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Cumulative Effects of Avian Predation on Upper Columbia River Steelhead

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Abstract
To investigate the cumulative effects of colonial waterbird predation on fish mortality and to determine what proportion of all sources of fish mortality (1 − survival) was due to bird predation, we conducted a mark–recapture–recovery study with upper Columbia River steelhead *Oncorhynchus mykiss* that were PIT-tagged and released ($N = 78{,}409$) at Rock Island Dam on the Columbia River, USA. We used a state–space Bayesian model that incorporated live detections and dead recoveries of tagged fish to jointly estimate predation and survival probabilities during smolt out-migration to the Pacific Ocean over an 11-year study period. Estimated cumulative (all colonies combined) avian predation probabilities ranged from 0.31 (95% credible interval [CRI] = 0.27–0.38) to 0.53 (95% CRI = 0.42–0.64) annually, indicating that avian predation was a substantial source of mortality. Of the predator species evaluated, predation by Caspian terns *Hydroprogne caspia* was often the highest, with predation probabilities ranging from 0.11 (95% CRI = 0.09–0.14) to 0.38 (95% CRI = 0.29–0.47). Probabilities of predation by double-crested cormorants *Phalacrocorax auritus* and mixed colonies of California gulls *Larus californicus* and ring-billed gulls *L. delawarensis* were generally lower than the probabilities for terns but were also substantial, with upwards of 0.04 (95% CRI = 0.03–0.07; cormorants) and 0.31 (95% CRI = 0.25–0.39; gulls) of steelhead consumed. Comparisons of total smolt mortality with mortality due to avian predation indicated that avian predation accounted for 42% (95% CRI = 30–56%) to 70% (95% CRI = 53–87%) of total mortality, suggesting that more steelhead were consumed by avian predators than died from all other mortality sources combined. Results indicate that avian predation, although not the original cause of steelhead declines in the basin, is now a factor limiting the survival of upper Columbia River steelhead. Using the analytical framework developed in this study, future studies can consider the cumulative impact of multiple mortality sources across large spatial and temporal scales to more fully understand the extent to which they limit fish survival.

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Identifying factors that affect the survival of juvenile Pacific salmonids *Oncorhynchus* spp., particularly populations listed under the U.S. Endangered Species Act (ESA), is necessary to develop effective recovery plans. Recent research suggests that avian predation may be a factor limiting the recovery of some ESA-listed salmonid populations in the Columbia River basin (Hostetter et al. 2015; Evans et al. 2016). Multiple species of piscivorous colonial waterbirds nest in the region, and previous research indicates that Caspian terns *Hydroprogne caspia*, double-crested cormorants *Phalacrocorax auritus*, California gulls *Larus californicus*, and ring-billed gulls *L. delawarensis* are the principal avian predators of juvenile salmonids in the Columbia River basin (Collis et al. 2001; Evans et al. 2012, 2016; Hostetter et al. 2015). Bird nesting colonies are located at numerous sites throughout the basin, with colony sizes ranging from less than 25 to well over 10,000 breeding pairs, depending on the species, site, and year (Collis et al. 2002; Adkins et al. 2014). The timing of the nesting season (April–August) also coincides with the peak smolt out-migration period, making most anadromous salmonids in the Columbia River basin susceptible to predation by colonial waterbirds (Lyons et al. 2007; Adkins et al. 2014; Evans et al. 2016).

Previous studies indicate that colonial waterbirds can consume large numbers of migrating juvenile salmonid smolts. For example, Caspian terns nesting on Rice Island in the Columbia River estuary consumed between 8.1 and 12.4 million Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, and steelhead *O. mykiss* smolts (all species combined) annually (Roby et al. 2003), while double-crested cormorants nesting on East Sand Island, also located in the estuary, consumed between 2.4 and 15.0 million smolts (all species combined) annually (Lyons 2010). Similarly, mark–recovery studies investigating avian predation rates or probabilities (i.e., proportion of available fish consumed) documented substantial levels of avian predation on some salmonid species. For example, California gulls and ring-billed gulls nesting on Miller Rocks Island (The Dalles Reservoir), consumed between 0.06 and 0.11 (i.e., 6–11%) of available juvenile steelhead smolts annually (Hostetter et al. 2015), while Caspian terns nesting on Goose Island in Potholes Reservoir (adjacent to the middle Columbia River) consumed upwards of 0.15 (i.e., 15%) of the available steelhead smolts annually (Evans et al. 2012). The system-wide cumulative impacts on smolt survival by multiple species and breeding colonies of piscivorous colonial waterbirds, however, are largely unknown but may be substantial based on the predation rates documented at individual breeding colonies in or near the Columbia River.

In addition to predation from piscivorous colonial waterbirds, salmonid smolts are subject to numerous other nonavian sources of mortality during out-migration. For example, mortality associated with hydroelectric dam passage, predation by piscivorous fish, and disease is well documented in the Columbia River basin (Ward et al. 1995; Muir et al. 2001; Dietrich et al. 2011). Determining the extent to which avian predation limits smolt survival relative to these other sources of mortality may be critical for prioritizing recovery actions for ESA-listed salmonid populations (Evans et al. 2016).

Mark–recapture–recovery studies have been used to identify and quantify specific sources of mortality for anadromous fish in the Columbia River basin (Mathur et al. 1996; Muir et al. 2001; Evans et al. 2016). These studies relied on marking (tagging) fish and then using subsequent recapture (or detection) and recovery events to estimate survival and cause-specific mortality (e.g., predation, harvest, and dam passage). Results from these studies provide critical information regarding where, when, and how many fish die from a specific cause. Such studies, however, often focus on the effects of a single mortality factor at a specific time and location. Investigating the cumulative effects of multiple mortality factors across larger spatial and temporal scales may provide data to more rigorously investigate the benefits or efficacy of reducing cause-specific mortality to increase fish survival. Understanding the cumulative effects of bird predation may be especially important for salmonid populations that undergo long-distance migrations, such as upper Columbia River steelhead, which must migrate hundreds of river kilometers (rkm) through the foraging ranges of multiple piscivorous waterbird colonies during smolt out-migration.

To investigate the cumulative effects of avian predation and to determine what proportion of total fish mortality (1 − survival) was due to avian predation, we conducted a mark–recapture–recovery study using steelhead smolts from the ESA-listed upper Columbia River population (NOAA 2011). Survival and predation rates were evaluated during an 11-year study period (2008–2018) across multiple river reaches where piscivorous waterbirds (Caspian terns, double-crested cormorants, California gulls, and ring-billed gulls) foraged from up to 14 different breeding colonies. Results provide a comprehensive, system-wide evaluation of the cumulative effects of colonial waterbird predation on the survival of steelhead smolts during out-migration to the Pacific Ocean.

STUDY AREA

We integrated multiple sources of data to estimate avian predation and survival of upper Columbia River steelhead, including detections of live fish passing multiple in-river detection sites, recoveries of tags from depredated fish on multiple bird colonies, and independent studies to estimate deposition and recovery rates of tags from depredated fish after consumption by piscivorous colonial waterbirds. We estimated predation rates and survival rates of steelhead smolts that were marked with PIT tags and released into the tailrace of Rock Island Dam on the middle Columbia River annually during 2008–2018 (Figure 1). River reaches were defined by the locations where PIT-tagged fish were detected or recovered after release and included (1) Rock Island Dam to McNary Dam, a 259-rkm section of the middle to lower Columbia River; (2) McNary Dam to Bonneville Dam, a 236-rkm section of the lower Columbia River; and (3) Bonneville Dam to the Pacific Ocean, a 234-rkm section of the lower Columbia River and estuary (hereafter, reaches 1, 2, and 3, respectively). Smolt survival and predation through reaches 1 and 2 were estimated based on live-fish detections at in-river PIT tag detection sites and recoveries of tags from depredated fish on multiple bird colonies (Figure 1). Smolt predation in reach 3 was based on recoveries of tags from depredated fish on bird colonies on East Sand Island in the Columbia River estuary. Smolt survival through reach 3, however, could not be estimated due to a lack of in-river PIT tag detection sites downstream of East Sand Island. The number of smolts surviving to adulthood (fish known to have survived out-migration to the Pacific Ocean) was determined based on PIT tag detections of returning adult steelhead in fishways or ladders located at Bonneville Dam (Figure 1).

METHODS

Mark–recapture–recovery.— The methods of Evans et al. (2014) were used to capture, tag, and release steelhead smolts at Rock Island Dam (Figure 1). Steelhead smolts were captured at the Rock Island Dam juvenile fish trap, anesthetized (with tricaine methanesulfonate), and PIT-tagged (12- × 2-mm tags [length × width]; 134.2 kHz) annually during 2008–2018. Fish were sampled for tagging daily from early April to mid-June of each year, with the duration of tagging dependent on the availability of steelhead smolts in the trap. Steelhead smolts were randomly selected for tagging (i.e., tagged regardless of their size, rearing type, or condition; see Evans et al. 2014 for details) and were tagged in proportion to the number of smolts collected in the trap each day. This sampling regime ensured that the tagged fish were representative of the run at large. After tagging, fish could recover from handling in a temporary holding tank for up to 12 h before being released into the tailrace of Rock Island Dam to resume out-migration to the Pacific Ocean.

After their release at Rock Island Dam, tagged steelhead could be detected (recaptured) alive at downstream sites with PIT tag antennas or arrays (a series of multiple antennas). Arrays were located at McNary Dam (rkm 470), John Day Dam (rkm 349), and Bonneville Dam (rkm 234) and at a vessel-towed paired-trawl net detector system in the Columbia River estuary (rkm 85; Figure 1). Adult steelhead returning to the Columbia River after ocean residency were detected at arrays located in fishways (ladders) at Bonneville Dam 1–3 years after their release as smolts at Rock Island Dam (Figure 1). Recapture records were retrieved from the PIT Tag Information System, a regional mark–recapture–recovery database maintained by the Pacific States Marine Fisheries Commission (PSMFC 2019).

