

ARTICLE

Relative Vulnerability of PIT-Tagged Subyearling Fall Chinook Salmon to Predation by Caspian Terns and Double-Crested Cormorants in the Columbia River Estuary

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Abstract

We quantified the percentage of PIT-tagged subyearling fall Chinook Salmon *Oncorhynchus tshawytscha* that were consumed by Caspian terns *Hydroprogne caspia* and double-crested cormorants *Phalacrocorax auritus* nesting on East Sand Island in the Columbia River estuary by electronically recovering PIT tags that were deposited on the bird colonies. We released 23 groups of PIT-tagged subyearling fall Chinook Salmon from hatcheries in the lower Columbia River downstream of Bonneville Dam from 2002 to 2010. Vulnerability to avian predation was compared between PIT-tagged subyearlings of two Columbia River basin stocks: tule and upriver bright (URB). Recoveries of PIT tags revealed that overall predation rates were significantly different between the tule stock (22%) and URB stock (3%); for fish that were detected as entering the lower Columbia River during the same week, predation rates also differed between stocks (tule: 21%; URB: 2%). Minimum predation rates on tule subyearlings originating from hatcheries downstream of Bonneville Dam were among the highest documented for any salmonid species in the Columbia River basin to date, occasionally exceeding 35% of the available fish. The ratio of URB fish consumed by the two avian predators indicated that the percentages were nearly equal (cormorant [%] : tern [%] = 51:49), whereas the ratio for tule-stock fish consumed by the two avian species was not uniform (cormorant : tern = 81:19). Differences in predation rates between the tule stock and the URB stock may be attributable to migration behaviors exhibited in the estuary. We estimate that more than 8 million tule fall Chinook Salmon subyearlings released from

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hatcheries annually are consumed by double-crested cormorants and Caspian terns nesting on East Sand Island; ongoing management actions by multiple federal, state, and tribal governments, if successful, will decrease predation on fall Chinook Salmon stocks.

During the early 1980s, large numbers of Caspian terns *Hydroprogne caspia* and double-crested cormorants *Phalacrocorax auritus* began nesting on islands in the Columbia River estuary (Gill and Mewaldt 1983; Carter et al. 1995), and populations of both species increased rapidly (Roby et al. 2005). These avian species have now established breeding colonies of several thousand pairs (Roby et al. 2005), and they consume all extant populations of Columbia River anadromous salmonids (Collis et al. 2001), including those listed under the Endangered Species Act (ESA). Combined consumption by Caspian terns and double-crested cormorants ranged from 7 to 15 million fish annually in 2006 and 2007 (Lyons 2010). Anadromous salmonid mortalities caused by predation from birds nesting in the Columbia River estuary represent a substantial loss to the recovery of ESA-listed populations in addition to commercial, recreational, and tribal harvest. Therefore, these avian colonies are managed by several federal agencies under the existing biological opinion for the Federal Columbia River Hydropower System (NMFS 2010).

Since 2001, nearly all nesting by Caspian terns and double-crested cormorants in the Columbia River estuary has occurred on East Sand Island. East Sand Island is located 8 km upstream of the Columbia River mouth in a brackish-water reach where marine forage fishes are available to avian predators as an alternative to salmonid prey (Roby et al. 2002). Caspian terns and double-crested cormorants generally arrive at the breeding colonies on East Sand Island in late March and remain there through September, although double-crested cormorants generally vacate the island later than Caspian terns (Roby et al. 2012). The breeding period coincides with the peak out-migration of the majority of Columbia River salmon (Collis et al. 2002). The two avian species have different foraging strategies: Caspian terns are plunge divers and are limited to preying on fish near the surface (Cuthbert and Wires 1999), whereas double-crested cormorants are foot-propelled pursuit divers and can access prey several meters below the water surface (DeGraaf et al. 1985). It is well established that salmonid species and ESA-listed populations differ in their vulnerability to avian predation in the Columbia River estuary (Collis et al. 2001, 2002; Roby et al. 2002, 2003; Ryan et al. 2003; Evans et al. 2012). Caspian terns disproportionately prey upon steelhead *Oncorhynchus mykiss*, whereas double-crested cormorants do not exhibit preferences for any particular salmon species (Ryan et al. 2003). During 2000–2010, the breeding population of Caspian terns on East Sand Island was relatively stable, ranging from 8,000 to 10,000 nesting pairs. In contrast, the breeding population of double-crested cormorants more than doubled from

5,000 nesting pairs in 2000 to 14,000 nesting pairs in 2007; this population has since stabilized at approximately 12,000 pairs (Lyons 2010; Roby et al. 2012).

Salmon and steelhead stocks or populations listed under the ESA exist within every major basin of the Columbia River. Several ESA-listed salmonid populations enter the lower Columbia River (LCR) downstream of Bonneville Dam (river kilometer [rkm] 234), including a large portion of the fall Chinook Salmon belonging to the LCR evolutionarily significant unit, which out-migrate to the Pacific Ocean as subyearlings. The majority of fall Chinook Salmon subyearlings in the Columbia River basin originate from two stocks: tule and upriver bright (URB). The tule stock is generally native to tributaries of the LCR, which extends from the eastern foothills of the Cascade Mountains west to the Columbia River estuary; in contrast, the URB stock (Columbia and Snake rivers) is native to tributaries east of the Cascade Mountains (Narum et al. 2004b; HSRG 2009). Fall Chinook Salmon populations form two distinct lineages on roughly the same geographic basis (LCR and interior Columbia River) despite their similarities in run timing and population structure (Waples et al. 2004).

Chinook Salmon are known to display a diversity of distinct life histories related to location and duration of freshwater residency (Carl and Healey 1984; Narum et al. 2004a; Bottom et al. 2005a; Hering et al. 2010). However, it is unknown whether the stocks of subyearling fall Chinook Salmon in the Columbia River exhibit different migration behaviors once they enter the estuary or whether the stocks are equally vulnerable to avian predators. Ryan et al. (2003) hypothesized that salmonids originating from tributaries in the LCR (i.e., tule stock) were more vulnerable to avian predation because they are more likely to rear in estuary habitats for prolonged periods than fall Chinook Salmon originating upstream from Bonneville Dam. Ryan et al. (2003) suggested that this hypothesis could be tested by PIT-tagging salmonids from LCR tributaries and comparing their relative vulnerability with that of fish originating upstream of Bonneville Dam. If this hypothesis is correct, it suggests that management actions focused on one or both avian species may be necessary to more effectively reduce salmonid losses due to avian predation.

