Transactions of the American Fisheries Society 141:975–989, 2012

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.676809

ARTICLE

Systemwide Evaluation of Avian Predation on Juvenile Salmonids from the Columbia River Based on Recoveries of Passive Integrated Transponder Tags

Allen F. Evans and Nathan J. Hostetter
Real Time Research, Inc., 52 Southwest Roosevelt Avenue, Bend, Oregon 97702, USA

Daniel D. Roby
U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA

Ken Collis*
Real Time Research, Inc., 52 Southwest Roosevelt Avenue, Bend, Oregon 97702, USA

Donald E. Lyons
Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA

Benjamin P. Sandford and Richard D. Ledgerwood
National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Boulevard, Seattle, Washington 98112-2097, USA

Scott Sebring
Pacific States Marine Fisheries Commission, 205 Southeast Spokane Street, Suite 100, Portland, Oregon 97202, USA

Abstract

We recovered passive integrated transponder (PIT) tags from nine piscivorous waterbird colonies in the Columbia River basin to evaluate avian predation on Endangered Species Act (ESA)-listed salmonid *Oncorhynchus* spp. populations during 2007–2010. Avian predation rates were calculated based on the percentage of PIT-tagged juvenile salmonids that were detected as passing hydroelectric dams and subsequently were consumed and deposited by birds on their nesting colonies. Caspian terns *Hydroprogne caspia* (hereafter, "terns") and double-crested cormorants *Phalacrocorax auritus* (hereafter, "cormorants") nesting on East Sand Island in the Columbia River estuary consumed the highest proportions of available PIT-tagged salmonids, with minimum predation rates ranging from 2.5% for Willamette River spring Chinook salmon *O. tshawytscha* to 16.0% for Snake River steelhead *O. mykiss*. Estimated predation rates by terns, cormorants, gulls of two species (California gull *Larus californicus* and ring-billed gull *L. delawarensis*), and American white pelicans *Pelecanus erythrorhynchos* nesting near the confluence of the Snake and Columbia rivers were also substantial; minimum predation rates ranged from 1.4% for Snake River fall Chinook salmon to 13.2% for upper Columbia River steelhead. Predation on ESA-listed salmonids by gulls and American white pelicans were minor (<2.0% per ESA-listed salmonid population) relative to predation by terns and cormorants. Cumulative impacts were greater for Snake River and upper Columbia River salmonids than for salmonids originating

*Corresponding author: ken@realtimeresearch.com
Received November 30, 2011; accepted March 13, 2012
Published online June 21, 2012

closer to the estuary because upriver salmonids must migrate past more bird colonies to reach the ocean. Predation rates adjusted for colony size (per capita rates) were significantly higher for terns and cormorants nesting at inland colonies (upstream of Bonneville Dam) than for those nesting in the estuary, suggesting that inland colonies have a greater reliance on salmonids as a food source. Management actions to increase salmonid survival by reducing avian predation in the estuary could be offset if birds that disperse from the estuary relocate to inland nesting sites on or near the Columbia River.

Predation on juvenile salmonids *Oncorhynchus* spp. during out-migration to the Pacific Ocean is considered a limiting factor in the recovery of Columbia River basin salmonid populations that are listed for protection under the U.S. Endangered Species Act (ESA; NOAA 2008). Studies of avian predation in the Columbia River basin have focused on colonial waterbirds that nest in the estuary (Collis et al. 2001; Roby et al. 2003; Ryan et al. 2003; Lyons et al. 2010), which currently hosts the largest known colonies of Caspian terns *Hydroprogne caspia* (hereafter, "terns") and double-crested cormorants *Phalacrocorax auritus* (hereafter, "cormorants") in western North America (Lyons et al. 2010). Previous research has demonstrated that cormorants and terns nesting on East Sand Island in the Columbia River estuary consume millions of juvenile salmonids annually (Lyons et al. 2010), including salmonids from evolutionarily significant units (ESUs) and distinct population segments (hereafter collectively referred to as ESUs; NOAA 2011) that are listed under the ESA. Breeding colonies of piscivorous colonial waterbirds, however, are not limited to the Columbia River estuary but are distributed throughout the Columbia River basin. Nearly 150,000 piscivorous colonial waterbirds representing five species at 20 different colonies were documented as nesting at inland sites (upstream of the estuary) during 2007–2010 (BRNW 2011). Published research on the impacts of predation by these inland bird colonies on survival of juvenile salmonids has been limited to the tern colonies on Crescent Island in the mid-Columbia River (Antolos et al. 2005) and on Goose Island in Potholes Reservoir, Washington (Maranto et al. 2010; Figure 1).

Since 1987, passive integrated transponder (PIT) tags have been placed in juvenile salmonids from the Columbia River basin to study their behavior and survival after release. Passive integrated transponder tags can provide specific information on individual fish, including species, run type, and migration timing (based on detections of live fish passing hydroelectric dams). Recoveries of PIT tags on bird colonies have previously been used to calculate minimum predation rates and to measure the relative susceptibility of different salmonid ESUs to avian predation (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Passive integrated transponder tags that were recovered from large tern and cormorant colonies in the Columbia River estuary revealed that steelhead *O. mykiss* ESUs were consumed disproportionately in comparison with other PIT-tagged salmonid ESUs. Predation rates on PIT-tagged steelhead detected as passing Bonneville Dam, the last Columbia River dam encountered by out-migrating salmonids, ranged from 9% to 15% depending on the year (Collis et al. 2001; Ryan et al. 2003). With the few exceptions noted above, similar trends in salmonid susceptibility to and overall impacts of predation from birds nesting at inland colonies have not yet been evaluated.

Previous studies of avian predation impacts on the survival of salmonids from the Columbia River basin have focused on individual nesting colonies (Collis et al. 2001; Roby et al. 2003; Antolos et al. 2005; Maranto et al. 2010) as opposed to the cumulative effects of numerous colonies located on or near the Columbia and Snake rivers. Information on salmonid losses to avian predation at larger spatial and temporal scales, however, is paramount in order to fully understand and effectively manage avian predation and thereby maximize the potential benefits to ESA-listed salmonid ESUs throughout the basin. Furthermore, the ephemeral nature of many of the colony sites and the frequency of intercolony movements documented in these bird species (Conover et al. 1979; Cuthbert 1988; Quinn and Sirdevan 1998; Wires et al. 2000) necessitate a systemwide assessment of avian predation management plans. For example, these data are crucial in order to confirm that increases in smolt survival associated with piscivorous waterbird management in the estuary are not offset by increased ESU-specific avian predation rates along the mid-Columbia and lower Snake rivers.

Resource management agencies and conservation groups working in the Columbia River basin recognize the importance of addressing avian predation in efforts to restore ESA-listed salmonid ESUs (USFWS 2005; NOAA 2008). Plans to recover ESA-listed ESUs have been developed by the United States government and specifically call for development of strategies to manage avian predation as a means to bolster juvenile salmonid survival (NOAA 2008, 2010). With the exception of terns nesting on East Sand Island in the Columbia River estuary (USFWS 2005), however, plans have not specified (1) which bird colonies pose the greatest risks to juvenile salmonid survival or (2) the potential benefits of management initiatives to reduce avian predation, particularly in terms of increased salmonid survival.

The main objectives of this study were to (1) determine colony-specific and cumulative predation rates on ESA-listed salmonids by avian predators located on or near the Columbia and Snake rivers, (2) evaluate relative differences in avian predation rates among salmonid ESUs, (3) assess whether differences in predation rates are based on the location of the bird colony (estuary versus inland), and (4) determine whether per capita

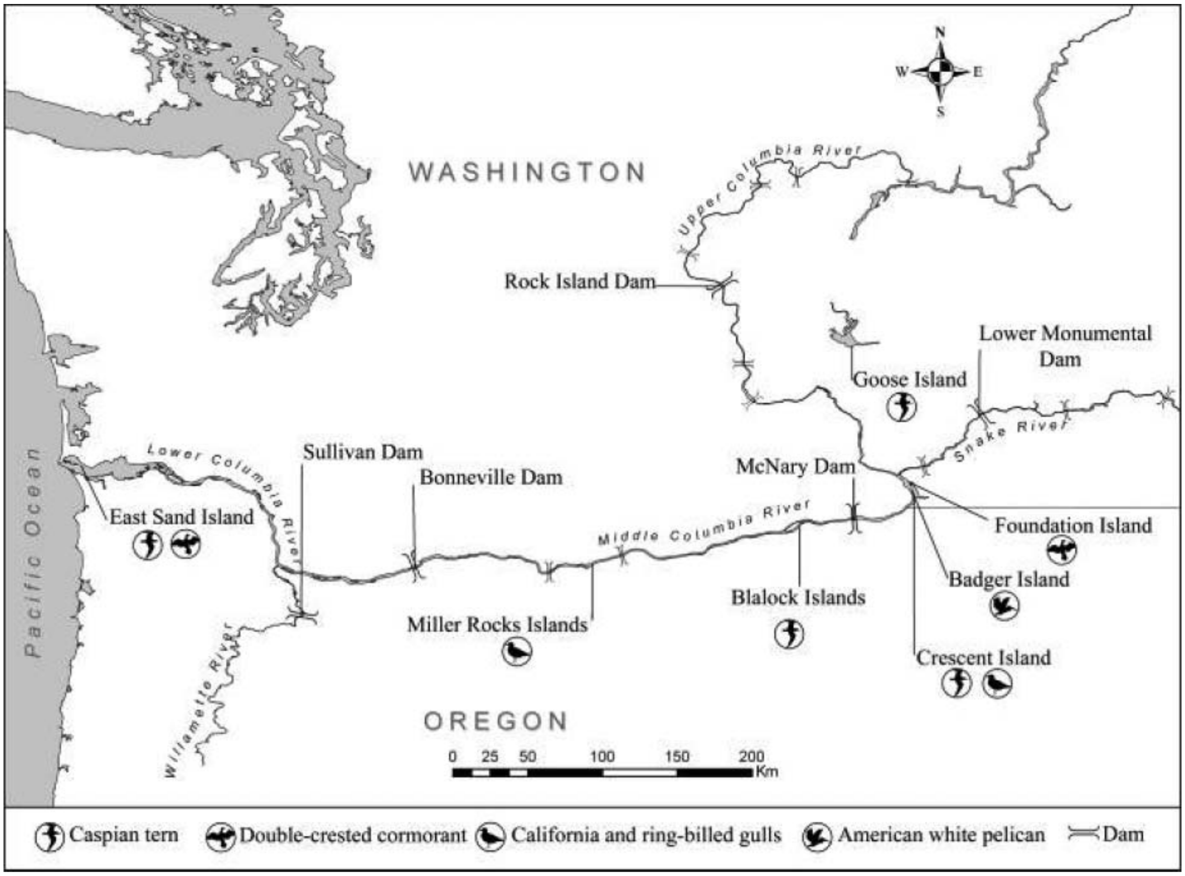

FIGURE 1. Map of the Columbia River basin, showing the bird colonies that were scanned for passive integrated transponder tags from consumed juvenile salmonids, the river systems associated with salmonid populations, and the hydroelectric dams that were used to determine smolt availability during 2007–2010.

