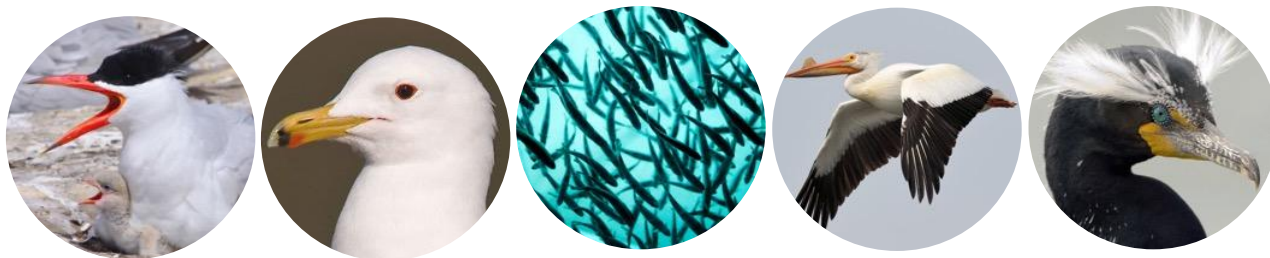


Cumulative Effects of Colonial Waterbird Predation on the Survival of Juvenile Upriver Bright Fall Chinook Salmon: An Updated Retrospective Analysis



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Table of Contents

Summary.....	3
Introduction.....	4
Methods.....	5
Study Area.....	5
Mark-Recapture-Recovery.....	7
Predation and Survival Estimation.....	8
Results & Discussion.....	10
Mark-Recapture-Recovery.....	10
Avian Predation.....	13
Total Mortality.....	17
Concluding Remarks.....	19
Acknowledgements.....	20
References.....	20
Supplementary Tables.....	26

Summary

In 2020, we conducted an analysis of the cumulative effects of avian predation on juvenile Upriver Bright (URB) Fall Chinook Salmon (*Oncorhynchus tshawytscha*) that were PIT-tagged and released in the middle Columbia River, USA. A state–space Bayesian model that incorporated live detections of tagged fish during out-migration and recoveries of dead tagged fish on piscivorous waterbird colonies was used to jointly estimate predation and survival probabilities over a 12-year study period (2008–2019). This report serves as an update to the original analysis, including an additional five years (2021–2025) of data to investigate how avian predation continues to impact the survival of juvenile URB Chinook. Predator species included Caspian Terns (*Hydroprogne caspia*, hereafter “CATE”), Double-crested Cormorants (*Nannopterum auritum*, hereafter “DCCO”), California Gulls (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*, collectively hereafter “LAXX”), American White Pelicans (*Pelecanus erythrorhynchos*, hereafter “AWPE”), and Great Blue Herons and Great Egrets (*Ardea herodias* and *Ardea alba*, collectively hereafter “ARXX”) that were nesting at up to 26 individual colonies or breeding sites. The findings of this updated analysis indicated that estimates of avian predation probabilities (proportion of tagged fish consumed by birds) on URB Chinook smolts have, on average, increased over the course of the last five years. Estimates of average annual cumulative predation probabilities (predation by all colonies combined) on hatchery smolts increased from 0.088 (95% credible interval = 0.078–0.102) during 2008–2019 to 0.153 (0.139–0.170) during 2021–2025. Similarly, predation on wild smolts increased from 0.152 (0.134–0.171) during 2008–2019 to 0.217 (0.194–0.248) during 2021–2025. Similar patterns in predation and survival trends were observed in all years (2008–2025), with wild fish significantly more likely to be predated and less likely to survive out-migration to Bonneville Dam on the lower Columbia River than their hatchery counterparts. Of the river reaches evaluated, predation was consistently highest from release in the middle Columbia River to McNary Dam on the lower Columbia River. Of the predator species evaluated, predation by AWPE was consistently the highest, followed by DCCO, LAXX, CATE, and ARXX. During the most recent period (2021–2025), multiple colonies moved location from one breeding site to another, and new colonies emerged. While avian predation was a substantial source of juvenile URB Chinook mortality in some years and river reaches, most URB Chinook mortality was presumably due to non-avian causes, with avian predation accounting for 16% to 28% of all mortality sources during smolt outmigration to Bonneville Dam, depending on the fish’s rear type and year. Collectively, results provided evidence that avian predation on URB Chinook smolts has increased in recent years, but that multiple factors threaten smolt survival during outmigration to the Pacific Ocean.

Introduction

Previous research indicates that predation by piscivorous colonial waterbirds limits the survival of some salmonid (*Oncorhynchus* spp.) populations in the Columbia River Basin (Evans et al. 2012, Evans et al. 2019, Payton et al. 2023). The magnitude of predation depends greatly on the salmonid species, avian predator species, and colony size and location (Evans et al. 2012; Payton et al. 2019, Payton et al. 2023). Piscivorous colonial waterbirds, like Caspian Terns (*Hydroprogne caspia*), Double-crested Cormorants (*Nannopterum auritum*), California Gulls (*Larus californicus*), Ring-billed Gulls (*L. delawarensis*), and American White Pelicans (*Pelecanus erythrorhynchos*), have breeding colonies located throughout the Columbia River Basin and consume juvenile (smolt) salmonids during their seaward migration (Collis et al. 2001, Evans et al. 2012). Colony sizes can range from less than 100 breeding pairs to well over 10,000 pairs per colony, and predation effects can range from less than 1% to more than 20% of available smolts per colony (Roby et al. 2021).

As one of the most productive Chinook Salmon (*O. tshawytscha*) stocks in the Pacific Northwest (Langness & Reidinger 2003), the Upriver Bright (URB) Fall Chinook Salmon stock, is important to commercial, sport, and tribal fisheries. Studies involving URB Chinook from the Hanford Reach of the Columbia River have been on-going since 1987, with tagging studies releasing fish and then using subsequent recapture and recovery events to estimate fish behavior and survival (Fryer 2024). Understanding cause specific mortality of URB Chinook has been a topic of high interest, as the survival of this stock is impacted by multiple sources, including mortality associated with dam passage, abiotic river conditions, and predation (Harnish et al. 2014, Payton et al. 2023). For instance, Payton et al. (2023) found that among avian predators, American White Pelicans (here after “AWPE”) and Double-crested Cormorants (hereafter “DCCO”) posed the greatest threat to URB Chinook survival, with predation rates or probabilities (percentage or proportion of available tagged fish consumed) in excess of 20% or 0.20 of available fish in some years during 2008–2019 (Payton et al. 2020, 2023). Additionally, biotic factors were shown to influence the susceptibility of URB Chinook to avian predation, particularly a fish’s rear type (i.e., hatchery vs wild), where wild fish were often more likely to be consumed than their hatchery counterparts (Payton et al. 2023).

