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ARTICLE

Susceptibility of Juvenile Steelhead to Avian Predation: the Influence of Individual Fish Characteristics and River Conditions

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Abstract

Identification of the factors that influence susceptibility to predation can aid in developing management strategies to recover fish populations of conservation concern. Predator–prey relationships can be influenced by numerous factors, including prey condition, prey size, and environmental conditions. We investigated these factors by using juvenile steelhead *Oncorhynchus mykiss* from the Snake River (Pacific Northwest, USA), a distinct population segment that is listed as threatened under the U.S. Endangered Species Act. During 2007–2009, steelhead smolts ($n = 25{,}909$) were captured, examined for external condition characteristics (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations), marked with passive integrated transponder (PIT) tags, and released to continue their out-migration. Recoveries of PIT tags on a downstream colony of Caspian terns *Hydroprogne caspia* ($n = 913$ tags) indicated that steelhead susceptibility to Caspian tern predation increased significantly with decreases in steelhead external condition, decreased water discharge, and decreased water clarity. Susceptibility to Caspian tern predation also increased with increasing steelhead fork length up to 202 mm but then decreased for longer steelhead. Recoveries of PIT tags on a downstream colony of double-crested cormorants *Phalacrocorax auritus* ($n = 493$ tags) indicated that steelhead susceptibility to double-crested cormorant predation increased significantly with declining external condition of steelhead, and that steelhead of hatchery origin were more susceptible than their wild counterparts. Results indicate that steelhead susceptibility to avian predation is dependent on fish condition and length and is influenced by river conditions and rearing environment.

Predation is a key ecological process influencing the size of fish populations and the composition of fish communities (Sih 1987). Predator–prey relationships are often influenced by numerous factors, including prey condition (see review by Mesa et al. 1994), prey size (see review by Sogard 1997), and environmental factors (Gregory 1993; Mesa 1994; Mesa and Warren 1997; Gregory and Levings 1998; De Robertis et al. 2003). An understanding of how these factors influence predator–prey

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relationships has important implications for fitness at both the individual and population levels and also provides valuable information regarding the efficacy of top-down ecosystem management (i.e., predator management).

The theory that predators disproportionately prey on individuals that are in substandard condition (e.g., weak, sick, stressed, or inexperienced; sensu Temple 1987) is widely accepted and has been well supported in fish predation studies (see review by Mesa et al. 1994). The occurrence and magnitude of condition-dependent predation may vary as a function of predator foraging strategy. In theory, predators that chase their prey should be more likely to disproportionately take individuals in poorer condition compared to predators that ambush their prey (Estes and Goddard 1967; Schaller 1968). Studies evaluating predator–prey interactions and the efficacy of predator management, however, rarely consider the influence of prey condition and predator foraging strategies (Mesa et al. 1994). For instance, the success of predator management efforts to increase prey populations would be diminished if the prey would have died from other causes (e.g., disease, competition, or other predators) regardless of the predation event (Errington 1956; Temple 1987). Thus, the degree to which the mortality caused by predation is compensatory is a primary consideration for programs that seek to restore prey populations through predator management.

Within populations of Pacific salmon *Oncorhynchus* spp., increased susceptibility to predation by piscivorous fish and birds has been attributed to differences in fish behavior, condition, size, rearing, and environmental conditions (Gregory and Levings 1998; Mesa et al. 1998; Collis et al. 2002; Schreck et al. 2006; Kennedy et al. 2007). Environmental conditions experienced by juvenile salmonids during out-migration (e.g., water flow, turbidity, or factors associated with migration timing) are known to increase stress, reduce fish performance, and increase susceptibility to predation (Raymond 1979; Gregory and Levings 1998; Budy et al. 2002; Schreck et al. 2006). The external condition (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations) of out-migrating juvenile steelhead *O. mykiss* has been linked to internal fish condition and to survival during out-migration (Hostetter et al. 2011). Although some studies have suggested that the condition of smolts influences their susceptibility to avian predation (Schreck et al. 2006; Kennedy et al. 2007), no direct link between external fish condition and susceptibility to avian predation has been documented in the wild.

Predator foraging strategy can play an important role in determining which factors influence prey susceptibility to predation (Estes and Goddard 1967; Schaller 1968; Temple 1987). In the Columbia River basin, Caspian terns *Hydroprogne caspia* and double-crested cormorants *Phalacrocorax auritus* are responsible for the majority of the avian predation mortalities among smolts (Collis et al. 2002; Evans et al. 2012), but the two waterbird species employ very different foraging behaviors. Double-crested cormorants are pursuit divers that actively hunt their prey underwater (Hatch 1999), whereas Caspian terns are plunge divers that capture (i.e., ambush) their prey at or near the water surface (Cuthbert and Wires 1999). In addition to foraging behavior, these predators also differ in size, gape width, and foraging range from the breeding colony (Cuthbert and Wires 1999; Hatch 1999), suggesting that factors influencing the susceptibility of juvenile salmonids to avian predation may differ between the two predator species.

Avian predation on salmonid smolts has been identified as one of several factors limiting recovery of salmonid evolutionarily significant units (ESUs) and steelhead distinct population segments (Waples 1991) within the Columbia River basin that are listed as threatened or endangered under the U.S. Endangered Species Act (ESA; Roby et al. 2003; Lyons 2010). Management efforts to reduce the impact of avian predation on survival of juvenile salmonids within the Columbia River estuary are currently being implemented (Roby et al. 2002; USFWS 2006). However, knowledge of how individual fish characteristics and environmental factors influence the susceptibility of juvenile salmonids to avian predation is extremely limited.

