimating Cause-Specific Mortality and Survival of Juvenile Fall Chinook Salmon: An Investigation of Avian Predation across Large Spatial Scales

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Abstract

To investigate the effects of piscivorous colonial waterbird predation on juvenile salmonids (smolts) and to determine what proportion of all sources of smolt mortality was due to predation, we analyzed a data set describing fall Chinook Salmon *Oncorhynchus tshawytscha* that were marked with PIT tags in the Columbia River, USA. We used a state-space Bayesian model that incorporated live detections of tagged fish and recoveries of tags from dead fish to jointly estimate predation and survival over multiple river reaches and years (2008–2019). By incorporating recoveries of tags on bird colonies, the model was also able to increase the precision and spatial extent of survival estimates compared with a more traditional capture–recapture model. Results indicated that the avian predation probability (proportion of available fish consumed) varied depending on the predator species, colony location, and the fish's rearing type. Estimates of cumulative predation probability ranged annually from 0.066 (95% credible interval = 0.049–0.089) to 0.283 (0.210–0.419), and predation accounted for 7.3% (4.3–11.9%) to 29.1% (19.7–40.2%) of all sources of smolt mortality during out-migration to Bonneville Dam. Probabilities of predation on wild smolts were significantly higher than those for hatchery smolts in most river reaches and years. Predation probabilities were the highest for colonies of American white pelicans *Pelecanus erythrorhynchos* and double-crested cormorants *Nannopterum auritum*, which were located near where wild smolts rear and congregate. Estimates of predation by Caspian terns *Hydroprogne caspia*, California gulls *Larus californicus*, and ring-billed gulls *L. delawarensis* were often <0.03 of available smolts annually. Collectively, results indicated that the cumulative effects of predation on Chinook Salmon smolts were substantial in some but not all river reaches and years. Future models that consider biological and environmental factors influencing smolt susceptibility to avian predation may provide a more holistic understanding of the degree to which predation limits fish survival.

Accurate assessment of cause-specific mortality is paramount to understanding factors that affect the survival of Pacific salmon *Oncorhynchus* spp. and the development of effective management plans. Numerous studies indicate that predation by piscivorous colonial waterbirds,

although not the original cause of salmonid declines (Nelson et al. 1991), is now a factor limiting the survival of some salmonid populations in the Columbia River basin, USA (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012, 2019; Payton et al. 2019). Multiple waterbird

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species nest in the region, with Caspian terns *Hydroprogne caspia* (CATE), double-crested cormorants *Nannopterum auritum* (DCCO), American white pelicans *Pelecanus erythrorhynchos* (AWPE), California gulls *Larus californicus*, and ring-billed gulls *L. delawarensis* (the two gull species are collectively referred to as “LAXX” hereafter) identified as the principal avian predators of juvenile salmonids during out-migration (Evans et al. 2012, 2019). Avian breeding colonies are located on numerous nesting sites spread throughout the middle and lower Columbia River, and the timing of the breeding season (April–September) coincides with the peak smolt out-migration period (April–August), making most anadromous juvenile salmonids (smolts) susceptible to predation by colonial waterbirds (Evans et al. 2012; Adkins et al. 2014).

Previous studies indicate that individual bird colonies can consume a large number and proportion of available smolts. For instance, Roby et al. (2003) estimated that CATE nesting on Rice Island in the Columbia River estuary consumed between 8.1 and 12.4 million smolts (Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, and steelhead *O. mykiss* combined) annually, while Lyons (2010) estimated that DCCO nesting on East Sand Island (ESI), also located in the estuary, consumed between 2.4 and 15.0 million smolts annually. In a study of avian predation rates or probabilities (proportion of available fish consumed), Evans et al. (2016) estimated that LAXX breeding on Miller Rocks Island (MRI), which is located in The Dalles Reservoir on the lower Columbia River, consumed 0.02–0.10 (equivalent to 2–10%) of available smolts, depending on the salmonid species and year. Evans et al. (2019) estimated that CATE nesting on Goose Island in Potholes Reservoir, located adjacent to the middle Columbia River, preyed upon more than 0.20 of the available smolts in some years. Previous research has largely focused on the effects 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 out-migration (Evans et al. 2019). The systemwide cumulative effects of multiple piscivorous colonial waterbirds on smolt survival are largely unknown but may be substantial given the documented high impacts from individual colonies. Previous studies have also largely focused on predation of Endangered Species Act-listed salmonids, whereas the effects of predation on nonlisted salmonid stocks are less understood.

The upriver bright (URB) fall Chinook Salmon stock is among the most productive salmon stocks in the Pacific Northwest (Langness and Reidinger 2003; Harnish et al. 2013). The URB stock is important for both regional and international commercial ocean fisheries as well as local sport and tribal fisheries (Dauble and Watson 1997).

The stock is also an integral part of the culture of Columbia River Tribes, which rely on salmon for ceremonial, subsistence, and economic reasons. Studies that involve the PIT tagging of URB Chinook Salmon rely on capturing and releasing smolts and then use subsequent recapture events to estimate fish behavior and survival (Fryer 2019). Although the results of these studies provide critical information, the specific causes of URB Chinook Salmon mortality—particularly the mortality of juveniles—remain largely unknown (Harnish et al. 2014). As such, having a better understanding of the effects of avian predation on URB Chinook Salmon mortality may be important for identifying and developing effective management plans. In addition to avian predation, salmonid smolts are subject to numerous other nonavian sources of mortality (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). Therefore, determining the degree to which avian predation limits smolt survival relative to these other sources of mortality may also be critical for prioritizing management actions for URB Chinook Salmon and other salmonid species and stocks in the Columbia River basin (Evans et al. 2019).

To investigate the cumulative effects of avian predation and in turn determine what proportion of total mortality ($1 - \text{survival}$) is due to avian predation, we conducted a mark–recapture–recovery analysis of hatchery and wild (i.e., naturally produced) URB Chinook Salmon smolts that were PIT-tagged and released into the Columbia River. Data were from a historical data set that included 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 CATE, DCCO, AWPE, and LAXX breeding at up to 13 individual colonies. In some cases, mixed-species nesting areas (i.e., locations where multiple avian predator species co-nested) were present, requiring careful consideration of tag recoveries to accurately estimate predation probabilities for the predator species present at each site. Collectively, results of this study provide a comprehensive, systemwide evaluation of the cumulative effects of avian predation on URB Chinook Salmon smolts at different spatial scales across a 12-year study period (2008–2019).

In addition to estimating spatially explicit predation probabilities, the modeling methods used herein incorporated tag recoveries from bird colonies. These recoveries can be used to generate more accurate and precise estimates of smolt survival compared with the more ubiquitous Cormack–Jolly–Seber (CJS) capture–recapture methods (Hostetter et al. 2018; Payton et al. 2019). For instance, recoveries of smolt PIT tags on bird colonies can be used to increase detections of fish after release, thus

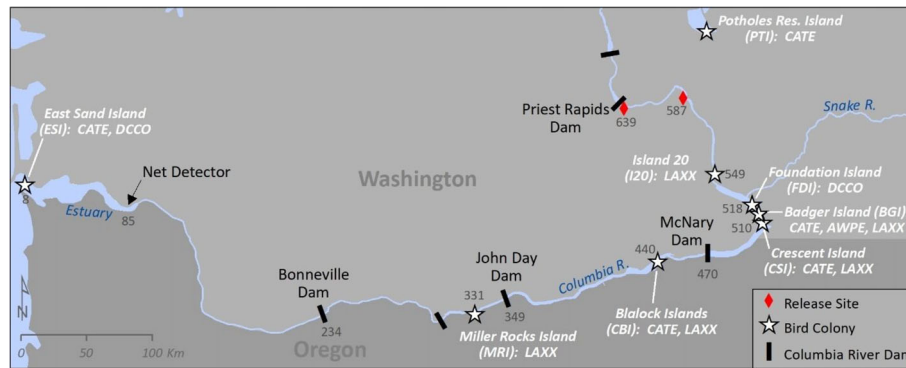


FIGURE 1. Mark–recapture–recovery locations of PIT-tagged hatchery and wild Chinook Salmon smolts released downstream of Priest Rapids Dam during 2008–2019. Release sites included the Priest Rapids Hatchery and the Hanford Reach section of the middle Columbia River. Recapture locations include McNary Dam, John Day Dam, Bonneville Dam, and a pair-trawl net detection system in the lower Columbia River. Recovery locations include Caspian tern (CATE), double-crested cormorant (DCCO), California gull and ring-billed gull (LAXX), and American white pelican (AWPE) colonies. Distances represent river kilometers from the Pacific Ocean.

providing additional information to evaluate spatially explicit survival. These newly developed Bayesian capture–recapture–recovery models may be especially important for cases in which sample sizes of tagged fish are small and/or recapture probabilities are low (Hostetter et al. 2018). To assess the effectiveness of and quantify the additional information provided by incorporating tag recoveries on bird colonies, we conducted a statistical simulation study comparing estimates of URB Chinook Salmon smolt survival as generated from a traditional CJS capture–recapture model (based solely on live detections of tagged fish) to estimates generated by the joint mortality and survival (JMS) capture–recapture–recovery model (based on detections of live and dead tagged fish) used herein.

