September 3, 2015

Avian Predation on Juvenile Salmonids in the Columbia River: A Spatial and Temporal Analysis of Impacts in Relation to Fish Survival

PREPARED FOR:

Public Utility District No. 2 of Grant County and the Priest Rapids Coordinating Committee

P.O. Box 87830, Ephrata, WA 98823

WITH IN-KIND SUPPORT FROM:

Bonneville Power Administration

905 Northeast 11th Portland, OR 97232

U.S. Army Corps of Engineers - Walla Walla District

201 N 3rd Ave Walla Walla, WA 99362

PREPARED BY:

Allen Evans, Quinn Payton, Aaron Turecek, Brad Cramer, and Ken Collis

Real Time Research, Inc.

231 SW Scalehouse Loop, Suite 101 Bend, OR 97702

Daniel Roby and Peter Loschl

Department of Fisheries and Wildlife, Oregon State University

104 Nash Hall Oregon State University Corvallis, OR 97331

WITH SUPPORT FROM:

John Skalski and Richard Townsend

School of Aquatic and Fishery Science, University of Washington

1325 4th Ave, Suite 1515, Seattle, WA 98101

Leah Sullivan

Blue Leaf Environmental, Inc.

2301 W Dolarway Rd, Suite 3 Ellensburg, WA 98926

Mark Weiland

Pacific Northwest National Laboratory

390 Evergreen Dr., PO Box 241, North Bonneville, WA 98639

Suggested citation:

Evans, A., Q. Payton, A. Turecek, B. Cramer, K. Collis, D. Roby, P. Loschl, L. Sullivan, M. Weiland, J. Skalski and R. Townsend. 2015. Avian predation on juvenile salmonids in the Columbia River: A spatial and temporal analysis of impacts in relation to fish survival. Final Technical Report submitted to Grant County Public Utility District No. 2. Available on-line at www.birdresearchnw.org

SUMMARY

To address concerns over the impact of avian predation on juvenile salmonids in the Columbia River Basin, we evaluated predation probabilities on steelhead, yearling Chinook salmon, and subyearling Chinook salmon by piscivorous birds from 11 different breeding colonies. Salmonid smolts were tagged and released as part of survival studies using the Juvenile Salmonid Acoustic Telemetry System, a network of hydrophones that provided detections of acoustic-tagged fish at various spatial and temporal scales during seaward migration. Fish were released and tracked during passage through a 251 kilometer (km) section of the lower Snake River and lower Columbia River in 2012, a 192 km section of the lower Columbia River in 2014, and a 184 km section of the middle Columbia River during 2014. Detections of tagged smolts at telemetry arrays, coupled with the recovery of tags on nearby bird colonies, were used to quantify where avian predation occurred, when it occurred, and the cumulative impact of predation by colonial waterbirds on the survival of tagged fish. Results were also used to estimate unaccounted for smolt mortality (total smolt mortality – mortality due to colonial waterbirds), which was due in part to factors other than bird predation (e.g., piscine predation, mortality during dam passage, and other non-avian mortality factors).

Impacts of avian predation on survival of tagged smolts varied by fish species/age-class, species of avian predator (i.e., Caspian tern, double-crested cormorant, American white pelican, California gull, ring-billed gull), colony location, river reach, week, and year, demonstrating that predator-prey interactions were dynamic at both spatial and temporal scales. Results indicated that avian predation was a substantial source of smolt mortality, especially for steelhead, with reach-specific predation probabilities or rates of 5.5%, 10.9%, and 27.7% of the available tagged fish released into sections of the middle Columbia River, lower Columbia River, and lower Snake River, respectively. For yearling Chinook salmon, predation by colonial waterbirds was lower than juvenile steelhead, with corresponding reach-specific predation rates of 2.8%, 5.8%, and 9.1% of the available tagged fish. For subyearling Chinook salmon, predation by colonial waterbirds was the lowest among the three species/age-classes evaluated in this study (less than 5.3% of available tagged fish in all three reaches studied).

An investigation of predation hotspots indicated higher probabilities of avian predation on smolts near dams on the lower Columbia River and on smolts in the lower Snake River near its confluence with the Columbia River. In general, California and ring-billed gulls disproportionately consumed smolts near dams, while Caspian terns disproportionately consumed smolts in the reservoirs. No clear predation hotspots were evident for colonies of American white pelicans or double-crested cormorants, with the exception that cormorants disproportionately preyed on tagged smolts in the lower Snake River relative to the lower Columbia River.

A comparison of smolt mortality due to colonial waterbird predation with total smolt mortality (1-survival) indicated that in some cases avian predation was one of the greatest, if not the single greatest, sources of mortality affecting survival of steelhead and yearling Chinook salmon during out-migration. Colonial waterbird predation on subyearling Chinook salmon, however, was generally low and a minor component of total smolt mortality, suggesting that factors other than bird predation (e.g., piscine predation) were responsible for the high mortality of subyearling Chinook salmon during out-migration in 2012 and 2014.

TABLE OF CONTENTS

TABLE OF FIGURES

TABLE OF TABLES

TABLE OF APPENDICES

INTRODUCTION

Tagging studies are commonly used to quantify survival rates in fish species of conservation concern. In particular, substantial resources have been allocated to conduct telemetry studies in the Columbia River Basin to quantify the survival of Endangered Species Act (ESA)-listed juvenile salmonids (*Oncorhynchus* spp.) during out-migration to the Pacific Ocean (Skalski et al. 2002; McMichael et al. 2010). The proximate cause of smolt mortality (predation, dam passage, disease, or other causes) in these studies is generally unknown, as tagged fish are generally not recaptured following release. Accurate assessment of specific mortality factors, however, is vital in order to prioritize recovery actions for ESA-listed species (Yoccoz et al. 2001; Hostetter et al. 2015). Consequently, data on the proximate cause of fish mortality, coupled with information on where and when this mortality occurs, can be paramount for effective fish recovery plans.

Survival standards for ESA-listed juvenile salmonids have been established under various Biological Opinions (BiOp) relating to the operation of hydroelectric dams in the Columbia River Basin. Survival standards vary by region and fish species and are set to help ensure an adequate number and percentage of anadromous fish survive out-migration (NOAA 2008). In sections of the middle Columbia River, survival standards are project-specific (dam and reservoir combined) and require that ≥ 93% of juvenile steelhead (*O. mykiss)* and yearling Chinook salmon (*O. tshawytscha)* survive passage (NMFS 2004). In sections of the lower Columbia River, survival standards are dam-specific (dam only) and require that ≥ 96% of juvenile steelhead and yearling Chinook salmon survive passage of the dam, and that ≥ 93% of subyearling Chinook salmon survive passage (NOAA 2008). To evaluate whether survival standards are being met, researchers tag salmonid smolts with acoustic transmitters via the Juvenile Salmonid Acoustic Telemetry System (JSATS; McMichael et al. 2010). Acoustic telemetry (AT) tags emit sound waves that are readily detectable via hydrophones that are placed in lines perpendicular to the shore (referred to as an "array"). Detection probabilities of AT-tagged fish passing arrays are often near 1.0 (McMichael et al. 2010; Hughes et al. 2013; Skalski et al. 2015), resulting in precise estimates of fish survival at different spatial- and temporal-scales. Because AT-tagged fish are not physically recaptured following release, however, the proximate cause of fish mortality in relation to these spatial- and temporal-scales is generally unknown (Hughes et al. 2013).

Research has indicated that smolt survival standards are not always met. For example, Timko et al. (2011) reported that 86% of AT-tagged juvenile steelhead survived passage through the Wanapum project (Wanapum dam and reservoir) in the middle Columbia River during 2010, falling short of the ≥ 93% survival standard. In 2014, survival standards for subyearling Chinook salmon passing McNary and John Day dams were not met, with 92% passage survival of AT-tagged subyearling Chinook salmon estimated at each dam (Skalski et al. 2014a; Skalski et al. 2014b). Cumulative or total losses of smolts passing multiple dams and reservoirs can also be substantial. For example, Skalski et al. (2015) estimated that greater than 30% of subyearling Chinook salmon died during passage through the McNary and John Day projects in 2014. In an investigation of where smolt losses were the highest, Hughes et al. (2013) reported consistently lower survival of juvenile steelhead and yearling Chinook salmon in a particular segment of the John Day reservoir in 2012, a segment where piscivorous waterbird colonies resided on islands in the river (Hostetter et al. 2015). Hughes et al. (2013) also reported that mortality rates were higher for juvenile steelhead, a species known to be particularly susceptible to bird predation (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012).

Avian predation has been identified as a limiting factor in the recovery of some ESA-listed salmonid populations from the Columbia River Basin (NOAA 2008). Caspian terns (*Hydroprogne caspia)*, double-crested cormorants (*Phalacrocorax auritus)*, American white pelicans (*Pelecanus erythrorhynchos)*, California gulls (*Larus californicus),* and ring-billed gulls (*L. delawarensis)* nesting in colonies on or near the Columbia River are known to consume ESA-listed smolts (Antolos et al. 2005; Evans et al. 2012; Hostetter et al. 2015). Evans et al. (2012) reported predation rates as high as 16% of available smolts by Caspian terns nesting in colonies within commuting distance of the middle Columbia River in 2009. Hostetter et al. (2015) reported predation rates as high as 10% of available smolts by California gulls nesting in a colony on an island in the lower Columbia River near John Day Dam in 2014.

Previous studies of avian predation have relied on recoveries of passive integrated transponder (PIT) tags from smolts on bird colonies to estimate impacts to survival of juvenile salmonids from the Columbia River Basin (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 20012; Sebring et al. 2013; Hostetter et al. 2015). Unlike AT tags, which generally have a short tag life (e.g., 30 days; McMichael 2010), PIT tags have an indefinite life (Prentice 1990), allowing researchers to detect them on bird colonies months or even years after the tagged fish was consumed by a bird and the PIT tag was deposited on its nesting colony. The location of predation events based on PIT tag recoveries on-colony, however, is often unknown because PIT tag antennas do not span the length and breadth of the Columbia River (i.e., detection probabilities are low, generally < 0.40; Smith et al. 2006), and because PIT tag antennas are typically located at hydroelectric dams, resulting in a greater spatial distance between interrogation events with PIT tag data as compared to AT tag data.

As part of JSATS survival studies conducted in the Columbia River Basin during 2012 and 2014, researchers tagged smolts with both AT and PIT tags (i.e., double-tagged fish), providing an opportunity to determine what proportion of total fish mortality (1-survival) can be attributed to predation by colonial waterbirds by recovering PIT tags on bird colonies. More specifically, the objectives of this study were to: (1) calculate avian predation rates on juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon at different spatial and temporal scales, (2) to quantify unaccounted for mortality (total mortality – mortality due to colonial waterbird predation) at these same spatial and temporal scales, and (3) to identify potential hotspots of avian predation on smolts (e.g., predation at dams or particular segments of the river). Collectively, results were used to identify where smolts losses are occurring, when during out-migration they occur, and the proximate cause of smolt mortality (colonial waterbird predation or unaccounted for mortality).

METHODS

Study area

We investigated predation on double-tagged (AT and PIT tags, hereafter "tagged") juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon within three different sections or river reaches: (1) a 251 kilometer (km) section of the lower Snake River and lower Columbia River, (2) a 192 km section of the lower Columbia River, and (3) a 184 km section of the middle Columbia River (Figure 1). Acoustic arrays in the lower Columbia River spanned from below Ice Harbor Dam (river km {Rkm} 525) or upstream of McNary Dam (Rkm 498 or 472, depending on the year) to the forebay of The Dalles Dam (Rkm 311). Acoustic arrays in the middle Columbia River spanned from Wanapum Dam (Rkm 670) to an array located near the confluence of the Snake and Columbia rivers (Rkm 545).

Bird predation on tagged smolts within each study area was investigated by recovering smolt PIT tags on bird breeding colonies previously identified as posing a risk to smolt survival within the study area (Evans et al. 2012; Hostetter et al. 2015). A total of six and 11 different piscivorous waterbird colonies were investigated in 2012 and 2014, respectively, as part of this study. Bird colonies that were part of the study included Caspian tern colonies on (1) Twinning Island (an "off-river" nesting site in Bank Lake), (2) Goose Island (an off-river nesting site in Potholes Reservoir), (3) Crescent Island (Rkm 510), and (4) Anvil Island (Rkm 440); California and ring-billed gull colonies on (5) Island 20 (Rkm 549), (6) Crescent Island, (7) Anvil Island, (8) Straight Six Island (Rkm 439), and (9) Miller Rocks Island (Rkm 331); a double-crested cormorant colony on (10) Foundation Island (Rkm 518); and an American white pelican colony on (11) Badger Island (Rkm 512; see Figure 1).

Fish capture, tagging, and release

Detailed methods regarding the collection, tagging, and release of smolts used in this study are presented in Hughes et al. (2013), Weiland et al. (2015), and Skalski et al. (2015). In brief, for releases on the lower Snake River and lower Columbia River, downstream migrating juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon were collected at John Day Dam (lower Columbia River) or Lower Monumental Dam (lower Snake River) by sampling fish out of the juvenile bypass facilities as described by Martinson et al. (2010). Fish were examined to ensure they met length (95 – 300 mm; fork length) and condition (no signs of disease, ≤ 20% descaling, no open wounds, hemorrhaging, or deformities) criteria suitable for acoustic tagging (see Weiland et al. 2015 for details). Fish were then anesthetized (tricaine methanesulfonate or MS-222), implanted with an acoustic tag (Acoustic Telemetry Systems model SS130/SS300; 11mm x 5mm x 3mm) and a PIT tag (Biomark model HPT12; 12mm x 2mm x 2mm), and held in a recovery tank for 18 to 24 hours. Following recovery, fish were transported by truck and released via boat at a designated release site. In 2012, releases occurred in the lower Snake River at Rkm 562, in the lower Columbia River in McNary Reservoir at Rkm 503, in the tailrace of McNary Dam at Rkm 468, in John Day Reservoir at Rkm 422, and in the tailrace of John Day Dam at Rkm 346 (Figure 1a). In 2014, releases occurred in the lower Columbia River in McNary Reservoir at Rkm 503, in the tailrace of McNary Dam at Rkm 468, in John Day Reservoir at Rkm 449, and in the tailrace of John Day Dam at Rkm 346 (Figure 1b). Tagged juvenile steelhead were released daily from 27 April to 2 June in 2012, and from 27 April to 28 May in 2014. Tagged yearling Chinook salmon were released daily from 27 April to 28 May in 2012, and from 30 April to 29 May in 2014. Tagged subyearling Chinook salmon were released daily from 10 June to 9 July in 2012, and from 11 June to 9 July in 2014.

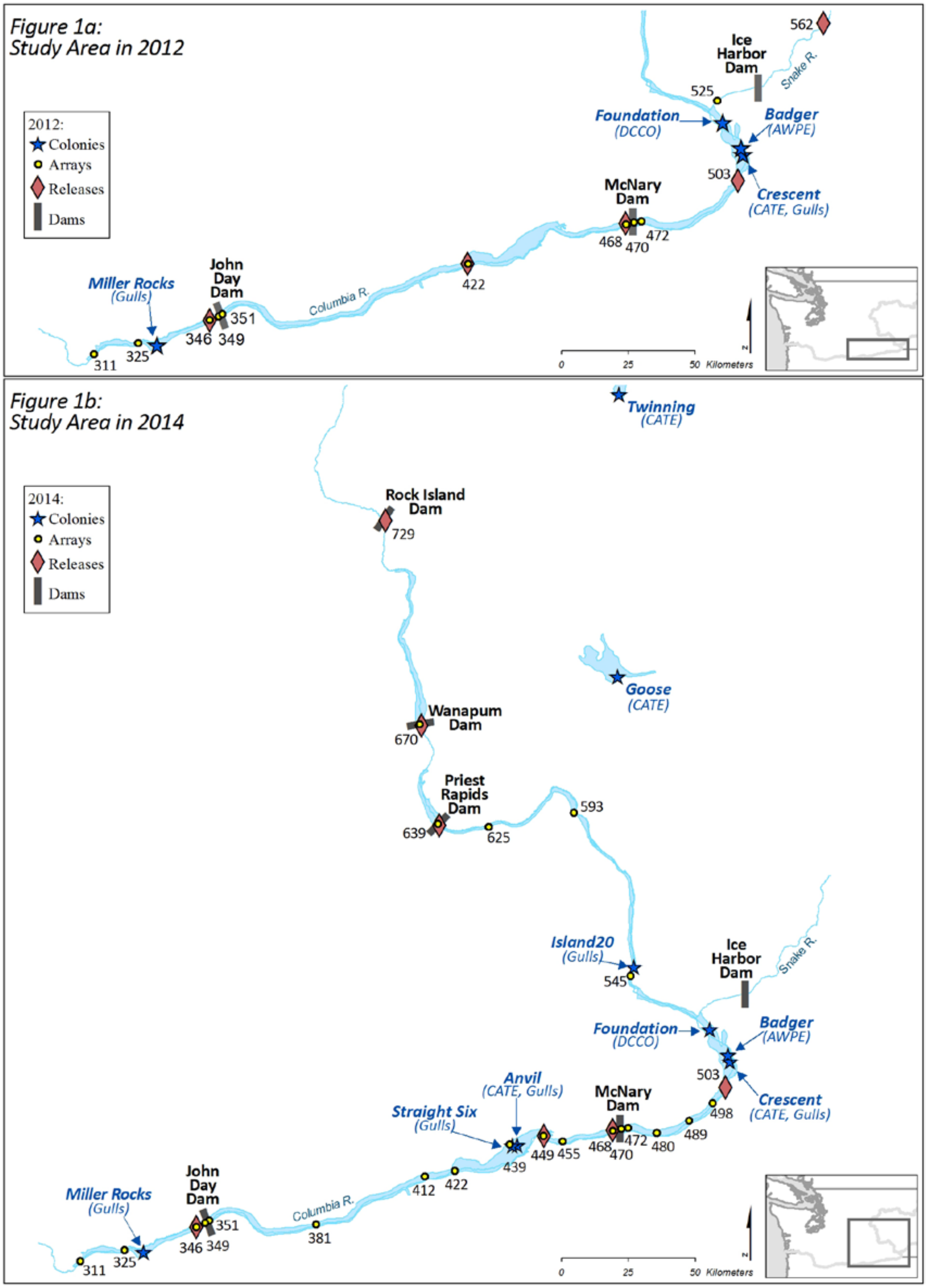

Figure 1. Study area in 2012 (Figure 1a) and 2014 (Figure 1b). Locations of smolt release sites, acoustic arrays, hydroelectric dams, and fish-eating bird colonies are noted. Species of colonial waterbirds evaluated include Caspian terns (CATE), double-crested cormorants (DCCO), California and ring-billed gulls (Gulls), and American white pelicans (AWPE).