In the present study, we tested three hypotheses regarding the predator–prey relationship between piscivorous birds (e.g., Caspian terns and double-crested cormorants) and anadromous salmonids (e.g., steelhead) in the Columbia River basin. Hypothesis 1 was that the probability of a smolt being consumed by an avian predator is influenced by both individual fish characteristics (e.g., size, rearing type [hatchery versus wild], and external condition) and environmental factors (e.g., turbidity and water discharge rate). Hypothesis 2 was that avian predation on salmonid smolts is condition dependent, such that the probability of a smolt being consumed by an avian predator increases with declining external condition of the smolt. Hypothesis 3 was that factors influencing smolt susceptibility to avian predation will vary with the species of avian predator. Snake River steelhead were selected for this study because prior research suggested that among salmonids in the mid-Columbia River, steelhead smolts were the most susceptible to avian predation (Antolos et al. 2005). In addition, data describing the impact of avian predation are needed to evaluate recovery options for Snake River steelhead, which are listed as threatened under the ESA (Good et al. 2005).

METHODS

Study area.—Our research efforts focused on out-migrating juvenile steelhead from the Snake River basin, which were guided into juvenile collection facilities at either Lower Monumental Dam (LMN; river kilometer [rkm] 589) or Ice Harbor Dam (ICH; rkm 538) on the lower Snake River, Washington (Figure 1). We investigated two piscivorous waterbird breeding colonies on two different islands in the mid-Columbia River: a Caspian tern colony on Crescent Island (rkm 510) and a double-crested cormorant colony on Foundation Island (rkm 518; Figure 1). These islands were situated in an impoundment formed

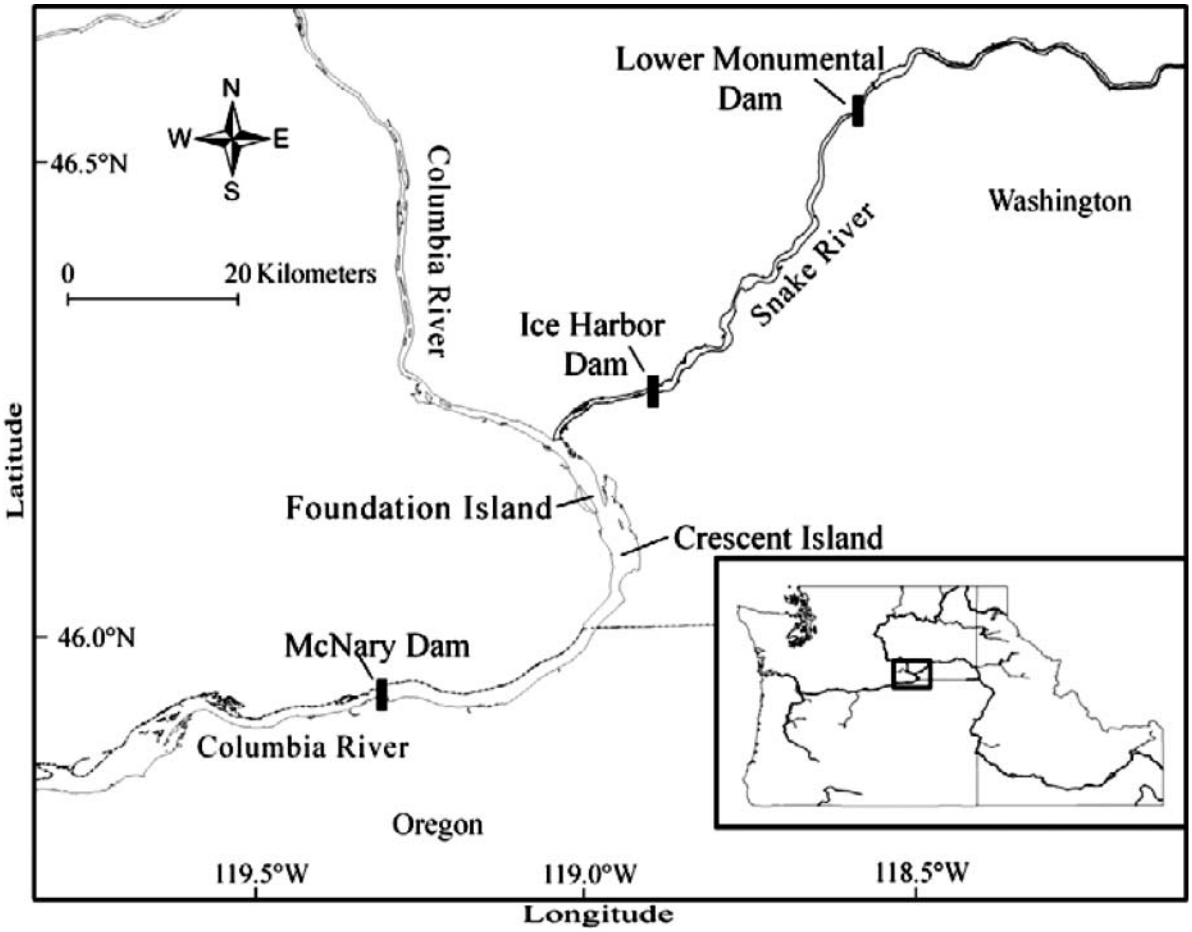

FIGURE 1. Map of the main-stem Columbia and Snake rivers, showing locations of the hydroelectric dams (bars) noted in the text. The Caspian tern colony was located at Crescent Island, and the double-crested cormorant colony was located at Foundation Island.

by McNary Dam (hereafter, "McNary Pool"), just downstream of the Snake River–Columbia River confluence and downstream of the smolt capture and release sites. The smolt capture and release locations (Figure 1) were specifically selected because they were directly upstream of the two nesting colonies in McNary Pool and were within the documented foraging ranges of the two waterbird species (Hatch 1999; Anderson et al. 2004; Lyons et al. 2007; Maranto et al. 2010).