METHODS

Study area.— We investigated predation and survival of hatchery and wild URB Chinook Salmon smolts that were marked with PIT tags and released into the middle Columbia River during 2008–2019 (Figure 1). Hatchery fish were released at the Priest Rapids Hatchery (PRH) downstream of Priest Rapids Dam at river kilometer (rkm) 639, whereas wild fish were captured in the Hanford Reach (HR) between rkm 557 and 639 and released at boat ramps between rkm 576 and 587 (Figure 1). After release, survival and predation were evaluated through four river reaches during smolt out-migration from the middle Columbia River to the Columbia River estuary: (1) from release to McNary Dam (rkm 470), (2) from McNary Dam to John Day Dam (rkm 349), (3) from John Day Dam to Bonneville Dam (rkm 234), and (4) from passage below Bonneville Dam as smolts to their return to Bonneville Dam as adults (Figure 1). River

reaches were defined by the locations of PIT tag detection sites and the locations of bird colonies that were capable of foraging on tagged fish within each river reach (see Figure 1 for bird colony locations).

Mark–recapture–recovery.— Hatchery smolts from PRH and wild smolts that were captured with seine nets in the HR were PIT-tagged (134-kHz, full-duplex tags; Biomark) and released annually into the middle Columbia River during 2008–2019. During 2008 and 2009, wild smolts were tagged with both 12- × 2-mm (length × width) and 8.5- × 2.0-mm tags. During 2010–2019, all smolts (hatchery and wild) were tagged with 12- × 2-mm tags. At the time of tagging, hatchery smolts ranged in size from 45 to 139 mm FL, with a mean of 79 mm FL. Wild smolts ranged in size from 44 to 136 mm FL, with a mean of 67 mm FL. After tagging, hatchery fish were held in captivity for an additional 2–4 weeks prior to release, whereas wild fish were held in tanks with recycled river water for 24 h prior to release. In most years (2008–2016), hatchery fish were released during a 2-week period in the latter half of June; in 2017–2019, fish were released during a 4-week period from mid-May to mid-June. Wild fish were released during a 1-week period in early June during all years.

After release, a proportion of tagged smolts was detected (passively recaptured) alive at downstream detection sites equipped with PIT tag arrays (a series of antennas), which delineated the spatial segments for which predation and survival probabilities were estimated. Arrays were located at the McNary Dam, John Day Dam, and Bonneville Dam juvenile fish bypass facilities; at a corner collector (a spill-like route) at Bonneville Dam only; and in a vessel-towed pair-trawl net detection system in the lower Columbia River (rkm 75; Figure 1). Adult URB Chinook Salmon returning to the Columbia River after ocean residency were also detected at arrays located

in fishways at Bonneville Dam 1–5 years after their release as smolts. Smolt survival and predation probabilities were estimated based on (1) detections of live fish passing tag arrays located at dams and (2) recoveries of tags from dead fish on bird colonies (see below for details). Although recapture data from the pair-trawl detection system in the upper Columbia River estuary were included in the model, low recapture probabilities and numerous weeks of nonoperation of the trawl resulted in small sample sizes of tagged fish and consequently imprecise estimates of survival. To present our results in a more informative and intuitive manner, we defined four river reaches. The first three reaches corresponded directly with the first three delineated river segments. Reach 4, however, was defined to be the passage of smolts downstream of Bonneville Dam to the Pacific Ocean and their return to Bonneville Dam as adults. Recapture records and dates of operation for the pair-trawl system were retrieved from the PIT Tag Information System, a regional mark-recapture–recovery database maintained by the Pacific States Marine Fisheries Commission (PSMFC 2021).

After release, a proportion of tags implanted in URB Chinook Salmon smolts was also recovered on bird colonies (i.e., tags from dead fish). Colonies included in the study were those previously identified as posing a potential threat to juvenile salmonid survival during out-migration (Evans et al. 2012, 2019). Bird species and colonies included CATE associated with nesting areas on (1) Pot-holes Reservoir Island, (2) Badger Island (BGI), (3) Crescent Island, (4) Central Blalock Islands, and (5) ESI; LAXX associated with nesting areas on (6) Island 20, (7) BGI, (8) Crescent Island, (9) Central Blalock Islands, and (10) MRI; DCCO associated with nesting areas on (11) Foundation Island (FDI) and (12) ESI; and AWPE nesting on (13) BGI (Figure 1). Additional tags and modeling considerations (see *Predation and Survival Estimation* below) were also needed for a 14th nesting area on BGI, where the colonies of LAXX and AWPE partially overlapped (i.e., an area of co-nesting) in some years.

The methods of Evans et al. (2012) were used to recover PIT tags from each nesting area. 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 was scanned for tags following each breeding season, with a minimum of two complete sweeps or passes of each site conducted in each year. The land area occupied by birds during each breeding season was determined based on aerial images and/or ground surveys of nesting areas conducted during the peak period of the breeding season in May–June (see also Adkins et al. 2014).

Not all active bird colonies were scanned for smolt PIT tags in all years during 2008–2019. The two notable examples were the AWPE colony on BGI in 2013 and the

DCCO colony on FDI during 2013 and 2015–2019, where large numbers of birds nested, but there were no efforts to recover fish tags after the breeding season. To address this data gap, we assumed that the average annual predation probabilities observed from years when the colony was scanned were similar to those in years when the colony was not scanned. Estimates of colony size (number of breeding adults) indicated that the DCCO colony on FDI has remained relatively stable in size since 2008, ranging from 308 to 390 breeding pairs annually (Evans et al. 2019). The BGI AWPE colony, however, increased in size from a low of 1,349 breeding pairs in 2008 to a high of 3,330 pairs in 2018 (Cramer et al. 2021). Estimates of average predation from these two colonies in these specific years represent “best guess” estimates of predation and are explicitly labeled as such in the tables and figures (see *Results* below).

Recovery of PIT tags ingested by avian predators was the result of two stochastic processes: that is, not all PIT tags ingested by avian predators were deposited on the nesting colony (i.e., deposition probabilities were <1.0), and not all deposited tags were detected by researchers after the breeding season (i.e., detection probabilities were <1.0). For instance, some proportion of consumed tags was regurgitated or defecated at off-colony loafing or roosting sites, deposited tags were removed or damaged by wind or water erosion, or deposited tags were missed (i.e., not detected) by researchers during the scanning process (Hostetter et al. 2015). Given these known sources of tag loss, an accurate estimate of the total number of tagged fish that were consumed by birds required an adjustment or correction for both PIT tag deposition and detection probabilities on bird colonies. The methods and data of Hostetter et al. (2015) and Evans et al. (2019, 2022b) were used to estimate colony-specific detection probabilities and predator-specific (CATE, DCCO, LAXX, and AWPE) deposition probabilities.

Unlike deposition probabilities, results of detection probability studies indicated that detection varied within and between years, necessitating empirically derived estimates of detection probability at each colony during each year (Hostetter et al. 2015; Payton et al. 2019). To estimate detection probabilities, as part of independent studies, PIT tags were intentionally sown in nesting areas by researchers prior to, during (when possible), and after the breeding season each year at each of the colonies included in this study (Evans et al. 2012, 2019, 2022a, 2022b). Recoveries of sown tags during scanning efforts after the nesting season were then used to model the probability of detecting a tag that was deposited on the colony during the breeding season (see also *Predation and Survival Estimation* below). The colony-specific PIT tag detection probabilities and predator-specific PIT tag deposition probabilities (collectively referred to as “recovery probabilities”) used

in this study were those previously reported by Evans et al. (2019, 2022a).