(per bird) predation rates differ among bird species and colony locations. Objectives 1 and 2 address the paucity of knowledge regarding which ESA-listed salmonid ESUs are most affected by avian predation on a systemwide scale. Objectives 3 and 4 will aid current and future management efforts by identifying which bird species and colonies pose the greatest risk to salmonid populations in the region and by specifying where reductions in avian predation would most enhance juvenile salmonid survival.

STUDY AREA

Our study area included breeding colonies of piscivorous waterbirds from the mouth of the Columbia River to the upper Columbia River, a distance of approximately 730 river kilometers (rkm; Figure 1). In total, nine individual bird colonies were surveyed for this study. These colonies were selected based on previous surveys for PIT tags (Ryan et al. 2003; Antolos et al. 2005; Maranto et al. 2010), the large size of the colonies, the close proximity of the colonies to out-migrating salmonids, or a combination of large size and close proximity. Colonies were located in the Columbia River estuary, inland along the mid-Columbia River (between Bonneville Dam and McNary Dam), and near the confluence of the Snake and Columbia rivers (hereafter, "the confluence"; Figure 1). Specific breeding colonies that were scanned for PIT tags included tern colonies on East Sand Island (rkm 8; estuary), the Blalock Islands (rkm 445; mid-Columbia River), Crescent Island (rkm 510; confluence), and Goose Island (an off-river colony in Potholes Reservoir, Washington, near the confluence); cormorant colonies on East Sand Island and Foundation Island (rkm 518; confluence); gull colonies (i.e., California gulls *Larus californicus* and ring-billed gulls *L. delawarensis*; hereafter, "gulls") on Miller Rocks Islands (rkm 333; mid-Columbia River) and Crescent Island; and a colony of American white pelicans *Pelecanus erythrorhynchos* (hereafter, "pelicans") on Badger Island (rkm 511; confluence; Figure 1).

The designation of ESUs for ESA-listed salmonids followed those of the National Oceanic and Atmospheric Administration (NOAA; NOAA 2011) and included both wild and hatchery-reared fish. Passive integrated transponder tagged salmonids that originated from within the geographic boundary of the NOAA-defined ESU were included in the study. All ESA-listed salmonid ESUs that originated entirely upstream of Bonneville Dam on the Columbia River were included in the study (Figure 1). Upper Willamette River spring Chinook salmon *O. tshawytscha* were also included, as the majority of fish from this ESU originates above Sullivan Dam on the Willamette River (Figure 1). However, upper Willamette River steelhead were excluded from the study due to the small sample sizes of PIT-tagged individuals. Overall, eight different ESA-listed salmonid ESUs were evaluated by this study: Snake River steelhead, Snake River sockeye salmon *O. nerka*, Snake River spring–summer Chinook salmon, Snake River fall Chinook salmon, upper Columbia River steelhead, upper Columbia River spring Chinook salmon, mid-Columbia River steelhead, and upper Willamette River spring Chinook salmon.

METHODS

Scanning of PIT tags was conducted after birds dispersed from their breeding colonies following the nesting season (August–November) during 2007–2010 (hereafter, "the study period"). We used the methods described by Ryan et al. (2001), whereby flat-plate and pole-mounted PIT tag antennas were used to detect PIT tags in situ by systematically scanning the area that was occupied by birds during the nesting season. The area occupied by birds on each colony was determined based on aerial photographs of the colony and visits to the colony during the nesting season. The entire colony area occupied by nesting birds was scanned for PIT tags (referred to as a "pass"). Numerous passes were then conducted until the number of previously undetected PIT tags that were found during a pass was less than or equal to 5% of the total number of PIT tags that were found during all previous passes. The effort required to achieve this criterion ranged from 2–6 passes/colony, which took from 1 to 5 d to complete each year depending on the size (surface area) of the colony.

Passive integrated transponder tag detection efficiency.—Not all PIT tags deposited by birds on the nesting colony are subsequently found by researchers after the nesting season. For example, tags can be blown off of the colony's nesting area during wind storms; washed away during high tides, rain storms, or other flooding events; or otherwise damaged or lost during the course of the nesting season. Furthermore, the detection methods used to find PIT tags on bird colonies are not 100% efficient, as some proportion of detectable tags is missed by researchers during the scanning process (Ryan et al. 2003). To address these factors, PIT tags with known tag codes were intentionally sown on each bird colony (hereafter, "control tags") throughout the nesting season to quantity PIT tag detection efficiency. Control tags had the same dimension and length as PIT tags used to mark juvenile salmonids from the Columbia River basin (12-mm, 134.2-kHz, full-duplex tags). The sowing of control tags was conducted during several discrete stages of the birds' nesting season: (1) prior to the initiation of egg laying (March–April), (2) during the egg incubation period (April–May), (3) during the chick rearing period (May–June), and (4) immediately after the fledging of young (July–August). These periods were selected because they encompassed the time periods when juvenile salmonids were out-migrating and therefore available as prey to nesting birds. The total number of control PIT tags that were sown varied by colony and year, with sample sizes ranging from 100 to 600 PIT tags/colony in any given year. The number of discrete time periods during which control tags were sown also varied but was no less than two (at the beginning and end of the nesting season) and no more than four. During each release, control tags were randomly sown throughout the entire area occupied by nesting birds during the breeding season. Priorities for sowing control tags were based on colony size (with larger colonies receiving the most control tags) and our a priori expectation of salmonid predation at that colony, with tern and cormorant colonies generally receiving more control tags than gull or pelican colonies (Collis et al. 2002).

Not all PIT tags egested by birds are subsequently deposited on their nesting colony. An unknown number of tags are presumably damaged during digestion or are regurgitated or defecated off-colony at loafing, staging, or other areas utilized by birds during the breeding season. The number of consumed PIT tags that were deposited off-colony during this study was unknown. Therefore, predation rate estimates are minimum estimates of salmonid losses to colonial waterbirds.

Availability of PIT-tagged salmonids.—We queried the regional salmonid PIT Tag Information System (PTAGIS) database (maintained by the Pacific States Marine Fisheries Commission) to acquire data on interrogations of ESA-listed PIT-tagged salmonids that were released in the Columbia River basin during the study period. Availability of PIT-tagged salmonids to predation by birds nesting on different colonies was determined by interrogations of PIT-tagged fish at the nearest upstream hydroelectric dam with juvenile fish interrogation capabilities. Therefore, fish availability to birds nesting at East Sand Island in the estuary was based on detections of PIT-tagged salmonids at Bonneville Dam (rkm 225) on the lower Columbia River or at Sullivan Dam (rkm 206) on the Willamette River (Figure 1). For bird colonies on Miller Rocks Islands and the Blalock Islands in the mid-Columbia River, salmonid availability was determined based on detections of PIT-tagged fish at McNary Dam (rkm 470; Figure 1). For bird colonies near the confluence (Crescent, Badger, Foundation, and Goose islands), availability was determined from detections of PIT-tagged fish at Lower Monumental Dam (rkm 589) on the Snake River and at Rock Island Dam (rkm 730) on the upper Columbia River (Figure 1). Data on impacts to mid-Columbia River steelhead were limited to predation impacts by birds in the Columbia River estuary because the majority of PIT-tagged fish from this population entered the migration corridor downstream of McNary Dam.

The distance between the dam used to determine fish availability and the downstream bird colony surveyed varied from a minimum of 25 rkm (McNary Dam to the Blalock Islands) to a maximum of 220 rkm (Rock Island Dam to Crescent Island; Figure 1). For most colonies in this study, the distance between the dam and the colony was beyond the maximum published foraging radius for the bird species (Baird 1976; Gill 1976; Ryder 1993; Anderson et al. 2004; Scoppettone et al. 2006), suggesting that birds from downstream colonies rarely consumed juvenile salmonids upstream of these dams.