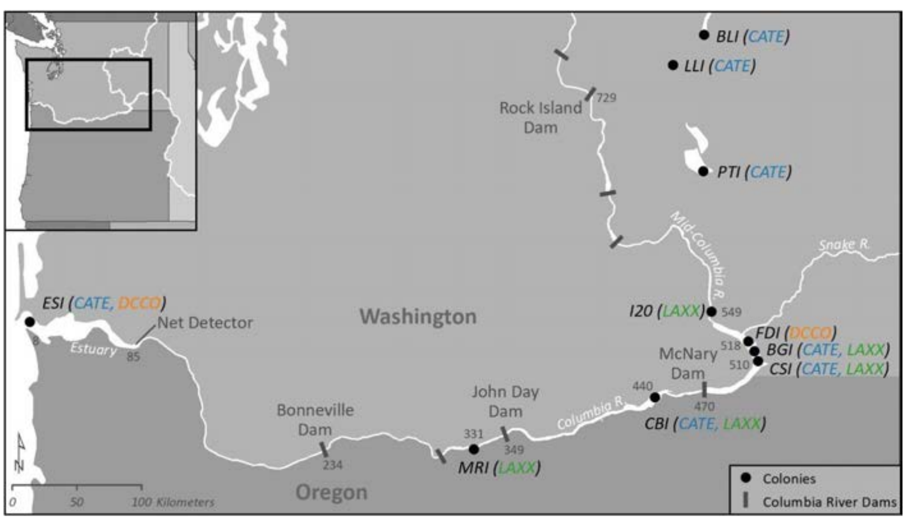

FIGURE 1. Mark–recapture–recovery locations of PIT-tagged steelhead released at Rock Island Dam. Recapture locations include McNary Dam, John Day Dam, and Bonneville Dam as well as a towed net detection system in the Columbia River estuary. Recovery locations include Banks Lake Island (BLI), Potholes Reservoir (PTI), Lenore Lake Island (LLI), Island 20 (I20), Foundation Island (FDI), Badger Island (BGI), Crescent Island (CSI), central Blalock Islands (CBI), Miller Rocks Island (MRI), and East Sand Island (ESI). Avian species studied include Caspian terns (CATE), double-crested cormorants (DCCO), and mixed California gulls and ring-billed gulls (LAXX). Distances represents river kilometers from the Pacific Ocean.

Steelhead tags were also recovered on piscivorous waterbird colonies located throughout the Columbia River basin. In total, 14 different bird colonies were included in the study; all colonies were previously identified as posing a potential threat to steelhead survival during out-migration (Figure 1; Evans et al. 2012; Hostetter et al. 2015). The methods of Evans et al. (2012) were used to recover PIT tags from each bird colony. Hand-held or flat-plate PIT tag antennas were used to detect tags on bird colonies after birds dispersed after the breeding season (August–October). The entire land area occupied by nesting birds was scanned for tags after each nesting season, with a minimum of two complete sweeps or passes of each colony site conducted each year. The land area occupied by birds during each nesting season was determined based on aerial photography surveys and/or ground-based surveys of the colony, which were carried out during the peak of the nesting season (i.e., late April to early June; see below for additional details).

Not all fish PIT tags that are ingested by birds are deposited on the bird's nesting colony (i.e., deposition probabilities for consumed fish tags are less than 1.0), and not all tags deposited at the colony are detected by researchers after the nesting season (i.e., detection probabilities for deposited fish tags are less than 1.0; Hostetter et al. 2015). We followed previously published methods for estimating colony-specific PIT tag deposition and detection probabilities (Hostetter et al. 2015; Evans et al. 2016; Payton et al. 2019). Recoveries of PIT-tagged salmonids that were intentionally fed to nesting Caspian terns, double-crested cormorants, and California gulls throughout the nesting season at multiple colonies and years were used to estimate PIT tag deposition probabilities (Hostetter et al. 2015). To estimate detection probabilities, PIT tags were sown on each bird colony by researchers prior to, during (when possible), and after the nesting season. Recoveries of these 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 nesting season. Colony-specific PIT tag recovery probabilities are provided in Appendix Table A.1.

Birds nesting at some of the colonies included in this study were capable of foraging in multiple river reaches (i.e., upstream and downstream of an array used to delineate a river reach; Evans et al. 2016; Hostetter et al. 2018), which required predation rates to be partitioned by river reach (Figure 2). A benefit of this partitioning was that predation rates delineated by river reach could be summed to evaluate colony-specific and cumulative predation rates (Figure 2).

Bird colony size.— The methods of Adkins et al. (2014) were used to estimate the size (number of breeding pairs) of piscivorous waterbird colonies included in the study. Estimates of colony size were obtained late in incubation, when the greatest numbers of adults are aggregated at nesting colonies (Gaston and Smith 1984). Numbers of breeding pairs of Caspian terns at colonies were estimated either from counts of nesting birds via high-resolution orthorectified digital aerial photography or from ground counts of attended nests late in incubation. Colony size estimates from digital photography were either direct counts of all incubating birds or direct counts of all adults on-colony, corrected using simultaneous ground counts of incubating and nonincubating birds in plots. All ground counts were made from an observation blind or a boat situated near the colony. The number of breeding pairs of double-crested cormorants was determined from direct counts of attended nests in digital aerial photography or direct ground counts of attended nests (i.e., from an observation blind or a boat) around the peak of incubation. We could not correct counts from aerial photography to estimate the number of breeding pairs for California gulls and ring-billed gulls because representative counts of incubating and nonincubating gulls from the ground were not

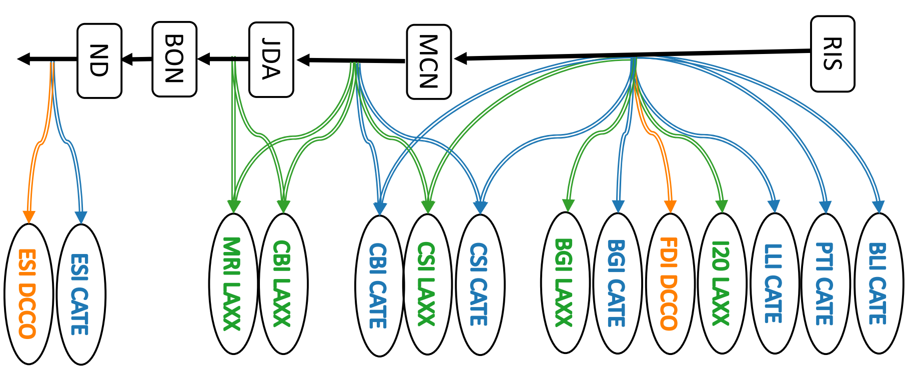

FIGURE 2. Schematic of mark–recapture–recovery sites used to estimate steelhead smolt predation and survival rates for fish tagged and released at Rock Island Dam (RIS). Arrows depict colonies (color coded by species) that were capable of consuming fish above and below recapture sites. Recapture locations include McNary Dam (MCN), John Day Dam (JDA), and Bonneville Dam (BON), plus a paired-trawl net detector (ND) system in the Columbia River estuary. Recovery location codes (three letters) and avian species codes (four letters) are defined in Figure 1.

available. As such, colony size estimates for gulls were based on counts of adult gulls from aerial photography and used as an index of the number of breeding pairs utilizing the colony (Adkins et al. 2014).

Predation and survival estimation.— The joint mortality and survival estimation technique of Payton et al. (2019) was used to estimate reach-specific and cumulative steelhead predation and survival rates. This hierarchal Bayesian modeling approach incorporated both live detections and dead recoveries of tagged fish in space and time to simultaneously estimate rates of predation and survival. In brief, the state–space model used two vectors, $\mathbf{m}_i$ and $\mathbf{d}_i$, to describe a fish's recapture history after release at Rock Island Dam at each of the 5 downstream live-recapture sites and each of the 14 bird colony recovery sites under consideration. The vector $\mathbf{m}_i$ was a 5-length vector, where m_j was an indicator variable of a fish's recapture at recapture opportunity j, and $\mathbf{d}_i$ was a 15-length vector, where for $h \in \{1, 2, \ldots, 14\}, d_{i,h}$ was an indicator variable of recovery from colony h and $d_{i,15}$ indicated that a fish was unrecovered. The model provided inference about $\mathbf{z}_i$, the unobserved 5-length vector, where $z_{i,j}$ was an indicator variable of whether the fish was still alive at recapture opportunity j.

Parameters used in the model were as follows:

- Φ, defined as a 5-length vector, where Φ_j represented the probability that a fish alive at recapture opportunity $j-1$ (where release from Rock Island Dam is defined as the 0th recapture opportunity) survived to recapture opportunity j;
- Θ, a 15×5 matrix, where $\Theta_{j,h}$ represented the probability that a fish alive at recapture opportunity $j-1$ survived to recapture opportunity j and then succumbed to mortality cause h;
- $\mathbf{p}$, a 5-length vector, where p_j represented the probability that a fish alive at recapture opportunity j was successfully recaptured; and
- $\boldsymbol{\lambda}$, a 15-length vector, where for $h \in \{1, 2, \ldots, 14\}$, λ_h represented the probability of recovering a fish that died due to mortality cause h and $\lambda_{15} = 0$ represented the lack of recoveries of fish that died from all other unspecified causes.

