System-wide Effects of Avian Predation on the Survival of Upper Columbia River Steelhead: Implications for Predator Management

Prepared for: Grant County Public Utility District and the Priest Rapid Coordinating Committee
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Preface

Predator-prey interactions involving piscivorous colonial waterbirds and anadromous juvenile salmonids (*Oncorhynchus* spp.) have been the subject of numerous research, monitoring, and evaluation studies in the Columbia River basin. Previous research has identified predation by Caspian terns (*Hydroprogne caspia*), double-crested cormorants (*Phalacrocorax auritus*), California gulls (*Larus californicus*), and ring-billed gulls (*L. delawarensis*) as a significant mortality factor for some salmonid populations during smolt outmigration to the Pacific Ocean. This previous work was largely focused on quantifying the impacts of piscivorous birds from specific nesting colonies on smolt mortality, but some salmonid populations, like the Endangered Species Act (ESA)-listed Upper Columbia River (UCR) steelhead trout (*O. mykiss*), must migrate through the foraging ranges of breeding birds from multiple colonies during outmigration. The system-wide, cumulative impacts of piscivorous colonial waterbirds on smolt survival are largely unknown. Juvenile salmonids are also subject to numerous other non-avian sources of mortality during outmigration (e.g., hydroelectric dam passage, predation by piscivorous fish, disease, and other factors) and determining to what extent avian predation limits fish survival relative to these other sources of mortality is critical for prioritizing recovery actions for ESA-listed salmonid populations in the region.

To address concerns over Caspian tern predation on juvenile salmonids, management plans have been implemented to reduce the size or eliminate the largest Caspian tern nesting colonies in the Columbia River basin. A critical but unanswered question regarding management is whether mortality due to avian predation is an additive or compensatory source of smolt mortality. For instance, would reductions in predation rates on steelhead smolts by Caspian terns result in higher rates of smolt survival (i.e. tern predation adds to smolt mortality) or are smolts that are consumed by terns destined to die during outmigration or before returning as adults regardless of tern predation (i.e. tern predation is compensated for by other sources of mortality)? If the latter is true, efforts to reduce Caspian tern predation rates by reducing the size of nesting colonies in the Columbia River basin would have little effect on fish survival. Conversely, if terns are consuming smolts that would otherwise survive outmigration and return as adults to spawn, then reductions in tern predation rates due to avian predation management actions may be an important component in efforts to recover ESA-listed salmonid populations in the Columbia River basin.

As part of a multi-year, system-wide study of avian predation funded by Grant County Public Utility District and the Priest Rapids Coordinating Committee, we investigated the cumulative effects of avian predation on the survival of UCR steelhead smolts and estimated what proportion of total mortality (1-survival) was due to avian predation during smolt outmigration. We also investigated to what degree predation by Caspian terns, a managed colonial waterbird species, was an additive versus compensatory source of steelhead mortality and whether avian predation management actions that have been implemented to-date have been successful at reducing predation on UCR steelhead smolts. These two objectives are addressed in two separate, but related, chapters entitled “Cumulative Effects of Avian Predation on Upper Columbia River Steelhead” and “Additive Effects of Caspian Tern Predation on the Survival of Upper Columbia River Steelhead: Implications for Predator Management.”

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CHAPTER 1: Cumulative Effects of Avian Predation on Upper Columbia River Steelhead

Abstract

Predator-prey interactions involving piscivorous colonial waterbirds and anadromous juvenile salmonids (*Oncorhynchus spp.*) have been the subject of numerous studies in the Columbia River basin. Previous research has identified predation by Caspian terns (*Hydroprogne caspia*), double-crested cormorants (*Phalacrocorax auritus*), California gulls (*Larus californicus*), and ring-billed gulls (*L. delawarensis*) as a significant mortality factor for juvenile salmonids during the smolt outmigration. Previous research has focused on the impacts of piscivorous birds from specific nesting colonies, but some salmonid populations, like the Endangered Species Act (ESA)-listed Upper Columbia River (UCR) steelhead trout (*O. mykiss*), must out-migrate through the foraging ranges of breeding birds from multiple colonies on their way to the Pacific Ocean. These cumulative, system-wide impacts of avian predation on smolt survival are largely unknown. Juvenile salmonids are also subject to numerous other non-avian sources of mortality during outmigration (e.g., hydroelectric dam passage, predation by piscivorous fish, disease, and other factors) and determining to what degree avian predation limits smolt survival relative to these other sources of mortality may be critical for prioritizing recovery actions for ESA-listed salmonid populations.

To investigate the cumulative effects of colonial waterbird predation and to estimate what proportion of all sources of smolt mortality (1-survival) were due to avian predation, we conducted a mark-recapture-recovery study with UCR steelhead smolts marked with passive integrated transponder (PIT) tags (n = 78,409) and released into the tailrace of Rock Island Dam on the middle Columbia River during 2008-2018. We used a state-space, hierarchal Bayesian model with live and dead detections of PIT-tagged fish to jointly estimate predation and survival probabilities (rates) during smolt passage through three river segments or reaches: (1) a 259 river kilometer (Rkm) section of the middle and lower Columbia River between Rock Island Dam and McNary Dam, (2) a 236 Rkm section of the lower Columbia River between McNary Dam and Bonneville Dam, and (3) a 234 Rkm section of the lower Columbia River downstream of Bonneville Dam to the Pacific Ocean. Multiple avian predator species (Caspian terns, double-crested cormorants, California and ring-billed gulls) nesting at up to 14 different colonies were included in the study.

Estimates of cumulative avian predation rates (all bird species combined) ranged annually from 0.31 (95% credible interval [CRI] = 0.27–0.38) to 0.53 (95% CRI = 0.42–0.64), indicating that birds consumed between 31% and 53% of all UCR steelhead smolts during outmigration from Rock Island Dam to the Pacific Ocean. Predation impacts were highly variable by river reach, avian predator species, bird colony, and year. By river reach, cumulative avian predation rates ranged annually from 0.07 (95% CRI = 0.05–0.10) to 0.36 (95% CRI = 0.27–0.45) of available UCR steelhead smolts during passage from Rock Island Dam to McNary Dam, from 0.08 (95% CRI = 0.05–0.11) to 0.38 (95% CRI = 0.27–0.53) during passage from McNary Dam to Bonneville Dam, and from 0.10 (95% CRI = 0.07–0.14) to 0.28 (95% CRI = 0.21–0.39) during passage from Bonneville Dam to the Pacific Ocean. Caspian terns generally consumed the largest proportion of available smolts relative to double-crested cormorants, California gulls, and ring-billed gulls, with aggregate (all Caspian tern colonies combined) tern predation rates ranging annually from 0.11 (95% CRI = 0.09–0.14) to 0.38 (95% CRI = 0.29–0.47). Of the 14 individual bird colonies evaluated, predation rates by Caspian terns nesting on East Sand Island in the Columbia River estuary and on Goose Island in Potholes Reservoir were the highest observed, with upwards of 0.21 (95% CRI = 0.16–0.30) and 0.26 (95% CRI = 0.19–0.35) of

available smolts consumed, respectively, in some years. Aggregate predation by California and ring-billed gulls from mixed species colonies were also substantial in some years, with aggregate gull predation rates ranging annually from 0.07 (95% CRI = 0.05–0.11) to 0.31 (95% CRI = 0.25–0.39). Predation rates by double-crested cormorants were highly variable among breeding colonies, with colony-specific estimates ranging from less than 0.01 for a small colony located upstream of McNary Dam on Foundation Island to upwards of 0.10 (95% CRI = 0.07–0.16) for the large cormorant colony located on East Sand Island in the Columbia River estuary.

Comparisons of total annual UCR steelhead smolt mortality to mortality due to avian predation indicated avian predation accounted for 42% (95% CRI = 30–56%) to 70% (95% CRI = 53–87%) of all mortality sources during smolt outmigration from Rock Island Dam to Bonneville Dam, indicating that more UCR steelhead were consumed by colonial waterbirds than died from all other mortality sources (e.g., dam passage, predation by piscivorous fish, disease, and other factors) combined in most years. Collectively, results from this system-wide investigation indicate that predation by colonial waterbirds was one of the greatest, and in many years the single greatest, direct source of mortality for UCR steelhead smolts during outmigration to the Pacific Ocean. Using the analytical framework applied in this study, future studies can consider the cumulative impact of multiple mortality factors on various ESA-listed salmonid stocks across large spatial- and temporal-scales to more fully understand to what extent they limit fish survival.

Introduction

Identifying factors that affect the survival of juvenile salmonids, 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, double-crested cormorants, California gulls, and ring-billed gulls are the principal avian predators of juvenile salmonids in the Columbia River basin (Collis et al. 2001; Roby et al. 2003b; Evans et al. 2012; Hostetter et al. 2015; Evans et al. 2016). Bird nesting colonies are located at numerous sites throughout the basin, with colony sizes ranging from less than 25 breeding pairs to well over 10,000 pairs, depending on the species, site, and year (Collis et al. 2002; Adkins et al. 2014). The timing of the nesting season (April to August) also coincides with the peak smolt outmigration 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 birds from particular breeding colonies can consume large numbers of out-migrating juvenile salmonid smolts. For example, Caspian terns nesting on Rice Island in the Columbia River estuary consumed between 8.1 million and 12.4 million smolts annually (Roby et al. 2003a), while double-crested cormorants nesting on East Sand Island, also located in the estuary, consumed between 2.4 million and 15.0 million smolts 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 and ring-billed gulls nesting on Miller Rocks in the Dalles Reservoir, consumed between 0.06 and 0.11 (6–11%) of available juvenile steelhead trout 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 (15%) of the available steelhead smolts annually (Evans et al. 2012). The system-wide, cumulative impacts on smolt survival of multiple species and breeding colonies of piscivorous colonial waterbirds, however, is largely unknown, but may be substantial based on the predation rates documented at individual breeding colonies on or near (i.e. with foraging range) the Columbia River. In addition to predation from piscivorous colonial waterbirds, salmonid smolts are subject to numerous other non-avian sources of mortality during outmigration. For example, mortality associated with hydroelectric dam passage, predation by piscivorous fish, and disease are well documented in the Columbia River basin (Ward et al. 1995; Muir et al. 2001; Dietrich et al. 2011). Determining to what extent 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; Hostetter et al. 2015). These studies relied on marking (tagging) fish and then using subsequent recapture and recovery events to estimate both survival and cause-specific mortality (e.g., harvest, dam passage, predation). Results from these studies provide critical information regarding where, when, and how many fish die from a specific cause. These studies, however, often focused 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 UCR steelhead trout that must migrate hundreds of river kilometers through the foraging ranges of multiple piscivorous waterbird colonies during smolt outmigration.

To investigate the cumulative effects of avian predation and to determine what proportion of total mortality (1-survival) was due to avian predation, we conducted a mark-recapture-recovery study using steelhead smolts from the ESA-listed UCR steelhead 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 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 UCR steelhead smolts during outmigration to the Pacific Ocean.

Methods

Study Area – We integrated multiple sources of data to estimate avian predation and survival of UCR 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 probabilities of tags from depredated fish following consumption by piscivorous colonial waterbirds. We estimated predation rates and survival rates of UCR steelhead smolts marked with passive integrated transponder (PIT) tags and released into the tailrace of Rock Island Dam on the middle Columbia River during 2008-2018 (*Figure 1.1*). River reaches were defined by the locations were PIT-tagged fish were detected/recovered following release and included (1) Rock Island Dam to McNary Dam, a 259 Rkm section of the middle and 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 (hereafter Reach 1, 2, and 3, respectively). Smolt survival and predation through Reach 1 and Reach 2 were estimated based on live fish detections at in-stream PIT tag detection sites and recoveries of tags from depredated fish on multiple bird colonies (*Figure 1.1*). 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-stream PIT tag detection sites downstream of East Sand Island in the Columbia River estuary. The number of smolts surviving to adulthood were determined based on PIT tag detections of returning adult steelhead in fishways or ladders located at Bonneville Dam, the lower most dam on the Columbia River (*Figure 1.1*).

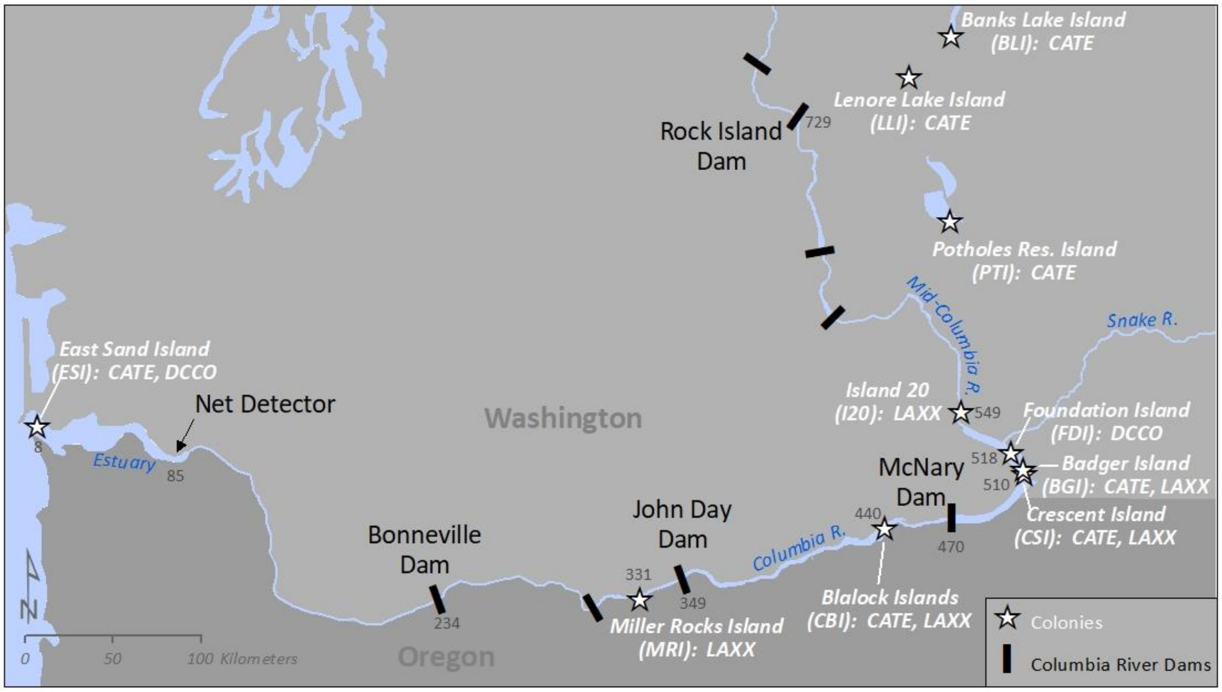


Figure 1.1. Mark-recapture-recovery locations of PIT-tagged steelhead released at Rock Island Dam (RIS). Recapture locations include McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and a towed net detection (ND) system in the upper Columbia River estuary. Recovery locations include bird colonies on 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 included in this study include Caspian terns (CATE), double-crested cormorants (DCCO), and California and ring-billed gulls (LAXX). Distances represents river kilometers from the Pacific Ocean.

Mark-Recapture-Recovery – The methods of Evans et al. (2014) were used to capture, mark (tag), and release UCR steelhead smolts at Rock Island Dam (*Figure 1.1*). In brief, steelhead were captured at the Rock Island Dam juvenile fish trap, anesthetized (tricaine methanesulfonate), and PIT tagged (12-mm [length] × 2-mm [width], 134.2 kHz) during 2008-2018. Fish were sampled for tagging daily from early-April to mid-June 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, rear-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. Following tagging, fish were allowed to recover from handling in a temporary holding tank for up to 12 hours before being released into the tailrace of Rock Island Dam to resume outmigration to the Pacific Ocean.

Following 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), Bonneville Dam (Rkm 234), and at a vessel towed pair-trawl net detection system in the upper Columbia River estuary (Rkm 85; *Figure 1.1*). Adult steelhead returning to the Columbia River following ocean residency were detected at arrays located in fishways at Bonneville Dam one to three years following release as smolts at Rock Island Dam (*Figure 1.1*). Recapture records were retrieved from the PIT Tag Information System, a regional mark, recapture, recovery database maintained by Pacific States Marine Fisheries Commission (PSMFC 2018).

Steelhead tags were also recovered on piscivorous waterbird colonies located throughout the Columbia River basin. A total of 14 different bird colonies were included in the study, all colonies previously identified as posing a potential threat to steelhead survival during outmigration (*Figure 1.1*; Evans et al. 2012; Evans et al. 2016). The methods of Evans et al. (2012) were used to recover PIT tags from each bird colony. In brief, hand-held or flat plate PIT tag antennas were used to detect tags after birds dispersed from their breeding colonies at the end of the nesting season (August–October). The entire land area occupied by nesting birds was scanned for tags following 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 surveys of the colony carried out during the peak of the nesting season (i.e. late-April to early-June; see also *Colony Sizes* for additional details).

Not all fish PIT tags ingested by birds are deposited on the bird's nesting colony (i.e. deposition probabilities for consumed fish tags were less than 1.0) and not all tags deposited on the colony are detected by researchers after the nesting season (i.e. detection probabilities for deposited fish tags were 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, 2018; Payton et al. 2019). In brief, 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 following 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 A, Table A1*.

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 1.2*). 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 1.2*).

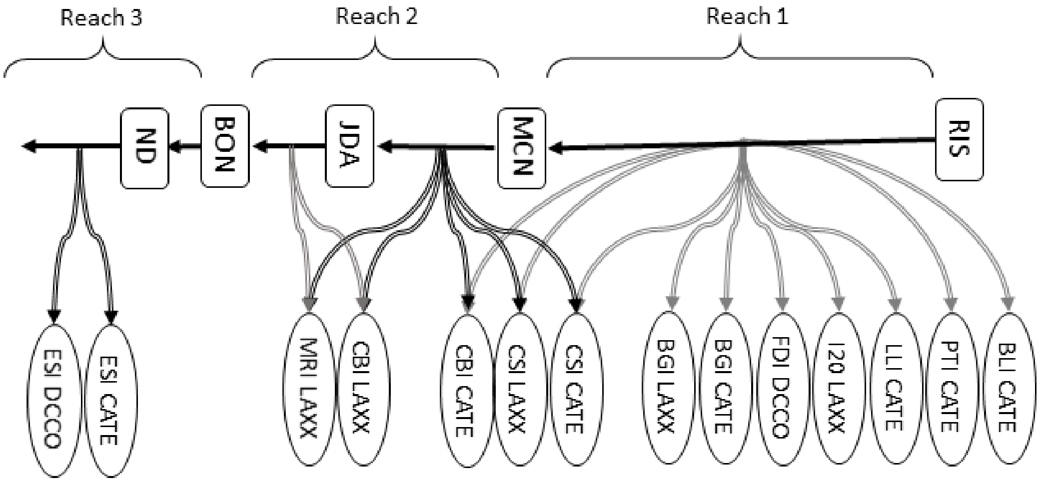


Figure 1.2. Schematic of mark-recapture-recovery sites used to estimate UCR steelhead smolt predation and survival rates for fish tagged and released at Rock Island Dam (RIS). Recapture locations include McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and a towed net detection (ND) system in the upper 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 included in this study include Caspian terns (CATE), double-crested cormorants (DCCO), and California and ring-billed gulls (LAXX). Double arrows depict colonies capable of consuming fish above and below recapture locations.

Colony Sizes – 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 number of nesting adults are aggregated at the colony (Gaston and Smith 1984). The number of breeding pairs of Caspian terns at colonies were estimated from either 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 non-incubating birds in plots. All ground counts were made from an observation blind or boat situated near the colony. The number of breeding pairs of double-crested cormorants were 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 and ring-billed gulls because representative counts of incubating and non-incubating gulls from the ground were not available. As such, colony size estimates for gulls were based on counts of adult gulls from aerial photography and used as an index to the number of breeding pairs utilizing the colony (Adkins et al. 2014).

Predation and Survival Estimation – The joint mortality and survival (JMS) 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 and dead detections of tagged fish in space and time to simultaneously estimate rates of predation and survival. In brief, the state-space model used two vectors, $\mathbf{m}_\mathrm{i}$ and $\mathbf{d}_\mathrm{i}$, to describe a fish's recapture history following release at Rock Island Dam at each of the five downstream live recapture sites and each of the 14 bird colony recovery sites under consideration. The vector $\mathbf{m}_\mathrm{i}$ was a 5-length vector, where $m_{i,j}$ was an indicator variable of the i^{th}

fish's recapture at recapture opportunity j, and $\mathbf{d}_{\mathrm{i}}$ was a 15-length vector, where, for $h \in \{1,2,\dots,14\}$, $d_{i,h}$ was an indicator variable of recovery from colony *h* and $d_{i,15}$ indicated the i^{th} fish was unrecovered. The model provided inference about $\mathbf{z}_{\mathrm{i}}$, the unobserved 5-length vector, were $z_{i,j}$ was an indicator variable of whether the i^{th} fish was still alive at recapture opportunity j.

Parameters used in the model were:

$\boldsymbol{\Phi}$, defined to be 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*,

$\boldsymbol{\Theta}$**,** a 15x5 matrix where $\Theta_{\boldsymbol{j},\boldsymbol{h}}$ represented the probability that a fish alive at recapture opportunity $j-1$ survived to recapture opportunity *j*, and then succumbed to mortality cause *h*,

p, a 5-length vector where p_j represented the probability that a fish alive at recapture opportunity *j* was successfully recaptured

$\boldsymbol{\lambda}$, a 15-length vector where, for $h \in \{1,2,\dots,14\}$, λ_h represented the probability of recovering a fish that died due to mortality cause *h,* and λ_{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 $\Theta_{j,15} = 1 - \phi_{\mathrm{j+1}} - \sum_{h\leq 14} \Theta_{j,h}\ \forall j$.