Avian predation rates.—Predation rates on PIT-tagged salmonids were calculated using a multistep approach. First, for each ESA-listed ESU, the proportion of PIT-tagged fish that were consumed by avian predators on day j ($\hat{q}_j$) was estimated by dividing the number of PIT-tagged fish detected at a dam on day j that were subsequently recovered on a bird colony (recovered$_j$) by the total number of salmonids detected as passing that dam on day j (available$_j$):

$$\hat{q}_j = \frac{\text{recovered}_j}{\text{available}_j}. \tag{1}$$

Second, we used logistic regression to estimate colony-specific daily detection efficiencies, whereby a binary response of detections (detected or not detected) was modeled as a function of time since control tags were placed on the bird colony:

$$\hat{p}_j = \frac{e^{(\beta_0+\beta_1 t_j)}}{1+e^{(\beta_0+\beta_1 t_j)}}, \tag{2}$$

where $\hat{p}_j$ is the probability of detecting a control tag that was deposited on day j, β_0 is the regression intercept, β_1 is the regression slope, and t_j is the independent variable for deposition date. To calculate colony-specific adjusted daily predation rates ($\hat{r}_j$), the proportion of available PIT-tagged salmonids whose tags were recovered from a bird colony on day j ($\hat{q}_j$) was corrected for colony-specific detection efficiency on day j ($\hat{p}_j$):

$$\hat{r}_j = \frac{\hat{q}_j}{\hat{p}_j}. \tag{3}$$

To calculate annual predation rates, daily estimates of the total number of PIT-tagged salmonids consumed were summed and divided by the total number of salmonids that were available within that same time period. Reach-specific (estuary, mid-Columbia River, and confluence) predation rates were calculated by summing predation rates from bird colonies in the same reach per salmonid ESU. Confidence intervals for predation rates were estimated by a bootstrapping simulation technique (Efron and Tibshirani 1986; Manly 1998). The bootstrapping analysis consisted of 2,000 iterations of the model calculation, with each iteration representing a unique bootstrap resample (random sample with replacement) of the observed detection efficiency and salmonid PIT tag data sets. The 2.5th and 97.5th quartiles were used to represent the limits of a bootstrapped 95% confidence interval. Predation rate estimates and 95% confidence intervals were calculated for each unique ESA-listed ESU of PIT-tagged fish consumed by a bird colony in each year. A study period estimate and 95% confidence interval were then generated for each bird colony by using all available PIT-tagged salmonids for 2007–2010 to evaluate colony-specific impacts on smolt survival during the entire study period. For all instances in which a bird colony consumed less than 0.1% of a given ESA-listed ESU, predation rates are noted as being less than 0.1% and are presented without confidence intervals due to the proximity of the estimate to zero.

To control for imprecise results that might arise from small sample sizes, estimates of predation rates were only calculated for ESA-listed ESUs from which at least 500 PIT-tagged salmonids were interrogated while passing an upstream dam in a given year. Additionally, only PIT-tagged salmonids that were detected at a dam during the bird nesting season (1 March–31 August for colonies in the estuary; 1 April–31 July for inland colonies) were included in these analyses, as these fish were believed to be available to birds nesting at the colony. Analyses were conducted using R software, with statistical significance α set at 0.05.

Per capita predation rates.—Predation rates adjusted for differences in colony size (number of nesting adults) were generated for each bird colony and each year to address how potential changes in bird colony size might affect overall predation rates on ESA-listed ESUs. Colony-size-adjusted predation rates (per capita rates) were calculated by dividing predation rate estimates by the number of adult birds present at each colony in each year. The numbers of adult birds nesting at each colony in each year were obtained from Bird Research Northwest (BRNW 2011). Per capita predation rates were based on detections of all ESA-listed PIT-tagged salmonids that were interrogated while passing the nearest upstream dam(s).

Model assumptions.—Results from our multistep modeling procedure for estimating minimum avian predation rates on PIT-tagged salmonids were based on the following assumptions: (1) salmonid release and detection information obtained from PTAGIS was complete and accurate; (2) PIT-tagged salmonids that were detected while passing an upstream dam were available to avian predators nesting downstream of that dam; (3) the detection probability for control PIT tags was equal to the detection probability for PIT tags that were naturally deposited by birds on-colony; (4) off-colony PIT tag deposition rates (i.e., tags that were regurgitated or defecated by birds somewhere other than on the nesting colony) did not differ among bird species, among colonies, or among years; and (5) PIT tags from consumed fish were deposited on a bird colony on the same day that the PIT-tagged fish were detected as passing the upstream dam.

To verify assumption 1, irregular entries were either validated by tagging coordinators or eliminated from the analysis. Detections of PIT-tagged salmonids at dams upstream of bird colonies were deemed the most appropriate measure of fish availability given the downstream movement of juvenile salmonids, the ability to standardize data across all sites, and the ability to define unique groups of salmonids based on a known location and passage date (assumption 2). Detection efficiency estimates (assumption 3) were generally high at all colonies (see

Results); thus, possible violations of assumption 3 would have little effect on estimates of predation rates. Variation in the proportion of consumed PIT tags deposited off-colony among bird species and among colonies (assumption 4) could result in differences in minimum predation rate estimates. At this time, however, there are no data available to support or refute assumption 4 other than to note that during the nesting season, some PIT tags presumably are damaged during digestion, are deposited off-colony, or both. Assumption 5 relates to the use of the last date of live detection as a proxy for the date of PIT tag deposition on a bird colony; this assumption needed only to be roughly true because detection efficiency did not change dramatically on a daily basis (see Results).

RESULTS

In total, 1,058,808 PIT-tagged salmonids from the eight salmonid ESUs were used to determine fish availability to avian predators (Table 1). From these fish, 32,064 PIT tags were subsequently recovered by researchers on avian colonies during the study period. Snake River steelhead represented the ESU with the highest number of on-colony recoveries (n = 17,353 PIT tags), followed by Snake River spring–summer Chinook salmon (n = 4,858), upper Columbia River steelhead (n = 4,378), Snake River fall Chinook salmon (n = 2,728), mid-Columbia River steelhead (n = 1,965), upper Columbia River spring Chinook salmon (n = 399), Willamette River spring Chinook salmon (n = 200), and Snake River sockeye salmon (n = 183). By river reach and bird colony, the largest number of PIT tags was recovered from bird colonies in the Columbia River estuary (n = 20,733 PIT tags recovered on the East Sand Island tern and cormorant colonies), followed by colonies near the confluence (n = 8,831 PIT tags recovered on the Goose Island tern colony, Crescent Island tern and gull colonies, Foundation Island cormorant colony, and Badger Island pelican colony), and colonies in the mid-Columbia River between McNary and The Dalles dams (n = 2,500 PIT tags recovered on the Miller Rocks Islands gull colony and Blalock Islands tern colony). Interrogations of PIT-tagged salmonids overlapped almost completely with the nesting seasons of the avian colonies studied here; over 98% of all PIT-tagged salmonids were detected as passing dams during the nesting seasons.

Passive Integrated Transponder Tag Detection Efficiency

Detection efficiency of control PIT tags that were intentionally sown on bird colonies during the nesting season was unique to each bird colony and each year. In general, detection efficiencies were high across colonies and years (Table 2). Detection efficiency estimates ranged from a low of 46.5% at the Goose Island tern colony in 2009 to a high of 93.0% at the Blalock

TABLE 1. Numbers of PIT-tagged salmonids that were interrogated while passing Bonneville Dam (BON) on the lower Columbia River, Sullivan Dam (SUL) on the Willamette River (WR), McNary Dam (MCJ) on the mid-Columbia River (MCR), Lower Monumental Dam (LMJ) on the Snake River (SR), and Rock Island Dam (RIS) on the upper Columbia River (UCR) during 2007–2010. Salmonids were from Endangered Species Act-listed evolutionarily significant units (ESUs); dashes denote PIT-tagged ESUs with too few interrogations for analyses (<500 detections/year).

		Migration year				
Dam	ESU	2007	2008	2009	2010	Total
BON	SR spring–summer Chinook salmon	23,830	11,425	17,396	38,441	91,092
	SR fall Chinook salmon	2,005	24,136	16,314	17,974	60,429
	SR sockeye salmon	—	—	1,845	1,382	3,227
	SR steelhead	6,391	19,571	23,310	40,023	89,295
	MCR steelhead	2,277	2,435	3,570	9,112	17,394
	UCR spring Chinook salmon	2,268	1,662	2,064	5,972	11,966
	UCR steelhead	3,021	2,494	2,213	12,196	19,924
SUL	WR spring Chinook salmon	1,505	2,509	5,573	510	10,097
MCJ	SR spring–summer Chinook salmon	74,905	27,288	60,155	52,129	214,477
	SR fall Chinook salmon	7,374	36,857	43,461	29,587	117,279
	SR sockeye salmon	—	—	2,088	1,327	3,415
	SR steelhead	7,680	15,447	29,877	17,805	70,809
	UCR spring Chinook salmon	6,764	4,713	3,982	6,192	21,651
	UCR steelhead	3,102	3,204	3,220	3,942	13,468
LMJ	SR spring–summer Chinook salmon	22,730	30,142	20,753	8,562	82,187
	SR fall Chinook salmon	2,147	22,968	27,198	38,709	91,022
	SR sockeye salmon	—	767	2,651	568	3,986
	SR steelhead	17,120	28,652	52,220	10,950	108,942
RIS	UCR spring Chinook salmon	—	—	738	929	1,667
	UCR steelhead	3,781	7,742	7,226	7,732	26,481

TABLE 2. Average detection efficiency (proportion) of control PIT tags that were sown on colonies of Caspian terns (tern), double-crested cormorants (cormorant), American white pelicans (pelican), and California gulls and ring-billed gulls (gull) in the Columbia River basin during 2007–2010. Sample sizes are provided in parentheses. In-season variation in detection efficiency is denoted by footnotes.

Island	Bird colony	2007	2008	2009	2010
East Sand	Tern	0.89 (600)	0.92[a] (600)	0.90[a] (600)	0.84[a] (400)
East Sand	Cormorant	0.58[a] (200)	0.69[a] (600)	0.70 (600)	0.76[a] (400)
Miller Rocks	Gull	0.87 (200)	0.83 (200)	0.78[a] (200)	0.75[a] (200)
Blalock	Tern	0.88 (200)	0.93 (100)	0.84 (100)	0.88[c] (NA)
Crescent	Tern	0.70[a] (800)	0.62[a] (400)	0.71[a] (400)	0.75[a] (400)
Crescent	Gull	0.63[a] (200)	0.74[a] (200)	0.73[a] (200)	0.79[a] (200)
Badger	Pelican	0.65[a] (200)	0.68 (200)	0.85[a] (200)	0.75[a] (200)
Foundation	Cormorant	0.68 (400)	0.74 (400)	0.73[b] (400)	0.63 (400)
Goose	Tern	0.53[a] (100)	0.64[a] (400)	0.47[a] (400)	0.58[a] (400)

[a]Detection efficiency significantly ($P < 0.05$) increased with Julian date of tag deposition.
[b]Detection efficiency significantly ($P < 0.05$) decreased with Julian date of tag deposition.
[c]Detection efficiency was based on the average from previous years because no tags were sown on the colony in 2010.