Our objectives were to (1) quantify avian predation on LCR hatchery-reared subyearling fall Chinook Salmon; (2) test the null hypothesis posited by Ryan et al. (2003) that the vulnerability of fall Chinook Salmon subyearlings to avian predation in the Columbia River estuary is similar regardless of stock (tule or URB); and (3) evaluate whether the ratio of fish consumed is uniformly distributed between avian species.

METHODS

Two to four groups of approximately 3,000 subyearling fall Chinook Salmon at LCR hatcheries were PIT tagged each year from 2002 to 2010, with the exception of 2004, when no fall Chinook Salmon were PIT-tagged. The implanted PIT tags were 134.2-kHz Model ST tags measuring 2.1 mm in diameter and 12 mm in length (Prentice et al. 1990). We used dip nets to capture Chinook Salmon that were reared in concrete raceways prior to release. We then followed recommended PIT-tagging procedures (Prentice et al. 1990; CBFWA 1999), including anesthetizing the fish with tricaine methanesulfonate, implanting PIT tags with a 12-gauge veterinary needle, and recording FL measurements to the nearest millimeter. Fish were returned to raceways with the unmarked individuals and were held for at least 48 h prior to release.

The first 2 years of PIT-tagging effort were focused on groups of subyearling fall Chinook Salmon released within foraging range of the two avian colonies; these subyearlings were released at the Sea Resources Hatchery (rkm 12) and Big Creek Hatchery (rkm 43; Figure 1). During subsequent years, we PIT-tagged and released fish of different stocks and from different locations in the LCR to represent a broader sample of this evolutionarily significant unit. These additional tagging locations included Warrenton (rkm 16), Deep River (rkm 37), Elochoman (rkm 77), Kalama Falls (rkm 135), North Toutle (rkm 190), Washougal (rkm 225), and Bonneville (rkm 233) hatcheries. We also included large groups of tule-stock subyearlings that were tagged and released from Spring Creek National Fish Hatchery during 2008–2010.

Vulnerability to avian predation was compared between tule and URB fall Chinook Salmon subyearlings of similar size. In

addition to URB fish that were PIT-tagged at Bonneville Hatchery during 2005 and 2006, we identified URB stocks (described by Narum et al. 2004b) that were PIT-tagged at hydroelectric projects (Lower Granite Dam, Lower Monumental Dam, etc.) and hatcheries (i.e., Dworshak, Irrigon, Nez Perce Tribal, Oxbow, Priest Rapids, Prosser, and Umatilla hatcheries, etc.) in the Columbia and Snake rivers for research purposes unrelated to our study. We excluded fish that were released from Lyons Ferry Hatchery because they are reared to a larger size than other subyearling fall Chinook Salmon released in this region. Numbers of fish that were interrogated at the Bonneville Dam instream detection facilities during the study period were queried from the PIT Tag Information System (PTAGIS; PSMFC 2010). We classified fall Chinook Salmon as subyearling migrants if they were released after April 1 and if they were less than 120 mm FL at the time of tagging; this follows mark–recapture observations of Chinook Salmon in the Columbia River estuary from known release groups that enabled field determination of yearling and subyearling age-classes (Dawley et al. 1986).

Detection of PIT tags on avian colonies.—We used methods described by Ryan et al. (2001) and Evans et al. (2012) to electronically recover PIT tags from subyearling fall Chinook Salmon consumed by Caspian terns and double-crested cormorants and deposited on the East Sand Island breeding colonies before, during, or after the breeding season. Detection of PIT tags that were deposited by birds occurred each season after the breeding colonies were vacated. We used a flat-plate antenna towed by a tractor to detect PIT tags on the open, sandy substrate of the Caspian tern colony. We used pole-mounted antennas to detect PIT tags on the double-crested cormorant colony because substrates were too irregular or otherwise inaccessible for use of the flat-plate detection system (Ryan et al. 2001).

Sample efficiency measurement.—Using the methods described by Evans et al. (2012), we measured the efficiency of PIT tag detection on each bird colony by randomly sowing PIT tags (hereafter, “control tags”) on the colony surface during the nesting season. By doing so, we intended to simulate natural deposition of PIT tags and to quantify our recovery effort for PIT tags that were consumed by birds and subsequently deposited on the surface of breeding colonies. We assumed that electronic recovery of tag codes from randomly sown control tags accurately represented the recovery of PIT tags that were consumed by birds preying on tagged subyearlings and later deposited on breeding colonies. Control tags were of the same model as those implanted in salmonids and were sown before and after the nesting seasons on both avian colonies. On two occasions during the middle of each nesting season, additional control tags were sown on the Caspian tern colony. Releases of control tags on the double-crested cormorant colony were limited to the pre-season and post-season to avoid disturbing the nesting activity or causing abandonment of nests. Detection efficiency on each avian colony was estimated as the proportion of control tags sown that were subsequently detected and was



FIGURE 1. Locations of lower Columbia River hatcheries where subyearling fall Chinook Salmon were PIT-tagged and released during 2002–2010.

used to adjust for the number of PIT tags that were deposited on the colonies but not detected. The number of control PIT tags sown on each bird colony in each year varied but was no less than 200. Predation rates were adjusted dividing by the mean detection efficiency estimate specific to each avian colony for each weekly group of fish. Nonetheless, all predation rates should be considered minimum estimates because they did not account for PIT tags that were deposited off-colony at loafing, staging, or other areas used by birds during the breeding season.

Comparing vulnerability of fish by stock type.—We tested the null hypothesis that avian predation rates were not significantly different between the two stocks of PIT-tagged subyearling Chinook Salmon. We calculated predation rates by pooling fish that were released from LCR hatcheries or detected at Bonneville Dam into weekly groups. Pooling fish into weekly groups allowed us to compare predation rates (1) between the tule and URB stocks on an annual basis and (2) between groups of fish that were present in the estuary (and within foraging range of birds) during the same week. Comparison of predation rates on fish detected as entering the estuary during the same week allowed us to remove, as much as possible, bias related to temporal variability of alternate prey, avian population, or avian foraging behavior. A minimum sample size of 100 fish/week from LCR hatcheries or Bonneville Dam detections was used to ensure accurate statistical analysis (Ryan et al. 2003). All statistical comparisons were completed by using two-tailed *t*-tests ($\alpha < 0.05$). We estimated predation rates (pooled by week) by using the release date for fish originating from LCR hatcheries or by using the date of detection at Bonneville Dam for fish originating upstream of the dam.