Predation and survival estimation.—The JMS estimation methods of Payton et al. (2019) were used to estimate segment-specific and cumulative URB Chinook Salmon smolt predation and survival probabilities during 2008–2019. The model simultaneously estimated predation and survival probabilities by incorporating detections of live and dead PIT-tagged fish across space and time. Live PIT-tagged fish were possibly recaptured at up to five downstream passive detection sites that delineated the boundaries of the five spatial segments evaluated in the model. Predation on PIT-tagged fish was evaluated for up to four genera of avian predators (CATE, DCCO, AWPE, and LAXX) nesting on colonies across eight islands in the Columbia River. Each year, we estimated predation probabilities for up to 13 genus/island-specific avian colonies. To inform the genus/island-specific predation rates, tags were generally recovered from 13 single-genus nesting areas; however, in some years, the AWPE and LAXX colonies on BGI overlapped spatially, creating a 14th, “mixed” nesting area from which tags were recovered.

Hatchery and wild smolts were tagged and released at different times. Temporal variation both within and across years 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). We therefore defined cohorts (groups of fish that were assumed to have experienced equal rates of mortality/survival and recapture) by year, rearing type, and day of release. Here, we describe the data, parameters, and likelihood equations of the employed model for all fish released in a single given cohort.

The primary data informing our model consisted of two vectors, \mathbf{y} and \mathbf{r} , to describe each fish’s recapture (passive encounter) and tag recovery history. The vector \mathbf{y} was a 5-length vector, where y_j was an indicator variable of the successful recapture of the fish at recapture opportunity j , which delineated the end of segment j . The vector \mathbf{r} was a 15-length vector identifying the fish’s nesting area of recovery or lack thereof. As such, \mathbf{r} had a single element equal to 1, with the rest of the elements equal to 0, where $r_1 = 1$ indicated that a fish was unrecovered, $r_a = 1$ for $a \in \{2, \dots, 14\}$ indicated recovery on single-genus nesting area a , and $r_{15} = 1$ indicated recovery from the mixed-species nesting area on BGI (nesting area $a = 15$).

Two parameters were of primary importance in defining the model:

\mathbf{p} is a 5-length vector, where p_j represents the probability that a fish alive at recapture opportunity j was successfully recaptured. We assumed that $p_5 = 1$, as recapture probabilities for adults detected at Bonneville

Dam fishways were assumed to be effectively perfect. Additionally, for days in which the pair-trawl net detection system was not in operation, p_4 was assumed to be 0.

Θ is a 5×14 matrix, where $\Theta_{j,d}$ represents the probability (from release) that a fish entered segment j alive and then, prior to arrival at recapture opportunity j , subsequently succumbed to some unspecified cause of mortality for $d = 1$ or was preyed upon by (genus/island-specific) colony d for $d \in \{2, \dots, 14\}$. Implicit from this parameterization is that survival from release through segment k is equal to $1 - \sum_{j \leq k} \sum_d \Theta_{j,d}$.

Three additional parameter vectors were needed to enumerate the likelihood of recovering tags:

$\boldsymbol{\rho}$ is a 14-length vector, where, for $d \in \{2, \dots, 14\}$, ρ_d represents the proportion of tags consumed by birds from colony d that were subsequently deposited on their single-genus nesting areas (where $d = a$) versus the mixed nesting area ($a = 15$). Given that $d = 1$ represents unspecified mortalities, we let $\rho_1 = 1$ to simplify the likelihood expression. This vector is needed only to account for the two colonies responsible for tags recovered from the mixed colony on BGI in certain years; for all other colonies, $\rho_d = 1$. The full details on how the values of $\boldsymbol{\rho}$ were informed and estimated are provided as Appendix S1.

$\boldsymbol{\phi}$ is a 14-length vector, where ϕ_d represents the probability of a tag consumed by a bird from colony d being deposited on that bird’s nesting area for $d \in \{2, \dots, 14\}$. We let $\phi_1 = 0$ represent the disappearance of tags from fish that died due to unspecified causes. Informative prior distributions informing the values of $\boldsymbol{\phi}$ were taken from Hostetter et al. (2015) for CATE, DCCO, and LAXX and were taken from Evans et al. (2022a) for AWPE.

$\boldsymbol{\psi}$ is a 15-length vector, where ψ_a represents the probability of recovering a tag deposited on nesting area a for $a \in \{2, \dots, 15\}$. We let $\psi_1 = 0$ represent the lack of recoveries of fish that died from all other unspecified causes. Informative prior distributions that were used to inform the values of $\boldsymbol{\psi}$ were taken from Evans et al. (2022b).

The employed model can be expressed by incorporating these parameters into recursive functions, $\chi_{j,d}$, which are defined to represent the probability for the recovery of a fish that was not subsequently recaptured after entering segment j . The probability of a tag being recovered from a single-genus nesting area (i.e., where $a = d$ for $a \in \{2, \dots, 14\}$) can be expressed as

$$\chi_{j,a} = \rho_a \times \theta_{j,a} \times \phi_a \times \psi_a + (1 - p_{j+1}) \times \chi_{j+1,a}$$

The probability of a tag being recovered from the mixed nesting area ($a = 15$) can be expressed as

$$\chi_{j,15} = \sum_{d>1} (1-\rho_d) \times \theta_{j,d} \times \phi_d \times \psi_{15} + (1-p_{j+1}) \times \chi_{j+1,15}.$$

The probability of a tag going unrecovered can be expressed as

$$\chi_{j,1} = \sum_d \theta_{j,d} \times \left[\rho_d \times (1-\phi_d \times \psi_d) + (1-\rho_d) \times (1-\phi_d \times \psi_{15}) \right] + (1-p_{j+1}) \times \chi_{j+1,1}.$$

If we define m to be the final recapture opportunity at which the fish was seen, with $m = 0$ representing a fish that was never reseen (i.e., recaptured or recovered) after release, then the portion of the aggregate likelihood associated with the recapture/recovery history of each fish from a given cohort can be expressed as

$$L = \prod_a \chi_{m+1,a}^{r_a}$$

for $m = 0$;

$$L = \prod_{j \leq m} \left[p_j^{y_j} \times (1-p_j)^{(1-y_j)} \right] \times \prod_a \chi_{m+1,a}^{r_a}$$

for $m \in \{1, \dots, 4\}$; and

$$L = \prod_j \left[p_j^{y_j} \times (1-p_j)^{(1-y_j)} \right] \times \left(1 - \sum_j \sum_d \theta_{j,d} \right)$$

for fish surviving to adulthood. The former product describes a fish's recapture history prior to its final recapture, and the latter portion of the equation describes the fish's subsequent recovery or lack thereof after its final recapture.

There were considerable differences in how the probabilities of survival, mortality, recapture, and recovery were related among the temporal and biological cohorts. Probabilities of the recovery of consumed tags (deposition and detection combined) were assumed to be equal across rearing types and within each day of release. As described above, informed priors were employed to estimate the colony-specific values of deposition and the nesting area-specific values of detection, which explicitly account for the increasing likelihood of detecting tags that were deposited later in the year. Probabilities of recapture were assumed to be independent from year to year and between rearing types. For a given rearing type in a given year, the

log-odds of recapture at a given recapture opportunity site on a given day were assumed to be equal to the log-odds for the previous day plus (or minus) some random error,

$$\ln\left(\frac{p_{i+1}}{1-p_{i+1}}\right) = \ln\left(\frac{p_i}{1-p_i}\right) + \epsilon_i,$$

where i denotes the daily cohort, $\epsilon_i \sim \text{Normal}(0, \sigma_\epsilon)$, and the prior distribution for the probability of recapture on the first day was assumed to be $\text{Uniform}(0, 1)$. Aggregate survival/mortality probabilities were also assumed to be independent from year to year and between rearing types. Similar to the modeling of recapture probabilities, serial correlation among days was accounted for with a log-odds random-walk approach, as described by Payton et al. (2019). Additionally, the informed partitioning methods of Evans et al. (2022b) were also used to allow for the sharing of information among years to increase the precision of segment-specific estimates. In brief, a vector of aggregate life path possibilities was constructed, including the probability of survival to return as an adult, the cumulative probability (across all segments) of predation by each colony, and segment-specific probabilities of death from unspecified sources, to be the basis for modeling variations across days. The cumulative probability of predation by each colony was subsequently partitioned across river segments. For a given rearing type in a given year, the log-odds of each aggregate life path possibility on a given day were assumed to be equal to the respective log-odds in the previous day plus (or minus) some random error,