Islands tern colony in 2008 (Table 2). Within-season temporal differences in detection efficiency were also observed at some colonies but varied by colony and year (Table 2). Logistic regression results indicated that estimated detection efficiency could increase, decrease, or remain stable throughout the nesting season (Table 2). The most common temporal trend was increasing detection efficiency through the nesting season, and this relationship was observed in all 4 years at the Crescent Island tern colony, the Crescent Island gull colony, and the Goose Island tern colony (Table 2).

Avian Predation Rates

Results indicated that avian predation on ESA-listed salmonids varied by bird colony, colony location or river reach, and salmonid ESU. By bird colony and location, minimum predation rates were highest from terns and cormorants nesting on East Sand Island in the Columbia River estuary. Terns and cormorants nesting on East Sand Island consumed a minimum of 2.5–16.0% (depending on the ESU) of the available PIT-tagged salmonids that were last detected as passing Bonneville Dam or Sullivan Dam during the study period (Figure 2). Of the eight ESA-listed ESUs evaluated, minimum predation rates were highest on Snake River steelhead, with an estimated 16% consumed by terns and cormorants nesting on East Sand Island (Figure 2). Although combined losses were greatest for Snake River steelhead, similar losses to terns and cormorants nesting in the estuary were also observed for mid-Columbia River steelhead (14.1%) and upper Columbia River steelhead (13.8%; Figure 2). Among avian predators in the estuary, predation on steelhead ESUs was significantly higher from terns (9.7–10.7%) than from cormorants (3.1–5.5%; Figure 2). Of the four ESA-listed Chinook salmon ESUs evaluated, minimum predation rates by terns and cormorants in the estuary were highest on Snake River spring–summer Chinook salmon at 4.6% (Figure 2). Conversely, minimum predation rates were lowest on Willamette River spring Chinook salmon at 2.5% (Figure 2). Terns and cormorants in the estuary consumed between 0.9% and 2.4% of available PIT-tagged Chinook salmon ESUs (Figure 2), which suggests that Chinook salmon ESUs exhibited similar susceptibility to predation by terns and predation by cormorants. The combined minimum predation rate on Snake River sockeye salmon by terns and cormorants in the estuary was estimated at 3.0% (Figure 2); the predation rate on sockeye salmon was higher for cormorants (2.1%) than for terns (0.9%; Appendix Table A.1). Annual variability in predation rates was observed during the 4-year study, and predation rates by cormorants on salmonids (all ESUs) was lowest

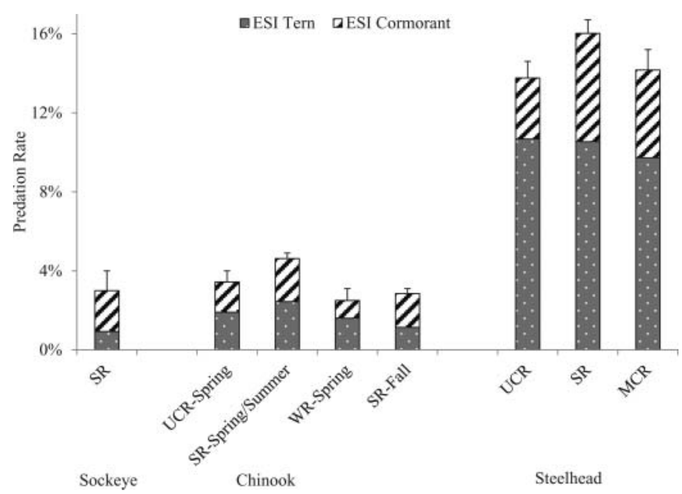

FIGURE 2. Estimated minimum predation rates (with upper 95% confidence limit) on PIT-tagged juvenile salmonids by Caspian terns (tern) and double-crested cormorants (cormorant) nesting on East Sand Island (ESI) in the Columbia River estuary during 2007–2010; prey availability was calculated based on the number of PIT-tagged salmonids that were last interrogated while passing Bonneville Dam (Columbia River) or Sullivan Dam (Willamette River [WR]). Salmonid evolutionarily significant units (ESUs) are provided (SR = Snake River; UCR = upper Columbia River; MCR = mid-Columbia River). Only ESUs with at least 500 PIT-tagged individuals interrogated in any given year (see Table 1) are presented.

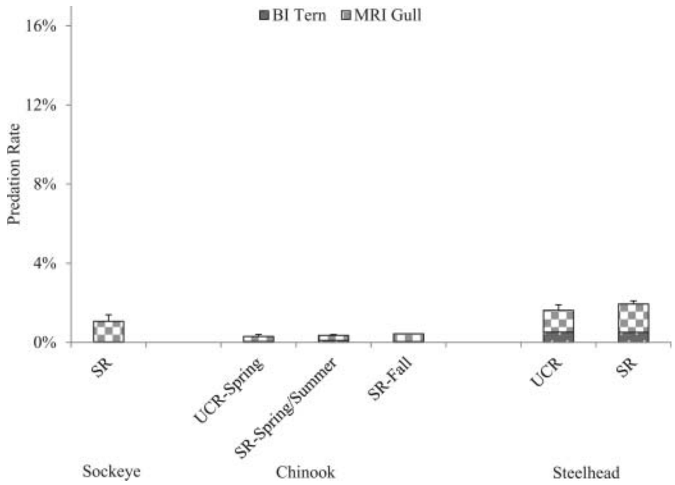

FIGURE 3. Estimated minimum predation rates (with upper 95% confidence limit) on PIT-tagged juvenile salmonids by Caspian terns (tern) nesting on the Blalock Islands (BI) and California gulls and ring-billed gulls (gull) nesting on Miller Rocks Islands (MRI) in the mid-Columbia River during 2007–2010; prey availability was calculated based on the number of PIT-tagged salmonids that were last interrogated while passing McNary Dam. Salmonid ESUs are provided (SR = Snake River; UCR = upper Columbia River). Only ESUs with at least 500 PIT-tagged individuals interrogated in any given year (see Table 1) are presented.

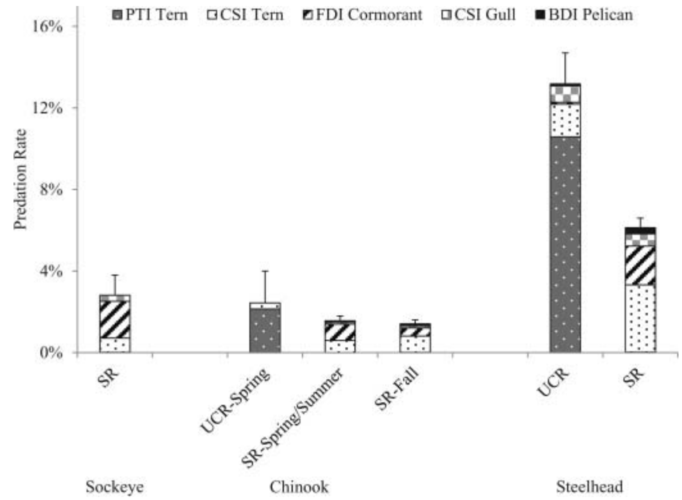

FIGURE 4. Estimated minimum predation rates (with upper 95% confidence limit) on PIT-tagged juvenile salmonids by Caspian terns (tern), double-crested cormorants (cormorant), California gulls and ring-billed gulls (gull), and American white pelicans (pelican) nesting on islands near the Snake River–Columbia River confluence during 2007–2010 (PTI = Goose Island, Potholes Reservoir; CSI = Crescent Island; FDI = Foundation Island; BDI = Badger Island); prey availability was calculated based on the number of PIT-tagged salmonids that were last interrogated while passing Lower Monumental Dam (Snake River [SR]) or Rock Island Dam (upper Columbia River [UCR]). Salmonid ESUs are provided. Only ESUs with at least 500 PIT-tagged individuals interrogated in any given year (see Table 1) are presented.

in 2007 (Table A.1). Annual predation rates on salmonids by East Sand Island terns were less variable than predation rates by cormorants, but significant differences in annual predation rates among years and among salmonid ESUs were also noted (Table A.1). The trend in which terns had the highest predation rates on steelhead ESUs, however, was evident during each of the four study years.

Predation on ESA-listed PIT-tagged salmonids by the two avian colonies in the mid-Columbia River between McNary and The Dalles dams (gulls on Miller Rocks Islands; terns on Blalock Islands) was relatively minor (<2.0% of available fish per salmonid ESU; Figure 3) during the study period in comparison with predation rates by terns and cormorants nesting on East Sand Island. Similar to avian predation in the estuary, however, minimum predation rates by terns and gulls in the mid-Columbia River were significantly greater on steelhead ESUs (1.6–1.9%) than on salmon ESUs (0.3–1.1%; Figure 3), with Blalock Islands terns and Miller Rock Islands gulls both consuming disproportionately more steelhead relative to their availability downstream of McNary Dam. During the study period, minimum predation rates from Blalock Islands terns and Miller Rocks Islands gulls were less than 0.5% for the three ESA-listed Chinook salmon ESUs evaluated (upper Columbia River spring, Snake River fall, and Snake River spring–summer ESUs). Predation on Snake River sockeye salmon (1.1%), especially by gulls on Miller Rocks Islands, was higher than that on Chinook salmon ESUs, although data were limited to two of the four study years due to inadequate numbers of PIT-tagged Snake River sockeye salmon in 2007 and 2008 (Table 1). Very little variation in annual predation rate estimates was observed for these colonies during the study period (<1.0% difference in ESU-specific predation rates in all yearly comparisons; Table A.1). The lack of variability in annual predation rate estimates is associated with the close proximity of these estimates to zero.