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 $\boldsymbol{\theta}^{cumulative}$ to be a 15-sized vector, where $\theta_h^{cumulative}$ represented the probability that a fish released at Rock Island Dam succumbed to mortality cause h*.* Then, for each colony h, the 5-length vector $\boldsymbol{\rho}_h$ was used to define the partitioning of $\theta_h^{cumulative}$. That is,

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

where

$$\boldsymbol{\rho}_h \sim \mathrm{dirichlet}\left(\boldsymbol{\alpha}^h\right).$$

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

$$z_{i,j} \sim \mathrm{bernoulli}\left(z_{i,(j-1)} * \phi_j\right),$$
$$m_{i,j} \sim \mathrm{bernoulli}\left(z_{i,j} * p_j\right),$$

and

$$d_{i,h} \sim \mathrm{bernoulli}\Big(\sum_{j=1}^{M-1} \left(z_{i,j+1} - z_{i,j}\right) * \Theta_{j,h} * \lambda_d\Big).$$

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 $\mathbf{\Theta}_{\mathrm{y,w}}$, $\mathbf{p}_{y,w}$, 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 were accounted for through a weekly random walk process (Payton et al. 2019). Temporal variation in detection rates were 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 and *Appendix A, Table A1*). Estimated detection probabilities at each colony were interpolated from the logistic curve 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 cases, intra-seasonal variation in recovery rates based on information from similar colonies in the same year or information from the same colony in different years were used to estimate weekly variation in colony-specific detection probabilities (see Payton et al. 2019 and *Appendix A, Table A1*).

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 $\mathrm{uniform}(0{,}1)$. Analogously, the prior distribution assigned for the life paths simplexes in the initial week of each year was assumed to be $\mathrm{Dirichlet}(\mathbf{1})$, where $\mathbf{1}$ was an appropriately sized vector of ones. Weakly informative priors of half-normal $(0, 5)$ were also implemented for all variance parameters.

Simulated samples from the posterior distribution were derived using the software Stan (Stan Development Team 2015), accessed through R version 3.1.2 (R Development Core Team 2014), using the rstan package (version 2.17.3; Stan Development Team 2015). We ran four parallel Hamiltonian Monte Carlo (HMC) 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 given Gelman-Rubin statistics for all parameters valued less than 1.01, and zero (0) divergent transitions 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 Interval [CRI]).

Model Assumptions – The accuracy and precision of survival and predation rate estimates depend in part on the validity of the following assumptions:

A1. Smolt survival, predation, and recapture/recovery probabilities were independent.
A2. Fish tagged and released within the same week had identical recapture/recovery probabilities.
A3. Intra-annual variation in survival, predation, and recapture/recovery probabilities can be described as a 'random walk' process.
A4. Sampled fish were representative of all fish (tagged and un-tagged) 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 (A1). 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 (A2; Hostetter et al. 2015). The random walk framework allowed for inter-weekly fluctuations in survival, predation, and recapture/recovery probabilities, so assumption A3 only needs to be approximately true for rates to be unbiased. Assumption A4 rests on the random selection of steelhead for PIT-tagging at Rock Island Dam, whereby fish were tagged regardless of their rear-type, size, or condition and fish were tagged in proportion to the number available each week, each year (see also Evans et al. 2014 and *Appendix B* for additional information). This sampling scheme helped to ensured 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 each fish, however, were inestimable. A significant number of losses due to handling/tagging would result in an overstatement of fish availability and consequently underestimate predation and survival to an unknown degree.

Results

Mark-recapture-recovery – In total, 78,409 UCR steelhead smolts were captured, PIT tagged, and released into the tailrace of Rock Island Dam during 2008–2018 (*Table 1.1*). Sample sizes ranged annually from 5,893 to 7,756 tagged UCR steelhead smolts, with the number of weekly releases ranging from 9 to 11 weeks per year (*Table 1.1*). Following release, there were 11,525 downstream tag recapture events at in-river PIT tag antennas/arrays and 8,129 tag recovery events at bird colonies (*Table 1.1*). The number of UCR steelhead smolts detected at downstream recapture sites varied considerably by river reach and year, as did the number of UCR steelhead tags recovered on bird colonies (*Table 1.1 and Appendix A, Table A2*). The largest number of UCR steelhead tags were recovered on bird colonies located upstream of McNary Dam in Reach 1 (n = 3,871; *Table 1.1*). Conversely, the smallest number of steelhead smolts were recaptured alive at the pair-trawl net detector in the Columbia River estuary in Reach 3 (n = 1,067; *Table 1.1*). Only a small number (n = 629) and proportion of steelhead smolts tagged and released at Rock Island Dam returned to Bonneville Dam as adults, with the number of adult returns ranging from 5 to 220 adults per smolt release year (*Table 1.1*).

Table 1.1. Number of UCR steelhead smolts tagged and released at Rock Island Dam that were subsequently recaptured (detected) alive at PIT tag detection arrays or whose tags were recovered on bird colonies during 2008-2018. The number of steelhead smolts returning as adults to Bonneville Dam are also provided; dashed-line denotes that complete adult returns from a particular 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	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

Recapture and recovery probabilities for smolt PIT tags at in-stream arrays and on bird colonies are reported in *Appendix A, Table A1*. Recapture probabilities were generally low (posterior medians less than 0.20 for most recapture sites and years). Recovery probabilities were generally higher than recapture probabilities, but were also variable depending on the bird species, bird colony, and year (range of posterior medians of 0.07 to 0.65; *Appendix A, Table A1*).

Colony sizes – The estimated size of bird colonies (number of breeding pairs) included in the study varied by predator species, colony location, and year (*Table 1.2*). In Reaches 1 and 2, the largest colonies of piscivorous waterbirds were mixed colonies of California and ring-billed gulls (3,733–16,558 breeding pairs per colony, per year), followed by Caspian tern colonies (2–677 breeding pairs per colony, per year) and double-crested cormorant colonies (308-390 breeding pairs per colony, per year; *Table 1.2*). 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 per colony, per year for terns and cormorants, respectively) and were generally an order of magnitude greater than tern and cormorant colonies located in Reaches 1 and 2 (*Table 1.2*). Although the size of bird colonies varied by location, bird species, and year, the breeding chronology of birds were 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.

Table 1.2. Number of piscivorous waterbirds counted on breeding colonies by river reach (Re) and year. Bird colony 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). Cells highlighted in grey indicate the colony was active that year but was not scanned for PIT tags. NA denotes the colony was active 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 [1]	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 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 [2]	2	10,950	12,087	13,596	13,045	12,301	14,916	13,626	12,150	9,772	544	3,672

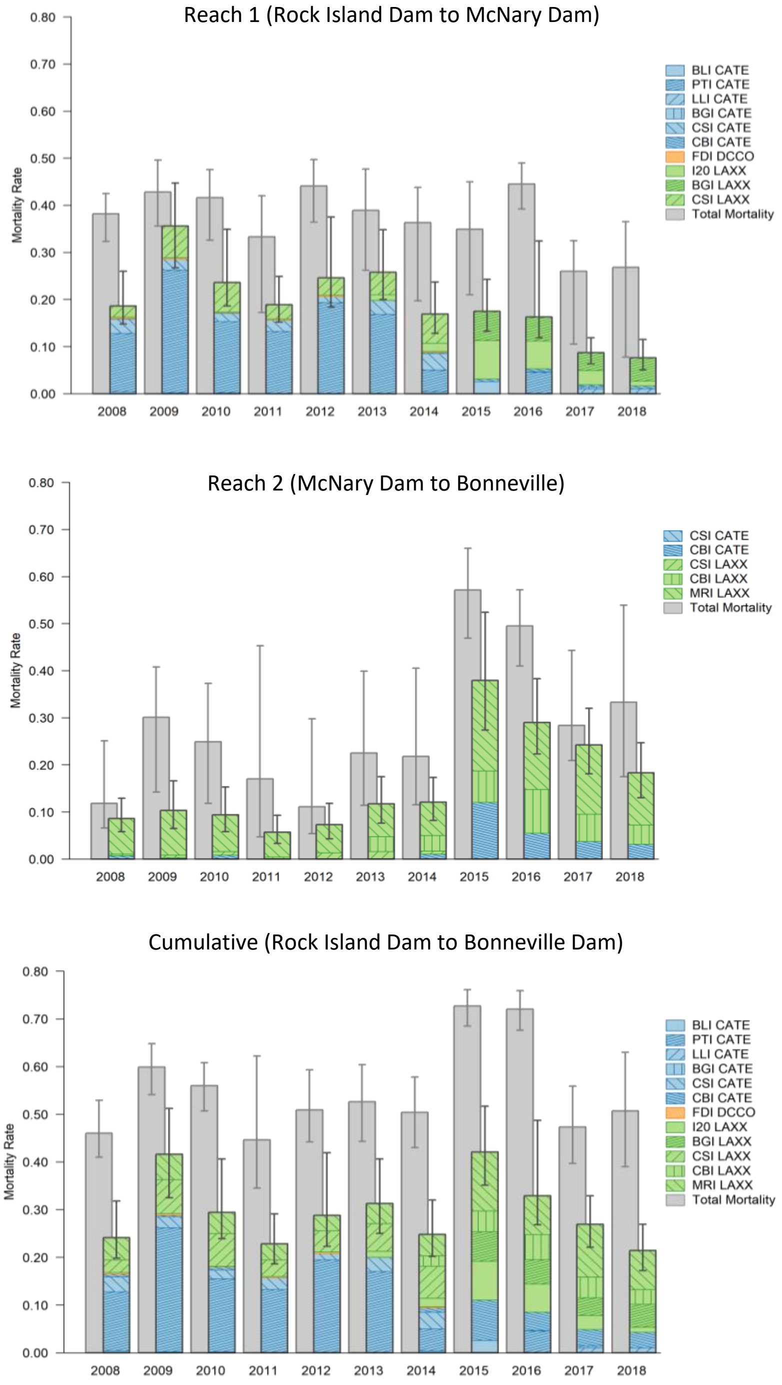
[1] Caspian terns nested either on Goose Island in Potholes Reservoir (2008-2015) or an unnamed island in Potholes Reservoir (2016)

[2] Double-crested cormorants temporarily dispersed from the colony site during the peak nesting period in 2016–2018

Not all colony sites had nesting birds in all study years, nor were all sites scanned for PIT tags in all years. Specifically, California and ring-billed gull colonies on Island 20 and the central Blalock Islands were not scanned for PIT tags during 2008–2012 (*Table 1.2*), 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 and again during 2015–2018, preventing estimation of predation rates by cormorants in those years. Double-crested cormorants nesting on East Sand Island temporarily dispersed from the colony site either partially or entirely during the peak of the traditional 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 June and July (Turecek et al. 2018, 2019). As such, although the East Sand Island cormorant colony was scanned for PIT tags in all years, the total number of steelhead smolts consumed by cormorants foraging in Reach 3 in 2016-2018 were unknown, resulting in minimum estimates of cormorant predation rates in those years. Unlike gull and cormorant colonies, all large Caspian tern colonies (those greater than 20 breeding pairs) were scanned for PIT tags in all study years (*Table 1.2*).

Predation Impacts – Of the birds from colonies foraging in Reach 1 (Rock Island Dam to McNary Dam), the highest estimated predation rates on UCR steelhead smolts were those of Caspian terns nesting on islands in Potholes Reservoir, with annual predation rate estimates ranging from 0.04 (95% CRI = 0.02–0.06) to 0.26 (95% CRI = 0.18–0.34; *Figure 1.3,* see also *Appendix A, Table A3*). Predation rate estimates at the Crescent Island tern colony ranged from 0.01 (95% CRI = 0.01–0.02) to 0.03 (95% CRI = 0.02–0.05; *Figure 1.3*). Predation rate estimates were lowest for Caspian terns nesting at Banks Lake and Lenore Lake, with predation rate estimates less than 0.01 in most years (*Figure 1.3*). Aggregate estimated predation impacts from all Caspian tern colonies in Reach 1 on UCR steelhead smolts ranged from 0.02 (95% CRI = 0.01–0.04) to 0.28 (95% CRI = 0.21–0.37). Of the mixed California/ring-billed gull colonies evaluated in Reach 1, UCR steelhead smolt consumption estimates were the highest for gulls nesting on Island 20, with predation estimates of 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 Crescent Island gulls (annual range = 0.02–0.07) and Badger Island gulls (annual range = 0.01–0.07; *Figure 1.3*). Aggregate UCR steelhead smolt predation rate estimates by all California 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 rate estimates on UCR steelhead smolts were consistently the lowest for double-crested cormorants nesting on Foundation Island, with estimates less than 0.01 (*Figure 1.3*). Cumulative predation rate estimates on UCR steelhead smolts (predation by birds from all colonies combined) indicated that a large proportion of available steelhead were consumed by piscivorous colonial waterbirds in Reach 1, with annual estimates ranging from 0.07 (95% CRI = 0.05–0.10) to 0.36 (95% CRI = 0.27–0.45) during 2008–2018 (*Figure 1.3*). Cumulative predation rate estimates did not include consumption by gulls nesting on Island 20 during 2008–2012 or double-crested cormorants nesting on Foundation Island during 2013 and 2015–2017, and thus are minimum estimates of the total impact of birds from all colonies on UCR steelhead mortality in Reach 1 during those years.

Of the birds from colonies foraging in Reach 2 (McNary Dam to Bonneville Dam), predation rate estimates on UCR steelhead smolts were the highest for California and ring-billed gulls nesting at the mixed colony on Miller Rocks, with annual steelhead predation rates ranging from 0.05 (95% CRI = 0.03–0.08) to 0.18 (95% CRI = 0.13–0.29; *Figure 1.3*, see also *Appendix A, Table A3*). Estimates of consumption by gulls from the mixed species colony in the central Blalock Islands ranged from 0.03 (95% CRI = 0.02–0.05) to 0.09 (95% CRI = 0.06–0.14; *Figure 1.3*), during those years when PIT tag data were available (2013–2018). Aggregate predation rates of PIT-tagged UCR steelhead smolts from all mixed colonies of California and ring-billed gulls in Reach 2 was estimated to range 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 rate estimates on UCR steelhead smolts were the highest and the most variable by terns nesting at the central Blalock Islands, with annual predation rate estimates ranging from <0.01 to 0.12 (95% CRI = 0.07–0.20; *Figure 1.3*). Estimates of the cumulative impact of all piscivorous colonial waterbirds on UCR steelhead smolt survival in Reach 2 were highly variable across the study period, with annual predation rate estimates ranging from 0.06 (95% CRI = 0.03–0.10) to 0.38 (95% CRI = 0.27–0.53; *Figure 1.3*). Analogous to estimates of cumulative predation in Reach 1, not all California and ring-billed gull colonies were scanned for PIT tags in all study years in Reach 2 (i.e. the gull colony in the central Blalock Islands during 2009–2012) and, therefore, estimates of cumulative predation by piscivorous colonial waterbirds were minimums in those years.


Reach 1 (Rock Island Dam to McNary Dam)

Reach 2 (McNary Dam to Bonneville)

Cumulative (Rock Island Dam to Bonneville Dam)

Figure 1.3. Estimated total mortality (grey bars) and mortality attributed to colonial waterbird predation (colored bars) on UCR steelhead smolts in Reach 1 (Rock Island Dam to McNary Dam), Reach 2 (McNary Dam to Bonneville Dam), and Reaches 1 and 2 combined (cumulative). Colony 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 include Caspian terns (CATE), double-crested cormorants (DCCO), and California and ring-billed gulls (LAXX). Error bars represent 95% credible intervals for total mortality and cumulative avian predation.

Gulls and terns nesting on Crescent Island in Reach 1 foraged both upstream and downstream of McNary Dam, but only a small proportion of available steelhead were consumed by these two colonies downstream of McNary Dam in Reach 2, estimated to be less than 0.01 of available smolts, per year, per colony (*Appendix A, Table A3*). Similarly, predation rate estimates indicated that terns nesting in the central Blalock Islands in Reach 2 foraged upstream of McNary Dam in Reach 1, but predation estimates were less than 0.02 in all study years (*Appendix A, Table A3*). Collectively, results indicate foraging on UCR steelhead smolts was concentrated within the river reach nearest 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 UCR steelhead smolts, with a minimum, one-way commuting distance of 34 to 67 km, depending on the colony (*Figure 1.1* above).

Of the colonies foraging in Reach 3 (Bonneville Dam to the Pacific Ocean), predation rate estimates on UCR steelhead smolts were the highest by Caspian terns nesting on East Sand Island, with annual estimates ranging from 0.07 (95% CRI = 0.05–0.13) to 0.21 (95% CRI = 0.16–0.30; *Figure 1.4*, see also *Appendix A, Table A3*). Predation on UCR steelhead smolts by double-crested cormorants on East Sand Island were generally lower than those for terns but were substantial in years (2008–2015) when cormorants were present on-colony throughout the smolt outmigration period, with estimates ranging from 0.03 (95% CRI = 0.02–0.05) to 0.10 (95% CRI = 0.07–0.16; *Figure 1.4*). Due to several *en masse* dispersal events away from the East Sand Island cormorant colony during the peak nesting and smolt outmigration periods in 2016–2018, predation rates on UCR steelhead smolts by double-crested cormorants nesting on East Sand Island should be considered minimum estimates. During these colony dispersal events, most double-crested cormorants remained in the Columbia River estuary (see Turecek et al. 2018, 2019) where they presumably continued to consume steelhead in Reach 3, but consumed PIT tags from UCR steelhead smolts were not being deposited on the East Sand Island cormorant colony.

Annual cumulative avian predation rate estimates (predation by all 14 colonies combined) on UCR steelhead during smolt passage from Rock Island Dam to the Pacific Ocean were substantial, ranging 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, predation rate estimates on UCR steelhead smolts were often the highest by Caspian tern colonies, with annual aggregate tern predation rates ranging from 0.11 (95% CRI = 0.09–0.14) to 0.38 (95% CRI = 0.29–0.47) (*Figure 1.4*). Predation estimates on UCR steelhead smolts by all gull colonies were also substantial, ranging from 0.07 (95% CRI = 0.05–0.10) to 0.31 (0.25–0.39), but gull consumption could not be fully evaluated across all study years and river reaches due to a lack of PIT tag recoveries from the Island 20 and central Blalock Islands gull colonies during 2008–2012. The estimated cumulative impact of double-crested cormorants from the two colonies included in the study (Foundation Island and East Sand Island) on UCR steelhead smolts was consistently less than that of the seven tern and five gull colonies included in the study, ranging from 0.01 (95% CRI = 0.01–0.02) to 0.04 (95% CRI = 0.03–0.07). Analogous to several gull colonies, estimates of predation rates by cormorants nesting on Foundation Island were not available in all study years, so in those years cumulative predation rates by cormorants were minimum estimates. In the case of the large cormorant colony on East Sand Island in Reach 3, predation rates on UCR steelhead smolts from PIT tag recoveries in 2016–2018 also represent minimum losses due to colony abandonment events in those three years.

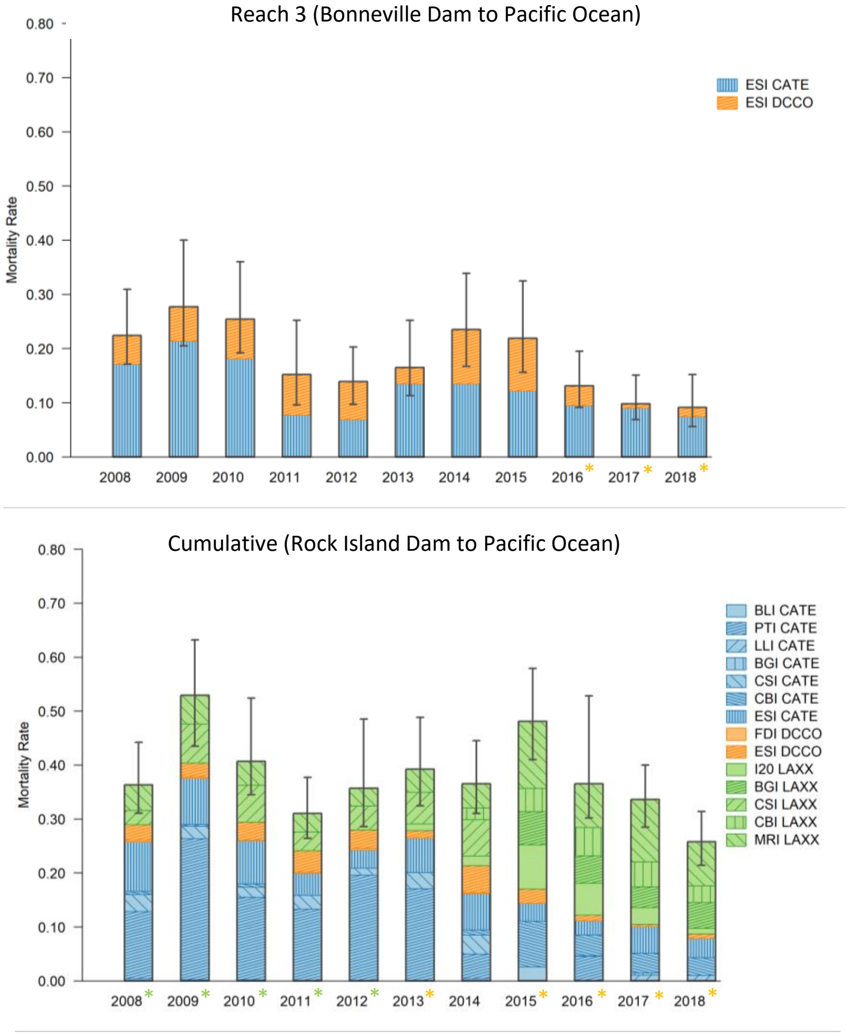


Figure 1.4. Estimated mortality of UCR steelhead smolts due to predation by colonial waterbirds in Reach 3 (Bonneville Dam to the Pacific Ocean) and cumulative mortality from all 14 bird colonies on steelhead smolts during passage from Rock Island Dam to the Pacific Ocean. Colony locations include Banks 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 include Caspian terns (CATE), double-crested cormorants (DCCO), and California and ring-billed gulls (LAXX). Error bars represent 95% credible intervals for cumulative avian predation.