We also evaluated predation ratios to determine whether the tule and URB fish consumed were equally distributed between the two avian predators (i.e., double-crested cormorant [%] : Caspian tern [%] = 50:50). Two-tailed *t*-tests ($\alpha < 0.05$) were used to compare predation ratios for each fall Chinook salmon stock and between the two stocks. Differences in predation ratios were evaluated for fish from both stocks detected as entering the LCR during the same week as well as for the entire study period (April 2002–September 2010).

Analysis of avian predation by fish size.—We evaluated the effect of fish size (FL) on vulnerability to avian predation to determine whether the consumption of subyearling fall Chinook Salmon by either avian species was biased by fish length. We calculated predation rates for 1-mm FL increments weighted by the number of individuals that were available to both avian species, and we used logistic regression (Hosmer and Lemeshow 2000) to determine statistical relationships between rates of predation by the two bird species. We tested model terms for fish length, stock (tule or URB), and year as well as two-way interactions of these terms. With logistic regression, the response variable *p* (the proportion of fish consumed) was modeled as a function of explanatory variables x_i ($i = 1, \dots, n$; where $n =$

the total number of terms in the model):

$$p(x_1, \dots, x_n) = \frac{\exp(\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n)}. \quad (1)$$

Alternatively, equation (1) can be viewed by using the logit link (*g*) to obtain a linear response as

$$\begin{aligned} g[p(x_1, \dots, x_n)] &= \log_e \left[\frac{p(x_1, \dots, x_n)}{1 - p(x_1, \dots, x_n)} \right] \\ &= \beta_0 + \beta_1 x_1 + \dots + \beta_n x_n + \varepsilon. \end{aligned} \quad (2)$$

Unlike standard linear regression, where the error term is assumed to be normally distributed, the error term (ε) in the logistic regression model is assumed to be binomially distributed. The best model was chosen by first fitting the full model and then using likelihood ratio tests to remove terms that were not significant ($\alpha < 0.05$; Hosmer and Lemeshow 2000).

An assumption inherent in conducting this analysis was that postrelease growth of fish did not bias the results. Obtaining appropriate sample sizes of fish detected as passing Bonneville Dam each week precluded (1) the use of the relatively few length measurements from fish collected at the Bonneville Dam instream collection facilities and (2) the estimation of length for all URB fish based upon a subsample of individuals. Available data on size-specific selectivity suggest that significantly larger fish (i.e., 220 mm) are generally preferred by Caspian terns (Roby et al. 2012), yet neither avian species is known to exhibit size-selective preferences within the size range represented by subyearling tule and URB fall Chinook Salmon. Although we suspect that size-selective predation may be biased toward URB-stock fish originating from the upper Columbia River or Snake River, as those fish have greater potential for posttagging growth prior to entering the LCR, underestimation of the length of URB fish would not significantly affect this analysis unless an intra-annual stock \times length interaction is observed.

Assumptions in predation rate calculations.—In our predation rate calculations and statistical comparisons between tule and URB fall Chinook Salmon subyearlings, we made assumptions similar to those of Evans et al. (2012): (1) data obtained from PTAGIS were complete and accurate; (2) all PIT-tagged subyearlings entering the LCR were equally available to avian predators; (3) no bias existed in the ability to detect control tags in comparison with tags that were regurgitated or egested by birds onto the colony surface; (4) off-colony deposition rates of PIT tags did not differ between the two avian species; (5) PIT tag deposition by birds onto the colony surface occurred during the week in which the fish were ingested; and (6) fish were properly identified as subyearling migrants.

To address our first assumption, we maintained multiple copies of PIT-tag release data obtained from PTAGIS and used the most current and reliable sources. Mean travel time of subyearling Chinook Salmon to the Columbia River estuary is

approximately 4 d, and variation in survival rate exists both temporally and spatially (McMichael et al. 2010). However, because foraging ranges for Caspian terns in the Columbia River basin are known to exceed 70 km (Roby et al. 2012), the application of spatial or temporal criteria necessary for adjusting postrelease survival rates of fish released from LCR hatcheries was deemed arbitrary and potentially misleading (assumption 2). Detection efficiencies for PIT tags on East Sand Island are generally high, increased throughout our study period after improvement in detection techniques and equipment, and show occasional effects over the course of the entire avian breeding season (late March to early September; Evans et al. 2012). Therefore, use of mean annual detection efficiency is appropriate, particularly for groups of fish entering the LCR in the same week during the middle of the avian breeding season (assumption 3). Although it is known that some PIT tags may become damaged during or after deposition on the colony surface, at this time there are no data quantifying differences (or a lack thereof) in deposition rates between the two avian species (assumption

4). Assumption 5 addresses classification of fish into weekly groups based on the last date of live detection at Bonneville Dam and using the date as a proxy for the week in which PIT tags were deposited on the colony surface. This assumption need only be approximate because detection efficiencies varied little over short periods (Evans et al. 2012).

RESULTS

Between 2002 and 2010, we PIT-tagged and released a total of 72,076 subyearling fall Chinook Salmon from 23 release groups at nine hatcheries in the LCR (Table 1). The majority of release groups consisted of the tule stock ($N = 63,052$ fish), although we did release two groups of PIT-tagged URB-stock fish from Bonneville Hatchery ($N = 6,554$ fish). The majority of fish that were detected at Bonneville Dam juvenile bypass facilities belonged to the URB stock ($N = 81,289$), although large numbers of tule-stock fish released from Spring Creek

TABLE 1. Annual number of tule-stock fall Chinook Salmon subyearlings released and the rates of predation (adjusted for PIT tag detection efficiency) by Caspian terns and double-crested cormorants. Numbers of fish available included (1) subyearlings that were released from lower Columbia River hatcheries or (2) Spring Creek National Fish Hatchery subyearlings that were detected as passing Bonneville Dam.

Release year	Release site	Releases (<i>N</i>)	Adjusted predation rate (%)		Total predation rate (%)	Annual mean predation rate (%)	SE
			Tern	Cormorant			
2002	Big Creek	2,927	5.4	26.2	31.5	32.6	1.4
	Sea Resources	2,388	5.2	28.4	33.5		
2003	Big Creek	2,974	3.7	11.0	14.7	22.8	8.1
	Sea Resources	2,873	7.6	23.2	30.9		
2005	Big Creek	2,999	3.2	18.8	22.1	NA	NA
2006	Big Creek	3,031	3.2	30.0	33.2	NA	NA
2007	Big Creek	3,028	3.1	15.3	18.4	14.8	4.4
	Kalama Falls	3,013	5.0	16.4	21.3		
	North Toutle	3,278	0.4	1.3	1.7		
	Washougal	3,011	3.3	14.7	17.9		
2008	Big Creek	3,055	5.2	29.7	34.9	15.2	3.5
	Elochoman	3,069	5.4	33.2	38.5		
	Kalama Falls	3,039	3.8	28.8	32.5		
	Spring Creek	25,395	1.9	7.2	9.1		
2009	Big Creek	3,038	2.9	20.3	23.2	12.2	2.7
	Deep River	3,162	5.8	19.9	25.7		
	Kalama Falls	2,902	5.4	16.1	21.5		
	Spring Creek	13,369	1.3	4.5	5.8		
	Warrenton	3,014	6.6	16.7	23.3		
2010	Big Creek	3,051	3.9	23.4	27.3	21.8	2.0
	Deep River	3,085	7.9	18.0	25.9		
	North Toutle	3,073	2.8	12.7	15.5		
	Spring Creek	1,243	4.0	17.1	21.7		
	Warrenton	3,042	5.4	13.6	18.9		