Fish capture, tagging, and external examination.—In general, juvenile steelhead were sampled 6 d/week at LMN and 2 d/week at ICH during the steelhead out-migration period in 2007–2009. Sampling corresponded with the run-at-large, starting in early April and ending either in early July or when capture numbers dropped below 100 steelhead/week. Steelhead were collected daily, and prior to sampling they were held for up to 24 h in the holding tanks (supplied with flow-through river water) at each dam's juvenile collection facility. Daily samples of captured juvenile steelhead were then separated into small batches (10–50 fish) via a slide gate, were anesthetized with tricaine methanesulfonate (MS-222), and were tagged with a 12- × 2-mm (length × width) passive integrated transponder (PIT) tag (134.2 kHz) via a modified hypodermic syringe equipped with a 12-gauge needle (Prentice et al. 1990a, 1990b; Nielsen 1992). To reduce disease transmission, needles were soaked for a minimum of 10 min in a 70% solution of ethyl alcohol prior to PIT tag loading.

Methods for the noninvasive examination of steelhead smolts followed those of Hostetter et al. (2011) and are briefly summarized here. After a steelhead was PIT-tagged, it was placed in a sample tray, measured (fork length [FL]; nearest mm), weighed (nearest g), classified according to rearing environment (i.e., natural origin: indicated by the presence of an adipose fin; hatchery origin: indicated by the absence of an adipose fin or by characteristics associated with hatchery rearing practices, including the erosion of pectoral, pelvic, caudal, or dorsal fins), and digitally photographed (Canon EOS Rebel XTi camera; Canon EF 50-mm f/2.5 Compact Macro lens; Bencher Copymate II copy stand with fluorescent light source). Digital photographs were taken of both sides of each fish to allow for classification of external symptoms (by type and severity) after the fish was released; the total handling time for each fish was therefore reduced (<30 s). Detailed information on the external condition of each steelhead (body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations; classifications are described in Table 1) was collected by analyzing the digital photographs. Each steelhead smolt was scored for overall external condition (good, fair, or poor; modified from Evans et al. 2004) based on the scores for the five external condition categories (see Table 1).

After the examination process, daily groups of PIT-tagged steelhead were placed in a holding tank with flow-through river water for at least 1 h and were then released into the tailrace of the dam via the juvenile bypass facility's outflow pipe. Release times alternated between mornings and evenings to reduce possible bias in steelhead predation susceptibility associated with release time. Release times at LMN alternated between (1) 1800–2300 hours Pacific Daylight Time (PDT) on the day of processing and (2) 0700–1100 hours PDT on the day after processing. Release times at ICH alternated between 0900–1300 and 1800–2200 hours PDT on the day of processing. All mortalities and ejected PIT tags were removed from temporary holding tanks prior to the release of fish, and these individuals and tags were excluded from further analyses.

Recovery of PIT tags.—A PIT-tagged steelhead smolt was considered to have been consumed by a Caspian tern or a double-crested cormorant if the unique PIT tag associated with that individual was detected on the avian colony at Crescent Island or Foundation Island. During each year of the study, PIT tags were recovered from the colonies after nesting birds had dispersed (i.e., July–August, after the breeding season). A detailed description of the methods used to recover PIT tags from bird colonies is provided by Ryan et al. (2001); thus, the methods are only briefly summarized here. On the Caspian tern colony, PIT tags were recovered by systematically scanning the area occupied during the nesting season with a flat-plate PIT tag detector mounted on a four-wheel-drive vehicle. Pole-mounted, hand-held transceivers were then used to detect PIT tags in areas that were inaccessible to the flat-plate detector. The thick woodland on Foundation Island prevented the use of a vehicle; therefore, the entire double-crested cormorant colony was scanned using pole-mounted, hand-held transceivers.

Detection efficiency.—Recoveries of PIT tags on bird colonies provide a minimum estimate of predation on PIT-tagged smolts because (1) an unknown proportion of consumed

TABLE 1. Description and prevalence (%) of external condition characteristics of steelhead ($n = 25{,}909$) that were captured and PIT-tagged at Lower Monumental Dam or Ice Harbor Dam during 2007–2009. External condition descriptions are from Hostetter et al. (2011).

External condition	Category	Tagged fish	Prevalence (%)	Description
Body injury	Absent	20,963	81	No visible hemorrhages, scars, or other damage to the head, trunk, operculum, or eyes
	Moderate	3,025	12	Closed or healed scars to the head, trunk, operculum, or eyes
	Severe	1,921	7	Deformity, open wound, or large surface area scars on head, trunk, operculum, or eyes
Descaling	<5%	16,975	65	Scale loss on less than 5% of the body
	5–20%	7,916	31	Scale loss on 5–20% of the body
	>20%	1,018	4	Scale loss on over 20% of the body
Disease	Absent	24,917	96	No external symptoms of bacterial, fungal, or viral infections
	Moderate	349	1	Visible infection limited to one external area
	Severe	643	3	Visible infection in multiple areas or symptoms that suggest a systemic infection
Ectoparasites	Absent	25,217	97	No visible ectoparasites
	Moderate	523	2	Visible ectoparasites found in one area
	Severe	169	1	Visible ectoparasites in more than one area or on the gills
Fin damage	Absent	5,762	22	Fin wear and damage less than 50% on any fin
	Moderate	14,553	56	Fin wear and damage greater than 50% on one or two fins
	Severe	5,594	22	Fin wear and damage greater than 50% on three or more fins
Integrated condition[a]	Good	15,228	59	No noticeable external injury or symptoms of disease; descaling of no more than 10% of body surface
	Fair	7,197	28	Minor scars or other closed external damage; descaling of greater than 10% but no more than 50% of body surface
	Poor	3,484	13	Any steelhead with externally apparent fungal, parasitic, or bacterial infections; or descaling of greater than 50% of body surface; or open external body lesions

[a] Modified version of the procedure developed by Evans et al. (2004) for scoring external condition in adult steelhead.