To avoid over-parameterization, $\Theta_{j,15}$ was defined as $\Theta_{j,15} = 1 - \phi_{j+1} - \sum_{h \le 14} \Theta_{j,h} \forall j$.

Low recapture rates are detrimental to partitioning the impact of predation by birds from colony h among the river reaches comprising each bird colony's foraging range. Previous research indicated that predation rates by birds from particular colonies were spatially proportionate amongst river reaches across years (Evans et al. 2016; Hostetter et al. 2018). Therefore, a beta-binomial distribution was used to facilitate an "informed partitioning" method. Informed partitioning involved first defining $\theta^{cumulative}$ as a 15-length vector, where $\theta_h^{cumulative}$ represented the probability that a fish released at Rock Island Dam succumbed to mortality cause h. For each colony h, the 5-length vector $\boldsymbol{\rho}_h$ was then used to define the partitioning of $\theta_h^{cumulative}$. That is,

$$\Theta_{j,h} = \theta_h^{cumulative} \rho_{h,j} \prod_{k<j} \phi_k, \quad \forall j, h$$

where

$$\boldsymbol{\rho}_h \sim \text{Dirichlet}(\alpha^h).$$

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

$$z_{i,j} \sim \text{Bernoulli}\left[z_{i,(j-1)} \times \phi_j\right],$$

$$m_{i,j} \sim \text{Bernoulli}\left(z_{i,j} \times p_j\right),$$

and

$$d_{i,h} \sim \text{Bernoulli}\left[\sum_{j=1}^{M-1} \left(z_{i,j+1} - z_{i,j}\right) \times \Theta_{j,h} \times \lambda_d\right].$$

We allowed for temporal variation in mortality (Evans et al. 2014; Hostetter et al. 2015), recapture (Sandford and Smith 2002), and recovery (Ryan et al. 2003; Evans et al. 2012) probabilities. Steelhead were grouped into weekly release cohorts under the assumption that fish released within the same week experienced similar rates of mortality/survival, recapture, and recovery (Hostetter et al. 2015; Payton et al. 2019). The week-specific rates were accordingly denoted $\Theta_{y,w}$, $\mathbf{p}_{\mathbf{y},\mathbf{w}}$, and $\boldsymbol{\lambda}_{y,w}$. Rates of mortality, recapture, and recovery from weeks closer in time were assumed to be more alike than those temporally further apart. Serial correlation in survival/mortality and recapture rates was accounted for through a weekly random walk process (Payton et al. 2019). Temporal variation in detection rates was estimated more directly from recovery of intentionally sown PIT tags on each colony before, after, and (in some instances) within each nesting season (see Hostetter et al. 2015; Table A.1). Estimated detection probabilities at each colony were interpolated from the logistic curve that was estimated from recoveries of intentionally sown tags. In some rare instances, researchers were unable to sow PIT tags prior to the nesting season. In these few cases, intraseasonal variation in recovery rates based on information from similar colonies in the same year or information from the same colony in different years was used to estimate weekly variation in colony-specific detection probabilities (see Payton et al. 2019; Table A.1).

Weakly informative priors were assigned to most of the parameters of the model (Gelman et al. 2017; Payton et al. 2019). The prior for the initial week's detection probability in each year was defined to be Uniform (0, 1). Analogously, the prior distribution assigned for the life path simplexes in the initial week of each year was assumed to be Dirichlet (**1**), where **1** was an appropriately sized vector of ones. Weakly informative priors of Half-normal (0, 5) were also implemented for all variance parameters.

Simulated samples from the posterior distribution were derived using the software Stan (SDT 2015), accessed through R version 3.1.2 (RDCT 2014), using the rstan package (version 2.17.3; SDT 2015). We ran four parallel Hamiltonian Monte Carlo simulations (Betancourt and Girolami 2015). Each chain contained 2,000 adaptation iterations, followed by 2,000 posterior iterations. Chain convergence was visually evaluated and verified using the Gelman–Rubin statistic (Gelman et al. 2013). Chains were only considered valid if Gelman–Rubin statistics for all parameters were valued less than 1.01 and if zero divergent transitions were reported. Posterior predictive checks were used to assure model fit with respect to site-specific annual recapture counts and site-specific annual recovery counts (Gelman et al. 2013). Bayesian P-values were all deemed to be of little concern (P-values $\in$ [0.1, 0.9]). We present estimated results as posterior medians along with 95% highest (posterior) density intervals (95% credible intervals [CRIs]).

Model assumptions.— The accuracy and precision of survival and predation rate estimates depend in part on the validity of the following assumptions: (1) smolt survival, predation, and recapture/recovery probabilities are independent; (2) fish tagged and released within the same week have identical recapture/recovery probabilities; (3) intra-annual variation in survival, predation, and recapture/recovery probabilities can be described as a "random walk" process; and (4) sampled fish are representative of all fish (tagged and untagged) in the population at-large.

The fate of each tagged fish was assumed to be independent of the fate of other tagged fish in the sample (assumption 1 above). This assumption is ubiquitous amongst mark–recapture studies, but there is rarely evidence to support or refute the validity of this assumption (Payton et al. 2019). Lack of independence would likely overstate estimates of precision and bias predation and survival estimates to an unknown degree. Detection probabilities did not change dramatically on a weekly basis, and there was no evidence of inter- or intra-annual changes in deposition probabilities across colonies of the same species of avian predator (assumption 2; Hostetter et al. 2015). The random walk framework allowed for interweekly fluctuations in survival, predation, and recapture/recovery probabilities, so assumption 3 only needs to be approximately true for rates to be unbiased (Payton et al. 2019). Assumption 4 rests on the random selection of steelhead for PIT tagging at Rock Island Dam, whereby fish were tagged regardless of their rearing type, size, or condition, and fish were tagged in proportion to the number available each week to account for differences in run timing each year (see also Evans et al. 2014). This sampling scheme helped to ensure that steelhead included in the study were representative of steelhead in the population at-large (tagged and untagged) passing Rock Island Dam. The effects of handling and PIT tagging of each fish, however, were inestimable. If this was an issue, then smolt losses due to handling or tagging would result in an overstatement of fish availability, thereby leading to the underestimation of predation and survival to an unknown degree.

RESULTS

Mark–Recapture–Recovery

In total, 78,409 steelhead smolts were captured, PIT-tagged, and released into the tailrace of Rock Island Dam during 2008–2018 (Table 1). Sample sizes ranged annually from 5,893 to 7,756 tagged smolts, with the number of weekly releases ranging from 9 to 11 weeks/year (Table 1). After release, there were 11,525 downstream smolt recapture events at in-river PIT tag arrays and 8,129 recovery events at bird colonies (Table 1). Numbers of steelhead detected in-river varied considerably by river reach and year, as did the number of smolt tags recovered on individual bird colonies (Table A.2). The largest numbers of smolt tags were recovered on bird colonies located upstream of McNary Dam in reach 1 ($N = 3{,}871$; Table 1). Conversely, the smallest number of smolts was recaptured alive at the paired-trawl net detector in the Columbia River estuary in reach 3 ($N = 1{,}067$; Table 1). Only a small number and proportion of steelhead smolts that were tagged and released at Rock Island Dam returned to Bonneville Dam as adults, with the number of adult returns ($N = 629$) ranging from 5 to 220 adults per smolt release year (Table 1).

Recapture and recovery probabilities for smolt PIT tags at in-stream arrays and on bird colonies, respectively, are reported in Table A.1. Recapture probabilities were generally low (posterior medians <0.20 for most recapture sites and years). Recovery probabilities were generally higher than recapture probabilities but were also highly variable depending on the bird species, bird colony, and year (range of posterior medians = 0.07–0.65; Table A.1).

Bird Colony Size

The estimated size of bird colonies (number of breeding pairs) included in the study (see Figure 1) varied by predator species, colony location, and year (Table 2). In reaches

TABLE 1. Numbers of steelhead smolts that were tagged and released at Rock Island Dam and subsequently recaptured (live) at PIT tag detection arrays or whose tags were recovered on bird colonies (dead) during 2008–2018. The numbers of smolts returning as adults to Bonneville Dam are also provided; an en dash (–) denotes that complete adult returns from a cohort were not available.

		Reach 1 (Rock Island Dam to McNary Dam)		Reach 2 (McNary Dam to Bonneville Dam)		Reach 3 (Bonneville Dam to Pacific Ocean)		Adult returns
Year	Number released (weeks)	Live	Dead	Live	Dead	Live	Dead	Live
2008	7,271 (11)	636	479	390	68	81	489	220
2009	7,114 (11)	668	616	427	52	110	431	77
2010	7,365 (11)	366	517	977	56	104	397	88
2011	7,756 (11)	358	493	153	31	72	270	46
2012	6,712 (10)	401	372	348	25	96	178	67
2013	5,893 (10)	332	474	396	42	118	165	61
2014	7,663 (10)	352	346	528	91	137	338	65
2015	7,069 (10)	385	204	701	425	103	190	5
2016	6,764 (9)	779	214	711	227	87	97	–
2017	7,436 (10)	314	105	406	215	77	168	–
2018	7,366 (10)	246	51	584	155	82	148	–
Total	78,409 (113)	4,837	3,871	5,621	1,387	1,067	2,871	629

1 and 2, the largest colonies of piscivorous waterbirds were mixed colonies of California gulls and ring-billed gulls (3,733–16,558 breeding pairs·colony^{-1}·year^{-1}), followed by Caspian tern colonies (2–677 breeding pairs·colony^{-1}·year^{-1}) and double-crested cormorant colonies (308–390 breeding pairs·colony^{-1}·year^{-1}; Table 2). In reach 3, Caspian tern and double-crested cormorant colonies were the largest anywhere in the Columbia River basin (3,500–10,688 and 544–14,916 breeding pairs·colony^{-1}·year^{-1}, respectively) and were generally an order of magnitude greater than tern and cormorant colonies located in reaches 1 and 2 (Table 2). Although the size of bird colonies varied by location, bird species, and year, the breeding chronology of birds was similar across species, with courtship and nest building observed in April, egg laying and incubation observed in May, and chick rearing and fledging observed from June to early August but occasionally extending into September.