Steelhead Survival – Estimated UCR steelhead smolt survival rates 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 1.3 above*). Estimated annual cumulative survival rates of UCR steelhead smolts from release at Rock Island Dam to Bonneville Dam ranged 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 UCR steelhead smolts died prior to reaching Bonneville Dam (*Figure 1.3 above*). An estimate of UCR steelhead 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 located on East Sand Island. Estimated smolt-to-adult survival (SAR) of UCR steelhead from Rock Island Dam (as smolts) to Bonneville Dam (as adults), ranged from 0.01 (95% CRI = 0.0.1–0.01) to 0.03 (95% CRI = 0.03–0.03) during 2008–2015 (the years with complete adult returns available for analysis). Estimated SARs of UCR steelhead from Bonneville Dam (as smolts) to Bonneville Dam (as adults) indicated that steelhead smolts that survived outmigration to Bonneville Dam (i.e., through the hydrosystem) were more likely to return as adults than steelhead just starting outmigration at Rock Island Dam, with SARs ranging from 0.01 (95% CRI = 0.01–0.02) to 0.06 (95% CRI = 0.04–0.07) during 2008–2015.

Comparisons of total UCR steelhead smolt mortality (1-survival) and mortality due to colonial waterbird predation indicated that avian predation was often the greatest direct source of steelhead mortality during outmigration through both Reach 1 and Reach 2 (*Figure 1.3*). In Reach 1, predation by colonial waterbirds was the dominant mortality factor in many, but not all, study years, with birds accounting for an estimated 28% (95% CRI = 14–93%) to 87% (95% CRI = 64–100%) of all UCR steelhead smolt mortality during passage from Rock Island Dam to McNary Dam in 2008–2018. In some years, predation by Caspian terns from the colonies in Potholes Reservoir alone was estimated to be the single greatest direct source of steelhead mortality in Reach 1, accounting for as much as 62% of all estimated steelhead mortality in 2009 (*Figure 1.3*). In Reach 2, bird predation was also estimated to be the dominant mortality factor in many, but not all years, with colonial waterbird predation accounting for 35% (95% CRI = 19–90%) to 91% (95% CRI = 47–100%) of all estimated UCR steelhead smolt mortality during 2008–2018 (*Figure 1.3*). In Reach 1, Caspian tern predation was the dominate source of UCR steelhead smolt mortality due to bird predation during 2008–2013, and California and ring-billed gull predation was the dominate 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 gull predation on UCR steelhead mortality during 2008–2012. Estimates of total UCR steelhead smolt mortality in Reach 1 provided an upper bound for the level of unaccounted for gull consumption in those years, however, whereby unaccounted for gull consumption cannot exceed estimates of total steelhead 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 rates on UCR steelhead smolts that were greater than the point estimate of total UCR steelhead smolt mortality in Reach 1.

Comparisons of total UCR steelhead smolt mortality from Rock Island Dam to Bonneville Dam indicated that predation by colonial waterbirds was the one of the greatest, and in many years the single greatest, direct sources of steelhead mortality, with predation from the colonial waterbird species and colonies included in the study accounting for an estimated 42% (95% CRI = 30–56%) to 70% (95% CRI = 53–87%) of all UCR steelhead smolt mortality during 2008–2018. As such, results indicate that the direct impact of colonial waterbird predation on UCR steelhead smolt was greater than the direct impact of all other mortality sources combined in most study years.

Discussion

Numerous mortality factors have been linked to the decline in steelhead populations in the Columbia River basin, including harvest, habitat loss and degradation, hatchery practices, 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, is a factor that is currently limiting the survival and recovery of ESA-listed UCR steelhead. Predation by colonial waterbirds was estimated to be the single greatest source of direct mortality for UCR steelhead smolts during outmigration from Rock Island Dam to Bonneville Dam, with avian predation estimated to account for more than 50% of all mortality (1-survival) in 9 of the 11 years of this study. For instance, estimated UCR steelhead smolt losses to piscivorous colonial waterbirds included in this study were greater than 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 other piscivorous waterbird species that were not included in the study (America 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 Columbia River upstream of Bonneville Dam, the impact of piscivorous colonial waterbirds on UCR steelhead smolts in the free-flowing section of the Columbia River downstream of Bonneville Dam were substantial, with Caspian terns and double-crested cormorants nesting on East Sand Island in the estuary consuming between an estimated 0.09 and 0.28 of available UCR steelhead smolts annually. Even at these high levels, predation impacts reported herein should be considered minimum estimates due to a lack of smolt PIT tag recoveries from several large gull and cormorant colonies during the study period and due to unaccounted for predation from non-breeding, failed breeders, and/or prospecting piscivorous colonial waterbirds that were not associated with one of the colonies included in the study (see also *Chapter 2* for additional discussion).

Previous research indicates that steelhead are especially susceptible to colonial waterbird predation (Collis et al. 2001; Evans et al. 2012; Freschette et al. 2012; Evans et al. 2016). For example, predation by Caspian terns and California and ring-billed gulls on steelhead smolts were reported to be 2-5 times greater than those of sockeye salmon (*O. nerka*) and Chinook salmon (*O. tshawytscha*) smolts during passage through the same river reaches (Evans et al. 2012; Evans et al. 2016). Freschette et al. (2012) observed higher predation rates by western gulls (*L. occidentalis*) on steelhead compared with coho salmon (*O. kisutch*) 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 salmonids. Hostetter et al. (2012) noted prey size-selectivity by Caspian terns (see also *Appendix B*)*,* 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 meter of the water column (Winkler 1996; Cuthbert and Wires 1999). 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 were substantially greater on UCR 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 are necessary to evaluate to what extent 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 this study provided data to identify which bird species (Caspian terns, double-crested cormorants, California and ring-billed gulls) and individual breeding colonies posed the greatest risk to UCR steelhead survival during outmigration. Comparisons of UCR steelhead losses by predator species indicated that Caspian terns often, but not always, consumed a larger proportion of available steelhead compared with California and 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 estimated to have been the single greatest direct 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 and ring-billed gulls and double-crested cormorants, indicating a higher per capita (per bird) impact by Caspian terns on 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), 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 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 UCR steelhead was consistently less than that of Caspian terns from nearby colonies (e.g., Crescent Island terns versus Foundation Island cormorants; 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 the large size of the cormorant colony (in excess of 14,000 breeding pairs in 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 and ring-billed gulls are generalists omnivores that scavenge food in addition to depredating 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 UCR steelhead smolts by California 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, it was estimated that California and ring-billed gulls nesting at the Miller Rocks colony annually consumed between 0.05 and 0.18 of available UCR steelhead smolts during passage from McNary Dam to Bonneville Dam, while Caspian terns that nested on the nearby central Blalock Islands annually consumed between an estimated 0.04 and 0.12 of available UCR steelhead smolts. Hostetter et al. (2015) attributed high consumption rates by gulls on steelhead smolts to the relatively large size (tens of thousands of breeding pairs) of gull colonies, coupled with the behavioral flexibility to exploit temporarily available food sources (Winkler 1996). In a spatially-explicit investigation of smolt predation by California and ring-billed gulls nesting at colonies in the Columbia River, Evans et al. (2016) observed that gulls nesting on Miller Rocks 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 delays in travel times associated with forebay passage, smolt injury and mortality associated with turbine passage, or 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 fish, making it difficult to equate estimates of consumption to those of predation.

In addition to the suite of biotic factors that influence fish susceptibility to bird predation (i.e. colony sizes, prey availability, and individual fish characteristics; see also *Appendix B*), abiotic factors can also contribute to the susceptibility of fish to bird predation and thus smolt survival during outmigration. Petrosky and Schaller (2010) observed a relationship between increasing river flows in the Columbia River and higher rates of steelhead survival during outmigration, a relationship that has been linked to predation rates 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 UCR 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 dam passage made fish more susceptibility to bird predation. Collectively, results from these studies indicate that numerous biotic and abiotic factors experienced by smolts during outmigration influence their susceptibility to avian predation. Although not the focus of this study, the modeling approach used to jointly estimate predation and survival in the present study could also be used to identify and test the strength of interactions between various biotic and abiotic factors and predation rates, potentially providing important insight to the suite of factors or mechanisms that influence steelhead smolt survival during outmigration.

Concluding Remarks – Results from this study indicate that predation by colonial waterbirds was one of, and in many cases, the single greatest direct source of mortality for UCR steelhead smolts during outmigration. Predation probabilities were highly variable based on the avian predator species, colony location, river reach, and year, indicating dynamic predator-prey interactions that occurred at both local (i.e., reservoir specific) and system-wide (i.e., freshwater migration corridor) scales. Given the magnitude of cumulative predation effects by colonial waterbirds observed in this study, particularly when compared to non-avian 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 UCR 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 UCR steelhead smolt survival in the Columbia River basin; predation probabilities from several 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, non-avian salmonid management actions being implemented in the region (e.g., changes in dam operational strategies, habitat improvements, improved hatchery practices, reductions in harvest). Conversely, by not accounting for avian predation when evaluating the efficacy of other, non-avian management actions, it is likely that the benefits of these actions would be confounded or otherwise masked due to unaccounted for fluctuations in avian predation.

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APPENDIX A: Supplemental Tables

Table A1. Average annual recapture and recovery probabilities (95% credible intervals) of PIT-tagged UCR 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 Columbia River estuary, and smolt-to-adult returns (SAR) to BON. Recovery probabilities are from Caspian terns (CATE), California and ring-billed gulls (LAXX), and/or double-crested cormorants (DCCO) nesting at 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). Recovery probability is shown as the deposition probability multiplied by the annual weighted average of detection probability.

Recapture	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
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)
BON (SAR)	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table A1 Continued...

Recovery	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
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)[1]	0.50 (0.35-0.65)	0.51 (0.35-0.66)		
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)[1]		0.48 (0.29-0.66)		
LLI CATE									0.54 (0.37-0.70)[1]	0.46 (0.31-0.63)[1]	0.35 (0.22-0.47)
I20 LAXX						0.12 (0.08-0.16)	0.12 (0.08-0.16)[1]	0.12 (0.08-0.17)	0.12 (0.08-0.16)	0.12 (0.09-0.17)	0.14 (0.1-0.19)
FDI DCCO	0.37 (0.24-0.50)	0.36 (0.23-0.48)	0.31 (0.20-0.43)	0.23 (0.13-0.33)	0.18 (0.11-0.26)		0.10 (0.05-0.14)				
BGI LAXX								0.12 (0.08-0.17)[1]	0.07 (0.04-0.11)[1]	0.11 (0.07-0.14)	0.08 (0.05-0.1)
BGI CATE				0.51 (0.36-0.66)	0.49 (0.35-0.63)					0.62 (0.45-0.79)[1]	
CSI LAXX	0.12 (0.08-0.16)	0.10 (0.07-0.14)	0.12 (0.08-0.16)	0.11 (0.07-0.15)	0.11 (0.07-0.15)	0.10 (0.07-0.14)	0.13 (0.09-0.17)				
CSI CATE	0.41 (0.29-0.52)	0.49 (0.34-0.63)	0.5 (0.36-0.63)	0.56 (0.39-0.71)	0.43 (0.29-0.56)	0.54 (0.38-0.67)	0.57 (0.4-0.73)				
CBI LAXX						0.12 (0.09-0.17)	0.14 (0.11-0.18)	0.14 (0.1-0.19)	0.14 (0.1-0.18)	0.14 (0.1-0.18)[1]	0.14 (0.1-0.18)[1]
CBI CATE	0.67 (0.49-0.84)	0.64 (0.45-0.8)	0.56 (0.3-0.79)[1]	0.58 (0.42-0.74)		0.62 (0.45-0.78)[1]	0.47 (0.26-0.67)[1]	0.46 (0.27-0.63)	0.46 (0.32-0.59)	0.32 (0.21-0.41)	0.23 (0.16-0.31)
MRI LAXX	0.12 (0.09-0.17)	0.12 (0.08-0.15)	0.11 (0.08-0.15)	0.12 (0.08-0.16)	0.12 (0.08-0.16)	0.12 (0.08-0.16)	0.13 (0.09-0.17)	0.13 (0.09-0.18)	0.12 (0.08-0.16)	0.11 (0.07-0.15)	0.12 (0.08-0.16)
ESI CATE	0.65 (0.48-0.81)	0.63 (0.45-0.79)	0.55 (0.39-0.69)	0.54 (0.39-0.67)	0.49 (0.35-0.63)	0.38 (0.26-0.49)	0.42 (0.31-0.54)	0.58 (0.41-0.72)	0.50 (0.36-0.65)	0.46 (0.32-0.58)	0.47 (0.32-0.6)
ESI DCCO	0.32 (0.21-0.43)	0.31 (0.19-0.44)	0.35 (0.22-0.48)	0.35 (0.23-0.49)	0.33 (0.2-0.45)	0.33 (0.21-0.45)	0.35 (0.22-0.48)	0.34 (0.19-0.48)	0.30 (0.19-0.4)	0.33 (0.21-0.45)	0.44 (0.28-0.6)

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

Table A2. Number of PIT-tagged steelhead smolts released below Rock Island Dam (see Table 1.1 for samples sizes) that were subsequently detected (recaptured) alive at PIT tag arrays or recovered dead on bird colonies during 2008–2018. Bird colonies include those of Caspian terns, double-crested cormorants, and California and ring-billed gulls. See Figure 1.2 for map of recapture and recovery locations. Dashed-line denotes that scanning for PIT tags was not conducted that year, but the colony site was active. Blank cells indicate the colony site was not active (i.e. no breeding birds present).

Recaptured	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
McNary Dam	636	668	366	358	401	332	352	385	779	314	246
John Day Dam	827	430	310	1131	554	225	345	86	207	984	500
Bonneville Dam	390	427	977	153	348	396	528	701	711	406	584
Net Detector	81	110	104	72	96	118	137	103	87	77	82
Recovered	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Caspian terns											
Banks Lake	6	6	6	-	3	-	14	89	3		
Lenore Lake									4	33	16
Potholes Reservoir	347	468	378	350	294	340	103		141		
Badger Island										18	
Crescent Island	97	86	69	111	38	92	151				
Central Blalock Islands	27	11	21	1	-	1	30	278	117	84	52
East Sand Island	425	377	318	164	106	138	211	130	87	159	123
California and ring-billed gulls											
Island 20	-	-	-	-	-	8	15	68	44	26	10
Badger Island								47	22	28	25
Crescent Island	22	50	61	28	32	34	62				
Central Blalock Islands	-	-	-	-	-	12	21	40	47	44	30
Miller Rocks	41	41	35	30	25	29	40	107	63	87	73
Double-crested cormorants											
Foundation Island	7	6	3	4	5	-	1	-	-	-	-
East Sand Island	64	54	79	106	72	27	127	60	20 [1]	9 [1]	25 [1]

[1] Minimum estimate due to colony dispersal events at the East Sand Island double-crested cormorant colony in 2016-2018.

Table A3. Estimated colony- and reach-specific avian predation probabilities or rates (95% creditable intervals) on UCR steelhead smolts released at Rock Island Dam during 2008–2018. Estimates are the proportion of available fish within each reach consumed by birds from each colony. Bird colonies include Caspian terns (CATE), California and ring-billed gulls (LAXX), and/or double-crested cormorants (DCCO) nesting at 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).

						Reach 1 (Rock Island Dam to McNary Dam)					
Colony	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
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		
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)		
LLI CATE									<0.01	0.01 (0.01-0.02)	0.01 (0-0.03)
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)
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)				
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)
BGI CATE				<0.01	<0.01					< 0.01 (0-0.01)	
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)				
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)
All Birds	*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)					
Colony	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
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)				
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 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)
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)
All Bird Colonies	*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)*

Table A3 Continued…

					Reach 3 (Bonneville Dam to the Pacific Ocean)						
Colony	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
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 [1] (0.02-0.07)	0.01 [1] (0-0.02)	0.02 (0.01-0.03)
All Bird Colonies	*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)*

[1] Minimum estimate due to colony dispersal events at the East Sand Island double-crested cormorant colony during 2016-2018.

APPENDIX B: Analysis of Individual Fish Characteristics

The primary purpose of randomly or haphazardly selecting UCR steelhead smolts for PIT-tagging at Rock Island Dam was to ensure that the sample of fish used to estimate steelhead predation and survival rates were representative of all steelhead smolts (tagged and untagged) in the population at-large. This was necessary because previous research has demonstrated that hatchery-reared and injured or diseased steelhead may be more susceptible to bird predation (Hostetter et al. 2012), less likely to survive outmigration (Hostetter et al. 2011; Hostetter et al. 2015), and less likely return as adults (Evans et al. 2014). In addition to random sampling, UCR steelhead smolts were also tagged in proportion to the run passing Rock Island Dam, with more fish tagged when more fish were available in-river. This sampling approach eliminated the need to weight estimates of predation and survival rates based on the number and run-timing of steelhead smolts each year.

Although not the primary focus of this study, data regarding the rear-type, external condition, and size (length) of steelhead smolts – coupled with predation probabilities from the Joint Mortality and Survival model – provided an opportunity to investigate the relationship between individual fish characteristics and susceptibility to bird predation during the study.

Methods

An investigation of the role of individual fish characteristics in the susceptibility to avian predation is predicated on the assumption that characteristics remain unchanged after a fish is tagged and released (Hostetter et al. 2012). For example, significant changes in the external condition of individual fish following release could potentially confound or mask the ability to detect a relationship between fish condition and susceptibility to predation. For this reason, we limited the geographic scope of this analysis to predation rates within Reach 1 (Rock Island Dam and McNary Dam), the first river reach that smolts migrated through following tagging, condition assessment, and release into the tailrace of Rock Island Dam. We further limited the analysis to the four bird colonies where the highest predation rates on UCR steelhead smolts released into Reach 1 were recorded, that is Caspian tern colonies on islands in Potholes Reservoir and on Crescent Island and the mixed California and ring-billed gull colonies on Island 20 and on Crescent Island. Data from the other piscivorous waterbird colonies in Reach 1 and data from all colonies in Reach 1 during 2018 were constrained by the lack of smolt PIT tags recovered on those colonies (see *Appendix A, Table A2*) and the relatively low proportion of wild fish and fish of compromised condition consumed by those colonies, and thus available for analyses (see *Results* below).

Assessment of steelhead condition at the time of tagging was performed according to the non-invasive examination methods of Hostetter et al. (2011) and Evans et al. (2014). In brief, data on the presence and severity of body injuries, descaling, fin damage, and disease were recorded for each tagged UCR steelhead smolt prior to release below Rock Island Dam. For the purposes of this analysis, external condition factors were grouped into a single categorical variable indicating a fish was in a "compromised" or "uncompromised" condition (see also Hostetter et al. 2015). Compromised fish were those that had (1) severe body injuries (defined as deformities, open wounds, or scarring on a large surface area of the head, trunk, operculum, or eyes), (2) significant descaling (defined as a loss of scales on more than 20% of the body), (3) evidence of disease (defined by any external signs of bacterial, fungal, or viral infections), or (4) severe fin damage (defined as fin wear and damage greater than 50% on three or more fins).

Uncompromised fish were those that did not meet any of the criteria listed for compromised fish. Fish size was measured as fork-length (mm) and each fish was classified by rear-type as hatchery (indicated by the absence of an adipose fin or by characteristics associated with hatchery rearing practices, including the removal or erosion of pectoral, pelvic, or dorsal fins) or wild (indicated by the presence of fully intact fins).

Statistical Analysis – To model the relationships between individual steelhead characteristics and avian predation probabilities, we used logistic regression. For each colony under consideration, we assumed

$$k_{w|y,v} \sim binomial(n_{w|y,v}, f(\theta^0_{w|y}, v) * \phi * \psi_{w|y})$$

where $n_{w|y,v}$ is the number of recovered tags from the $n_{w|y,v}$ release for cohort v in week w of year y and $f(\theta_{w|y}, v)$ is the functional relationship between the variable under consideration and the weekly predation rate. ϕ and $\psi_{w|y}$ are the deposition rate and detection rate parameters, respectively, and are estimated as described above. We employed an autoregressive model to describe the average weekly fluctuations in baseline predation rates for steelhead.

$$\theta^0_{w|y} = logit^{-1}\left(logit\left(\theta^0_y\right) + \sum_{i \le w} \epsilon_{y,i} \right).$$

For the categorical covariate analyses (rear-type and condition), we defined

$$f\left(\theta^0_{w|y}, v\right) = logit^{-1}(logit(\theta^0_{w|y}) + \rho * x_v)$$

where x_v is a cohort identifier variable ($x_v = 0$ for the wild cohort or uncompromised steelhead cohort, and x_v = 1 for hatchery-reared or steelhead in compromised condition). Results are interpreted as the average proportional difference in the odds of predation by a bird colony, with a value less than or greater than 1.0 indicating a higher susceptibility for a group of fish and a value of 1.0 showing no difference between groups in susceptibility. For example, a value of 1.50 indicates that the odds of a fish being consumed were 50% greater for that group of fish (e.g., a hatchery fish relative to a wild fish). Confidence intervals that overlap 1.0 indicate that the odds were not statistically significant (alpha = 0.05).

For the continuous covariate analysis (fork-length), we defined

$$f\left(\theta^0_{w|y}, v\right) = logit^{-1}(logit(\theta^0_{w|y}) + \beta_1 * x_v + \beta_2 * x_v^2)$$

where x_v is fork-lengths centered at 195 mm, the median fork-length of all steelhead smolts released over the 10-year study period (i.e. x_v= fork length – 195).