$$\ln\left(\frac{\bar{\theta}_i^*}{\bar{\theta}_{\text{ref}_i}^*}\right) = \ln\left(\frac{\bar{\theta}_i^*}{\bar{\theta}_{\text{ref}_i}^*}\right) + \bar{\epsilon}_i,$$

where $\theta^* = \text{vec}(\theta)$ (i.e., a vectorization of θ), with θ_{ref}^* denoting the reference level, defined to be death from an unspecified source in the final segment; i denotes the daily cohort; and $\delta_{d,i} \sim \text{Normal}(0, \sigma_\epsilon)$. See Payton et al. (2019) for more detail. Each vector representing the probabilities for the aggregated life path possibilities is a simplex, and the prior distribution for the initial day's simplex was assumed to be $\text{Dirichlet}(\mathbf{1})$, where $\mathbf{1}$ is an appropriately sized vector of ones. Weakly informative priors of $\text{Half-Normal}(0, 5)$ were also implemented for all random-walk variance parameters. Previous testing and applications of the JMS model have demonstrated that given sufficient data, the information provided by prior distribution assignments has negligible impacts on predation and survival estimates but is valuable for computational efficiency. Annual estimates were calculated as weighted averages, defined by weekly release counts within each biological cohort. We refer to the summation of predation

TABLE 1. Numbers of PIT-tagged hatchery (H) and wild (W) Chinook Salmon smolts released in the middle Columbia River that were subsequently recaptured alive (i.e., detected) at PIT tag arrays during out-migration or when returning as an adult or whose tags were recovered (i.e., representing dead fish) on bird colonies. The PIT tag arrays were located at McNary Dam (MCJ), John Day Dam (JDA), Bonneville Dam (BON), and a pair-trawl net detection system in the estuary (EST). Avian predator species include Caspian terns (CATE), double-crested cormorants (DCCO), California gulls and ring-billed gulls (LAXX), American white pelicans (AWPE), and mixed-species colonies of AWPE and LAXX (MIX) that were present during 2015–2019. See Figure 1 for a map of release, recapture, and recovery locations.

Year	Rearing type	Released	Fish recaptured alive					Tags recovered on bird colonies				
			MCJ	JDA	BON	EST	Adult ^a	CATE	DCCO	LAXX	AWPE	MIX
2008	H	2,994	340	154	191	10	37	27	29	5	5	
	W	16,651	862	544	274	37	128	38	250	17	64	
2009	H	2,994	450	142	183	13	14	43	15	3	5	
	W	13,728	916	401	213	31	41	69	168	2	131	
2010	H	2,956	391	149	172	10	32	14	22	4	14	
	W	4,851	271	127	101	19	36	16	53	1	91	
2011	H	2,994	262	182	135	3	113	18	24	0	13	
	W	10,337	599	446	228	0	140	66	82	0	161	
2012	H	42,844	3,034	4,078	1,613	69	795	305	249	24	252	
	W	4,891	179	239	94	5	25	22	70	2	38	
2013	H	42,906	4,925	2,589	859	102	900	215	266	85	0	
	W	4,183	236	151	115	13	40	9	8	6	0	
2014	H	42,903	6,431	2,707	2,168	197	149	245	154	96	208	
	W	9,940	880	455	341	29	38	41	37	21	107	
2015	H	42,621	2,720	2,028	663	14	36	389	108	181	60	76
	W	4,965	77	77	24	0	2	17	5	16	54	35
2016	H	42,955	4,128	1,912	1,488	65	112	249	45	157	19	101
	W	9,926	330	166	99	6	15	22	4	29	66	144
2017	H	42,840	2,840	2,095	3,019	50	254	228	1	133		363
	W	9,989	537	317	355	0	13	31	1	19		260
2018	H	42,895	2,370	1,915	1,689	39	160	186	33	129	30	522
	W	9,987	289	224	128	0	9	13	6	8	17	380
2019	H	42,850	890	1,314	1,304	0	39	103	12	110	11	514
	W	9,989	95	194	110	0	0	16	2	19	11	327
All		464,189	34,052	22,606	15,566	712	3,128	2,382	1,644	1,067	1,357	2,722

^aAdult returns were incomplete during 2017–2019.

and survival across multiple interarray segments as “cumulative” estimates. We refer to the summation of predation across multiple colonies as “aggregate” estimates of predation.

All models were implemented with the software Stan accessed through R version 4.1.0 (R Core Team 2021) using RStan version 2.21.1 (Stan Development Team 2020). All estimates presented here represent posterior distribution medians, with 95% credible intervals (CRIs) representing the highest density intervals calculated with HDInterval version 0.2.2 (Meredith and Kruschke 2020). To simulate random draws from the joint posterior distribution, we ran four Hamiltonian Monte Carlo–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. 1995), and all accepted chains reported zero divergent transitions. Reported estimates represent simulated posterior medians along with 95% highest (posterior) density intervals (95% CRIs).

Survival model comparisons.—We further investigated how incorporating the recoveries of smolt PIT tags on bird colonies by using the JMS model affected the accuracy and precision of survival estimates compared to methods in common use. We developed a series of simulated data sets with which we compared estimates of survival probabilities provided by the Bayesian JMS model to estimates provided by a frequentist CJS model. Specifically, we simulated data sets that were constructed to resemble a variety of tagging efforts for wild Chinook Salmon smolts (average annual sample size = 9,040 PIT-tagged fish; range = 4,183–16,651; Table 1). Simulations

were constructed to represent data attained within a migration year; as such, recaptures were limited to the first four opportunities, ending with the pair-trawl detection system. We wanted to represent a broad array of relevant survival, recapture, and recovery rates; to represent the duration and magnitude of release numbers; and to reflect diversity in the location and magnitude of predation. Therefore, prescribed probabilities for simulations were based on estimates from 4 years of data: 2008, 2013, 2015, and 2017. These years were chosen to represent years with relatively lower predation and greater survival (2008), lower predation and lower survival (2013), greater predation and greater survival (2017), and greater predation and lower survival (2015). Five-hundred simulated data sets were developed from each set of prescribed rates.

Estimates of cumulative survival were then developed for each simulated data set using (1) the JMS model as described above and (2) the CJS model, with estimates derived using program RMark (Laake 2013). Single-release CJS estimates (using an identity link function) are commonly used to estimate annual survival in the Columbia River basin (Northwest Fisheries Science Center 2022). However, the inclusion of recoveries in the JMS model necessarily requires a recognition of the day of release, as recovery probabilities can vary considerably throughout the migration season. As the prescribed probabilities varied considerably throughout the year, we believed that it would not be a fair comparison to allow the JMS model to account for this variation while the CJS model assumed that there was none. Therefore, we independently modeled daily cohorts with the CJS model and defined annual estimates to be geometric means using sample sizes as weights and variance estimates approximated per the delta method.

Metrics of the accuracy and precision of model results were examined to assess the relative performance of each model in estimating survival. Metrics relating to the accuracy of estimates included the average error (estimated value minus the prescribed value; i.e., bias), average absolute error, and maximum error. Metrics relating to the precision of estimates included average uncertainty and coverage probability. Average uncertainty was defined as the average width of the estimated 95% uncertainty intervals (confidence intervals for the CJS model results and CRIs for the JMS model results). Coverage was defined as the proportion of uncertainty intervals that contained the prescribed parameter value.

RESULTS

Mark–Recapture–Recovery

In total, 464,189 URB Chinook Salmon smolts were PIT-tagged and released during 2008–2019 (Table 1). Of

these, 354,792 were hatchery fish from PRH and 109,437 were wild fish from the HR of the middle Columbia River (Figure 1). Release numbers varied considerably by year (range = 7,807–52,882 fish/year; Table 1) and rearing type (range = 2,956–42,955 fish·year⁻¹ rearing type⁻¹). Numbers of tagged fish detected alive at downstream recapture sites also varied by detection site and year, as did the number of tags (representing dead fish) recovered on bird colonies (Table 1). In total, 9,172 tags (range = 435–1,325 tags/year) were recovered on bird colonies. Only a small number and proportion of smolts released at PRH and in the HR returned to Bonneville Dam as adults; adult returns ranged from 38 to 940 fish/release year (Table 1). Numbers of tags recovered from each avian predator genus (CATE, DCCO, LAXX, and AWPE) are provided in Table 1, while the numbers recovered on each individual colony are provided in Table S1. Recovery probabilities of tagged fish are provided in Table S2.