The goal of this study was to update the results of Payton et al. (2023) with data collected during 2021–2025. Changes in colony locations and the advent of new predator species (Great Blue Herons [*Ardea herodias*] and Great Egrets [*A. alba*] here after “ARXX”) have occurred in recent years. As such, extending the avian predation studies of Payton et al. (2023) to include the most recent data available improved our understanding of the effects

of avian predation on URB Chinook smolts and to what degree avian predation limits the survival of URB Chinook in the Columbia River basin. Specifically, the goals of this updated analysis were to (1) generate spatially explicit estimates of colony-specific predation rates, (2) estimate the cumulative effects of avian predation (i.e., predation by all predator species and colonies combined), and to (3) estimate what proportion of all URB Chinook smolt mortality (1 - survival) was due to avian predation during 2021–2025.

Methods

Study Area – We investigated predation and survival of hatchery and wild URB Chinook smolts marked with passive integrated transponder (PIT) tags during 2021–2025; updating the dataset (2008–2019) used by Payton et al. (2023). The study area described in Payton et al. (2023) was the same used herein. In brief, hatchery fish were released at the Priest Rapids Hatchery downstream of Priest Rapids Dam (PRD) at River kilometer (Rkm) 639 and wild fish were captured in the Hanford Reach (HR) between Rkm 557 and 639 and released at boat ramps at Rkm 576 and 587 (Figure 1). Following release, survival and predation were evaluated through four river reaches or sections of the Columbia River: (1) release to McNary Dam (MCJ; Rkm 470), (2) MCJ to John Day Dam (JDA; Rkm 349), (3) JDA to Bonneville Dam (BON; Rkm 234), and (4) BON to the Pacific Ocean. 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. 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 in the Columbia River estuary (Rkm 8), 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.



Figure 1. Mark-recapture-recovery locations of PIT-tagged hatchery and wild Upriver Bright Fall Chinook Salmon released downstream of Priest Rapids Dam during 2021–2025. Release sites included the Priest Rapids Hatchery and the Hanford Reach section of the Columbia River. Recapture locations include McNary Dam (MCJ), John Day Dam (JDA), Bonneville Dam (BON), plus a net detection system in the lower Columbia River and estuary. Recovery locations include Caspian Tern (CATE), Double-crested Cormorant (DCCO), California and Ring-billed Gull (LAXX), American White Pelican (AWPE), and Great Blue Heron and Great Egret (ARXX) colonies.

Mark-Recapture-Recovery – The same mark-recapture-recovery dataset described in Payton et al. (2023), updated with URB Chinook releases from 2021–2025, were used in the present study. Although the dataset from Payton et al. (2023) ended in 2019, no URB Chinook were tagged and released in 2020 due to Covid-19 constraints that year, thus the updated dataset starts in 2021. Hatchery URB Chinook from Priest Rapids Hatchery were tagged and released during a four-week period from mid-May to mid-June in all years. Wild fish, which rear in the Hanford Reach prior to outmigration, were captured, tagged, and released during a one-week period in early June in all years, except for 2025 when no (zero) fish were tagged due to the inability to find a site where the project could be conducted after a late denial of access at the federal sites on the Hanford Nuclear Reservation, where the project had been run since 1987. 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 MCJ, JDA, and BON juvenile bypass fish facilities or at a corner collector (a spill-like route; BON only) and in the Columbia River estuary as a combination of the towed pair-trawl net detection system and antennas on pile dikes. Adult URB Chinook returning to the Columbia River following ocean residency were detected at arrays located in fishways at the BON adult fish facility one to five years following release as a smolt. Recapture records were retrieved from the PIT Tag Information System (PTAGIS), a regional mark, recapture, recovery database maintained by Pacific States Marine Fisheries Commission (PSFMC 2026).

The methods of Evans et al. (2012) were used to recover PIT tags from each bird colony included in the study (see [Figure 1](#) for a list of colonies). 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 (Adkins et al. 2014). Not all PIT tags ingested by avian predators are 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). 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 both PIT-tag deposition and detection probabilities on bird colonies. Data from Hostetter et al. (2015), Payton et al. (2023), and Evans et al. (2026) were used to estimate colony-specific detection probabilities and predator-specific (CATE, DCCO, LAXX, AWPE, ARXX) deposition probabilities (see also Payton et al. 2023).

Predation and Survival Estimation –. The joint mortality and survival (JMS) estimation methods of Payton et al. (2019, 2023) were used to generate reach-specific, colony-specific, and cumulative URB 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, $\mathbf{y}$ and $\mathbf{r}$, to describe each fish's recapture and recovery history throughout each downstream river reach and each of the bird colony recovery sites under consideration. Each vector $\mathbf{y}$ was a J -length vector ($J = 5$) where y_j was an indicator variable of a fish's recapture at recapture opportunity j for $j \in \{1, 2, \dots, J - 1\}$ and $y_j = 0$ as there was no live recapture site downstream of the net detector in the Columbia River estuary. Recoveries were indicated by $\mathbf{r}$, a D -length vector, where D represents the number of recovery areas each year, with a single element equal to one and the rest of the elements are zero, where $r_d = 1$ indicated recovery on colony d for $d \in \{1, 2, \dots, D - 1 = 14\}$, and $r_D = 1$ indicated a fish was unrecovered. Parameters used in the model included:

$\boldsymbol{\theta}$, a $D \times J$ matrix where $\theta_{d,j}$ represented the probability (from release) that a fish survived to recapture opportunity $j - 1$ – where $-j = 0$ represents release – and then subsequently succumbed to predation by colony d for $d \in \{1, 2, \dots, D - 1\}$ or some other cause of mortality for $d = D$, prior to arrival at recapture opportunity $j + 1$. Implicit from this parameterization is that survival from release through segment k is equal to $1 - \sum_{j \leq k} \sum_d \theta_{j,d}$.

$\mathbf{p}$, a J -length vector where p_j represented the probability that a fish alive at recapture opportunity j was successfully recaptured. This study defines $p_J = 0$, as there is no recapture opportunity downstream of the Net Detector.

$\boldsymbol{\gamma}$, a D -length vector where γ_d represented the probability of recovering a fish which died due to predation by colony d for $d \in \{1, 2, \dots, D - 1\}$, and $\gamma_{15} = 0$ represented the lack of recovery opportunity for fish which died from all other unspecified causes.

The model employed can be expressed by incorporating these parameters into recursive functions, $X_{j,d}$, defined to represent the probability a fish entering segment j is not subsequently recaptured and is recovered on colony d (i.e. $r_d = 1$), such that

$$X_{j,d} = \theta_{j,d} \cdot \gamma_d + (1 - p_{j+1}) \cdot X_{j+1,d} \quad \text{for } d \in 1, \dots, D - 1,$$

or not recovered at all (i.e. $r_{15} = 1$), such that

$$X_{j,D} = \sum_d \theta_{j,d} \cdot (1 - \gamma_d) + (1 - p_{j+1}) \cdot X_{j+1,D}.$$

Then, if m is defined as the final recapture opportunity at which the fish was seen, with $m = 0$ representing a fish never recaptured following release, the portion of the aggregate likelihood associated with each fish's recapture/recovery history can be expressed as

$$L = \prod_{j \leq m} \left(p_j^{y_j} \cdot (1 - p_j)^{(1-y_j)} \right) \cdot \prod_d X_{m+1,d}^{r_d},$$

where the former product describes a fish's recapture history prior to its final recapture and the latter product describes the fish's subsequent recovery or lack thereof following its final recapture.