PIT tags are deposited off-colony; (2) PIT tags that are deposited on the colony may be lost due to wind and water erosion; (3) either before or after deposition, some PIT tags are damaged to the point of being unreadable; and (4) detection efficiency for functioning PIT tags on the colony is less than 100% due to signal collision and other factors (Ryan et al. 2003; Evans et al. 2011). To better account for possible interannual differences in tag loss and damage, we measured detection efficiency in each year of the study by systematically sowing known PIT tags (of identical dimensions and design to those implanted in steelhead) on each of the colonies ($n = 400$ tags·colony^{-1}·year^{-1}, except at the Crescent Island colony in 2007 and 2008, when 800 tags/year were sown). To investigate possible intraseasonal variation in PIT tag detection efficiency, known PIT tags were sown on each colony (1) prior to the birds' arrival at the colony (March), (2) during the incubation period (May), (3) near the time of chick fledging (June), and (4) once the birds had left the colony after the nesting season (late July to early August). Recoveries of sown tags during PIT tag recovery allowed the estimation of weekly detection efficiencies by interpolation using logistic regression. Weekly estimates of detection efficiency were then included as fixed effects in all models to account for seasonal variation in colony-specific detection efficiency.

Environmental factors.—Environmental variables that were evaluated as part of this study included (1) steelhead release location (LMN or ICH), (2) steelhead abundance, (3) water discharge (hereafter, "discharge"), (4) Caspian tern or double-crested cormorant abundance, (5) water clarity, and (6) migration year. Steelhead were PIT-tagged and released at two locations upstream of the avian colonies (ICH and LMN) to evaluate whether either bird species disproportionately consumed steelhead released at one of the two dams. Measurements of the number of in-river juvenile steelhead passing McNary Dam (prey abundance) and the water discharge (kilo cubic feet per second [kcfs]; 1 kcfs = 28.3 m^3/s) at LMN were obtained from the Fish Passage Center website (www.fpc.org) and the Data Access in Real Time website (www.cbr.washington.edu/dart). In-river juvenile steelhead abundance was calculated as a weekly (Sunday–Saturday) average of the estimated number of juvenile steelhead that passed McNary Dam each day. Although the in-river steelhead index at McNary Dam is not an exact measurement of the overall abundance of juvenile steelhead in McNary Pool, it does provide a quantitative estimate of the relative numbers of in-river juvenile steelhead within and between migration years. The McNary Dam passage index was selected (relative to passage indices at other dams) because it includes steelhead from both the Snake and Columbia rivers and because this dam is located just downstream of and within the presumed foraging radius of the avian colonies on Crescent and Foundation islands (Figure 1). Discharge measurements were obtained from LMN instead of ICH, as measurements were correlated between dams (Pearson's product-moment correlation coefficient $r > 0.80$) and the majority of PIT-tagged steelhead were released from LMN. Data on weekly Caspian tern and double-crested cormorant abundance (hereafter, "predator abundance") were obtained from the Bird Research Northwest website (www.birdresearchnw.org). These data were estimated by averaging three to eight weekly counts of the number of adult and juvenile birds present on each colony; counts were conducted from observation blinds located at the periphery of the colonies. Water clarity was estimated using averages of two to four weekly Secchi depth measurements (nearest 0.25 m) taken from a boat in the main channel of the Snake River just upstream from its confluence with the Columbia River. Water clarity measurements were also taken at other locations within the McNary Pool but were correlated between locations (Pearson's $r > 0.70$ during peak out-migration periods). We therefore used water clarity measurements that were taken in the main channel of the Snake River—a location that was used by all out-migrating steelhead smolts in this study. Discharge, water clarity, predator abundance, and prey abundance variables were not highly correlated with one another (Pearson's $r < 0.60$; Figure 2).

Susceptibility to avian predation.—A suite of logistic regression models was used to evaluate the influence of environmental factors and individual fish characteristics on the probability of recovering a PIT-tag (i.e., representing an individual steelhead) on the Crescent Island Caspian tern colony or the Foundation Island double-crested cormorant colony. We considered a null model that included colony-specific detection efficiency, number of birds on-colony, in-river steelhead abundance, and migration year (hereafter, "base model") due to the biological importance of these variables in predicting steelhead susceptibility to avian predation (Ryan et al. 2003; Antolos et al. 2005). Variables that were included in the base model were also included in all candidate models; this allowed us to account for variation in steelhead predation susceptibility associated with these variables prior to investigating relationships between predation susceptibility and explanatory variables of interest.

We fit logistic regression functions,

$$\text{logit}\,(p_i) = \beta_0 + \beta_1 D_i + \beta_2 P_i + \beta_3 S_i + \beta_4 Y_i \ldots + \beta_p X_i,$$

where p_i is the probability that steelhead i would be detected on a specific bird colony, β_0 is the regression intercept, $\beta_1 D_i$ is the regression coefficient for the weekly colony-specific detection efficiency for steelhead i, $\beta_2 P_i$ is the regression coefficient for the weekly colony-specific predator abundance for steelhead i, $\beta_3 S_i$ is the regression coefficient for the weekly in-river steelhead abundance for steelhead i, $\beta_4 Y_i$ is the regression coefficient for the migration year of steelhead i, and $\beta_p X_i$ is the regression coefficient for the independent explanatory variable X associated with steelhead i. Independent explanatory variables evaluated in this study included the river conditions and the individual fish characteristics described above.