Predation Probabilities

Cumulative predation probabilities, measured as predation by all 13 bird colonies on URB Chinook Salmon smolts from release to the Pacific Ocean, averaged 0.089 (95% CRI = 0.078–0.102) for hatchery smolts, ranging from 0.066 (0.049–0.089) to 0.133 (0.102–0.170), and averaged 0.153 (0.134–0.172) for wild-reared smolts, ranging from 0.082 (0.057–0.120) to 0.283 (0.210–0.419). Of the bird taxa evaluated (CATE, DCCO, LAXX, and AWPE), aggregated (taxon-specific) predation probabilities were often—but not always—highest for the AWPE and DCCO colonies (Figure 2). Annual aggregate effects of AWPE, which were limited to a lone colony on BGI, averaged 0.026 (95% CRI = 0.021–0.033) for hatchery smolts and 0.081 (0.066–0.097) for wild smolts, with impacts as high as 0.214 (0.146–0.347). Aggregate impacts of DCCO predation, which included two colonies, averaged 0.025 (95% CRI = 0.020–0.029) for hatchery smolts and 0.045 (0.037–0.056) for wild smolts and were as high as 0.079 (0.051–0.140) for wild smolts. The aggregate effects of predation by all LAXX colonies were high in some but not all years, with predation probabilities averaging 0.023 (95% CRI = 0.019–0.036) and 0.018 (0.013–0.024) for hatchery and wild smolts, respectively, and estimated probabilities as high as 0.042 (0.033–0.054) were observed for wild smolts. In general, the aggregate effects of predation by all CATE colonies were the lowest among the four predator taxa evaluated, averaging 0.014 (95% CRI = 0.013–0.016) for hatchery smolts and 0.008 (0.007–0.009) for wild smolts, with the highest estimate being 0.027 (0.019–0.039) for hatchery smolts in 2009 (Figure 2).

Of the colonies that were capable of foraging in reach 1 (release to McNary Dam), the highest predation probabilities were those of the AWPE colony on BGI, with annual predation probabilities ranging from 0.006 (95%

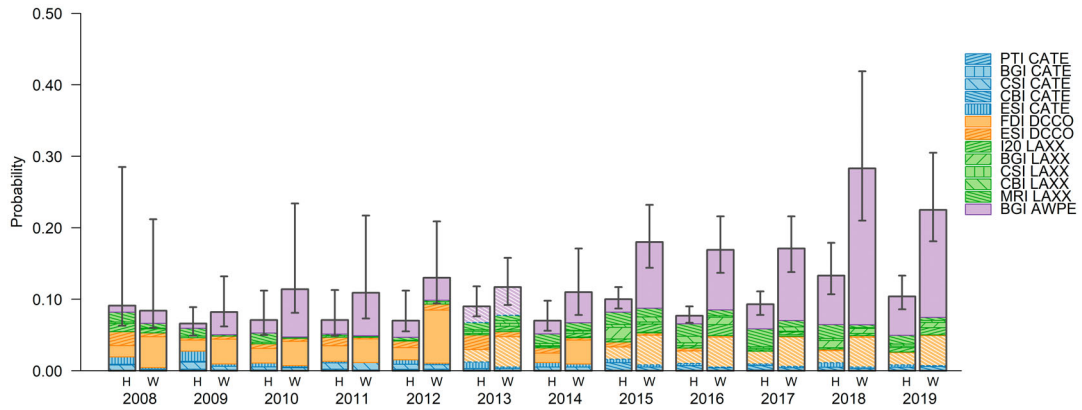


FIGURE 2. Estimated cumulative mortality due to avian predation (proportion of available fish consumed) of PIT-tagged hatchery (H) and wild (W) Chinook Salmon smolts during 2008–2019. Predator species include Caspian terns (CATE), double-crested cormorants (DCCO), California gulls and ring-billed gulls (LAXX), and American white pelicans (AWPE; see Figure 1 for definition of colony abbreviations). Error bars represent 95% credible intervals. White cross-hatching represents “best guess” estimates of predation based on cases in which empirical data for that colony in the specified year were lacking, so the average rate from past years was used (see Methods).

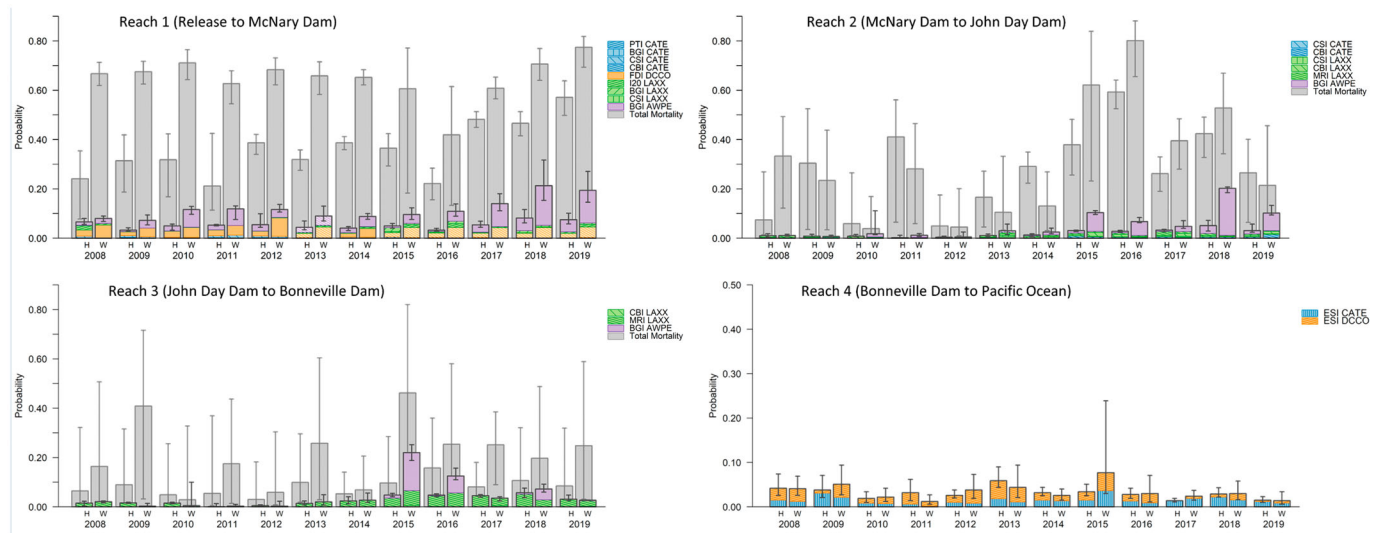


FIGURE 3. Estimated reach-specific total mortality (gray bars) and mortality due to avian predation (colored bars) of PIT-tagged hatchery (H) and wild (W) Chinook Salmon smolts during 2008–2019. Predator species include Caspian terns (CATE), double-crested cormorants (DCCO), California gulls and ring-billed gulls (LAXX), and American white pelicans (AWPE; see Figure 1 for definition of colony abbreviations). Error bars represent 95% credible intervals. White cross-hatching represents “best guess” estimates of predation based on cases in which empirical data for that colony in the specified year were lacking, so the average rate from past years was used (see Methods).