Two further modelling considerations beyond those of Payton et al. (2019) were included to better inform the spatially explicit estimates of predation effects. First, the informed partitioning methods of Evans et al. (2022) were also used to allow for a sharing of information across years to increase the precision of segment-specific estimates. In brief, a vector of aggregate life-path possibilities is 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 modelling variations across days. The cumulative probability of predation by each colony is subsequently partitioned across river segments with proportionate impacts among reaches assumed to be similar among years. Second, pelicans and gulls occurred in co-nesting areas on Badger Island during 2015–2024 and on Crescent Island in 2025, with portions of each genus' colonies overlapping spatially, creating “mixed” genus areas. This study employed the methods of Payton et al. (2023) to incorporate supplemental data (i.e., aerial nest count surveys) to inform what proportion of each genus was nesting in the single-genus areas versus the “mixed” areas. Then, by assuming the odds of a tag consumed by a given genus was deposited in the single-genus portions of each colony versus in the “mixed” area was similar to the odds of a bird of that genus nesting in the single-genus portion, it was possible to estimate the portion of tags recovered from the “mixed” portion of the colony were attributable to each predator genera.

To measure inter-annual temporal variation in probabilities, fish were partitioned into weekly release groups with the assumption that fish released within the same week experienced similar rates of mortality/survival, recapture, and recovery (Payton et al. 2019). While all rates were assumed to be independent among years, weekly cohorts

closer in time were assumed to be more alike than those further apart. The serial correlation in probabilities was assumed and accounted for as described by Payton et al. (2019). The prior distribution 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 $D(\mathbf{1})$, where $\mathbf{1}$ was an appropriately sized vector of ones. Weakly-informative priors of half – normal(0, 1.5) were implemented for the variance parameters describing inter-weekly variation.

The recovery parameters, γ_d , represent the combined probability that a consumed tag was deposited on colony, d , and the probability that the tag is subsequently detected (recovered) by researchers following the breeding season given tag deposition on a colony. The simulated posterior distributions of deposition probabilities and colony-specific detection probabilities which were derived, summarized, and presented in previous studies were employed here as informative prior distributions in the derivation of predation probability estimates.

Models were analyzed using the software STAN, accessed through R version 4.6.0, and using the rstan package (version 2.32.7) (R Development Core Team 2014, Stan Development Team 2025). To simulate random draws from the joint posterior distribution, four Hamiltonian Monte Carlo (HMC) Markov Chain processes were run. Each chain contained 4,000 warm-up iterations followed by 4,000 posterior iterations thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2014); only chains with zero reported divergent transitions were accepted. Posterior predictive checks compared simulated and observed annual aggregate raw recapture and recovery numbers to ensure model estimates reflected the observed data. Reported estimates represent simulated posterior medians along with 95% highest (posterior) density intervals (95% Credible Intervals [CRI]) calculated using the HDInterval package (version 0.2.4) (Meredith & Kruschke 2022).

Results & Discussion

Mark-Recapture-Recovery –. In total, 253,772 URB Chinook smolts were PIT-tagged and released during 2021–2025 (Table 1). Of these, 213,990 were hatchery fish released from the Priest Rapid Hatchery and 39,782 were wild fish captured and released into the Hanford Reach of the Columbia River downstream of Priest Rapids Dam (Figure 1). Hatchery fish were, on average, larger in length than wild fish, with average fork lengths of 78.0 mm (SD = 7.4 mm, range 43 – 234 mm) and 65.2 mm (SD = 5.6 mm, range 46 – 374), respectively. Release numbers were consistent each year, ranging from 42,472 to 42,976

hatchery smolts and 9,778 and 9,990 wild smolts annually, with notable exception of 2025 when no (zero) wild smolts were captured and released. Numbers of tagged Chinook detected alive at downstream recapture sites varied greatly by location and year, while the number of tags recovered dead on bird colonies were similar in most, but not all, years ([Table 1](#)). The largest numbers of tags that were recovered dead on bird colonies were on mixed (co-nesting) AWPE and LAXX breeding sites located upstream of McNary Dam on Badger Island and Crescent Island in Reach 1 (n=7,755; [Table 1](#), see also [Supplemental Table S.1](#) for recoveries by colony). Conversely, the smallest number of smolts were recaptured alive at the pair-trawl net detector and pile dikes in the Columbia River estuary in Reach 3 (n=557; [Table 1](#)). Only a small number and proportion of smolts released returned to BON as adults, with returns ranging from 0–261 adults per release year and rear type, though adult returns for 2022–2025 were incomplete at the time of this analysis ([Table 1](#)). Recapture and recovery probabilities of tags on each bird colony, data used to estimate predation probabilities (see [Methods](#)), are provided in the [Supplemental Tables, Table S2](#).

Table 1. Numbers of PIT-tagged Upriver Bright Fall Chinook smolts that were subsequently detected alive at PIT-tag arrays or recovered dead on bird colonies (see Figure 1 for a map of release, recapture, and recovery locations). The PIT tag arrays were located at McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and pair-trawl and pile dike detections system in the Columbia River estuary (EST). Bird colonies include Caspian Terns (CATE), American White Pelicans (AWPE), Double-crested Cormorants (DCCO), Brandt's Cormorants (BRAC), Great Blue Herons and Great Egrets (ARXX), California and Ring-billed Gulls (LAXX) or colonies that were a combination of mixed or co-nesting AWPE and LAXX. Dashed line denotes that the colony was not scanned for tags that year but may have been active. Adult returns are incomplete during 2022–2025. The number of PIT tags recovered on bird colonies presented in this table are raw counts and not adjusted to account for tag loss due to on-colony detection and deposition probabilities (see *Supplemental Table S.2*), thus represent minimum numbers of tagged fish consumed by birds.

Year	Rear	Released	Recaptured Alive					Recovered Dead on Bird Colonies						
			MCN	JDA	BON	EST	Adult	CATE	DCCO	BRAC	ARXX	LAXX	AWPE	AWPE/LAXX
2021	W	9,878	94	122	173	0	13	19	36	0	-	33	7	672
	H	42,873	1,013	1,264	1,229	13	248	68	185	0	-	164	11	1,263
2022	W	9,918	286	245	117	3	11	26	69	0	-	40	12	294
	H	42,971	1,438	1,214	758	19	155	150	323	2	-	159	35	1,029
2023	W	9,996	77	42	29	10	0	7	20	0	-	27	17	748
	H	42,976	730	581	636	209	112	91	227	0	-	96	28	1,272
2024	W	9,990	49	45	46	9	0	7	88	0	-	43	1	352
	H	42,698	365	641	516	200	14	42	374	2	-	152	0	1,261
2025	H	42,472	524	545	421	217	4	36	472	4	112	128	50	864
ALL		253,772	4,576	4,699	3,925	680	557	446	1,794	8	112	842	161	7,755