Of the three river reaches examined, predation rates associated with bird colonies near the confluence were the most variable: minimum predation rates on ESA-listed ESUs ranged from 1.4% to 13.2% during the study period (Figure 4). Of the five avian colonies in the confluence reach, the terns nesting on Goose Island in Potholes Reservoir demonstrated the highest single colony-specific predation rate of 10.6%, which was observed for upper Columbia River steelhead (Figure 4). Predation by Goose Island terns was almost exclusively on salmonid ESUs originating from the upper Columbia River (2.1–10.6%), whereas their predation rates on Snake River ESUs were significantly lower (<0.3%; Figure 4). The Crescent Island tern colony and Foundation Island cormorant colony were associated with the highest predation rates on ESUs originating from the Snake River (Figure 4), and they consumed disproportionately more Snake River sockeye salmon, Snake River spring–summer Chinook salmon, Snake River fall Chinook salmon, and Snake River steelhead compared with upper Columbia River ESUs. Predation by Crescent Island terns was highest on Snake River steelhead, as a minimum of 3.3% of available PIT-tagged individuals were consumed during the study period (Figure 4).

With the exception of upper Columbia River spring Chinook salmon, which were predominately consumed by Goose Island terns, predation by Foundation Island cormorants on salmon (Chinook salmon and sockeye salmon) ESUs was similar to or greater than predation by terns (Crescent and Goose islands) on the same salmon ESUs (Figure 4). Significant annual variation in predation rates was observed at bird colonies in the confluence reach. Predation rates on upper Columbia River steelhead by Goose Island terns were particularly variable, ranging from a low of 7.5% in 2008 to a high of 15.7% in 2009 (Table A.1). Similar to results in the estuary, the trend of higher predation rates on steelhead populations, particularly by terns, was evident in all study years.

Overall predation impacts were often greater on ESUs originating upstream of the confluence than on ESUs originating lower in the basin (mid-Columbia River or Willamette River), as upriver ESUs (Snake River and upper Columbia River) were susceptible to predation by birds from several inland colonies that did not prey upon fish from lower-river ESUs (Figures 2–4). Relative to their availability, upper Columbia River steelhead and Snake River steelhead suffered the greatest cumulative impacts from the nine avian colonies evaluated here. Reach-specific minimum predation rates on Snake River steelhead were 6.1% by avian colonies near the confluence, 1.9% by mid-Columbia River colonies, and 16.0% by estuarine colonies (Figures 2–4). Minimum predation rates on upper Columbia River steelhead were 13.2, 1.6, and 13.8% by avian colonies near the confluence, in the mid-Columbia River, and in the estuary, respectively (Figures 2–4). Cumulative avian predation impacts were greater for upper Columbia River steelhead than for Snake River steelhead due to the high predation rates on upper Columbia River steelhead by terns nesting on Goose Island (Figure 4). Predation rates by the nine avian colonies evaluated here were often significantly less for ESA-listed Chinook salmon and sockeye salmon ESUs than for steelhead populations but were still in excess of 2.0% for most ESUs in most river reaches.

Per Capita Predation Rates

After accounting for differences in the size of each avian colony, per capita (per bird) predation rates were highest for Crescent Island terns, Foundation Island cormorants, Blalock Islands terns, and Goose Island terns—all inland colonies (Figure 5). Predation rates adjusted for colony size were an order of magnitude greater for Crescent Island and Blalock Islands terns than for East Sand Island terns (Figure 5). A similar difference was evident between Foundation Island cormorants and

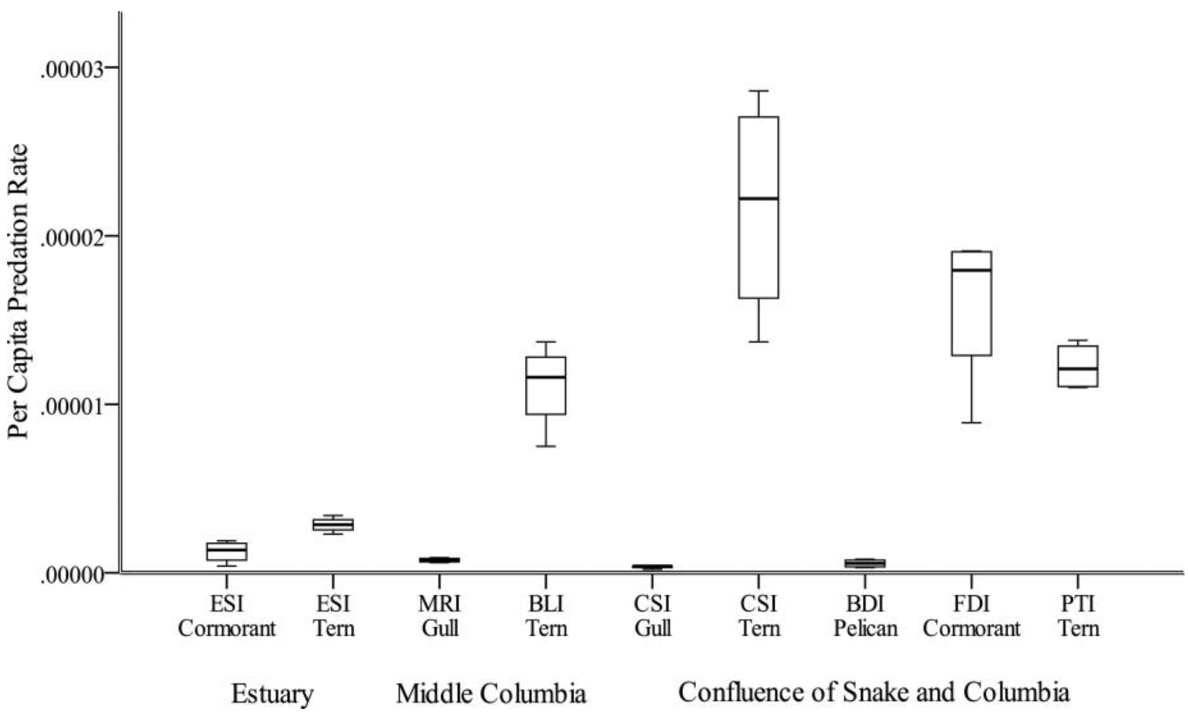

FIGURE 5. Box-and-whisker plot showing annual estimated minimum per capita predation rates on PIT-tagged juvenile salmonids (Chinook salmon, sockeye salmon, and steelhead combined) by Caspian terns (tern), double-crested cormorants (cormorant), California gulls and ring-billed gulls (gull), and American white pelicans (pelican) nesting on islands in the Columbia River estuary (ESI = East Sand Island), in the mid-Columbia River (MRI = Miller Rocks Islands; BLI = Blalock Islands), or near the Snake River–Columbia River confluence (CSI = Crescent Island; BDI = Badger Island; FDI = Foundation Island; PTI = Goose Island, Potholes Reservoir) during 2007–2010. Predation rates were calculated based on the number of PIT-tagged salmonids that were detected as passing Bonneville and Sullivan dams (for estuarine colonies), McNary Dam (for mid-Columbia River colonies), or Lower Monumental and Rock Island dams (for colonies near the confluence). The sizes of bird colonies (number of nesting adults) were from Bird Research Northwest (BRNW 2011). Lines within the box represent the median, ends of the box represent the interquartile, and the whiskers represent the minimum and maximum.

East Sand Island cormorants; per capita predation rates were approximately 13 times higher for cormorants nesting at the inland location (Foundation Island) relative to those nesting at the estuarine location (East Sand Island; Figure 5). Per capita salmonid predation rates by gull and pelican colonies, regardless of river reach, remained extremely low in comparison with those by tern and cormorant colonies (Figure 5).

DISCUSSION

This study is among the first to document predation rates on different ESA-listed fish populations by multiple bird species nesting throughout a large river system. Predation impacts on PIT-tagged salmonids were evaluated for five previously unstudied piscivorous waterbird colonies in the Columbia River basin (gulls nesting at colonies on Miller Rocks Islands and Crescent Island, cormorants nesting on Foundation Island, terns nesting on the Blalock Islands, and pelicans nesting on Badger Island) and compared them with updated predation rates from four colonies evaluated in the published literature (tern and cormorant colonies on East Sand Island, terns on Crescent Island, and terns on Goose Island in Potholes Reservoir). Results demonstrate that avian predation by these nine colonies was a substantial source of mortality for ESA-listed salmonids during out-migration.

Passive Integrated Transponder Tag Detection Efficiency

Overall, the efficiency of PIT tag detection on avian colonies was high, as the majority of control tags sown on-colony during the nesting season were subsequently recovered by researchers after the nesting season. Variation in on-colony detection efficiency of PIT tags among colonies and among years was likely due to the unique characteristics of each island, including substrate type (sand, rock, or soil-based nesting substrate) and weather conditions. The loss of PIT tags during the birds' nesting season (i.e., losses to wind storms, rain storms, or other factors) and the missed detections of functional PIT tags on-colony have not been incorporated into previously published studies (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Although Evans et al. (2011) documented substantial loss of coded wire tags on a Caspian tern colony in San Francisco Bay, published studies of on-colony loss and detection probabilities of PIT tags were lacking. Our results demonstrate that when detection efficiency is ignored, predation rates based on PIT tag recoveries can underestimate smolt losses to avian predators. Predation rates by terns nesting on Crescent and Goose islands were especially influenced by within-season differences in detection efficiency and the relatively low estimates of detection efficiency ($<60\%$) in comparison with the other bird colonies evaluated. Salmonid smolt out-migration occurs across several months; therefore, data describing the variation in detection efficiency of PIT tags deposited on bird colonies during these time periods are necessary to make more accurate comparisons across ESUs and across years.

Even after adjustments for on-colony detection efficiency are made, an unknown number of PIT tags consumed by colonial waterbirds are presumably damaged during digestion, deposited off-colony, or both. Biology and foraging behavior differ among the five avian species evaluated here, and theoretically these differences could influence the degree to which predation rates are underestimated due to off-colony deposition and tag damage. Thus, although adjustments for detection efficiency increase the accuracy of predation rate estimates, the predation rates based on PIT tags recovered from bird nesting colonies still constitute minimum estimates of predation. Further study is needed to quantify off-colony PIT tag deposition and tag damage for comparisons among avian species, among colonies, and among different environmental conditions.