Results and Discussion

Most UCR steelhead smolts captured, tagged, and released into the tailrace of Rock Island Dam were hatchery-reared, comprising 72.2–77.7% of all tagged fish annually during 2008–2017 (*Table B1*). Ratios of hatchery to wild fish were relatively consistent across the study period. Most of the fish were in good external condition, with 76.9–96.2% of fish classified as being in uncompromised condition in each year (*Table B1*). Unlike the ratio of hatchery to wild fish, however, there was considerable inter-annual variation in the proportion of fish in compromised condition, ranging from just 3.6% in 2014 to 23.1% in

2011. Of those fish in compromised condition, the most common anomalies were body injuries (average of 5.5%), followed by descaling (2.5%), disease (2.3%), and fin damage (2.0%). Results were similar to and, in the case of data from 2008–2010, identical to those presented in Evans et al. (2014), but Evans et al. (2014) provided a more detailed assessment of individual fish condition (i.e. multiple categories of damage).

Table B1. Individual fish characteristics of UCR steelhead smolts tagged and released at Rock Island Dam, including rear-type (hatchery, wild), external condition (uncompromised [Uncomp], compromised [Comp]), and median fork-length (range = minimum to maximum).

	Rear-type		External Condition		Fork-Length mm
Year	Hatchery (%)	Wild (%)	Comp (%)	Uncomp (%)	Median (Min - Max)
2008	5,373 (73.9%)	1,898 (26.1%)	774 (10.6%)	6,497(89.4%)	193 (88-302)
2009	5,150 (72.4%)	1,964 (27.6%)	434 (6.1%)	6,680 (93.9%)	195 (96-291)
2010	5,387 (73.1%)	1,978 (26.9%)	615 (8.4%)	6,750 (91.6%)	197 (70-297)
2011	5,961 (76.9%)	1,795 (23.1%)	1,792 (23.1%)	5,964 (76.9%)	204 (102-320)
2012	5,107 (76.1%)	1,605 (23.9%)	652 (9.7%)	6,060 (90.3%)	196 (92-320)
2013	4,284 (72.7%)	1,609 (27.3%)	422 (7.2%)	5,471 (92.8%)	193 (90-320)
2014	5,686 (74.2%)	1,977 (25.8%)	276 (3.6%)	7,387 (96.4%)	191 (77-308)
2015	5,105 (72.2%)	1,964 (27.8%)	963 (13.6%)	6,106 (86.4%)	193 (86-300)
2016	4,965 (73.4%)	1,799 (26.6%)	429 (6.3%)	6,335 (93.7%)	196 (119-340)
2017	5,776 (77.7%)	1,660 (22.3%)	518 (7.0%)	6,918 (93.0%)	194 (87-310)

There was considerable variation in fork-length of the tagged sample, with individual fish ranging from 70 mm to 340 mm (*Table B1* above *and Figure B1*). Hatchery-reared steelhead were, on average, larger than wild steelhead, but fork-lengths were also more variable amongst wild fish, with wild fish having both the smallest and largest individuals in the sample (Figure B1).

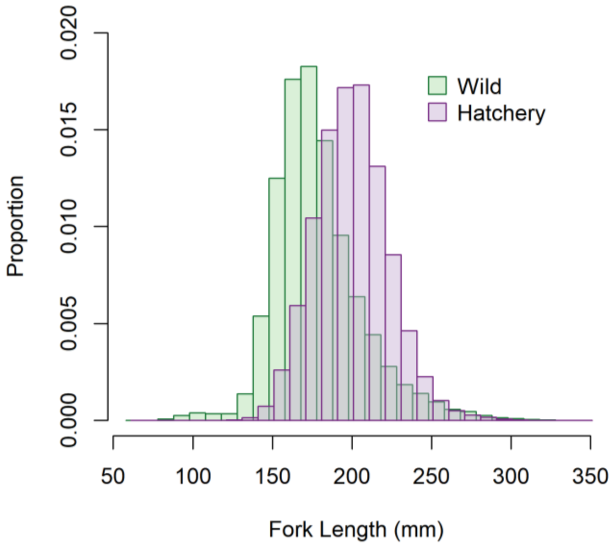

Figure B1. Length distribution of wild and hatchery-reared UCR steelhead smolts tagged and released at Rock Island Dam during 2008-2017. Density is shown as the proportion of fish sampled.

Comparisons of the susceptibility of hatchery versus wild UCR steelhead smolts to predation by birds indicated that hatchery fish were more likely to be consumed than their wild counterparts (*Table B2*). Differences were statistically significant for both types of avian predator species (Caspian terns, California and ring-billed gulls) and each colony evaluated (*Table B2*; see also *Figure B2* for weekly comparisons). Although results were statistically significant, the magnitude of differences in relative susceptibility were often small (based on the proximity of estimates to 1.0) and varied by colony, with hatchery fish estimated to have been 1.05 (95% CI = 1.00–1.09) to 1.29 (95% CI = 1.17–1.43) times more likely to be consumed than their wild counterparts across all study years, depending on the colony (see *Figure B2* for weekly and yearly comparisons). There was also some evidence that compromised fish were more likely to be consumed by birds than uncompromised fish. Differences in susceptibility based on fish condition, however, were inconsistent, with compromised fish more likely to be consumed than uncompromised fish in some, but not all, weekly and yearly comparisons (*Figure B3*). When smolt condition data from all weeks and years were considered, results were statistically significant only for Caspian terns nesting in Potholes Reservoir, whereby compromised fish were more likely to be consumed by Caspian terns than uncompromised fish (*Table B2*). Analogous to differences based on rear-type, the magnitude of relative differences in susceptibility based on condition were small, with compromised steelhead estimated to have been just 1.01 (95% CI = 0.96–1.06) to 1.07 (0.95–1.16) times more likely to be consumed by birds than uncompromised fish (*Table B2*).

Table B2. Estimated odds ratio of predation by birds (95% confidence intervals) based on the individual fish characteristics of rear-type (hatchery, wild) and external condition (compromised [Comp], uncompromised [Uncomp]). Values > 1 indicate greater odds of predation for hatchery fish and compromised fish, values < 1 indicate greater odds of predation for wild fish and uncompromised fish. Avian predators include Caspian terns (CATE) and California and ring-billed gulls (LAXX) nesting at colonies on or near the middle Columbia River and foraging on smolts between Rock Island Dam and McNary Dam during 2008-2017 (see Figure 1.1 for map of colony locations).

Years	Species	Nesting Site	Rear-type Hatchery / Wild	Condition Comp / Uncomp
2008-2016	CATE	Potholes Reservoir	1.10 (1.07-1.12)	1.04 (1.01-1.07)
2008-2014		Crescent Island	1.05 (1.00-1.09)	1.01 (0.96-1.06)
2013-2017	LAXX	Island 20	1.29 (1.17-1.43)	1.07 (0.95-1.16)
2008-2014		Crescent Island	1.22 (1.14-1.32)	1.03 (0.93-1.11)

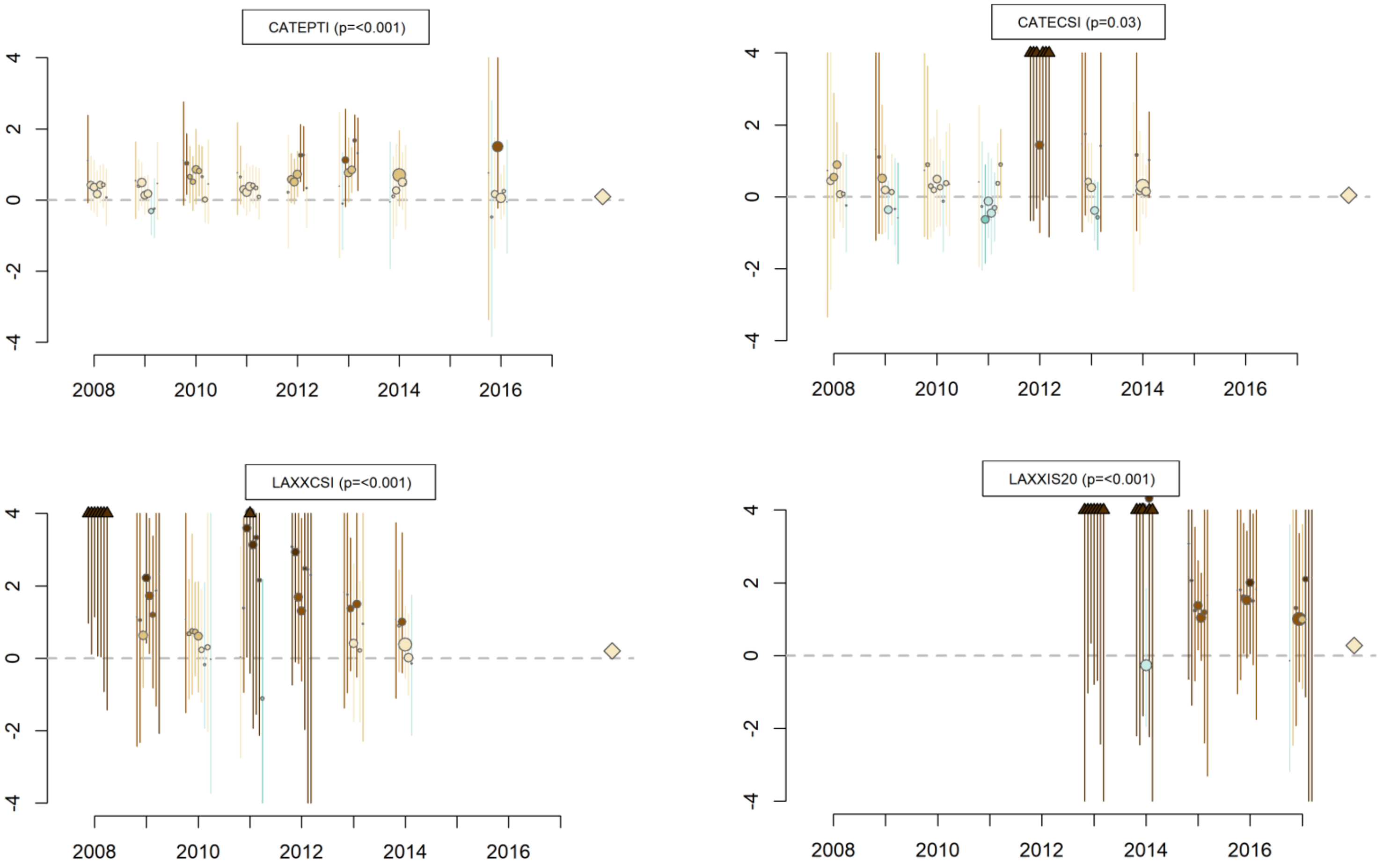

Figure B2. Weekly estimates of log odds ratio of predation on hatchery-reared versus wild UCR steelhead smolts by Caspian terns (CATE) or California or ring-billed gulls (LAXX) nesting on Crescent Island (CSI), Island 20 (IS20), or islands in Potholes Reservoir (PTI). Values greater than 0 indicate a preference for hatchery-reared steelhead with darker brown points and bars associated with greater preference. Point sizes are proportional to sample sizes; only weeks with combined weekly sample sizes greater than 100 are shown. Arrows represent points exceeding the range of the y-axis. Diamonds and bars represent the estimated average log-odds ratio during the study period.

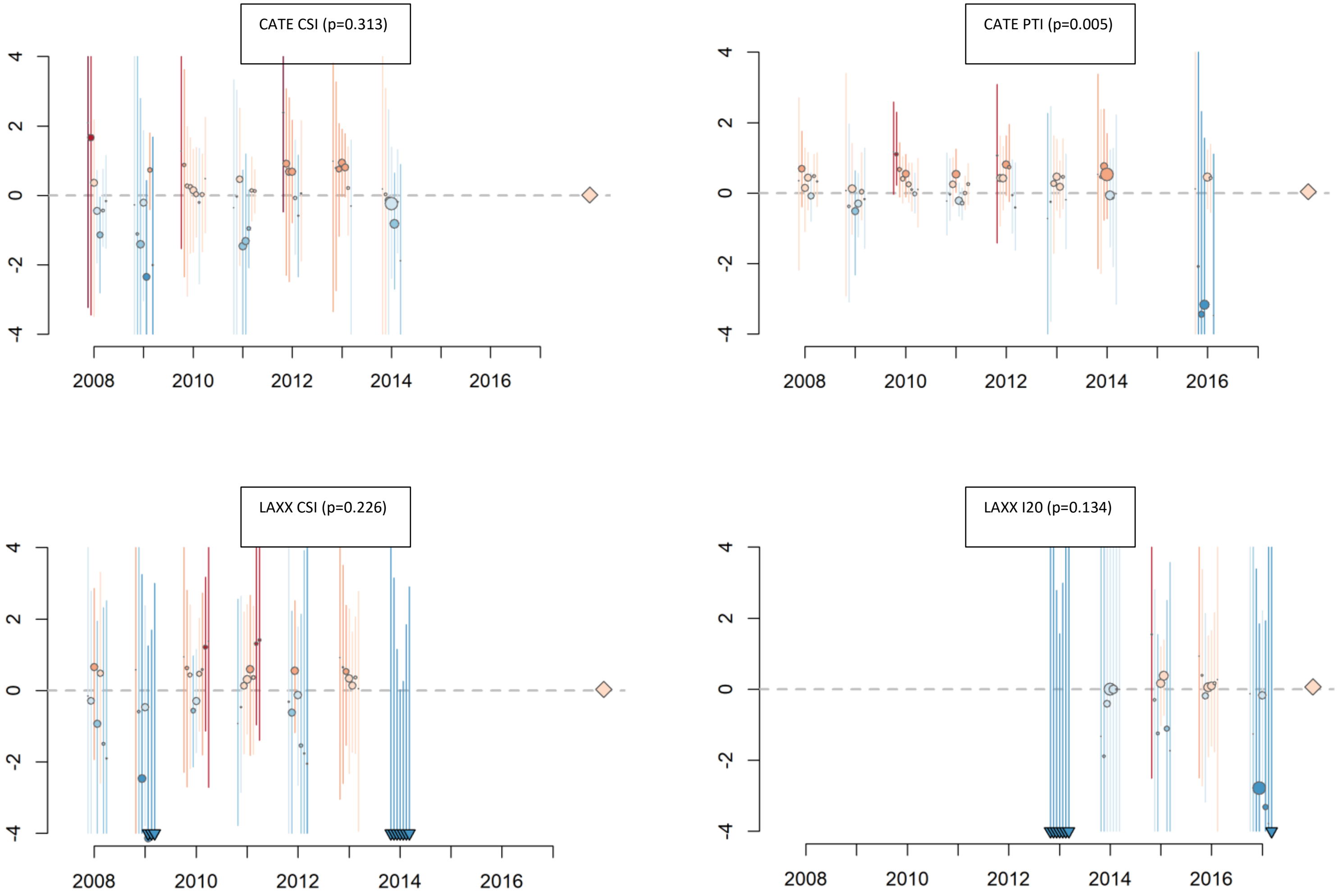

Figure B3. Weekly estimates of log odds ratio of predation on compromised versus uncompromised UCR steelhead smolts by Caspian terns (CATE) or California or ring-billed gulls (LAXX) nesting on Crescent Island (CSI), Island 20 (IS20), or islands in Potholes Reservoir (PTI). Values greater than 0 indicate a preference for compromised steelhead with darker brown points and bars associated with greater preference. Point sizes are proportional to sample sizes; only weeks with combined weekly sample sizes greater than 100 are shown. Arrows represent points exceeding the range of the y-axis. Diamonds and bars represent the estimated average log-odds ratio during the study period.

An analysis of steelhead length data indicated that, on average, larger fish were more susceptible to predation by both terns and gulls than smaller fish, but only up to a threshold where the odds of predation decreased as fish size increased (*Table B3* and *Figure B4*). For example, a 150 mm steelhead was significantly less likely to be consumed by birds than a 210 mm steelhead, but a 210 mm steelhead was significantly more likely to be consumed than a 250 mm steelhead. Results indicated that steelhead with fork-lengths of 200 mm and 215 mm were the most susceptible to predation by terns and gulls, respectively, with gulls preferring slightly larger fish than terns when data from all years and colonies were considered (*Table B3*). Gulls were also capable of consuming steelhead that were greater than 300 mm, while the maximum size consumed by Caspian terns was approximately 280 mm (*Figure B4*).

Table B3. Estimated fork-length of UCR steelhead smolts at which the odds of predation by birds (95% CR) was highest (maximum susceptibility) for each bird colony studied, along with odd ratios demonstrating predation associated with smaller-sized (150 mm) and larger-sized (250 mm) fish relative to the size of maximum susceptibility.

Years	Species	Nesting Site	Max Susceptible	Odds Ratio	
				150 mm	250 mm
2008-2016	CATE	Potholes Reservoir	200 (196-205)	0.55 (0.47-0.63)	0.56 (0.45-0.67)
2008-2015		Crescent Island	210 (200-223)	0.49 (0.35-0.61)	0.73 (0.53-0.95)
2013-2017	LAXX	Island 20	215 (191-274)	0.38 (0.18-0.63)	0.76 (0.37-1.30)
2008-2015		Crescent Island	215 (203-231)	0.22 (0.12-0.34)	0.65 (0.35-1.00)

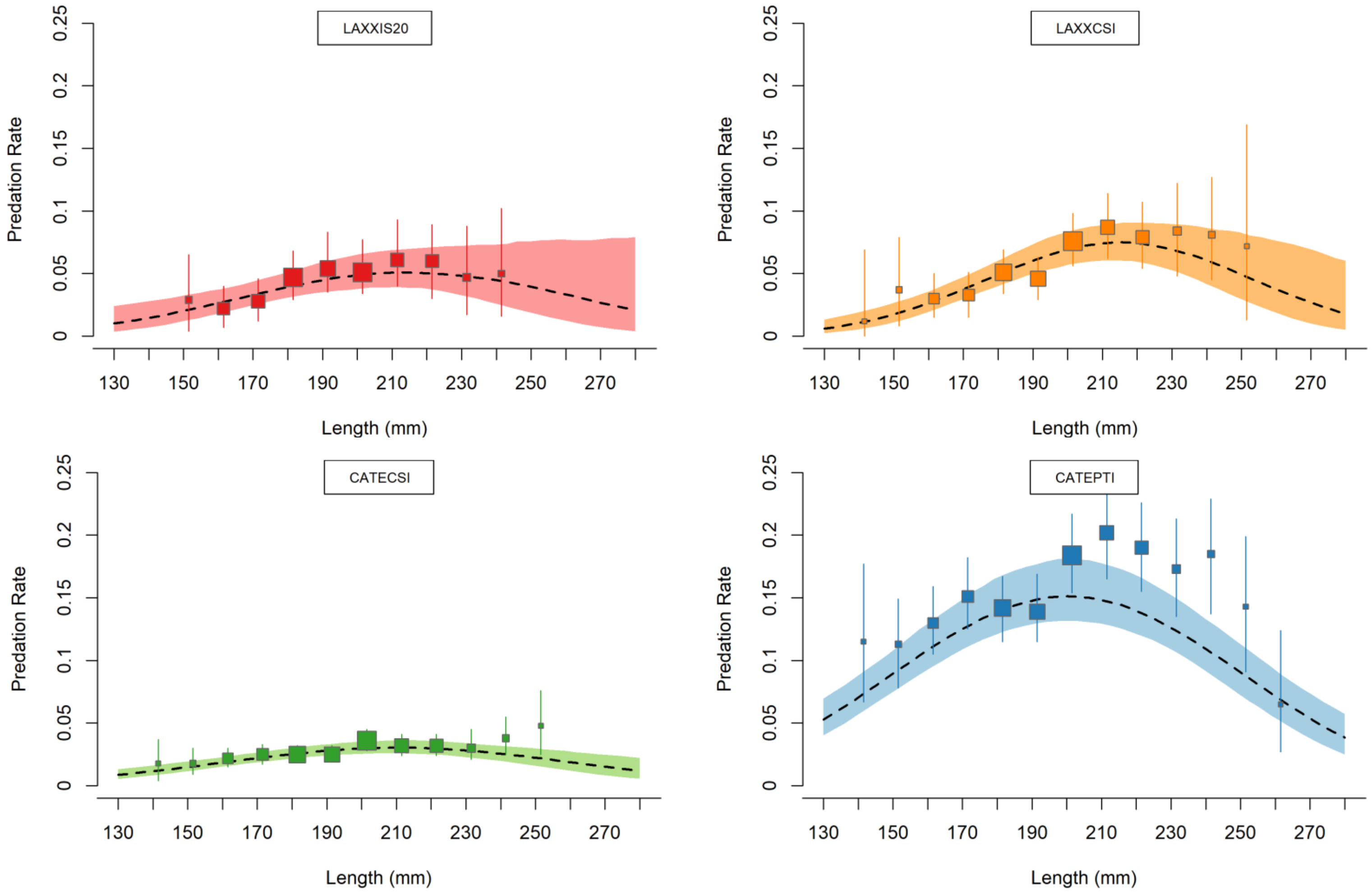

Figure B4. Weighted average annual estimates of bird predation rates (boxes, error bars represent 95% Credible Intervals) for steelhead grouped by fork-length (rounded to nearest cm) for Caspian terns (CATE) or California or ring-billed gulls (LAXX) nesting on Crescent Island (CSI), Island 20 (IS20), or islands in Potholes Reservoir (PTI). Point sizes are proportional to sample sizes; only estimates with combined sample sizes greater than 500 across all years are shown. Dashed curves represent the best fit from a logistic regression model with the shaded regions representing the 95% Credible Intervals.