Not all colony sites had nesting birds in all study years, and not all sites were scanned for smolt PIT tags in all years. Specifically, California gull/ring-billed gull colonies on Island 20 and the central Blalock Islands were not scanned for PIT tags during 2008–2012 (Table 2), preventing estimation of predation rates in those years by birds from those colonies. The Foundation Island double-crested cormorant colony was not scanned for PIT tags during 2013 or during 2015–2018, thus preventing estimation of predation rates in those years by birds from that colony. Double-crested cormorants nesting on East Sand Island temporarily abandoned the colony site either partially or entirely during the peak of the nesting season in 2016–2018, corresponding with the peak of the smolt outmigration period, before cormorants returned to nest on East Sand Island starting in July (Turecek et al. 2018, 2019). Therefore, although the East Sand Island cormorant colony was scanned for PIT tags in all years, the total numbers of steelhead smolts consumed by cormorants foraging in reach 3 during 2016–2018 were unknown, resulting in minimum estimates of cormorant predation rates in those years. Unlike the gull and cormorant colonies, all large Caspian tern colonies (those with >20 breeding pairs) were scanned for smolt PIT tags in all study years (Table 2).

Predation Probabilities

Of the birds from colonies foraging in reach 1 (Rock Island Dam to McNary Dam), the highest predation probabilities were those of Caspian terns nesting on islands in Potholes Reservoir, with annual probabilities ranging from 0.04 (95% CRI = 0.02–0.06) to 0.26 (95% CRI = 0.18–0.34; Figure 3; Table A.3). Predation probabilities at the Crescent Island Caspian tern colony on the lower Columbia River ranged from 0.01 (95% CRI = 0.01–0.02) to 0.03 (95% CRI = 0.02–0.05; Figure 3). Predation probabilities were lowest for Caspian terns nesting at Banks and Lenore lakes, with values less than 0.01 in most years (Figure 3). Aggregate predation impacts from all Caspian tern colonies in reach 1 ranged from 0.02 (95% CRI = 0.01–0.04) to 0.28 (95% CRI = 0.21–0.37). Of the mixed California gull/ring-billed gull colonies evaluated in reach 1, smolt consumption was the highest for gulls nesting on Island 20 on the lower Columbia River, with predation probabilities of

TABLE 2. Numbers of piscivorous waterbirds counted on breeding colonies by river reach (Re) and year. Colonies include Caspian terns, mixed California gulls/ring-billed gulls, and double-crested cormorants nesting at Banks Lake Island (BLI), Lenore Lake Island (LLI), Potholes Reservoir (PTI), Island 20 (I20), Foundation Island (FDI), Badger Island (BGI), Crescent Island (CSI), central Blalock Islands (CBI), Miller Rocks Island (MRI), and East Sand Island (ESI). Cells highlighted in gray indicate that the colony was active during that year but was not scanned for smolt PIT tags. "NA" denotes that the colony was active during that year, but colony size estimates were not available.

Colony	Re	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Caspian terns												
BLI	1	27	61	34	19	22	13	66	64	6	0	0
LLI	1	0	0	0	0	0	0	0	16	39	123	91
PTI[a]	1	293	487	416	422	463	340	159	2	144	0	0
BGI	1	0	0	0	0	0	0	0	0	0	41	0
CSI	1	388	349	375	419	422	393	474	0	0	0	0
CBI	2	104	79	136	20	6	26	45	677	483	449	313
ESI	3	10,668	9,854	8,283	6,969	6,416	7,387	6,269	6,240	5,915	3,500	4,960
California gulls and ring-billed gulls												
I20	1	20,999	19,341	NA	NA	NA	14,039	14,475	16,558	14,316	11,176	13,069
BGI	1	0	0	0	0	0	0	0	3,740	4,126	4,505	5,908
CSI	1	8,567	8,575	8,108	7,108	7,187	5,707	6,404	0	0	0	0
CBI	2	0	1,631	NA	NA	8,989	6,896	6,020	7,376	6,741	4,163	3,408
MRI	2	4,443	6,016	5,532	5,742	4,509	4,810	4,132	4,433	3,733	3,435	4,284
Double-crested cormorants												
FDI	1	357	309	308	318	390	386	390	NA	NA	NA	NA
ESI[b]	2	10,950	12,087	13,596	13,045	12,301	14,916	13,626	12,150	9,772	544	3,672

[a]Caspian terns nested either on Goose Island in Potholes Reservoir (2008–2015) or on an unnamed island in Potholes Reservoir (2016).
[b]All or some of the double-crested cormorants temporarily abandoned the colony site during the peak nesting period in 2016–2018.

PIT-tagged steelhead ranging from 0.01 (95% CRI = 0.01–0.02) to 0.08 (95% CRI = 0.05–0.12), followed closely by gulls nesting on Crescent Island (annual range = 0.02–0.07) and those nesting on Badger Island on the lower Columbia River (annual range = 0.01–0.07; Figure 3). Aggregate probabilities of smolt predation by all California gulls and ring-billed gulls in reach 1 ranged from 0.02 (95% CRI = 0.01–0.04) to 0.14 (95% CRI = 0.10–0.21). Of the 10 individual waterbird colonies that foraged in reach 1, predation probabilities were consistently the lowest for double-crested cormorants nesting on Foundation Island on the lower Columbia River, with probabilities less than 0.01 (Figure 3). Cumulative predation probabilities (predation by birds from all colonies combined) indicated that a large proportion of available steelhead was consumed by piscivorous colonial waterbirds in reach 1, with annual probabilities ranging from 0.07 (95% CRI = 0.05–0.10) to 0.36 (95% CRI = 0.27–0.45) during 2008–2018 (Figure 3). Cumulative predation estimates on upper Columbia River steelhead did not include consumption by gulls nesting on Island 20 during 2008–2012 or by double-crested cormorants nesting on Foundation Island during 2013 and 2015–2017; thus, these are minimum estimates of the total impact of birds from all colonies on steelhead mortality in reach 1 during those years.

Of the birds from colonies foraging in reach 2 (McNary Dam to Bonneville Dam), predation probabilities were the highest for California gulls and ring-billed gulls nesting at the mixed colony on Miller Rocks Island on the lower Columbia River, with probabilities ranging annually from 0.05 (95% CRI = 0.03–0.08) to 0.18 (95% CRI = 0.13–0.29; Figure 3; Table A.3). Consumption by gulls from the mixed-species colony in the central Blalock Islands on the lower Columbia River ranged annually from 0.03 (95% CRI = 0.02–0.05) to 0.09 (95% CRI = 0.06–0.14; Figure 3) in those years when PIT tag data were available for analysis (2013–2018). Aggregate predation on PIT-tagged smolts by all mixed colonies of California gulls and ring-billed gulls in reach 2 ranged from 0.06 (95% CRI = 0.03–0.10) to 0.25 (95% CRI = 0.17–0.38). Of the Caspian tern colonies foraging in reach 2, predation rates were the highest and the most variable by terns nesting at the central Blalock Islands, with predation probabilities ranging annually from less than 0.01 to 0.12 (95% CRI = 0.07–0.20; Figure 3). Estimates of the cumulative impact of all piscivorous colonial waterbirds on steelhead survival in reach 2 were highly variable across the study period, with predation probabilities ranging annually from 0.06 (95% CRI = 0.03–0.10) to 0.38 (95% CRI = 0.27–0.53; Figure 3). Analogous to estimates of cumulative predation in reach 1, not all California gull/ring-billed gull colonies were scanned for PIT tags during all study years in reach 2 (i.e., the gull colony in the central Blalock Islands during 2009–2012); therefore, estimates of cumulative steelhead