The influence of individual fish characteristics and environmental factors on the probability of recovering a PIT tag on a bird colony was evaluated by using three sets of a priori general models and a best-fit model from backwards stepwise selection

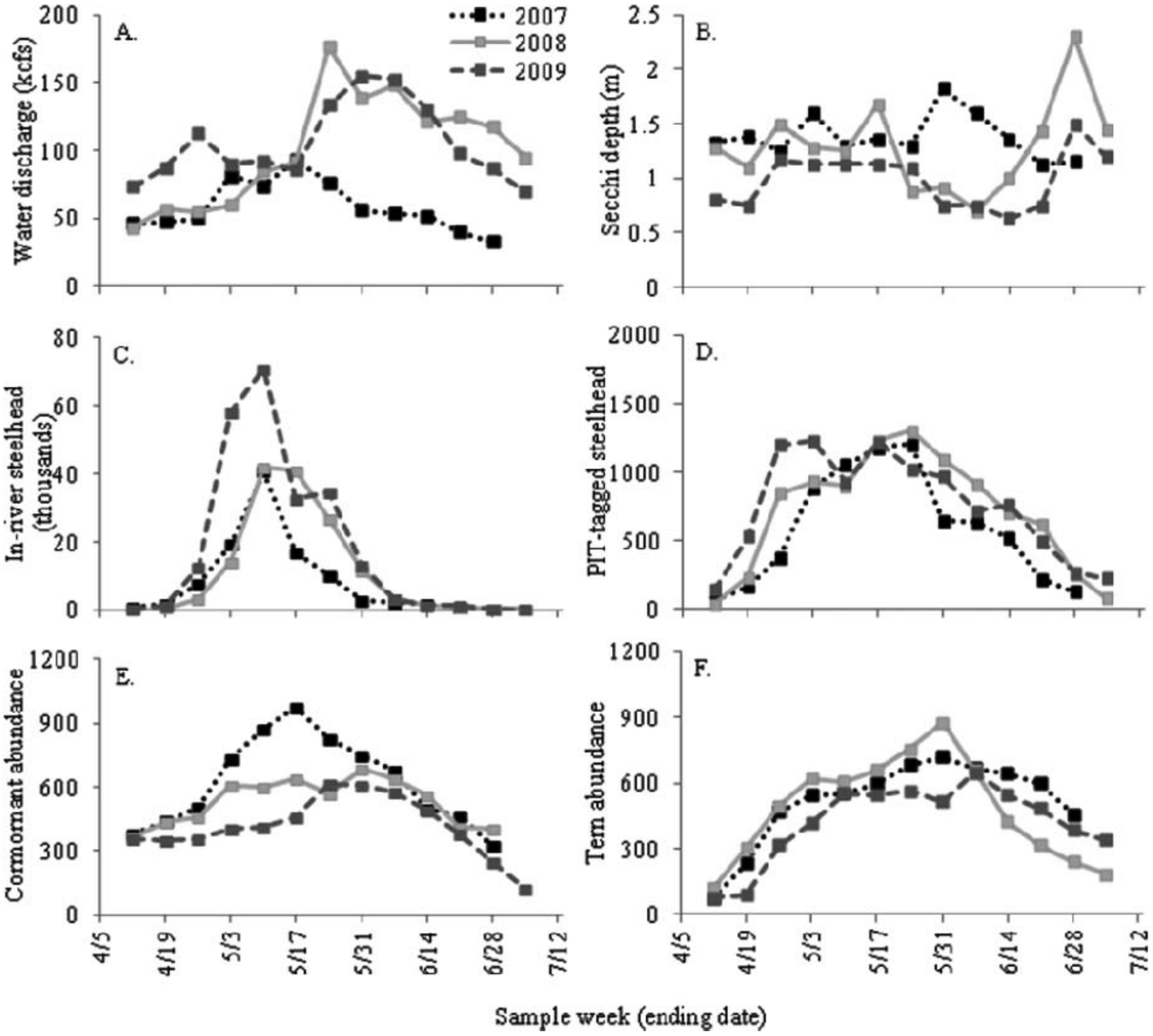

FIGURE 2. Weekly averages of **(A)** water discharge (kilo cubic feet per second [kcfs]; 1 kcfs = 28.3 m^3/s) at Lower Monumental Dam, **(B)** water clarity (Secchi depth, m), **(C)** number of in-river steelhead smolts, **(D)** number of steelhead smolts that were PIT-tagged and released as part of this study, **(E)** number of double-crested cormorants at the nesting colony on Foundation Island, and **(F)** number of Caspian terns at the nesting colony on Crescent Island. Data points are plotted on the last day of each sample week. See Methods for complete descriptions of the variables.

(following the methods used by Keefer et al. 2008 for adult steelhead). The general models included (1) the previously described base model, (2) a global additive model that included all variables of interest, and (3) individual models that evaluated each explanatory variable irrespective of other individual fish characteristics and environmental factors of interest (Table 2). The best-fit model from a backwards stepwise selection process that began with the global additive model was also examined. Only additive models were investigated due to the small proportion of PIT tags that were recovered on bird colonies (~2–4% per colony per year) and the high number of explanatory variables that were evaluated. Logistic regression models were evaluated for goodness of fit (Pearson's χ^2), and the covariance matrices were corrected if overdispersion was detected (Hosmer and Lemeshow 2000). All models were ranked and compared by using Akaike's information criterion corrected for small sample size (AIC_c) and by using the AIC_c difference (ΔAIC_c; Burnham and Anderson 2002). Relative differences in the probability of recovering a PIT tag on a bird colony were further investigated through probabilities, odds, and odds ratios of specific explanatory variables. Evaluation of explanatory variables by AIC_c values, stepwise selection, and odds ratios allowed us to address our hypotheses by identifying the most influential explanatory variables while also assessing the direction and strength of these variables for explaining steelhead susceptibility to each avian predator species. All analyses were conducted in the Statistical Analysis System version 9.2 (SAS Institute, Inc.) with statistical significance α set at 0.05.

TABLE 2. Model selection results used to evaluate the influence of individual fish characteristics and environmental factors on the susceptibility of juvenile steelhead to predation by Caspian terns or double-crested cormorants (FL = fork length; AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = AIC_c difference). External condition characteristics are defined in Table 1.