CRI = 0.002–0.018) to 0.214 (0.146–0.347), and the DCCO colony on FDI, with annual predation probabilities ranging from 0.013 (0.007–0.025) to 0.071 (0.043–0.132), depending on the colony, year, and rearing type (Figure 3). Probabilities of predation by all other colonies foraging in reach 1 were generally <0.010 per colony in each year. Cumulative estimates of predation (predation by all colonies foraging in reach 1 combined) ranged from a low of 0.033 (95% CRI = 0.028–0.040) on hatchery smolts in 2016 to a high of 0.213 (0.153–0.317) on wild

smolts in 2018 (Figure 3). In reach 2 (McNary Dam to John Day Dam), predation probabilities were generally low (<0.010) in most years, with the exception of predation by the AWPE colony on BGI, which had predation probabilities as high as 0.176 (95% CRI = 0.094–0.332), and, to a lesser degree, the LAXX colonies on MRI, which had predation probabilities as high as 0.016 (0.002–0.030; Figure 3). Similarly, 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 as 0.158 (95% CRI = 0.076–0.295) and 0.061 (0.021–0.146) on wild smolts by the AWPE colony on BGI and the LAXX colonies on MRI, respectively (Figure 3). Predation probabilities in reach 3 were especially high on wild smolts in 2015 and 2016, with cumulative estimates of 0.125 (95% CRI = 0.11–0.157) and 0.22 (0.188–0.252), respectively. Results indicate that despite the location of the BGI colony in McNary Reservoir, birds were regularly commuting to forage on smolts downstream of John Day Dam, over 150 rkm from their nesting site (Figure 1). Cumulative estimates of avian predation on wild smolts in 2018 were the highest reach-specific estimates observed during the 12-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) and relatively sparse recaptures, which resulted in imprecise estimates of predation in reach 3. Of the colonies foraging in reach 4 (Bonneville Dam to the Pacific Ocean), predation probabilities were generally the highest for DCCO nesting on ESI, with probabilities ranging annually from <0.001 to 0.040 (95% CRI = 0.012–0.134) depending on the year and the fish's rearing type (Figure 3). Cumulative estimates of predation by both DCCO and CATE in reach 4 ranged annually from 0.014 (95% CRI = 0.011–0.019) to 0.059 (0.040–0.090) on hatchery smolts and from 0.012 (0.006–0.027) to 0.077 (0.030–0.239) on wild smolts (Figure 3). Analogous to the results for reaches 2 and 3, small sample sizes of fish surviving to below Bonneville Dam resulted in imprecise estimates of predation in reach 4, particularly for wild fish.

Comparisons of predation between hatchery and wild smolts indicated that wild fish were often but not always more likely to be consumed than hatchery fish, with statistically significant differences in predation probabilities observed in multiple river reaches and years (Figures 2 and 3). There was also evidence that predation, particularly on wild smolts, increased during the study period, with cumulative average annual predation estimates increasing from 0.111 (95% CRI = 0.091–0.136) during 2008–2014 to 0.208 (0.181–0.239) during 2015–2019 for wild fish. Increases in predation during the latter part of the study period were largely associated with the AWPE colony on BGI.

Total Mortality

Estimated total mortality (1 – survival) of URB Chinook Salmon smolts was highly variable depending on the river reach, year, and rearing type (Figure 3). Total mortality was consistently the highest in reach 1 (release to McNary Dam), averaging 0.357 (95% CRI = 0.328–0.381) annually in hatchery smolts, with a range from 0.212 (0.110–0.410) to 0.571 (0.500–0.639), and averaging 0.644 (0.610–0.676) annually in wild smolts, with a range from

0.419 (0.149–0.626) to 0.774 (0.705–0.826). Results indicated that more than 50% of all wild smolts died prior to reaching McNary Dam in 11 of the 12 study years evaluated (Figure 3). Total mortality was often but not always lower in reaches 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 smolts died prior to reaching Bonneville Dam: estimates averaged 0.579 (95% CRI = 0.552–0.612) for hatchery smolts, ranging from 0.369 (0.190–0.524) to 0.728 (0.690–0.782), and averaged 0.821 (0.803–0.837) for wild smolts, ranging from 0.723 (0.681–0.768) to 0.926 (0.855–0.978). Coincident with increases in predation, there was some evidence that total mortality, particularly the mortality of wild smolts, increased during the study period, with estimates from the years 2015–2018 significantly higher than estimates from the years 2008–2014 in reaches 2 and 3 (Figure 3). An estimate of total smolt mortality through reach 4 could not be calculated because there was no smolt PIT tag detection site downstream of the bird colonies in the lower Columbia River estuary (Figure 1). Estimated total mortality to adulthood, based on the proportion of smolts released that died before returning to Bonneville Dam as adults, ranged annually from 0.962 (95% CRI = 0.958–0.969) to 0.996 (0.996–0.997) for hatchery fish and from 0.986 (0.984–0.988) to 0.997 (0.996–0.998) for wild fish during 2008–2016 (2016 was the last year with complete adult return data available; Table 1). These translate into smolt-to-adult survival percentages of 0.3% to 3.6%, depending on the out-migration year and rearing type.

Coincident with trends in predation, wild smolts were considerably more likely to die than hatchery smolts during out-migration in most but not all river reaches and years (Figure 3). For instance, in reach 1, wild fish were significantly more likely to die than hatchery fish during 11 of the 12 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 2015–2019, wild fish were again more likely to die relative to their hatchery counterparts. Collectively (in all reaches and years), the results indicated that hatchery smolts were more likely to survive out-migration to Bonneville Dam and their probabilities of returning as adults were generally higher than those for wild smolts.

Annual comparisons of the total mortality of URB Chinook Salmon smolts and the mortality due to bird predation indicated that avian predation accounted for 7.3% (95% CRI = 4.3–11.9%) to 16.2% (12.0–21.3%) of hatchery fish mortality and for 8.0% (5.5–12.4%) to 29.1% (19.7–40.2%) of wild fish mortality during smolt out-migration from 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%

(95% CRI = 5.9–25.0%) to 28.6% (19.8–40.3%) of total mortality per year. In reaches 2 and 3, avian predation accounted for <20% of total mortality in most years, with the exception of 2015 and 2016, when increases in predation probabilities coincided with increases in total mortality (Figure 3). Results indicate that although the cumulative effects of bird predation were a substantial source of smolt mortality in some river reaches and years, it was not the dominant source of mortality, with most fish dying from nonavian causes during out-migration to Bonneville Dam.

Survival Model Comparisons

In general, the CJS model tended to produce less-biased estimates of survival across all years compared to the JMS model (Table 2). However, the average absolute error of the JMS model estimates was less than that of the CJS model estimates for 9 of the 12 comparable year \times reach combinations (Table 2), suggesting that the JMS model generally produced more accurate estimates. Error for both models was generally small in magnitude (<0.03), with the exception of the 2015 data sets. These metrics suggest that although the CJS estimates were less biased than the JMS estimates in relation to the prescribed parameter values in aggregate, the estimates of the JMS model displayed less error for each simulation individually (i.e., displayed less absolute error). Furthermore, the maximum level of error in any given river reach and year was generally greater for the CJS estimates than for the JMS estimates (Table 2; Figure 4). The estimates produced by the JMS model were more consistent, with the most egregious error measuring 0.19. In contrast, estimates produced by the CJS model could be substantially different from the prescribed estimate, overestimating survival to John Day Dam by up to 0.82 in the 2015 simulations (Table 2).

The uncertainty intervals for the JMS model were also consistently narrower than those of the CJS model (Figure 3). For all 12 comparable year \times reach combinations, the average uncertainty interval widths produced by the JMS model were less than those produced by the CJS model, with some year \times reach combinations generating uncertainty intervals that were, on average, two to four times the size of the intervals produced by the JMS model for the same data set (Table 2). The CJS model often produced very wide 95% confidence intervals (Figure 4). This was especially true for estimates of survival to Bonneville Dam, with CJS estimates ranging from 0% 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, as the estimated uncertainty interval coverage associated with the JMS model was generally greater than that of the CJS model. The annual estimates with reduced JMS coverage probabilities were associated with the widest CJS intervals in which many overlapped

one limit or both limits of the unit interval (Figure 4). The JMS model consistently produced compact 95% CRIs throughout the system, including estimates of survival to the pair-trawl net detection system in the Columbia River estuary. Estimates of survival to the pair-trawl system, however, could not be generated using the CJS model due to a lack of live detection sites downstream of the pair-trawl in the lower Columbia River estuary (Figure 4).

DISCUSSION

Numerous factors have been linked to URB fall Chinook Salmon 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 Chinook Salmon—was substantial in some river reaches and years. Predation probabilities were highly variable, however, with cumulative estimates indicating that birds consumed as few as 6.6% to as many as 28.3% of available smolts each year. Comparisons of total mortality (1 – survival) with mortality due to colonial waterbird predation indicated that avian predation accounted for 7.3–29.1% of all sources of smolt mortality annually during out-migration to Bonneville Dam. Even after passage through the hydrosystem, predation impacts by colonial waterbirds in the estuary were high in some years, with upwards of 7.7% of available smolts consumed by birds in the estuary. Collectively, results indicated that the cumulative effects of avian predation were an important factor in the survival of URB fall Chinook Salmon smolts in some but not all river reaches and years.