Avian Predation –. During the updated time series, 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) from 2021–2024 and Crescent Island in 2025 (CSI), followed by LAXX on Island 20 (IS20) in 2021, 2022, and 2024, the DCCO colony on Foundation Island (FDI) from 2021–2022, DCCO from Hanford (HAN) in 2021–2024, and the DCCO CSI from 2024–2025 (Figure 1). Annual, colony-specific predation probabilities ranged from 0.011 (95% CRI = 0.008–0.014) to 0.184 (0.141–0.259), depending on the colony and smolt rear type (Figure 2). The shift in colony locations of AWPE and LAXX from BGI to CSI, which occurred in 2025, was likely the result of the presence of coyotes (*Canis latrans*) on the island during the breeding season, while the movement of DCCO from FDI to CSI, which occurred during 2023 to 2024, was likely due the presence of nesting Bald Eagles (*Haliaeetus leucocephalus*) on FDI (Trenton DeBoer, Yakima Nation, pers. comm., Evans et al. 2026). Predation probabilities by all other colonies foraging in Reach 1 were less than 0.010 per colony, per year, per rear type. Cumulative estimates of predation (predation by all colonies foraging in Reach 1 combined) ranged from 0.110 (0.089–0.146) on hatchery smolts in 2025 to 0.235 (0.182–0.321) on wild smolts in 2021 (Figure 2). This range is shifted notably higher than the 2008–2019 estimate range of 0.033 (0.027–0.040) on hatchery smolts in 2013 to 0.183 (0.136–0.247) on wild smolts in 2017.

In Reach 2 (McNary Dam to John Day Dam), predation probabilities were consistently lower than those of Reach 1 throughout 2021–2025 (Figure 2). This trend is generally consistent with that of the previous time frame (2008–2019), though predation by AWPE was occasionally high some years past (e.g., 2015, 2018, 2019; see also Supplemental Table S.3 for average annual reach-specific estimates by time periods). Predation by all avian colonies in this reach ranged from 0.010 (0.002–0.031) on wild smolts in 2022 to 0.037 (0.019–0.065) on hatchery smolts in 2023. The primary colonies responsible for predation in this reach were AWPE from BGI and LAXX from Miller Rocks (MRI), though most predation effects from these colonies take place in Reaches 1 and 3, respectively. From all AWPE predation in Reach 2, estimates ranged from <0.001 (0–0.009) to 0.028 (0.012–0.055) across all years and rear types during the updated time series. Predation estimates from LAXX in Reach 2 were slightly higher those of AWPE (ranging from 0.004 [<0.001–0.018] to 0.016 [<0.001–0.054] across all years and rear types), but still low relative to other reaches.

Predation probabilities in Reach 3 (John Day Dam to Bonneville Dam) from 2021–2025 were, like Reach 1, generally shifted higher in comparison to earlier estimates (2008–2019). Like estimates in years past, however, predation was highest from the MRI LAXX colony, ranging from 0.030 (0.009–0.072) on wild smolts in 2022 to 0.107 (0.540–0.178) on

hatchery smolts in 2025. Estimates of predation from the DCCO colony on Murdock Towers (MUT), a colony that formed in 2023, were 0.033 (0.009–0.093) on wild smolts in 2024 and 0.046 (0.031–0.076) on hatchery smolts in 2025. In 2023 only, predation estimates from the BGI AWPE colony were notable at 0.022 (0.002–0.010). Congruent with evidence from 2015, 2016, and 2018, AWPE from BGI were commuting to forage on smolts downstream of John Day Dam, over 150 Rkm from their nesting site, in some years. Predation estimates from all other colonies from 2021–2025 were less than 0.010 per rear type. It should be noted that estimates in Reach 3 were based on small sample sizes of wild fish (those surviving passage to below John Day Dam), which resulted in imprecise estimates of predation, as noted by the wide 95% CRI (Figure 2).

Estimates of predation in Reach 4 (Bonneville Dam to the Pacific Ocean) during 2021–2025 ranged annually from 0.030 (0.014–0.070) to 0.257 (0.089–0.756). Of the colonies foraging in Reach 4, predation probabilities were often the highest by DCCO nesting on the Astoria-Megler Bridge (AMB), a colony that rapidly increased in size during the updated time series, with probabilities ranging annually from 0.018 (0.008–0.111) to 0.125 (0.016–0.515) depending on the year and rear type. Predation estimates from DCCO nesting on Troutdale Towers (TTOWER), a colony that formed in 2022, were also substantial in some years, with predation estimates of up to 0.067 (0.010–0.394). The emergent significance of the AMB and TTOWER DCCO colonies are especially apparent when comparing the 2021–2025 predation impacts to those from 2008–2019, where East Sand Island (ESI) DCCO were the primary threat of avian predation to URB Chinook smolts in Reach 4. This upriver shift in the DCCO colonies may explain this apparent increase in predation, as colonies that are located in freshwater are more likely to consume juvenile salmonids on per capita (per bird) basis compared with colonies that forage in marine waters (Evans et al. 2026). For instance, recent research indicates per capita predation probabilities by DCCO on juvenile salmonids were 2–5 times higher by birds breeding in the upper estuary and lower Columbia River compared to those breeding on East Sand Island in the lower estuary (Evans et al. 2026). Similar to estimates in Reach 3, however, estimates of predation in Reach 4 should be interpreted with caution, as small sample sizes resulted in wide credible intervals, particularly with wild fish (Figure 2).

Cumulative, system-wide predation probabilities, measured as the impact of all 26 bird colonies combined on URB fall Chinook mortality from release to the Pacific Ocean, ranged annually from 0.140 (0.117–0.168) to 0.170 (0.144–0.205) for hatchery fish and from 0.172 (0.140–0.211) to 0.261 (0.211–0.349) for wild fish during 2021–2025 (Figure 3). Of the bird species evaluated (CATE, DCCO, LAXX, AWPE, ARXX), aggregated (species-specific) predation probabilities on were often, but not always, the highest by AWPE and DCCO. The

aggregate effects of predation by all LAXX colonies were also appreciable in some years with predation probabilities as high as 0.037 (0.027–0.057). In general, the aggregate effects of predation by CATE and ARXX colonies were the lowest of the five predator species evaluated, although data from ARXX were limited to 2025 only (Figure 3).

Consistent with previous findings, the updated analysis comparing predation between hatchery and wild smolts indicated that wild fish were often more likely to be predated than hatchery fish (Figure 2, Figure 3). Relative differences in predation by pelican colonies were especially pronounced, with wild fish often twice as likely to be consumed as their hatchery counterparts. Hatchery fish were, on average, 12.8 mm longer than wild fish and previously published studies have indicated that smaller Chinook smolts may be more susceptible to pelican predation (Payton et al. 2021, Payton et al. 2023). Although smolt length had an inverse relationship to predation probabilities in these studies (i.e., smaller sized fish were more susceptible to predation), higher predation probabilities among wild smolts were still evident after accounting for differences in length, suggesting additional factors may be associated with higher predation on wild URB Chinook smolts (Payton et al. 2023). Payton et al. (2023) hypothesized that wild smolts reside and rear in the Hanford Reach and that fish may congregate in shallow water habitat, areas where fish may be more susceptible to pelican predation. Unlike predation by pelicans, hatchery smolts were as equally susceptible as wild smolts to predation by LAXX (Figure 2 and 3). Gulls are known to disproportionately consume actively migrating smolts near dams, areas where both wild and hatchery smolts congregate in space and time (Evans et al. 2016).