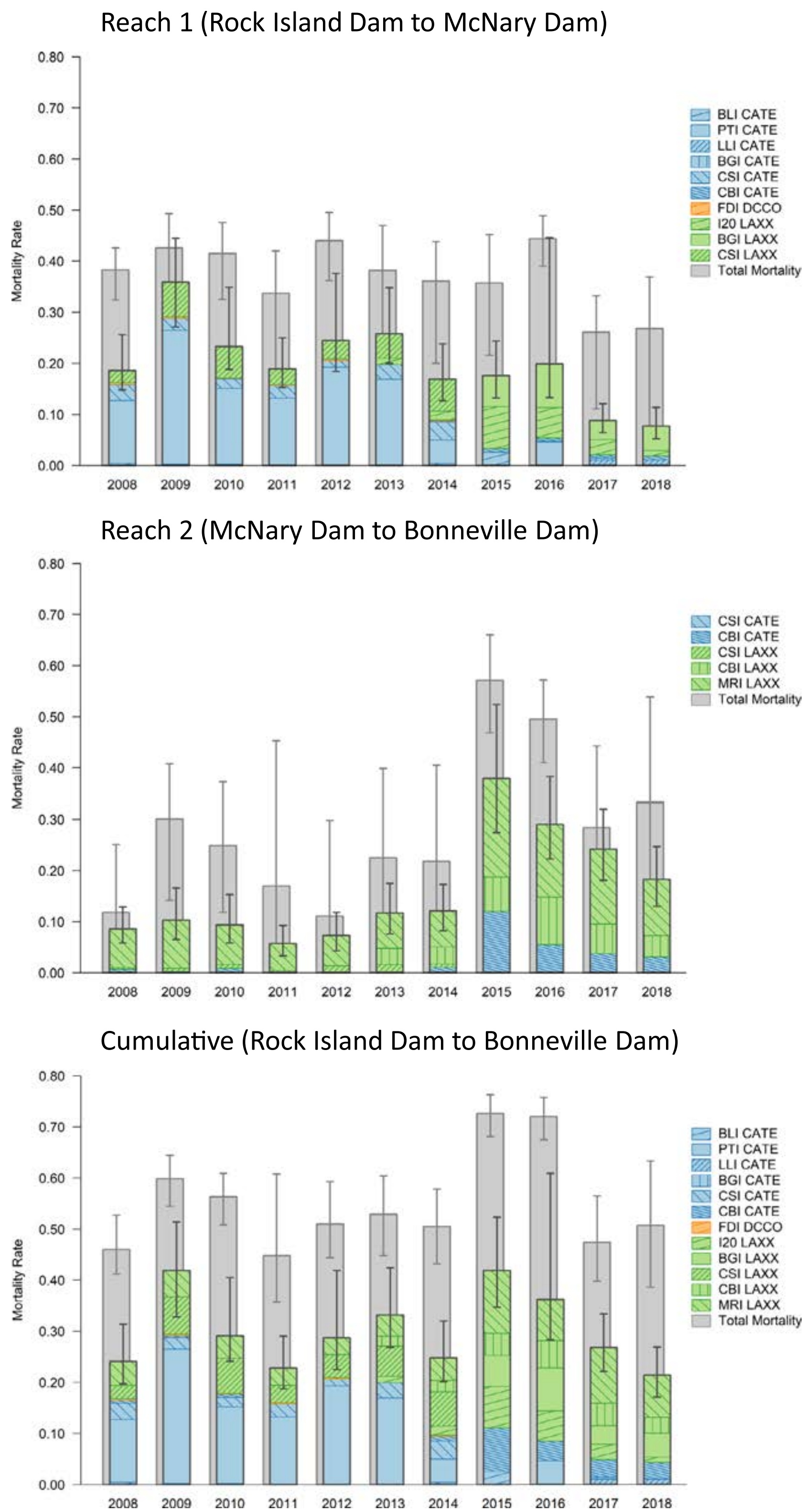

FIGURE 3. Estimated total mortality and mortality attributed to predation by colonial waterbirds on steelhead smolts during out-migration in reach 1, reach 2, and reaches 1 and 2 combined (cumulative). Colony location codes (three letters) and avian species codes (four letters) are defined in Figure 1. Error bars represent 95% credible intervals for total mortality and for mortality due to avian predation.

predation by piscivorous colonial waterbirds were minimum estimates in those years.

Gulls and Caspian terns nesting on Crescent Island in reach 1 foraged both upstream and downstream of McNary Dam, but only a small proportion of available steelhead was consumed by these colonies downstream of McNary Dam in reach 2: less than 0.01 of available smolts per year (Table A.3). Similarly, predation probabilities indicated that terns nesting in the central Blalock Islands in reach 2 foraged upstream of McNary Dam in reach 1, but predation probabilities were less than 0.02 in all study years (Table A.3). Collectively, results indicate that foraging on steelhead was concentrated within the river reach nearest to the colony. In the case of terns nesting on islands in waterbodies adjacent to the Columbia River (Banks Lake, Potholes Reservoir, and Lenore Lake), however, birds traveled a considerable distance from their breeding colony to forage on steelhead smolts in the Columbia River, with a minimum one-way commuting distance of 34–67 km, depending on the colony (Figure 1).

Of the colonies foraging in reach 3 (Bonneville Dam to the Pacific Ocean), predation probabilities were the highest for Caspian terns nesting on East Sand Island in the Columbia River estuary, with probabilities ranging annually from 0.07 (95% CRI = 0.05–0.13) to 0.21 (95% CRI = 0.16–0.30; Figure 4; Table A.3). Probabilities of predation by double-crested cormorants on East Sand Island were generally lower than those for Caspian terns but were substantial in years when cormorants were present on-colony throughout the smolt out-migration period, with estimates ranging from 0.03 (95% CRI = 0.02–0.05) to 0.10 (95% CRI = 0.07–0.16; Figure 4). Due to dispersal events by double-crested cormorants away from the East Sand Island colony during the peak nesting and smolt out-migration periods in 2016–2018, predation rates on steelhead smolts by double-crested cormorants nesting on East Sand Island should be considered minimum estimates in those years. During these colony abandonment events, most double-crested cormorants remained in the Columbia River estuary (see Turecek et al. 2018) and presumably continued to consume steelhead in reach 3, but the consumed smolt PIT tags were not being deposited on the East Sand Island cormorant colony and could not be recovered at their alternative nesting or roosting sites in the estuary.

Cumulative bird predation probabilities based on smolt PIT tag recoveries from all 14 bird colonies during smolt passage from Rock Island Dam to the Pacific Ocean were substantial, ranging annually from 0.31 (95% CRI = 0.26–0.37) to 0.53 (95% CRI = 0.44–0.63). Of the piscivorous colonial waterbird species evaluated, cumulative predation probabilities on steelhead were often—but not always—the highest for Caspian tern colonies, with terns consuming 0.11 (95% CRI = 0.09–0.14) to 0.38 (95% CRI = 0.29–0.47) of all steelhead smolts per year (Figure 4). The cumulative predation on steelhead by gulls from all colonies in reaches 1 and 2 was also substantial, ranging from 0.07 (95% CRI = 0.05–0.10) to 0.31 (95% CRI = 0.25–0.39), but gull consumption could not be fully evaluated across all study years due to a lack of tag recoveries from the Island 20 and central Blalock Islands gull colonies during 2008–2012. The cumulative predation on steelhead by double-crested cormorants from the two colonies included in the study (Foundation Island and East Sand Island) was consistently less than that of the seven tern and five gull colonies in the study, ranging from 0.01 (95% CRI = 0.01–0.02) to 0.04 (95% CRI = 0.03–0.07). Analogous to the cumulative consumption by all gull colonies, estimates of predation by cormorants nesting on Foundation Island were not available in all study years, so in those years the cumulative probabilities of predation by cormorants were minimum estimates. In the case of the large cormorant colony on East Sand Island in reach 3, predation probabilities from PIT tag recoveries in 2016–2018 also represent minimum losses due to colony abandonment events in those years.

Steelhead Survival

Estimated steelhead smolt survival ranged annually from 0.56 (95% CRI = 0.51–0.61) to 0.74 (95% CRI = 0.66–0.87) in reach 1 and from 0.42 (95% CRI = 0.32–0.49) to 0.87 (95% CRI = 0.76–0.94) in reach 2 (Figure 3). Estimated cumulative survival from release at Rock Island Dam to Bonneville Dam ranged annually from 0.27 (95% CRI = 0.23–0.31) to 0.55 (95% CRI = 0.38–0.65), indicating that a large proportion—and in many years the majority—of steelhead smolts died prior to reaching Bonneville Dam (Figure 3). An estimate of smolt survival through reach 3 could not be calculated because there were no PIT tag detection sites in the lower Columbia River estuary downstream of the bird colonies on East Sand Island. Estimated smolt-to-adult survival from Rock Island Dam (as smolts) to Bonneville Dam (as adults) ranged annually from 0.01 (95% CRI = 0.0.1–0.01) to 0.03 (95% CRI = 0.03–0.03) during 2008–2015 (the last year with complete adult returns). Estimated smolt-to-adult survival from Bonneville Dam (as smolts) to Bonneville Dam (as adults) was also available and ranged annually from 0.01 (95% CRI = 0.01–0.02) to 0.06 (95% CRI = 0.04–0.07) during 2008–2015.

Comparisons of total smolt mortality (1 − survival) and mortality associated with colonial waterbird predation indicated that avian predation was often the greatest source of steelhead mortality during out-migration through both reach 1 and reach 2 (Figure 3). In reach 1, predation by colonial waterbirds was the dominant mortality factor in many but not all study years, with birds