Results presented here were consistent with other studies that indicated fish susceptibility to colonial waterbird predation was associated with individual fish characteristics (Hostetter et al. 2012; Osterback et al. 2014). For example, Hostetter et al. (2012) observed that hatchery-reared steelhead originating from the Snake River were more susceptible to Caspian tern predation than wild steelhead, differences that were attributed to the larger average size of hatchery steelhead compared to wild steelhead. In a study of predation by western gulls (*L. occidentalis*), Osterback et al. (2014) observed that larger-sized steelhead were more susceptible to gull predation than smaller-sized steelhead up to a threshold where predation susceptibility decreased as fish sizes reached or exceeded the maximum size of fish consumed by gulls. In the present study, most steelhead (74%), particularly wild steelhead (91%), were less than 210 mm, indicating that numerically, terns and gulls disproportionately consumed larger-sized steelhead, particularly larger-sized wild steelhead. Previous research indicates that larger-sized steelhead smolts are more likely to survive outmigration (Zabel et al. 2005; Hostetter et al. 2015) and more likely to return as adults than smaller-sized smolts (Evans et al. 2014). The disproportionate consumption of larger-sized steelhead smolts by Caspian terns also supports the finding that tern predation was an additive source of mortality for juvenile steelhead between Rock Island Dam and Bonneville Dam (see *Chapter 2* for details), whereby terns may be disproportionately depredated fish with a higher likelihood of survival.

In a study of external maladies (body injuries, disease, descaling), Hostetter et al. (2012) observed that compromised fish were more likely to be depredated by either Caspian terns or double-crested cormorants than uncompromised fish. Similar to results from this study, however, the magnitude of difference in predation rates between compromised and uncompromised fish was relatively small (i.e. compromised fish were only slightly more susceptible to bird predation than uncompromised fish; Hostetter et al. 2012). It should be noted that in both studies the vast majority of steelhead sampled and released were in uncompromised condition. Collectively, results from this and other studies provide evidence of size- and condition-dependent selectivity by colonial waterbirds (Caspian terns, California and ring-billed gulls) on steelhead smolts. The overall impact on the steelhead population of size selectivity by avian predators may be more important in limiting smolt survival than that of condition selectivity, given that terns and gulls disproportionately consumed larger-sized steelhead and larger steelhead smolts have been shown to be more likely to survive outmigration than smaller steelhead smolts (Hostetter et al. 2011; Evans et al. 2014). Conversely, the overall impact of condition selectivity by avian predators may be relatively minor (depending on how prevalent smolts in poor condition are in any given year) because only a small fraction of steelhead smolts had external abnormalities (less than 10% in most years) and because the magnitude of difference in susceptibility to avian predation between fish with and without external maladies was generally small or not detectable in this and other studies.

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CHAPTER 2: Additive Effects of Caspian Tern Predation on the Survival of Upper Columbia River Steelhead: Implications for Predator Management

Abstract

We investigated the degree to which Caspian tern (*Hydroprogne caspia*) predation was an additive versus compensatory source of mortality for juvenile Endangered Species Act (ESA)-listed Upper Columbia River (UCR) steelhead trout (*Oncorhynchus mykiss*) during outmigration to the Pacific Ocean. The dataset included UCR steelhead smolts tagged with passive integrated transponders (PIT) tags (n=78,409) and released at Rock Island Dam on the middle Columbia River during 2008–2018. We used a hierarchical, multinomial state-space model to jointly estimate probabilities of steelhead survival, predation by Caspian tern colonies, and mortality from other causes among time-stratified cohorts, measuring the strength, magnitude, and direction of relationships among these probabilities. Predation and survival probabilities or rates (proportion of available fish) were evaluated during UCR steelhead outmigration through three different river reaches of the Columbia River: (1) a 259-river kilometer (Rkm) section of the middle and lower Columbia River between Rock Island Dam and McNary Dam, (2) a 236 Rkm section of the lower Columbia River between McNary Dam and Bonneville Dam, and (3) a 234 Rkm section of the lower Columbia River between Bonneville Dam and the Pacific Ocean.

Annual predation rates by the seven individual Caspian tern colonies included in the study were highly variable across the study period, ranging from less than 0.01 to 0.26 (95% credible interval [CRI] = 0.18–0.34) of the available UCR steelhead smolts, per colony, per year. Weekly estimates of Caspian tern predation rates were also highly variable depending on the colony, river reach, and year, ranging from less than 0.01 to 0.49 (95% CRI = 0.16–0.82) of the available UCR steelhead smolts, per week. The cumulative impact of all seven Caspian tern colonies on UCR steelhead smolts during outmigration to the Pacific Ocean were substantial, with annual cumulative predation rates ranging from 0.11 (95% CRI = 0.09–0.14) to 0.38 (95% CRI = 0.29–0.47) during the 11-year study period. Comparisons of total steelhead mortality (1-survival) to mortality due to predation by Caspian terns indicated that tern predation was one of the greatest direct sources of steelhead mortality during outmigration, with more smolts succumbing to predation by Caspian terns than from all other sources of mortality combined in some river reaches and years.

There was strong evidence of additive (***a***) mortality to UCR steelhead from Caspian tern predation, with increases in tern predation associated with a statistically significant decrease in steelhead survival for all river reaches and years evaluated. Estimates of **a**, the magnitude of the negative linear relationship between predation and survival, were significantly greater than zero (0) in all years and river reaches, with annual estimates of smolt survival and smolt-to-adult returns (SAR) consistently lower than the respective baseline estimates (survival in the absence of tern predation). Average annual baseline UCR steelhead smolt survival rates between Rock Island Dam and McNary Dam were estimated to be 0.16 greater (95% CRI: 0.12–0.20) than observed smolt survival rates with tern predation, equivalent to a 48% annual average increase in smolt survival in the absence of predation from the five tern colonies that foraged in Reach 1. Average annual baseline steelhead smolt survival rates between Rock Island Dam and Bonneville Dam were estimated to be 0.19 (95% CRI = 0.14–0.25) greater than observed smolt survival rates with tern predation, equivalent to a 45% annual average increase in smolt survival in the absence of

predation from the six tern colonies that foraged in Reach 1 and Reach 2. Average annual baseline SAR rates, which accounted for predation from all seven tern colonies, were estimated to be 0.02 (95% CRI = 0.01–0.03) greater than observed SAR rates, equivalent to 243% annual average increase in adult UCR steelhead returns to Bonneville Dam in the absence of all tern predation in the Columbia River basin. Results provide the first evidence of its kind that Caspian tern predation on UCR steelhead smolts was an additive source of mortality during the smolt life-stage and was a partially additive source of mortality to the adult life-stage.

To address concerns over Caspian tern predation on UCR steelhead and other salmonid populations in the Columbia River basin, management plans have been implemented to reduce the number of Caspian terns nesting at the three largest colonies in the basin, those on (1) East Sand Island in the Columbia River estuary, (2) Crescent Island in McNary Reservoir on the lower Columbia River, and (3) Goose Island and other islands in Potholes Reservoir; the latter are within foraging range of the middle Columbia River. To investigate the efficacy of these plans to reduce Caspian tern predation on UCR steelhead smolts, we compared predation rates and smolt survival rates prior to and following implementation of management actions at each tern colony and within the river reaches where management actions occurred. We also measured changes in tern colony sizes, tern predation rates, and steelhead survival rates at four unmanaged tern colonies in the basin: (1) Badger Island located in McNary Reservoir on the lower Columbia River, (2) the central Blalock Islands located in John Day Reservoir on the lower Columbia River, (3) Twinning Island located in Banks Lake, and (4) a small unnamed island in Lenore Lake; both of the latter two colonies are within foraging range of the middle Columbia River.

Tern predation rates on UCR steelhead smolts PIT-tagged and released at Rock Island Dam were significantly reduced or eliminated concurrent with reductions in tern colony sizes at the three managed colony sites (East Sand, Crescent, and Goose islands). Steelhead smolt survival rates were also, on average, significantly higher in river reaches where tern management actions were implemented and where smolt survival rates could be estimated. An unintended consequence of management actions, however, was an increase in the size of unmanaged Caspian tern colonies in the region, whereby a proportion of terns dissuaded from managed colony sites dispersed to nearby unmanaged colony sites, where terns continued to consume steelhead smolts. In particular, there was an eight-fold increase in the size of the Caspian tern colony in the central Blalock Islands, from an average of 59 breeding pairs prior to management to an average of 481 breeding pairs following management. Consequently, tern predation rates on steelhead smolts in Reach 2 increased significantly and reach-specific survival rates decreased significantly following implementation of management actions at the Crescent Island and Goose Island tern colonies in Reach 1. Collectively, results indicated that management actions accomplished their goal of decreasing tern predation rates at managed colonies and increasing smolt survival in the reaches where those birds foraged. Overall benefits of tern management, however, were offset to some degree by increases in tern predation and decreases in smolt survival associated with terns from managed colonies relocating to unmanaged colony sites within the Columbia Plateau region. Collectively, results from this study suggest that further reductions in Caspian tern predation are possible and, if successful, would likely result in increased survival of UCR steelhead smolts and greater returns of adult steelhead to Bonneville Dam in the future. A system-wide, adaptive management approach for Caspian terns nesting at unmanaged colonies, however, will be needed to achieve these goals.

Introduction

Predator-prey dynamics are fundamental to evolutionary and ecological processes (Holling 1959), yet the impact of predation on prey populations has been a topic of ongoing debate (Serrouya et al. 2015). Assessing the effects of predation on prey populations generally requires information about (1) the number or proportion of available prey consumed, (2) which individuals or life-stages are targeted by which predators, and (3) the levels at which other mortality sources or vital rates may compensate for predation (Caswell 2001; Mills 2012). Even relatively large predation probabilities, however, do not necessarily mean that predators are a limiting factor for prey populations. Quantifying varying levels of predation and its association with prey population dynamics may provide more accurate insight into the role of predation in driving prey population dynamics (Serrouya et al. 2015). For example, if mortality from predation is approximately 100% compensatory, there is little effect on prey populations at any level of predation. Conversely, when predation is a substantial source of mortality and predominately additive, it may depress prey survival and population growth rates (Taylor 1984).

In the Columbia River basin, predator-prey interactions involving piscivorous colonial waterbirds and anadromous juvenile salmonids (*Oncorhynchus spp.*) have been the subject of numerous studies. Previous research has identified predation by Caspian terns (*Hydroprogne caspia*) as a substantial source of mortality for juvenile steelhead trout (*O. mykiss*) during smolt outmigration to the Pacific Ocean. For example, several studies have documented predation probabilities in excess of 20% of available Endangered Species Act (ESA)-listed steelhead smolts (Collis et al. 2001; Evans et al. 2012; Hostetter et al. 2015; Evans et al. 2016; Payton et al. 2019; see also *Chapter 1*). Despite such documented high levels of predation, it is currently unknown to what degree Caspian tern predation is an additive versus a compensatory source of mortality for steelhead smolts. In other words, would reductions in predation rates on steelhead smolts by Caspian terns result in higher rates of smolt survival (i.e. tern predation adds to mortality) or are smolts consumed by terns destined to die regardless of tern predation (i.e. tern predation is compensated for by other mortality sources)? The additive (a) mortality hypothesis predicts that predation is proportionately related to survival in space and time ($a = 1.0$; *Figure 2.1*; Sandercock et al. 2011). The compensatory mortality hypothesis predicts that predation and survival are unrelated, at least up to the point where predation exceeds natural mortality, whereby survival must decrease ($a = 0$; *Figure 2.1*, shaded boxes). The hypothesis of partial additive mortality lies between these two extremes, where a reduction in predation is associated with some proportional increase in survival. Hypotheses of super additivity ($a > 1.0$) or over-compensation ($a < 0$) predict that non-predated animals will either be less likely to survival or more likely to survive, respectively, than predated animals (Burnham and Anderson 1984; Schaub and Pradel 2004; Sandercock et al. 2011; Peron 2013; Wolfe et al. 2015). Extending these hypotheses to migratory species such as juvenile salmonids, we expect the level of additive mortality due to predation to vary across spatial scales as baseline survival at local scales may be high (e.g., during migration through a specific river reach) but low at life-cycle scales (e.g., smolt-to-adult return rates [SARs]). The efficacy of predator management actions for achieving management or conservation goals may therefore vary by the spatial scale and life-stage under consideration, and assessments at multiple levels of each may be required to fully understand the potential benefits of predator management.

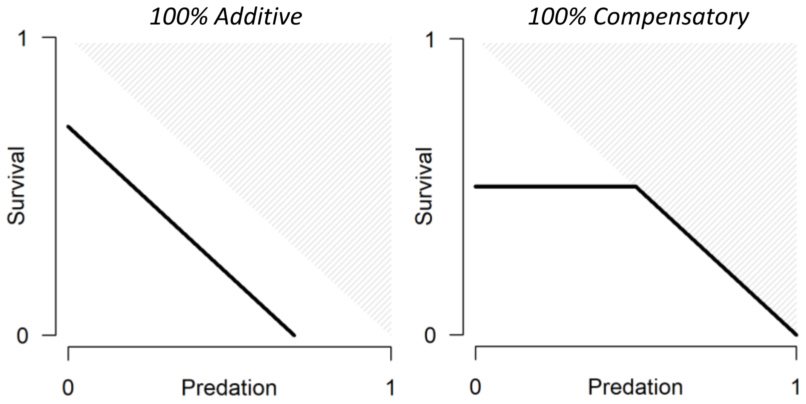

Figure 2.1. Hypothetical relationships of prey survival rates as a function of mortality rates due to predation under assumptions of 100% additive mortality and 100% compensatory mortality from predation. Shaded areas denote the region outside the parameter space, where predation exceeds total mortality (see also Sandercock et al. 2011).

Recent advances in integrated mark-recapture-recovery models provide novel approaches to investigate predator-prey dynamics, compensation, and the impacts of predation on prey populations (Schaub and Pradel 2004; Sandercock et al. 2011; Peron 2013; Evans et al. 2016; Payton et al. 2019; *Chapter 1* of this study). To investigate to what degree Caspian tern predation was an additive versus compensatory source of fish mortality, we used a state-space, mark-recapture-recovery model that jointly estimated rates of predation and survival for ESA-listed Upper Columbia River (UCR) steelhead. Our methods build upon previously published studies assessing compensation in harvest mortality (Burnham and Anderson 1984; Sedinger et al. 2010; Sandercock et al. 2011), where cause-specific mortality and survival were assessed in the same group of marked animals over space and time. In our study, we evaluated the impacts of predation by Caspian terns from seven different breeding colonies on the survival of steelhead during outmigration and smolt-to-adult return rates. Collectively, results provide a comprehensive, system-wide evaluation of the effects of Caspian tern predation on the survival of UCR steelhead at different spatial-scales, life-stages (smolt, SAR), and across an 11-year study period (2008-2018). It is also the first study of its kind to attempt to quantify the degree to which bird predation was an additive versus compensatory source of fish mortality; data paramount to evaluating the efficacy of predator management actions aimed at increasing salmonid survival in the Columbia River basin.

To address concerns over Caspian tern predation on steelhead and other fishes of conservation concern in the Columbia River basin, management plans have been developed and are being implemented to reduce the number of Caspian terns nesting at three of the largest colonies in the region, those on (1) East Sand Island in the Columbia River estuary (USFWS 2006), (2) Crescent Island in McNary Reservoir in the lower Columbia River (USACE 2014), and (3) Goose Island and surrounding islands in Potholes Reservoir, which is within foraging distance of the middle Columbia River (USACE 2014). Management plans have utilized non-lethal nest dissuasion techniques to encourage terns to disperse from their colonies to alternative colony sites created for tern nesting outside the Columbia River basin (USFWS 2006; USACE 2014; Collis et al. 2019; Roby et al. 2019). To date, the efficacy of tern management actions in both reducing avian predation rates and increasing fish survival are not well understood. As part of this study, and using the estimates of steelhead predation and survival rates from the aforementioned 11-year study of UCR steelhead, we investigated changes (i.e. before versus after management) in Caspian tern colony size (number of breeding pairs), tern predation rates on steelhead smolts, and reach-specific steelhead survival rates to assess whether tern management achieved its objectives and what adaptive management initiatives might be worth considering to further increase smolt survival rates.

Methods

Mark-Recapture-Recovery – The same mark-recapture-recovery field methods and data described in *Chapter 1* were used to model the relationship between Caspian tern predation rates on UCR steelhead smolts and UCR steelhead survival rates as part of this Chapter. In brief, we used an 11-year dataset (2008–2018) of uniquely marked (tagged) juvenile UCR steelhead and their subsequent recapture (detections of live fish) and recoveries (detections of dead fish) to evaluate survival, predation, and the relationship between these processes. Each spring (April – June), migrating steelhead smolts were captured at Rock Island Dam on the middle Columbia River (river kilometer [Rkm] 729, as defined by distance to the Pacific Ocean), marked with PIT tags, and released into the tailrace of the dam to resume their out-migration to the Pacific Ocean (*Figure 1.1*). Fish were tagged in proportion to the run-at-large volitionally passing RIS each week. Following release, tagged steelhead could be recaptured (passively detected alive) as smolts at McNary Dam (Rkm 470), at John Day Dam (Rkm 349), at Bonneville Dam (Rkm 234), at a vessel-towed pair-trawl net detection system in the Columbia River estuary (Rkm 75), and as returning adults at Bonneville Dam following one- to three-years of ocean residency. Additionally, each year following the breeding season of piscivorous colonial waterbirds (August – September), PIT tags from depredated steelhead smolts were recovered from up to seven different breeding colonies of Caspian terns and from up to seven other breeding colonies of piscivorous waterbirds, including those of California gulls *Larus californicus*, ring-billed gulls *L. delawarensis*, and double-crested cormorants *Phalacrocorax auritus* (*Figure 1.1*).

The recovery of PIT tags from depredated fish on piscivorous waterbird colonies is the result of two stochastic processes (Hostetter et al. 2015). First, a PIT tag consumed by a bird must be deposited on the bird's breeding colony. Second, the deposited tag must be recovered by researchers on the breeding colony following the breeding season. Independent annual probabilities of tag deposition for each colony included in this study were informed by previous research (Hostetter et al. 2015; see also *Chapter 1, Table A3*), incorporated here through informative Beta priors, and assumed constant within each year. Probabilities of tag recovery varied within each year, with tags deposited earlier in a breeding season less likely to be retrieved than those deposited later. For each bird colony in each year, parameters defining unique logistic retrieval probability functions were estimated based on the intentional sowing of tags on each colony prior to, during (when possible), and after the breeding season (Hostetter et al. 2015; Payton et al. 2019; see also *Chapter 1, Table A3*).

Additive/Compensatory Mortality Modelling – An adaptation of the joint mortality and survival modelling methods of Payton et al. (2019) were used to estimate weekly UCR steelhead smolt survival probabilities (ϕ) and weekly colony-specific predation probabilities (Θ_d), where d indicates the mortality source. Of the 14 different piscivorous colonial waterbird colonies included in the study, seven colonies were those of Caspian terns ({TERNS}; $\Theta^{\{\mathrm{TERNS}\}} = \sum_{d\in\{\mathrm{TERNS}\}} \Theta_d$) and the other seven were those of other waterbird species ({OTHER}, $\Theta^{\{OTHER\}} = \sum_{d\in\{OTHER\}} \Theta_d$). A third and final category, referred to as "unexplained mortality," was defined as the unaccounted for remainder of the unit interval partition,

$(\Theta^{unexplained} = 1 - \phi - \sum_{d \in \{\{\text{TERNS}\} \cup \{OTHER\}\}} \Theta_d)$.

Parameters were measured across three imbricate spatial scales representing two anadromous salmonid life-stages: (1) smolt outmigration from Rock Island Dam to arrival at McNary Dam, (2) smolt outmigration from Rock Island Dam to arrival at Bonneville Dam, and (3) smolt-to-adult migration from Rock Island Dam (as smolts) to return at Bonneville Dam (as adults). For the smolt outmigration life-stage, all tag recaptures and recoveries were used only to inform probabilities of recapture at, and smolt survival to, McNary and Bonneville dams. For the smolt-to-adult return (SAR) life-stage, all recoveries were used to inform predation probabilities and only recaptures of returning adults at Bonneville Dam were evaluated to estimate survival. Recapture probabilities of the returning adults were assumed to be 1.0, allowing for precise survival-to-adulthood estimates (Keefer et al. 2008).

Simultaneous estimation of survival and predation within the same model allows for the measurement of functional relationships between these processes (e.g., $\phi = f(\boldsymbol{\theta})$). The mathematical expression of the classic compensatory mortality model was described by Anderson & Burnham (1976), $\phi = \phi^0 - a\theta$, where, θ denotes the predation probability (replacing anthropogenic harvest, K, used by Anderson & Burnham, [1976]), ϕ^0 is baseline survival probability (the expected probability of survival in the absence of predation), and a defines the constant linear relationship between predation and survival, ϕ. Direct measurements of the population-level impact on prey survival that can be attributed to the predator are measured with ϕ^Δ. This impact is inferred from the difference between baseline survival probabilities (expected survival probabilities in the absence of the predator) and the observed probabilities of survival (measured in the presence of the predator; i.e. $\phi^\Delta = \phi^0 - \phi$).