For releases on the middle Columbia River, downstream migrating steelhead and yearling Chinook salmon were collected at Wanapum and Priest Rapids dams by dip-netting smolts from the wheel gate slots at each dam. Length and condition criteria for acoustic tagging were the same as those described for smolts captured at dams on the lower Snake River and lower Columbia River, except that the size criteria for tagging was based on weight (15 – 89 g) and not length, which resulted in the inclusion of yearling Chinook salmon and steelhead of about 100 - 230 mm (fork length). Fish were anesthetized (MS-222), implanted with an acoustic tag (Lotek model L-AMT-1.421; 11mm x 5mm x 4mm), and a PIT tag (Biomark model HPT12), and held in a recovery tank for 18 to 24 hrs. Following recovery, fish were transported by truck and subsequently released by helicopter into designated release sites in the tailrace of Rock Island Dam (Rkm 729), Wanapum Dam (Rkm 670), and Priest Rapids Dam (Rkm 639; Figure 1b). Tagged steelhead were released daily during 7 - 28 May 2014, and tagged yearling Chinook salmon from 30 April to 24 May in 2014.

Bird colony sizes

Counts of piscivorous waterbirds at their breeding colonies were derived from aerial and ground surveys conducted during the egg incubation period (April-May), the stage of the nesting cycle when the greatest numbers of breeding adults are generally found on-colony (Gaston and Smith 1984; Adkins et al. 2014). Estimates of the size of Caspian tern and double-crested cormorant breeding colonies were based on the number of active breeding pairs counted from an observation blind located adjacent to each colony. Estimates of the size of American white pelican, California gull, and ring-billed gull breeding colonies were based on the number of adults counted on-colony from aerial photography taken with a high-resolution digital camera from a fixed-wing aircraft. Aerial and ground surveys were also used to gather basic information on nesting chronology (timing of nesting building, egg laying, chick rearing, and check fledging) at each colony and year, where possible.

Recovery of tags on bird colonies

The recovery or detection of smolt tags on waterbird colonies followed the methods of Evans et al. (2012). In brief, scanning for PIT tags was conducted after birds dispersed from their breeding colonies following the nesting season (August - November). The entire land area of each bird colony (i.e., land area occupied by nesting birds based on aerial and ground surveys conducted during the breeding season) was scanned using pole-mounted PIT tag antennas and transceivers (Biomark model HPR) by conducting a minimum of two complete passes or sweeps of the colony area.

Not all smolt tags ingested by birds are subsequently deposited on their nesting colonies. Tags can be regurgitated or defecated off-colony at loafing, staging, or roosting areas utilized by breeding birds during the nesting season (Hostetter et al. 2015). Ingested tags can also be damaged during avian digestion, and thereby rendered non-functional even if deposited on the colony (BRNW 2014). Data to correct or adjust for the proportion of consumed tags subsequently deposited by birds on-colony and in working order (i.e., deposition probabilities) were derived from results reported in Hostetter et al. (2015). In brief, salmonids injected with PIT tags of known codes were fed to nesting Caspian terns, double-crested cormorants, and California/ring-billed gulls during discrete daily time periods (morning or evening) and throughout the peak nesting season (April - June) at multiple colonies and years (2004 - 2013). The numbers of these ingested tags subsequently found by researchers on the breeding colony at the end of the nesting season were used to estimate tag deposition probabilities. The appropriate deposition probability reported from Hostetter et al. (2015) was then applied to the number of tagged fish recovered as part of this study on each bird colony (see Predation Probabilities below for modeling details). No deposition probabilities, however, were available for American white pelicans nesting on Badger Island and, consequently, estimates of the impact of white pelican predation on survival of tagged smolts are minimums (i.e., corrected for on-colony detection probabilities only; see below).

Not all smolt PIT tags deposited by birds on their nesting colony are subsequently found by researchers after the nesting season. Tags can be blown off of the nesting area or otherwise damaged or lost during the course of the nesting season (Ryan et al. 2003; Evans et al. 2012). Furthermore, methods used to detect tags on bird colonies are not 100% efficient, with some proportion of detectable PIT tags missed by researchers during the scanning process (i.e., detection probabilities < 1.0). The probability that a tag was detected by researchers given that the tag was deposited on-colony in working order required post-nesting surveys of on-colony tags that were deposited on-colony by researchers during the nesting season. PIT tags identical to those implanted in study fish (Biomark model HPT12) were sown across each bird colony by researchers during 1 – 4 discrete tag-sowing events during the nesting season. Recoveries of these tags during scanning efforts after birds dispersed from the colony were used to model the probability of detecting a tag that was deposited in working order on the bird colony during the nesting season (see Predation Probabilities below for modeling details).

Predation probabilities

Multiple acoustic arrays that detect AT-tagged fish in-river and recoveries of PIT tags from juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon on bird colonies provided data to evaluate survival and avian predation probabilities at various spatial and temporal scales within each river reach and year. Availability of tagged smolts within each spatial scale was based on releases and/or detections of live tagged fish at each array (Figure 1). Because releases of tagged study fish within each reach were conducted in two different years with different array configurations, analyses of avian predation probabilities were performed independently for each river reach and year.

To model survival and colonial waterbird predation probabilities, we employ a Bayesian analytical approach as an extension of the Cormack-Jolly-Seber (CJS) model, a mark-recapture estimation technique (Burnham 1987). For each year, we partitioned n_T tagged fish among *M* releases that potentially traversed a total of *J* sequential arrays. We refer to the number of tagged fish associated with a particular release *r* as n_r. The total number of tagged fish released is then $n_T = \sum_{r=1}^{M} n_r$. The detection history, death (all mortality sources), and tag recovery (mortality from colonial waterbird predation) associated with each tagged fish was modeled using several Bernoulli random variables.

We let S_{ij} be an indicator variable for the continued survival of tagged fish *i* at the jth array. That is, S_{ij} = 1 if tagged fish *i* is alive at array *j* and S_{ij} = 0 otherwise. This implies that ($S_{ij} \mid S_{i(j-1)} = 1$) ~ Bernoulli(ω_{rj}), where ω_{rj} is the probability of survival by a tagged fish from release location *r* through the *j*th segment, given it was alive at the preceding array. The $\overrightarrow{\boldsymbol{S}_i} = [S_{i0}, S_{i1}, \dots, S_{iJ}]$ vectors are not directly observed. We must make inferences about the survival of each tagged fish based on the detections at each interrogation array.

We let X_{ij} be the random variable associated with any interrogation of fish *i* at the *j*th array. We assumed (X_{ij}| S_{ij} = 1) ~ Bernoulli(δ_{rj}), where δ_{rj} is the probability detection at the *j*th interrogation array associated with all fish from the *r*th release. Treating the observed vector $\vec{\boldsymbol{X}}_i$ = [$X_{i0}, X_{i1}, \dots, X_{iJ}$] as recaptures allows us to employ the Cormack-Jolly-Seber model to adequately model probabilities of survival and interrogation array detection.

To account for tagged fish consumed by colonial waterbirds, we let D_{ijc} be the variable indicating whether fish *i* was taken from the *j*th segment by the *c*th bird colony. We let $D_{ijother}$ be an additional variable indicating whether tagged fish *i* was removed from the system within segment *j* by a cause not associated with colonial waterbirds included in the study (i.e., unaccounted for mortality). Letting $\vec{\boldsymbol{D}}_{ij}$ = [D_{ij1}, D_{ij2}, … , $D_{ijother}$], then ($\vec{\boldsymbol{D}}_{ij}$ | S_{ij} = 0) ~ multinomial(1, $\vec{\boldsymbol{\theta}}_{rj} / 1-\omega_{\text{rj}}$), where $\vec{\boldsymbol{\theta}}_{rj}$ = [$\theta_{j1}, \theta_{j2}, \dots$ $\theta_{rjother}$], θ_{jc} is the average predation probability for colony *c* in segment *j*, and $\theta_{rjother}$ is the "other" mortality in the *j*th segment associated with the *r*th release of tagged smolts.

We can then use non-informative priors for the survival and mortality parameters, letting {ω_{rj}, $\vec{\boldsymbol{\theta}}_{rj}$} ~ Dirichlet ($\vec{\mathbf{1}}$) where $\vec{\mathbf{1}}$ is an appropriately vector of ones. This implies that $\theta_{rjother}$ ~ uniform(0,1) ∀ r,j, θ_{jc} ~ uniform(0,1) ∀ *j,c*, and ω_{rj} ~ uniform(0,1) ∀ *r,j*, as previously stated.

The $\vec{\boldsymbol{D}}_{ij}$ vectors are not directly observed. We must infer the cause of mortality for a tagged fish from tag recoveries on breeding colonies. We let $\vec{\boldsymbol{R}}_i$ = {R_{ic} | *c* = 1, 2, … , # foraging colonies} be the vector indicating whether the tag associated with the fish *i* was recovered on any colony *c*. This means the entries of $\vec{\boldsymbol{R}}_i$ are binary with at most one non-zero value. As noted by Hostetter et al. (2015), not all smolt tags ingested by birds are subsequently deposited on their nesting colony. Furthermore, not all tags deposited by birds on their nesting colony are later detected by researchers after the nesting season (Evans et al. 2012). We therefore assume that (R_{ic} | $\sum_{j \in segments} D_{ijc}$ = 1) ~ Bernoulli ($\phi_c \psi_{cw.}$), where $\phi_c$represents the probability that a tag consumed by a bird from colony *c* is deposited on the colony, ψ_{cw} is the probability a tag deposited on colony *c* in week *w* is detected at the end of the nesting season, and *w*.= $\sum_{j \in segments} w_{ij} * D_{ijc}$, where w_{ij} is the week when fish *i* is expected to have passed through segment *j*. We assume w_{ij} to be equal to the week of the last recorded upstream detection.

The probability, ψ_{cw}, that a tag that was eaten in week *w* and deposited on-colony is detected is assumed to be a logistic function of week. That is:

$$\psi_{cw} = \beta_0 + \beta_1 * (w - mid.week_c),$$

where $mid.week_c$ is the median week of the breeding season at colony *c*, and β_0 and $\beta_1$are inferred from PIT tags intentionally sown to measure detection efficiency at each bird colony (see Results).

Imperfect rates of deposition and detection lead to positive estimates of predation for all segments in which birds from a particular colony were assumed to forage. We estimated positive rates of predation even when no direct evidence existed (i.e., when none of the tags whose detection history ended in a given segment were recovered on the colony of interest). Therefore the estimated total predation by colonial waterbirds from all colonies in a segment was directly related to the number of colonies assumed to forage there. It follows then that we must be cautious in our assumptions about which bird colonies provide foragers in each segment. We assumed that birds from each colony foraged along a continuous, uninterrupted range of the river. The limits of this range were set equal to the first and last segments in which at least one tag's detection ended and the tag was subsequently found on the colony (i.e., confirmation of predation by birds from that colony).

Estimates of $\vec{\boldsymbol{S}}_i$ and $\vec{\boldsymbol{D}}_{ij}$ were calculated as the respective medians of the joint posterior distribution. We used non-informative priors for each ω_{rj} and δ_{rj}. That is, we assumed ω_{rj} ~ uniform(0,1) ∀ *r,j* and δ_j ~ uniform(0,1) ∀ *j*. Informative Beta priors were used to infer deposition probabilities ϕ_c for each bird species and colony (see Hostetter et al. 2015). The mean and standard deviation for these prior distributions was assumed to be mean = 0.71 and standard deviation = 0.09 for Caspian tern colonies, mean = 0.51 and standard deviation = 0.09 for double-crested cormorant colonies, and mean = 0.15 and standard deviation = 0.03 for gull colonies (Hostetter et al. 2015). The deposition probability for American white pelicans was assumed to be 1.0, as data on deposition probability for this species were not available.

We calculated colonial waterbird predation probabilities on fish from the *r*[th] release over a given range/set of segments, $\boldsymbol{H}$, based on aggregated estimates of the $\vec{\boldsymbol{D}}_{ij}$ vectors.

$$\widehat{Predation}_{\boldsymbol{H},release\ r,colony\ c} = \sum_{j\,\in\,\boldsymbol{H}} \sum_{i\,\in\ release\ r} \widehat{D}_{ij1} \Big/ \sum_{i\,\in\ release\ r} S_{ih_o}$$

where h_0 is the initial release point in $\boldsymbol{H}$.

We implemented all predation probability models in a Bayesian framework using the software JAGS accessed through R version 3.1.2 (R Core Team 2014) using the R2jags (Su 2012) and dclone (Solymos 2010) R packages. We ran three parallel chains for 50,000 iterations each and a burn-in of 5,000 iterations. Chains were thinned by 20 to reduce autocorrelation of successive Markov chain Monte Carlo samples, resulting in 6,750 saved iterations. Chain convergence was tested using the Gelman-Rubin statistic ($\hat{R}$; Gelman et al. 2004). We report results as posterior medians along with the 2.5 and 97.5 percentiles, which are referred to as 95% Credible Intervals (95% CI).

Total mortality (1-survival) and mortality due to predation by colonial waterbirds were modeled using the approach detailed above at each of the following spatial scales:

1. Reach – Predation on fish consumed between the upper most release site to the last array in that section of river; reaches evaluated spanned from (1) the lower Snake River (Rkm 562) to an array located near the forebay of The Dalles Dam in the Columbia River (Rkm 311; Figure 2) in 2012, (2) the lower Columbia River near the mouth of the Walla Walla River (Rkm 503) to an array located in the forebay of The Dalles Dam (Rkm 311; Figure 3) in 2014, and (3) the middle Columbia River from the tailrace of Rock Island Dam (Rkm 729) to an array located upstream of the confluence of the Snake and Columbia rivers (Rkm 545; Figure 4) in 2014.

2. Project – Avian predation on tagged smolts within each dam and reservoir combined; projects evaluated included the Wanapum project in 2014, the Priest Rapids project in 2014, the McNary project in 2012, and the John Day project in 2012 and 2014.

3. Reservoir – Avian predation on tagged smolts within each reservoir; reservoirs evaluated included McNary reservoir in 2012 and John Day reservoir in 2012 and 2014.

4. Near-Dam – Predation on fish between arrays bracketing a dam (forebay-to-tailrace); dams evaluated included McNary Dam and John Day Dam in 2012 and 2014.

5. Segment – Avian predation on fish between any two adjacent arrays. The number of segments evaluated varied by reach and year.

To investigate temporal trends, the dependence between estimates of total mortality and avian predation were depicted by plotting weekly, reach-specific total mortality rates and weekly avian predation rates for each species/age-class and year. An analysis was then conducted to quantify the amount of variation in weekly estimates of smolt survival (1-mortality) which can be explained by colonial waterbird predation after accounting for river reach and year. A randomization test (Good 2005) was used to test the null hypothesis of no relationship between survival and colonial waterbird predation.

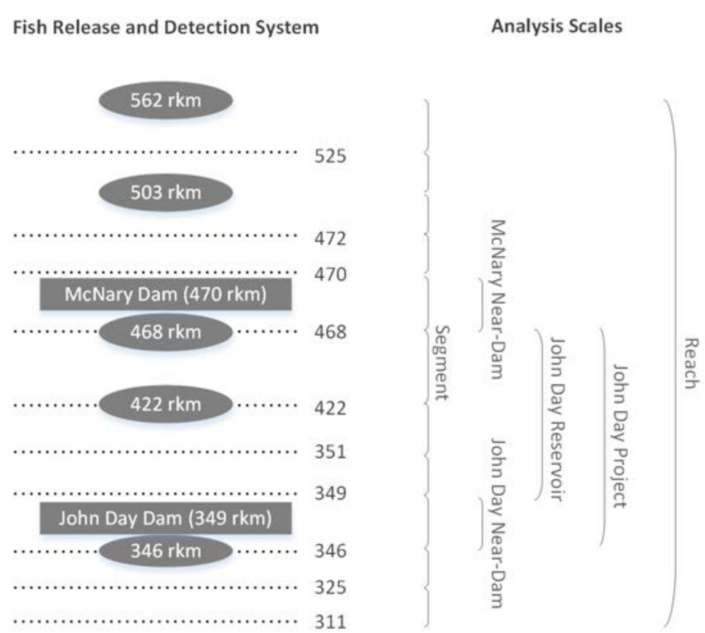

Figure 2. Schematic diagrams showing smolt release and detection arrays, with corresponding study area spatial scales, for tagged smolt releases in the lower Snake River and lower Columbia River in 2012. Grey ovals represent smolt release sites, dashed lines represent acoustic arrays, and grey rectangles represent dams.

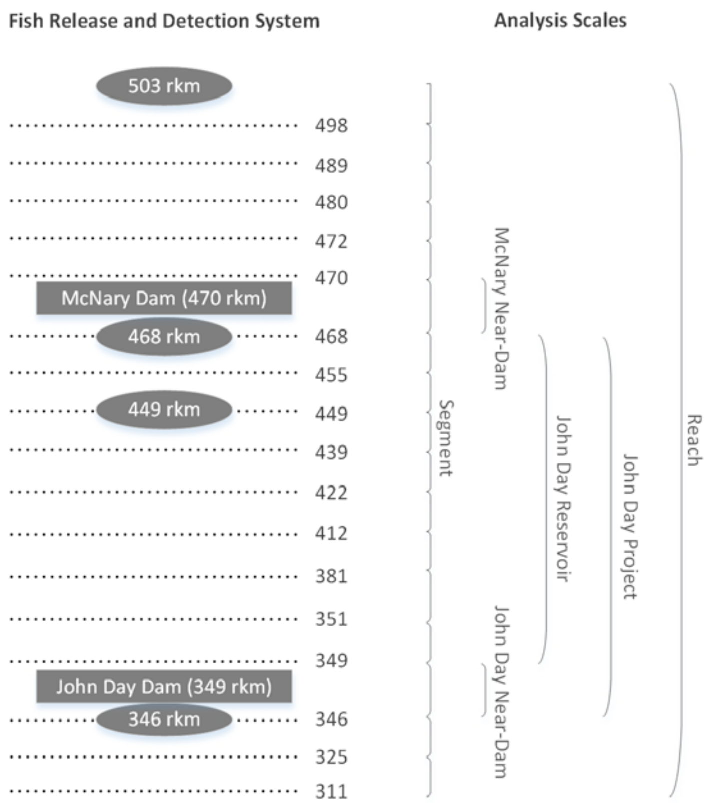

Figure 3. Schematic diagrams showing smolt release and detection arrays, with corresponding study area spatial scales, for tagged smolt releases in the lower Columbia River in 2014. Grey ovals represent smolt release sites, dashed lines represent acoustic arrays, and grey rectangles represent dams.

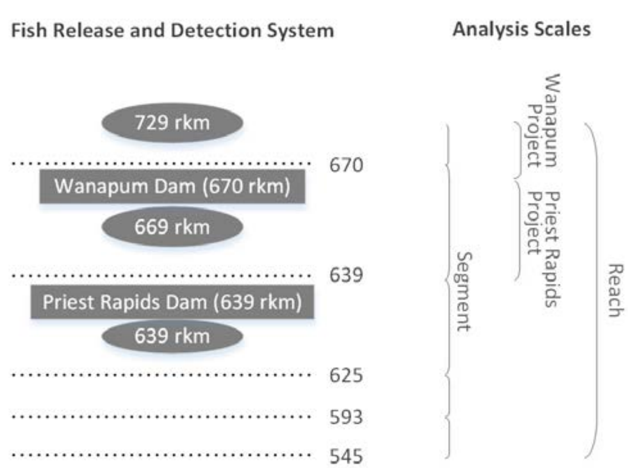

Figure 4. Schematic diagrams showing smolt release and detection arrays, with corresponding study area spatial scales, for tagged smolt releases in the middle Columbia River in 2014. Grey ovals represent smolt release sites, dashed lines represent acoustic arrays, and grey rectangles represent dams.