There was evidence that avian predation on both hatchery and wild URB Chinook has increased in recent years. For instance, the average annually cumulative predation probability on hatchery smolt has increased from 0.088 (0.078–0.102) during 2008–2019 to 0.153 (0.139–0.170) during 2021–2025. Similarly, predation on wild smolts increased from 0.152 (0.134–0.171) during 2008–2019 to 0.217 (0.194–0.248) during 2021–2025. Increases in predation during the latter part of the study period were largely associated with AWPE. Increases in predation at the BGI colony are coincident with increases in the size of the colony (number of breeding pelicans). For instance, the AWPE colony on BGI increased over the course of the study period, with the number of breeding birds observed in 2008 (ca. 1,349 birds) more than twice the number observed in 2024 (ca. 3,205) (Collis et al. 2021, Evans et al. 2025). Due to low estimated survival to Bonneville Dam (see *below*), predation in the Columbia River estuary was a relatively small overall component of cumulative predation, but predation by DCCO has increased markedly over the study period, with the highest levels observed in recent years due to the emergence of the large (> 10,000 breeding birds) colony on the AMB (Evans et al. 2026).

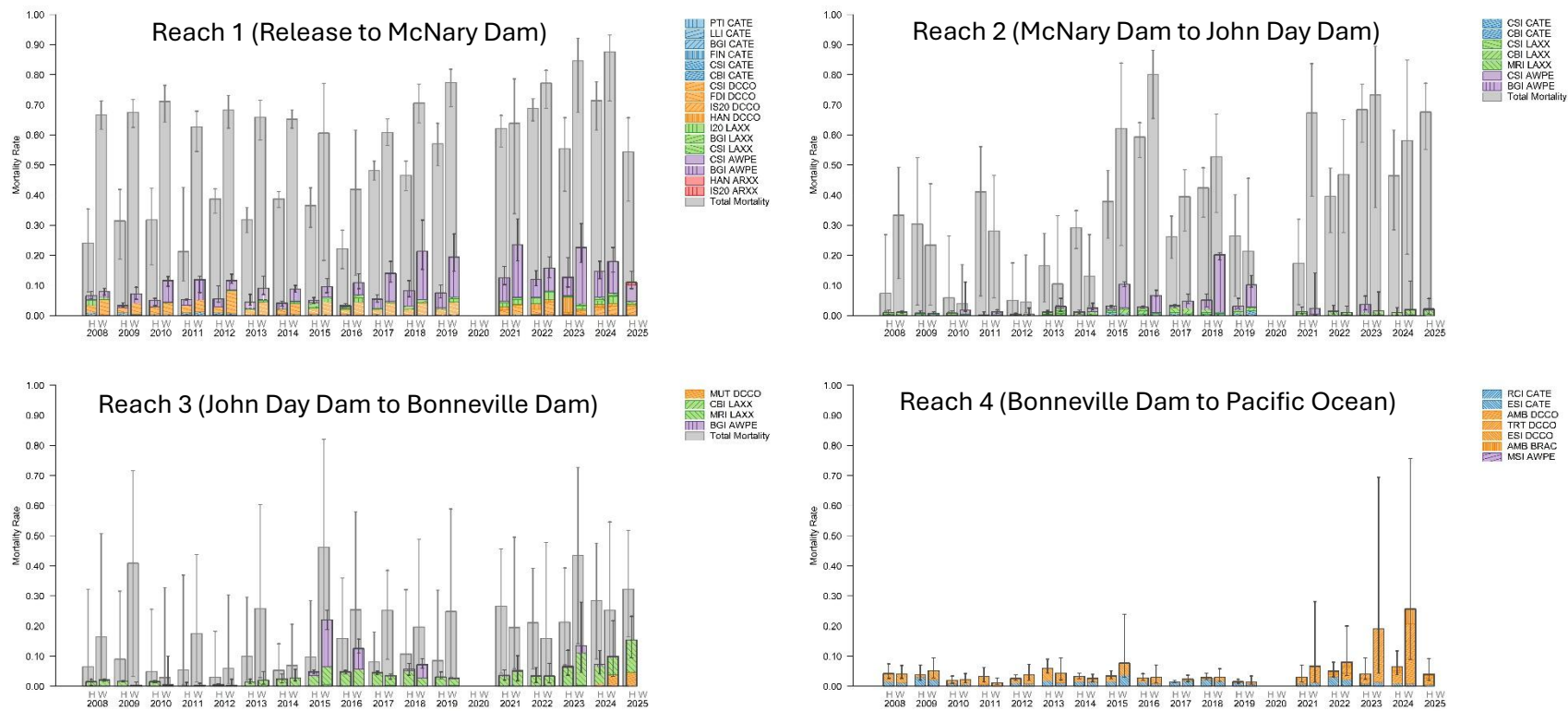


Figure 2. Estimated reach-specific total mortality (grey bars) and mortality due to avian predation (colored bars) of PIT-tagged hatchery (H) and wild (W) juvenile URB Fall Chinook smolts during 2008–2025. Estimates represent the proportion of available fish by rear type and year. Predator species include 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. 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).

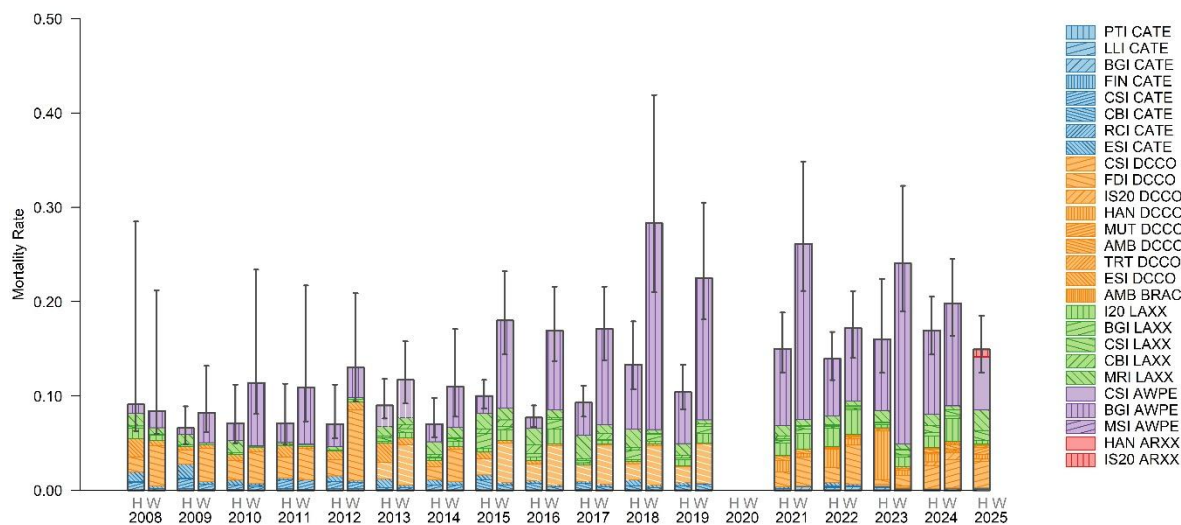


Figure 3. Estimated cumulative mortality due to avian predation (proportion of available fish consumed) of PIT-tagged hatchery (H) and wild (W) juvenile Upriver Bright Fall Chinook during 2008–2025. Estimates represent the proportion of available fish consumed by rear type and year. Predator species include Caspian Terns (CATE), Double-crested Cormorants (DCCO), California and Ring-billed Gulls (LAXX), and American White Pelicans (AWPE). Error bars represent 95% credible intervals.

Total Mortality–. Total mortality (1 - survival) was highly variable depending on year, river reach, and rear type. Cumulative total mortality estimates indicated that the majority of URB Chinook smolts died prior to reaching Bonneville Dam, with 2021–2025 estimates ranging from 0.770 (0.704–0.825) to 0.978 (0.962–0.987) across all years and rear types. Total mortality was consistently the highest in Reach 1 (Release to McNary Dam), ranging annually from 0.544 (0.380–0.657) to 0.714 (0.615–0.776) in hatchery smolts and 0.638 (0.338–0.786) to 0.876 (0.713–0.932) in wild smolts. Results indicated more than 50% of all wild smolts died prior to reaching McNary Dam in 16 of the 17 study years evaluated. Total mortality was often, but not always, lower in Reach 2 and 3, though generally trending higher in the most recent time series (2021–2025) compared to the original analysis (2008–2019; Figure 1, see also Payton et al. 2023). Estimates of smolt mortality through Reach 4 could not be calculated because there were no PIT tag detection sites downstream of the bird colonies in the lower Columbia River estuary (Figure 1). Because complete adult returns were not available during 2022–2025 (see Methods), total mortality to adulthood during the most recent time period could not be fully evaluated. During 2008–2021, the proportion of smolts released that die prior to returning to Bonneville Dam as an adult ranged annually from 0.975 (0.966–0.982) to 0.997 (0.994–0.998) in hatchery fish and 0.985 (0.973–0.992) to 0.998 (0.989–0.999). These translate into smolt-to-adult survival percentages of just 0.2% to 2.5%, depending on the out-migration year and the fish’s rear type.

Analogous to increases in predation, there was also evidence that total mortality of URB Chinook smolts has increased in recent years. For instance, on average, total mortality of hatchery and wild smolts from release to Bonneville Dam was estimated at 0.613 (0.584–0.639) and 0.835 (0.817–0.851), respectively, during 2008–2019 compared with 0.860 (0.841–0.875) and 0.936 (0.922–0.951), respectively, during 2021–2025. 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 outmigration in most, but not all, river reaches and years (Figure 1). Predation probabilities were also, on average, higher on wild smolts than hatchery smolts, which explains some, but not all, of the relative differences in total mortality. For instance, in years when predation probabilities were higher on wild fish, total mortality was often also higher on wild fish (Figure 1), but avian predation alone was not the dominate source of URB Chinook smolt mortality. For instance, comparisons of total URB Chinook smolt mortality and mortality due to bird predation indicated that avian predation accounted for 15.5% (12.9–18.8%) to 18.5% (15.4–23.4%) of total hatchery fish mortality and 18.2% (14.7–22.6%) to 28.0% (22.5–37.0%) of total wild fish mortality during smolt outmigration from the release to Bonneville Dam. Of the reaches evaluated, the relative effects of avian predation were often the greatest on wild smolts in Reach 1, with bird predation accounting for 17.4% (14.3–21.6%) to 36.8% (28.5–50.3%) of total mortality per year. In Reach 2, avian predation accounted for less than 10% of total mortality in 2021–2025. Although avian predation accounted for a larger share of total mortality in Reach 3 in some years (ranging from 13.6% [7.9–20.6%] to 47.9% [29.3–72.2%]), the wide credible intervals surrounding these estimates warrant caution in their interpretation (Figure 1).

In addition to avian predation, salmonid smolts are subject to numerous other non-avian sources of mortality during outmigration, such as hydroelectric dam passage, predation by piscivorous fish, disease, and other factors (Dietrich et al. 2011, Harnish et al. 2014, Muir et al. 2001, Ward et al. 1995). Previous studies have indicated that subyearling Chinook are more susceptible to piscivorous fish predation than other salmonid age-classes and species (Harnish et al. 2014, McMichael 2018, Rieman et al. 1991). Variation in abiotic factors, such as flow and temperature, have also been associated with subyearling Chinook survival in other systems, with drought conditions having a negative impact on survival (Connor et al. 2003, Notch et al. 2020). Biotic factors also play an important role in URB Chinook survival during outmigration, with fish length being positively correlated with survival (Harnish et al. 2014). 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 Chinook and other salmonid species and populations in the Columbia River basin (Evans et al. 2016, 2019). Finally, although non-avian sources were

presumably the primary cause of URB Chinook mortality, it should be noted that estimates of avian predation presented herein are minimum estimates because not all active colonies within foraging distance of URB Chinook smolts were scanned for PIT-tags in all years, nor were all avian predator species in the region included in the study (see also Payton et al. 2023). The colonial waterbird breeding season also generally starts in early April (Adkins et al. 2014), so some unknown proportion of wild smolts were susceptible to avian predation two months before they were PIT-tagged in the Hanford Reach in June. Given our finding that wild URB Chinook smolts were more susceptible to AWPE predation than their hatchery counterparts, additional research to quantify the effects of colonial waterbird predation on wild smolt during their resident, pre-smolt life-stage is warranted (Payton et al. 2023).

Concluding Remarks –. This updated analysis extending the URB Fall Chinook smolt predation time series from 2008–2019 through 2025 reinforces several key findings from Payton et al. (2023) while also revealing notable shifts in colony dynamics that warrant consideration. Across the full study period (2008–2025), avian predation remained a substantial, but not the primary, source of URB Chinook smolt mortality. The majority of smolt mortality during outmigration was attributable to non-avian causes, with bird predation accounting for roughly 15–28% of total mortality, depending on rear type and year. Despite this, the cumulative effects of predation in some reaches and years, particularly in Reach 1, were ecologically significant, with wild smolts bearing a disproportionately higher predation risk than their hatchery counterparts in most years and reaches. Among predator species, AWPE and DCCO continued to pose the greatest threat to URB Chinook smolts during the updated time series, consistent with earlier findings. LAXX remained a moderate but meaningful predation source in some years, while CATE and the newly investigated ARXX exhibited low predation impacts in most years. The updated analysis also demonstrated improved precision in predation estimates relative to Payton et al. (2023), attributable to the additional five years of data and the refined statistical approach for attributing predation at mixed-species colonies.