Several levels of temporal correlation were explicitly recognized in our iteration of this model. The yearly number of UCR steelhead smolts was apportioned into weekly cohorts for which we developed estimates of year (y)- and week (w)-specific survival probabilities ($\phi_{y,w}$), tern predation probabilities ($\Theta_{y,w}^{\{TERNS\}}$), probabilities of predation by other bird species ($\Theta_{y,w}^{\{OTHER\}}$), and probabilities of dying due to an unexplained source mortality ($\Theta_{y,w}^{unexplained}$). Weekly cohorts were not assumed to be mutually independent; instead, the temporal correlation among probabilities of predation, other mortality, and recapture were addressed through logistic random-walk models (see Payton et al. 2019). The assumption of a single, constant probability of baseline survival, common to compensatory mortality models, was relaxed in two ways. First, by incorporating weekly variation in Caspian tern predation probabilities and steelhead survival probabilities we could account for annual differences in the relationship between predation and survival. To this end, annual probabilities of baseline survival, ϕ_y^0, were assumed to be mutually independent. Second, we relaxed the assumption of a constant baseline survival probability within each year by incorporating a weekly random effect,

$$\operatorname{logit}(\phi_{y,w}^0) = \operatorname{logit}(\phi_y^0) + \epsilon_{y,w}$$

where $\epsilon_{y,w} \sim \text{normal}(0, \sigma_\phi^2)\ \forall y, w$. Annual values of additivity were assumed to be unique but similar among years,

$$a_y \sim \text{normal}(\mu_a, \sigma_a^2).$$

This approach allowed for a further evaluation of associations between baseline survival, $\boldsymbol{\phi^0}$, $\mathbf{a}$, or tern predation probabilities (e.g., was variation in levels of baseline survival or tern predation associated with variation in levels of additivity). Finally, under this framework, predation due to other waterbird species ($\Theta_{y,w}^{\{OTHER\}}$) represented a subset of all baseline mortality and thus provided a minimum estimate of "other mortality," analogous to non-harvest mortality or "natural" mortality in other studies (Sandercock et al. 2011; Anderson and Burnham 1976). This compensatory model could be expressed by defining weekly survival as a piecewise function,

$$\phi_{y,w} = \begin{cases} \phi_{\mathrm{y,w}}^0 - a_y \Theta_{y,w}^{\{\mathrm{TERNS}\}}, & \text{when } \Theta_{y,w}^{\{\mathrm{TERNS}\}} \le \theta_{y,w}^{saturation} \\ 1 - \Theta_{y,w}^{\{OTHER\}} - \Theta_{y,w}^{\{\mathrm{TERNS}\}}, & \text{when } \Theta_{y,w}^{\{\mathrm{TERNS}\}} > \theta_{y,w}^{saturation} \text{ and } a < \phi_{y,w}^0 \\ 0, & \text{when } \Theta_{y,w}^{\{\mathrm{TERNS}\}} > \theta_{y,w}^{saturation} \text{ and } a \ge \phi_{y,w}^0 \end{cases}.$$

Here, the first sub-function is the classic compensatory mortality model described by Anderson and Burnham (1976), while the second and third sub-functions enforce the boundary constraints whereby survival, tern predation, and the measured subset of other mortality must sum to 1. The delineations of these parameter space boundaries are defined by

$$\theta^{saturation} = \begin{cases} \dfrac{1-\phi^0}{1-a}, & \text{when } a < \phi^0 \\ \dfrac{\phi^0}{a}, & \text{when } a \ge \phi^0 \end{cases}.$$

Model Implementation and Assumptions– Prior distributions for all probabilities were defined to be either uniform for univariate parameters (i.e. baseline survival, recapture) or Dirichlet(**1**) for multivariate parameters (i.e. survival and mortality). We assigned $\mu_a \sim \mathrm{normal}(\frac{1}{2}, 3)$ as the enumeration of a vague *a priori* assumption that predation by Caspian terns was likely equal parts additive and compensatory mortality, with less prior credibility given to hypotheses of over-compensatory or super-additive mortality mechanisms. As with the random errors in the joint mortality and survival model, we assumed a weakly-informative prior of $\mathrm{half\ normal}(0, 5)$ for both σ_ϕ^2 and σ_a^2.

Models were analyzed using the software STAN (Stan Development Team 2015), accessed through R version 3.1.2 (R Development Core Team 2014), and using the rstan package (version 2.8.0; Stan Development Team 2015). To simulate random draws from the joint posterior distribution, we ran four Hamiltonian Monte Carlo (HMC) Markov Chain processes. Each chain contained 4,000 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. 2013); 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 Interval [CRI]) calculated using the HDInterval package (version 0.1.3; Meredith and Kruschke 2016).

The accuracy and precision of the model depends, in part, on the validity of the following assumptions:

- A1. Within each year there was a baseline mortality rate with independent weekly variation. The magnitude of inter-week variation was similar among years (i.e. σ^{ϵ} is constant across years).
- A2. The additive rate of tern predation was defined as the proportion of steelhead consumed by Caspian terns that would have otherwise survived in the absence of tern predation.
- A3. Relationships between steelhead survival rates and tern predation rates accurately describe the mechanistic relationships between fish survival and tern predation.

To confirm assumption A1, we used a Bayesian equivalent of the Durbin-Watson test to identify serial correlation among weeks and found little evidence of correlation. We additionally found little credibility that the magnitude of weekly variation about the baseline mortality was different among years. For steelhead survival and tern predation in Reaches 1 and 2, we found some evidence that the additive rate of predation was different among years; however, this was highly correlated with reduced range and variance in weekly predation rates. We therefore allowed additivity rates to differ among years, but shared information amongst years to increase precision. A3 concerns the lack of experimental manipulation and controls required to separate correlation and causation in observational studies.

Evaluation of Caspian Tern Management Actions – We evaluated methods to discourage Caspian terns from nesting on East Sand Island in the Columbia River estuary, Crescent Island in McNary Reservoir, and Goose Island and surrounding islands in Potholes Reservoir based on observed changes in the size of each tern colony (number of breeding pairs) prior to and following implementation of management actions at each colony. These methods included passive dissuasion (stakes, rope, flagging, fencing, vegetation, and other habitat modification techniques) and active dissuasion (human hazing and egg collection) to discourage terns from nesting at managed colonies (see Roby et al. 2019 and Collis et al. 2019 for a detailed description of management actions and techniques used at each colony). The same methods and estimates of Caspian tern colony sizes presented in *Chapter 1* were used herein to estimate colony sizes prior to and following implementation of management actions. Periods of this study were defined as pre- and post-management based on when passive and active nest dissuasion actions were implemented to reduce colony size and based on corresponding UCR steelhead predation and survival rates during each of those periods. For the Caspian tern colony on East Sand Island, pre- and post-management periods were 2008-2011 and 2012-2018, respectively. For the Caspian tern colony on Crescent Island, pre- and post-management periods were 2008-2014 and 2015-2018, respectively. For Caspian terns on Goose Island and other surrounding islands in Potholes Reservoir, pre- and post-management periods were 2008-2013 and 2014-2018, respectively. Annual and weekly Caspian tern predation rates on UCR steelhead smolts and steelhead smolt survival rates were also compared prior to and following implementation of management actions at each colony and within each river reach where terns from these colonies foraged. It should be noted that for this study, effects of management were assessed using the 11-year (2008-2018) dataset of UCR steelhead smolts PIT tagged at Rock Island Dam, but the pre-management period dates back much further for some Caspian tern colonies (e.g., Caspian terns first nested on Crescent Island in 1985 and the tern colony on East Sand Island was restored in 1999; Antolos et al. 2004). Also, Caspian terns consume juvenile salmonids from multiple ESA-listed salmonid ESUs/DPSs, but results presented here are germane to UCR steelhead smolts only.

Results

Mark-Recapture-Recovery – A total of 78,409 UCR steelhead smolts were captured, PIT tagged, and released into the tailrace of RIS during 2008–2018 (*Table 2.1*). Annual sample sizes of PIT-tagged smolts released ranged from 5,893 to 7,756 smolts, with the number of weekly releases per year ranging from 9 to 11 weeks (*Table 2.1*). Weekly sample sizes of PIT-tagged UCR steelhead smolts varied considerably from 5 to 2,780 smolts, depending on run-timing in any given year. The median weekly sample size of PIT-tagged steelhead smolts was 421. The number of UCR steelhead smolts detected alive at downstream recapture sites varied by river reach and year, as did the number of smolt PIT tags recovered on Caspian tern breeding colonies (*Table 2.1*). The largest number of UCR steelhead smolt PIT tags (n = 3,263) were recovered on the five Caspian tern colonies located in Reach 1 (Crescent Island, Potholes Reservoir islands, Badger Island, Banks Lake islands, Lenore Lake islands), followed by the Caspian tern colony on East Sand Island in Reach 3 (n = 2,238), and then the Caspian tern colony located on the central Blalock Islands in Reach 2 (n = 622; *Table 2.1*; see also *Appendix A, Table A2* for colony-specific PIT tag recoveries). The largest number of recaptured tags were in Reach 2 with detections from John Day Dam and Bonneville Dam combined (n = 5,621), followed by detections at McNary Dam in Reach 1 (n = 4,839), and at that the pair-trawl net detector in the Columbia River estuary in Reach 3 (n = 1,067; *Table 2.1*). Only a small number and proportion of UCR steelhead smolts tagged and released at Rock Island Dam returned to Bonneville Dam as adults (n = 629 or 0.85%), with the number of returning adults ranging from 5 (<0.1%) to 220 (3.0%) adults per smolt release year (*Table 2.1*).

Table 2.1. Number of UCR steelhead smolts PIT tagged and released at Rock Island Dam and subsequently recaptured alive at downstream PIT tag detection arrays or recovered dead on Caspian tern breeding colonies. The number of tagged UCR steelhead smolts that returned as adults to Bonneville Dam are also provided; dashes indicate that complete adult returns for those cohorts were not yet available.

		--- Reach 1 ---		--- Reach 2 ---		--- Reach 3 ---		
		Rock Island Dam to McNary Dam		McNary Dam to Bonneville Dam		Bonneville Dam to Pacific Ocean		Adult Returns
Year	Released (Weeks)	Live	Dead	Live[1]	Dead	Live	Dead	Live
2008	7,271 (11)	636	450	390	27	81	425	220
2009	7,114 (11)	668	560	427	11	110	377	77
2010	7,365 (11)	366	453	977	21	104	318	88
2011	7,756 (11)	358	461	153	1	72	164	46
2012	6,712 (10)	401	335	348	0	96	106	67
2013	5,893 (10)	332	432	396	1	118	138	61
2014	7,663 (10)	352	268	528	30	137	211	65
2015	7,069 (10)	385	89	701	278	103	130	5
2016	6,764 (9)	779	148	711	117	87	87	-
2017	7,436 (10)	314	51	406	84	77	159	-
2018	7,366 (10)	246	16	584	52	82	123	-
Total	78,409 (113)	4,837	3,263	5,621	622	1,067	2,238	629

[1] *Includes recaptures at both John Day and Bonneville dams*

Recapture probabilities at in-stream PIT tag detection arrays and recovery probabilities of PIT tags at bird colonies are reported in *Appendix A, Table A1*. Recapture probabilities were generally low (posterior medians < 0.20 for most detection sites and years). Estimated recovery probabilities were consistently higher than recapture probabilities but were also highly variable by tern colony and year (range of posterior medians of 0.22 to 0.65; *Appendix A, Table A1*).

Survival and Predation – Upper Columbia River steelhead smolt survival rate estimates varied by river reach and year, ranging 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 1.3*). Comparisons of survival rate estimates between reaches in the same year indicated that survival was higher in Reach 2 compared with Reach 1 during 2008–2014. The opposite trend was observed during 2015-2018, with survival rate estimates higher in Reach 1 compared with Reach 2. Differences were statistically significant in many, but not all, yearly comparisons by reach. Estimated cumulative UCR steelhead smolt survival rates from 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 UCR steelhead smolts tagged at Rock Island Dam died prior to reaching Bonneville Dam (*Appendix C, Table C1* and *Figure 1.3*). An estimate of UCR steelhead smolt survival rates through Reach 3 could not be calculated because there were no PIT tag detection sites in the Columbia River estuary downstream of the bird colonies on East Sand Island. Estimated SAR rates for UCR steelhead from Rock Island Dam (as smolts) to Bonneville Dam (as adults) ranged from 0.01 (95% CRI = 0.01–0.01) to 0.03 (95% CRI = 0.03–0.03) during 2008–2015 (the years with complete adult returns available for analysis). Estimated SARs from Bonneville Dam (as smolts) to Bonneville Dam (as adults) indicated that, as expected, those smolts that survived out-migration to Bonneville Dam were more likely to return as adults compared to smolts just starting out-migration at Rock Island Dam, with SARs ranging from 0.01 (95% CRI = 0.01–0.02) to 0.06 (95% CRI = 0.04–0.07) during 2008–2015.

Estimated Caspian tern predation rates on UCR steelhead smolts were the highest by terns nesting on Goose Island in Potholes Reservoir in Reach 1, with upwards of 0.26 (95% CRI = 0.19–0.35) of available steelhead smolts consumed in some years, followed closely by terns nesting on East Sand Island with upwards of 0.21 (95% CRI = 0.16–0.30) of available smolts consumed in some years (*Appendix A, Table A3*). Predation rate estimates were consistently the lowest for Caspian terns nesting at the unmanaged colonies on Twinning Island in Banks Lake, on an unnamed islands in Lenore Lake, and on Badger Island in McNary Reservoir in Reach 1; estimates of annual predation rates were generally less than 0.01 of available steelhead for terns from these colonies (*Appendix A, Table A3*). Cumulative Caspian tern predation rate estimates on UCR steelhead smolts during passage from Rock Island Dam to McNary Dam ranged from 0.02 (95% CRI = 0.01–0.04) to 0.28 (95% CRI = 0.21–0.37; *Appendix C, Table C1*) during 2008–2018.

Cumulative Caspian tern predation rate estimates on UCR steelhead smolts during passage from Rock Island Dam to Bonneville Dam ranged annually from 0.04 (95% CRI = 0.03–0.07) to 0.30 (95% CRI = 0.21–0.37; *Appendix C, Table C1*). Cumulative Caspian predation rate estimates by all seven tern colonies during UCR steelhead smolt passage from Rock Island Dam to the Pacific Ocean ranged annually from 0.08 (95% CRI = 0.06 –0.11) to 0.38 (95% CRI = 0.29–0.47; *Appendix C, Table C1*). These results indicate that despite the relatively small colony- and reservoir-specific tern predation rates on UCR steelhead smolts observed in some years, the cumulative, system-wide impact of Caspian terns from all colonies in the basin was a substantial source of smolt mortality during steelhead outmigration. Weekly cumulative Caspian tern predation rate estimates on UCR steelhead were also highly variable by river reach and year, ranging from less than 0.01 to 0.49 (95% CRI = 0.16–0.82) of available steelhead smolts per week, depending on the reach and year (*Figure 2.2* and *Figure 2.3*). Estimated cumulative predation probabilities on steelhead from all colonial waterbird species (Caspian terns, double-crested cormorants, California and ring-billed gulls) and colonies combined ranged annually from 0.31 (95% CRI = 0.27–0.38) to 0.53 (95% CRI = 0.42–0.64; see *Chapter 1* for a more detailed summary of predation rate results associated with all 14 colonies).

Comparison of total smolt mortality (1-survival) to mortality due to Caspian tern predation indicated that in some years and river-reaches, predation by Caspian terns was the single greatest direct source of UCR steelhead mortality, with estimated mortality rates from tern predation greater than that of all other direct sources of mortality combined. In 2009, for example, Caspian terns accounted for an estimated 68% (95% CRI = 48–87%) of all mortality during UCR steelhead passage from Rock Island Dam to McNary Dam (*Appendix C, Table C1* and *Figure 1.3.*). In other years, however, the proportion of all mortality that was attributable to Caspian tern predation was relatively small. In 2016, for example, we estimated Caspian terns accounted for just 11% (95% CRI = 9–16%) of all mortality during UCR steelhead passage from Rock Island Dam to McNary Dam (*Appendix C, Table C1*). The annual proportion of total steelhead smolt mortality attributable to Caspian tern predation in Reach 2 was also highly variable, ranging from 9% (95% CRI = 5–13%) to 48% (95% CRI = 34–64%; *Appendix C, Table C1* and *Figure 1.3*). Comparisons of total UCR steelhead mortality from Bonneville Dam (as smolts) to Bonneville Dam (as adults) and predation rates by Caspian terns nesting on East Sand Island in the Columbia River estuary (i.e. tern predation on steelhead smolts that occurred downstream of Bonneville Dam but prior to smolts reaching the Pacific Ocean) indicated that Caspian terns nesting in the estuary accounted for an estimated 7% (95% CRI = 4–11%) to 22% (95% CRI = 15–30%) of all UCR steelhead mortality from Bonneville Dam (as smolts) back to Bonneville Dam (as adults).

Additive/Compensatory Mortality Modelling – There was strong evidence of additive mortality to UCR steelhead from Caspian tern predation for all spatial scales, years, and life-stages evaluated. Estimates of **a**, the magnitude of the negative linear relationship between predation and survival, were significantly greater than zero (0) in all years and spatial scales, with annual estimates of smolt survival and SAR probabilities consistently lower than the respective baseline estimates (*Figure 2.2*, *2.3*, and *2.4*).

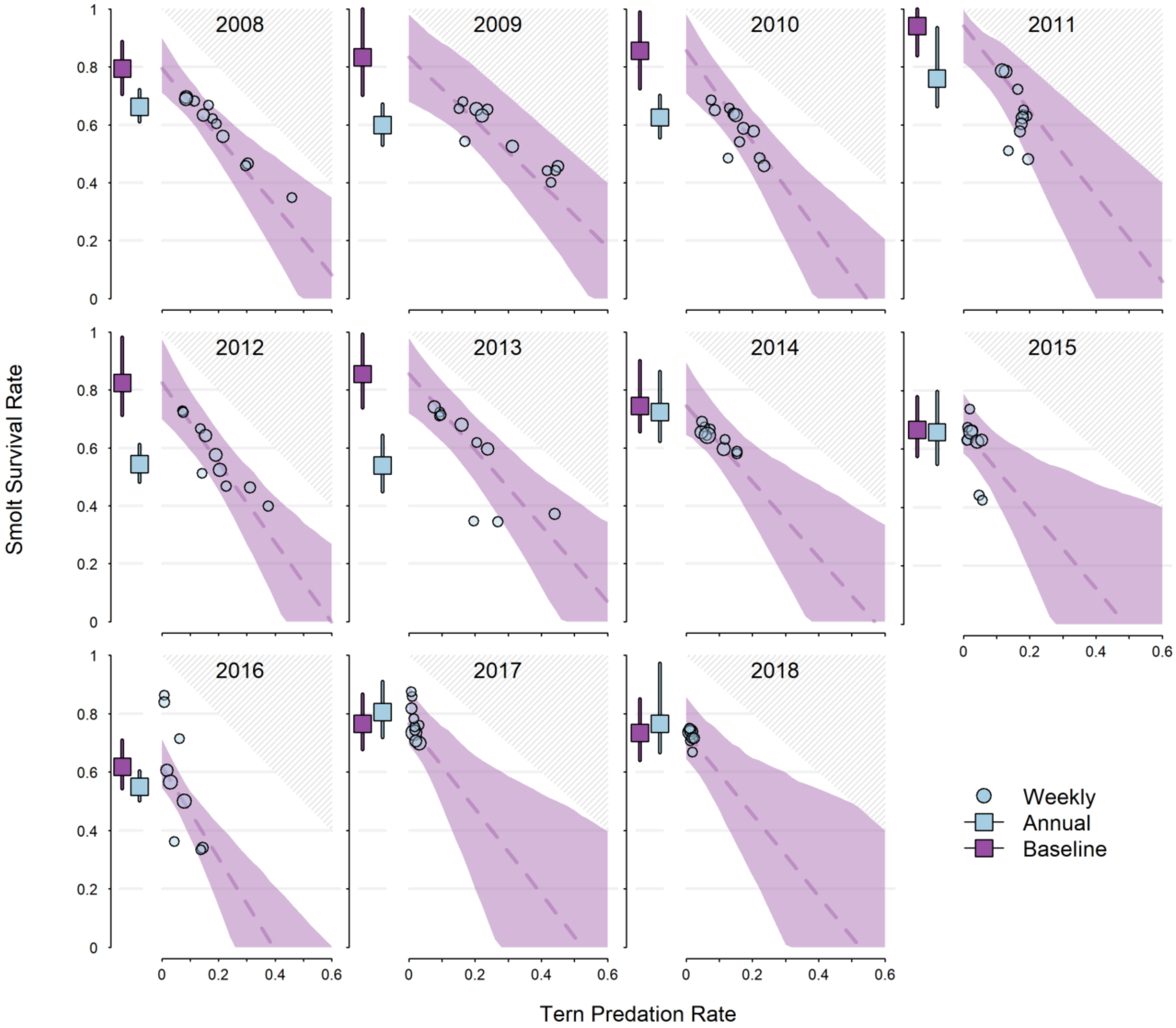

Figure 2.2. Estimated annual relationships between UCR steelhead smolt survival and Caspian tern predation rates during outmigration from Rock Island Dam to McNary Dam. The size of blue circles depicts relative number of tagged steelhead smolts released each week at Rock Island Dam. Dashed lines represent the best fit estimate of the linear relationship and shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of UCR steelhead smolt survival rates with tern predation (blue box) and baseline smolt survival rates in the absence of tern predation (purple box) are also provided (error bars denote 95% CRI).