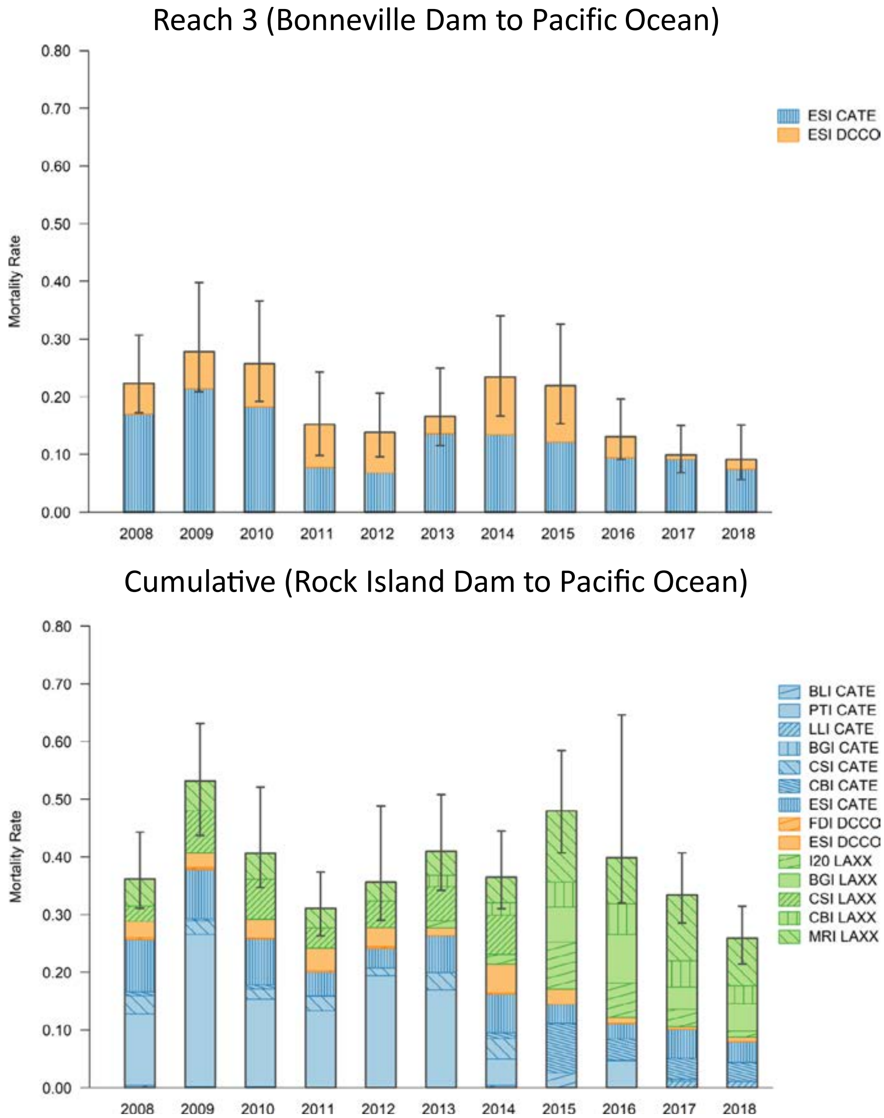

FIGURE 4. Estimated predation by colonial waterbirds on steelhead smolts in reach 3 and mortality from all avian species and colonies on steelhead smolts in reaches 1, 2, and 3 combined (cumulative). Colony location codes (three letters) and avian species codes (four letters) are defined in Figure 1. Error bars represent 95% credible intervals for mortality due to avian predation.

accounting for 28% (95% CRI = 14–93%) to 87% (95% CRI = 64–100%) of all smolt mortality sources during passage from Rock Island Dam to McNary Dam during 2008–2018. In some years, predation by Caspian terns from the colony at Potholes Reservoir alone was the single greatest source of steelhead mortality in reach 1, accounting for as much as 62% of all steelhead mortality in 2009 (Figure 3). In reach 2, bird predation was also the primary mortality factor in many but not all years, with bird predation accounting for 35% (95% CRI = 19–90%) to 91% (95% CRI = 47–100%) of all smolt mortality during 2008–2018 (Figure 3). In reach 1, Caspian tern predation was the dominant source of smolt mortality due to bird predation during 2008–2013, and California gull and ring-billed gull predation was the foremost source during 2014–2018. A lack of tag recovery data from the Island 20 and central Blalock Islands gull colonies, however, resulted in underestimates of predation by all gulls on steelhead during 2008–2012. Estimates of total smolt mortality in reach 1 provided an upper bound for the level of unaccounted-for consumption by gulls in those years, as unaccounted-for gull consumption cannot exceed estimates of total smolt mortality. For instance, in 2012, point estimates of predation by gulls from the central Blalock Islands colony in reach 2 could not have been greater than 0.04 because that would have resulted in cumulative avian predation probabilities on smolts that were greater than the point estimate of total smolt mortality in reach 1.

Comparisons of total smolt mortality from Rock Island Dam to Bonneville Dam indicated that predation by colonial waterbirds was among the most important mortality factors—and, in many cases, the single greatest mortality factor—for steelhead smolts, with predation by birds accounting for 42% (95% CRI = 30–56%) to 70% (95% CRI = 53–87%) of all smolt mortality during 2008–2018.

DISCUSSION

Impacts from Bird Predation

Numerous mortality factors have been linked to the decline in steelhead populations in the Columbia River basin, including harvest, habitat loss and degradation, poor water quality, and passage restrictions and mortality associated with hydroelectric dams (Nelson et al. 1991). Results from this study indicate that predation from piscivorous colonial waterbirds, although not the original cause of steelhead declines in the Columbia River basin, is a factor that is currently limiting the survival and recovery of ESA-listed upper Columbia River steelhead. Predation by colonial waterbirds was estimated to be the single greatest source of mortality for steelhead during smolt out-migration from Rock Island Dam to Bonneville Dam, with bird predation accounting for more than 50% of all mortality sources in 9 of the 11 study years evaluated. Estimated upper Columbia River steelhead smolt losses to piscivorous colonial waterbirds were greater than direct losses associated with passage through five hydroelectric dams (Wanapum, Priest Rapids, McNary, John Day, and Bonneville dams), predation from piscivorous fish (Northern Pikeminnow *Ptychocheilus oregonensis*, Smallmouth Bass *Micropterus dolomieu*, Walleye *Sander vitreus*, and others), predation by piscivorous waterbird species that were not included in the study (American white pelicans *Pelecanus erythrorhynchos*, common mergansers *Mergus merganser*, great blue herons *Ardea herodias*, and others), mortality from disease, and all remaining mortality factors. Even after passage through the impounded sections of the middle and lower Columbia River upstream of Bonneville Dam, the impact of piscivorous colonial waterbirds on survival of steelhead smolts in the free-flowing section of the Columbia River downstream of Bonneville Dam was substantial, with Caspian terns and double-crested cormorants nesting on East Sand Island annually consuming upwards of 0.28 of available steelhead smolts in the estuary. Even at these high levels, predation impacts reported herein should be considered minimum estimates due a lack of smolt PIT tag recoveries from several gull and cormorant colonies during the study period and due to unaccounted-for predation from piscivorous colonial waterbirds that were nonbreeding, failed breeders, and/or prospecting and therefore were not associated with one of the 14 study colonies.

Previous research indicates that steelhead are especially susceptible to colonial waterbird predation (Collis et al. 2001; Evans et al. 2012, 2016; Freschette et al. 2012). For example, estimated probabilities of predation by Caspian terns and California gulls/ring-billed gulls on steelhead smolts were two to five times higher than those of juvenile salmon species during passage through the same river reaches (Evans et al. 2012, 2016). Freschette et al. (2012) observed higher predation by western gulls *L. occidentalis* on steelhead compared with Coho Salmon smolts along the California coast. Possible explanations for the greater susceptibility of steelhead smolts to colonial waterbird predation include differences in the size (length) and behavior of steelhead compared with other species of salmonid smolts. Hostetter et al. (2012) noted prey size selectivity by Caspian terns, with larger smolts depredated at higher rates than smaller smolts; juvenile steelhead are, on average, larger than other juvenile salmonids (Quinn 2005). Beeman and Maule (2006) observed that steelhead smolts were more surface oriented compared with salmon smolts, and surface orientation is believed to render fish more vulnerable to predation by terns and gulls—species that forage in the top 1 m of the water column (Winkler 1996; Cuthbert and Wires 1999; Pollet et al. 2012). Given the greater susceptibility of steelhead to colonial waterbird predation observed in these studies, it is likely that the cumulative impact from the 14 colonies evaluated in the present study was substantially greater on upper Columbia River steelhead compared with other species of salmonids. Research to quantify cumulative predation and survival rates in salmon species and in other steelhead populations (e.g., ESA-listed Snake River steelhead), however, is currently lacking but is necessary to evaluate the extent to which colonial waterbird predation limits the survival of the 12 other ESA-listed anadromous salmonid populations that reside in the Columbia River basin (NOAA 2011).

A system-wide evaluation of colonial waterbird predation across the spatial scales evaluated in the current study provided data to identify which bird species (Caspian terns, double-crested cormorants, and California gulls/ring-billed gulls) and individual breeding colonies posed the greatest risk to upper Columbia River steelhead survival during out-migration. Comparisons of steelhead losses by predator species indicated that Caspian terns often—but not always—consumed a larger proportion of available steelhead compared with California gulls/ring-billed gulls or double-crested cormorants foraging in the same river reach and year. In some cases, predation by Caspian terns from a single breeding colony was the single greatest source of all steelhead mortality in that reach and year. Caspian tern colonies, however, were consistently smaller in size (number of breeding pairs) than nearby colonies of California gulls/ring-billed gulls and double-crested cormorants, indicating a higher per-capita (per-bird) impact by Caspian terns on the survival of steelhead smolts. Previous research has also documented higher per-capita losses of salmonid smolts to Caspian terns relative to both gulls or cormorants (Evans et al. 2012), with differences attributable to a greater reliance on juvenile salmonids as a food source by Caspian terns compared with other avian predators in the Columbia River basin (Collis et al. 2002; Lyons 2010). Like Caspian terns, double-crested cormorants are strictly piscivorous, but previous studies have indicated that juvenile salmonids comprised less than 20% of cormorant diets (by mass) compared with 30–80% of Caspian tern diets for colonies foraging within the same river reaches (Collis et al. 2002; Lyons et al. 2007). Although the impact of double-crested cormorants on survival of upper Columbia River steelhead was consistently less than that of Caspian terns from nearby colonies (e.g., Crescent Island terns versus Foundation Island cormorants; and East Sand Island terns versus East Sand Island cormorants), predation rates on steelhead smolts by double-crested cormorants nesting on East Sand Island were still substantial in some years due to the large size of the cormorant colony (in excess of 14,000 breeding pairs during some years) and the greater energetic demands of double-crested cormorants compared to Caspian terns (Lyons 2010).

Unlike Caspian terns and double-crested cormorants, which are not known to eat dead fish (Cuthbert and Wires 1999; Dorr et al. 2014), California gulls and ring-billed gulls are generalist omnivores that scavenge food in addition to consuming live prey (Winkler 1996; Pollet et al. 2012). Previous studies found that juvenile salmonids comprised less than 10% (by mass) of the diet of gulls nesting at colonies on the Columbia River (Collis et al. 2002). Despite low per-capita impacts, predation rates on steelhead smolts by California gulls and ring-billed gulls nesting at some colonies were similar to or greater than predation rates by Caspian terns and double-crested cormorants nesting at nearby colonies. For example, California gulls and ring-billed gulls nesting at the Miller Rocks Island colony annually consumed between 0.05 and 0.18 of available steelhead smolts during passage from McNary Dam to Bonneville Dam, while Caspian terns that nested on the nearby central Blalock Islands annually consumed between 0.04 and 0.12 of available steelhead smolts. Hostetter et al. (2015) attributed high rates of steelhead smolt consumption by gulls to the relatively large size (tens of thousands of breeding pairs) of gull colonies, coupled with the gulls' behavioral flexibility to exploit temporarily available food sources (Winkler 1996; Pollet et al. 2012). In a spatially explicit investigation of smolt predation by California gulls and ring-billed gulls nesting at colonies in the Columbia River, Evans et al. (2016) observed that gulls nesting on Miller Rocks Island disproportionately consumed steelhead near John Day Dam, located just 18 rkm upstream of the colony site. Several studies have hypothesized that smolts may be more vulnerable to gull predation near dams due to (1) delays in travel time associated with forebay passage, (2) smolt mortality and injury associated with turbine passage, or (3) smolts being temporarily stunned or disoriented by hydraulic conditions in the tailrace of dams (Ruggerone 1986; Zorich et al. 2011; Evans et al. 2016). Given that gulls scavenge for food and disproportionately forage near dams where smolts may be more vulnerable to predation, some fraction of fish consumed by gulls could be dead or moribund individuals, making it difficult to equate estimates of consumption to those of predation.

In addition to the suite of biotic factors that influence the susceptibility of steelhead to predation by birds (i.e., colony sizes, prey availability, and individual fish characteristics), abiotic factors can also contribute to the susceptibility of steelhead to bird predation and thus smolt survival during out-migration. Petrosky and Schaller (2010) observed a relationship between increasing river flows in the Columbia River and higher rates of steelhead survival during out-migration, a relationship that has been linked to rates of predation by colonial waterbirds, whereby higher river flows decrease fish travel times and consequently lower the exposure of smolts to bird predation. For instance, Hostetter et al. (2012) observed that increased river flows were related to a decrease in Caspian tern predation rates on steelhead smolts originating from the Snake River. Payton et al. (2016) observed that faster water transit times (a measure of flow in relation to reservoir levels) were associated with lower predation rates by Caspian terns on steelhead smolts passing through the Wanapum and Priest Rapids reservoirs in the middle Columbia River. Ferguson et al. (2006) observed delayed mortality in smolts that passed through turbines at hydroelectric dams and hypothesized that injury and stress associated with dam passage made fish more susceptible to bird predation. Collectively, results from these studies indicate that numerous biotic and abiotic conditions experienced by smolts during out-migration influence their susceptibility to avian predation. Although not the focus of this study, the mortality and survival modeling approach used to jointly estimate predation and survival could also be used to identify and test the strength of interactions between various biotic and abiotic factors and predation rates, potential providing important insight into the suite of factors or mechanisms that influence steelhead smolt survival during out-migration.

Conclusions

Results from this study indicate that predation by colonial waterbirds was one of the greatest sources of mortality—and, in many cases, the single greatest source —for upper Columbia River steelhead smolts during out-migration to the Pacific Ocean. Predation probabilities were highly variable based on the avian predator species, colony location, river reach, and year, indicating the dynamic predator–prey interactions that occurred at both local (e.g., reservoir-specific) and system-wide (e.g., freshwater migration corridor) scales. Given the magnitude of cumulative predation effects by colonial waterbirds observed in the present study, particularly when compared to nonavian sources of mortality at the same spatial and temporal scales, reducing avian predation should be a high priority for those concerned with the recovery of ESA-listed steelhead. It should be noted, however, that Caspian terns, double-crested cormorants, California gulls, and ring-billed gulls are all native species protected by the U.S. Migratory Bird Treaty Act and not all piscivorous waterbird colonies pose a risk to upper Columbia River steelhead smolt survival in the Columbia River basin; predation probabilities from several of the colonies included in the study were estimated to be less than 0.01. Irrespective of the need for avian predation management to reduce smolt mortality, accounting for factors that limit fish survival to the degree observed in this study may be paramount for interpreting the results and measuring the efficacy of other, nonavian salmonid management actions being implemented in the region (e.g., changes in dam operational strategies, habitat improvements, improved hatchery practices, and reductions in harvest). Conversely, by not considering avian predation when evaluating the efficacy of nonavian management actions, the benefits of such actions would likely be confounded or otherwise masked due to unaccounted-for fluctuations in avian predation.

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Appendix: Additional Data

TABLE A.1. Average annual recapture and recovery probabilities (with 95% credible intervals in parentheses) of PIT-tagged steelhead released at Rock Island Dam. Recapture probabilities are from McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), a paired-trawl net detector (ND) in the estuary, and smolt-to-adult returns (SAR) to BON. Recovery probabilities are from Caspian tern (CATE), mixed California gull/ring-billed gull (LAXX), and double-crested cormorant (DCCO) colonies at Banks Lake Island (BLI), Lenore Lake Island (LLI), Potholes Reservoir (PTI), Island 20 (I20), Foundation Island (FDI), Badger Island (BGI), Crescent Island (CSI), central Blalock Islands (CBI), Miller Rocks Island (MRI), and East Sand Island (ESI). Recovery probability is shown as the deposition probability multiplied by the annual weighted average of detection probability.

Location	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Recapture											
MCN	0.15 (0.13–0.16)	0.16 (0.14–0.18)	0.09 (0.07–0.1)	0.07 (0.06–0.09)	0.11 (0.09–0.13)	0.10 (0.08–0.12)	0.07 (0.06–0.09)	0.09 (0.07–0.1)	0.21 (0.19–0.23)	0.06 (0.05–0.07)	0.05 (0.04–0.07)
JDA	0.20 (0.18–0.22)	0.14 (0.12–0.16)	0.08 (0.07–0.1)	0.24 (0.21–0.28)	0.16 (0.14–0.18)	0.07 (0.06–0.09)	0.08 (0.07–0.1)	0.03 (0.02–0.04)	0.07 (0.06–0.08)	0.22 (0.19–0.25)	0.11 (0.09–0.13)
BON	0.10 (0.09–0.12)	0.15 (0.13–0.17)	0.30 (0.27–0.34)	0.04 (0.03–0.05)	0.11 (0.09–0.13)	0.14 (0.12–0.18)	0.14 (0.12–0.17)	0.36 (0.31–0.42)	0.40 (0.34–0.47)	0.11 (0.09–0.13)	0.16 (0.13–0.22)
ND	0.03 (0.02–0.04)	0.04 (0.03–0.06)	0.03 (0.03–0.05)	0.02 (0.01–0.04)	0.03 (0.02–0.05)	0.04 (0.03–0.06)	0.04 (0.03–0.05)	0.06 (0.05–0.09)	0.09 (0.06–0.15)	0.05 (0.02–0.08)	0.03 (0.02–0.04)
SAR	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Recovery											
BLI CATE	0.29 (0.10–0.50)	0.51 (0.34–0.68)	0.50 (0.32–0.68)				0.50 (0.34–0.66)[a]	0.50 (0.35–0.65)	0.51 (0.35–0.66)		
LLI CATE									0.54 (0.37–0.70)[a]	0.46 (0.31–0.63)[a]	0.35 (0.22–0.47)
PTI CATE	0.38 (0.25–0.51)	0.25 (0.18–0.34)	0.34 (0.23–0.45)	0.35 (0.25–0.45)	0.22 (0.13–0.3)	0.33 (0.22–0.45)	0.35 (0.2–0.5)[a]		0.48 (0.29–0.66)		
BGI CATE				0.51 (0.36–0.66)	0.49 (0.35–0.63)					0.62 (0.45–0.79)[a]	
CSI CATE	0.41 (0.29–0.52)	0.49 (0.34–0.63)	0.5 (0.36–0.63)	0.56 (0.39–0.71)	0.43 (0.29–0.56)	0.54 (0.38–0.67)	0.57 (0.4–0.73)				
CBI CATE	0.67 (0.49–0.84)	0.64 (0.45–0.8)	0.56 (0.3–0.79)[a]	0.58 (0.42–0.74)		0.62 (0.45–0.78)[a]	0.47 (0.26–0.67)[a]	0.46 (0.27–0.63)	0.46 (0.32–0.59)	0.32 (0.21–0.41)	0.23 (0.16–0.31)
ESI CATE	0.65 (0.48–0.81)	0.63 (0.45–0.79)	0.55 (0.39–0.69)	0.54 (0.39–0.67)	0.49 (0.35–0.63)	0.38 (0.26–0.49)	0.42 (0.31–0.54)	0.58 (0.41–0.72)	0.50 (0.36–0.65)	0.46 (0.32–0.58)	0.47 (0.32–0.6)
I20 LAXX						0.12 (0.08–0.16)	0.12 (0.08–0.16)[a]	0.12 (0.08–0.17)	0.12 (0.08–0.16)	0.12 (0.09–0.17)	0.14 (0.1–0.19)
BGI LAXX								0.12 (0.08–0.17)[a]	0.07 (0.04–0.11)[a]	0.11 (0.07–0.14)	0.08 (0.05–0.1)
CSI LAXX	0.12 (0.08–0.16)	0.10 (0.07–0.14)	0.12 (0.08–0.16)	0.11 (0.07–0.15)	0.11 (0.07–0.15)	0.10 (0.07–0.14)	0.13 (0.09–0.17)				
CBI LAXX						0.12 (0.09–0.17)	0.14 (0.11–0.18)	0.14 (0.1–0.19)	0.14 (0.1–0.18)	0.14 (0.1–0.18)[a]	0.14 (0.1–0.18)[a]
MRI LAXX	0.12 (0.09–0.17)	0.12 (0.08–0.15)	0.11 (0.08–0.15)	0.12 (0.08–0.16)	0.12 (0.08–0.16)	0.12 (0.08–0.16)	0.13 (0.09–0.17)	0.13 (0.09–0.18)	0.12 (0.08–0.16)	0.11 (0.07–0.15)	0.12 (0.08–0.16)
FDI DCCO	0.37 (0.24–0.50)	0.36 (0.23–0.48)	0.31 (0.20–0.43)	0.23 (0.13–0.33)	0.18 (0.11–0.26)		0.10 (0.05–0.14)				
ESI DCCO	0.32 (0.21–0.43)	0.31 (0.19–0.44)	0.35 (0.22–0.48)	0.35 (0.23–0.49)	0.33 (0.2–0.45)	0.33 (0.21–0.45)	0.35 (0.22–0.48)	0.34 (0.19–0.48)	0.30 (0.19–0.4)	0.33 (0.21–0.45)	0.44 (0.28–0.6)

[a]Variation in detection probability was partially inferred from other years.

TABLE A.2. Numbers of PIT-tagged steelhead smolts released at Rock Island Dam (see Table 1 for sample sizes) and subsequently recaptured (live) at PIT tag arrays or recovered on bird colonies (dead) during 2008–2018. Recaptures are from McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), a paired-trawl net detector (ND) in the estuary, and smolt-to-adult returns (SAR) to BON. Colony (recovery) location codes (three letters) and avian species codes (four letters) are defined in Table A.1. An en dash (–) denotes that scanning for PIT tags was not conducted during that year, but the colony site was active. Blank cells indicate that the colony site was not active (i.e., no breeding birds were present).

Location	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
					Recapture						
MCN	636	668	366	358	401	332	352	385	779	314	246
JDA	827	430	310	1,131	554	225	345	86	207	984	500
BON	390	427	977	153	348	396	528	701	711	406	584
ND	81	110	104	72	96	118	137	103	87	77	82
					Recovery						
BLI CATE	6	6	6	–	3	–	14	89	3		
LLI CATE									4	33	16
PTI CATE	347	468	378	350	294	340	103		141		
BGI CATE										18	
CSI CATE	97	86	69	111	38	92	151				
CBI CATE	27	11	21	1	–	1	30	278	117	84	52
ESI CATE	425	377	318	164	106	138	211	130	87	159	123
I20 LAXX	–	–	–	–	–	8	15	68	44	26	10
BGI LAXX								47	22	28	25
CSI LAXX	22	50	61	28	32	34	62				
CBI LAXX	–	–	–	–	–	12	21	40	47	44	30
MRI LAXX	41	41	35	30	25	29	40	107	63	87	73
FDI DCCO	7	6	3	4	5	–	1	–	–	–	–
ESI DCCO	64	54	79	106	72	27	127	60	20[a]	9[a]	25[a]

[a]Minimum estimate due to colony dispersal events during the peak nesting period in 2016–2018.

TABLE A.3. Estimated colony- and reach-specific avian predation probabilities (with 95% credible intervals in parentheses) on steelhead released at Rock Island Dam during 2008–2018. Estimates are the proportion of available fish within each reach that were consumed by birds from each colony. Colony location codes (three letters) and avian species codes (four letters) are defined in Table A.1. "TOT" indicates all bird colonies combined.

Colony	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Reach 1 (Rock Island Dam to McNary Dam)											
BLI CATE	<0.01 (0–0.01)	<0.01	<0.01		<0.01		<0.01 (0–0.01)	0.02 (0.01–0.04)	<0.01		
LLI CATE									<0.01	0.01 (0.01–0.02)	0.01 (0–0.03)
PTI CATE	0.12 (0.09–0.19)	0.26 (0.19–0.35)	0.15 (0.11–0.25)	0.13 (0.1–0.19)	0.19 (0.14–0.32)	0.17 (0.12–0.25)	0.04 (0.02–0.07)		0.04 (0.03–0.07)		
BGI CATE				<0.01	<0.01					<0.01 (0–0.01)	
CSI CATE	0.03 (0.02–0.05)	0.02 (0.02–0.04)	0.02 (0.01–0.03)	0.02 (0.02–0.04)	0.01 (0.01–0.02)	0.03 (0.02–0.04)	0.03 (0.02–0.05)				
CBI CATE	<0.01	<0.01	<0.01	<0.01		<0.01	<0.01 (0–0.01)	0.01 (0–0.03)	0.01 (0–0.02)	<0.01 (0–0.02)	0.01 (0–0.02)
I20 LAXX						0.01 (0.01–0.03)	0.02 (0.01–0.03)	0.08 (0.05–0.12)	0.06 (0.04–0.09)	0.03 (0.02–0.05)	0.01 (0–0.02)
BGI LAXX								0.06 (0.04–0.09)	0.07 (0.04–0.13)	0.04 (0.02–0.06)	0.05 (0.03–0.08)
CSI LAXX	0.02 (0.01–0.04)	0.07 (0.04–0.11)	0.06 (0.04–0.10)	0.03 (0.02–0.05)	0.04 (0.02–0.06)	0.05 (0.02–0.08)	0.06 (0.04–0.09)				
FDI DCCO	<0.01 (0–0.01)	<0.01 (0–0.01)	<0.01	<0.01 (0–0.01)	<0.01 (0–0.01)		<0.01 (0–0.01)				
TOT	0.19 (0.15–0.26)	0.35 (0.27–0.44)	0.23 (0.19–0.34)	0.19 (0.15–0.25)	0.24 (0.19–0.38)	0.26 (0.2–0.35)	0.16 (0.12–0.21)	0.17 (0.13–0.22)	0.18 (0.13–0.25)	0.09 (0.06–0.12)	0.08 (0.05–0.12)
Reach 2 (McNary Dam to Bonneville Dam)											
CSI CATE	<0.01	<0.01	<0.01 (0–0.01)	<0.01 (0–0.01)	<0.01	<0.01 (0–0.01)	<0.01 (0–0.01)				
CBI CATE	0.01 (0–0.01)	<0.01 (0–0.01)	0.01 (0–0.02)	<0.01		<0.01	0.01 (0–0.02)	0.12 (0.07–0.20)	0.06 (0.04–0.09)	0.04 (0.02–0.06)	0.03 (0.01–0.06)
CSI LAXX	<0.01 (0–0.02)	0.01 (0–0.04)	0.01 (0–0.05)	0 (0–0.02)	0.01 (0–0.05)	0.02 (0–0.06)	0.01 (0–0.04)				
CBI LAXX						0.03 (0.02–0.06)	0.03 (0.02–0.05)	0.07 (0.04–0.11)	0.09 (0.06–0.14)	0.06 (0.04–0.09)	0.04 (0.02–0.07)
MRI LAXX	0.07 (0.05–0.12)	0.09 (0.06–0.15)	0.07 (0.05–0.12)	0.05 (0.03–0.08)	0.06 (0.03–0.10)	0.07 (0.04–0.11)	0.07 (0.04–0.11)	0.18 (0.13–0.29)	0.14 (0.09–0.23)	0.15 (0.10–0.22)	0.11 (0.07–0.17)
TOT	0.09 (0.06–0.13)	0.10 (0.07–0.17)	0.09 (0.05–0.14)	0.06 (0.03–0.10)	0.07 (0.04–0.12)	0.12 (0.08–0.18)	0.12 (0.08–0.18)	0.38 (0.27–0.53)	0.29 (0.22–0.4)	0.25 (0.18–0.32)	0.19 (0.13–0.27)
Reach 3 (Bonneville Dam to the Pacific Ocean)											
ESI CATE	0.17 (0.13–0.25)	0.21 (0.16–0.30)	0.18 (0.13–0.26)	0.08 (0.05–0.12)	0.07 (0.05–0.10)	0.13 (0.09–0.20)	0.13 (0.10–0.20)	0.12 (0.09–0.18)	0.09 (0.07–0.15)	0.08 (0.06–0.14)	0.07 (0.05–0.13)
ESI DCCO	0.05 (0.03–0.09)	0.06 (0.04–0.12)	0.07 (0.05–0.12)	0.07 (0.05–0.13)	0.07 (0.04–0.12)	0.03 (0.02–0.05)	0.10 (0.07–0.16)	0.10 (0.06–0.18)	0.04[a] (0.02–0.07)	0.01[a] (0–0.02)	0.02[a] (0.01–0.03)
TOT	0.22 (0.18–0.31)	0.28 (0.21–0.39)	0.25 (0.2–0.35)	0.15 (0.11–0.23)	0.14 (0.1–0.2)	0.17 (0.12–0.25)	0.24 (0.18–0.32)	0.22 (0.16–0.31)	0.13 (0.10–0.19)	0.10 (0.07–0.14)	0.09 (0.06–0.15)

[a]Minimum estimate due to colony dispersal events during the peak nesting period in 2016–2018.