TABLE 2. Annual numbers of upriver-bright-stock fall Chinook Salmon subyearlings that were detected at Bonneville Dam or released from Bonneville Hatchery and the mean annual rates of predation (adjusted for PIT tag detection efficiency) by Caspian terns and double-crested cormorants.

Year	Detections (<i>N</i>)	Adjusted predation rate (%)		Mean predation rate (%)	SE
		Tern	Cormorant		
2002	13,102	0.9	1.5	2.5	0.4
2003	8,850	1.7	0.6	2.2	0.3
2005	878	1.3	2.3	3.6	1.1
2006	6,298	4.1	2.9	1.2	0.7
2007	3,322	2.9	1.2	4.1	0.7
2008	22,959	1.1	2.3	3.4	0.5
2009	13,301	1.6	3.1	4.7	1.1
2010	13,336	0.4	2.4	2.8	0.6

National Fish Hatchery were detected during 2008–2010 ($N = 40,007$; Table 2; PSMFC 2010).

Predation rates on juvenile Chinook Salmon were adjusted for detection efficiency by using the proportion of control PIT tags distributed by researchers on the avian nesting colonies. The detection efficiency for control PIT tags on the open, sandy substrate of the Caspian tern colony was often greater than 90% (Table 3). Detection efficiency of control PIT tags on the combined bare-sand, driftwood, and rip-rap substrate of the double-crested cormorant colony gradually increased throughout the duration of the study period, with a mean value of 55%.

Although tule-stock subyearlings were generally observed to migrate through the LCR earlier in the migration season than URB-stock fish, both groups were detected as entering the LCR during June (Figure 2). Overall, 62 weekly groups of PIT-tagged URB-stock fish were detected at Bonneville Dam during the study period from late May to August. These fish were

consistently consumed by the avian species in low proportions (mean = 3.3%; SE = 0.2; range = 0.5–12%). The two groups of URB-stock fish from Bonneville Hatchery were released to migrate through the LCR during June and experienced similar predation rates (mean = 4.5%; SE = 0.8; range = 3.6–5.2%). A total of 19 groups of PIT-tagged tule-stock fish released from Spring Creek National Fish Hatchery during 2008–2010 were detected at Bonneville Dam from March 2 to May 4, earlier than any other group. The predation rates on Spring Creek National Fish Hatchery tule subyearlings (mean = 9.2%; SE = 1.5; range = 1.2–25.6%) were initially low and gradually increased over the migration period and in general were greater than the rates of predation on the URB stock. Tule-stock subyearlings were released from hatcheries in the LCR from March 2 to July 6. Predation rates on LCR tule-stock fish were high (mean = 24.8%; SE = 1.9; range = 1.7–38.5%) even though these fish frequently overlapped with the URB stock in the LCR.

In total, seven groups of URB-stock fall Chinook Salmon subyearlings and eight groups of tule-stock subyearlings were detected as passing Bonneville Dam or were released from hatcheries into the LCR during the same week over the study period (Table 4). Predation rates were significantly different ($P < 0.001$) between the weekly groups of URB-stock (mean = 3.4%) and tule-stock (mean = 21.8%) fish. The ratio of URB-stock fish consumed by the two avian predators (double-crested cormorant [%]: Caspian tern [%] = 50:50) was not significantly different than a uniform distribution ($P = 0.989$). In contrast, the ratio for consumed tule-stock fish (double-crested cormorant : Caspian tern = 78:22) was significantly different than a uniform distribution ($P < 0.001$). The predation ratios for tule and URB subyearlings that were detected as entering the LCR during the same week were also significantly different ($P = 0.025$).

In addition, we tested differences in predation rates between stocks of fish throughout the entire study period, regardless of when the fish entered the LCR. The ratio of URB-stock fish consumed by the avian predators (double-crested cormorant [%] : Caspian tern [%] = 51:49) did not significantly differ

TABLE 3. Percentage of control PIT tags that were recovered from the Caspian tern and double-crested cormorant breeding colonies on East Sand Island during 2002–2010. The PIT tags were intentionally sown on the surface of each colony to measure detection efficiency; the number of tags sown on the colony is listed in parentheses.

Year	Percentage of control PIT tags recovered (number sown)	
	Cormorant	Tern
2002	35 (300)	95 (300)
2003	45 (300)	85 (300)
2004	36 (600)	92 (1,100)
2005	55 (800)	83 (1,200)
2006	52 (600)	64 (1,200)
2007	58 (200)	89 (600)
2008	69 (600)	92 (600)
2009	70 (600)	90 (600)
2010	76 (400)	84 (400)
Mean	55	86

TABLE 4. Mean weekly avian predation rates on fall Chinook Salmon subyearlings and the predation ratio for consumed fish (double-crested cormorant [%] : Caspian tern [%]); data are presented for PIT-tagged tule-stock and upriver-bright-stock subyearlings that migrated through the lower Columbia River during the same week. During 2007 two groups of tule stock were released and are shown as separate groups in Figures 2 and 3.