		Caspian tern		Double-crested cormorant	
Model[a]	df	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
Individual characteristics					
Body injury	8	6,881.7	262.8	4,861.7	68.3
Descaling	8	6,881.3	262.4	4,865.4	72.0
Disease	8	6,883.3	264.4	4,829.2	35.8
Ectoparasites	8	6,881.9	263.0	4,861.1	67.7
Fin damage	8	6,882.7	263.8	4,858.7	65.3
Integrated condition	8	6,878.6	259.7	4,848.9	55.5
Rearing type (hatchery or wild)	7	6,880.3	261.4	4,854.7	61.3
FL	7	6,769.9	151.0	4,864.9	71.5
FL + FL^2	8	6,635.8	16.9	4,863.5	70.1
Environmental factors					
Discharge	7	6,881.1	262.2	4,865.4	72.0
Water clarity	7	6,875.0	256.1	4,861.5	68.1
Release location	7	6,878.8	259.9	4,834.1	40.7
A priori models					
Base model[a]	6	6,881.9	263.0	4,863.3	70.0
Global model[b]	23	6,627.0	8.1	4,804.0	10.6
Backward stepwise models					
FL + FL^2 + integrated condition + discharge + water clarity	12	6,618.9	0.0		
Disease + release location + rearing type	10			4,793.4	0.0

[a] All models controlled for detection efficiency, predator abundance, prey abundance, and migration year (base model).

[b] Additive model that included all individual characteristics and environmental factors.

RESULTS

Steelhead Capture and Condition

In total, 25,909 juvenile steelhead were PIT-tagged and released from either LMN ($n = 22{,}401$) or ICH ($n = 3{,}508$) as part of this study. Sampling effort was relatively consistent across the 3-year study, with annual releases of 7,065 PIT-tagged steelhead in 2007, 9,143 fish in 2008, and 9,701 fish in 2009. Released PIT-tagged steelhead consisted of more hatchery-reared smolts ($n = 22{,}135$) than wild smolts ($n = 3{,}774$), corresponding to the relative abundances of these two rearing types among run-of-the-river steelhead sampled at lower Snake River dams during the study period (FPC 2011). Of the PIT-tagged steelhead, 59% were classified as being in good condition, 28% were in fair condition, and 13% were in poor condition (Table 1). The most prevalent external fish condition was fin damage (78% of the tagged fish), followed by descaling of 5% or greater (35% of the tagged fish), body injuries (19%), external symptoms of disease (4%), and ectoparasite infestations (3%; Table 1). Average FL of hatchery-reared steelhead (mean = 225 mm) was 21.2% greater than that of wild steelhead (mean = 185 mm; 95% CI of difference = 20.7–21.7%; two-tailed *t*-test: $P < 0.001$). Despite this difference, the range of FLs of hatchery-reared and wild steelhead overlapped considerably (hatchery-reared fish: 132–375 mm FL; wild fish: 131–354 mm FL).

Tag Recoveries

Of the 25,909 PIT-tagged steelhead that were released, PIT tags representing 913 steelhead (3.5%) were recovered on the Crescent Island Caspian tern colony and PIT tags from 493 steelhead (1.9%) were recovered on the Foundation Island double-crested cormorant colony. There was a positive association between the detection efficiency of PIT tags sown on the Crescent Island colony and the date of sowing, indicating that the probability of smolt PIT tag recovery was higher for tags that were deposited later in the nesting season. This trend was significant in 2007 ($\chi^2 = 140.9$, df = 1, $P < 0.001$), 2008 ($\chi^2 = 153.1$, df = 1, $P < 0.001$), and 2009 ($\chi^2 = 92.1$, df = 1, $P < 0.001$). Results from the Foundation Island colony indicated that the probability of PIT tag recovery on this colony was inversely related to the date of sowing. This relationship was significant in 2009 ($\chi^2 = 5.0$, df = 1, $P = 0.03$) but was not significant in 2007 ($\chi^2 = 1.8$, df = 1, $P = 0.17$) or 2008 ($\chi^2 = 3.3$, df = 1, $P = 0.07$).

Susceptibility to Caspian Tern Predation

Steelhead susceptibility to predation by Caspian terns was associated with six different individual fish characteristics and environmental factors (Tables 2, 3). Fork length, discharge, water clarity, and integrated condition category (good, fair, or poor) were the most influential explanatory variables in predicting steelhead susceptibility to predation by Caspian terns (Table 2). A quadratic function of steelhead FL was the most important individual fish characteristic in predicting susceptibility to Caspian tern predation. Steelhead FL was highly significant in the top model (Table 3), and the model with FL had the lowest AIC$_c$ value of any model based on a single explanatory variable (Table 2). Results indicated that the relationship between steelhead FL and susceptibility to Caspian tern predation was convex: the greatest susceptibility was at FLs of around 202 mm, whereas lower susceptibility was observed at greater and lesser FLs (Figure 3). For example, the odds of recovering a PIT tag from a 202-mm steelhead on the Caspian tern colony was more than twice the odds of recovering a PIT tag from a steelhead smaller than 150 mm FL or larger than 250 mm FL (Figure 3).