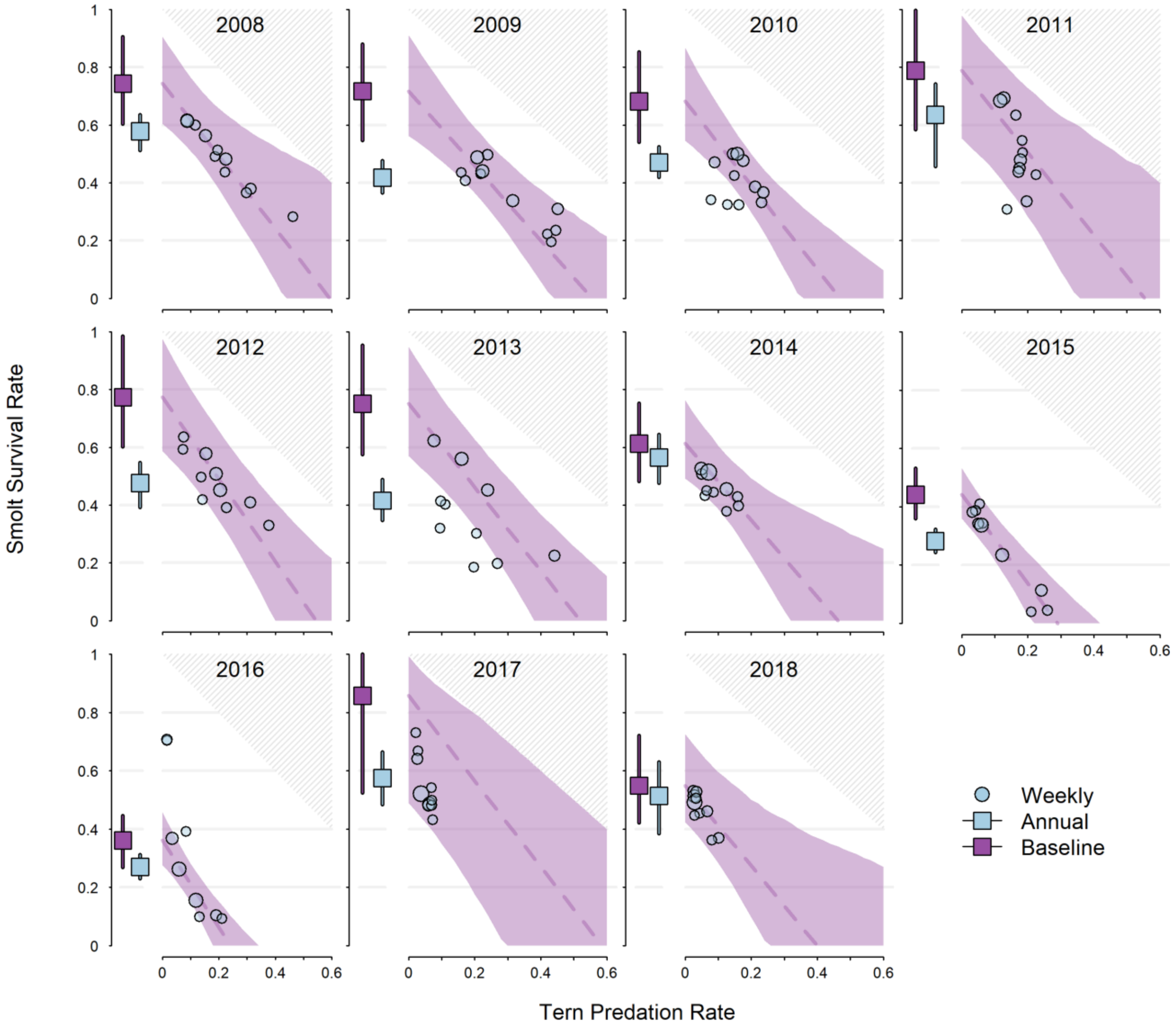

Figure 2.3. Estimated annual relationships between UCR steelhead smolt survival rate and Caspian tern predation rate during out-migration from Rock Island Dam to Bonneville Dam. The size of blue circles depicts relative number of steelhead smolts tagged and released each week at Rock Island Dam. Dashed lines represent the best fit estimate of the linear relationship and shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of UCR steelhead smolt survival with tern predation (blue box) and baseline smolt survival in the absence of tern predation (purple box) are also provided (error bars denote 95% CRI).

For smolt survival, estimates of $\mathbf{a}$ ranged from 1.08 (95% CRI = 0.02–1.66) to 1.50 (95% CRI = 0.96–2.88) during UCR steelhead smolt passage from Rock Island Dam to McNary Dam and from 1.25 (95% CRI =0.25–1.91) to 1.50 (95% CRI = 0.94–2.12) during smolt passage in from Rock Island Dam to Bonneville Dam (*Table 2.2*), suggesting that predation by Caspian terns foraging on UCR steelhead smolts upstream of Bonneville Dam was a super-additive source of mortality ($a > 1$). Estimates of $\mathbf{a}$ were not significantly correlated with estimates of $\boldsymbol{\phi}^0$ or with estimates of annual predation probabilities by Caspian terns ($\hat{r}^2$ = 0.03 [95% CRI = -0.55–0.59] and $\hat{r}^2$ = -0.10 [95% CRI = -0.70–0.49], respectively). Estimates of $\boldsymbol{\phi}^\Delta$ (the difference between baseline and observed survival) for UCR steelhead smolts were consistently greater than zero in all years, ranging nominally from 0.06 (95% CRI = 0.01–0.12) to 0.31 (95% CRI = 0.17–0.46;

Table 2.2). Consequently, observed annual survival probabilities were estimated to be 29% (95% CRI= 23–34%) less than baseline survival probabilities on average (*Figures 2.2* and *2.3*).

Table 2.2. Estimates of the magnitude of the association between Caspian tern predation probabilities on UCR steelhead survival ($\boldsymbol{a}$, additivity), and the difference in steelhead survival probabilities from estimated baseline survival probabilities ($\boldsymbol{\Phi}^{\Delta}$). Values are reported as medians with 95% credible intervals. Dashes denote cohorts where complete adult returns were not yet available.

	Estimates of $\boldsymbol{a}$			Estimates of $\boldsymbol{\Phi}^{\Delta}$		
Year	McNary Dam	Bonneville Dam	SAR	McNary Dam	Bonneville Dam	SAR
2008	1.21 (0.67-1.71)	1.26 (0.53-1.86)	0.19 (0.11-0.31)	0.18 (0.10-0.26)	0.19 (0.08-0.29)	0.05 (0.03-0.08)
2009	1.11 (0.29-1.75)	1.29 (0.68-1.82)	0.09 (0.05-0.16)	0.27 (0.13-0.41)	0.31 (0.17-0.46)	0.03 (0.02-0.05)
2010	1.53 (0.94-2.39)	1.45 (0.81-2.27)	0.12 (0.04-0.18)	0.27 (0.15-0.40)	0.24 (0.11-0.40)	0.03 (0.01-0.04)
2011	1.46 (0.71-2.46)	1.41 (0.61-2.29)	0.11 (0.05-0.25)	0.23 (0.12-0.36)	0.22 (0.11-0.39)	0.02 (0.01-0.05)
2012	1.39 (0.82-2.04)	1.43 (0.76-2.12)	0.11 (0.04-0.18)	0.26 (0.16-0.39)	0.28 (0.13-0.42)	0.03 (0.01-0.05)
2013	1.32 (0.75-1.94)	1.44 (0.84-2.13)	0.06 (0.01-0.10)	0.23 (0.14-0.35)	0.26 (0.14-0.4)	0.01 (0-0.02)
2014	1.32 (0.51-2.15)	1.34 (0.50-2.08)	0.12 (0.07-0.19)	0.11 (0.04-0.21)	0.13 (0.04-0.23)	0.02 (0.01-0.03)
2015	1.36 (0.41-2.55)	1.51 (0.98-2.15)	0.13 (0.05-0.36)	0.05 (0-0.10)	0.17 (0.10-0.23)	0.01 (0-0.03)
2016	1.54 (0.92-2.39)	1.48 (0.88-2.21)	-	0.07 (0-0.15)	0.11 (0.03-0.19)	-
2017	1.44 (0.52-2.76)	1.40 (0.62-2.35)	-	0.03 (0-0.08)	0.14 (0.04-0.29)	-
2018	1.38 (0.36-2.52)	1.38 (0.52-2.32)	-	0.03 (-0.01-0.07)	0.06 (0.01-0.13)	-
Average	1.39 (0.99-1.81)	1.40 (0.99-1.83)	0.09 (0.06-0.12)	0.16 (0.12-0.20)	0.19 (0.14-0.25)	0.02 (0.01-0.03)

Estimates of $\mathbf{a}$ for the analysis of SAR probabilities were also significantly greater than zero in all years with complete adult returns (2008–2015; *Figure 2.4* and *Table 2.2*). Results provide strong evidence that higher Caspian tern predation probabilities on UCR steelhead smolts were associated with lower SAR rates in all years. The weighted average of annual estimates of $\mathbf{a}$ was 0.09 (95% CRI = 0.06–0.12), with a negative linear relationship between Caspian tern predation rates and SARs, even in years of markedly low adult returns (*Figure 2.4*). Nominal estimates of $\boldsymbol{\phi}^{\Delta}$ ranged from 0.01 (95% CRI = 0–0.02) to 0.05 (95% CRI = 0.03–0.08; *Figure 2.4* and *Table 2.2*. Years of lower estimated UCR steelhead SARs, or lower estimated Caspian tern predation rates, were associated with relatively smaller estimates of $\boldsymbol{\phi}^{\Delta}$. For example, UCR steelhead smolts released in 2015, a year in which mortality from sources other than tern predation was among the highest estimated, had estimated weekly SARs that were considerably lower than average. The estimate of ϕ^{Δ}_{2015}, however, was still measurable and almost certainly larger than zero ($\widehat{\phi}^{\Delta}_{2015}$ = 0.01 [95% CRI = 0.00–0.03]; $\hat{p}\left[\phi^{\Delta}_{2015} \leq 0\right] < 0.001$). After accounting for predation from all seven Caspian tern colonies, including the large Caspian tern colony at East Sand Island in the Columbia River estuary, the observed steelhead SARs were, on average, 71% (95% CRI = 65–77%) less than the respective estimated baseline probabilities (*Figure 2.4*). Collectively, these results provide strong evidence that weekly cohorts of tagged UCR steelhead smolts returned to the Columbia River as adults in smaller proportions after experiencing higher rates of Caspian tern predation as smolts (*Table 2.2* and *Figure 2.4*). As with smolt outmigration, estimates of $\mathbf{a}$ and $\boldsymbol{\phi}^{0}$ were not significantly correlated among years or with estimates of annual predation probabilities by Caspian terns ($\hat{r}^2$ = 0.08 [95% CRI = -0.67–0.81] and $\hat{r}^2$ = 0.06 [95% CRI = -0.73–0.75], respectively).

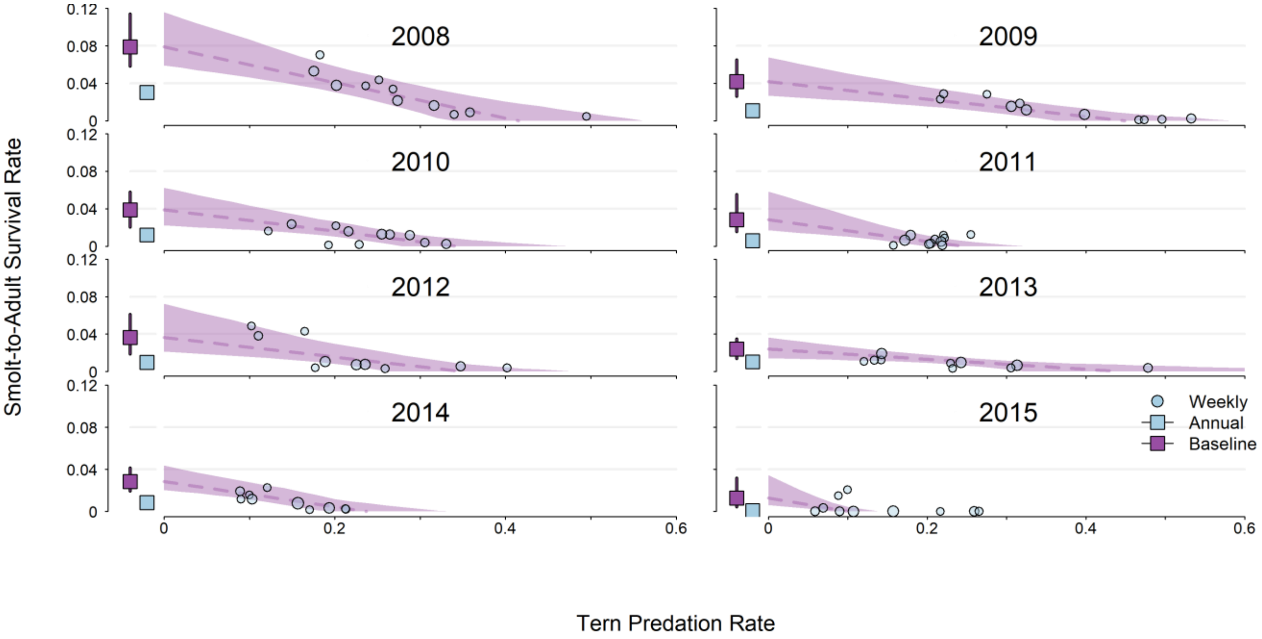

Figure 2.4. Estimated annual relationships between smolt-to-adult survival rates of UCR steelhead from Rock Island Dam (as smolts) to Bonneville Dam (as adults) and cumulative Caspian tern predation rates during smolt out-migration from Rock Island Dam to the Pacific Ocean. The size of the blue circles depicts the relative number of UCR steelhead tagged and released each week at Rock Island Dam. Dashed lines represent the estimate of the best linear fit to the data and shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of steelhead survival with tern predation (blue box) and baseline survival in the absence of tern predation (purple box) are also provided (error bars denote 95% CRI).

Caspian Tern Management Actions – Passive and active dissuasion to discourage Caspian terns from nesting at specific, historical colony sites were successful, with tern colony sizes (i.e. number of breeding pairs) greatly reduced or eliminated following implementation of management actions at each colony site. The Caspian tern colony on Goose Island was incrementally reduced from an average of 404 breeding pairs (range = 293–422 pairs; 2009-2013) prior to management to 0 (zero) breeding pairs during the later stages of management (2016-2018; *Figure 2.5*). In 2016, however, an incipient tern colony of 159 breeding pairs formed on an unnamed island in northeastern Potholes Reservoir, but adaptive management actions were successful at preventing reformation of that colony in 2017 and 2018 (see also Collis et al. 2019). At Crescent Island, management actions eliminated the colony (i.e. no nesting by terns) in the first year of management and in each subsequent year; colony size was reduced from an average of 403 breeding pairs (range = 349–474 pairs) pre-management (2008-2014) to 0 (zero) pairs during the management period (2015-2018; *Figure 2.5*).

The greatest numerical reduction in Caspian tern colony size was associated with management actions implemented at the East Sand Island tern colony in the Columbia River estuary, where the colony was reduced from an average of 9,601 breeding pairs (range = 8,283–10,668 pairs) prior to management (2008-2010) to 5,957 breeding pairs (range = 3,500–7,387 pairs) after management (2011-2018; *Figure 2.5*). However, perhaps because of management to reduce the size of the East Sand Island colony, several hundred to several thousand Caspian terns attempted to nest in the upper Columbia River estuary on

Rice Island (Rkm 34) in Reach 3 during the management period (Roby et al. 2019). As part of the Caspian Tern Management Plan for the Columbia River Estuary (USFWS 2006), adaptive management was successfully implemented to prevent a Caspian tern colony from forming on Rice Island during the late management period (P. Schmidt, USACE, pers. comm.; Harper and Collis 2018). Regardless, Caspian terns that attempted to nest on Rice Island consumed juvenile salmonids, including UCR steelhead smolts, and the level of smolt mortality caused by Caspian terns that roosted and attempted to nest at that site were unknown. Given the large number of Caspian terns observed attempting to nest on Rice Island during the management period (Harper and Collis 2018), predation rates on steelhead smolts may have been substantial in some years.

Analogous to the use of Rice Island by Caspian terns in the estuary, an unintended consequence of tern management actions at Goose and Crescent islands was the relocation of a large number of Caspian terns from these two managed colonies to both extant and incipient colonies within the Columbia Plateau region. For example, following the implementation of management actions at the Goose Island Caspian tern colony site in 2014, two new colonies formed: (1) the aforementioned colony site in northeastern Potholes Reservoir in 2016 and (2) a colony on an unnamed island in Lenore Lake during 2015-2018 (Schniedermeyer 2018; *Figure 2.5*). Also, following management at Crescent Island tern colony in 2015, the extant tern colony site in the central Blalock Islands in John Day Reservoir (within Reach 2) increased 8-fold, from an average of 59 breeding pairs (range = 0–66 breeding pairs) prior to management (2008-2014) to an average of 481 breeding pairs (range = 313–677 pairs) following management (2015-2018; *Figure 2.5*). The dispersal and relocation of nesting Caspian terns from managed colony sites on Goose and Crescent islands to the above-mentioned unmanaged colony sites was confirmed by re-sightings of Caspian terns marked with field-readable leg bands (Roby et al. 2017; Schniedermeyer 2018) and by tracking of Caspian terns that were satellite-tagged at the two colonies prior to management (Roby et al. 2017). For example, of the 510 Caspian terns banded with field-readable leg bands that were resighted on central Blalock Island in 2016, 58% were previously banded on Crescent Island prior to the initiation of management in 2015 and 36% were previously banded on Goose Island prior to the initiation of management in 2014 (Roby et al. 2017). Two other previously extant, unmanaged Caspian tern colonies were also active in Reach 1 during the study period, one on Twinning Island in Banks Lake and the other on Badger Island in McNary Reservoir (*Figure 1.1*). These two colonies remained relatively small (range = 0–66 breeding pairs), however, with little or no change in colony size observed from the pre-management to the post-management period (*Figure 2.5*).

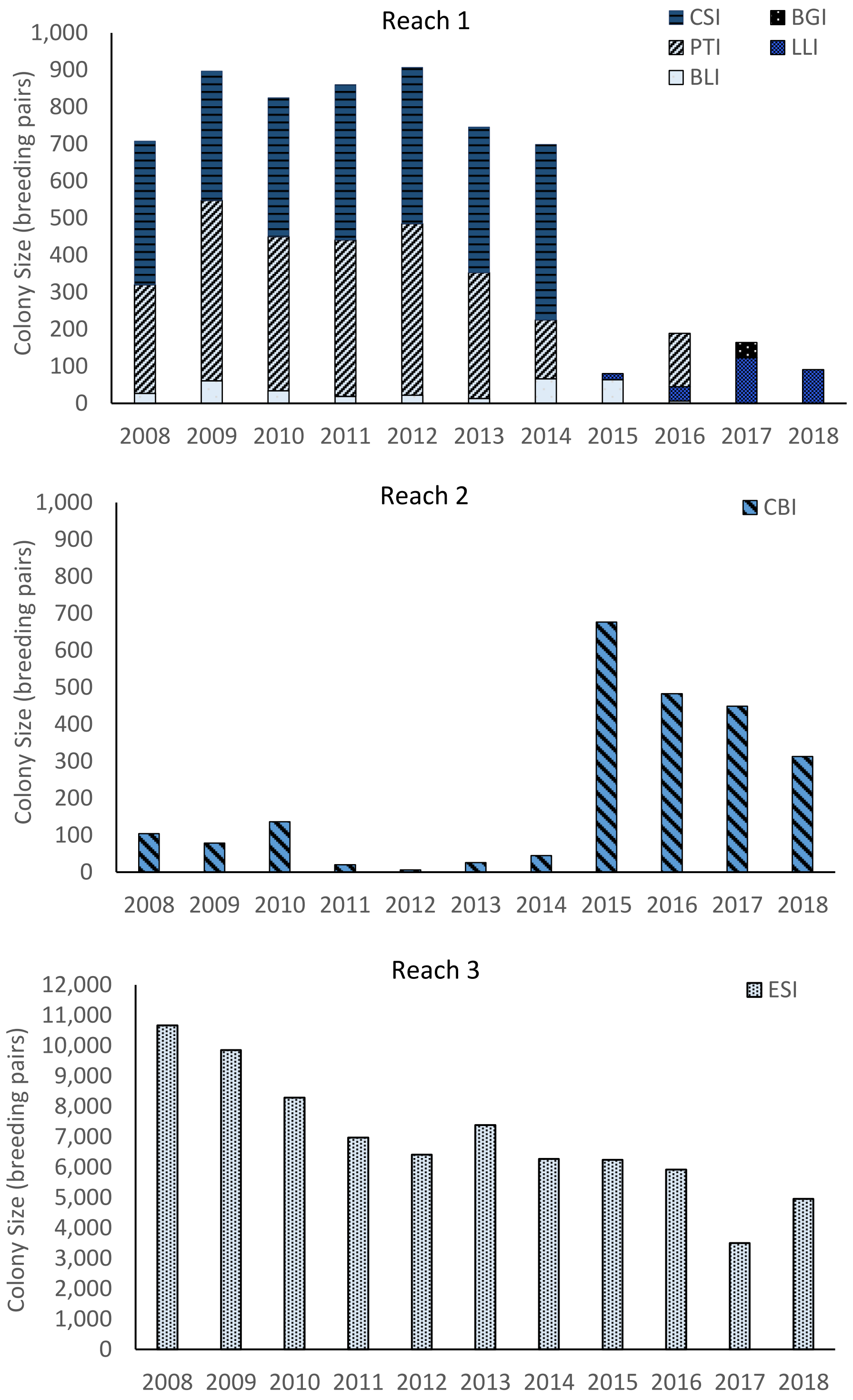

Figure 2.5. Caspian tern colony size (number of breeding pairs) at colonies within foraging distance of UCR steelhead smolts migrating through Reach 1 (Rock Island Dam to McNary Dam), Reach 2 (McNary Dam to Bonneville Dam), and Reach 3 (Bonneville Dam to the Pacific Ocean) of the Columbia River. Management actions that reduced tern colony sizes were initiated in Reach 1 at Potholes Reservoir islands (PTI) in 2014, in Reach 1 at Crescent Island (CSI) in 2015, and in Reach 3 at East Sand Island (ESI) starting in 2011. See Figure 1.1 for a map of colony locations and names.