Year	Week	Predation rate (%) on the tule stock			Predation rate (%) on the upriver bright stock		
		Cormorant	Tern	Ratio	Cormorant	Tern	Ratio
2003	Jun 16–22	23.3	7.7	75:25	0	1.7	0:100
2007	Jun 18–24	16.4	5.0	77:23	0.9	2.9	24:76
	Jun 18–24	1.3	0.4	76:24			
	Jul 9–15	14.7	3.3	82:18	0.8	0.7	51:49
2008	Jul 7–13	28.8	3.8	88:12	1.6	1.7	48:52
2009	Jun 15–21	16.7	6.6	72:28	1.5	1.0	59:41
2010	Jun 28–Jul 4	18.0	7.9	69:31	0.4	0.1	89:11
	Jul 5–11	12.7	2.8	82:12	1.6	0.5	78:22
Mean		16.5	4.7	78:22	1.0	1.2	50:50
Total			21.1			2.2	

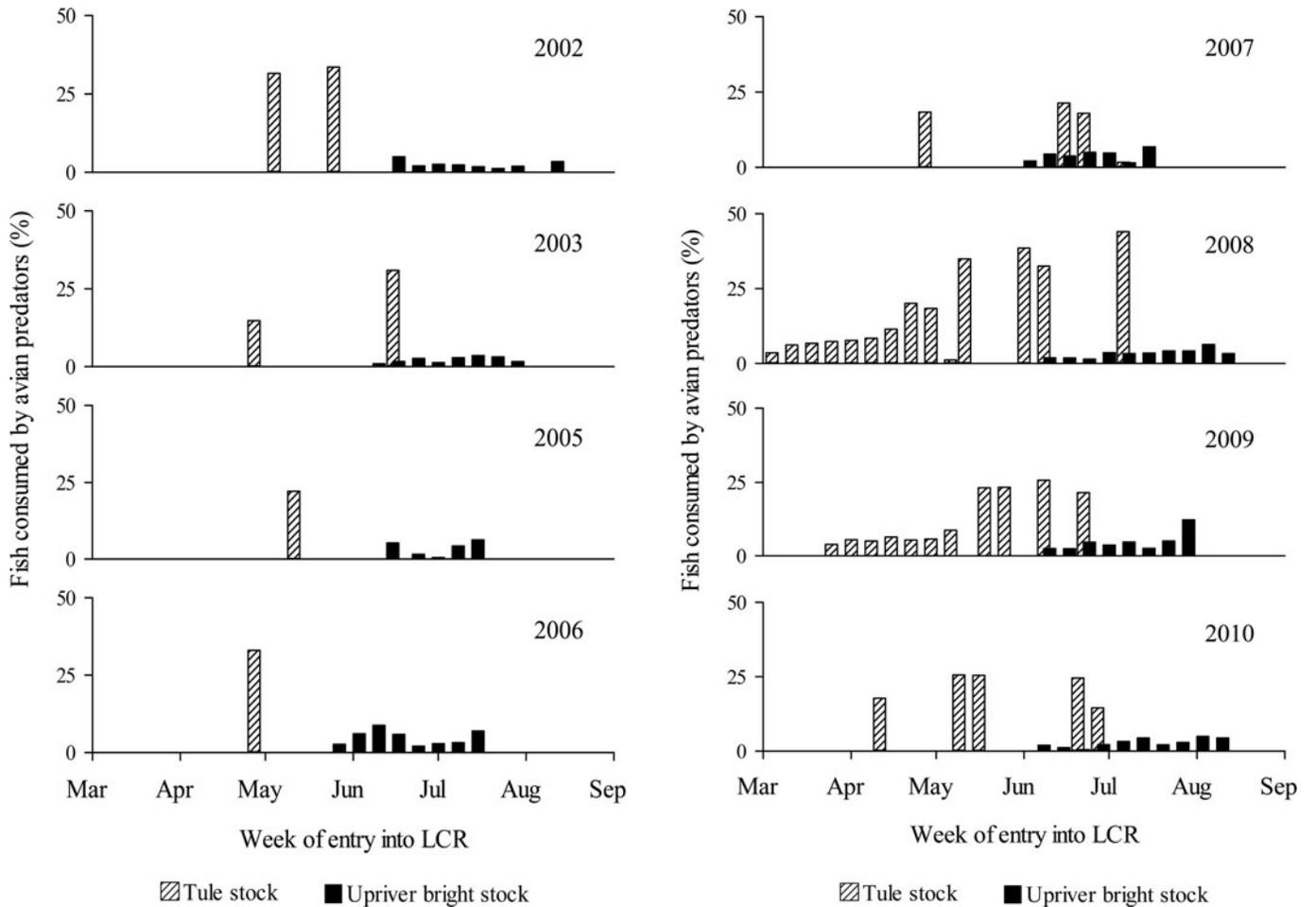


FIGURE 2. Rates of avian predation (%) on PIT-tagged tule-stock and upriver-bright-stock fall Chinook Salmon subyearlings (grouped by week) that were released into the lower Columbia River (LCR) or detected as passing Bonneville Dam, 2002–2010.

TABLE 5. Annual mean predation ratio (with SE; double-crested cormorant [%] : Caspian tern [%]) for consumed fish from pooled weekly groups (*N*) of PIT-tagged tule-stock and upriver-bright-stock fall Chinook Salmon subyearlings that were released into the Columbia River, 2002–2010.

Year	Predation ratio for the tule stock				Predation ratio for the upriver bright stock			
	<i>N</i>	Cormorant	Tern	SE	<i>N</i>	Cormorant	Tern	SE
2002	2	84	17	0.50	8	50	50	11.6
2003	2	75	25	0	8	27	73	8.1
2005	1	85	15	NA	5	53	47	15.2
2006	1	90	10	NA	8	32	68	8.3
2007	4	80	21	1.8	7	38	62	7.9
2008	13	81	19	1.9	10	62	38	5.8
2009	11	77	23	1.5	8	63	37	5.6
2010	6	78	22	2.7	10	83	17	3.6
Mean		81	19			51	49	

from a uniform distribution ($P = 0.900$; Table 5). The ratio of tule-stock fish consumed by the avian species (double-crested cormorant : Caspian tern = 81:19) was significantly different than a uniform distribution ($P < 0.001$). The predation ratios by avian species on tule and URB fish observed throughout the study period were also significantly different ($P < 0.001$).

Analysis of Avian Predation in Relation to Fish Size

We observed that size at the time of tagging for tule-stock subyearlings released during 2002–2010 was similar (mean = 78 mm FL; SE = 1.7; range = 53–118 mm) to that for URB

fish (mean = 84 mm FL; SE = 1.4; range = 45–119 mm; Figure 3). Logistic regression analysis revealed that the same model terms (year \times length; year \times stock) were included in the best-fitting model for both Caspian terns and double-crested cormorants, indicating that differences in size of juvenile Chinook Salmon did not significantly affect vulnerability to either bird species. Therefore, we pooled predation rates for both bird species and evaluated predation rates relative to fish size using the same logistic regression on an annual basis. The best-fitting model from logistic regression included the model terms year \times length and year \times stock ($P = 0.959$; Table 6). The

TABLE 6. Logistic regression models that incorporated three explanatory variables and their bivariate interactions to evaluate avian predation on subyearling fall Chinook Salmon in the Columbia River estuary (year [Y] = 2002–2010; stock [S] = tule or upriver bright; length [L] = FL, mm). The relative statistical significance of each model was evaluated by using likelihood ratio tests ($\log[L] = \log$ likelihood). Due to the nested structure of the models, the tests evaluated the significance of individual terms. The binomial overdispersion estimate was 1.48. The asterisk indicates the best-fitting model.

Model	Logistic regression $\log(L)$	Parameters	Likelihood ratio test versus full model	<i>P</i> -value
Y, S, L, Y \times S, Y \times L, S \times L	–31,738.73	25		
Y, S, L, Y \times S, Y \times L*	–31,738.73	24	0.003	0.959
Y, S, L, Y \times S, S \times L	–31,839.62	18	136.32	<0.001
Y, S, L, Y \times L, S \times L	–31,772.05	18	45.03	<0.001
Y, S, L, Y \times S	–31,851.72	17	152.67	<0.001
Y, S, L, Y \times L	–31,772.05	17	45.03	<0.001
Y, S, L, S \times L	–31,868.62	11	175.51	<0.001
Y, S, L	–31,898.87	10	216.37	<0.001
Y, S, Y \times S	–31,954.71	16	291.82	<0.001
Y, L, Y \times L	–34,341.19	16	3,516.30	<0.001
S, L, S \times L	–31,945.70	4	279.65	<0.001
Y, S	–31,982.44	9	329.29	<0.001
Y, L	–35,231.11	9	4,718.70	<0.001
S, L	–31,959.80	3	298.70	<0.001
Y	–35,307.25	8	4,821.58	<0.001
S	–32,029.81	2	393.30	<0.001
L	–35,593.90	2	5,208.88	<0.001

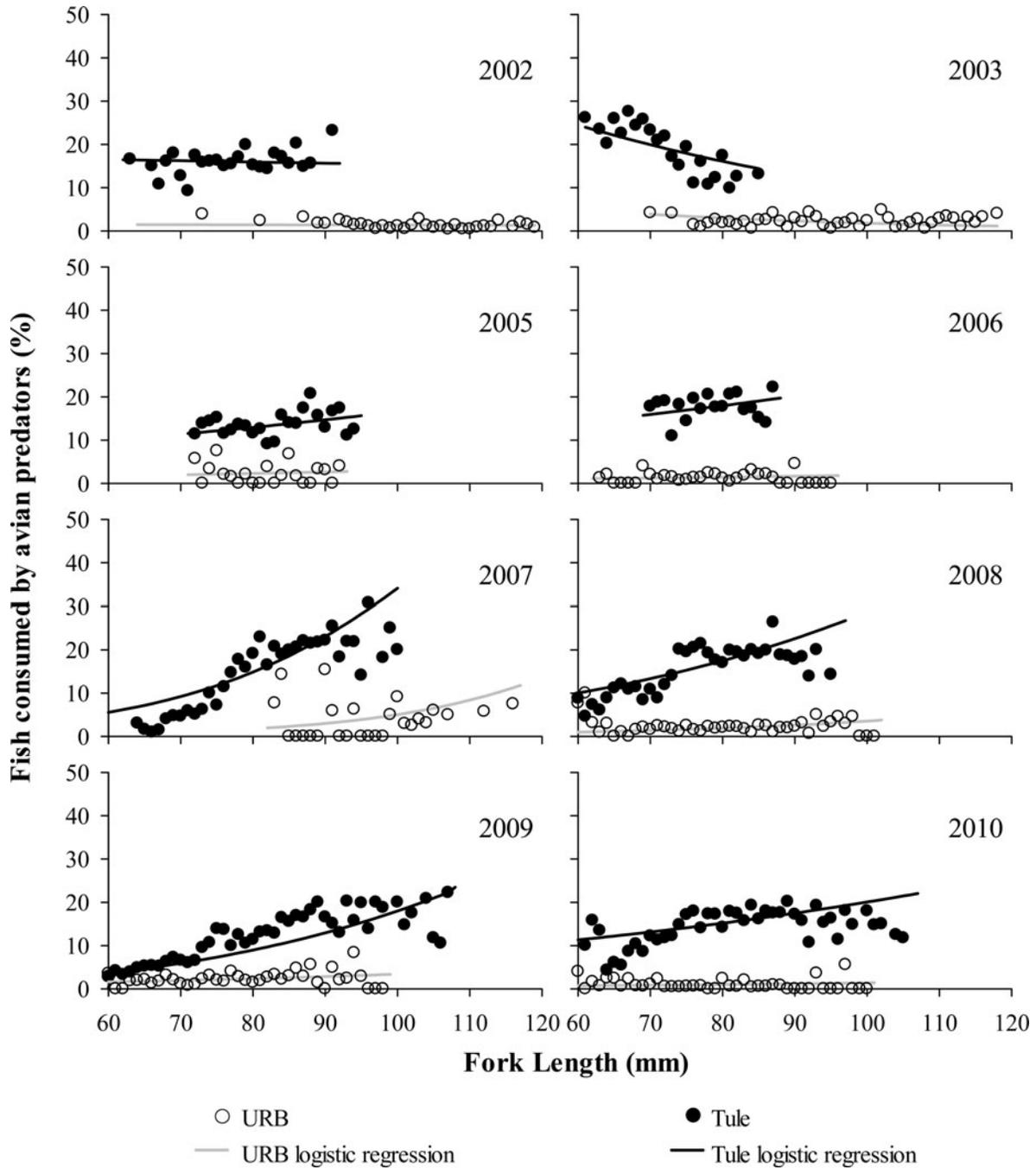


FIGURE 3. Percentage of PIT-tagged tule-stock and upriver-bright (URB) stock fall Chinook Salmon subyearlings that were consumed by avian predators as a function of fish FL (mm) measured at the time of tagging, 2002–2010.

interaction of year \times length yielded significantly different relationships ($P < 0.001$), which were positive, neutral, or negative depending on the year (Table 7). The year \times stock interaction was also significantly different ($P < 0.001$), although there appeared to be a greater effect of length on predation rate for the tule stock during some years (i.e., 2006 and 2007). These results indicate that the effects of length and stock on vulnerabil-

ity to predation varied each year and were significantly different throughout the study period. However, the stock \times length interaction was not included in the best-fitting model, which suggests that within any given year, the relationship between length and vulnerability to predation was similar regardless of stock type. This result remains valid even if length is biased low because fish were measured at the time of PIT-tagging.

TABLE 7. Best-fitting model terms (year, stock, length, year \times stock, and year \times length; see Table 6) from logistic regression analysis used to evaluate bias in avian predation on subyearling fall Chinook Salmon. Each *P*-value was adjusted for over-dispersion by 1.22.