Colony-specific foraging

Foraging locations for piscivorous waterbirds from specific breeding colonies were investigated based on the percentage of available tagged smolts consumed within each river segment per colony, and by species/age-class of fish (yearling, subyearling). To account for differences in the relative size (length) of each river segment evaluated, colony-specific predation impacts are presented as predation probabilities per river kilometer in that reach. Results represent approximate foraging locations on tagged smolts because the actual foraging path of each bird was not known and the exact location of predation events between any two adjacent acoustic arrays within a segment was not known.

Assumptions

Methods to calculate total smolt mortality and mortality due to colonial waterbird predation were based on the following assumptions:

A1. Tagged smolts were actively out-migrating and tags were functional during the study period.

A2. Smolt survival, smolt predation, tag deposition, and tag detection were independent.

A3. Mortality due to handling and tagging was negligible and is included in the “other” mortality probability designation.

A4. Smolt tags were deposited on bird colonies within the same week that the smolt tag was consumed, and tag detection probabilities followed a logistic trend over time.

A5. Tag deposition probabilities on bird colonies did not vary spatially (by consumption location) or temporally (by consumption week).

To confirm assumption A1, directionality and travel times of smolts were investigated and confirmed that tagged smolts were actively out-migrating during the study period. Tests were conducted on a random sample of tags to confirm tag life and functionality was as specified by the tag’s manufacture (23 - 33 days, depending on the model and manufacture; see Hughes et al. 2013 and Skalski et al. 2015). The fate of each tag implanted in a smolt was assumed to be independent. The interrogation and survival of all tagged smolts were assumed to be mutually independent (A2). Likewise, the deposition and subsequent detection of tags from all depredated smolts were also assumed to be mutually independent (A2). Lack of independence among tagged smolts could potentially bias survival and predation probabilities to an unknown degree and overstate estimates of precision. Mortality after release that was potentially associated with handling and tagging is inestimable, which necessitates assumption A3. A significant number of losses due to handling and tagging would result in an overstatement of availability and consequently bias estimates of predation probabilities down. Assumption A4 only needs to be approximately accurate, as on-colony detection probabilities were generally high (see Results) and did not change dramatically on a weekly basis. Based on results from Hostetter et al. (2015), there was no evidence of inter- or intra-annual changes in deposition probabilities across colonies within a given species of avian predator (A5). If, however, deposition probabilities of tagged smolts used in this study differed significantly from those reported in Hostetter et al. (2015), predation probabilities could be biased to an unknown degree.

RESULTS

Fish capture, tagging, and release

Complete descriptions of smolt capture, tagging, and releases are summarized in Hughes et al. (2013), Weiland et al. (2015), and Skalski et al. (2015). In brief, analyses of bird predation based on fish releases in the lower Snake River and the lower Columbia River in 2012 included tagged smolts from five different release locations (Rkms 346, 422, 468, 503, and 562), totaling 5,799 juvenile steelhead, 5,795 yearling Chinook salmon, and 9,372 subyearling Chinook salmon (Table 1). In the middle Columbia River in 2014, bird predation analyses included tagged smolts from three different release locations (Rkms 639, 669, and 729), totaling 1,720 juvenile steelhead and 1,716 yearling Chinook salmon (Table 1). Bird predation analyses in the lower Columbia River in 2014 included tagged smolts from up to four different locations (Rkms 346, 449, 468, and 503), totaling 6,498 juvenile steelhead, 6,502 yearling Chinook salmon, and 7,490 subyearling Chinook salmon (Table 1).

Table 1. Numbers of tagged juvenile steelhead (Sthd), yearling Chinook salmon (Chin 1), and subyearling Chinook salmon (Chin 0) released and subsequently recovered (in parentheses) on piscivorous waterbird colonies during 2012 and 2014. Tag recoveries only include those smolt tags that were recovered in the same year that the tagged smolt migrated. River kilometer (Rkm) is the distance from the tagged smolt release site to the Pacific Ocean.

		Reach									
Year	**Species /age**	**Middle Columbia River**			**Lower Snake and Lower Columbia Rivers**						**Totals**
		Rkm 729	Rkm 669	Rkm 639	Rkm 562[1]	Rkm 503	Rkm 468	Rkm 449	Rkm 422	Rkm 346	
2012	Sthd				1,002 (82)	1,400 (34)	1,199 (15)		1,198 (7)	1,000 (3)	5,799 (141)
	Chin 1				1,001 (15)	1,399 (8)	1,198 (2)		1,200 (5)	997 (0)	5,795 (30)
	Chin 0				1,885 (27)	2,524 (18)	1,993 (3)		1,984 (3)	986 (2)	9,372 (53)
2014	Sthd	399 (16)	771 (38)	550 (39)		2,499 (62)	1,999 (38)	2,000 (30)			8,218 (223)
	Chin 1	398 (2)	769 (4)	549 (2)		2,500 (14)	2,000 (7)	2,002 (10)			8,218 (39)
	Chin 0					2,517 (32)	1,995 (15)	1,997 (14)		981 (3)	7,490 (64)

[1]Release site was on the lower Snake River, 40 Rkm upstream from the confluence of the Snake and Columbia rivers and 562 Rkm from the Pacific Ocean.

Bird colony sizes

The size of each bird breeding colony (number of breeding pairs or adults on-colony) varied by species (Caspian tern, double-crested cormorant, California/ring-billed gull, American white pelican), colony location, and year. In general, the largest piscivorous waterbird colonies in the study area were California and ring-billed gull colonies (range = 1,566 – 14,475 adults on-colony), followed by colonies of American white pelicans (range = 2,075 – 2,447 adults on-colony), Caspian terns (range = 6 – 463 breeding pairs on-colony), and double-crested cormorants (390 breeding pairs on-colony; Table 2).

Although the sizes of colonies varied by year and species, the arrival timing and general nesting chronology of birds at each breeding site was similar across species, with courtship and nest building activities observed in late March/ April, egg laying and incubation in late April/May, and chick rearing and fledging in June/July. Peak colony sizes were observed during the egg laying and incubation periods, which coincided the peak steelhead and yearling Chinook salmon out-migration periods in both 2012 and 2014. Most colonies abandoned their nesting sites by early August, although American white pelicans were observed on Badger Island through September and early October.

Table 2. Numbers of piscivorous waterbirds counted on-colony at the peak of nesting during the 2012 and 2014 breeding seasons. Counts of Caspian terns and double-crested cormorants represent the number of breeding pairs, while counts of American white pelicans and California/ring-billed gulls represent the number of individual adults on-colony. An asterisk denotes that the colony was not scanned for tags during that year. NA denotes that a colony count was not available that year due to lack of aerial- or ground-based surveys.

Location (Rkm)	Species	2012	2014
Twinning Island, Banks Lake (off-river)	Caspian terns	22*	66
Goose Island, Potholes Reservoir (off-river)	Caspian terns	463	159
Island 20, middle Columbia River (549)	California and ring-billed gulls	NA*	14,475
Foundation Island, lower Columbia River (518)	Double-crested cormorants	390	390
Badger Island, lower Columbia River (512)	American white pelicans	2,075	2,447
Crescent Island, lower Columbia River (510)	Caspian terns	422	474
Crescent Island, lower Columbia River (510)	California and ring-billed gulls	7,187	6,404
Anvil Island, lower Columbia River (440)	Caspian terns	6*	45
Anvil Island, lower Columbia River (440)	California and ring-billed gulls	7,282*	4,454
Straight Six Island, lower Columbia River (439)	California and ring-billed gulls	1,707*	1,566
Miller Rocks, lower Columbia River (331)	California gulls	4,509	4,132

Recovery of tags on bird colonies

The number of bird colonies scanned for tags from study fish varied by year, with a total of six colonies scanned for tags following the 2012 nesting season and 11 colonies scanned for tags following the 2014 nesting season (Table 2 and Appendix A, Table A1). In total, tags from 364 juvenile steelhead, 69 yearling Chinook salmon, and 117 subyearling Chinook salmon were recovered on bird colonies during the same year the tagged smolts migrated and were included in analyses of avian predation probabilities (Table 1). More smolt tags were recovered on bird colonies in 2014 (n = 326; all species/age-classes combined) compared with 2012 (n = 224; all species/age-classes combined), due in part to greater sampling effort at bird colonies in 2014, but also because more tagged smolts were released in 2014, including releases in the middle Columbia River (Table 1). A summary of the number of smolt PIT tags recovered by fish species/age-class, bird colony, and year, including tags recovered on bird colonies located outside of the study area (e.g., East Sand Island in the Columbia River estuary at Rkm 8), are provided in Appendix A, Table A1.

Detection probabilities of PIT tags sown on bird colonies ranged from a low of 0.24 at the Goose Island Caspian tern colony during the first week of smolt releases to a high of 0.99 at the Straight Six Island gull colony during the last week of smolt releases (Table 3). In general, detection probabilities were high (ca.

0.70) for most bird colonies and years (Table 3). There was a positive relationship between detection probability and time since deposition; the probability of recovering a tag was lower for tags deposited early in the smolt run compared with tags deposited late in the smolt run (Table 3).

Table 3. Range of median weekly detection probabilities (first to last week of smolt releases) for PIT tags sown on bird colonies in 2012 and 2014. The total number of PIT tags sown (n) and the number of tag releases (r) to model detection probabilities are shown. NA denotes that the colony was not scanned for PIT tags that year.

Location	Bird species	2012	2014
Twinning Island	Caspian tern	NA	0.44-0.91 (n=100; r=2)
Goose Island	Caspian tern	0.24-0.80 (n=400; r=4)	0.49-0.97 (n=100; r=2)
Island 20	California gull	NA	0.73-0.90 (n=100; r=2)
Foundation Island	Double-crested cormorant	0.37-0.41 (n=200; r=2)	0.20-0.20 (n=100; r=1)
Badger Island	American white pelican	0.68-0.74 (n=100; r=2)	0.69-0.76 (n=100;r=2)
Crescent Island	Caspian tern	0.50-0.91 (n=200; r=4)	0.77-0.94 (n=200; r=4)
Crescent Island	California gull	0.63-0.95 (n=100; r=2)	0.73-0.98 (n=100; r=2)
Anvil Island	Caspian tern	NA	0.85-0.86 (n=100; r=2)
Anvil Island	California gull	NA	0.90-0.98 (n=100; r=2)
Straight Six Island	California gull	NA	0.87-0.98 (n=100; r=2)
Miller Rocks Island	California gull	0.74-0.89 (n=100; r=2)	0.83-0.87 (n=100; r=2)

Predation probabilities

The main focus of this study was to model total mortality and mortality due to colonial waterbird predation and not survival probabilities. Survival estimates, however, were very similar, if not identical, to those reported by Hughes et al. (2013), Weiland et al. (2015), and Skalski et al. (2015).

Estimated colonial waterbird predation probabilities varied by river segment, fish species/age-class, and year, with predation probabilities ranging from less than 0.01 to greater than 0.16 (95% CI = 0.11 – 0.19), per river segment (Figures 5-7). Within the same spatial scale and year, estimated avian predation probabilities were consistently higher on steelhead compared with yearling Chinook salmon and subyearling Chinook salmon. For instance, avian predation on juvenile steelhead was generally 2 to 4 times higher than that on yearling Chinook salmon and 2 to 5 times higher than that on subyearling Chinook salmon. Estimated impacts of avian predation were also consistently the highest (0.02 – 0.16, depending on the species/age-class of fish) on tagged smolts in a segment of the lower Snake River (Rkm 562-525), relative to other river segments evaluated, due to the close proximity and subsequent consumption of tagged smolts by colonial waterbirds nesting on Foundation and Crescent islands, located just below the confluence of the Snake and Columbia rivers (Figure 5; see Appendix B1, Table B1 for colony-specific results).

In addition to higher probabilities of predation by colonial waterbirds in the lower Snake River, avian predation probabilities were also higher in the tailrace of McNary Dam (Rkm 470-468; Figures 5-6) and John Day Dam (Rkm 349-346; Figures 5-6) in both 2012 and 2014, and, in 2014, a section of the John Day Reservoir (Rkm 412-449; Figure 6). In 2012, there were fewer arrays in the John Day Reservoir and the gull colonies on Anvil and Straight Six islands (located in the Blalock Islands complex) were not scanned for tags that year, so the total impact of colonial waterbird predation on smolt survival in this particular section of the John Day reservoir during 2012 is unknown, but higher than that presented herein because smolt tags released in 2012 were detected on gull colonies in the Blalock Islands during scans in 2014 (i.e., the fish were consumed by birds in 2012 but the tags were not detected on-colony until 2014 and were thus not included in predation probability calculations; Appendix A, Table A1).

Estimated probabilities of predation by colonial waterbirds for all bird colonies combined were generally lower on fish out-migrating through the middle Columbia River (0.03 and 0.06 for yearling Chinook salmon and juvenile steelhead, respectively) compared with fish out-migrating through the lower Snake River (0.05 – 0.28, depending on the fish species/age-class; Appendix B, Table B1) and lower Columbia River (0.05 – 0.11, depending on fish species/age-class and year; Appendix B, Table B1). It should be noted, however, that the precision of predation estimates on tagged smolts released into the middle Columbia River was lower due to smaller numbers of steelhead and yearling Chinook released as part of this study. For instance, 95% creditable intervals for reach-specific predation probabilities on yearling Chinook salmon and steelhead in the middle Columbia River were 0.01 – 0.06 and 0.04 – 0.09, respectively (Figure 7 and Appendix B, Table B1).

The amount of total mortality (1-survival) explained by colonial waterbird predation also varied by spatial-scale, fish species/age-class, and year (Figures 5-7 and Table 4). For juvenile steelhead, predation by colonial waterbirds accounted for the majority (> 50%) of smolt losses in many of the spatial-scale/years evaluated. For example, colonial waterbird predation on tagged juvenile steelhead accounted for an estimated 11 – 85% of total mortality, depending the river reach and year. At finer spatial scales (e.g., the lower Snake River and near McNary and John Day dams), colonial waterbird predation accounted for nearly all (100%) of juvenile steelhead losses (Figures 5 and 6; see also Appendix B, Table B1). In the Wanapum and Priest Rapids projects in 2014, predation by colonial waterbirds accounted for 31% and 25% of all documented steelhead mortality, respectively (Table 4).

For yearling Chinook salmon, the proportion of total smolt mortality explained by colonial waterbird predation was generally lower than that for juvenile steelhead (Figures 5-7 and Table 4), although in some segments and years, avian predation accounted for > 50% of yearling Chinook salmon losses (e.g., near McNary Dam in 2012 and 2014; Figures 5-7 and Table 4). For subyearling Chinook salmon, particularly in the John Day project, estimated colonial waterbird predation accounted for only a small proportion (generally < 0.10, depending on the spatial scale) of smolt losses (Figures 5-6 and Table 4). Total mortality of subyearling Chinook salmon, however, was generally higher than that observed in steelhead and yearling Chinook salmon, based on comparisons at the same release/interrogation sites (Figures 5-6 and Appendix B). This suggests that something other than bird predation was responsible for most mortality of subyearling Chinook salmon, particularly in 2014, when all known waterbird colonies within foraging distance of subyearling Chinook salmon tagged in this study were included in the analysis.

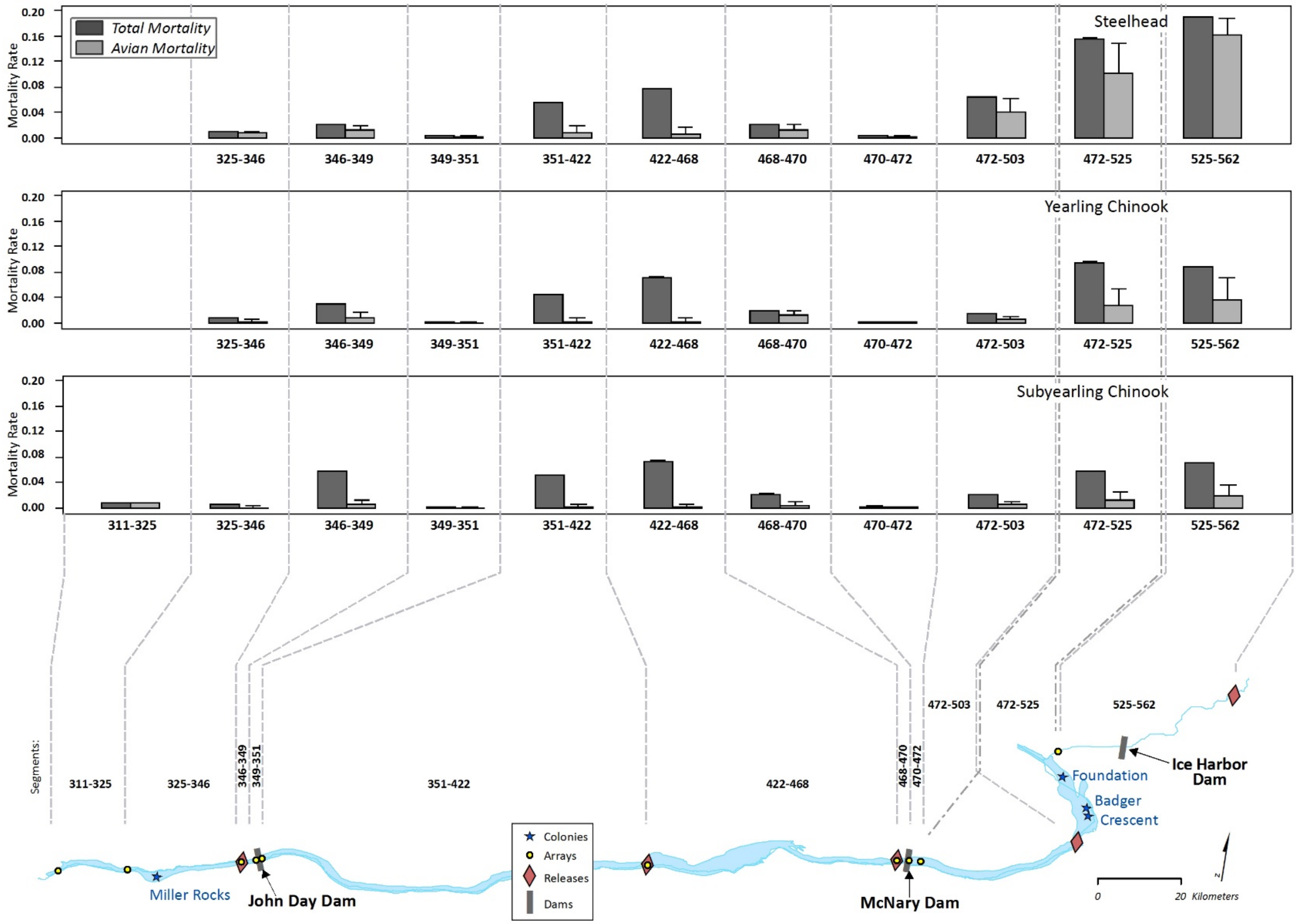

Figure 5. Estimated total mortality and mortality due to predation by birds from six breeding colonies on tagged smolts in sections of the lower Snake River and lower Columbia River in 2012. Locations of smolt release sites (red diamonds), acoustic arrays (yellow dots), bird colony sites (blue stars), and hydroelectric dams (grey bars) are shown.

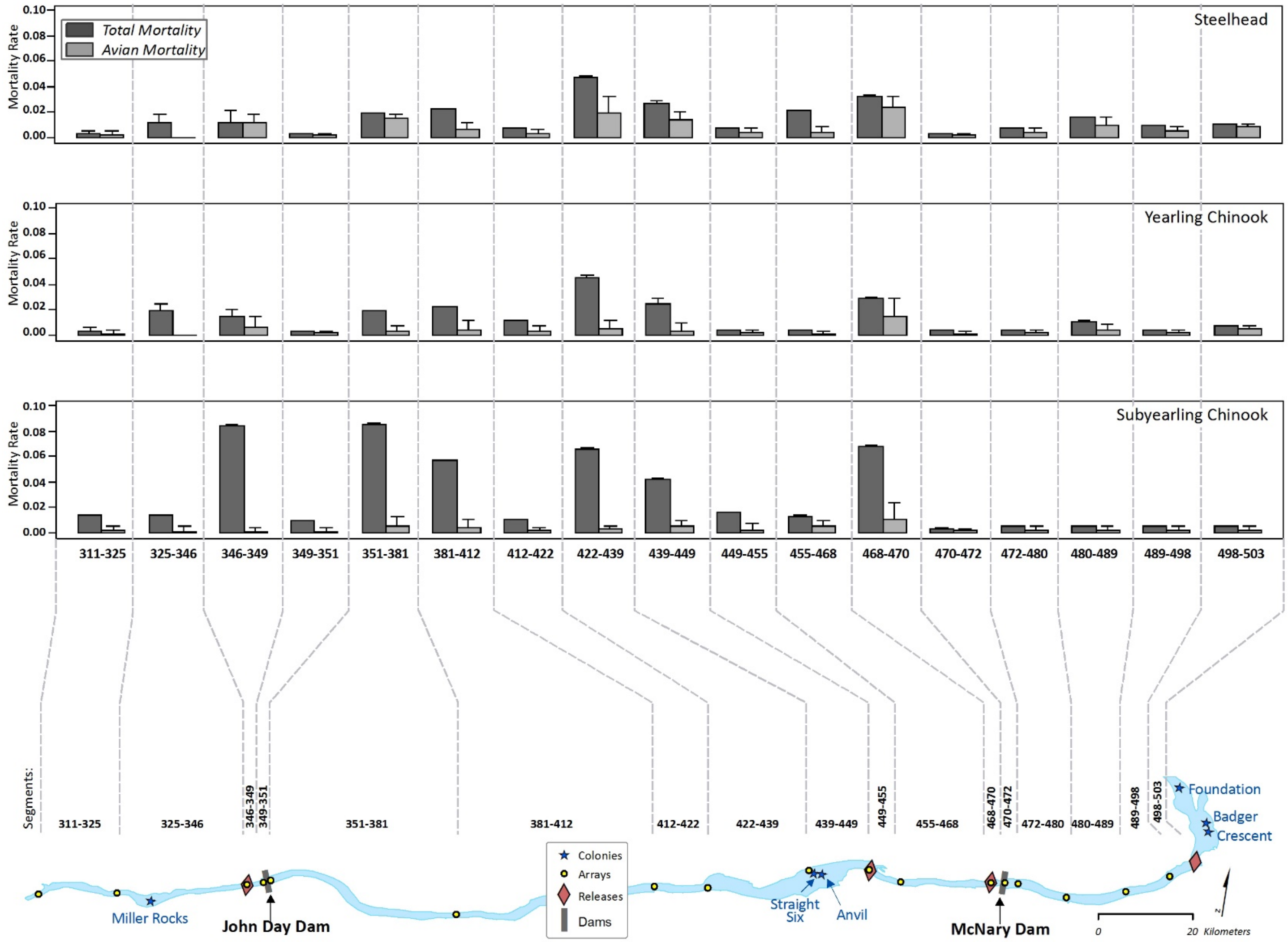

Figure 6. Estimated total mortality and mortality due to predation by birds from 11 breeding colonies on tagged smolts in a section of the lower Columbia River in 2014. Locations of smolt release sites (red diamonds), acoustic arrays (yellow dots), bird colony sites (blue stars), and hydroelectric dams (grey bars) are shown.

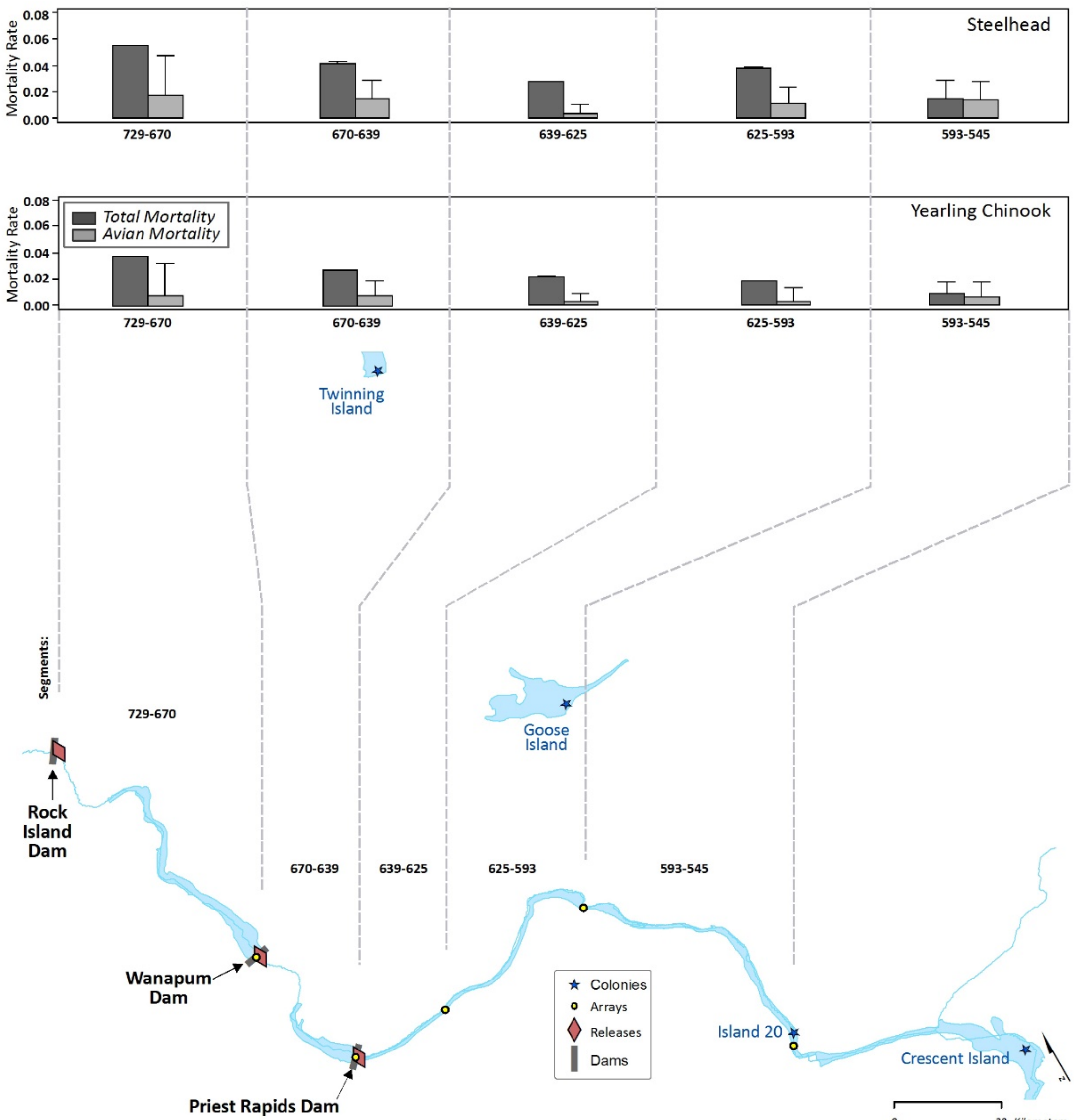

Figure 7. Estimated total mortality and mortality due to predation by birds from four breeding colonies on tagged smolts in a section of the middle Columbia River in 2014. Locations of smolt release sites (red diamonds), acoustic arrays (yellow dots), bird colony sites (blue stars), and hydroelectric dams (grey bars) are shown.

Comparisons of inter-annual differences (2012 versus 2014) in predation by colonial waterbirds for near-dam, reservoir, and project-specific impacts indicated that for most species/age-classes, predation probabilities and the percentage of total mortality explained by mortality from avian predation was generally higher in 2014 compared with 2012 (Table 4). An increase in avian predation probabilities in 2014 relative to 2012 was in large part due to the number of bird colonies scanned for tags in 2014; two additional gull colonies and one additional Caspian tern colony were included in 2014 analyses, colonies that were not included in the 2012 analyses (see Appendix B1, Table B1 for colony-specific results). The one exception to an over-all increase in colonial waterbird predation probabilities in 2014 compared with 2012 was predation on subyearling Chinook salmon near John Day Dam, where a decrease in avian predation probabilities occurred in 2014 relative to 2012. Consumption of subyearling Chinook salmon near John Day Dam by colonial waterbirds was almost exclusively due to predation by gulls nesting on Miller Rocks Island in both 2012 and 2014 (Appendix B, Table B1). The last known detections of tagged smolts consumed by gulls nesting on Miller Rocks Island indicated a shift in foraging behavior in 2014 relative to 2012; gulls nesting on Miller Rocks Island disproportionately consumed tagged smolts downstream of the last array in the forebay of The Dalles Dam in 2014 (i.e., outside of the study area). In 2012, 57.1% of the PIT tags from subyearling Chinook salmon that were recovered on the Miller Rocks Island gull colony were consumed upstream of The Dalles Dam, whereas in 2014, only 10.5% of the PIT tags from subyearling Chinook salmon that were recovered on the Miller Rocks gull colony were consumed upstream of The Dalles Dam. Consequently, in 2014, the focus of smolt predation by gulls nesting on Miller Rocks Island was further downstream, below The Dalles Dam, than it was in 2012.

Table 4. Estimated predation probabilities (proportion of available tagged fish consumed) of juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon by colonial waterbirds at project-, reservoir-, and near-dam spatial scales and the percentage of total smolt mortality (1-survival) explained by bird predation (in parentheses) in 2012 and 2014 (see Appendix B, Table B1 for colony-specific results and 95% credible intervals associated with each estimate).

			Steelhead		Yearling Chinook		Subyearling Chinook	
Reservoir	**Scale**	**Rkm**	**2012**	**2014**	**2012**	**2014**	**2012**	**2014**
Wanapum	Project	729-670		0.018 (31%)		0.008 (17%)		
Priest Rapids	Project	670-639		0.011 (25%)		0.007 (31%)		
McNary	Near-Dam	472-468	0.016 (64%)	0.025 (70%)	0.014 (65%)	0.017 (59%)	0.006 (23%)	0.014 (18%)
	Reservoir [1]	525-472	0.100 (65%)		0.029 (31%)		0.013 (28%)	
	Project [1]	525-470	0.104 (65%)		0.030 (33%)		0.016 (29%)	
John Day	Near-Dam	351-346	0.015 (61%)	0.014 (85%)	0.008 (26%)	0.008 (40%)	0.006 (10%)	0.003 (2%)
	Reservoir	468-351	0.013 (11%)	0.056 (42%)	0.005 (4%)	0.021 (18%)	0.003 (2%)	0.026 (10%)
	Project	468-349	0.016 (12%)	0.058 (42%)	0.005 (4%)	0.023 (19%)	0.003 (3%)	0.027 (10%)

[1] The acoustic array at Rkm 525 was located on the lower Snake River, 9 Rkm downstream of Ice Harbor Dam.

An investigation of temporal changes in the impact of avian predation on tagged smolts indicates that a positive relationship existed between the week when tagged smolts were released and predation probabilities by colonial waterbirds, whereby predation impacts generally increased with time. Results indicated that smolts released during the latter half of the study were more susceptible to bird predation than smolts released during the few weeks of the study (Appendix C, Figures C1-C3). This trend was particularly pronounced for juvenile steelhead, with predation rates significantly higher for smolts released in May compared with those released in April. For example, median reach-specific avian predation probabilities on tagged steelhead released into the lower Snake River were 0.12 during the first week of tagged smolt releases and increased to 0.49 during the last week of releases (Appendix C, Figure C1). Temporal trends in avian predation were less evident for yearling Chinook and subyearling Chinook salmon; however, the general trend of increasing impacts of avian predation with release week were evident in both species.

Temporal trends in colonial waterbird predation rates were consistent with seasonal trends in total mortality for juvenile steelhead and yearling Chinook salmon out-migrating through the lower Snake and Columbia rivers in 2012 and 2014, with increases in weekly total mortality commensurate with weekly bird predation probabilities (Appendix C, Figures C1-C2). Trends were less obvious in steelhead and yearling Chinook migrating through the middle Columbia River, although analyses were limited to just three weeks of releases from a single year (Appendix C, Figure C3).

Results of the randomization test indicates that a large proportion of the variation in weekly estimates of smolt survival (1-mortality) can be explained by variation in avian predation rates (Figure 8). Results were particularly pronounced for steelhead, with an R^2 of 0.95 and p-value = < 0.001. A statistically significant relationship was also observed for yearling Chinook salmon (R^2 = 0.64, p = 0.001) and subyearling Chinook salmon (R^2 = 0.63, p = 0.01). Results for subyearling Chinook salmon should be viewed more cautiously, however, as the predation rate estimate observed during the last week of releases in 2014 (30% of available fish) was highly influential.

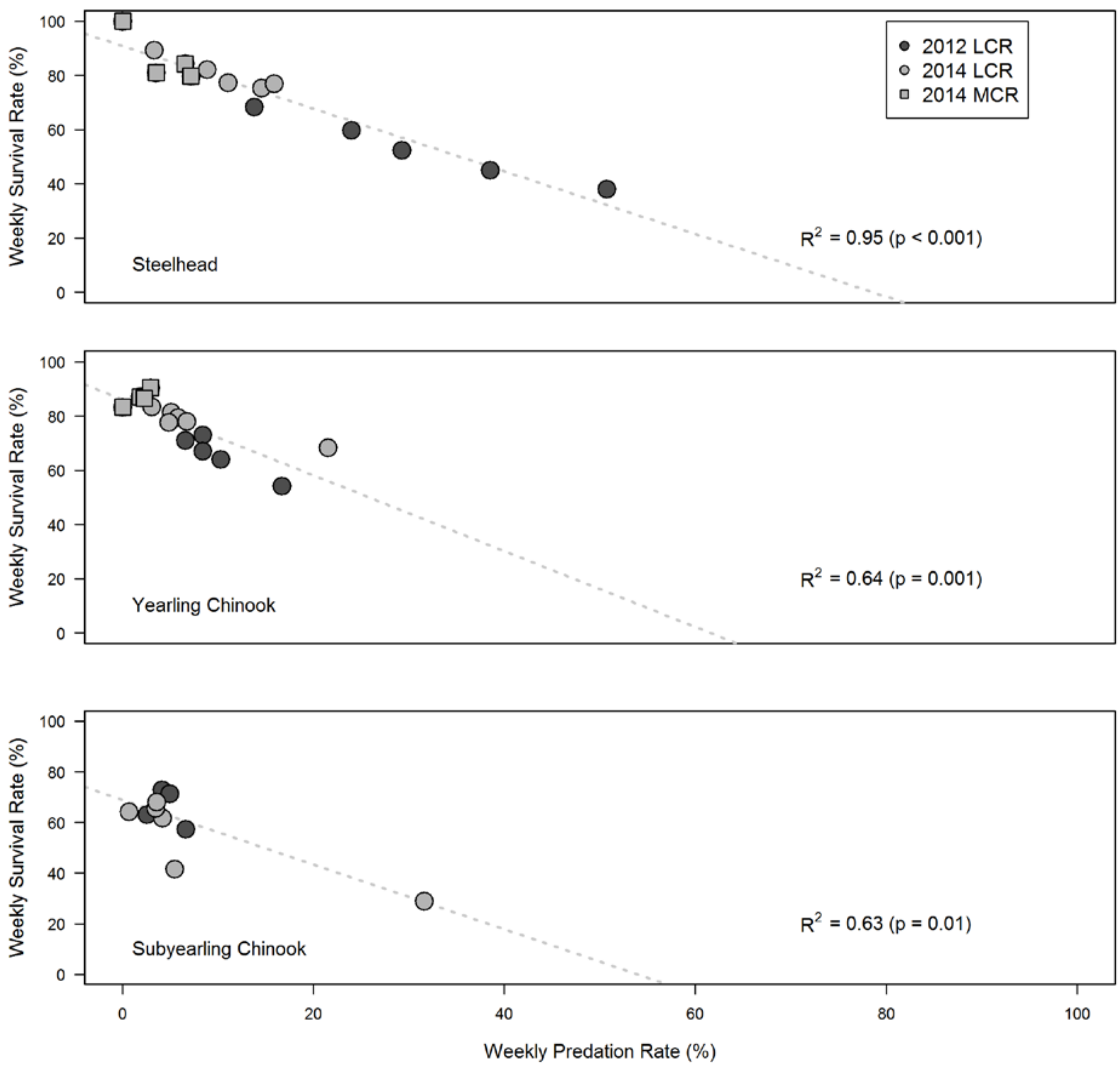

Figure 8. Weekly estimated survival (1-mortality) and avian predation rates for tagged juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon traveling through the middle Columbia River (MCR) and lower Snake River and lower Columbia River (LCR) during 2012 and 2014.

Colony-specific foraging

Bird colony-specific predation probabilities, adjusted for the length of each river segment, indicated several foraging hotspots for colonial waterbirds in the study area (Figure 9). In general, gull colonies disproportionately consumed tagged juvenile steelhead near dams, while Caspian terns disproportionately consumed tagged smolts in the reservoirs (Figure 9). No clear hotspot for predation by nesting double-crested cormorants or American white pelicans within the study area was identified, however (Figure 9).

In 2012, hotspots of bird predation on tagged juvenile steelhead were identified in the lower Snake River and in the section of the lower Columbia River just below the confluence of the Snake River, with predation by Foundation Island cormorants, Crescent Island terns, and Crescent Island gulls among the highest observed in any reach evaluated (Figure 9). Results indicated that birds nesting on Foundation and Crescent islands disproportionately commuted upstream of their breeding colony to forage on steelhead in the lower Snake River (Figure 9). The other hotspot of avian predation identified in 2012 was the tailrace of John Day Dam, where gulls nesting on Miller Rocks disproportionately consumed tagged steelhead relative to other nearby river segments. Impacts of predation by Badger Island white pelicans were among the lowest observed in this river reach (lower Snake River and lower Columbia River), with no hotspot of predation identified. An evaluation of hotspots of avian predation in the lower Snake River in 2014 was not possible because there were no releases of tagged smolts in this river reach in 2014.

Similar to 2012, predation by Crescent Island Caspian terns was higher within McNary Reservoir in 2014 compared with the other spatial scales (e.g., near-dam) evaluated (Figure 9). Results from 2014 also indicated that Crescent Island gulls disproportionally consumed fish in the tailrace of McNary Dam (Figure 9). Also similar to 2012, predation by Miller Rocks gulls in 2014 was concentrated in the tailrace of John Day Dam relative to other nearby segments (Figure 9). Total predation impacts and relative foraging hotspots by Miller Rocks gulls, however, were not fully quantified, as a large proportion of the tagged smolts in the study (juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon) were depredated outside of the study area in 2014 (i.e., downstream of the array located in the forebay of The Dalles Dam). The other hotspot for avian predation identified in 2014 was predation by gulls and Caspian terns nesting on Anvil Island in the Blalock Islands complex in John Day Reservoir, with predation concentrated in a stretch of the river about 30 Rkm upstream and downstream of the island (Figure 8). These bird colonies were not scanned for tags in 2012, precluding a comparison of predation impacts by birds nesting at these colonies in John Day Reservoir between 2012 and 2014.

No bird colony-specific hotspots for predation were identified within the middle Columbia River, although fewer spatial-scales were available for analyses in this portion of the study area (Figure 9). Of the spatial-scales evaluated, colonial waterbird predation was more evenly distributed and relativity low in intensity compared with colonial waterbird predation on smolts in the lower Snake River and Lower Columbia River in 2014. Avian predation within Wanapum and Priest Rapids projects was limited to birds nesting at three colonies in 2014; Caspian terns nesting on Twinning Island, Banks Lake; Goose Island, Potholes Reservoir; and Crescent Island, McNary Reservoir. Despite its proximity to Priest Rapids Dam, there was no evidence that gulls nesting on Island 20 were commuting upstream to forage within the Wanapum or Priest Rapids projects (Figure 8). The number of tagged juvenile steelhead that were available to birds below Rock Island Dam (n = 399) and Wanapum Dam (n = 1,148) was small, however, and on-colony deposition probabilities for gulls was low, so results should be interpreted cautiously.

The foraging ranges of piscivorous waterbirds (distance from their breeding colony) also varied by colony, river reach, and year. In general, predation rates on tagged steelhead were highest in those river segments closest to each colony (Figure 9), with most predation occurring within a 40 to 50 km radius of the colony site. The foraging range of Caspian terns feeding on juvenile steelhead tended be the longest, followed by the foraging ranges of California/ring-billed gulls, American white pelicans, and double-crested cormorants (Figure 9). Sample sizes of tags recovered on the Badger Island white pelican colony and the Foundation Island cormorant colony were, however, small (Appendix A, Table A1); thus, inferences on the foraging ranges for white pelicans and double-crested cormorants should be made cautiously.

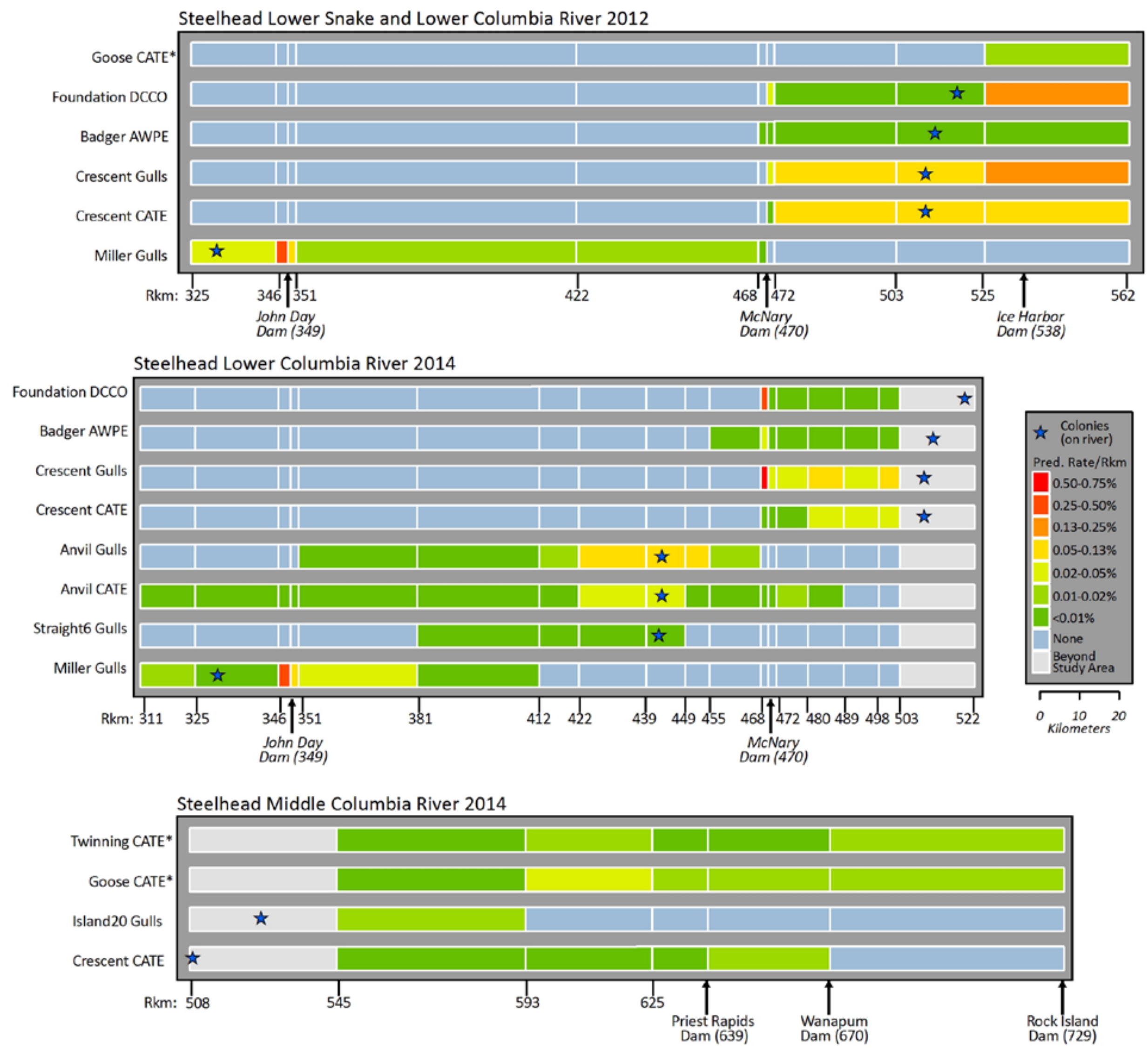

Figure 9. Bird colony-specific locations of predation on tagged juvenile steelhead in sections of the lower Snake River, lower Columbia River, and middle Columbia River during 2012 and 2014. Results are depicted as predation rates per river kilometer. Species of fish-eating colonial waterbirds evaluated include Caspian terns (CATE), double-crested cormorants (DCCO), California and ring-billed gulls (Gulls), and American white pelicans (AWPE). An asterisk next to a colony site denotes that the colony is located off-river.

DISCUSSION

Numerous factors have been linked to mortality of juvenile salmonids during seaward migration, including dam passage (Muir et al. 2001), disease (Dietrich et al. 2011), predation by fish (Rieman et al. 1991), and predation by birds (Evans et al. 2012). In the present study, predation by colonial waterbirds was a substantial source of mortality for tagged steelhead during out-migration, with reach-specific predation rates of 5.5%, 10.9%, and 27.7% of the available tagged fish released into the middle Columbia River, lower Columbia River, and lower Snake River, respectively. For yearling Chinook salmon, predation by colonial waterbirds was generally lower than that for juvenile steelhead, with reach-specific predation rates of 2.8%, 5.8%, and 9.1% of the available tagged fish. For subyearling Chinook salmon, predation probabilities by colonial waterbirds were the lowest among the three fish species/age-classes evaluated (< 5.3% of available fish in all reaches). Higher avian predation probabilities on juvenile steelhead compared with salmon species are well documented in the published literature (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012). Possible explanations for the greater susceptibility of juvenile steelhead to bird predation include differences in the size (length) and behavior of steelhead compared with other salmonid species; steelhead smolts are generally larger and more surface-oriented compared with salmon smolts (Beeman and Maule 2006).

Previous published studies about avian predation on juvenile salmonids, such as Evans et al. (2012) and Hostetter et al. (2015), could not evaluate bird predation at discrete spatial scales. Use of acoustic telemetry data, however, provided information on which section of the river a tagged smolt was depredated in by birds. Spatial analyses indicated that avian predation probabilities varied by river segment and bird colony. Caspian tern foraging was almost exclusively documented within the reservoirs and not near hydroelectric dams. Conversely foraging by California and ring-billed gulls was concentrated near hydroelectric dams. Ruggerone (1986) and Zorich et al. (2011) also documented gull predation on juvenile salmonids near dams and hypothesized that smolts may be more vulnerable near dams as a result of (1) increased smolt travel times or delayed migration in the forebay of dams, (2) injury or mortality associated with dam passage, or (3) smolts being temporarily stunned or disoriented by hydraulic conditions in the tailrace of dams. Gull predation on tagged smolts observed in the present study, however, was not limited to foraging near dams, with predation taking place within the reservoirs as well, including the free flowing section of the middle Columbia River downstream of Priest Rapids Dam, the Hanford Reach. There was also evidence that Caspian terns, gulls, and double-crested cormorants nesting on islands in McNary Reservoir disproportionality foraged upstream of their nesting sites on and near the lower Snake River. Higher predation probabilities on smolts by piscivorous waterbirds in this section of river may be related to (1) the proximity of Ice Harbor Dam on the lower Snake river to Foundation and Crescent islands (19 Rkm and 27 Rkm downstream from the dam, respectively), (2) the relative abundance of smolts originating from the Snake River compared with smolts originating from the middle Columbia River or (3) environmental conditions resulting in favorable foraging conditions for birds in the lower Snake River, like reduced flows and higher turbidity (Hostetter et al. 2012).

A previous spatial investigation of bird colony-specific predation probabilities indicated that foraging was concentrated within an approximate 40 - 50 km radius of each colony. Telemetry data on the foraging behavior of Caspian terns and double-crested cormorants also indicates that most birds will preferentially remain close to their nesting site to forage, if foraging conditions near the colony allow (Anderson et al. 2004; Adrean et al. 2011). If fish availability near the colony is low, however, Caspian terns have been reported to commute over 90 km from the nesting colony in order to forage (BRNW 2013). Data on foraging behavior and ranges in California gulls, ring-billed gulls, and American white pelicans are generally lacking, although American white pelicans have been documented to consume tagged fish over 300 km from their nesting site (Scoppettone et al. 2006). In the present study, some fraction of smolt tags deposited by birds on-colony may have been from non-breeders or from birds that visited the colony while prospecting for a nest site (BRNW 2015). Consequently, it is more challenging to use recoveries of fish tags on bird colonies as a measure of foraging behavior in nesting adults compared to studies where adult birds are tagged to track their movements. Nevertheless, results from this study suggest that foraging was concentrated within a 40 to 50 km radius of the colony, although some birds consumed tagged fish that were depredated upwards of 100 km from the breeding colony where the tag was recovered.

Smolt predation by gulls, which are omnivores and generalist predators, was similar to or greater than that of Caspian terns and double-crested cormorants, which are strictly piscivorous predators. Hostetter et al. (2015) also reported that predation probabilities for gulls were higher than documented in the published literature because previous estimates of gull predation probabilities did not include a measure of on-colony PIT tag deposition probabilities. High smolt predation probabilities for gulls nesting on colonies in the study area were likely associated with (1) relatively large colony sizes (gull colonies were an order of magnitude larger than those for Caspian terns, double-crested cormorants, and American white pelicans), (2) behavioral flexibility to exploit temporarily available prey (Osterback et al. 2013), and (3) the proximity of some gull colonies to hydroelectric dams (e.g., gulls nesting on Miller Rocks Island), where smolts may be particularly vulnerable to predation by gulls (Ruggerone 1986; Collis et al. 2002; Zorich et al. 2011). Not all of the gull colonies evaluated in this study had appreciable impacts on smolt survival, however, with predation rates by gulls nesting on Island 20 in the middle Columbia River and on Straight Six Island in John Day Reservoir in the lower Columbia River amongst the lowest observed.

Similar to data reported by Evans et al. (2012), of the various piscivorous waterbird species evaluated herein, impacts were lowest by American white pelicans nesting on Badger Island in McNary Reservoir. Evans et al. (2012) hypothesized that several factors may account for low predation probabilities on juvenile salmonids by American white pelicans nesting on Badger Island, including (1) the reliance of white pelicans on larger forage fish, (2) the tendency of white pelicans to forage in shallow water habitats where activity migrating smolts are relatively less abundant, (3) a lack of temporal or spatial overlap between white pelicans and salmonid smolts in the lower Snake and Columbia rivers, or (4) some combination of these factors. It is important to note, however, that estimates of smolt predation probabilities for white pelicans presented here and those presented by Evans et al. (2012) do not incorporate tag loss due to off-colony deposition and thus represent minimum estimates of predation probabilities. In a study of predation on cutthroat trout (*O. clarkii*) by American white pelicans in Idaho, Teuscher et al. (2015) estimated that average deposition and detection probabilities (a combined estimate for both parameters) for PIT tags implanted in trout were approximately 0.30 (range = 0.08 – 0.55). Applying this correction factor to the raw, unadjusted numbers of juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon tagged in this study and recovered on the Badger Island white pelican colony, however, would not increase predation probabilities to a significant extent, as predation rates would still be < 1% for all fish species/age-classes and all spatial scales evaluated as part of this study.

An investigation of weekly predation rates provided evidence of within-season temporal trends in predation probabilities, whereby predation probabilities generally increased with release date, particularly for steelhead. In a study of Caspian tern predation on juvenile salmonids, Evans et al. (2013) also observed a positive relationship between the week when tagged smolts were released and avian predation probabilities. Hostetter et al. (2012) linked weekly predation rates to the number of PIT-tagged smolts available in-river, whereby predation rates were generally lower when more PIT-tagged fish were present in-river, apparently producing a predator-swamping effect (Ims 1990). Variation in weekly predation probabilities have also been correlated with the number of adult birds counted on-colony, with higher predation rates linked to higher colony counts (Evans et al. 2013). Data on weekly colony attendance were not available for all the colonies evaluated in the present study, and similar numbers of tagged smolts were released each week, so the influence of colony size and variation in the number of tagged smolts available to birds on predation probabilities could not be investigated in the present study. Nevertheless, results provide strong evidence of intra-annual variation in predation rates, with late migrating smolts being more susceptible to colonial waterbird predation than early migrants.

Not all species of piscivorous waterbirds or all breeding colonies within the study area were included in the present study. As such, results presented here reflect minimum estimates of total bird predation on PIT-tagged smolts within the study area. Smolt predation probabilities for non-colonial or semi-colonial piscivorous waterbirds, such as common mergansers (*Mergus merganser)*, great blue herons (*Ardea Herodias)*, black-crowned night-herons (*Nycticorax nycticorax)*, and large grebes (*Aechmophorus* spp.), were not investigated as part of this study. While these species of piscivorous waterbirds are known to consume juvenile salmonids in the Columbia River Basin, their predation rates on smolts have been shown to be far less than those of colonial piscivorous waterbirds (Parrish 2006; Wiese et al. 2008), primarily because of smaller population sizes. Furthermore, not all colonies of piscivorous waterbirds that were identified within the study area during 2012 were scanned for smolt tags, including three bird colonies located in the John Day Reservoir (two gull colonies and a Caspian tern colony). Therefore, some fraction of unaccounted for mortality reported here was due to bird predation but based on the full suite of piscivorous waterbird colonies scanned for tags in 2014 and the low reported impacts from non- or semi-colonial piscivorous waterbird species on smolts, it was likely a minimal (in 2014) to moderate (in 2012) amount.

This study is amongst the first to document the impact of predation by colonial waterbirds in the context of overall smolt survival. Results provide strong evidence that a large proportion of the variation in smolt survival during out-migration was explained by colonial waterbird predation rates, particularly for steelhead. Comparisons of survival rates and avian predation rates indicated that predation on juvenile steelhead by colonial waterbirds was at times the single greatest mortality factor identified, with greater than 50% off all steelhead mortality attributed to colonial waterbird predation in a number of the river reaches and segments evaluated. Avian predation probabilities were more variable for yearling Chinook salmon, with the percentage of total mortality attributed to colonial waterbirds highest near hydroelectric dams and on smolts traveling through the lower Snake River. For subyearling Chinook salmon, predation by colonial waterbirds was generally low and a minor component of overall smolt mortality. For example, in the John Day Reservoir, total subyearling Chinook salmon mortality was estimated at 25.5% of available tagged fish in 2014, yet colonial waterbirds consumed only an estimated 2.6% of the available tagged smolts, providing strong evidence that something other than colonial waterbird predation was responsible for the vast majority of mortality to subyearling Chinook salmon in John Day Reservoir.

One likely component of unaccounted for mortality in the present study was predation by piscine predators, such as northern pikeminnow (*Ptychocheilus oregonensis),* smallmouth bass *(Micropterus dolomieu)*, walleye *(Sander vitreus),* and channel catfish *(Ictalurus punctatus).* Data on the impact of piscine predation on survival of juvenile salmonids in the Columbia River basin are from studies completed in the 1990s. Ward et al. (1995) estimated that impacts of pikeminnow predation on juvenile salmonids were greater in the lower Columbia River compared to the middle Columbia River and lower Snake River. Rieman et al. (1991) estimated that ca. 14% of juvenile salmonids passing through John Day Reservoir were consumed by pikeminnow, smallmouth bass, and walleye combined, with mortality rates highest on subyearling Chinook salmon. The shallow water habit that surround a number of islands in John Day Reservoir may provide optimal foraging conditions for piscine predators (Hughes et al. 2013), so more current studies of this source of mortality to salmonid smolts seem warranted.

Project-specific survival standards for juvenile steelhead in the middle Columbia River (≥ 93% survival) were not achieved in the Priest Rapids project during 2008 - 2010, nor in the Wanapum project in 2010 (Timko et al. 2011). Evans et al. (2013) estimated between 4.0% – 10.0% (depending on the project and year) of available juvenile steelhead in the Wanapum and Priest Rapids projects were annually consumed by Caspian terns during this three-year period. In 2014, survival standards for juvenile steelhead in the middle Columbia River were met (Skalski et al. 2015). Data presented in this study indicate that Caspian terns consumed an estimated 1.1% to 1.8% (depending on the project) of available juvenile steelhead in Wanapum and Priest Rapids projects during 2014. Reductions in predation rates on steelhead smolts by Caspian terns in 2014 were likely related to management efforts aimed at reducing the size of the Goose Island Caspian tern colony in nearby Potholes Reservoir, the largest tern colony within foraging distance of Wanapum and Priest Rapids projects. Management efforts were able to reduce the size of the Potholes Reservoir Caspian tern colony to 159 nesting pairs in 2014 from an average of 400 nesting pairs during 2008-2010 (BRNW 2014).

Survival standards for juvenile salmonids on the lower Columbia River are not project-specific, but instead dam-specific (≥ 96% survival per dam for steelhead and yearling Chinook salmon and ≥ 93% survival per dam for subyearling Chinook salmon). These survival standards were achieved for steelhead and yearling Chinook salmon in 2012 and 2014 for smolt passing McNary and John Day dams (Skalski et al. 2012; Skalski et al. 2014a; Skalski et al. 2014b). Standards, however, were not met for subyearling Chinook salmon passing McNary and John Day dams in 2014, falling approximately 1% short of the ≥ 93% standard at each dam (Skalski et al. 2014a; Skalski et al. 2014b). Avian predation rates near McNary and John Day dams, measured in the present study, were often below mortality thresholds set for juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon, ranging from 0.3% to 2.5% of available fish near each dam. Our estimates of smolt mortality due to predation by colonial waterbirds are not directly comparable to dam-specific survival standards, however, because bird predation was measured between arrays located in the forebay and tailrace of each dam, a greater area than that of the dam itself. Nevertheless, the percentage of total smolt mortality associated with colonial waterbird predation in the vicinity of McNary and John Day dams was often high, indicating that relative to other sources of smolt mortality near each dam, bird predation was a substantial cause of smolt mortality.

In the context of overall smolt survival, it is important to note that some fraction of predation on salmonid smolts is likely consumption of dead or moribund fish. If a significant fraction of tagged smolts that were consumed by birds (or other predators) were dead or moribund at the time of consumption, it would influence the interpretation of results. In particular, the expected benefits to smolt survival from reduced predation would be smaller (due to compensatory mortality) than those derived from adding estimates of predation rates back in to estimates of smolt survival rates. Research to quantifying what proportion of avian predation is a compensatory, as opposed to an additive, source of mortality is generally lacking in the Columbia River Basin (Hostetter et al. 2012; Lyons et al. 2014). Hostetter et al. (2012) observed differences in the susceptibility of juvenile steelhead to predation by Caspian terns and double-crested cormorants based on the external condition (body injuries, fungal infections, descaling) of tagged and released smolts, with smolts released in degraded condition more likely to be consumed by birds than apparently undamaged smolts. In the present study, only undamaged or good condition smolts were tagged and released, so an investigation of condition-dependent mortality was not possible, nor is it likely that results were influenced by a larger number or proportion of tagged fish in degraded condition. Furthermore, as part of JSATS survival studies, Hughes et al. (2013) and Skalski et al. (2015) released tagged dead smolts into the tailrace of McNary Dam (n = 180) and John Day Dam (n= 193) to evaluate detection probabilities of dead fish passing arrays. None (zero) of these dead fish were recovered on bird colonies as part of this study, providing evidence that dead smolts were not far more susceptible to consumption by piscivorous colonial waterbirds in the tailrace of dams compared to their live counterparts. Despite the lack of evidence in the present study that birds were disproportionately consumed moribund or dead fish, results from Hostetter et al. (2012) suggest that some fraction of avian predation is likely compensatory.

Future studies of avian predation on juvenile salmonids that utilize double-tagged (AT and PIT tags) fish would benefit from larger sample sizes of tagged smolts and a single release point upstream of the birds' maximum foraging range from their breeding colony. Evans et al. (2012) recommended that at least 500 tagged smolts be used in studies investigating predation rates in order to minimize unstable results that arise from small sample sizes, whereby the recovery of just few tags on-colony can greatly influence predation probabilities. Measurements of precision, like credible intervals, are also heavily influenced by the number of tagged smolts released (Hostetter et al. 2015) and the small sample sizes of tagged smolts released in the middle Columbia River in 2014 resulted in imprecise estimates of predation probabilities. Avian predation studies that release tagged fish just upstream of the maximum foraging range for nesting colonial waterbirds will result in more accurate and defensible measures of cumulative impacts on smolt survival by avian predators. In the present study, avian predation probabilities were heavily influenced by the location of release and interrogation sites, and cumulative impacts for some bird colonies could not be documented because birds were presumably foraging on tagged smolts upstream of the release point (e.g., double-crested cormorants nesting on Foundation Island) or downstream of the last array in the study area (e.g., gulls nesting on Miller Rocks Island). Finally, additional studies aimed at investigating factors that influence fish susceptibility to bird predation, like prey densities, river flows, travel times, route-specific passage histories, and size- and condition-dependent mortality, are warranted. Results from these types of investigations may not only broaden our understanding of mechanisms that regulate predator-prey interactions, but they may help in the development of management strategist to reduce predation impacts.

In summary, impacts of avian predation on smolt survival described in the present study varied by bird species, colony location, fish species/age-class, week, and year, demonstrating that predator-prey interactions were dynamic at both spatial and temporal scales. Predation by piscivorous colonial waterbirds on juvenile steelhead and yearling Chinook salmon was a substantial source of mortality and was one of the greatest, if not the single greatest, sources of mortality during passage through sections of the lower Snake River and the lower and middle Columbia rivers in 2012 and 2014. Predation probabilities by colonial waterbirds on subyearling Chinook salmon, however, were generally low and a minor overall component of total mortality. Assuming birds are not largely consuming dead or moribund fish and that other sources of mortality do not fill the niche created by a reduction in predation at any given bird colony, management of piscivorous colonial waterbirds will likely enhance survival of juvenile salmonids from the Columbia River Basin.

ACKNOWLEDGMENTS

This project was funded by Public Utility District No. 2 of Grant County with oversight and approval from the Priest Rapids Coordinating Committee. We especially want to thank Curt Dotson of Grant County PUD for his assistance and support. John Skidmore and David Roberts of Bonneville Power Administration and Eric Hockersmith and David Trachtenbarg of the U.S. Army Corps of Engineers - Walla Walla District also provided assistance for which we are grateful. We want to thank Cindy Fitzgerald of Blue Leaf Environmental for preparation of acoustic data and general support. Finally, this work would not have been possible without the hard work and dedication of numerous field researchers, for which we are grateful. Any use of trade, firm, or product names is for descriptive purposes and does not imply endorsement.

LITERATURE CITED

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

Adrean, L.J. 2011. Caspian tern (*Hydroprogne caspia*) foraging ecology and predation on juvenile salmonids in San Francisco Bay, California. Unpublished M.S. thesis, Oregon State University, Corvallis, Oregon.

Anderson, C.D., D.D. Roby, and K. Collis. 2004. Conservation implications of the large colony of double-crested cormorants on East Sand Island, Columbia River estuary, Oregon, USA. Waterbirds 27:155-160.

Antolos, M., D.D. Roby, D.E. Lyons, K. Collis, A.F. Evans, M. Hawbecker, and B.A. Ryan. 2005. Caspian tern predation on juvenile salmonids in the Mid-Columbia River. Transactions of the American Fisheries Society 134:466-480.

Beeman, J. W., and A. G. Maule. 2006. Migration depths of juvenile Chinook salmon and steelhead relative to total dissolved gas supersaturation in a Columbia River reservoir. Transactions of the American Fisheries Society 135:584–594.

BRNW (Bird Research Northwest). 2013. Research, Monitoring, and Evaluation of Avian Predation on Salmonid Smolts in the Lower and Mid-Columbia River, Final 2012 Annual Report. Submitted to Bonneville Power Administration, U.S. Army Corps of Engineers – Walla Walla District, and U.S Army Corps of Engineers – Portland District. Available on-line at www.birdresearchnw.org.

BRNW (Bird Research Northwest). 2014. Research, Monitoring, and Evaluation of Avian Predation on Salmonid Smolts in the Lower and Mid-Columbia River, Final 2013 Annual Report. Submitted to Bonneville Power Administration, U.S. Army Corps of Engineers – Walla Walla District, U.S Army Corps of Engineers – Portland District, and Grant County Public Utility District (GPUD)/Priest Rapids Coordinating Committee. Available on-line at www.birdresearchnw.org.

BRNW (Bird Research Northwest). 2015. Research, Monitoring, and Evaluation of Avian Predation on Salmonid Smolts in the Lower and Mid-Columbia River, Draft 2014 Annual Report. Submitted to the Bonneville Power Administration, the U.S Army Corps of Engineers – Portland District, and the Grant County Public Utility District. Available on-line at www.birdresearchnw.org.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., and Pollock, K. H. 1987. Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture. American Fisheries Society Monograph, 5.

Collis, K., D.D. Roby, D.P. Craig, B.A. Ryan, and R.D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society 130:385-396.

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

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

Evans, A.F., N.J. Hostetter, K. Collis, D.D. Roby, D.E. Lyons, B.P. Sandford, R.D. Ledgerwood, and S. Sebring. 2012. A system-wide evaluation of avian predation on juvenile salmonid in the Columbia River Basin based on recoveries of passive integrated transponder tags. Transactions of the American Fisheries Society 141:975-989.

Evans, A.F., N.J. Hostetter, and K. Collis. 2013. Caspian tern predation on Upper Columbia River steelhead in the Priest Rapids Project: a retrospective analysis of data from 2008-2010. Final Report to Grant County Public Utility District No. 2 and Blue Leaf Environmental, Inc. Available on-line at www.birdresearchnw.org.

Gaston, A. J., and G. E. J. Smith. 1984. The interpretation of aerial surveys for seabirds: Some effects of behavior. Canadian Wildlife Service Occasional Paper 53:1-20.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian Data Analysis, Second Edition. CRC Press.

Good, Phillip I. 2005. Permutation, Parametric and Bootstrap Tests of Hypotheses, 3rd ed., Springer.

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

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

Hughes, J.S., M.A. Weiland, C.M. Woodley, GR Ploskey, S.M. Carpenter, M.J. Hennen, E.F. Fischer, G.W. Batten III, T.J. Carlson, A.W. Cushing, Z. Deng, D.J. Etherington, T Fu, MJ Greiner, M Ingraham, J Kim, X Li, J Martinez, TD Mitchell, B Rayamajhi, A Seaburg, JR Skalski, RL Townsend, KA Wagner, and SA Zimmerman. 2013. Survival and passage of yearling and subyearling Chinook salmon and steelhead at McNary Dam, 2012. PNNL-22788. Report submitted by the Pacific Northwest National Laboratory to the U.S. Army Corps of Engineers, Walla Walla, Washington.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator swamping strategy. American Naturalist 136:485–498.

Lyons, D.E., D.D. Roby, A.F. Evans, N.J. Hostetter, and K. Collis. 2014. Benefits to Columbia River anadromous salmonids from potential reductions in predation by double-crested cormorants nesting at the East Sand Island colony in the Columbia River estuary. Report to the U.S. Army Corps of Engineers, Portland District, Portland, OR.

Martinson, R.D., G.M. Kovalchuk, and D. Ballinger. 2010. Monitoring of downstream salmon and steelhead at Federal Hydroelectric Facilities. Annual Report. Project No. 87-127-01, Pacific States Marine Fisheries Commission, The Dalles, Oregon.

McMichael, G.A., B.M. Eppard, T.J. Carlson, B.D. Ebberts, R.S. Brown, M. Weiland, G.R. Ploskey, R.A. Harnish, and Z.D. Deng. 2010. The Juvenile Salmon Acoustic Telemetry System: A New Tool. Fisheries 35: 9-22.

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

NMFS (National Marine Fisheries Service). 2004. Biological Opinion and Magnuson-Steven Fishery Conservation and Management Act. Interim Protection Plan for Operation of the Priest Rapids Hydroelectric Project. May 3, 2004.

NOAA Fisheries. 2008. Biological Opinion (BiOp) on the operation of the Federal Columbia River Power System (FCRPS). U.S. Department of Commerce, National Marine Fisheries Service, Northwest Regional Office, Seattle, Washington.

Osterback, A.-M.K., D.M. Frechette, A.O. Shelton, S.A. Hayes, M.H. Bond, S.A. Shaffer, and J.W. Moore. 2013. High predation on small populations: Avian predation on imperiled salmonids. Ecosphere 4:art116.

Parrish, J. K. (Ed.) 2006. Avian predation final report: 2002-2004. Report to the Chelan County Public Utility District, University of Washington, Seattle, WA.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990a. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317–322 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Rieman, B.E., R.C. Beamesderfer, S. Viggs, and T.P. Poe. 1991. Estimated loss of juvenile salmonids by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:44-458.

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

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

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

Sebring, S.H., M.C. Carper, R.D. Ledgerwood, B.P. Sandford, G.M. Matthews, and A.F. Evans. 2013. Relative vulnerability of PIT-tagged subyearling fall Chinook salmon to predation by Caspian terns and double-crested cormorants in the Columbia River estuary. Transactions of the American Fisheries Society 142:1321-1334.

Skalski, J. R., R. Townsend, J. Lady, A. E. Georgi, J. R. Stevenson, and R. D. McDonald. 2002. Estimating route specific passage and survival probabilities at a hydroelectric project from smolt radio telemetry studies. Canadian Journal of Fisheries and Aquatic Sciences 59:1385-1393.

Skalski, JR, RL Townsend, AG Seaburg, JS Hughes, MA Weiland, GR Ploskey, CM Woodley, Z Deng, and TJ Carlson. 2012. Compliance monitoring of yearling and subyearling Chinook salmon and juvenile steelhead survival and passage at McNary Dam, 2012. PNNL-22125, Pacific Northwest National Laboratory, Richland, Washington.

Skalski, JR, RL Townsend, MA Weiland, CM Woodley, and J Kim. 2014a. Compliance monitoring of yearling and subyearling Chinook salmon and juvenile steelhead survival and passage at McNary Dam, 2014. PNNL-23979, Pacific Northwest National Laboratory, Richland, Washington.

Skalski JR, RL Townsend, MA Weiland, CM Woodley, and J Kim. 2014b. Compliance monitoring of subyearling Chinook salmon survival and passage at John Day Dam, 2014. PNNL-23951, Pacific Northwest National Laboratory, Richland, Washington.

Skalski, J.R., R. Townsend, J.M. Lady, M.A. Timko, L.S. Sullivan, K. Hatch. 2015. Survival of acoustic-tagged steelhead and yearling Chinook salmon smolts through the Wanapum-Priest Rapids Project in 2014. Report prepared for Public Utility District No. 2 of Grant County, Washington by Columbia Basin Research, University of Washington, Seattle, Washington and Blue Leaf Environmental, Inc, Ellensburg, Washington.

Smith, S.G, W.D. Muir, D.M. Marsh and J.G. Williams. 2006. Survival estimates for the passage of spring-migrating juvenile salmonids through the Snake and Columbia River dams and reservoirs, 2005. Report to Bonneville Power Administration. Available on-line at http://www.nwfsc.noaa.gov/assets/26/1267_07072010_153149_Smith.et.al.2006-rev.pdf

Sólymos, P. 2010. dclone: Data Cloning in R. The R Journal, 2(2), 29-37. URL http://CRAN. R-project. org/package= dclone

Su, Y. S., and M. Yajima. 2012. R2jags: A Package for Running jags from R. R package version 0.03-08, URL http://CRAN. R-project. org/package= R2jags.

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

Timko, M.A., L.S. Sullivan, S.E. Rizor, R.R. O'Connor, C.D. Wright, J.L. Hannity, C.A. Fitzgerald, M.M. Meagher, J.D. Stephenson, and J.R. Skalski, R.L. Townsend. 2011. Behavior and survival analysis of juvenile steelhead and sockeye salmon through the Priest Rapids Project in 2010. Report prepared for Public Utility District No. 2 of Grant County, Washington by Blue Leaf Environmental, Inc., Ellensburg, Washington.

USACE (U.S. Army Corps of Engineers). 2014. Inland Avian Predation Management Plan: Environmental Assessment, January 2014. U.S. Army Corps of Engineers, Walla Walla District, Northwestern Division, Walla Walla, Washington.

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

Weiland, M.A., C.M. Woodley, J.S. Hughes, E.F. Fischer, K.D. Hand, J. Kim, B. Rayamajhi, K.A. Wagner, S.A. Zimmerman, G.W. Batten III, T.J. Carlson, Z. Deng, D.J. Etherington, T. Fu, M.J. Greiner, J.M. Ingraham, X. Li, J.J. Martinez, J.R. Skalski, R.L. Townsend, and T.L. Lockhart. 2015. Survival and passage of yearling and subyearling Chinook salmon and steelhead at McNary Dam, 2014. Draft final report submitted by the Pacific Northwest National Laboratory to the U.S. Army Corps of Engineers, Walla Walla, Washington.

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

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16:446–453.

Zorich, N.A., M.R. Jonas, and P.L. Madson. 2011. Avian predation at John Day and The Dalles dams 2010: Estimating fish consumption using direct observations and diet analysis. Report to the U.S. Army Corps of Engineers, Portland District, Portland, Oregon.

APPENDICES

APPENDIX A: PIT tags recovered on bird breeding colonies by location and year

Table A1. Numbers of tagged juvenile steelhead (Sthd), yearling Chinook salmon (Chin 1), and subyearling Chinook salmon (Chin 0) released into the lower Snake River, middle Columbia River, and lower Columbia River that were subsequently recovered on bird colonies in 2012 and 2014, including colonies located outside of the study area (i.e., those depicted in Figure 1). Recoveries include tags found on breeding colonies and tags found on avian loafing/roosting sites. Bird species include Caspian terns (CATE), California and ring-billed gulls (Gulls), double-crested cormorants (DCCO), Brandt's cormorants (BRAC), and American white pelicans (AWPE). At loafing sites the species of avian predator was unknown (Unid). Asterisks indicate that a site was not scanned the same year that tagged smolts were released.

					2012			2014	
Location	**Avian Species**	**RKM**	**Type**	**Chin 0**	**Chin 1**	**Sthd**	**Chin 0**	**Chin 1**	**Sthd**
Twinning Island	CATE	NA	Nesting	*	*	*		1	5
Goose Island	CATE	NA	Nesting			1		1	12
	Gulls	NA	Nesting				*	*	*
	Unid	NA	Loafing	1					
North Potholes Res.	DCCO	NA	Nesting				*	*	*
Cabin Island	Unid	638	Loafing	*	*	*			
Unnamed Island	Unid	603	Loafing	*	*	*			
Island 20	Gulls	549	Nesting	*	*	*			4
Foundation Island	DCCO	518	Nesting	1	6	10		1	
	Unid	518	Loafing				*	*	*
Badger Island	AWPE	512	Nesting	1	2	4			4
	Unid	512	Loafing			2	*	*	*
Crescent Island	CATE	510	Nesting	33	7	53	1	7	55
	Gulls	510	Nesting	2	2	15		5	20
	Unid	510	Loafing	1					1
Anvil Island	CATE	440	Nesting	1*	4*	15*	33	8	38
	Gulls	440	Nesting	1*	*	1*	2	4	26
	Unid	440	Loafing	*	1*	8*	14	3	16
Sand Island	Unid	440	Loafing	*	*	*			
Straight Six Island	Gulls	439	Nesting	*	*	*		1	1
Miller Rocks Island	Gulls	331	Nesting	14	1	34	19	11	58
East Sand Island	CATE	8	Nesting	37	63	367	4	42	279
	DCCO	8	Nesting	78	48	15	43	194	193
	BRAC	8	Nesting	4	1	2	2	3	6

APPENDIX B: Avian predation rates by bird breeding colony and year

Table B1. Estimated predation rates (95% creditable intervals) of juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon released into the lower Snake River, lower Columbia River, and middle Columbia River and subsequently consumed by piscivorous colonial waterbirds during 2012 and 2014. Asterisks indicate river segments where releases of study fish occurred. N depicts the number of tagged fish alive at the upstream array within each river segment evaluated. Bird species and colonies included Caspian terns (CATE) nesting on Twinning Island (TWI), Goose Island (GSI), Crescent Island (CSI), and Anvil Island (ANI); California and ring-billed gulls (Gulls) nesting on Island 20 (I20), CSI, ANI, Straight Six Island (SIX), and Miller Rocks (MRI); double-crested cormorants (DCCO) nesting on Foundation Island (FDI); and American white pelicans (AWPE) nesting on Badger Island (BGI). Estimates of total mortality (1-survival) and the percentage of total mortality explained by colonial waterbird predation (% Colonies) are also provided.

2012 Steelhead Predation Rates in the Lower Snake and Columbia Rivers												
Spatial-Scale	Rkms	N	DCCO FDI	AWPE BGI	CATE CSI	Gulls CSI	Gulls MRI	CATE GSI	All Colonies	Total Mortality	% Colonies[1]
Segment *	562-525	1,002	5.4% (3.0-8.7)	0.2% (0.1-0.5)	2.8% (1.7-4.8)	6.2% (2.5-10.6)		0.6% (0.1-1.9)	16.1% (10.6-18.9)	19.1% (18.8-19.1)	84.8%
Segment	525-472	811	0.4% (0-1.2)	0% (0-0.2)	4.7% (3.1-6.5)	4.8% (2.1-10.2)			10% (6.9-15)	15.5% (15.5-15.8)	64.5%
Segment*	503-472	1,400	0.1% (0-0.6)	<0.1%	1.9% (1.3-2.9)	1.9% (0.8-4.2)			4.1% (2.6-6.2)	6.5% (6.4-6.5)	64.5%
McNary Near Dam	472-468	1,994	0.2% (0-0.8)	0.1% (0-0.2)	0.1% (0-0.4)	1.1% (0.4-1.9)			1.6% (0.7-2.3)	2.5% (2.3-2.5)	63.7%
McNary Reservoir	525-472	811	0.4% (0-1.2)	0% (0-0.2)	4.7% (3.1-6.5)	4.8% (2.1-10.2)			10% (6.9-15)	15.5% (15.5-15.8)	64.5%
McNary Project	525-470	811	0.4% (0-1.5)	0% (0-0.3)	4.7% (3.1-6.6)	4.9% (2.2-10.6)			10.4% (7.3-15.2)	16.0% (16-16.3)	64.9%
Segment	470-468	1,986	0.1% (0-0.8)	<0.1%	0.1% (0-0.3)	1.0% (0.3-1.7)			1.3% (0.4-2.0)	2.1% (1.9-2.2)	62.8%
Segment*	468-422	3,143		0% (0-0.2)			0.5% (0.1-1.6)		0.5% (0.2-1.6)	7.7% (7.7-7.8)	7.4%
Segment*	422-351	4,100					0.8% (0.3-1.9)		0.8% (0.3-1.9)	5.5% (5.5-5.6)	13.7%
John Day Near Dam	351-346	3,874					1.5% (0.9-2.2)		1.5% (0.9-2.2)	2.6% (2.5-2.6)	61.2%
John Day Reservoir	468-351	3,143		0% (0-0.2)			1.3% (0.6-2.5)		1.3% (0.6-2.6)	12.5% (12.5-12.7)	10.8%
John Day Project	468-349	3,143		0% (0-0.2)			1.5% (0.8-2.8)		1.6% (0.8-2.9)	12.9% (12.9-13)	12.0%
Segment	349-346	3,858					1.3% (0.7-1.9)		1.3% (0.7-1.9)	2.2% (2.0-2.2)	62.5%
Segment*	346-325	4,776					0.9% (0.5-1.1)		0.9% (0.5-1.1)	1.1% (1.0-1.1)	82.4%
Reach (Total)	562-325	1,002	6.0% (3.3-9.1)	0.3% (0.1-0.7)	6.8% (4.8-9.0)	11.3% (6.8-16.7)	2.4% (1.5-3.6)	0.6% (0.1-1.9)	27.7% (21.9-32.2)	44.2% (44.1-44.2)	62.5%

2012 Yearling Chinook Predation Rates in the Lower Snake and Columbia Rivers											
Spatial-Scale	Rkm	N	DCCO FDI	AWPE BGI	CATE CSI	Gulls CSI	Gulls MRI	CATE GSI	All Colonies	Total Mortality	% Colonies[1]
Segment *	562-525	1,001	1.7% (0.6-4.9)	0.3% (0.2-0.7)	0.5% (0.2-1.2)	0.4% (0-3.1)		0.2% (0-1.4)	3.7% (1.7-7.2)	8.9% (8.7-8.9)	42.7%
Segment	525-472	912	1.2% (0.4-3.3)	0% (0-0.2)	0.9% (0.3-2.4)	0.3% (0-2.2)			2.9% (1.4-5.4)	9.5% (9.5-9.7)	30.9%
Segment*	503-472	1,399	0.1% (0-0.5)	<0.1%	0.3% (0.2-0.6)	0.1% (0-0.3)			0.6% (0.3-1.0)	1.5% (1.5-1.5)	30.9%
McNary Near Dam	472-468	2,203	0.4% (0.1-0.9)	<0.1%	0% (0-0.3)	0.9% (0.3-1.6)			1.4% (0.7-2.1)	2.2% (2.0-2.2)	64.6%
McNary Reservoir	525-472	912	1.2% (0.4-3.3)	0% (0-0.2)	0.9% (0.3-2.4)	0.3% (0-2.2)			2.9% (1.4-5.4)	9.5% (9.5-9.7)	30.9%
McNary Project	525-470	912	1.2% (0.4-3.3)	0% (0-0.3)	1.0% (0.3-2.4)	0.4% (0-2.3)			3.0% (1.5-5.4)	9.8% (9.6-9.8)	32.5%
Segment	470-468	2,197	0.3% (0-0.9)	<0.1%	0% (0-0.3)	0.8% (0.2-1.5)			1.2% (0.5-1.9)	1.9% (1.8-2.0)	65.1%
Segment*	468-422	3,353		<0.1%			0.2% (0-0.7)		0.2% (0-0.7)	7.1% (7.1-7.2)	2.5%
Segment*	422-351	4,314					0.3% (0-0.9)		0.3% (0-0.9)	4.6% (4.6-4.7)	5.5%
John Day Near Dam	351-346	4,116					0.8% (0.3-1.7)		0.8% (0.3-1.7)	3.1% (3-3.1)	25.8%
John Day Reservoir	468-351	3,353		<0.1%			0.4% (0.1-1.3)		0.5% (0.1-1.3)	11% (11-11.1)	4.0%
John Day Project	468-349	3,353		<0.1%			0.5% (0.1-1.4)		0.5% (0.1-1.4)	11.1% (11.1-11.2)	4.3%
Segment	349-346	4,113					0.8% (0.3-1.6)		0.8% (0.3-1.6)	3.0% (3.0-3.0)	25.4%
Segment*	346-325	4,986					0.1% (0-0.6)		0.1% (0-0.6)	0.8% (0.6-0.8)	8.9%
Reach (Total)	562-325	1,001	3.4% (1.8-6.9)	0.4% (0.2-0.8)	1.4% (0.7-2.8)	1.7% (0.6-4.9)	1.2% (0.4-2.3)	0.2% (0-1.4)	9.1% (5.8-12.9)	31.9% (31.8-31.9)	28.5%

2012 Subyearling Chinook Predation Rates in the Lower Snake and Columbia Rivers											
Spatial-Scale	Rkm	N	DCCO FDI	AWPE BGI	CATE CSI	Gulls CSI	Gulls MRI	CATE GSI	All Colonies	Total Mortality	% Colonies[1]
Segment *	562-525	1,885	0.1% (0-0.6)	0% (0-0.2)	1.1% (0.7-1.8)	0.5% (0.1-2.4)		0% (0-0.2)	2% (1.2-3.7)	7% (6.9-7.0)	28.0%
Segment	525-472	4,277	0.1% (0-0.7)	<0.1%	0.7% (0.3-1.3)	0.4% (0-1.5)			1.3% (0.7-2.7)	5.8% (5.8-5.8)	28.1%
Segment*	503-472	2,524	0% (0-0.2)	<0.1%	0.5% (0.4-0.7)	0.2% (0-0.5)			0.7% (0.5-1.1)	2.1% (2.1-2.1)	28.1%
McNary Near Dam	472-468	4,124	0.1% (0-0.4)	<0.1%	0.3% (0.2-0.5)	0.2% (0-0.8)			0.6% (0.3-1.3)	2.4% (2.2-2.4)	22.5%
McNary Reservoir	525-472	4,277	0.1% (0-0.7)	<0.1%	0.7% (0.3-1.3)	0.4% (0-1.5)			1.3% (0.7-2.7)	5.8% (5.8-5.8)	28.1%
McNary Project	525-470	4,277	0.2% (0-0.8)	0.1% (0.1-0.2)	0.7% (0.4-1.3)	0.5% (0.1-1.6)			1.6% (1-2.9)	6% (5.8-6.2)	29.4%
Segment	470-468	4,116	0% (0-0.3)		0.2% (0.1-0.5)	0.1% (0-0.8)			0.5% (0.2-1.1)	2.2% (2.1-2.3)	19.9%
Segment*	468-422	6,019					0.1% (0-0.6)		0.1% (0-0.6)	7.4% (7.4-7.5)	1.8%
Segment*	422-351	7,557					0.1% (0-0.6)		0.1% (0-0.6)	5.3% (5.3-5.3)	1.8%
John Day Near Dam	351-346	7,160					0.6% (0.2-1.3)		0.6% (0.2-1.3)	5.9% (5.8-5.9)	10.3%
John Day Reservoir	468-351	6,019					0.3% (0.1-0.8)		0.3% (0.1-0.8)	12.1% (12.1-12.2)	2.2%
John Day Project	468-349	6,019					0.3% (0.1-0.9)		0.3% (0.1-0.9)	12.2% (12.2-12.3)	2.5%
Segment	349-346	7,149					0.5% (0.2-1.2)		0.5% (0.2-1.2)	5.7% (5.6-5.8)	9.6%
Segment*	346-325	7,728					0.1% (0-0.3)		0.1% (0-0.3)	0.5% (0.5-0.6)	9.8%
Segment*	325-311	8,669					0.8% (0.4-0.8)		0.8% (0.4-0.8)	0.8% (0.8-0.8)	82.9%
Reach (Total)	562-325	1,885	0.4% (0.1-1.1)	0.1% (0.1-0.3)	2% (1.4-2.9)	1.3% (0.5-3.2)	1.1% (0.6-2.1)	0% (0-0.2)	5.1% (3.7-7.1)	33.1% (33-33.1)	15.4%

							2014 Steelhead Predation Rates in the Columbia River						
Spatial-Scale	Rkm	N	DCCO FDI	AWPE BGI	CATE CSI	Gulls CSI	CATE ANI	Gulls ANI	Gulls SIX	Gulls MRI	All Colonies	Total Mortality	% Colonies[1]
Segment*	503-498	2,499	<0.1%	<0.1%	0.2% (0.1-0.4)	0.6% (0.2-0.9)					0.8% (0.4-1)	1.0% (1.0-1.0)	76.9%
Segment	498-489	2,473	<0.1%	<0.1%	0.2% (0.1-0.4)	0.3% (0-0.6)					0.5% (0.3-0.9)	0.9% (0.9-0.9)	60.9%
Segment	489-480	2,450	<0.1%	<0.1%	0.4% (0.2-0.7)	0.5% (0.1-1.1)	0.1% (0-0.3)				1% (0.5-1.6)	1.6% (1.6-1.6)	63.3%
Segment	480-472	2,411	<0.1%	<0.1%	<0.1%	0.3% (0-0.6)	0.1% (0-0.3)				0.5% (0.2-0.7)	0.7% (0.7-0.7)	58.8%
McNary Near-Dam	472-468	2,394	0.6% (0-2.3)	0.1% (0-0.3)	0% (0-0.2)	1.4% (0.6-2.5)	0% (0-0.2)				2.5% (1.3-3.4)	3.6% (3.6-3.6)	69.8%
Segment	470-468	2,386	0.6% (0-2.3)	0% (0-0.2)	0% (0-0.2)	1.3% (0.6-2.4)	<0.1%				2.3% (1.1-3.3)	3.3% (3.2-3.3)	72.4%
Segment*	468-455	4,307		0.1% (0.1-0.2)			0.1% (0-0.2)	0.1% (0-0.6)			0.4% (0.2-0.8)	2.1% (2.1-2.2)	19.6%
Segment	455-449	4,215					<0.1%	0.4% (0.1-0.7)			0.4% (0.1-0.8)	0.8% (0.8-0.8)	51.5%
Segment*	449-439	6,182					0.2% (0.1-0.5)	1% (0.5-1.7)	0.1% (0-0.3)		1.3% (0.8-2)	2.7% (2.5-2.8)	48.9%
Segment	439-422	6,017					0.5% (0.3-0.9)	1.3% (0.6-2.6)	0.1% (0-0.3)		1.9% (1.1-3.2)	4.7% (4.5-4.9)	40.4%
Segment	422-412	5,734					<0.1%	0.2% (0-0.5)	0.1% (0-0.4)		0.3% (0.1-0.6)	0.7% (0.7-0.7)	42.5%
Segment	412-381	5,694					0.2% (0.1-0.3)	0.1% (0-0.3)	0.2% (0.1-0.6)	0.1% (0-0.5)	0.6% (0.3-1.1)	2.2% (2.2-2.2)	24.4%
Segment	381-351	5,567					<0.1%	0.1% (0-0.4)		1.3% (0.8-1.8)	1.5% (0.9-1.8)	1.9% (1.9-1.9)	79.1%
John Day Near-Dam	351-346	5,461					<0.1%			1.4% (0.8-2.0)	1.4% (0.9-2.0)	1.4% (0.8-2.4)	85.0%
John Day Resevoir	468-351	4,307		0.1% (0.1-0.2)			1% (0.7-1.5)	2.8% (1.9-4)	0.4% (0.2-1)	1.2% (0.7-1.7)	5.6% (4.4-6.9)	13.3% (13.3-13.3)	41.9%
John Day Project	468-349	4,307		0.1% (0.1-0.2)			1% (0.7-1.5)	2.8% (1.9-4)	0.4% (0.2-1)	1.3% (0.8-1.8)	5.8% (4.4-7.0)	13.5% (13.5-13.5)	41.9%
Segment	349-346	5,445					<0.1%			1.2% (0.7-1.8)	1.1% (0.7-1.8)	1.2% (0.5-2.1)	81.3%
Segment	346-325	5,384					<0.1%			0.2% (0-0.7)	0.2% (0-0.7)	1.2 % (0.1-1.8)	15.4%
Segment	325-311	5,323					<0.1%			0.2% (0-0.5)	0.2% (0.1-0.5)	0.3% (0-0.5)	68.3%
Reach (Total)	503-311	2,499	0.6% (0-2.2)	0.2% (0-0.4)	0.8% (0.6-1.3)	3.1% (2.1-4.5)	1.1% (0.8-1.6)	2.2% (1.5-3.3)	0.4% (0.1-0.8)	2.2% (1.4-3)	10.9% (9.2-	20.2% (20-20.4)	53.1%
							2014 Yearling Chinook Predation Rates in the Columbia River						
Spatial-Scale	Rkm	N	DCCO FDI	AWPE BGI	CATE CSI	Gulls CSI	CATE ANI	Gulls ANI	Gulls SIX	Gulls MRI	All Colonies	Total Mortality	% Colonies[1]
Segment*	503-498	2,500	<0.1%	<0.1%	0.2% (0.1-0.4)	0.3% (0.1-0.5)	0% (0-0)				0.6% (0.3-0.7)	0.7% (0.7-0.7)	72.2%
Segment	498-489	2,482	<0.1%	<0.1%	0% (0-0.2)	0.1% (0-0.4)	0% (0-0)				0.2% (0-0.4)	0.4% (0.4-0.4)	36.4%
Segment	489-480	2,471	<0.1%	<0.1%	0.2% (0.1-0.4)	0.2% (0-0.6)	0% (0-0.2)				0.4% (0.1-0.9)	1.1% (1.1-1.1)	37.0%
Segment	480-472	2,444	<0.1%	<0.1%	<0.1%	0.1% (0-0.4)	0% (0-0.2)				0.2% (0-0.5)	0.5% (0.5-0.5)	45.5%
McNary Near-Dam	472-468	2,433	0.6% (0.1-2)	<0.1%	0% (0-0.2)	0.7% (0.1-2.3)	0% (0-0.2)				1.7% (0.6-2.9)	3.3% (3.3-3.3)	59.3%
Segment	470-468	2,423	0.6% (0.1-2)	<0.1%	0% (0-0.2)	0.6% (0.1-2.2)	0% (0-0.2)				1.5% (0.4-2.9)	2.9% (2.9-3.1)	61.1%
Segment*	468-455	4,352		<0.1%			<0.1%	0.1% (0-0.3)			0.1% (0-0.4)	0.4% (0.4-0.4)	31.6%
Segment	455-449	4,333					<0.1%	0.1% (0-0.4)			0.2% (0-0.4)	0.4% (0.4-0.4)	42.1%
Segment*	449-439	6,316					<0.1%	0.1% (0-0.7)	0.2% (0-0.6)		0.3% (0.1-1)	2.5% (2.3-2.9)	13.8%
Segment	439-422	6,159					0.1% (0.1-0.1)	0.3% (0.1-0.9)	0.1% (0-0.4)		0.5% (0.2-1.1)	4.6% (4.2-4.7)	10.5%
Segment	422-412	5,878						0.2% (0-0.6)	0.1% (0-0.5)		0.3% (0.1-0.7)	1.1% (1.1-1.1)	24.2%
Segment	412-381	5,812					<0.1%	0.1% (0-0.4)	0% (0-0.4)	0.2% (0.1-0.8)	0.4% (0.1-1.2)	2.2% (2.2-2.2)	20.9%
Segment	381-351	5,683						0.2% (0-0.6)		0.1% (0-0.4)	0.3% (0.1-0.8)	2% (2.0-2.1)	17.9%
John Day Near-Dam	351-346	5,571								0.8% (0.3-1.6)	0.8% (0.3-1.6)	1.7% (1.2-2.3)	40.0%
John Day Resevoir	468-351	4,352		<0.1%			0.2% (0.1-0.3)	1.2% (0.6-2)	0.4% (0-1.1)	0.3% (0.1-0.8)	2.1% (1.3-3.1)	12% (12-12.1)	18.2%
John Day Project	468-349	4,352		<0.1%			0.2% (0.1-0.3)	1.2% (0.6-2)	0.4% (0-1.1)	0.4% (0.1-1)	2.3% (1.5-3.2)	12.2% (12.2-12.3)	19.1%
Segment	349-346	5,556								0.6% (0.2-1.5)	0.6% (0.2-1.5)	1.4% (1.0-2.0)	35.1%
Segment	346-325	5,476					<0.1%			0.2% (0-0.7)	0.2% (0-0.7)	2.0% (1.4-2.4)	10.0%
Segment	325-311	5,369					<0.1%			0.1% (0-0.4)	0.1% (0-0.4)	0.3% (0-0.7)	27.3%
Reach (Total)	503-311	2,500	0.6% (0.1-1.9)	0.1% (0-0.3)	0.5% (0.3-0.8)	1.5% (0.6-2.9)	0.2% (0.1-0.4)	1.1% (0.6-1.8)	0.3% (0-0.9)	1.1% (0.5-1.9)	5.8% (4.2-7.4)	20.3% (20.0-20.6)	29.5%

2014 Subyearling Chinook Predation Rates in the Columbia River													
Spatial-Scale	Rkm	N	DCCO FDI	AWPE BGI	CATE CSI	Gulls CSI	CATE ANI	Gulls ANI	Gulls SIX	Gulls MRI	All Colonies	Total Mortality	% Colonies[1]
Segment*	503-498	2,517	<0.1%	<0.1%	0% (0-0.2)	0.2% (0-0.5)					0.2% (0-0.5)	0.6% (0.5-0.6)	29.7%
Segment	498-489	2,503	<0.1%	<0.1%	0.1% (0-0.2)	0.1% (0-0.4)					0.2% (0-0.5)	0.5% (0.5-0.5)	38.5%
Segment	489-480	2,490	<0.1%	<0.1%	<0.1%	0.1% (0-0.4)	0.1% (0-0.3)				0.2% (0.1-0.5)	0.5% (0.5-0.5)	46.2%
Segment	480-472	2,477	<0.1%	<0.1%	<0.1%	0.1% (0-0.4)	<0.1%				0.2% (0-0.5)	0.5% (0.5-0.5)	41.7%
McNary Near-Dam	472-468	2,465	0.2% (0-1.2)	<0.1%	0.6% (0.4-1.1)	0.2% (0-0.9)	0.1% (0-0.3)				1.4% (0.8-2.5)	7.1% (7.1-7.1)	17.7%
Segment	470-468	2,457	0.2% (0-1.2)	<0.1%	0.6% (0.4-1.1)	0.1% (0-0.7)	0.1% (0-0.3)				1.2% (0.7-2.3)	6.8% (6.8-6.9)	16.1%
Segment*	468-455	4,285					0.2% (0.1-0.3)	0.2% (0-0.8)			0.4% (0.2-1)	1.3% (1.3-1.4)	36.8%
Segment	455-449	4,228					0.2% (0.1-0.4)	0.1% (0-0.5)			0.3% (0.2-0.7)	1.6% (1.5-1.6)	14.9%
Segment*	449-439	6,158					0.4% (0.2-0.6)	0.2% (0-0.6)	0.1% (0-0.4)		0.6% (0.4-1.2)	4.2% (4.1-4.3)	12.3%
Segment	439-422	5,900					0.2% (0.1-0.4)	0.1% (0-0.6)	0.1% (0-0.3)		0.4% (0.2-0.9)	6.6% (6.5-6.7)	4.3%
Segment	422-412	5,510					<0.1%	0.1% (0-0.5)	0.1% (0-0.4)		0.2% (0.1-0.6)	1% (0.9-1.0)	16.1%
Segment	412-381	5,454					<0.1%	0.1% (0-0.5)	0% (0-0.4)	0.1% (0-0.5)	0.3% (0.1-1.0)	5.7% (5.6-5.7)	5.2%
Segment	381-351	5,144					0.1% (0-0.2)	0% (0-0.3)		0.3% (0.1-0.7)	0.4% (0.2-0.9)	8.5% (8.5-8.6)	5.3%
John Day Near-Dam	351-346	4,706					<0.1%			0.3% (0-0.8)	0.3% (0.1-0.9)	9.3% (9.2-9.4)	2.3%
John Day Resevoir	468-351	4,285					1% (0.7-1.3)	1% (0.3-1.9)	0.3% (0-0.6)	0.4% (0.1-0.9)	2.6% (1.9-3.9)	25.5% (25.4-25.5)	9.8%
John Day Project	468-349	4,285					1% (0.7-1.3)	1% (0.3-1.9)	0.3% (0-0.6)	0.4% (0.2-1)	2.7% (1.9-4)	26.2% (26.1-26.2)	9.8%
Segment	349-346	4,661					<0.1%			0.1% (0-0.8)	0.2% (0-0.8)	8.4% (8.4-8.5)	1.3%
Segment*	346-325	5,249					<0.1%			0.1% (0-0.4)	0.1% (0-0.5)	1.3% (1.3-1.4)	7.2%
Segment*	325-311	6,162					<0.1%			0.2% (0-0.6)	0.2% (0-0.6)	1.4% (1.2-1.4)	22.7%
Reach (Total)	503-311	2,517	0.2% (0-1.2)	0.1% (0-0.2)	0.8% (0.5-1.3)	0.9% (0.3-1.7)	1.2% (0.8-1.7)	0.9% (0.3-1.8)	0.2% (0-0.6)	0.7% (0.2-1.5)	5.2% (3.9-6.7)	41.3% (41.2-41.3)	11.9%

2014 Steelhead Predation Rates in the Middle Columbia River									
Spatial-Scale	Rkm	N	CATE TWI	CATE GSI	Gulls IS20	CATE CSI	All Colonies	Total Mortality	% Colonies[1]
Wanapum Project*	729-670	399	0.8% (0.3-3.8)	0.8% (0.3-2.9)			1.8% (0.6-4.8)	5.5% (5.3-5.5)	31.4%
Priest Rapids Project*[2]	670-639	1,148	0.2% (0-0.9)	0.5% (0.2-1.7)		0.3% (0.2-0.9)	1.1% (0.5-2.4)	3.8% (3.7-3.9)	25.0%
Segment*	639-625	1,654	0.1% (0-0.6)	0.2% (0.1-0.8)		0% (0-0.3)	0.4% (0.1-1.0)	2.7% (2.5-2.7)	13.6%
Segment	625-593	1,619	0.4% (0.1-1.6)	1.0% (0.6-1.9)		0% (0-0.2)	1.5% (0.9-2.8)	4.2% (4.1-4.3)	35.6%
Segment	593-545	1,555	0.4% (0.1-1.3)	0.1% (0-0.4)	0.9% (0.1-2.2)	0.1% (0.1-0.5)	1.4% (0.6-2.8)	1.4% (0.6-2.9)	88.3%
Reach (Total)	729-545	399	2.0% (0.8-5.3)	2.3% (1-4.6)	0.5% (0-1.3)	0.5% (0.3-1.6)	5.5% (3.8-9.2)	17.3% (16.0-18.0)	31.8%

2014 Yearling Chinook Predation Rates in the Middle Columbia River									
Spatial-Scale	Rkm	N	CATE TWI	CATE GSI	Gulls IS20	CATE CSI	All Colonies	Total Mortality	% Colonies[1]
Wanapum Project*	729-670	398	0.3% (0-2.9)	0.3% (0-1.5)			0.8% (0-3.3)	3.8% (3.5-3.8)	17.1%
Priest Rapids Project*[2]	670-639	1,152	0.4% (0.1-1.6)	0.3% (0.1-0.7)		0% (0-0.3)	0.7% (0.3-1.9)	2.8% (2.7-2.8)	31.3%
Segment*	639-625	1,669	0.1% (0-0.8)	0.1% (0-0.4)		0% (0-0.2)	0.2% (0-0.8)	2.2% (2.1-2.2)	11.1%
Segment	625-593	1,633	0.1% (0-1.0)	0.1% (0-0.4)		0% (0-0.3)	0.2% (0-1.3)	1.8% (1.8-1.9)	13.8%
Segment	593-545	1,604	0.1% (0-0.6)	0.1% (0-0.4)	0.3% (0-1.4)	0% (0-0.3)	0.6% (0.1-1.7)	0.8% (0.1-1.7)	57.1%
Reach (Total)	729-545	398	1.5% (0.3-4)	0.5% (0-2)	0.3% (0-1.0)	0% (0-0.8)	2.8% (1.0-5.9)	12.2% (11.3-12.6)	23.4%

[1] Mortality due to bird predation is a median of the posterior distribution of avian mortality proportion estimates and therefore may be different from the median avian predation estimate divided by the median mortality estimate

[2] Assumes no mortality between the 669 and 670 arrays

APPENDIX C: Weekly reach-specific avian predation rates and total mortality

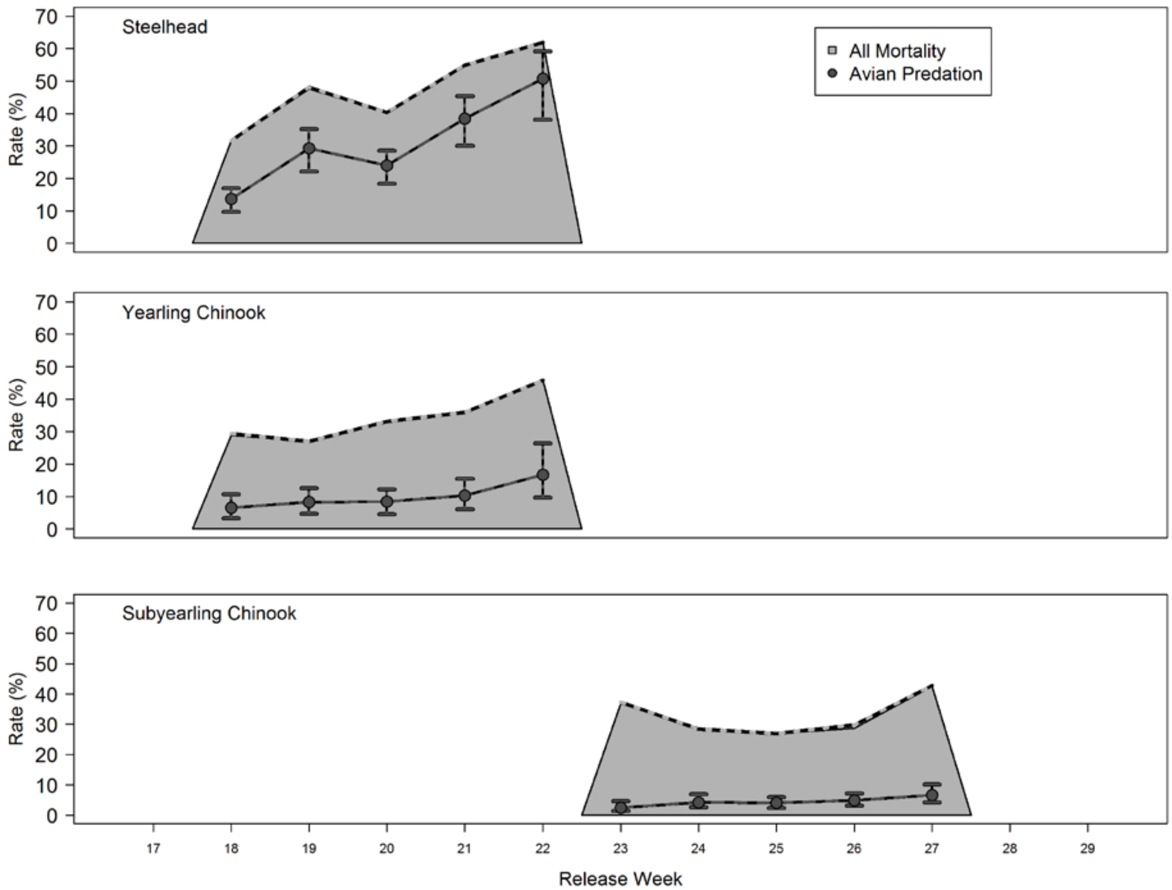

Figure C1. Weekly reach-specific avian predation rates (percentage of tagged fish consumed) and total mortality for tagged juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon released into the lower Snake River at river kilometer 562 in 2012. Release weeks are based on the Julian calendar, with week 17 starting on 23 April 2012.

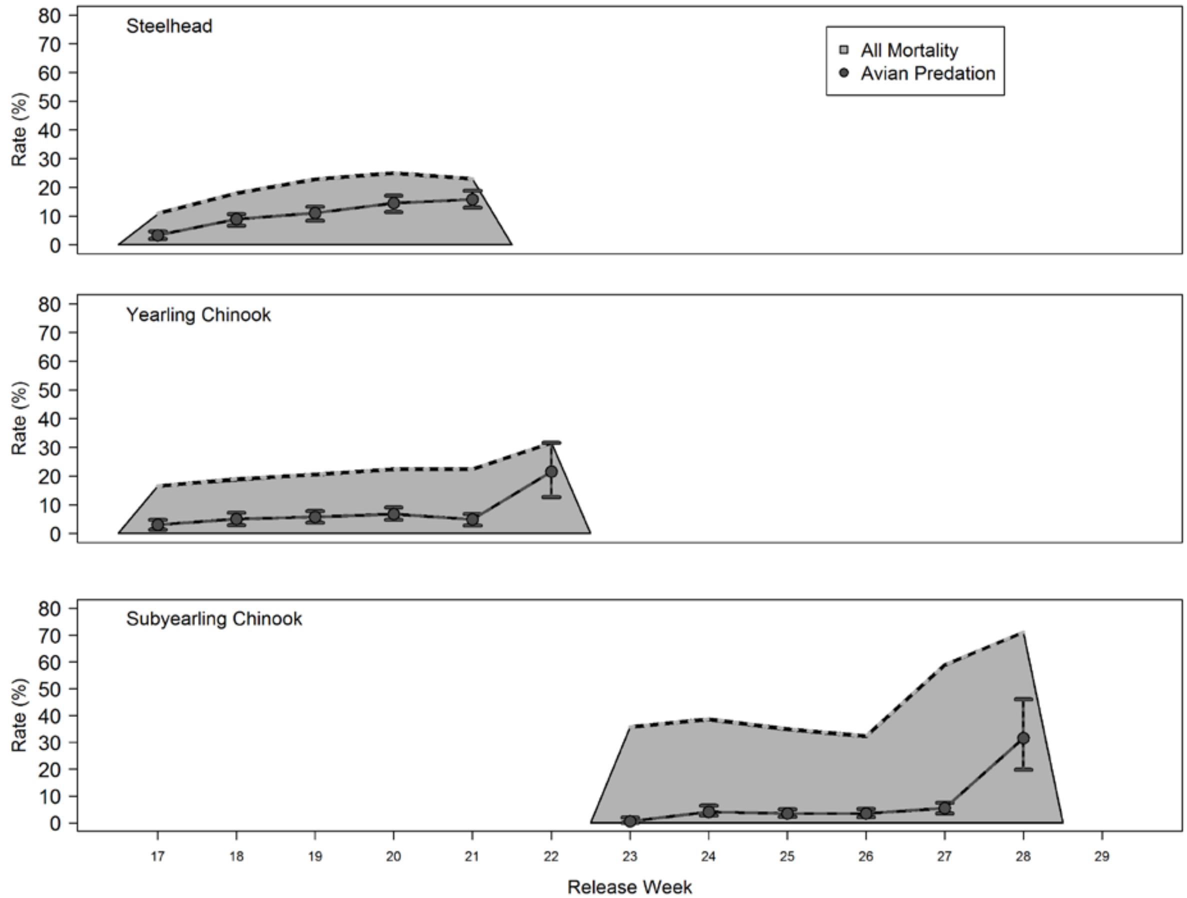

Figure C2. Weekly reach-specific avian predation rates (percentage of tagged fish consumed) and total mortality of tagged juvenile steelhead, yearling Chinook salmon, and subyearling Chinook salmon released into the lower Columbia River at river kilometer 503 in 2014. Release weeks are based on the Julian calendar, with week 17 starting on 24 April 2014.

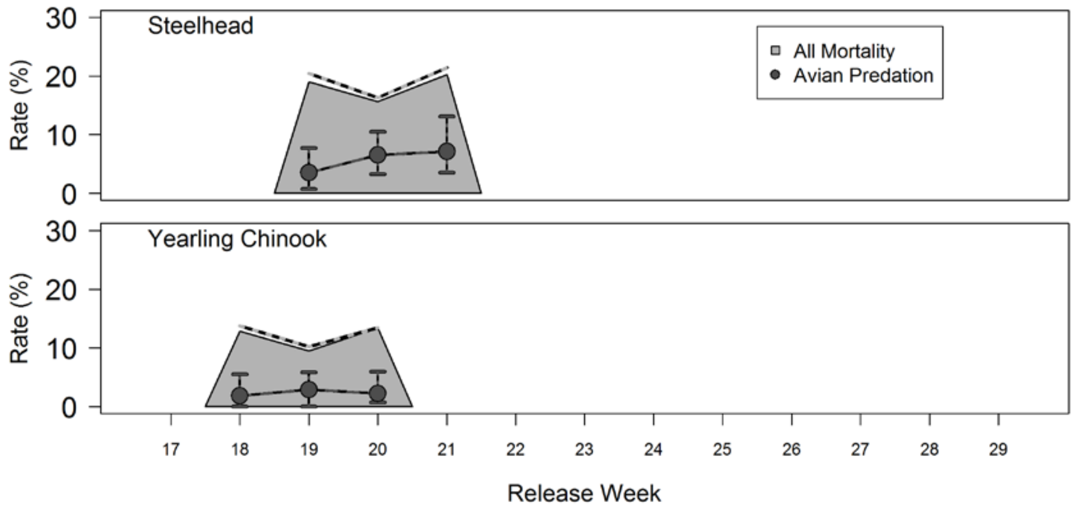

Figure C3. Weekly reach-specific avian predation rates (percentage of tagged fish consumed) and total mortality of tagged juvenile steelhead and yearling Chinook salmon released into the middle Columbia River at river kilometer 729 in 2014. Release weeks are based on the Julian calendar, with week 17 starting on 24 April 2014.