A key development during 2021–2025 was the geographic redistribution of several major colonies. The apparent collapse of the Foundation Island DCCO colony was largely offset by emergent colonies at Crescent Island, the Hanford Islands, and Murdock Towers, suggesting that the net predation threat from DCCOs in Reaches 1–3 has only slightly increased, despite this spatial reorganization. A more concerning trend involves the estuary, where the upriver shift of DCCO from East Sand Island to the Astoria-Megler Bridge and Troutdale Towers may signal increasing predation risk to URB Chinook in Reach

4. These estimates, however, carry considerable uncertainty due to small sample sizes of fish surviving to the lower river, and should be interpreted cautiously.

Collectively, these results highlight the dynamic nature of avian predation on URB Chinook smolts and the importance of continued long-term monitoring to track shifting colony distributions, changes in predator abundance, and their cumulative effects on smolt survival. Future work should prioritize improving sample sizes of wild smolts detected in the lower Columbia River and estuary, as the current data limitations preclude precise estimation of predation in Reach 4, a gap that constrains our ability to fully characterize system-wide mortality. Additionally, continued investigation of ARXX predation across a broader range of colonies and years could help determine whether this predator guild poses a greater threat than current evidence suggests. As both total mortality and avian predation appear to be increasing in the most recent years (2021–2025), understanding the relative contribution of avian predation versus other mortality sources, including piscivorous fish, dam passage, and abiotic factors, remains critical for informing management decisions that seek to improve the productivity and recovery of URB Chinook in the Columbia River basin.

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SUPPLEMENTAL TABLES

Table S.1. Numbers of PIT-tagged URB Chinook Salmon smolts recovered dead on nesting bird colonies in the Columbia River. Bird colonies include Caspian Terns (CATE), American White Pelicans (AWPE), Double-crested Cormorants (DCCO), Brandt's Cormorants (BRAC), California and Ring-billed Gulls (LAXX), Great Blue Herons and Great Egrets (ARXX), or mixed AWPE/LAXX colonies (see Figure 1 for map of colony locations). NC denotes there was no colony at the site and year. Dashed line denotes that colony was active but was not scanned for PIT tags and that average annual estimates of predation were used in those years (see *Methods*).

Colony	2021	2022	2023	2024	2025
AMB BRAC ¹	0	2	0	2	4
AMB DCCO ¹	4	1	4	8	2
ANV LAXX	18	5	5	NC	NC
BGI AWPE	18	46	45	0	NC
BGI CATE	46	76	44	NC	NC
BGI LAXX	5	3	3	1	NC
BGI AWPE/LAXX	1,935	1,323	2,020	1,613	NC
CSI AWPE	NC	NC	NC	1	50
CSI CATE	NC	36	32	20	10
CSI DCCO	NC	NC	34	259	276
CSI LAXX	9	8	8	46	13
CSI AWPE/LAXX	NC	NC	NC	0	864
ESI CATE	39	61	13	26	14
ESI DCCO	4	3	-	-	-
FDI DCCO	93	133	23	NC	NC
FIN CATE	NC	NC	NC	NC	11
HANIS DCCO	120	252	182	77	43
HANIS ARXX	-	-	-	-	3
IS20 DCCO	NC	NC	-	88	26
IS20 LAXX	95	137	33	95	23
IS20 ARXX	NC	NC	-	-	109
LEN-SHOAL CATE	0	0	0	1	0
MRI LAXX	70	46	74	53	92
MSI AWPE	0	1	0	0	0
MUT DCCO	NC	NC	-	27	119
NEP CATE	NC	NC	0	2	0
PTI CATE	2	0	2	0	1
RCI CATE ²	0	3	7	0	-
TTOWER DCCO	-	3	4	3	6

¹ Subsample of all available nests (see Evans et al. 2026)

² Active dissuasion occurred from 2021–2025.

Table S.2. Average annual recovery probabilities (95% credible intervals) of URB Chinook smolt PIT tags on colonial waterbird breeding sites. Recovery probabilities are from Caspian Tern (CATE), Double-crested Cormorant (DCCO), California and Ring-billed Gull (LAXX), American White Pelican (AWPE), mixed AWP/LAXX colonies, and Great Blue Heron and Great Egret (ARXX) colonies (see Figure 1 for map of colony locations and names). Recovery probability is reported as deposition probability multiplied by the detection probability. Dashed line indicates the colony sites was inactive or was not scanned for PIT tags that year (see *Table A1*). Data used to generate predation probabilities on URB Chinook during 2008–2019 are reported in Payton et al. (2023).

Recovery	2021	2022	2023	2024	2025
AMB BRAC	--	0.39	--	0.32	0.41
	--	(0.21 – 0.56)	--	(0.20 – 0.47)	(0.27 – 0.53)
AMB DCCO	0.36	0.33	0.25	0.27	0.24
	(0.23 – 0.49)	(0.20 – 0.44)	(0.15 – 0.34)	(0.20 – 0.39)	(0.13 – 0.34)
ANV LAXX	0.14	0.13	0.14	--	--
	(0.09 – 0.18)	(0.09 – 0.17)	(0.09 – 0.19)	--	--
BGI AWPE	0.37	0.42	0.41	--	--
	(0.27 – 0.50)	(0.28 – 0.54)	(0.28 – 0.53)	--	--
BGI CATE	0.51	0.53	0.43	--	--
	(0.37 – 0.65)	(0.36 – 0.67)	(0.26 – 0.58)	--	--
BGI LAXX	0.14	0.13	0.14	--	--
	(0.10 – 0.18)	(0.09 – 0.18)	(0.09 – 0.19)	--	--
BGI AWPE/LAXX	0.37	0.42	0.41	0.34	--
	(0.27 – 0.49)	(0.27 – 0.53)	(0.29 – 0.53)	(0.24 – 0.43)	--
CSI AWPE	--	--	--	0.34	0.38
	--	--	--	(0.24 – 0.46)	(0.27 – 0.49)
CSI CATE	--	0.59	0.44	0.38	0.18
	--	(0.42 – 0.77)	(0.28 – 0.60)	(0.25 – 0.51)	(0.10 – 0.28)
CSI DCCO	--	--	0.42	0.19	0.24
	--	--	(0.27 – 0.58)	(0.10 – 0.29)	(0.14 – 0.35)
CSI LAXX	0.13	0.14	0.11	0.12	0.12
	(0.09 – 0.17)	(0.10 – 0.18)	(0.07 – 0.15)	(0.08 – 0.15)	(0.09 – 0.16)
CSI AWPE/LAXX	--	--	--	--	0.38
	--	--	--	--	(0.27 – 0.50)
ESI CATE	0.48	0.33	0.56	0.59	0.64
	(0.34 – 0.62)	(0.23 – 0.45)	(0.40 – 0.71)	(0.40 – 0.74)	(0.48 – 0.80)
ESI DCCO	0.41	0.41	--	--	--
	(0.26 – 0.57)	(0.23 – 0.59)	--	--	--
FDI DCCO	0.09	0.13	0.08	--	--
	(0.06 – 0.15)	(0.06 – 0.18)	(0.04 – 0.13)	--	--
FIN CATE	--	--	--	--	0.60
	--	--	--	--	(0.42 – 0.80)
HANIS DCCO	0.22	0.29	0.09	0.21	0.21

Recovery	2021	2022	2023	2024	2025
	(0.12 – 0.34)	(0.17 – 0.43)	(0.03 – 0.16)	(0.13 – 0.32)	(0.11 – 0.32)
HANIS ARXX	--	--	--	--	0.20
	--	--	--	--	(0.11 – 0.31)
IS20 DCCO	--	--	--	0.40	0.33
	--	--	--	(0.23 – 0.54)	(0.21 – 0.47)
IS20 LAXX	0.14	0.13	0.14	--	0.14
	(0.09 – 0.19)	(0.09 – 0.17)	(0.11 – 0.19)	--	(0.10 – 0.19)
IS20 ARXX	--	--	--	--	0.34
	--	--	--	--	(0.22 – 0.49)
LEN-SHOAL CATE	--	--	--	0.47	--
	--	--	--	(0.33 – 0.64)	--
MRI LAXX	0.13	0.11	0.13	0.10	0.11
	(0.09 – 0.17)	(0.07 – 0.15)	(0.10 – 0.18)	(0.07 – 0.14)	(0.07 – 0.14)
MSI AWPE	--	0.45	--	--	--
	--	(0.31 – 0.56)	--	--	--
MUT DCCO	--	--	--	0.29	0.41
	--	--	--	(0.20 – 0.43)	(0.28 – 0.56)
PTI CATE	0.40	--	0.37	0.43	0.35
	(0.27 – 0.53)	--	(0.22 – 0.48)	(0.25 – 0.62)	(0.21 – 0.47)
RCI CATE	--	0.51	0.53	--	--
	--	(0.36 – 0.66)	(0.39 – 0.70)	--	--
TTOWER DCCO	--	0.18	0.11	0.16	0.18
	--	(0.11 – 0.28)	(0.04 – 0.20)	(0.09 – 0.24)	(0.10 – 0.27)

Table S.3.a. Estimated average annual (95% CRI) reach-specific survival and avian predation probabilities on hatchery and wild URB Chinook smolts during 2008–2019. Reaches include release to McNary Dam (MCJ), MCJ to John Day Dam (JDA), JDA to Bonneville Dam (BON), and from BON to adults returns to BON for survival and from BON to the Pacific Ocean for predation. Avian predators include American white pelicans (AWPE), California and ring-billed gulls (LAXX), Double-crested cormorants (DCCO), and all predator species combined within each reach (ALL).

2008 – 2019		Release to MCJ		MCJ to JDA		JDA to BON		FROM BON	
Survival	H	0.660	(0.634, 0.688)	0.701	(0.663, 0.740)	0.839	(0.786, 0.888)	0.025	(0.022, 0.028)
	W	0.377	(0.344, 0.420)	0.620	(0.573, 0.669)	0.732	(0.657, 0.806)	0.030	(0.025, 0.035)
Predation									
All Birds	H	0.052	(0.044-0.067)	0.012	(0.009-0.014)	0.011	(0.008-0.013)	0.014	(0.012-0.016)
	W	0.119	(0.103-0.137)	0.019	(0.015-0.024)	0.008	(0.006-0.011)	0.006	(0.005-0.007)
AWPE	H	0.022	(0.017-0.028)	0.004	(0.003-0.005)	0.001	(0-0.001)	NA	NA
	W	0.063	(0.051-0.078)	0.014	(0.011-0.019)	0.003	(0.002-0.006)	NA	NA
LAXX	H	0.007	(0.005-0.021)	0.006	(0.004-0.008)	0.01	(0.008-0.013)	NA	NA
	W	0.009	(0.006-0.015)	0.004	(0.003-0.005)	0.005	(0.003-0.006)	NA	NA
DCCO	H	0.017	(0.013-0.022)	NA	NA	NA	NA	0.007	(0.006-0.009)
	W	0.041	(0.033-0.052)	NA	NA	NA	NA	0.004	(0.003-0.004)
CATE	H	0.005	(0.004-0.006)	0.002	(0.002-0.003)	NA	NA	0.006	(0.005-0.007)
	W	0.004	(0.003-0.005)	0.001	(0.001-0.002)	NA	NA	0.002	(0.002-0.003)

Table S.3.b. Estimated average annual (95% CRI) reach-specific survival and avian predation probabilities on hatchery and wild URB Chinook Salmon smolts during 2021–2025. Reaches include release to McNary Dam (MCJ), MCJ to John Day Dam (JDA), JDA to Bonneville Dam (BON), and from BON to adults returns to BON for survival and from BON to the Pacific Ocean for predation. Adult returns, however, were incomplete at the time of this analysis. Avian predators include American white pelicans (AWPE), California and ring-billed gulls (LAXX), Double-crested cormorants (DCCO), and bird species combined within each reach (ALL). ALL includes predation by Great blue herons and Great Egrets (in 2025 only).

2021 – 2025		Release to MCJ		MCJ to JDA		JDA to BON		FROM BON	
Survival	H	0.378	(0.339, 0.426)	0.525	(0.468, 0.587)	0.74	(0.652, 0.836)	0.016	(0.013, 0.018)
	W	0.227	(0.169, 0.329)	0.393	(0.282, 0.556)	0.73	(0.558, 0.848)	0.009	(0.005, 0.014)
Predation									
All Birds	H	0.127	(0.114, 0.144)	0.021	(0.013, 0.029)	0.074	(0.055, 0.097)	0.029	(0.023, 0.039)
	W	0.201	(0.177, 0.232)	0.021	(0.006, 0.060)	0.083	(0.048, 0.132)	0.091	(0.046, 0.186)
AWPE	H	0.068	(0.058, 0.079)	0.008	(0.003, 0.014)	0.004	(0.002, 0.007)	0	(0, 0.001)
	W	0.135	(0.112, 0.162)	0.008	(0, 0.044)	0.009	(0.001, 0.032)	0	(0, 0.002)
LAXX	H	0.016	(0.013, 0.023)	0.012	(0.006, 0.021)	0.059	(0.042, 0.080)	NA	NA
	W	0.027	(0.021, 0.034)	0.009	(0.002, 0.026)	0.062	(0.031, 0.107)	NA	NA
DCCO	H	0.039	(0.031, 0.053)	NA	NA	0.011	(0.008, 0.017)	0.014	(0.009, 0.022)
	W	0.036	(0.027, 0.046)	NA	NA	0.008	(0.002, 0.023)	0.071	(0.028, 0.163)
CATE	H	0.003	(0.002, 0.003)	0	(0, 0.001)	NA	NA	0.013	(0.010, 0.017)
	W	0.003	(0.002, 0.004)	0.001	(0, 0.004)	NA	NA	0.014	(0.007, 0.027)