Best-fitting model terms	Coefficient	<i>P</i> -value
Constant		
Constant	-1.48831	0.024
Year		
2003	1.92786	0.017
2005	-1.59046	0.221
2006	-1.17706	0.298
2007	-4.61337	0.000
2008	-2.62965	0.000
2009	-1.77053	0.016
2010	-1.58504	0.033
Stock		
Tule	-2.56006	0.000
Length		
Length	-0.00217	0.769
Year \times stock		
2003 \times tule	0.73907	0.024
2005 \times tule	0.71711	0.073
2006 \times tule	-0.13350	0.690
2007 \times tule	0.27822	0.589
2008 \times tule	0.15785	0.598
2009 \times tule	0.54766	0.077
2010 \times tule	-0.32283	0.358
Year \times length		
2003	-0.02396	0.027
2005	0.01685	0.298
2006	0.01651	0.259
2007	0.05661	0.000
2008	0.03425	0.000
2009	0.02140	0.025
2010	0.01907	0.047

groups and to numerous local factors in the Columbia River estuary that affect the foraging efficiency of avian species. We suspect that vulnerability of the tule stock is particularly variable due to ephemeral abundances of alternate prey, especially marine forage fishes, such as Pacific Herring *Clupea pallasii*, Surf Smelt *Hypomesus pretiosus*, and Northern Anchovy *Engraulis mordax* (Weitkamp et al. 2012). For example, these marine species typically enter the Columbia River estuary during April, but in 2008 they did not enter the estuary until August due to high river flows (Weitkamp et al. 2012), the period in which the highest predation rates on tule stock throughout the entire study (34.8–44.0%) were documented. Therefore, we suggest that the abundance of alternate prey sources is an important mechanism affecting predation rates on the tule stock, perhaps more so than for other salmonids.

Although the two stocks of fall Chinook Salmon originate from different areas of the Columbia River and thus are exposed to numerous predation trials, research by Hostetter et al. (2011) suggested that individuals in poor condition were consumed by avian species more frequently than individuals in good condition. Thus, we cannot presume that tule-stock fish released directly into the Columbia River estuary in good condition would be significantly more vulnerable to predation by birds from large colonies and would be subjected to disproportionate predation relative to URB-stock fish. Low predation rates on URB-stock subyearlings that were released from Bonneville Hatchery suggest that disproportionate consumption of the tule stock is not merely the result of avian predators selecting the least-fit individuals. Indeed, URB fall Chinook Salmon are also exposed to the second-largest avian colonies in the Columbia River basin (the Caspian tern colony on Crescent Island and the double-crested cormorant colony on Foundation Island), which together constitute fewer than 800 breeding pairs—about 2% of the number of Caspian terns and double-crested cormorants nesting on East Sand Island (Roby et al. 2012). We believe that comparison of predation rates between the tule and URB stocks is reasonable because there is little natural experience that will train fish to evade so many predators.

Our observations indicate that stock-specific behaviors during seaward migration may be important factors influencing the vulnerability of subyearling fall Chinook Salmon to avian predation in the Columbia River estuary. However, because we did not directly measure the foraging behavior of the avian predators or the migration behavior, habitat use, and residency timing of the fish, we can only utilize the available information regarding these subjects to speculate about the factors that create differences in vulnerability between subyearlings of the two fall Chinook Salmon stocks.

Factors Affecting Adjustments to Predation Rates

Our estimates of predation rates on subyearling fall Chinook Salmon were adjusted for on-colony PIT tag detection efficiency, a factor that has not been accounted for in many of the previously published estimates of avian predation rates

DISCUSSION

Overview

Observed predation rates on the tule fall Chinook Salmon subyearlings that were PIT-tagged and released into the LCR during our study are among the highest documented for Columbia River basin salmonids (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012). Predation rates on the URB stock were consistent with those observed for other species (Ryan et al. 2003; Evans et al. 2012) and were significantly less than the rates of predation on the tule stock, regardless of when the fish entered the LCR. Predation rates on tule-stock subyearlings were significantly variable among years, as confirmed by logistic regression analysis. This high degree of variability is due to many factors that affect the survival of large hatchery release

based on PIT tag data (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Maranto et al. 2010). However, even after accounting for on-colony detection efficiency, predation rates are still minimum estimates because the number of PIT tags deposited off-colony by avian predators is unknown (Evans et al. 2012). Research to quantify off-colony PIT tag deposition rates by Caspian terns and double-crested cormorants is currently in progress; preliminary results suggest that off-colony deposition rates by Caspian terns are in excess of 25% of the consumed PIT tags (Collis et al. 2007). Because similar data from double-crested cormorants are not available and research is currently ongoing, we did not adjust for off-colony deposition of PIT tags for either of the avian species examined in this study.

We found that PIT tag detection efficiency measurements on East Sand Island were higher and more consistent on the Caspian tern colony than on the double-crested cormorant colony. The gradual increase in detection efficiency on the double-crested cormorant colony throughout the study period was likely the result of greater effort and the use of updated pole-mounted detection equipment, which we presume accurately represented the detection of PIT tags that were naturally deposited on-colony. Although detection efficiencies varied among years, the process of adjusting predation rates allowed for unbiased comparisons that were not affected by annual differences in equipment or effort.

Factors Affecting Vulnerability to Avian Predation

An understanding of the foraging ecology of both avian species within the Columbia River estuary may elucidate important aspects affecting the predation vulnerability of large groups of hatchery-produced fish. Rates of Caspian tern and double-crested cormorant predation on salmonids are affected by many factors, including the avian population size, alternate sources of prey, and avian foraging behavior. During the study period, the breeding population of Caspian terns in the Columbia River estuary remained relatively stable at about 9,000 breeding pairs, whereas the population of double-crested cormorants increased from about 10,000 breeding pairs in 2002 to approximately 12,000 breeding pairs (Roby et al. 2012). The proportion of salmonids in the diets of avian predators is generally greatest during the peak salmon migration season in April and May and decreases during June (Lyons 2010); however, predation rates on subyearling fall Chinook Salmon—particularly the tule stock—increased as the season progressed into June and July, while the proportion of other salmonids consumed by birds decreased.