Similar trends were observed when investigating discrete associations between steelhead susceptibility to Caspian tern predation and individual fish characteristics or environmental factors. Once again, the quadratic function of steelhead FL was the most important variable in predicting the relative susceptibility of steelhead smolts to predation by Caspian terns (Table 2; Appendix Table A.1). Individual fish characteristics, including severe body injuries, over 20% descaling, and the integrated condition category, were associated with higher susceptibility to Caspian tern predation, supporting the hypothesis that steelhead susceptibility to avian predation is condition dependent (Table A.1). Specifically, on the Caspian tern colony, the odds of recovering a PIT tag from a steelhead in poor condition was 1.31 times the odds of recovering a PIT tag from a steelhead in good condition (95% CI = 1.08–1.58; $P = 0.006$). Similarly, the odds of recovering a PIT tag from a steelhead with over 20% descaling and severe body injuries was 1.40 times (95% CI = 1.02–1.92; $P = 0.035$) and 1.24 times (95% CI = 0.99–1.55; $P = 0.057$), respectively, the odds of recovering a PIT tag from a steelhead without descaling or body injuries. Several individual fish characteristics were not included in the top model and were also not significantly associated with steelhead susceptibility to Caspian tern predation in the discrete models (Table 3; Table A.1). For instance, rearing type was not included in the top model (Table 3), and only a small and suggestive relationship was detected in the discrete model, indicating that the odds of recovering a PIT tag from a hatchery-reared steelhead was 0.83 times the odds of recovering a PIT tag from a wild steelhead (95% CI = 0.68–1.00; $P = 0.053$; Table A.1).

For all models, the results indicated that high river flows, high water clarity, and large numbers of out-migrating steelhead smolts reduced steelhead susceptibility to predation by Caspian terns (Table 3; Table A.1). For instance, results from the top model indicated that steelhead susceptibility to Caspian

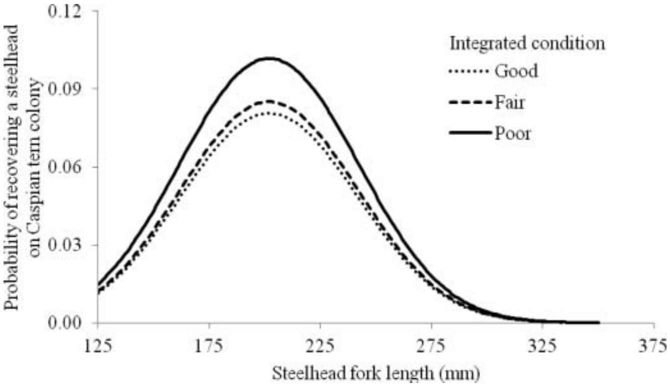

FIGURE 3. Regression lines for the relationship between juvenile steelhead fork length and susceptibility to predation by Caspian terns (i.e., probability of PIT tag recovery on the Crescent Island nesting colony). Regression lines for each integrated condition category (defined in Table 1) were calculated while other variables in the top model (colony-specific PIT tag detection efficiency, number of steelhead smolts in-river, number of Caspian terns on the colony, water clarity, and discharge) were held constant at their respective median values.

TABLE 3. Results from the top model used to evaluate susceptibility of juvenile steelhead to predation by Caspian terns. See Methods for variable descriptions (kcfs = kilo cubic feet per second [1 kcfs = 28.3 m^3/s]).

Variable	Effect	df	χ^2	Odds ratio	95% CI	P
FL	1-cm increase	1	83.1	3.95	2.94–5.31	<0.001
FL^2	1-cm increase	1	96.4	0.97	0.96–0.97	<0.001
Steelhead abundance	1,000-fish increase	1	61.6	0.97	0.96–0.98	<0.001
Water clarity	1-m increase in Secchi depth	1	13.2	0.56	0.41–0.77	<0.001
Discharge	10-kcfs increase	1	12.3	0.95	0.92–0.98	<0.001
Migration year	2008 vs. 2007	1	44.2	2.60	1.96–3.44	<0.001
	2009 vs. 2007	1	3.5	1.34	0.99–1.83	0.060
Integrated condition	Fair vs. good	1	0.5	1.06	0.90–1.25	0.494
	Poor vs. good	1	6.7	1.29	1.06–1.57	0.010
Caspian tern abundance	100-bird increase	1	0.8	1.03	0.97–1.09	0.380

tern predation increased when in-river steelhead abundance decreased ($P < 0.001$), water clarity decreased ($P < 0.001$), and discharge decreased ($P < 0.001$; Table 3). However, there was no evidence of a relationship between the number of Caspian terns on Crescent Island and the susceptibility of steelhead to Caspian tern predation after accounting for other variables in the model ($P = 0.380$; Table 3). Although release location was not included in the top model, there was a significant relationship between release location and steelhead susceptibility to Caspian tern predation in the discrete model (Table A.1). This result indicated that the odds of recovering a PIT tag from a steelhead released at LMN (i.e., farther upriver from the Caspian tern colony) was 1.32 times the odds of recovering a PIT tag from a steelhead released at ICH (i.e., closer to the colony; 95% CI = 1.03–1.69; $P = 0.028$).

Susceptibility to Double-Crested Cormorant Predation

Steelhead susceptibility to predation by double-crested cormorants was also associated with a select group of individual fish characteristics and environmental factors. External symptoms of disease appeared to be the most important individual fish characteristic for predicting steelhead susceptibility to double-crested cormorant predation. Variables for both moderate and severe external symptoms of disease were highly significant ($P < 0.001$) in the top model (Table 4), and the model that included disease had the lowest AIC_c value of any individual characteristic model (Table 2). Results from the top model indicated that on the double-crested cormorant colony, the odds of recovering a PIT tag from a steelhead with moderate or severe external symptoms of disease was 2.78 times (95% CI = 1.67–4.65; $P < 0.001$) and 2.94 times (95% CI = 2.05–4.24; $P < 0.001$), respectively, the odds of recovering a PIT tag from a steelhead without external symptoms of disease (Table 4). Results from the top model also indicated that the odds of recovering a PIT tag from a hatchery-raised steelhead on the double-crested cormorant colony was 1.54 times the odds of recovering a PIT tag from a wild steelhead (95% CI = 1.14–2.09; $P = 0.005$; Table 4).