Caspian tern predation rates on UCR steelhead smolts declined significantly following implementation of management actions at all three managed tern colonies (see *Appendix A, Table A3* for estimates of annual predation rates all seven Caspian tern colonies included in the study). On average, annual predation rate estimates by Caspian terns nesting on islands in Potholes Reservoir (Goose Island and an unnamed island in northeastern Potholes Reservoir) declined from 0.16 (95% CRI = 0.14–0.20) prior to management to 0.04 (95% CRI = 0.03–0.06) following management. Predation rates by Caspian terns nesting on Crescent Island were eliminated (i.e. were zero) following management actions, as Crescent Island was not used by nesting or roosting terns during the management period (2015-2018). Nevertheless, a significant increase in predation rates on UCR steelhead smolts by Caspian terns nesting at the unmanaged colony site in the central Blalock Islands in Reach 2 were observed during the post-management period of 2015-2018, a period that coincided with elimination of the Crescent Island tern colony as part of management actions in Reach 1. Predation rate estimates on UCR steelhead smolts by Caspian terns nesting on the central Blalock Islands increased from an average of just 0.01 (95% CRI = 0–0.01) prior to management to 0.07 (95% CRI = 0.06-0.09) following management. Relatively low predation rates on steelhead smolts (less than 0.02) were documented for Caspian terns nesting at the new colony site on Lenore Lake and at the extant colony on the Banks Lake islands during the post-management period (see *Appendix A, Table A3*). Predation rates on steelhead smolts by Caspian terns nesting on East Sand Island were significantly lower following the management period (2011-2018) compared to the pre-management period (2008-2010); the average estimated annual predation rate declined from 0.19 (95% CRI = 0.16-0.23) prior to management to 0.10 (95% CRI = 0.09-0.12) after management. Predation rates on UCR steelhead smolts by Caspian terns that attempted but failed to nest on Rice Island in Reach 3, however, were unknown and off-set total reductions in steelhead predation rates by terns in Reach 3 to an unknown degree.

Comparisons of weekly and annual Caspian tern predation rate estimates provide strong evidence that predation rates on UCR steelhead smolts significantly decreased in Reach 1 following management that reduced the size of the Caspian tern colonies in Potholes Reservoir and at Crescent Island (*Figure 2.6*). Correspondingly, estimated weekly and annual survival rates of UCR steelhead smolts passing through Reach 1 were, on average, significantly higher following reductions in predation rates by Caspian terns in Reach 1 (*Figure 2.6*). The reverse trends for estimated predation rates and survival rates were observed in Reach 2, however, where Caspian tern predation rates on steelhead smolts increased significantly and steelhead survival rates decreased significantly; these changes were attributable to the elimination of the Caspian tern colony on Crescent Island and the subsequent dispersal of terns from Crescent Island in Reach 1 to the central Blalock Islands in Reach 2 (*Figure 2.5* and *Figure 2.6*). Comparisons of weekly and annual Caspian tern predation rates on steelhead smolts and smolt survival rates in Reach 3 are not available due to the lack of smolt survival estimates from Bonneville Dam to the Pacific Ocean.

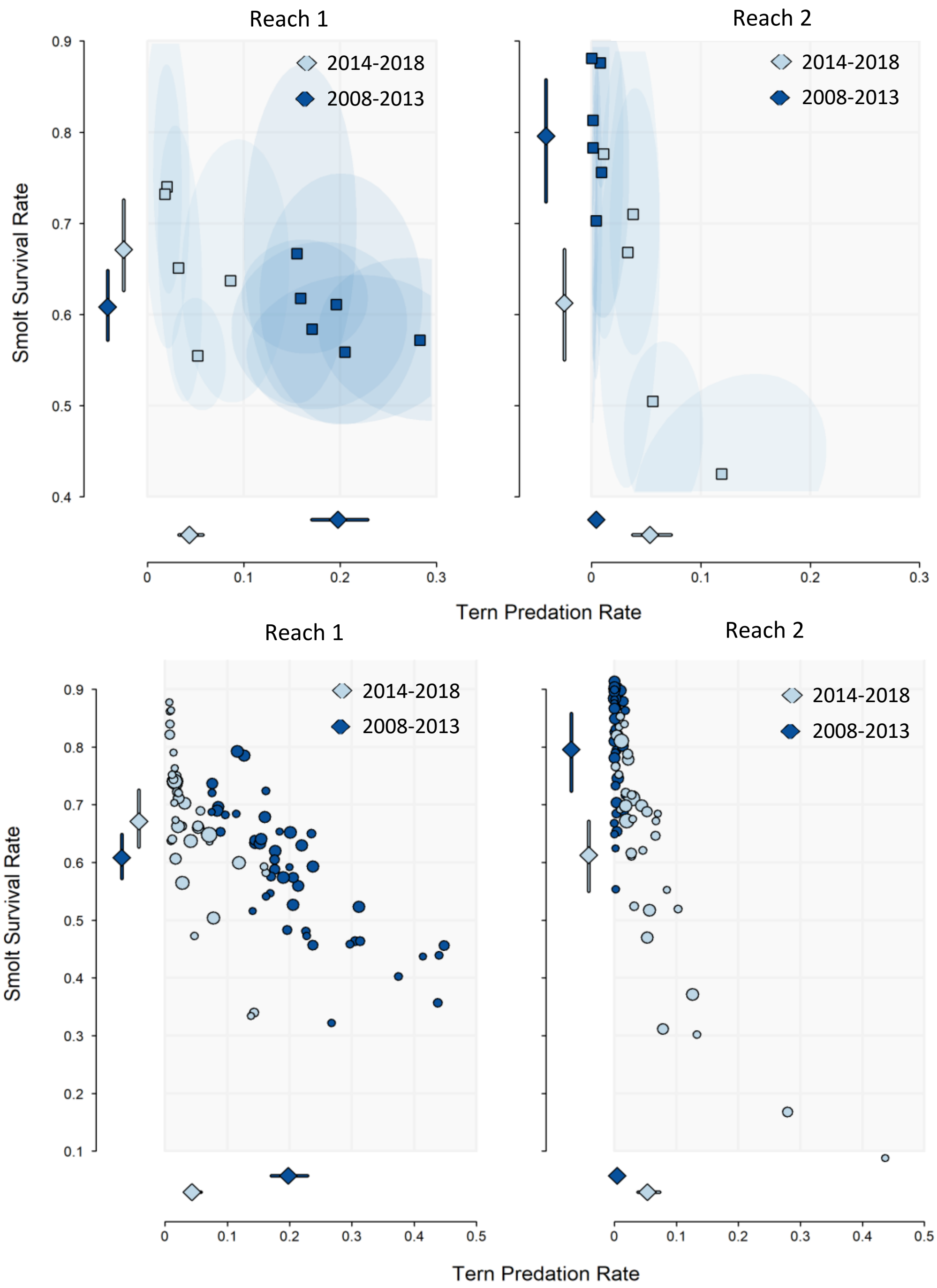

Figure 2.6. Steelhead survival rates and Caspian tern predation rates during UCR steelhead smolt passage in the Columbia River from Rock Island Dam to McNary Dam (Reach 1, left) and McNary Dam to Bonneville Dam (Reach 2, right) prior to (light-blue) and following (dark-blue) management actions that reduced the size of tern colonies in Reach 1. Median annual rates (boxes, top row of graphs), weekly rates (circles, bottom row of graphs), and rates for the entire study period (diamonds) are shown. Error bars represent 95% credible intervals for annual averages, and shaded ellipses represent 95% credible regions for the joint estimation of survival and predation in each river reach and year.

Discussion

Caspian Tern Predation Rates

– Several studies have documented high rates of predation on juvenile salmonids by Caspian terns nesting at particular breeding colonies in the Columbia River basin (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012; Hostetter et al. 2015). Because UCR steelhead smolts must migrate past multiple Caspian tern breeding colonies during their long-distance migration to the Pacific Ocean, we estimated the cumulative magnitude of tern predation to better understand system-wide impacts of bird predation on fish survival. Results indicate that the cumulative impact of multiple Caspian tern colonies was one of the greatest and, in some river reaches and years, the single greatest direct source of UCR steelhead smolt mortality during outmigration; more smolts succumbed to tern predation than directly died from all other sources of mortality combined in some years. Predation by Caspian terns occurred throughout much of the smolt outmigration corridor, with high levels of tern predation (upwards of 0.20 of available fish) observed in multiple river reaches.

Understanding the effects of predators on prey populations requires quantifying survival probabilities, predation probabilities, and the relationship between these two processes. The relevance of these relationships may be scale-dependent, with different mechanisms of compensation acting with varying significance, contingent on scope. Large-scale, density-dependent additive mortality can be quantified based on changes in population growth rates (which incorporate survival, movement, and reproduction), whereas in population ecology, inference is drawn more typically from shorter time scales, such as evaluating what proportion of losses were part of the "doomed surplus" versus losses that could have been avoided (Errington and Hamerstrom 1935). Thus, the scale at which the relationship between predation and survival is evaluated can have important implications for inferences with respect to the impact of predation on prey populations and prospective conservation intervention on behalf of the prey. Furthermore, linking mortality in one life-stage to cumulative survival across multiple life-stages is especially important for populations of anadromous salmonids, where mortality rates are high, the specific cause(s) and locations of mortality are often unknown, and the rate at which smolts survive to adulthood is a principle factor influencing population growth and persistence (Kareiva et al. 2000).

The estimated additive effects of Caspian tern predation on UCR steelhead were statistically significant within and across two different salmonid life-stages, despite tern predation occurring only during the smolt life-stage. Independent of baseline survival conditions and the magnitude of Caspian tern predation each year, a persistent pattern was evident: for each additional 10 UCR steelhead smolts consumed by Caspian terns, approximately 14 fewer smolts from that cohort survived outmigration to Bonneville Dam. This result has important implications for management actions focused on increasing UCR steelhead survival through the Columbia River (see *Management Implication* below for additional discussion). Further, Caspian tern predation on UCR steelhead during the smolt life stage was estimated to be a partially additive source of mortality at the scale of smolt-to-adult returns, with estimated observed survival probabilities significantly lower than estimates of baseline survival (survival in the absence of tern predation) in all study years. Again, regardless of baseline survival conditions and the level of Caspian tern predation, a pattern was consistently observed whereby, on average, for every 10 UCR steelhead smolts consumed by terns, one less individual from that cohort returned to the Columbia River as an adult. Over a scale as large as smolt-to-adult return, representing the vast majority of an anadromous salmonid's potential lifespan, any source of mortality will be mostly compensatory. Considering the low rate in which juvenile salmonids survive to adulthood (Quinn 2005), even small additive impacts to recruitment may be of large consequence to the viability of endangered salmonid species (NOAA 2014).

Mechanisms of super-additivity over large scales are generally driven by density-dependent processes relating to population regulation (Kokko and Johnstone 2001; Liermann and Hilborn 2001). In contrast, there are fewer predation-related super-additive mechanisms within a single lifespan (i.e. prior to reproduction), whereby predation also reduces the average probability of survival for those not consumed by the predator in question (Sandercock et al. 2011). Caspian terns plunge-dive to capture prey and often, perhaps a majority of the time, fail in their attempts (Smith and Mudd 1978; Cuthbert and Wires 1999). This unsuccessful foraging can result in some proportion of fish lethally- or sub-lethally injured (*Figure 2.7*), despite the fish not being consumed by the predator (i.e. latent mortality). This latent mortality is analogous to 'crippling losses' seen in harvest management (game injured or killed but not retrieved; Williams et al. 2002; Servanty et al. 2010). Latent smolt mortality associated with Caspian tern foraging activity was likely correlated with fluctuations in Caspian tern predation rates in the present study, but remains unobserved, unmeasured, and unaccounted for (Reimchen 1988). With harvest management, crippling loss may be minimized through hunter training or estimated via reward tags (Norton and Thomas 1994; Williams et al. 2002); however, data sufficient for estimation of crippling loss from predation due to Caspian terns were not available as part of this study.

Figure 2.7. Steelhead smolt injured by the bill of an avian predator.

An additional mechanism of super-additivity in the present study was prey theft, fish that were captured but not consumed by Caspian terns (i.e. kleptoparasitism). For example, an unknown, but possibly substantial, proportion of smolts captured by Caspian terns and brought back to the breeding colony to feed mates or young was kleptoparasitized by communally-nesting gulls *Larus* spp. (Garcia et al. 2010; Patterson 2012; Adkins et al. 2014). These smolt losses, however, were not incorporated into tern predation rates, but rather enumerated as consumed by gulls. The theft of killed prey is common in predator-prey systems and, as another mechanism of super-additivity, can increase predation probabilities and potentially increase the impact of predation on prey populations (Krofel et al. 2012; Tallian et al. 2017). In addition to super-additive mechanisms, it is also possible that predation from non-breeding terns – birds that foraged on steelhead smolts but that did not visit breeding colonies and deposit tags (Roby et al. 2017) – also occurred during the study and that predation by these non-breeding terns were correlated with estimates of predation by breeding Caspian terns. If true, predation probabilities by breeding Caspian terns presented herein could under estimate the total impacts of all Caspian terns (breeding and non-breeding) on steelhead smolts.

Identifying a negative relationship between survival and predation does not by itself indicate that predation is an additive source of mortality that affects prey populations (Sandercock et al. 2011; Serrouya et al. 2015). Negative relationships may also be consistent with some other ecological process driving both declines in survival and increases in predation. In other words, observational studies, without appropriate experimental controls and prescribed manipulation of treatment parameters, do not allow for definitive statements about causation. The introduction of management actions to reduce predation by reducing the number of Caspian terns nesting in the Columbia River basin (see details below), however, did result in a greater experimentally-driven range of estimates of tern predation probabilities. This wider range of observed probabilities facilitated the development of broader inferences and may mitigate some concerns of extrapolation inherent to the interpretation of baseline survival probabilities. Furthermore, the similarity in the annual relationships across 11 years of outmigration data and eight years of smolt-to-adult returns, suggests that Caspian tern predation on juvenile steelhead has had appreciable, consistent impacts on smolt survival probabilities during outmigration and smolt-to-adult return probabilities.

Management Implications – From a management perspective, results from this study support efforts to reduce Caspian tern predation rates on UCR steelhead smolts in the Columbia River basin. The most pertinent inference to be made from additive/compensatory mortality modelling was that reductions of Caspian tern predation rates by a factor of x were associated with an increase in smolt or smolt-to-adult survival rates by $x * \mathbf{\Phi}^{\Delta}$. The expected increases in survival rates in the absence of Caspian tern predation provide the means to evaluate the potential efficacy or benefits of reducing tern predation rates to increase fish survival within specific river reaches and salmonid life-stages. In the present study, we modeled baseline survival of steelhead smolts in the absence of all predation by nesting terns foraging within a specific river reach. It may not be possible, however, to completely eliminate tern predation within a given river reach, but modelling results presented herein can also be used to make inferences about varying levels of tern predation associated with specific Caspian tern breeding colonies or predation within and across specific river reaches, a potentially powerful tool for resource managers.

Management of Caspian terns in the Columbia Plateau region was successful at eliminating nesting by terns at Goose Island in Potholes Reservoir and at Crescent Island in McNary Reservoir, formerly the two largest nesting sites for the species in the region (Adkins et al. 2014). Results from this study provide evidence that, on average, predation rates on UCR steelhead smolts by terns nesting at Goose and Crescent islands were lower and that smolt survival rates were higher following implementation of management actions at these two tern colonies starting in 2014 and 2015, respectively. Reductions in tern predation rates following management were likely responsible for managers achieving survival goals for steelhead smolts during passage through the Priest Rapids and Wanapum projects (dams and reservoirs) in 2014, the first time this was achieved since steelhead survival assessments were first initiated in 2008 (Skalski et al. 2015; Evans et al. 2016). It should be noted, however, that decreases in tern predation rates on steelhead smolts between Rock Island Dam and McNary Dam during 2014–2017 were not commensurate with increases in steelhead smolt survival rates. This was largely due to an increase in gull predation on steelhead smolts during 2015–2016 (see *Chapter 1*), increases in predation by Caspian terns nesting at the central Blalock Islands following management, and, potentially, increases in unaccounted for smolt mortality due to predation by non-breeding terns displaced by management actions at Goose and Crescent islands. It should also be noted that although predation from colonial waterbirds, particularly predation by Caspian terns, was the dominant mortality factor for UCR steelhead smolts, it was not the only source of smolt mortality. For example, in the absence of all measurable avian predation between Rock Island Dam and McNary Dam, direct mortality from other sources was still substantial and thus a threat to the survival of steelhead smolts. It should also be noted that previous research indicates that juvenile steelhead are especially susceptible to predation by Caspian terns, with estimated tern predation rates on steelhead smolts 2-5 times greater than that on salmon (Chinook [*O. tshawytscha*], sockeye [*O. nerka*], and coho [*O. kisutch*]) smolts (Collis et al. 2001; Antolos et al. 2005; Evans et al. 2012; Evans et al. 2016). As such, the benefits of managing Caspian terns to increase salmon smolt survival in the Columbia River basin are likely much lower than that of steelhead smolts.

Caspian tern predation in the Columbia River estuary is of particular concern to fisheries managers (USFWS 2006) because these smolts had survived outmigration through the hydrosystem and have a higher probability of returning as adults (i.e. higher reproductive value) compared to smolts that had not yet migrated through the hydrosystem. As such, although predation rates on UCR steelhead smolts by Caspian terns foraging upstream and downstream of Bonneville Dam were similar in a number of study years, predation losses in the estuary were more likely to affect the population on per capita (i.e. per fish) basis. The size of the Caspian tern colony (i.e. number of breeding pairs) on East Sand Island in the Columbia River estuary was reduced as a result of management actions. Predation rates on UCR steelhead smolts by terns nesting on East Sand Island were also significantly lower, on average, as a consequence of management. Smolt survival between Bonneville Dam and the Pacific Ocean, however, could not be estimated due to a lack of PIT tag detection sites at the mouth of the Columbia River downstream of East Sand Island. Despite this uncertainty, the consistent and significant relationship between predation rates from all seven Caspian tern colonies, including East Sand Island, and SAR rates demonstrates the important role of tern predation in limiting UCR steelhead survival both upstream and downstream of Bonneville Dam.

Concluding Remarks – Our results provide new information about the impacts of predation on survival of prey using a Bayesian, multinomial state-space model and mark-recapture-recovery dataset involving multiple predators, spatial scales, years, and animal life-stages. In this model, mortality from predation was additive and, therefore, had a significant impact on prey survival. Predator-prey models should account for, or at least assess, additive effects of predation across life-stages in order to avoid exaggerating the potential benefits from management actions aimed at reducing predator populations as a means to enhance prey populations. As such, it is important to design studies that concurrently estimate survival and predation to evaluate these relationships and inform the efficacy of management strategies aimed at the reduction of predation impacts on prey populations of conservation concern. Finally, Caspian terns have a long history of nesting in the Columbia River basin (Collis et al. 2002; Antolos et al. 2004) and there is strong fidelity to and connectivity among the various breeding colony sites (Roby et al. 2003; Lyons 2010; Suzuki et al. 2018), so it will be difficult, if not impossible, to eliminate tern predation in the basin. Furthermore, not all Caspian tern colonies in the basin are the source of significant smolt mortality; some colonies are too small or located too far from the Columbia River to pose a threat to steelhead smolt survival. As demonstrated by the documented movements of Caspian terns from managed to unmanaged breeding colonies in the present study, a system-wide, adaptive approach to managing Caspian terns nesting in the basin will be needed if the goal of reducing the impact of tern predation on survival of steelhead smolts in the Columbia River basin is to be fully realized.

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APPENDIX C: Supplemental Tables

Table C1. Estimated cumulative predation rates (95% creditable intervals) by Caspian terns and total mortality (1-survival) of tagged UCR steelhead smolts released at Rock Island Dam during 2008–2018. See Appendix A, Table A3 for colony-specific estimates of tern predation rates. Estimates of total UCR steelhead smolt mortality between Bonneville Dam and the Pacific Ocean were not available (NA; see Methods).

	Rock Island Dam to McNary Dam										
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Tern Predation Mortality	0.16 (0.12-0.22)	0.29 (0.2-0.36)	0.17 (0.12-0.24)	0.16 (0.12-0.21)	0.20 (0.14-0.3)	0.20 (0.14-0.28)	0.08 (0.06-0.11)	0.03 (0.02-0.05)	0.05 (0.03-0.08)	0.02 (0.01-0.03)	0.01 (0-0.03)
All Mortality	0.38 (0.32-0.43)	0.42 (0.35-0.49)	0.41 (0.34-0.48)	0.33 (0.17-0.42)	0.44 (0.37-0.5)	0.38 (0.26-0.48)	0.37 (0.25-0.46)	0.36 (0.22-0.46)	0.44 (0.39-0.49)	0.26 (0.17-0.34)	0.27 (0.08-0.37)
	Rock Island Dam to Bonneville Dam										
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Tern Predation Mortality	0.16 (0.12-0.23)	0.29 (0.2-0.37)	0.17 (0.13-0.24)	0.16 (0.12-0.21)	0.20 (0.14-0.3)	0.20 (0.14-0.28)	0.09 (0.06-0.11)	0.11 (0.08-0.16)	0.08 (0.06-0.11)	0.05 (0.04-0.06)	0.04 (0.03-0.06)
All Mortality	0.46 (0.41-0.52)	0.60 (0.55-0.65)	0.56 (0.51-0.61)	0.45 (0.35-0.6)	0.51 (0.43-0.59)	0.53 (0.45-0.61)	0.51 (0.44-0.58)	0.73 (0.69-0.77)	0.72 (0.68-0.76)	0.47 (0.39-0.56)	0.51 (0.4-0.63)
	Rock Island Dam to Pacific Ocean										
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Tern Predation Mortality	0.27 (0.22-0.34)	0.39 (0.30-0.48)	0.27 (0.22-0.35)	0.22 (0.18-0.28)	0.23 (0.17-0.34)	0.22 (0.17-0.29)	0.17 (0.14-0.21)	0.15 (0.11-0.2)	0.11 (0.09-0.14)	0.12 (0.10-0.15)	0.08 (0.06-0.11)
All Mortality	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA