ARTICLE

Avian Predation on Juvenile Salmonids: Spatial and Temporal Analysis Based on Acoustic and Passive Integrated Transponder Tags

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Abstract

We evaluated the impact of predation on juvenile steelhead *Oncorhynchus mykiss* and yearling and subyearling Chinook Salmon *O. tshawytscha* by piscivorous waterbirds from 11 different breeding colonies in the Columbia River basin during 2012 and 2014. Fish were tagged with both acoustic tags and PIT tags and were tracked via a network of hydrophone arrays to estimate total smolt mortality (1 – survival) at various spatial and temporal scales during out-migration. Recoveries of PIT tags on bird colonies, coupled with the last known detections of live fish passing hydrophone arrays, were used to estimate the impact of avian predation relative to total smolt mortality. Results indicated that avian predation was a substantial source of steelhead mortality, with predation probability (proportion of available fish consumed by birds) ranging from 0.06 to 0.28 for fish traveling through the lower Snake River and the lower and middle Columbia River. Predation probability estimates ranged from 0.03 to 0.09 for available tagged yearling Chinook Salmon and from 0.01 to 0.05 for subyearlings. Smolt predation by gulls *Larus* spp. was concentrated

near hydroelectric dams, while predation by Caspian terns *Hydroprogne caspia* was concentrated within reservoirs. No concentrated areas of predation were identified for double-crested cormorants *Phalacrocorax auritus* or American white pelicans *Pelecanus erythrorhynchos*. Comparisons of total smolt mortality relative to mortality from colonial waterbirds indicated that avian predation was one of the greatest sources of mortality for steelhead and yearling Chinook Salmon during out-migration. In contrast, avian predation on subyearling Chinook Salmon was generally low and constituted a minor component of total mortality. Our results demonstrate that acoustic and PIT tag technologies can be combined to quantify where and when smolt mortality occurs and the fraction of mortality that is due to colonial waterbird predation relative to non-avian mortality sources.

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

To evaluate survival probabilities for juvenile salmonids, researchers tag 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, which are placed in lines perpendicular to the shore (referred to as "arrays"). Detection probabilities of AT-tagged fish passing arrays are often close to 1.0 (McMichael et al. 2010; 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 after release, the cause of fish mortality in relation to these spatial and temporal scales is generally unknown (Hughes et al. 2013).

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* that nest 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 that predation probability (the proportion of available fish that are consumed) was as high as 0.16 from Caspian terns nesting at a colony within commuting distance of the middle Columbia River in 2009. Hostetter et al. (2015) reported predation probabilities as high as 0.10 from California gulls nesting on an island in the lower Columbia River near John Day Dam in 2014.

Previous studies of avian predation on smolts have relied on PIT tag recoveries (detections) at bird colonies to estimate impacts on the survival of juvenile salmonids from the Columbia River basin (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012; Sebring et al. 2013; Hostetter et al. 2015). Unlike AT tags, which generally have a short tag life (e.g., 30 d; McMichael et al. 2010), PIT tags have an indefinite life (Prentice 1990), thus allowing them to be detected at a bird colony months or even years after consumption of the tagged fish and deposition of the PIT tags on the colony (Collis et al. 2001). The location of predation events based on PIT tag recoveries from bird colonies is often unknown because (1) 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 (2) PIT tag antennas are typically located at hydroelectric dams, resulting in a greater spatial distance between in-river PIT tag interrogation events relative to AT tag detections.

As part of JSATS survival studies conducted in the Columbia River basin during 2012 and 2014, researchers tagged smolts with both AT tags and PIT tags (double-tagging), thereby providing an opportunity to determine the proportion of total fish mortality (1 – survival) that could be attributed to predation by colonial waterbirds via tag recoveries from bird colonies. More specifically, the objectives of the present study were to (1) calculate avian predation rates on juvenile steelhead and yearling/subyearling Chinook Salmon at different spatial and temporal scales in the Columbia River basin, (2) quantify unaccounted-for mortality (total mortality – mortality due to colonial waterbird predation) at these same spatial and temporal scales, and (3) identify specific areas within the river where predation impacts were elevated or concentrated (e.g., predation at dams or in particular river segments). Collectively, results were used to identify where and when smolt losses occurred during the out-migration period and the cause of smolt mortality (colonial waterbird predation or unaccounted-for mortality).

STUDY AREA

We investigated predation on double-tagged (hereafter, "tagged") juvenile steelhead and yearling/subyearling Chinook Salmon within three different sections or reaches of the Columbia River basin: (1) a 251-km section of the lower Snake and lower Columbia rivers (Figure 1) in 2012; (2) a 192-km section of the lower Columbia River (Figure 2) in
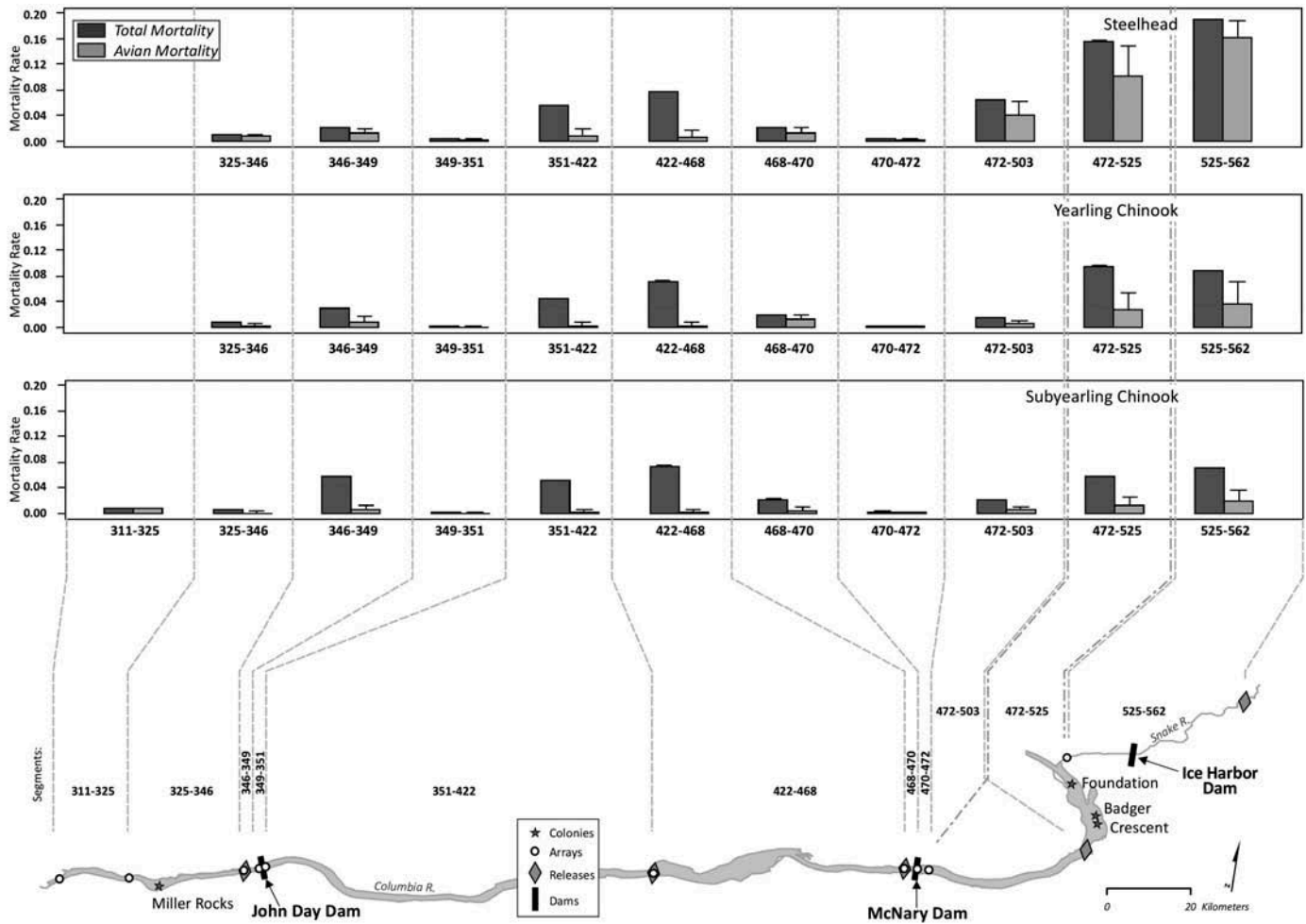
FIGURE 1. Estimated total mortality (+95% credible interval) of tagged juvenile steelhead, yearling Chinook Salmon, and subyearling Chinook Salmon in sections (x-axis labels = river kilometer range) of the lower Snake and lower Columbia rivers during 2012 and the estimated mortality of tagged smolts that was attributable to predation by birds from six breeding colonies. The map below the bar graphs depicts the locations of smolt release sites (diamonds), acoustic arrays (circles), bird colonies (stars), and hydroelectric dams (bars).

2014; and (3) a 184-km section of the middle Columbia River (Figure 3) in 2014. Acoustic arrays in the lower Columbia and lower Snake rivers were located below Ice Harbor Dam (river kilometer [rkm] 525) on the Snake River or upstream of McNary Dam (rkm 498 or 472, depending on the year) on the Columbia River to The Dalles Dam forebay (rkm 311) on the Columbia River. Acoustic arrays in the middle Columbia River spanned from Wanapum Dam (rkm 670) to an area near the confluence of the Snake and Columbia rivers (rkm 545).

METHODS

Fish Capture, Tagging, and Release

Details on the smolt collection, tagging, and release methods used in this study were presented by Hughes et al. (2013), Skalski et al. (2015), and Weiland et al. (2015). In brief, for releases on the

lower Snake and lower Columbia rivers, 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 at the juvenile bypass facilities as described by Martinson et al. (2010). Fish were examined to ensure that they met length (95–300 mm FL) and condition (no signs of disease; ≤20% descaling; no open wounds, hemorrhaging, or deformities) criteria reflecting fish suitability for acoustic tagging (Weiland et al. 2015). Fish were then anesthetized (tricaine methanesulfonate), implanted with an acoustic tag (Acoustic Telemetry Systems Model SS130/SS300; 11 × 5 × 3 mm) and a PIT tag (Biomark Model HPT12; 12 × 2 × 2 mm), and held in a recovery tank for 18–24 h. After recovery, fish were transported by truck and released from a boat at a designated release site. During 2012, releases in the lower Snake River occurred in Ice Harbor Reservoir at rkm 562; releases in the lower Columbia River
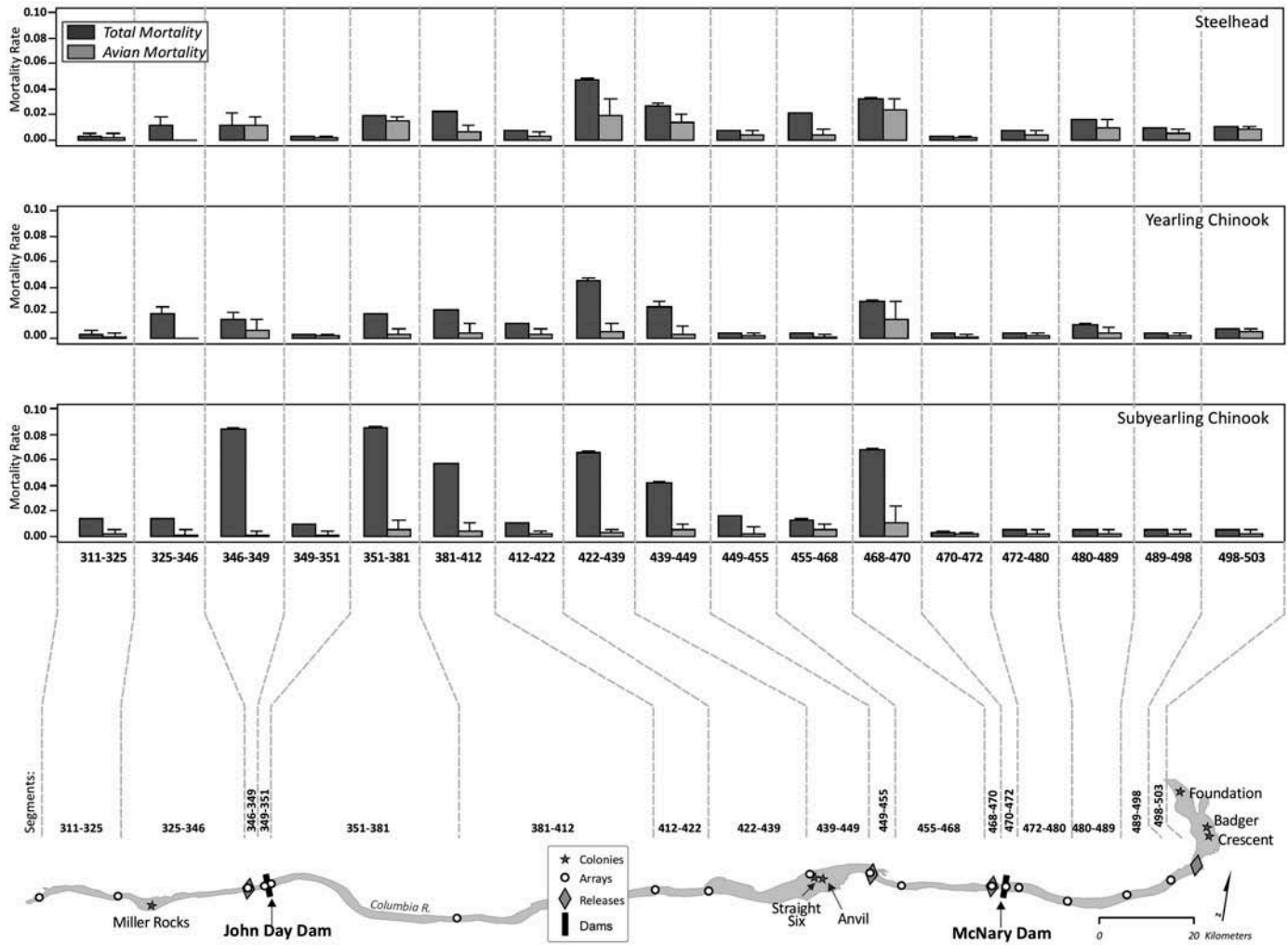
FIGURE 2. Estimated total mortality (+95% credible interval) of tagged juvenile steelhead, yearling Chinook Salmon, and subyearling Chinook Salmon in sections (x-axis labels = river kilometer range) of the lower Columbia River during 2014 and the estimated mortality of tagged smolts that was attributable to predation by birds from 11 breeding colonies. The map below the bar graphs depicts the locations of smolt release sites (diamonds), acoustic arrays (circles), bird colonies (stars), and hydroelectric dams (bars).

occurred in McNary Reservoir at rkm 503, the McNary Dam tailrace at rkm 468, John Day Reservoir at rkm 422, and the John Day Dam tailrace at rkm 346 (Figure 1). During 2014, releases in the lower Columbia River occurred in McNary Reservoir at rkm 503, the McNary Dam tailrace at rkm 468, John Day Reservoir at rkm 449, and the John Day Dam tailrace at rkm 346 (Figure 2). Tagged juvenile steelhead were released daily from April 27 to June 2 in 2012 and from April 27 to May 28 in 2014. Tagged yearling Chinook Salmon were released daily from April 27 to May 28 in 2012 and from April 30 to May 29 in 2014. Tagged subyearling Chinook Salmon were released daily from June 10 to July 9 in 2012 and from June 11 to July 9 in 2014. Approximately equal numbers of fish were released each day and week (see Results).

For releases on the middle Columbia River, downstream-migrating steelhead and yearling Chinook Salmon were collected at Wanapum and Priest Rapids dams by dipnetting 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 lower Snake and lower Columbia River dams, except that the size criterion for tagging was based on weight (15–89 g) rather than length; this resulted in the inclusion of 100–230-mm FL yearling Chinook Salmon and steelhead. Fish were anesthetized, implanted with an acoustic tag (Lotek Model L-AMT-1.421; $11 \times 5 \times 4$ mm) and a PIT tag (Biomark Model HPT12; $12 \times 2 \times 2$ mm), and held in a recovery tank for 18–24 h. After recovery, fish were transported by truck and subsequently released via helicopter at designated release sites in the tailraces of Rock Island Dam (rkm 729), Wanapum Dam (rkm 670), and Priest Rapids Dam (rkm 639; Figure 3). Tagged steelhead were released daily from May 7 to May 28 in 2014; tagged yearling Chinook
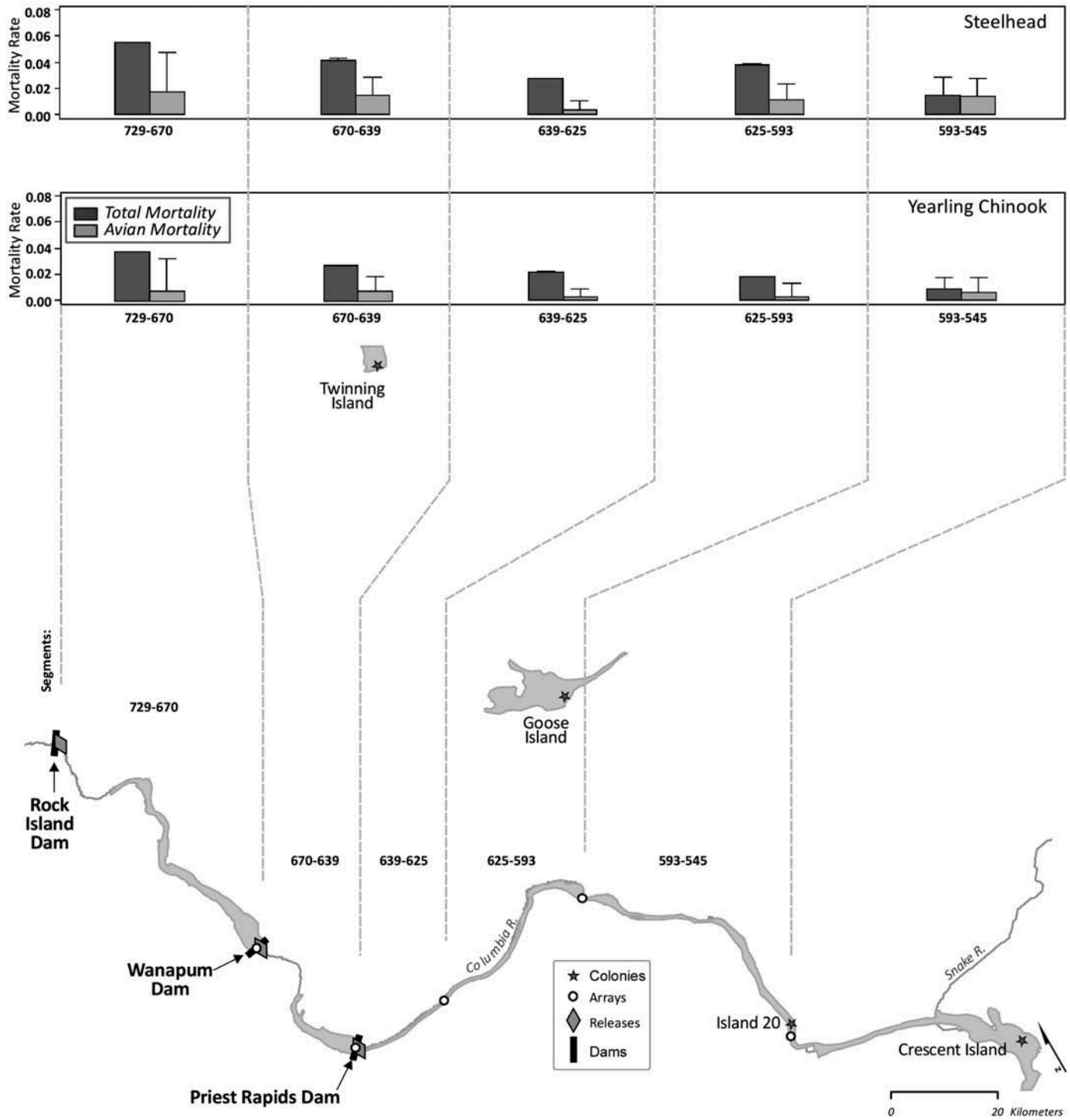
FIGURE 3. Estimated total mortality (+95% credible interval) of tagged juvenile steelhead, yearling Chinook Salmon, and subyearling Chinook Salmon in sections (*x*-axis labels = river kilometer range) of the middle Columbia River during 2014 and the estimated mortality of tagged smolts that was attributable to predation by birds from four breeding colonies. The map below the bar graphs depicts the locations of smolt release sites (diamonds), acoustic arrays (circles), bird colonies (stars), and hydroelectric dams (bars).

Salmon were released daily from April 30 to May 24 in 2014. Approximately equal numbers of fish were released each day and each week (see Results).

Bird Colony Location and Size

We evaluated bird breeding colonies previously identified as posing a risk to smolt survival in the region (Evans et al. 2012;

Hostetter et al. 2015). In total, 6 and 11 different breeding colonies were investigated in 2012 and 2014, respectively. Colonies included Caspian terns nesting on (1) Twinning Island (an "off-river" nesting site in Banks Lake), (2) Goose Island (an off-river nesting site in Potholes Reservoir), (3) Crescent Island (rkm 510), and (4) Anvil Island (in the Blalock Islands complex at rkm 440); California gull and ring-billed gull colonies on (5) Island 20 (rkm 549), (6) Crescent Island, (7) Anvil Island, (8) Straight Six Island (in the Blalock Islands complex at rkm 439), and (9) Miller Rocks Island (rkm 331); (10) a double-crested cormorant colony on Foundation Island (rkm 518); and (11) an American white pelican colony on Badger Island (rkm 512; see Figures 1–3).

Counts of piscivorous waterbirds at each breeding colony 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 breeding colony sizes for Caspian terns and double-crested cormorants were based on the number of active breeding pairs counted from an observation blind located adjacent to each colony. Breeding colony sizes for American white pelicans, California gulls, and ring-billed gulls were estimated based on the number of adults counted on-colony via aerial photographs 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 (initiation of nest building, egg laying, chick rearing, and chick fledging) at each colony during each year, where possible.

Recovery of PIT Tags on Bird Colonies

Once deposited on a bird colony, AT tags can no longer be detected by electronics; hence, PIT tags were used to measure predation probabilities for the study fish. The detection of smolt PIT tags on waterbird colonies followed the methods of Evans et al. (2012). In brief, scanning for PIT tags was conducted after the birds had dispersed from their breeding colonies (August–November after the nesting season). The entire land area of each bird colony (i.e., the area occupied by nesting birds based on aerial and ground surveys conducted during the breeding season) was scanned with pole-mounted PIT tag antennas and transceivers (Biomark Model HPR), conducting a minimum of two complete passes or sweeps of the entire 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 used by breeding birds during the nesting season (Hostetter et al. 2015). Ingested PIT tags can also be damaged during digestion and thereby rendered nonfunctional even if they are deposited on the avian colony. Data to correct or adjust for the proportion of consumed PIT tags that were subsequently deposited on-colony and in working order (i.e., the deposition probability) were derived from the results reported by Hostetter et al. (2015). In brief, salmonids with PIT tags of

known codes were fed to nesting Caspian terns, double-crested cormorants, California gulls, and ring-billed gulls during discrete daily time periods (morning or evening) and throughout the peak nesting season (April–June) at multiple colonies during 2004–2013. The numbers of these ingested tags that were subsequently found by researchers on each breeding colony at the end of the nesting season were used to estimate the tag deposition probabilities. The appropriate deposition probability reported by Hostetter et al. (2015) was then applied to the number of tags that were recovered from each colony as part of this study (see the Predation Probabilities section below for modeling details). No deposition probabilities were available for American white pelicans nesting on Badger Island; consequently, the estimated impacts of American white pelican predation on the survival of tagged smolts are minimum values.

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 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 that are used to detect tags on bird colonies are not 100% efficient, and some proportion of detectable PIT tags are missed by researchers during the scanning process (detection probability < 1.0). The probability that a tag was detected by researchers given that the tag was deposited on-colony in working order required postnesting surveys of on-colony tags that were sown on the colony by researchers during the nesting season (Hostetter et al. 2015). Passive integrated transponder tags that were identical to those implanted in study fish (Biomark Model HPT12) were sown across each bird colony by researchers during one to four discrete tag-sowing events during the nesting season. Recoveries of these tags during scanning efforts conducted after the birds had 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 section for modeling details).

Predation Probabilities

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

We employed a two-stage Bayesian analytical approach to modeling total mortality and the mortality due to colonial

waterbird predation. Total mortality was first modeled by using the standard Cormack–Jolly–Seber (CJS) mark–recapture model (Burnham et al. 1987). We used the posterior distribution of the fish that were alive at the upriver boundary of each river segment to determine smolt availability. Avian predation probabilities were then modeled by using a multinomial predation approach similar to that described by Hostetter et al. (2015).

For each year, there were M releases of fish that potentially traversed a total of J sequential arrays. The number of tagged fish associated with release r is represented with the symbol n_r. The total number of tagged fish released (n_T) is then calculated as $\sum_{r=1}^{M} n_r$. The detection history, total mortality history (mortality from all sources combined), and avian predation mortality history (from tags found on bird colonies) associated with each tagged fish were modeled with a standard CJS model. That is, we estimated each Z_{rj}, the number of tagged fish from release r that were alive at array j; $Z_{rj} \sim \text{Binomial}(Z_{r[j-1]}, S_{rj})$, where S_{rj} is the probability that a tagged fish from release r and alive at segment $j - 1$ was still alive at segment j. We let Y_{ij} represent the number of fish from release r that were interrogated at array j; $Y_{ij} \sim \text{Binomial}(Z_{rj}, p_j)$, where p_j is the probability of detection at the jth interrogation array associated with all fish from the rth release. We assumed that $p_j \sim \text{Uniform}(0, 1) \; \forall \; j$.

We modeled colonial waterbird consumption of tagged fish by using a multinomial extension of the methods detailed by Hostetter et al. (2015). We let D_{rjc} be the number of fish from release r that were taken from the jth segment by the cth bird colony ($c \in \{1, 2, \ldots, C_j\}$, where C_j represents the number of colonies under consideration from segment j). We let $D_{rj,other}$ represent the number of tagged fish from release r that died within segment j from a cause other than colonial waterbird predation (i.e., unaccounted-for mortality). Letting $\bar{\mathbf{D}}_{rj} = [D_{rj1}, D_{rj2}, \ldots, D_{rj,other}]$, then $\bar{\mathbf{D}}_{rj} \sim \text{Multinomial}$ with $n = Z_{r(j-1)} - Z_{rj}$ and $\boldsymbol{p} = \bar{\theta}_{rj}/(1 - S_{rj})$, where $\bar{\theta}_{rj} = [\theta_{rj1}, \theta_{rj2}, \ldots, \theta_{rj,other}]$ and θ_{rjc} is the predation probability for colony c in the jth segment associated with the rth release of tagged smolts. The probabilistic values of each Z_{rj} are estimated by the CJS model described above. The symbol $\theta_{rj,other}$ represents the probability of other (non-avian) mortality in the jth segment associated with the rth release of tagged smolts, and the value of $\theta_{rj,other}$ is inferred from the difference between $(Z_{r[j-1]} - Z_{rj})$ and $\sum_{i=1}^{C} D_{rji}$.

We used noninformative priors for the survival and mortality parameters, letting $\{S_{rj}, \bar{\theta}_{rj}\} \sim \text{Dirichlet}(\bar{1})$, where $\bar{1}$ is $(C_j + 2) \times 1$ vector of ones. This implies that jointly, $\theta_{rj,other} \sim \text{Uniform}(0, 1) \; \forall \; r, j$; $\theta_{jc} \sim \text{Uniform}(0, 1) \; \forall \; j, c$; and $S_{rj} \sim \text{Uniform}(0, 1) \; \forall \; r, j$, as previously stated.

To account for deposition and detection probabilities, ϕ_c represents the probability that a tag consumed by a bird from colony c was deposited on the colony and ψ_{cw} is the probability that a tag deposited on colony c in week w was detected at the end of the nesting season. This requires partitioning each D_{rjc} into $\overrightarrow{D_{r_wjc}}$, where r_w represents the fish last seen in

week w from release r (note that $D_{rjc} = \overrightarrow{D_{r_wjc}} \, 1^T$). We assumed that $R_{r_wjc} \sim \text{Binomial}(D_{r_wjc}, \phi_c\psi_{cw})$, where R_{r_wjc} is the number of fish recovered from release r that were last seen in week w and known to be alive when entering segment j and whose tags were recovered on colony c.

Informative beta priors were used to infer the deposition probability ϕ_c for each bird species and each colony (see Hostetter et al. 2015). The means (and SDs) for these prior distributions were assumed to be 0.71 (SD = 0.09) for Caspian tern colonies, 0.51 (SD = 0.09) for double-crested cormorant colonies, and 0.15 (SD = 0.03) for gull colonies (Hostetter et al. 2015). The ϕ_c for American white pelicans was assumed to be 1.0, as data on deposition probability for this species were not available.

The probability that a tag consumed during week w and deposited on-colony is detected (ψ_{cw}) was assumed to be a logistic function of week,

$$\psi_{cw} = \beta_{c0} + \beta_{c1} \cdot (w - \text{mid}_c),$$

where mid_c is the median week of the breeding season at colony c; and β_{c0} and β_{c1} are inferred from PIT tags that were intentionally sown to measure detection efficiency at each bird colony. We used uninformative priors for the logistic parameters, letting $\beta_{ci} \sim \text{Normal}(0, 1{,}000) \; \forall \; c, i$.

Imperfect rates of deposition and detection led 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 for which the detection history ended in a given segment was recovered on the colony of interest). Therefore, the estimated total predation by waterbirds from all colonies in a segment was directly related to the number of colonies that were assumed to forage there. Thus, it was necessary for us to be cautious in our assumptions about which bird colonies provided foragers in each river 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 was deposited and subsequently found by researchers on the colony (i.e., confirmation of predation by birds from that colony).

Estimates of $\bar{\mathbf{Z}}_r$ and $\bar{\mathbf{D}}_{rj}$ were calculated as the respective medians of the joint posterior distribution. We calculated colonial waterbird predation probabilities on fish from the rth release over a given range or set of segments H based on aggregated estimates of the $\bar{\mathbf{D}}_{ij}$ vectors:

$$\widehat{\text{Predation}}_{H,r,c} = \sum_{j \in H} \hat{D}_{rjc}/Z_{rh_0},$$

where h_0 is the initial release point in H.

We implemented all predation probability models in a Bayesian framework by using JAGS software accessed through R version 3.1.2 (RDCT 2014) and using the R2jags (Su and Yajima 2012) and dclone (Sólymos 2010) packages. We ran three parallel chains for 50,000 iterations each and employed 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 by using the Gelman–Rubin statistic ($\hat{R}$; Gelman et al. 2014). We report results as posterior medians along with the 2.5th and 97.5th percentiles (i.e., 95% credible interval [CI]) . To evaluate model fit, we conducted a Bayesian P-values approach to posterior predictive checking wherein the estimated distribution of fish among the segment-relevant causes of mortality was compared with that of simulated data sets by using Pearson's chi-square statistic as the discrepancy function (Gelman and Meng 1996). Uniformly distributed Bayesian P-values provided sufficient evidence of a well-fit model.

Spatial predation.—Total mortality (1 – survival) and mortality due to predation by colonial waterbirds were modeled using the approach detailed above at each of five spatial scales: (1) reach; (2) project (dam plus reservoir); (3) reservoir; (4) near-dam; and (5) segment. The reach scale encompassed predation on fish that were consumed between the uppermost release site to the last array in that section of river; evaluated reaches spanned (a) from the lower Snake River (rkm 562) to an array located near The Dalles Dam forebay (rkm 311) on the Columbia River (Figure 1) in 2012, (b) from the lower Columbia River near the mouth of the Walla Walla River (rkm 503) to an array located in The Dalles Dam forebay (rkm 311; Figure 2) in 2014, and (c) from the tailrace of Rock Island Dam (rkm 729) on the middle Columbia River to an array located upstream of the Snake River–Columbia River confluence (rkm 545; Figure 3) in 2014. The project scale comprised avian predation on tagged smolts within each dam and reservoir combined; evaluated projects 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. The reservoir scale addressed avian predation on tagged smolts within each reservoir, including McNary Reservoir in 2012 and John Day Reservoir in 2012 and 2014. The near-dam scale encompassed avian predation on fish between arrays bracketing a dam (forebay to tailrace); McNary Dam and John Day Dam were evaluated at this scale in 2012 and 2014. The segment scale comprised predation on fish between any two adjacent arrays; the number of segments evaluated varied depending on the reach and the year.

Temporal predation.—To illustrate temporal trends in mortality, estimates of total mortality and avian predation were depicted by plotting weekly, reach-specific total mortality rates and weekly avian predation rates for each group of tagged salmonids (steelhead and yearling or subyearling Chinook Salmon) and year. We used R^2 values and a randomization test (Good 2005) to evaluate the null hypothesis of no relationship between total mortality and colonial waterbird predation after accounting for river reach and year.

Colony-specific predation.—Foraging areas used by the specific breeding colonies included in the study were investigated based on predation probabilities for each river segment and year. To account for differences in the relative size (length) of each river segment evaluated, colony-specific predation impacts were presented as predation probabilities per river kilometer. Results represent approximate locations of foraging on tagged smolts because (1) the actual foraging path of each bird was unknown and (2) the exact location of predation events between any two adjacent acoustic arrays within a segment was unknown.

Model assumptions.—Methods for calculating total smolt mortality and the mortality due to colonial waterbird predation were based on five assumptions: (1) tagged smolts were actively out-migrating and their tags were functional during the study period; (2) smolt survival, tag deposition, and tag detection were independent; (3) mortality due to fish handling and tagging was negligible and is included in the "other mortality" probability designation; (4) smolt tags were deposited on bird colonies within the same week that the tag was consumed, and tag detection probabilities followed a logistic trend over time; and (5) probabilities of tag deposition on bird colonies did not vary spatially (by consumption location) or temporally (by consumption week).

To confirm assumption 1, directionality and travel times of smolts were investigated to ensure that the tagged smolts were actively out-migrating during the study period. Tests were conducted on a random sample of tags to confirm that tag life and functionality were as specified by the tag's manufacturer (23–33 d depending on the model and manufacturer; see Hughes et al. 2013, 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 (assumption 2). Likewise, the deposition and subsequent on-colony detection of tags from all consumed smolts were also assumed to be mutually independent (assumption 2). Lack of independence among tagged smolts could potentially bias total mortality and predation probabilities to an unknown degree and could lead to overestimation of precision. Postrelease mortality that was potentially associated with handling and tagging was inestimable, thus necessitating assumption 3. A significant number of losses due to handling and tagging would result in an overstatement of smolt availability and consequently would cause predation probability estimates to be biased downward. Assumption 4 need only 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 interannual or intra-annual changes in deposition probabilities across colonies of a given waterbird species (assumption 5). If, however, tag deposition probabilities for the smolts used in this study differed significantly from those reported by Hostetter et al. (2015), then our predation probabilities could be biased to an unknown degree.

RESULTS

Fish Capture, Tagging, and Release

Complete descriptions of smolt capture, tagging, and releases from the AT studies conducted in 2012 and 2014 were given by Hughes et al. (2013), Skalski et al. (2015), and Weiland et al. (2015). In brief, analyses of bird predation based on fish releases in the lower Snake and lower Columbia rivers in 2012 included tagged smolts from five different release locations (rkm 346, 422, 468, 503, and 562), totaling 5,799 steelhead (mean = 1,160 fish/week for 5 weeks); 5,795 yearling Chinook Salmon (mean = 1,159 fish/week for 5 weeks); and 9,372 subyearling Chinook Salmon (mean = 1,874 fish/week for 5 weeks; Table 1). In the middle Columbia River during 2014, avian predation analyses included tagged smolts from three different release locations (rkm 639, 669, and 729), totaling 1,720 steelhead (mean = 573 fish/week for 3 weeks) and 1,716 yearling Chinook Salmon (mean = 572 fish/week for 3 weeks; Table 1). Analyses of waterbird predation in the lower Columbia River during 2014 included tagged smolts from four release locations (rkm 346, 449, 468, and 503), totaling 6,498 steelhead (mean = 1,083 fish/week for 6 weeks); 6,502 yearling Chinook Salmon (mean = 1,084 fish/week for 6 weeks); and 7,490 subyearling Chinook Salmon (mean = 1,249 fish/week for 6 weeks; Table 1).

Bird Colony Location and Size

The number and locations of avian breeding colonies included in the study varied by year, with a total of six colonies scanned for tags after the 2012 nesting season and 11 colonies scanned for tags after the 2014 nesting season (Figure 1; Table 2). The size of each breeding colony (number of breeding pairs or number of adults on-colony) varied among species (Caspian tern, double-crested cormorant, California gull/ring-billed gull, or American white pelican) and between years. In general, the largest piscivorous water-bird colonies in the study area were California gull and ring-billed gull colonies (range = 1,566–14,475 adults on-colony), followed by the American white pelican colony (range = 2,075–2,447 adults on-colony), Caspian tern colonies (range = 6–463 breeding pairs), and the double-crested cormorant colony (390 breeding pairs; Table 2).

The nesting chronology of birds at each breeding site was similar across species and years: courtship and nest-building activities were observed during late March and April, egg laying and incubation took place during late April and May, and chick rearing and fledging occurred in June and July. Peak colony sizes were observed during the egg laying and incubation periods, which coincided with releases of tagged steelhead and yearling Chinook Salmon in both 2012 and 2014. Most birds completely abandoned their nesting sites by early August, although American white pelicans were observed on Badger Island through September and early October.

Recovery of PIT Tags on Bird Colonies

In total, PIT tags from 364 juvenile steelhead, 69 yearling Chinook Salmon, and 117 subyearling Chinook Salmon were recovered from bird colonies during the tagged smolts' year of out-migration; these tags were included in analyses of avian predation probability (Table 1). More smolt tags were

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TABLE 1. Numbers of tagged juvenile steelhead (STHD), yearling Chinook salmon (CHIN-1), and subyearling Chinook salmon (CHIN-0) that were released and the numbers that were subsequently recovered (in parentheses) from piscivorous waterbird nesting colonies during 2012 and 2014. Tag recoveries only include tags that were recovered during the same year in which the tagged smolts out-migrated. River kilometer (rkm) is the distance from the release site to the Pacific Ocean.

| Species | Middle Columbia River release site (rkm) | | | Lower Snake River/lower Columbia River release site (rkm) | | | | | | Total |
	729	669	639	562	503	468	449	422	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)

TABLE 2. Numbers of piscivorous waterbirds that were counted at the peak of nesting (peak date) during the 2012 and 2014 breeding seasons. Counts of Caspian terns (CATE) and double-crested cormorants (DCCO) represent the number of breeding pairs; counts of American white pelicans (AWPE) and California gulls/ring-billed gulls (GULL) represent the number of adults that were on-colony. Survey types to determine colony size are differentiated between aerial (A) and ground-based (G), with the number of independent counts for each estimate shown in parentheses. An asterisk denotes that the colony was not scanned for PIT tags during the specified year; "NA" denotes that an aerial or ground-based survey count was not conducted during the specified year.

		2012			2014		
Location	Avian species	Count	Peak date	Type (no.)	Count	Peak date	Type (no.)
Twinning Island (off-river)	CATE	22*	May 14	A (3)	66	May 18	A (3)
Goose Island (off-river)	CATE	463	May 26	G (2)	159	May 19	A (3)
Island 20 (rkm 549)	GULL	NA*	NA*	NA*	14,475	May 20	A (3)
Foundation Island (rkm 518)	DCCO	390	May 1	G (2)	390	May 14	G (2)
Badger Island (rkm 512)	AWPE	2,075	May 18	A (3)	2,447	May 20	A (3)
Crescent Island (rkm 510)	CATE	422	May 22	G (2)	474	May 20	G (5)
	GULL	7,187	May 18	A (3)	6,404	May 20	A (3)
Anvil Island (rkm 440)	CATE	6*	May 30	G (1)	45	June 11	A (2)
	GULL	7,282*	May 18	A (3)	4,454	May 20	A (3)
Straight Six Island (rkm 439)	GULL	1,707*	May 18	A (3)	1,566	May 20	A (3)
Miller Rocks Island (rkm 331)	GULL	4,509	May 18	A (3)	4,132	May 20	A (3)

recovered from bird colonies in 2014 (n = 326 tags; all three salmonid groups combined) than in 2012 (n = 224 tags; all salmonid groups combined), partly because greater sampling effort was expended at bird colonies in 2014 (11 colonies) than in 2012 (6 colonies) but also because more tagged smolts were released in 2014 (n = 23,926 smolts; all salmonid groups combined) than in 2012 (n = 20,966 smolts; all salmonid groups combined; Table 1).

In general, probabilities of PIT tag detection on bird colonies were high (~0.70) for most colony × year combinations (Table 3). Detection probability 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). There was a relationship between detection probability and the time since tag deposition; the probability of tag recovery was lower for PIT tags that were deposited during the first release than for tags that were deposited during the last release (Table 3).

Predation Probabilities

Estimated predation by colonial waterbirds varied among river segments, among salmonid groups (steelhead and yearling or subyearling Chinook Salmon), and between years. Avian predation probability ranged from less than 0.01 to over 0.16 (95% CI = 0.11–0.19) per river segment (Figures 1–3). Within the same spatial scale and year, estimated probabilities of avian predation were consistently higher for steelhead than for yearling or subyearling Chinook Salmon. For instance, avian predation on juvenile steelhead was generally two to four times higher than predation on yearling Chinook Salmon and two to five times higher than predation on subyearling Chinook Salmon. Estimated impacts of avian

predation were also consistently the highest (0.02–0.16, depending on the salmonid species or age-class) on tagged smolts between rkm 525 and rkm 562 of the lower Snake River relative to the other river segments evaluated. This difference was attributable to the close proximity and subsequent consumption of tagged smolts by colonial waterbirds nesting on Foundation and Crescent islands, which are located just below the confluence of the Snake and Columbia rivers (Figure 1; see Supplementary Tables S.A.1–S.A.3 in Supplement A available in the online version of this article for colony-specific results).

In addition to the higher probabilities of colonial waterbird predation on smolts in the lower Snake River, predation probabilities were also higher in the tailraces of McNary Dam (rkm 468–470; Figures 1, 2) and John Day Dam (rkm 346–349; Figures 1, 2) during 2012 and 2014 and in a section of John Day Reservoir (rkm 412–449; Figure 2) during 2014. In 2012, there were fewer arrays in John Day Reservoir, and the gull colonies on Anvil and Straight Six islands (in the Blalock Islands complex) were not scanned for tags during that year, so the total impact of avian predation on smolt survival in rkm 412–449 of John Day Reservoir during 2012 is unknown. However, the predation impact was higher than that presented herein because smolt tags released in 2012 were detected at gull colonies on both Anvil and Straight Six 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 thus were not included in predation probability calculations).

Estimated probabilities of predation for all waterbird colonies combined were generally lower on fish out-migrating through the middle Columbia River (0.03 for yearling

TABLE 3. Range of median weekly probabilities (from the first week to the last week of smolt releases) of PIT tag detection on piscivorous waterbird colonies. The total number of PIT tags that were sown (n) and the number of tag releases (r) that were used to model detection probability are shown; "NA" denotes that the colony was not scanned for PIT tags during the specified year. Avian species codes are defined in Table 2.

Location (rkm)	Avian species	2012	2014
Twinning Island (off-river)	CATE	NA	0.44–0.91
			($n = 100; r = 2$)
Goose Island (off-river)	CATE	0.24–0.80	0.49–0.97
		($n = 400; r = 4$)	($n = 100; r = 2$)
Island 20 (rkm 549)	GULL	NA	0.73–0.90
			($n = 100; r = 2$)
Foundation Island (rkm 518)	DCCO	0.37–0.41	0.20–0.20
		($n = 200; r = 2$)	($n = 100; r = 1$)
Badger Island (rkm 512)	AWPE	0.68–0.74	0.69–0.76
		($n = 100; r = 2$)	($n = 100; r = 2$)
Crescent Island (rkm 510)	CATE	0.50–0.91	0.77–0.94
		($n = 200; r = 4$)	($n = 200; r = 4$)
	GULL	0.63–0.95	0.73–0.98
		($n = 100; r = 2$)	($n = 100; r = 2$)
Anvil Island (rkm 440)	CATE	NA	0.85–0.86
			($n = 100; r = 2$)
	GULL	NA	0.90–0.98
			($n = 100; r = 2$)
Straight Six Island (rkm 439)	GULL	NA	0.87–0.98
			($n = 100; r = 2$)
Miller Rocks Island (rkm 331)	GULL	0.74–0.89	0.83–0.87
		($n = 100; r = 2$)	($n = 100; r = 2$)

Chinook Salmon and 0.06 for juvenile steelhead) than for fish out-migrating through the lower Snake River (0.05–0.28, depending on the salmonid species or age-class; Table S.A.1) and lower Columbia River (0.05–0.11, depending on the salmonid species or age-class and the year; Tables S.A.1, S.A.2). The precision of estimated predation on tagged smolts that were released into the middle Columbia River was lower due to the smaller numbers of steelhead and yearling Chinook Salmon released. For instance, 95% CIs for reach-specific predation probabilities in the middle Columbia River were 0.01–0.06 for yearling Chinook Salmon and 0.04–0.09 for steelhead (Figure 3; Table S.A.3).

The amount of total smolt mortality (1 − survival) that was explained by colonial waterbird predation also varied among spatial scales, among salmonid groups, and between years. For juvenile steelhead, waterbird predation accounted for the majority (>50%) of smolt losses at many of the spatial scale × year combinations evaluated (Figures 1–3). For example, avian predation on tagged juvenile steelhead in the lower Snake and lower Columbia rivers accounted for an estimated 11–85% of total mortality, depending on the river reach and the year (Tables S.A.1–S.A.3). In 2014, colonial waterbird predation accounted for 31% and 25%, respectively, of all documented steelhead mortality at the Wanapum and Priest

Rapids projects (Table S.A.3). At finer spatial scales (e.g., near McNary Dam and John Day Dam), waterbird predation accounted for nearly all (100%) losses of juvenile steelhead (Figures 1, 2).

The proportion of smolt mortality explained by colonial waterbird predation was generally lower for yearling Chinook Salmon than for juvenile steelhead (Figures 1–3), although for some river segment × year combinations, avian predation accounted for over 50% of yearling Chinook Salmon losses (e.g., near McNary Dam in 2012 and 2014; Figures 1, 2). For subyearling Chinook Salmon, particularly at the John Day Project, estimated avian predation accounted for only a small proportion (generally < 0.05, depending on the spatial scale) of smolt losses (Figures 1, 2). Despite this, the estimated total mortality of subyearling Chinook Salmon was often higher than the total mortality estimated for steelhead and yearling Chinook Salmon, particularly in 2014—a year when all known bird colonies within foraging distance of subyearling Chinook Salmon were included in the study. This result suggests that something other than colonial waterbird predation was responsible for the mortality of most Chinook Salmon subyearlings during the study.

Comparisons of interannual (2012 versus 2014) differences in predation by colonial waterbirds for near-dam, reservoir, and project-specific impacts indicated that for the three

salmonid groups, the predation probability and the percentage of total mortality that was explained by avian predation were generally higher in 2014 than in 2012 (Tables S.A.1, S.A.2). The greater avian predation probability in 2014 relative to 2012 was largely due to the number of bird colonies that were scanned for tags in 2014: two additional gull colonies and one additional Caspian tern colony were included in the 2014 analyses but not in the 2012 analyses (see Supplement A for colony-specific results). The one exception to the overall increase in colonial waterbird predation probability in 2014 relative to 2012 was predation on subyearling Chinook Salmon near John Day Dam, for which the avian predation probability was lower in 2014 than in 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 (Tables S.A.1, S.A.2). Detection histories of smolts consumed by gulls nesting on Miller Rocks Island indicated that foraging behavior shifted in 2014 relative to 2012; Miller Rocks Island gulls disproportionately consumed tagged smolts downstream of the last array in the The Dalles Dam forebay (rkm 311; i.e., outside of the study area) in 2014. For subyearling Chinook Salmon, among the PIT tags that were recovered from the Miller Rocks Island gull colony, 57% were consumed upstream of The Dalles Dam in 2012, whereas only 11% were consumed upstream of that dam in 2014. Consequently, the focus of smolt predation by gulls nesting on Miller Rocks Island was further downstream (below the array in The Dalles Dam forebay) in 2014 than in 2012.

A positive relationship existed between the week of tagged smolt release and the avian predation probability, as predation impacts generally increased with time (Figures S.B.1–S.B.3 in Supplement B available in the online version of this article). Smolts that were released during the latter half of the study were more susceptible to bird predation than smolts that were released during the first few weeks of the study. This trend was particularly pronounced for juvenile steelhead; predation rates were significantly higher for steelhead smolts released in May than for those released in April. For example, the median reach-specific probability of avian predation on tagged steelhead released into the lower Snake River was 0.12 during the first week of smolt releases and increased to 0.49 during the last week of releases (Figure S.B.1). Temporal trends in avian predation were less evident for yearling and subyearling Chinook Salmon; however, the general trend of greater avian predation impacts on fish released during later weeks was evident in both age-classes (Figures S.B.1–S.B.3).

Temporal trends in colonial waterbird predation were consistent with seasonal trends in total mortality for juvenile steelhead and yearling Chinook Salmon migrating through the lower Snake and Columbia rivers in 2012 and 2014; increases in weekly total mortality were commensurate with weekly bird predation probabilities (Figures S.B.1, S.B.2).

Trends were less apparent for steelhead and yearling Chinook Salmon migrating through the middle Columbia River, although analyses were limited to just 3 weeks of releases from a single year (Figure S.B.3). A randomization test indicated that a large proportion of the variation in weekly estimates of total smolt mortality could be explained by variation in avian predation probability. Results were particularly pronounced for steelhead, with an R^2 of 0.95 ($P < 0.001$). Significant relationships were also observed for Chinook Salmon yearlings ($R^2 = 0.64$, $P = 0.001$) and subyearlings ($R^2 = 0.63$, $P = 0.01$). Results for subyearling Chinook Salmon should be viewed more cautiously, as the predation probability observed during the final week of releases in 2014 (0.20 of the available fish were consumed by birds) was highly influential (Figure S.B.2).

Colony-Specific Foraging

Analysis of colony-specific predation probability (adjusted for the length of each river segment) identified several areas where predation probabilities were elevated or concentrated (Figure 4). In general, gull colonies disproportionately consumed steelhead near dams, whereas Caspian terns disproportionately consumed steelhead in the reservoirs. No concentrated areas of foraging were identified for double-crested cormorants or American white pelicans, although probabilities of predation by double-crested cormorants were higher in the lower Snake River than in the lower Columbia River.

During 2012, predation impacts on steelhead within the lower Snake River and within the lower Columbia River section just below the Snake River confluence were higher than impacts in other nearby river segments (Figure 4). Results indicated that Caspian terns nesting on Crescent Island and double-crested cormorants nesting on Foundation Island disproportionately commuted upstream of their breeding colonies to forage on smolts. Predation was also concentrated in the John Day Dam tailrace, where gulls nesting on Miller Rocks Island disproportionately consumed tagged steelhead relative to other nearby river segments. Similar to 2012, predation by Crescent Island Caspian terns in 2014 was higher within segments of McNary Reservoir than in near-dam segments (Figure 4). Results from 2014 also indicated that Crescent Island gulls disproportionally consumed fish in the tailrace of McNary Dam (Figure 4). Similarly, predation by Miller Rocks Island gulls in 2014 was concentrated in the John Day Dam tailrace relative to other nearby segments (Figure 4). However, we should note that the total impact of Miller Rocks Island gulls on tagged smolts (steelhead and yearling/subyearling Chinook Salmon) was not evaluated because a large proportion of consumed fish were preyed upon outside of the study area (i.e., downstream of the lowermost array, located in The Dalles Dam forebay at rkm 311). The other area of concentrated foraging identified in 2014 was predation by gulls and Caspian terns nesting on Anvil Island
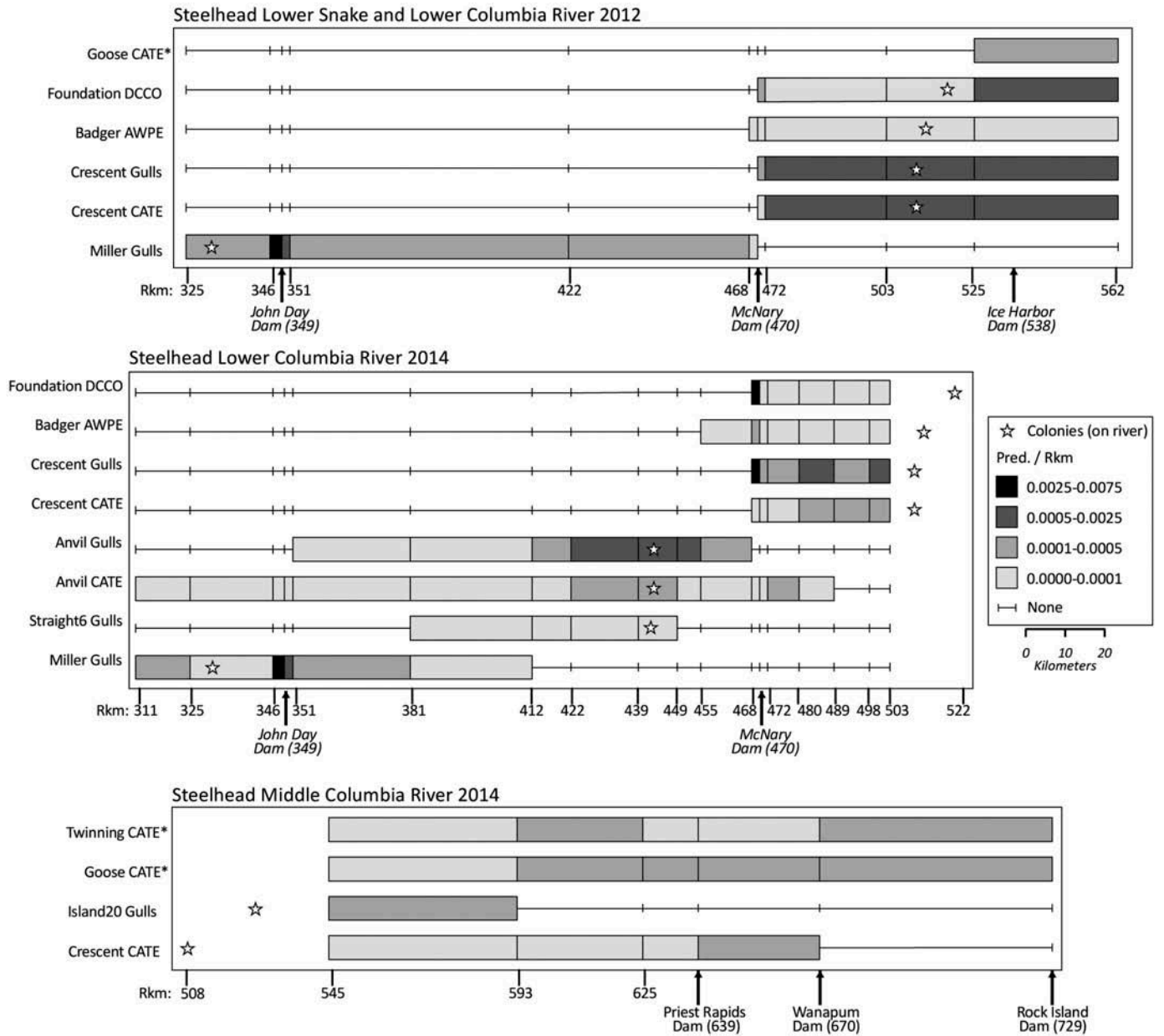
FIGURE 4. Bird colony-specific locations of predation on tagged juvenile steelhead in sections of the lower Snake River and the lower and middle Columbia River during 2012 and 2014. Results are depicted as the predation probability per river kilometer within each spatial scale. Piscivorous colonial waterbirds include Caspian terns (CATE), double-crested cormorants (DCCO), California gulls and ring-billed gulls (Gulls), and American white pelicans (AWPE). Asterisks denote nesting colonies that were located off-river. Vertical bars depict the acoustic array locations that were used to define spatial scale.

(Blalock Islands complex) in John Day Reservoir; predation by these birds was concentrated in a river segment about 30 rkm upstream and downstream of the island (Figure 4). The Anvil Island colonies were not scanned for tags in 2012, thus precluding an interannual comparison of predation impacts from birds nesting at these colonies.

No areas of elevated or concentrated predation were identified within the middle Columbia River, although fewer river segments or spatial scales were available for analyses

(Figure 3). For the spatial scales evaluated, colonial waterbird predation on smolts was more evenly distributed and relativity low in intensity compared with predation occurring in the lower Snake and lower Columbia rivers during 2014. Avian predation at the Wanapum and Priest Rapids projects was limited to Caspian terns nesting at three colonies in 2014: Twinning Island in Banks Lake; Goose Island in Potholes Reservoir; and Crescent Island in McNary Reservoir on the lower Columbia River. Despite the proximity of Island 20 to

Priest Rapids Dam, there was no evidence that gulls nesting on Island 20 were commuting upstream to forage at the Wanapum Project or the Priest Rapids Project (Figure 4). The numbers of tagged juvenile steelhead that were available to birds below Rock Island Dam ($n = 399$) and Wanapum Dam ($n = 1,148$) were small, and the on-colony deposition probability for tags consumed by gulls was low, so the results should be interpreted cautiously.

The foraging ranges of piscivorous waterbirds (distance from the breeding colony) varied depending on the colony, river reach, and year. In general, rates of predation on tagged steelhead were highest in river segments that were closest to each colony (Figure 4), and most predation occurred within a roughly 40–50-km radius of the colony site. The foraging range of Caspian terns feeding on juvenile steelhead tended to be the longest, followed by the foraging ranges of California gulls/ring-billed gulls, American white pelicans, and double-crested cormorants (Figure 4). However, the sample sizes of tags recovered from the Badger Island American white pelican colony and the Foundation Island double-crested cormorant colony were low.

DISCUSSION

Numerous factors have been linked to the mortality of juvenile salmonids during seaward migration, including dam passage (Muir et al. 2001), disease (Dietrich et al. 2011), predation by piscivorous fish (Rieman et al. 1991; Ward et al. 1995), and predation by piscivorous birds (Evans et al. 2012; Hostetter et al. 2015). In the present study, predation by colonial nesting waterbirds was a substantial source of mortality for tagged steelhead during their out-migration. Colonial waterbird predation on yearling Chinook Salmon was generally lower than predation on juvenile steelhead. Among the three salmonid groups evaluated, subyearling Chinook Salmon had the lowest probabilities of waterbird predation. Greater avian predation impacts on juvenile steelhead relative to salmon species has been well documented in the published literature (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012). Possible explanations for the higher susceptibility of juvenile steelhead to bird predation include differences in the size (length) and behavior of steelhead compared with other salmonids: steelhead smolts are generally larger and more surface oriented than salmon smolts (Beeman and Maule 2006). Surface orientation renders fish more vulnerable to predation by Caspian terns, gulls, and American white pelicans, which feed in the uppermost 1 m of the water column (Evans and Knopf 1993; Winkler 1996; Cuthbert and Wires 1999).

Previous studies of avian predation on juvenile salmonids (e.g., Evans et al. 2012; Hostetter et al. 2015) were unable to evaluate bird predation at discrete spatial scales. Use of AT data in the present study provided information on the river sections in which the tagged smolts were consumed by birds.

Spatial analyses indicated that avian predation probability varied significantly depending on the river segment and bird colony. Caspian tern foraging was documented to occur almost exclusively within reservoirs and not near hydroelectric dams. Conversely, foraging by California gulls and ring-billed gulls was concentrated near the 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 forebays of dams, (2) injury or mortality associated with dam passage, or (3) the temporary stunning or disorientation of smolts by hydraulic conditions in the tailraces of dams. Gull predation on tagged smolts in the present study, however, was not limited to foraging near dams, as predation also occurred within the reservoirs. We also found evidence that Caspian terns, gulls, and double-crested cormorants nesting on islands within McNary Reservoir disproportionately foraged upstream of their nesting sites, consuming fish in or near the lower Snake River. Higher probabilities of avian predation on smolts in this section of river may be related to (1) the proximity of Ice Harbor Dam (lower Snake River) to Foundation Island (19 rkm downstream from the dam) and Crescent Island (27 rkm downstream from the dam); (2) the relative abundance of smolts originating from the Snake River versus the middle Columbia River; or (3) environmental conditions (e.g., reduced flows and higher turbidity) that resulted in favorable foraging conditions for birds in the lower Snake River (Hostetter et al. 2012).

A 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 indicate that most birds will preferentially remain close to their nesting sites to forage, if foraging conditions near the colony allow (Anderson et al. 2004; Adrean 2011). However, Caspian terns reportedly commuted over 90 km from the nesting colony in order to forage when fish availability near the colony was low (BRNW 2014). Data on foraging behavior and foraging ranges in California gulls, ring-billed gulls, and American white pelicans are generally lacking, but 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 that were deposited on-colony by birds may have been from nonbreeders or from birds that visited the colony while prospecting for a nest site. Consequently, it is more challenging to use recoveries of fish tags on bird colonies as a measure of foraging behavior in nesting adults compared with studies in which adult birds are tagged to track their movements. Nevertheless, results from our study suggest that avian foraging was concentrated within a 40–50-km radius of the colony, although some birds consumed tagged fish upwards of 100 km from the breeding colony where the tags were recovered.

Gulls, which are omnivores and generalist predators, displayed smolt predation levels that were similar to or greater than those of Caspian terns and double-crested cormorants, which are strictly piscivorous predators. Hostetter et al. (2015) also reported that probabilities of predation by gulls were higher than documented in the published literature because previous predation probability estimates did not include a measure of on-colony PIT tag deposition probability. High probabilities of smolt predation by gulls nesting on colonies in the study area were likely associated with (1) large colony sizes (gull colonies were an order of magnitude larger than Caspian tern, double-crested cormorant, and American white pelican colonies); (2) behavioral flexibility to exploit temporarily available prey (Winkler 1996); and (3) the proximity of some gull colonies to hydroelectric dams (e.g., the Miller Rocks Island gull colony), where smolts may be particularly vulnerable to predation by gulls (Ruggerone 1986; Collis et al. 2002). Not all of the gull colonies evaluated in this study had appreciable impacts on smolt survival: predation rates by gulls nesting on Island 20 (middle Columbia River) and Straight Six Island (John Day Reservoir, lower Columbia River) were among the lowest observed.

Similar to data reported by Evans et al. (2012), we observed that among the various piscivorous waterbird species evaluated, American white pelicans nesting on Badger Island (McNary Reservoir) exerted the lowest impacts on salmonid smolts. Evans et al. (2012) hypothesized that several factors could account for low probabilities of juvenile salmonid predation by American white pelicans nesting on Badger Island, including (1) the pelicans' reliance on larger forage fish, (2) the pelicans' tendency to forage in shallow-water habitats where actively migrating smolts are relatively less abundant, (3) the lack of spatial overlap between pelican foraging locations and salmonid smolts that out-migrate through the lower Snake and Columbia rivers, or (4) some combination of these factors. In our study and the Evans et al. (2012) study, the probabilities of smolt predation by American white pelicans do not incorporate tag loss due to off-colony deposition (i.e., deposition probability was assumed to 1.0) and therefore represent minimum estimates. In a study of American white pelican predation on PIT-tagged Cutthroat Trout *O. clarkii* in Idaho, Teuscher et al. (2015) estimated that the average tag deposition and detection probability (a combined estimate for both parameters) was approximately 0.30 (90% confidence interval = 0.08–0.55). Applying this correction factor to the raw, unadjusted numbers of juvenile steelhead and subyearling/yearling Chinook Salmon whose tags were recovered from the Badger Island American white pelican colony would not appreciably increase predation probabilities, as they would still be less than 0.01 for all three salmonid groups and all spatial scales evaluated as part of this study.

An investigation of weekly predation probability provided evidence of within-season temporal trends in which predation probabilities generally increased with release date, particularly for steelhead. Hostetter et al. (2012) linked variation in weekly predation rates to the number of PIT-tagged smolts that were available in-river; predation impacts were generally lower when more PIT-tagged fish were present in the Columbia 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 (Hostetter et al. 2012). Data on weekly colony attendance were unavailable for the waterbird colonies we evaluated, and similar numbers of tagged smolts were released each week; therefore, we could not investigate the influence of colony size or variation in the number of tagged smolts on predation probabilities. Nevertheless, the present results provide strong evidence of intra-annual variation in predation impacts, with late-migrating smolts being more susceptible to colonial waterbird predation than early migrants.

Not all piscivorous waterbird species and not all breeding colonies within the study area were included in the present study. For instance, we did not investigate smolt predation probabilities for non-colonial or semi-colonial piscivorous waterbirds, such as the common merganser *Mergus merganser*, great blue heron *Ardea herodias*, black-crowned night-heron *Nycticorax nycticorax*, and grebes *Aechmophorus* spp. Although these piscivorous waterbirds are also known to consume juvenile salmonids in the Columbia River basin, their predation impacts on smolts have been shown to be far less than the impacts of colonial nesting piscivorous waterbirds (Wiese et al. 2008), primarily because the non-colonial and semi-colonial nesting species have smaller regional populations. Furthermore, not all piscivorous waterbird colonies that were identified within the study area during 2012 were scanned for smolt tags, including three colonies (two gull colonies and a Caspian tern colony) located in John Day Reservoir. Therefore, some fraction of the unaccounted-for mortality reported here was due to additional predation by waterbirds. Based on the full suite of piscivorous waterbird colonies scanned for tags in 2014 and the low reported smolt predation impacts from non-colonial or semi-colonial piscivorous waterbirds, this fraction of unaccounted-for mortality was presumably minimal (in 2014) to moderate (in 2012).

Our study is among the first to document the impact of predation by colonial waterbirds in the context of overall smolt mortality. Comparisons of total mortality to colonial waterbird predation mortality indicated that in several of the river reaches and segments evaluated, over 50% of all steelhead mortality was attributable to avian predation. Given this level of predation, results provided strong evidence that a large proportion of the variation in steelhead mortality during out-migration was explained by colonial waterbird predation. Avian predation probabilities were more variable for yearling Chinook Salmon; the percentage of total mortality attributed to predation by colonial waterbirds was highest near hydroelectric dams and for smolts traveling through the lower Snake

River. Colonial waterbird predation on subyearling Chinook Salmon was generally low and constituted a minor component of overall smolt mortality. For example, total mortality of subyearling Chinook Salmon in John Day Reservoir was estimated at 0.26 of available tagged fish in 2014, yet colonial waterbirds consumed only an estimated 0.03 of the available tagged smolts, providing strong evidence that a factor other than colonial waterbird predation was responsible for the vast majority of subyearling mortality in the reservoir.

One likely component of unaccounted-for mortality in the present study—especially for subyearling Chinook Salmon—is predation by piscivorous fishes, such as the Northern Pikeminnow *Ptychocheilus oregonensis*, Smallmouth Bass *Micropterus dolomieu*, Walleye *Sander vitreus*, and Channel Catfish *Ictalurus punctatus*. Data describing piscine predation impacts on the survival of juvenile salmonids in the Columbia River basin are from studies completed in the 1990s. Ward et al. (1995) estimated that the impacts of Northern Pikeminnow predation on juvenile salmonids were greater in the lower Columbia River than in the middle Columbia River or lower Snake River. Rieman et al. (1991) estimated that approximately 14% of juvenile salmonids passing through John Day Reservoir were consumed by Northern Pikeminnow, Smallmouth Bass, and Walleyes combined and that mortality rates were highest for subyearling Chinook Salmon. The shallow-water habitat that surrounds a number of islands within John Day Reservoir may provide optimal foraging conditions for piscivorous fish (Hughes et al. 2013); more-current studies of this smolt mortality source may be warranted.

Some fraction of the smolt losses due to predation may consist of dead or moribund fish. If true, the expected benefits to smolt survival from reduced predation would be smaller (due to compensatory mortality) than those derived from adding predation probability estimates to smolt survival estimates. Hostetter et al. (2012) observed differences in juvenile steelhead susceptibility to predation by Caspian terns and double-crested cormorants based on the external condition (body injuries, fungal infections, and descaling) of tagged smolts, as smolts that were released in severely degraded condition were more likely to be consumed by birds than smolts with little or no external damage. In the present study, however, only smolts with little to no external damage were tagged and released. Furthermore, the vast majority of smolts in the Columbia River have little or no external damage (Hostetter et al. 2012) and therefore are capable of navigating the hydrosystem and returning as adults (Evans et al. 2014). Despite the good overall condition of most smolts in the river, these seemingly healthy fish are consumed by avian predators at significant rates (Hostetter et al. 2012; this study). As part of a related JSATS survival study, Hughes et al. (2013) and Skalski et al. (2015) released double-tagged (AT- and PIT-tagged), dead smolts into the tailraces of McNary Dam (*n* = 180) and John Day Dam (*n* = 193) to evaluate detection probabilities for dead fish passing hydrophone arrays. None of the PIT tags from those dead fish was recovered on bird colonies as part of this study, thereby providing evidence that dead smolts were not more susceptible than their live counterparts to being consumed by colonial waterbirds in dam tailraces. Thus, although some portion of smolt mortality due to avian predation may reflect the consumption of dead or moribund fish, the majority of consumed smolts are seemingly healthy at the time of consumption. Future studies could more rigorously address condition-dependent predation mortality by tagging fish that represent all types of condition, including dead fish, and then comparing their predation probabilities.

Future avian predation studies that utilize double-tagged juvenile salmonids would benefit from (1) larger sample sizes of tagged smolts and (2) use of a single release point upstream of the waterbirds' maximum foraging range from their breeding colony. Evans et al. (2012) recommended that at least 500 tagged smolts be used in studies investigating predation probability in order to minimize the instability of results that arise from small sample sizes, as the recovery of just a few tags on-colony can greatly influence the estimated predation probability. Measurements of precision (e.g., 95% CIs) are also heavily influenced by the number of tagged smolts that are released (Hostetter et al. 2015); for example, the small number of tagged smolts released into the middle Columbia River during 2014 resulted in imprecise estimates of predation probability. Avian predation studies in which tagged fish are released just upstream of the maximum foraging range for nesting colonial waterbirds will result in more accurate and defensible measures of the avian predators' cumulative impacts on smolt survival. In our study, avian predation probabilities were heavily influenced by the locations of the release and interrogation sites, and cumulative impacts from some of the 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 lowermost 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—such as prey densities, travel time, river flow, turbidity, and size- and condition-dependent mortality (Hostetter et al. 2012; Osterback et al. 2014)—are warranted. Results from these types of investigation may not only broaden our understanding of mechanisms that regulate predator–prey interactions but may also help in the development of management strategies to reduce predation impacts.

In summary, use of AT and PIT tag technologies can assist fisheries managers and researchers in quantifying where and when predation occurs and the fraction of total mortality that is due to predation by colonial waterbirds. In the present study, avian predation impacts on smolt survival varied depending on the bird species, colony location, salmonid species/age-class, week, and year, demonstrating that predator–prey interactions were dynamic at both spatial and temporal scales. Colonial

waterbird predation on juvenile steelhead and yearling Chinook Salmon was one of the greatest sources of mortality—if not the single-greatest source—during smolt passage through sections of the lower Snake River and the lower and middle Columbia River in 2012 and 2014. In contrast, the probabilities of colonial waterbird predation on subyearling Chinook Salmon were generally low and represented a minor overall component of total mortality, suggesting that factors other than avian predation (e.g., consumption by piscivorous fishes) were responsible for subyearling mortality. Assuming that birds are not largely consuming dead or moribund fish and that other sources of mortality would not fill the niche created by a reduction in predation impacts from any given bird colony, a decrease in the number of piscivorous colonial waterbirds in the Columbia River basin will enhance the survival of ESA-listed juvenile salmonids.

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