Avian Predation Rates

Results demonstrated that minimum rates of avian predation on salmonids varied considerably by bird colony, location (estuary, mid-Columbia River, or near the confluence), and salmonid ESU. In general, the highest avian predation rates were observed for steelhead ESUs. It is well documented that steelhead have a higher susceptibility to avian predation than other salmonid ESUs in the Columbia River basin (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Possible reasons for the greater susceptibility of steelhead in comparison with salmon include differences in smolt behavior during out-migration and differences in the relative size (length) of salmonids. Collis et al. (2001) hypothesized that steelhead were more susceptible to avian predation because of their larger size (length) and their greater surface orientation in comparison with Chinook salmon and sockeye salmon. The positive association between average fish length and avian predation rates described by Ryan et al. (2003) supports this hypothesis, with steelhead being larger on average and preyed upon at a higher rate than salmon. In a study of salmonid migration depth in the Columbia River, Beeman and Maule (2006) observed that steelhead migrated closer to the surface than Chinook salmon during daylight hours, when bird predation occurs.

Of the eight ESA-listed salmonid ESUs evaluated here, Snake River steelhead and upper Columbia River steelhead experienced the highest proportional reach-specific and cumulative losses to avian predation. Steelhead from the Snake River and upper Columbia River must pass all nine bird colonies during out-migration to the Pacific Ocean, and fish from these two ESUs experienced avian predation rates greater than 14% in the estuary and greater than 6% near the confluence. Relative to other documented factors that influence mortality during out-migration, avian predation—particularly by tern and cormorant colonies—was a substantial source of mortality for out-migrating steelhead. Muir et al. (2001) estimated a 2–5% mortality rate for juvenile steelhead as they passed dams on the Snake River. Rieman et al. (1991) estimated that piscivorous fish (northern pikeminnow *Ptychocheilus oregonensis*, walleye *Sander vitreus*, and smallmouth bass *Micropterus dolomieu*) consumed 11%

of available juvenile steelhead in John Day Reservoir on the Columbia River.

All of the ESA-listed salmonid populations included in this study comprise a mixture of wild and hatchery-raised fish (NOAA 2011). As such, an evaluation of bird predation on ESA-listed ESUs required the inclusion of both rearing types. Other studies in the Columbia River basin have noted that hatchery-reared salmonids are occasionally more susceptible to avian predation than their wild counterparts (Collis et al. 2001; Ryan et al. 2003; Kennedy et al. 2007). Differences in the relative susceptibility of wild and hatchery-raised fish in these studies, however, generally were not statistically significant and were not consistently observed across salmonid species, avian colonies, or years.

Of the nine piscivorous waterbird colonies investigated, the colonies of terns and cormorants nesting on East Sand Island consumed the highest proportions of available PIT-tagged salmonids. Smolt losses to tern and cormorant predation in the estuary as presented here were higher than those reported by Ryan et al. (2003), who investigated predation by terns and cormorants on East Sand Island during 1998–2000. The increases in predation rates between these studies are likely due to the growing number of cormorants nesting on East Sand Island (14,324 adults in 1998; 27,192 adults in 2010; BRNW 2011) and the fact that PIT tag detection efficiency was not incorporated into the 1998–2000 estimates.

Predation rate estimates based on PIT tag recoveries have excluded ESA-listed ESUs originating from the lower Columbia River (lower Columbia River chum salmon *O. keta*, coho salmon *O. kisutch*, Chinook salmon, and steelhead; Collis et al. 2001; Ryan et al. 2003). Lower Columbia River salmonid populations were not considered in this study due to a lack of adequate PIT tag interrogation sites downstream of Bonneville and Sullivan dams. Predation rates may differ to an unknown degree for salmonids originating from the lower Columbia River ESUs and those originating from ESUs upstream of Bonneville and Sullivan dams. In a study of smolt consumption (numbers of fish) in the estuary, Lyons et al. (2010) concluded that coho salmon and subyearling Chinook salmon, two abundant lower Columbia River salmonids, were the most numerous salmonid prey type in the diets of cormorants nesting on East Sand Island.

Avian predation in the Columbia River estuary affects juvenile salmonids that have survived freshwater migration and presumably have a higher probability of surviving to return as adults relative to those fish that have yet to complete outmigration (Roby et al. 2003). Additionally, juvenile salmonids belonging to every ESA-listed Columbia River basin ESU must pass through the Columbia River estuary and are therefore susceptible to predation by birds nesting on East Sand Island. At current colony sizes, management efforts focused on terns and cormorants in the Columbia River estuary will consequently benefit a greater number of salmonid ESUs than will management of inland bird colonies (Roby et al. 2003; USFWS 2005; Lyons et al. 2010).

The highest estimated predation rates on PIT-tagged salmonids by birds nesting at inland colonies were from terns nesting on Crescent and Goose islands and cormorants nesting on Foundation Island. Of the six ESA-listed salmonid populations that were evaluated while passing inland avian colonies, upper Columbia River steelhead received the highest observed predation rates during the study period (10.6%; range = 7.5–15.7%) from terns nesting on Goose Island in Potholes Reservoir. The predation rate estimate for upper Columbia River steelhead was surprising because of the relatively small size of the tern colony (<500 breeding pairs; BRNW 2011) and the location of the colony (at least 35 km from the upper Columbia River). Our estimates of predation rates on salmonid populations by terns nesting on Goose Island differ considerably from rates previously reported by Maranto et al. (2010); those authors estimated an average predation rate of 0.6% (range = 0.4–1.1%) on upper Columbia River steelhead by terns nesting on an island in Potholes Reservoir during 2003–2006. There are several explanations for this apparent discrepancy. First, during 2003–2006, the location of the tern colony in Potholes Reservoir shifted from Solstice Island in the northern portion of the reservoir to Goose Island in the southern portion of the reservoir (6 km closer to the upper Columbia River). This move corresponded with a change in the birds' diet composition, as salmonid prey types were more commonly observed in the diets of terns nesting on Goose Island (~24% of prey items) compared with terns nesting on Solstice Island (~2% of prey items; Maranto et al. 2010). Second, the size of the Goose Island tern colony increased from a maximum of 323 breeding pairs in 2006 (Maranto et al. 2010) to a maximum of 487 breeding pairs in 2009 (BRNW 2011). Third, measures of PIT tag detection efficiency were not available prior to 2007—a substantial factor given that detection efficiency was less than 65% during 2007–2010. Finally, smolt availability to terns nesting at Potholes Reservoir was calculated differently in the two studies. Maranto et al. (2010) based their predation rate estimates on all PIT-tagged salmonids released into the upper Columbia River, regardless of the distance of the fish's release point to the tern colony at Potholes Reservoir. We limited our analysis to PIT-tagged salmonids that were last detected as passing Rock Island Dam, which is 70 km from Goose Island and therefore is near the estimated upper foraging range of terns nesting in Potholes Reservoir (Maranto et al. 2010).

Avian predation rates on Snake River and upper Columbia River salmonid ESUs only included salmonids that migrated past inland bird colonies. However, not all Snake River salmonids pass inland bird colonies; a portion of salmonids are collected at Snake River dams and are transported (via barges or trucks) to release locations downstream of Bonneville Dam (Buchanan et al. 2006). Estimates of the percentage of Snake River salmonids that are transported past inland bird colonies vary by ESU and year, and average transportation estimates for Chinook salmon, sockeye salmon, and steelhead during the study period ranged from approximately 60% in 2008 to 40% in 2010 (FPC 2011). Consequently, the effects of predation on

Snake River salmonids by inland bird colonies apply only to the portion of the smolt population that is not transported around bird colonies (Antolos et al. 2005); during the study period, roughly half of all Snake River salmonids were not transported. However, all (100%) of the salmonids originating from the upper Columbia River must out-migrate in-river past inland bird colonies in the confluence reach. Similarly, because transported Snake River salmonids are released just downstream of Bonneville Dam, all salmonids must out-migrate past bird colonies in the estuary.

Predation rates associated with tern and cormorant colonies were almost always significantly higher than predation rates associated with gull and pelican colonies, regardless of salmonid ESU or river reach. Previous research indicates that fish, and salmonids in particular, constitute a very small proportion of the diets of California gulls and ring-billed gulls nesting on inland islands of the Columbia River (Collis et al. 2002). Gut content analysis of gulls nesting at Miller Rocks Islands and Crescent Island (Collis et al. 2002) indicated that juvenile salmonids comprised less than 4% (by mass) of food biomass. In contrast, salmonids comprised 74% (by mass) of the diets of Caspian terns nesting on Crescent Island (Antolos et al. 2005). Predation rates on PIT-tagged salmonids by the Badger Island pelican colony—the only breeding colony of American white pelicans in Washington State (Ackerman 1997)—were the lowest observed among the nine bird colonies investigated during our study. Pelican predation rates were 0.1% or less for five of the six ESA-listed salmonid populations evaluated, and the predation rate on Snake River steelhead was only slightly higher (0.2%). Low predation rates on out-migrating salmonids by pelicans nesting on Badger Island may be due to several factors, including (1) a reliance on larger fish (Scoppettone et al. 2006) or on fish that congregate in shallow-water habitats (Knopf and Evans 2004), (2) differences in foraging behavior that reduce the habitat overlap between Badger Island pelicans and out-migrating salmonids from the upper Columbia and Snake rivers, or (3) a combination of these.

Per Capita Predation Rates

The per capita predation rates on juvenile salmonids (i.e., rates adjusted for differences in colony size) were substantially higher at inland tern and cormorant colonies relative to their counterparts in the estuary. Per capita salmonid predation rates associated with gull and pelican colonies were much lower than those associated with tern and cormorant colonies, regardless of river reach. The higher per capita predation rates for inland tern and cormorant colonies are due to the higher prevalence of juvenile salmonids in the diets of terns and cormorants nesting at inland colonies versus estuarine colonies (Collis et al. 2002; Antolos et al. 2005; Lyons 2010). Differences in diet composition have been attributed to colony location, as food availability differs throughout the Columbia River basin (Collis et al. 2002; Roby et al. 2003; Lyons 2010; Maranto et al. 2010). A comparison of diet composition between Caspian terns nesting on Rice Island in the upper estuary (rkm 34) and those nesting on East Sand Island (rkm 8) revealed that East Sand Island terns were more reliant on marine forage fishes (northern anchovy *Engraulis mordax*, Pacific herring *Clupea pallasii*, etc.), whereas Rice Island terns had a greater reliance on freshwater fishes (Roby et al. 2002). Furthermore, diet composition varied substantially between the tern colonies in the estuary and those at inland sites (Collis et al. 2002).