In the Columbia River estuary, both Caspian terns and double-crested cormorants rely on marine and estuarine mixing zones as foraging habitat, particularly in the summer, when the numbers of migrating salmon have decreased (Lyons et al. 2005, 2007). Caspian terns primarily forage in areas near East Sand Island (Lyons et al. 2005), whereas double-crested cormorants (especially males) more often forage further upstream in the freshwater reach of the Columbia River estuary (Ander-

son et al. 2004), where large areas of tidal wetland habitat are located. These avian species are known to distribute foraging effort equally among habitats, but they also focus foraging effort on particular habitats (i.e., tidal flats and pile dikes) according to prey availability (Lyons et al. 2007). Studies of acoustic-tagged subyearling fall Chinook Salmon revealed that the majority of avian predation on subyearlings was from double-crested cormorants and occurred upstream of Tongue Point (rkm 27) in the freshwater reach of the Columbia River estuary (Ryan Harnish, Pacific Northwest National Laboratory, personal communication, March 2011). This reach of the estuary is characterized by tidal wetland habitats and shallow subtidal channels, which have little or no overhead cover and provide optimal depth and visibility conditions for mass fishing by double-crested cormorants (Van Eerden and Voslamber 1995). Both double-crested cormorants and great cormorants *Phalacrocorax carbo sinensis* are known to forage in large groups numbering from hundreds to thousands of individuals; this is a more efficient foraging strategy than solitary foraging, especially at high prey densities (Bartholomew 1942; Van Eerden and Voslamber 1995). Therefore, we suspect that the foraging efficiency of double-crested cormorants differs among Columbia River estuary habitats and may be a factor influencing the differences in vulnerability between the tule and URB stocks.

Although we found that avian predation rates were related to stock type, there is little understanding of how the stock-specific migration behaviors of subyearling Chinook Salmon within the Columbia River estuary affect their vulnerability to avian predation. Estuarine habitat use by fish may be critical to understanding the differences in vulnerability to avian predation because subyearling Chinook Salmon are known to reside in shallow wetland habitats for periods of weeks to months (Levy and Northcote 1982; Swales and Levings 1989; Bottom et al. 2005a; Sommer et al. 2005; Teel et al. 2009) and they exhibit site-specific fidelity while rearing in the estuary (Hering et al. 2010). Data from stationary PIT tag arrays located in tidal wetland channels demonstrated that subyearling fall Chinook Salmon can reside in such channels for periods of over 50 d in the Columbia River estuary upstream of Tongue Point (Regan McNatt, National Oceanic and Atmospheric Administration [NOAA] Fisheries, personal communication, June 2009) and in the Salmon River, Oregon (Hering et al. 2010).

Much like a slow migration rate, prolonged estuarine residence is a behavior that may increase predation exposure of subyearling fall Chinook Salmon if they reside for extended periods within foraging range of the birds nesting on East Sand Island. Prolonged residency in wetlands and estuaries is a common life history pattern throughout the range of Chinook Salmon (Carl and Healey 1984; Dawley et al. 1986; Sommer et al. 2001; Bottom et al. 2005b). Wetlands are highly productive habitats where subyearlings experience greater growth rates relative to main-channel habitats (Sommer et al. 2001). Prolonged wetland residency seems to benefit subyearling Chinook Salmon by decreasing size-dependent predation by aquatic predators (Fisher

and Pearcy 1988), especially when ocean productivity is relatively poor (Holtby et al. 1990).

Smolt development (as measured by gill Na^+ , K^+ -ATPase activity level) and migration rate are interrelated factors in behavior and physiology that may determine the duration of estuarine residency (Wagner et al. 1969; Zaugg 1989) and, presumably, the period for which the fish are exposed to avian predation. Kennedy et al. (2007) found that higher gill Na^+ , K^+ -ATPase activity levels in steelhead decreased their vulnerability to predation by Caspian terns and double-crested cormorants nesting on East Sand Island. In addition, Kennedy et al. (2007) suggested that steelhead with lower gill Na^+ , K^+ -ATPase activity levels were more likely to utilize freshwater habitats, thereby increasing their vulnerability to shallow-water foraging avian predators. Smolt development is also known to increase during active migration (Zaugg et al. 1985; Tiffan et al. 2000), indicating that a longer migration distance decreases the likelihood of prolonged estuarine residency. Dawley et al. (1986) observed that the migration rates of subyearling fall Chinook Salmon increased in proportion to distance from the Pacific Ocean. During 2008 and 2009, the mean migration time of PIT-tagged URB fish from Bonneville Dam to rkm 75 was approximately 2 d (SE = 0.03; $n = 297$), whereas tule-stock fish from Spring Creek National Fish Hatchery took approximately 24 d (SE = 2.98; $n = 61$) to migrate the same distance (Matthew Morris, Pacific States Marine Fisheries Commission [PSMFC], personal communication, July 2009). Thus, for tule fall Chinook Salmon subyearlings, including those released from Spring Creek National Fish Hatchery, the period of exposure to avian predators in the Columbia River estuary was likely longer than that for the URB stock. We therefore suspect that the migration rate and smoltification status of subyearling fall Chinook Salmon may also be important factors influencing the duration of vulnerability to avian predators.

Although we did not directly measure the factors affecting vulnerability of subyearling fall Chinook Salmon to avian predation, based on available information we hypothesize that fish stock type affects several interrelated factors of migration behavior: smoltification, migration rate, duration of estuarine residence, and estuary habitat use. We hypothesize that migration behaviors exhibited by the tule stock result in a greater likelihood that these fish will exhibit spatial and temporal overlap with avian predators, particularly double-crested cormorants, thereby resulting in higher predation rates relative to those on the URB stock. However, more research is needed to determine (1) whether these factors are indeed related to the greater vulnerability of tule-stock fall Chinook Salmon subyearlings compared with URB-stock subyearlings and (2) whether examining other groups of PIT-tagged fish would yield evidence of unexpected vulnerability to avian predation.

Management Implications

Releases of hatchery-reared tule-stock fall Chinook Salmon during the past decade have averaged nearly 37 million fish an-

nually (CBR 2010). If conservative estimates of avian predation rates on PIT-tagged tule subyearlings are representative of the predation rates on tule-stock fish released for annual hatchery production, then extrapolation of the mean annual predation rate (21.8%) yields an estimate of approximately 8 million fish (range = 3.3–10.0 million fish) being consumed annually by avian predators during 2002–2010. If this estimate is accurate, tule-stock subyearlings undoubtedly constitute a significant proportion of the 15 million salmonid smolts that are consumed each year by avian predators nesting on East Sand Island (Collis et al. 2009). Numerous federal, state, and tribal governments are currently addressing mortality of all salmonids from predation by Caspian terns and double-crested cormorants nesting on East Sand Island by relocating both colonies to areas outside of the Columbia River basin (USFWS 2005; NMFS 2010; Lyons et al. 2011). If these efforts are successful, it is likely that predation on tule-stock fall Chinook Salmon subyearlings prior to ocean entry will substantially decrease.

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