A systemwide evaluation of colonial waterbird predation across multiple river reaches provided data to identify which bird taxa (CATE, DCCO, LAXX, and AWPE) and individual colonies posed the greatest risk to URB Chinook Salmon smolts. Comparisons of smolt losses attributable to the four predator taxa indicated that the AWPE colony on BGI and the DCCO colonies on FDI and ESI often consumed the largest proportions of available smolts compared with the other predator taxa and colonies evaluated. There was also evidence that predation increased during the latter half (2014–2019) of the study period—particularly predation associated with the AWPE colony on BGI. Increases in AWPE predation coincided with increases in the size (number of breeding adults) of the BGI colony; the count of AWPE increased from 1,349 birds in 2008 to 3,330 birds in 2018 (Cramer et al. 2021). Conversely, probabilities of predation by the CATE and LAXX colonies included in our study were generally the

TABLE 2. Summary statistics of cumulative survival estimates for simulated data sets produced from Cormack–Jolly–Seber (CJS) and joint mortality and survival (JMS) models. Model performance was evaluated using average error, average absolute error, maximum (max) absolute error, coverage, and uncertainty. Values depicted in bold (for JMS) and italic (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 the given model for the specified river reach and year. Survival is of tagged wild Chinook Salmon smolts during out-migration from the Hanford Reach of the Columbia River to McNary Dam (MCJ), John Day Dam (JDA), Bonneville Dam (BON), and a pair-trawl net detection system in the Columbia River estuary (EST; see also Figure 1).

Statistic	Model	2008 simulations						2013 simulations						2015 simulations						2017 simulations								
		To		To		To		To		To		To		To		To		To		To		To		To		To		
		JDA	BON	BON	EST	MCJ	JDA	BON	BON	EST	EST	MCJ	JDA	BON	BON	EST	EST	MCJ	JDA	BON	BON	EST	EST	MCJ	JDA	BON	BON	EST
Average error	CJS	-0.01	-0.01	-0.01	NA	0.00	-0.01	0.01	NA	NA	0.11	0.03	0.08	0.08	NA	0.00	0.00	0.00	0.00	0.02	0.02	NA	0.00	0.00	0.00	0.02	0.02	NA
	JMS	0.00	0.01	-0.02	-0.04	0.06	-0.01	-0.03	-0.04	0.04	0.04	0.10	0.00	0.01	0.01	0.02	0.02	0.01	0.01	0.02	0.01	0.01	0.02	0.01	0.01	-0.03	0.00	0.00
Absolute error	CJS	0.02	0.02	0.04	NA	0.03	0.04	0.06	NA	0.20	0.06	0.08	0.08	NA	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	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	0.04	0.10	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.03	0.01	0.01
Max error	CJS	0.08	0.10	0.12	NA	0.26	0.19	0.24	NA	0.41	0.82	0.79	0.79	NA	0.09	0.08	0.08	0.08	0.08	0.08	0.13	0.09	0.08	0.08	0.08	0.13	NA	NA
	JMS	0.09	0.07	0.08	0.10	0.18	0.09	0.08	0.08	0.14	0.19	0.06	0.06	0.03	0.03	0.08	0.08	0.08	0.05	0.05	0.06	0.04	0.08	0.05	0.05	0.40	0.40	0.40
Coverage	CJS	0.88	0.91	0.80	NA	0.90	0.83	0.69	NA	0.55	0.84	0.70	0.70	NA	0.90	0.91	0.90	0.91	0.91	0.91	0.91	0.90	0.91	0.91	0.91	0.91	0.91	0.91
	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	0.99	0.99	0.99	0.83	0.94	0.94	0.94	0.94	0.99	0.83	0.94	0.94	0.52	0.99	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	0.23	NA	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.07	0.08	NA	NA
	JMS	0.09	0.09	0.09	0.12	0.15	0.13	0.10	0.11	0.26	0.19	0.06	0.06	0.04	0.04	0.06	0.06	0.06	0.07	0.07	0.05	0.04	0.06	0.07	0.07	0.05	0.08	0.08

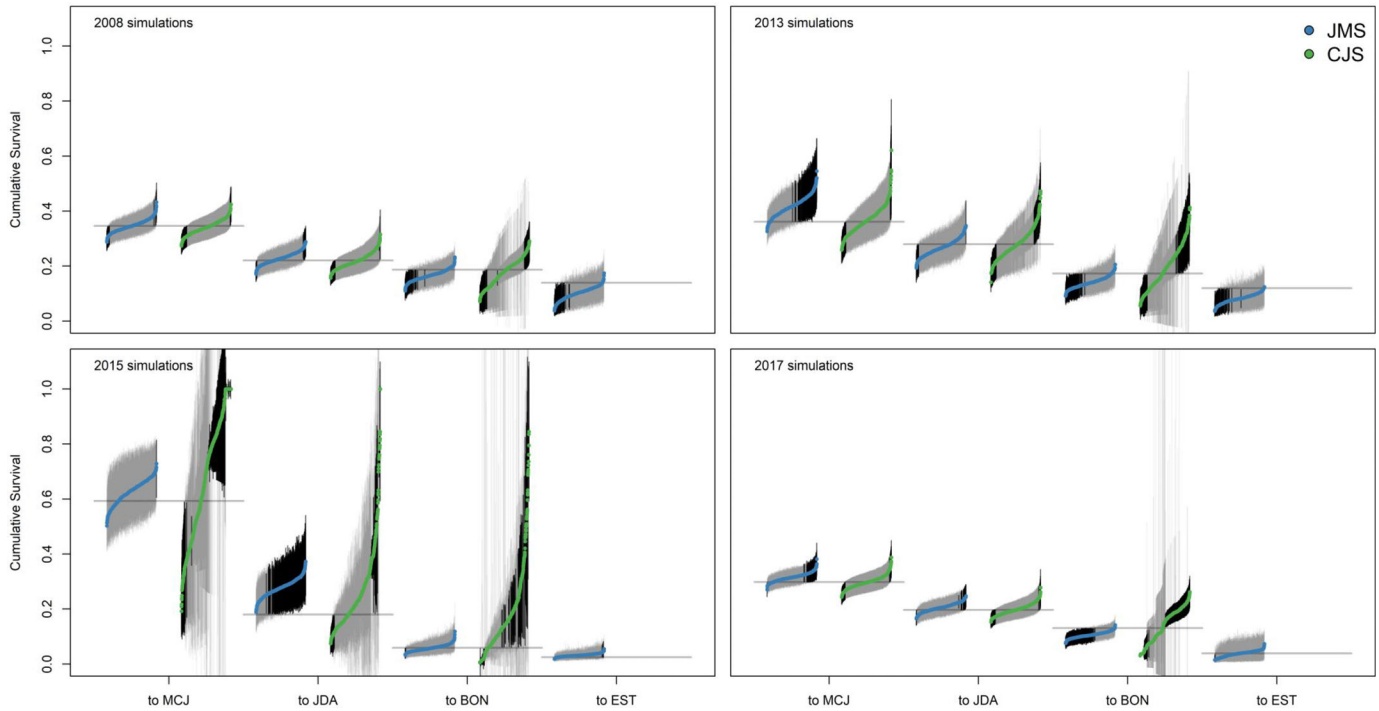


FIGURE 4. Graphical representations of the 500 simulated wild Chinook Salmon smolt survival estimates and associated uncertainty intervals produced according to the Cormack–Jolly–Seber (CJS) and joint mortality and survival (JMS) models for each reach × year combination. Comparisons are ordered by the magnitude of the point estimates. Horizontal gray line segments represent the prescribed parameter values, dots represent the estimates produced by each model (blue for JMS estimates; green for CJS estimates), and vertical line segments represent the associated uncertainty intervals, with gray indicating successful coverage of the prescribed parameter value and black indicating unsuccessful coverage. Survival is from the Hanford Reach of the Columbia River to McNary Dam (MCJ), John Day Dam (JDA), Bonneville Dam (BON), and a pair-trawl net detection system in the Columbia River estuary (EST; see also Figure 1).

lowest (<0.03) among the predator taxa evaluated, with the exception of the LAXX colonies on MRI. Evans et al. (2016) observed that LAXX nesting on MRI disproportionately consumed juvenile salmonids near John Day Dam, which is 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 time associated with forebay passage, mortality and injury due to turbine passage, or temporary stunning and disorientation of fish by hydraulic conditions in the tailrace of dams (Ruggerone 1986; Evans et al. 2016). Unlike CATE, DCCO, and AWPE, the LAXX are also known to scavenge dead fish and to engage in kleptoparasitism (i.e., stealing dead fish from other predators; Winkler 2020), so the proportion of smolts consumed by LAXX on MRI that were dead or moribund when consumed is unknown. Lower probabilities of predation by LAXX and CATE colonies compared with the DCCO and AWPE colonies may also be related to predator-specific foraging behavior, whereby LAXX and CATE are plunge-diving predators that disproportionately consume larger-sized smolts like steelhead (Hostetter et al. 2012; Evans et al. 2016), while DCCO and AWPE are pursuit divers

and communal foragers that are capable of consuming multiple smaller-sized fish during foraging bouts (Anderson 1991; Dorr et al. 2014).

There was evidence that wild URB Chinook Salmon smolts were more susceptible to avian predation than their hatchery counterparts in most of the river reaches and years evaluated. This finding was surprising, as other studies of avian predation have generally found that hatchery fish are more susceptible to avian predation than wild fish (Fritts et al. 2007; Hostetter et al. 2012) or that hatchery and wild fish are equally susceptible to avian predation (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012). Hatchery URB Chinook Salmon are, on average, considerably larger than their wild counterparts, and smolt length has been shown to be a factor in the predation susceptibility of other groups of fish (Hostetter et al. 2012; Osterback et al. 2014). In addition to differences in fish size, higher predation on wild smolts by birds nesting on BGI could also be due to the close proximity of the nesting site to the HR (where wild fish were captured, tagged, and released) compared with the tailrace of Priest Rapids Dam further upstream, where hatchery fish were released. Additionally, wild URB Chinook Salmon smolts were

captured and released in shallow-water habitats in the HR—areas where fish may be more susceptible to predation by AWPE, which are cooperative foragers that corral fish in shallow water (Knopf and Evans 2004). Evidence that wild 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 Salmon stocks in the Columbia River basin, natural-spawning URB fall Chinook Salmon outnumber hatchery-origin returning adults, as approximately 60–70% of adult returns are wild-origin fish (Stuart Ellis, Columbia River Inter-Tribal Fish Commission, personal communication). Given the higher avian predation probabilities observed for wild URB Chinook Salmon, efforts to reduce avian predation could have a greater benefit to the wild population, potentially leading to substantially more adult returns in the future.

The estimates of avian predation presented herein represent minimum estimates of predation by all piscivorous colonial waterbird species and colonies because (1) not all active colonies within foraging distance of URB Chinook Salmon smolts were scanned for PIT tags in all years and (2) not all avian predator species in the region were included in the study. For instance, we did not investigate smolt predation probabilities for noncolonial or semicolonial piscivorous waterbirds, such as common mergansers *Mergus merganser*, Forster's terns *Sterna forsteri*, great blue herons *Ardea herodias*, black-crowned night herons *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 been shown to be less than the impacts of colonial-nesting piscivorous waterbirds (Wiese et al. 2008), primarily because the noncolonial- and semicolonial-nesting species have smaller regional populations. It should be noted, however, that fall Chinook Salmon, which are smaller in size than most other salmonid smolts (Quinn 2005), are within the size range documented to occur in the diets of common mergansers and grebes, and studies regarding the predation impacts of these pursuit-diving species on smolts are currently lacking. As a result, the impact of other piscivorous waterbirds on URB Chinook Salmon smolt mortality is unknown but is likely less than those of CATE, DCCO, AWPE, and LAXX, the principal avian predators of actively migrating salmonid smolts documented by this and other studies (Collis et al. 2002; Roby et al. 2003; Wiese et al. 2008; Evans et al. 2016, 2022b; Payton et al. 2019). It should also be noted that wild juvenile URB Chinook Salmon reside in and otherwise rear in the HR for several months before being PIT-tagged and prior to out-migrating in June. The colonial waterbird breeding season, however, generally starts in early April (Adkins et al. 2014), so some unknown proportion of wild smolts was susceptible

to avian predation 2 months before the fish were PIT-tagged in the HR. Given our finding that wild URB Chinook Salmon were more susceptible to AWPE predation than their hatchery counterparts, additional research to quantify the effects of colonial waterbird predation on wild individuals during their resident presmolt life stage may be warranted.

Several other studies have documented that avian predation probabilities vary substantially based on the salmonid species of interest. For instance, Evans et al. (2012, 2016, 2022b) documented significantly higher rates of predation on steelhead compared to Chinook Salmon in the Columbia River basin. Evans et al. (2019) reported alarmingly high rates of avian predation on upper Columbia River steelhead, with more fish (>50%) succumbing to predation by colonial waterbirds than to all other non-avian sources of mortality combined during smolt out-migration from Rock Island Dam (rkm 729) to Bonneville Dam. In the present study, probabilities of avian predation on URB Chinook Salmon smolts were often but not always low (<0.10) and constituted a smaller (<20%) component of total mortality in most 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 sub-yearling Chinook Salmon relative to other salmonid species and age-classes. Harnish et al. (2014) estimated that there were large numbers of Northern Pikeminnow in the HR, with an estimate of 37,392 predatory fish annually. In addition to piscivorous fish and birds, other sources of mortality affect URB fall Chinook Salmon smolts, but data to quantify these impacts are generally lacking in the published literature.

Survival Models

The additional information provided by the inclusion of tag recoveries on bird colonies was associated with more precise estimates of survival compared with CJS model estimates that were based strictly on detections (recapture) of live fish. The JMS model often provided narrower uncertainty intervals across all simulations. Conversely, by relying solely on detections of live fish, the CJS model had difficulty in consistently producing informative confidence intervals and estimates near the prescribed parameter value. Furthermore, low survival of wild URB Chinook Salmon to Bonneville Dam, coupled with low detections of live fish in the estuary pair-trawl system

downstream of Bonneville Dam, resulted in too few detections with which to estimate survival to Bonneville Dam, while incorporation of tags on bird colonies in the estuary allowed for the increased spatial extent of survival estimates to Bonneville Dam in the JMS model. Our results are similar to those of Hostetter et al. (2018), who found that the information provided by the recovery of tags from bird colonies significantly increased the level of precision and the overall reliability and spatial extent of estimates of fish survival in the Columbia River basin. A common justification for using the more traditional or standard frequentist CJS model is that the estimates are asymptotically unbiased. Although the results of our simulation study confirmed that CJS estimates were on average (across all years) unbiased, they also demonstrated that this criterion, despite its statistical elegance, was of little practical value because the magnitude of the errors associated with individual CJS estimates was large and often resulted in survival estimates that were uninformative or lacking altogether. Collectively, results indicated that fish tag recoveries on bird colonies increased parameter precision and were able to generate survival estimates across larger spatial scales.

Differences in the precision and accuracy of estimates produced by the Bayesian JMS and frequentist CJS models may reflect a litany of differences between the two models beyond just the added information of known mortalities. For instance, the serial correlation in survival/mortality and recapture probabilities that was assumed in the JMS model constrains the probabilities to be similar to each other over time, whereas such assumptions are considerably more burdensome in the frequentist CJS model and, as such, were not used in the development of CJS model estimates. Furthermore, estimates produced by the JMS model are restricted to the unit interval through mathematical transformations, whereas the identity link was used in the CJS model, which allows for estimates of survival to be >100% and is needed for estimates to be considered statistically unbiased. Lastly, the interpretation of the CRIs produced by Bayesian methods differs markedly from the interpretation of frequentist confidence intervals, and the comparison of interval widths and coverage probabilities is necessarily difficult to parse. Comparisons of the JMS and CJS models within the Bayesian framework using the same transformations have been previously published (Hostetter et al. 2018). The simulation study herein is designed to supplement this field of comparative studies and should be recognized as such.

CONCLUDING REMARKS

Results of this study indicate that predation by colonial waterbirds was an important mortality factor for URB Chinook Salmon during the smolt life stage, although

impacts were highly variable based on the predator taxon, colony location, river reach, and year. Results suggest that wild fish were more likely to be consumed relative to their hatchery counterparts. Factors such as fish size, fish behavior, and predator-specific characteristics (e.g., colony location, size, and foraging strategies) may be related to rearing type and thus to differences in smolt susceptibility to avian predation. Results of this and other studies indicate that predators and prey do not occur in isolation but are nested inside complex multi-predator, multi-prey systems that include a variety of ecological processes and factors. Future studies should consider these factors with an aim toward application to both applied ecology and the potential management of predators to increase prey survival.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.