Differences in colonywide predation rates and per capita predation rates indicate that current management efforts to increase smolt survival by reducing the number of nesting birds on East Sand Island could be offset if those birds relocate to inland sites in large numbers. Increases in colony size at inland sites, where per capita predation rates are higher, could have a negative impact on smolt survival, especially for Snake River and upper Columbia River steelhead ESUs. Movement of terns from estuarine to inland nesting locations is plausible given the ephemeral nature of waterbird nesting habitats and the documented intercolony movements of waterbird species (Conover et al. 1979; Cuthbert 1988; Quinn and Sirdevan 1998; Wires et al. 2000).

Concluding Remarks

Predation rates based on PIT tag recoveries from bird colonies provide minimum estimates of the proportion of available fish that are consumed by avian predators and provide specific information on when and where salmonid populations are most susceptible to predation by colonial waterbirds. To more precisely measure predation impacts, additional research is needed to evaluate off-colony deposition of PIT tags by colonial waterbirds. Research is also needed to determine whether reductions in smolt losses to avian predation translate into commensurate increases in smolt survival and, ultimately, adult salmonid recruitment. For example, if avian predators are disproportionately consuming dead, diseased, injured, or otherwise moribund fish relative to healthy fish, efforts to reduce avian predation will not result in commensurate increases in smolt survival (Schreck et al. 2006). Similarly, reductions in smolt mortality by reducing predation at one bird colony could be countered by increases in predation at other colonies or by other piscivorous predators. Research aimed at addressing these uncertainties will help to determine the efficacy of avian management initiatives to recover ESA-listed salmonid ESUs.

ACKNOWLEDGMENTS

This project was funded by the U.S. Army Corps of Engineers (USACE) Walla Walla District with additional support from the Bonneville Power Administration (BPA), the USACE Portland District, and the Bureau of Reclamation. We especially thank Scott Dunmire, Rebecca Kalamasz, David Trachtenbarg, and Paul Schmidt (USACE) and John Skidmore (BPA) for their assistance and support. We are grateful to Dave Marvin of the Pacific States Marine Fisheries Commission for providing information on PIT tag releases in the region via PTAGIS; Brad Ryan, an important collaborator during the early phases of the project; Manuela Huso and Nick Som for providing consultation on the statistical methods used to estimate predation rates; and our field crews and field crew coordinators, particularly Brad Cramer, Pete Loschl, Jessica Adkins, James Tennyson, and Melissa Carper, for their valuable contributions to this study. The mention of trade or product names does not constitute endorsement by the U.S. Government. The study was performed under the auspices of the Institutional Animal Care and Use Committee, Oregon State University (Animal Care and Use Protocol Number 3718).

REFERENCES

Ackerman, S. M. 1997. Update: American white pelican colony. Washington Ornithological Society News 51 (October/November):1, 6. Available: wos.org/newsletterarchives.htm. (February 2011).

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.

Baird, P. A. 1976. Comparative ecology of California and ring-billed gulls (*Larus californicus* and *Larus delawarensis*). Doctoral dissertation. University of Montana, Missoula.

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). 2011. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River: colony counts from the 2007, 2008, 2009, and 2010 annual reports. BRNW, Bend, Oregon. Available: www.birdresearchnw.org/Project-Info/publications-reports/unpublished-reports/default.aspx. (August 2011).

Buchanan, R. A., J. R. Skalski, and S. G. Smith. 2006. Estimating the effects of smolt transportation from different vantage points and management perspectives. North American Journal of Fisheries Management 26:460–472.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. 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.

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.

Conover, M. R., B. C. Thompson, R. E. Fitzner, and D. E. Miller. 1979. Increased populations of ring-billed and California gulls in Washington State. Western Birds 10:31–36.

Cuthbert, F. J. 1988. Reproductive success and colony-site tenacity in Caspian terns. Auk 105:339–344.

Efron, B., and R. J. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Science 1:54–75.

Evans, A. F., D. D. Roby, K. Collis, B. M. Cramer, J. A. Sheggeby, L. J. Adrean, D. S. Battaglia, and D. E. Lyons. 2011. Recovery of coded wire tags at a Caspian tern colony in San Francisco Bay: a technique to evaluate impacts of avian predation on juvenile salmonids. North American Journal of Fisheries Management 31:79–87.

FPC (Fish Passage Center). 2011. FPC 2010 draft annual report. FPC, Portland, Oregon. Available: www.fpc.org. (June 2011).

Gill, R. E. 1976. Notes on the foraging of nesting Caspian terns *Hydroprogne caspia* (Pallas). California Fish and Game 62:155.

Kennedy, B. M., W. L. Gale, and K. G. Ostrand. 2007. Relationship between smolt gill Na^+, K^+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries Aquatic Sciences 64:1506–1516.

Knopf, F. L., and R. M. Evans. 2004. The birds of North America online: American white pelican (*Pelecanus erythrorhynchos*). Cornell Laboratory of Ornithology, Ithaca, New York. Available: bna.birds.cornell.edu/bna/species/057. (August 2011).

Lyons, D. E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Doctoral dissertation. Oregon State University, Corvallis. Available: www.birdresearchnw.org/Project-Info/publications-reports/graduate-student-theses. (February 2011).

Manly, B. F. J. 1998. Randomization, bootstrap and Monte Carlo methods in biology, 2nd edition. Chapman and Hall, London.

Maranto, C. J., T. P. Good, F. K. Wiese, and J. K. Parrish. 2010. Impact of the Potholes Reservoir Caspian tern breeding colony on out-migrating juvenile salmonids in the mid-Columbia River. Transactions of the American Fisheries Society 139:362–381.

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.

NOAA (National Oceanic and Atmospheric Administration). 2008. Biological opinion, Endangered Species Act section 7(a)(2) consultation: consultation on remand for operation of the federal Columbia River power system, 11 Bureau of Reclamation projects in the Columbia basin and ESA section 10(a)(1)(A) permit for juvenile fish transportation program. NOAA National Marine Fisheries Service, Northwest Region, F/NWR/2005/05883, Seattle, Washington. Available: https://pcts.nmfs.noaa.gov/pls/pcts-pub/pcts_upload.summary_list_biop?p_id=27149. (September 2010).

NOAA (National Oceanic and Atmospheric Administration). 2010. Endangered Species Act section 7(a)(2) consultation supplemental biological opinion: supplemental consultation on remand for operation of the federal Columbia River power system, 11 Bureau of Reclamation projects in the Columbia basin and ESA section 10(a)(I)(A) permit for juvenile fish transportation program. NOAA National Marine Fisheries Service, Northwest Region, Seattle, Washington.

NOAA (National Oceanic and Atmospheric Administration). 2011. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA National Marine Fisheries Service, Northwest Region, Seattle, Washington. Available: www.nwr.noaa.gov/Publications/Biological-Status-Reviews/Salmon.cfm. (September 2011).

Quinn, J. S., and J. Sirdevan. 1998. Experimental measurement of nesting substrate preference in Caspian terns, *Sterna caspia*, and the successful colonization of human constructed islands. Biological Conservation 85:63–68.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448–458.

Roby, D. D., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, A. M. Myers, and R. M. Suryan. 2002. Effects of colony relocation on diet and productivity of Caspian terns. Journal of Wildlife Management 66:662–673.

Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. Canadian Journal of Zoology 81:250–265.

Ryan, B. A., J. W. Ferguson, R. D. Ledgerwood, and E. P. Nunnallee. 2001. Detection of passive integrated transponder tags from juvenile salmonids on piscivorous bird colonies in the Columbia River basin. North American Journal of Fisheries Management 21:149–153.

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.

Ryder, J. P. 1993. The birds of North America online: ring-billed gull (*Larus delawarensis*). Cornell Laboratory of Ornithology, Ithaca, New York. Available: bna.birds.cornell.edu/bna/species/033. (August 2011).

Schreck, C. B., T. P. Stahl, L. E. Davis, D. D. Roby, and B. J. Clemens. 2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and estuary, 1992–1998: evidence for delayed mortality? Transactions of the American Fisheries Society 135:457–475.

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.

USFWS (U.S. Fish and Wildlife Service). 2005. Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary: final environmental impact statement. USFWS, Migratory Birds and Habitat Programs, Portland, Oregon.

Wires, L. R., and F. J. Cuthbert. 2000. Trends in Caspian tern numbers and distribution in North America: a review. Waterbirds 23:388–404.

APPENDIX: AVIAN PREDATION RATES ON JUVENILE SALMONIDS

TABLE A.1. Minimum annual predation rates (%; with 95% confidence intervals in parentheses) by bird colonies on PIT-tagged salmonids from Endangered Species Act-listed evolutionarily significant units (ESUs; SR = Snake River; MCR = mid-Columbia River; UCR = upper Columbia River; WR = Willamette River) during each year and across all years (study period, 2007–2010). Smolt availability for each river reach (Columbia River estuary [estuary], MCR, and SR–Columbia River confluence [confluence]) was based on the number of PIT-tagged salmonids that were interrogated at Sullivan Dam or Bonneville Dam (for estuarine colonies), McNary Dam (for MCR colonies), or Lower Monumental and Rock Island dams (for colonies near the confluence). Dashes denote PIT-tagged populations that were excluded from analysis because fewer than 500 individuals were interrogated during that year.

Salmonid ESU	2007	2008	2009	2010	Study period
Double-Crested Cormorants on East Sand Island (Estuary)					
SR spring–summer Chinook salmon	0.8 (0.6–1.0)	1.7 (1.4–2.1)	3.3 (3.0–3.7)	2.6 (2.4–2.9)	2.2 (2.0–2.3)
SR fall Chinook salmon	0.7 (0.3–1.3)	1.3 (1.1–1.5)	2.2 (1.9–2.5)	1.9 (1.7–2.2)	1.7 (1.6–1.9)
SR sockeye salmon	—	—	2.7 (1.9–3.7)	1.2 (0.6–1.9)	2.1 (1.5–2.7)
SR steelhead	1.7 (1.3–2.3)	7.3 (6.6–8.1)	8.1 (7.4–8.8)	3.7 (3.4–4.1)	5.5 (5.2–5.8)
MCR steelhead	1.3 (0.7–2.1)	6.6 (5.2–8.1)	6.4 (5.4–7.5)	3.9 (3.4–4.5)	4.4 (4.0–4.9)
WR spring Chinook salmon	0.4 (0.1–0.9)	1.6 (1.0–2.3)	0.7 (0.4–0.9)	1.8 (0.6–3.4)	0.9 (0.7–1.2)
UCR spring Chinook salmon	1.3 (0.7–2.0)	1.7 (1.0–2.6)	1.3 (0.7–1.9)	1.6 (1.2–2.0)	1.5 (1.3–1.8)
UCR steelhead	1.7 (1.1–2.4)	3.0 (2.2–3.9)	3.5 (2.6–4.6)	3.4 (2.9–3.8)	3.1 (2.8–3.4)
Caspian Terns on East Sand Island					
SR spring–summer Chinook salmon	2.2 (2.0–2.4)	1.8 (1.5–2.0)	3.3 (3.0–3.6)	2.4 (2.2–2.6)	2.4 (2.3–2.6)
SR fall Chinook salmon	2.3 (1.6–3.0)	1.3 (1.2–1.5)	1.4 (1.2–1.6)	0.5 (0.4–0.6)	1.1 (1.0–1.2)
SR sockeye salmon	—	—	0.8 (0.4–1.3)	1.1 (0.5–1.7)	0.9 (0.6–1.3)
SR steelhead	16.0 (15.0–17.2)	10.1 (9.6–10.7)	10.4 (9.9–10.9)	9.9 (9.3–10.6)	10.5 (10.2–10.9)
MCR steelhead	12.9 (11.5–14.4)	9.8 (8.6–11.0)	10.1 (9.0–11.2)	8.7 (8.0–9.6)	9.7 (9.2–10.3)
WR spring Chinook salmon	1.0 (0.5–1.5)	3.1 (2.4–3.8)	1.2 (0.9–1.5)	1.1 (0.2–2.3)	1.6 (1.4–1.9)
UCR spring Chinook salmon	1.3 (0.8–1.8)	1.2 (0.7–1.8)	2.6 (1.8–3.3)	2.1 (1.7–2.5)	1.9 (1.6–2.2)
UCR steelhead	11.1 (9.9–12.4)	11.7 (10.4–13.1)	14.0 (12.4–15.6)	9.8 (9.1–10.6)	10.7 (10.2–11.2)
California Gulls and Ring-Billed Gulls on Miller Rocks Islands (MCR)					
SR spring–summer Chinook salmon	0.2 (0.1–0.2)	0.3 (0.3–0.4)	0.3 (0.3–0.4)	0.3 (0.2–0.3)	0.3 (0.2–0.3)
SR fall Chinook salmon	0.5 (0.3–0.7)	0.4 (0.3–0.5)	0.6 (0.5–0.6)	0.1 (0.1–0.2)	0.4 (0.4–0.4)
SR sockeye salmon	—	—	1.3 (0.8–1.9)	0.6 (0.2–1.1)	1.0 (0.7–1.4)
SR steelhead	1.5 (1.2–1.8)	1.4 (1.2–1.6)	1.5 (1.3–1.7)	1.4 (1.2–1.6)	1.4 (1.3–1.5)
UCR spring Chinook salmon	0.3 (0.2–0.5)	0.2 (0.1–0.4)	0.4 (0.2–0.6)	0.2 (0.1–0.3)	0.3 (0.2–0.3)
UCR steelhead	1.3 (0.9–1.8)	1.1 (0.7–1.5)	1.0 (0.6–1.4)	1.1 (0.7–1.5)	1.1 (0.9–1.3)
Caspian Terns on Blalock Islands (MCR)					
SR spring–summer Chinook salmon	0.1 (0.0–0.1)	0.1 (0.1–0.1)	0.2 (0.2–0.2)	<0.1	0.1 (0.1–0.1)
SR fall Chinook salmon	0.1 (0.0–0.1)	0.1 (0.0–0.1)	<0.1	<0.1	<0.1
SR sockeye salmon	—	—	<0.1	0.1 (0.0–0.3)	<0.1
SR steelhead	0.6 (0.5–0.8)	0.5 (0.4–0.6)	0.4 (0.3–0.5)	0.6 (0.5–0.8)	0.5 (0.5–0.6)
UCR spring Chinook salmon	<0.1	<0.1	0.1 (0.0–0.2)	<0.1	0.1 (0.0–0.1)
UCR steelhead	0.7 (0.4–1.0)	0.4 (0.2–0.7)	0.3 (0.1–0.5)	0.7 (0.4–0.9)	0.5 (0.4–0.6)

TABLE A.1. Continued.

Salmonid ESU	2007	2008	2009	2010	Study period
Caspian Terns on Crescent Island (Near the Confluence)					
SR spring–summer Chinook salmon	0.3 (0.2–0.4)	0.6 (0.5–0.8)	1.0 (0.8–1.2)	0.3 (0.2–0.4)	0.6 (0.5–0.7)
SR fall Chinook salmon	0.6 (0.3–1.0)	1.1 (0.9–1.3)	0.7 (0.6–0.9)	0.7 (0.6–0.8)	0.8 (0.7–0.9)
SR sockeye salmon	—	1.0 (0.2–2.0)	0.6 (0.3–1.0)	0.9 (0.2–1.8)	0.7 (0.5–1.0)
SR steelhead	2.8 (2.5–3.1)	4.1 (3.8–4.6)	3.2 (2.9–3.5)	2.8 (2.4–3.2)	3.3 (3.1–3.5)
UCR spring Chinook salmon	—	—	<0.1	0.4 (0.0–1.0)	0.3 (0.0–0.6)
UCR steelhead	1.7 (1.2–2.2)	2.0 (1.6–2.5)	1.6 (1.2–1.9)	1.2 (1.0–1.6)	1.6 (1.5–1.8)
California Gulls and Ring-Billed Gulls on Crescent Island					
SR fall Chinook salmon	<0.1	0.1 (0.1–0.1)	0.1 (0.1–0.1)	<0.1	0.1 (0.0–0.1)
SR sockeye salmon	—	0.2 (0.0–0.5)	0.4 (0.1–0.7)	<0.1	0.3 (0.1–0.5)
SR steelhead	0.6 (0.4–0.8)	0.6 (0.5–0.7)	0.7 (0.6–0.8)	0.6 (0.4–0.7)	0.6 (0.6–0.7)
UCR spring Chinook salmon	—	—	<0.1	<0.1	<0.1
UCR steelhead	0.9 (0.5–1.3)	0.4 (0.2–0.5)	1.0 (0.7–1.3)	1.1 (0.8–1.4)	0.8 (0.7–1.0)
American White Pelicans on Badger Island (Near the Confluence)					
SR spring–summer Chinook salmon	<0.1	0.1 (0.0–0.1)	0.2 (0.1–0.2)	<0.1	0.1 (0.0–0.1)
SR fall Chinook salmon	<0.1	0.1 (0.0–0.1)	0.1 (0.0–0.1)	0.1 (0.0–0.1)	0.1 (0.0–0.1)
SR sockeye salmon	—	<0.1	<0.1	<0.1	<0.1
SR steelhead	0.3 (0.2–0.4)	0.2 (0.1–0.2)	0.3 (0.3–0.4)	0.3 (0.2–0.5)	0.3 (0.2–0.3)
UCR spring Chinook salmon	—	—	<0.1	<0.1	<0.1
UCR steelhead	0.1 (0.0–0.2)	0.1 (0.0–0.2)	0.3 (0.1–0.4)	0.1 (0.0–0.2)	0.1 (0.1–0.2)
Double-Crested Cormorants on Foundation Island (Near the Confluence)					
SR spring–summer Chinook salmon	0.7 (0.6–0.9)	1.0 (0.9–1.1)	0.9 (0.7–1.1)	0.8 (0.5–1.0)	0.8 (0.7–0.9)
SR fall Chinook salmon	0.9 (0.4–1.4)	0.4 (0.3–0.5)	0.5 (0.4–0.6)	0.4 (0.3–0.5)	0.4 (0.4–0.5)
SR sockeye salmon	—	1.1 (0.3–2.0)	2.1 (1.4–2.7)	1.7 (0.5–3.1)	1.8 (1.3–2.3)
SR steelhead	2.3 (2.0–2.7)	2.3 (2.1–2.6)	1.7 (1.6–1.9)	1.3 (1.0–1.6)	1.9 (1.8–2.1)
UCR spring Chinook salmon	—	—	<0.1	<0.1	<0.1
UCR steelhead	<0.1	0.1 (0.1–0.3)	0.1 (0.0–0.2)	0.1 (0.0–0.2)	0.1 (0.1–0.1)
Caspian Terns on Goose Island (Potholes Reservoir, Near the Confluence)					
SR spring–summer Chinook salmon	<0.1	<0.1	<0.1	<0.1	<0.1
SR fall Chinook salmon	0.1 (0.0–0.6)	<0.1	<0.1	<0.1	<0.1
SR sockeye salmon	—	0.2 (0.0–0.6)	<0.1	<0.1	<0.1
SR steelhead	<0.1	<0.1	<0.1	<0.1	<0.1
UCR spring Chinook salmon	—	—	3.6 (1.6–6.1)	1.0 (0.2–2.0)	2.1 (1.1–3.4)
UCR steelhead	9.1 (6.3–14.0)	7.5 (6.5–8.5)	15.7 (13.6–18.2)	9.6 (8.3–11.2)	10.6 (9.7–11.6)