Results from models based on individual explanatory variables provided additional support for the hypothesis that steelhead susceptibility to double-crested cormorant predation was condition dependent. Several external condition characteristics, including body injuries ($P = 0.050$), external symptoms of disease ($P < 0.001$), fin damage ($P = 0.012$), and the integrated condition category ($P < 0.001$), indicated that as the condition of steelhead declined, their susceptibility to double-crested cormorant predation increased (Appendix Table A.2). No relationship was detected between other individual fish characteristics and susceptibility to double-crested cormorant predation (Table A.2).

Environmental factors included in the top model indicated that steelhead susceptibility to predation by double-crested cormorants increased when the abundance of these birds increased ($P < 0.001$) and when steelhead were released closer to the double-crested cormorant nesting colony (i.e., released at ICH; $P < 0.001$). Unlike the results for Caspian terns, there was no evidence of predator swamping associated with double-crested cormorant predation on steelhead, as in-river steelhead abundance was not related to steelhead susceptibility to predation by double-crested cormorants ($P = 0.946$). Although water clarity was not included in the top model, this variable was associated with steelhead susceptibility to double-crested cormorant predation when modeled as a separate explanatory variable. Results from the model with water clarity as the single explanatory variable indicated that as water clarity increased, steelhead susceptibility to double-crested cormorant predation increased ($P = 0.047$; Table A.2). This result was opposite that obtained for Caspian terns, wherein steelhead susceptibility to Caspian tern predation decreased as water clarity increased (Table A.1). Finally, discharge was not associated with steelhead susceptibility to double-crested cormorant predation, as it was not included in the top model and was not significant when modeled as the single explanatory variable ($P = 0.959$; Table A.2).

DISCUSSION

This study tested hypotheses regarding the influence of individual fish characteristics and environmental factors on the relative susceptibility of steelhead smolts to avian predation. We found that the size and condition of juvenile steelhead as

TABLE 4. Results from the top model used to evaluate susceptibility of juvenile steelhead to predation by double-crested cormorants (LMN = Lower Monumental Dam; ICH = Ice Harbor Dam). See Methods for variable descriptions.

Variable	Effect	df	χ^2	Odds ratio	95% CI	P
Disease	Moderate vs. absent	1	15.3	2.78	1.67–4.65	<0.001
	Severe vs. absent	1	33.8	2.94	2.05–4.24	<0.001
Release location	LMN vs. ICH	1	33.7	0.53	0.43–0.66	<0.001
Double-crested cormorant abundance	100-bird increase	1	12.0	1.15	1.06–1.25	<0.001
Rearing type	Hatchery vs. wild	1	7.8	1.54	1.14–2.09	0.005
Release year	2008 vs. 2007	1	5.9	1.43	1.07–1.90	0.015
	2009 vs. 2007	1	3.2	1.45	0.97–2.16	0.072
Steelhead abundance	1,000-fish increase	1	0.0	1.00	0.99–1.01	0.946

well as the river conditions at the time of their release were related to a steelhead's probability of being eaten by an avian predator; however, the importance and strength of these factors differed between the two avian predator species. One consistent trend for both Caspian terns and double-crested cormorants was the disproportionate consumption of steelhead that exhibited degraded physical condition. These results corroborate previous work suggesting that the susceptibility of Chinook salmon *O. tshawytscha* smolts to predation by Caspian terns in the Columbia River estuary was influenced by the incidence of disease in the out-migrating smolts (Schreck et al. 2006). Kennedy et al. (2007) found similar relationships between decreased saltwater preparedness and increased susceptibility of juvenile steelhead to avian predation in the Columbia River estuary, thus supporting the hypothesis that salmonid susceptibility to avian predation is associated with individual fish characteristics and condition.

The results presented here support the theory that predator foraging strategies play an important role in the incidence and magnitude of condition-dependent predation (Estes and Goddard 1967; Schaller 1968; Temple 1987). Condition-dependent susceptibility of steelhead was more evident for double-crested cormorant predation (pursuit-diving foraging strategy) than for Caspian tern predation (plunge-diving foraging strategy). Four different external indices of health status (body injuries, external symptoms of disease, fin damage, and integrated condition category) were significantly associated with steelhead susceptibility to double-crested cormorant predation (Table A.2), but only one external health index (integrated condition category) was associated with susceptibility to Caspian tern predation (Table A.1). Furthermore, the magnitude and significance of condition-dependent susceptibility were greater for double-crested cormorant predation than for Caspian tern predation in the top models and the individual-variable models. For instance, on the double-crested cormorant colony, the odds of recovering a PIT tag from a steelhead in poor condition was 1.72 times the odds of recovering a tag from a steelhead in good condition (Table A.2), whereas the odds ratio was only 1.31 for recovery of these PIT tags on the Caspian tern colony (Table A.1). Taken together, these results indicate that both piscivorous bird species disproportionately consumed steelhead that were in degraded condition, but the magnitude of condition-dependent susceptibility varied between the avian predator species.

Selective predation can result from several conditional events, including differences in predator–prey encounter rates, attack rates, capture rates, or a combination of these (Temple 1987). For instance, the behavior of potential prey in poorer health could make them more conspicuous to predators, thus increasing encounter rates. Likewise, predators could selectively attack prey in poorer condition to enhance foraging efficiency (rate of successful attacks), expending less energy to capture substandard prey than healthy prey (Stephens and Krebs 1986). Finally, increased predation rates on prey in substandard condition could result when predators attack all encountered individuals of the prey population but have a higher capture rate for fish in poorer health (Temple 1987).

Although this study could not address the mechanisms influencing selective predation, Caspian terns and double-crested cormorants both disproportionately consumed steelhead that were in degraded condition. The external indices of steelhead health status used in this study were associated with other metrics of overall fish condition, including increased pathogen prevalence and reduced survival (Hostetter et al. 2011). Hostetter et al. (2011) demonstrated that the likelihood of survival was significantly less for juvenile steelhead with external symptoms of degraded condition than for relatively undamaged smolts. These previous results, coupled with the condition-dependent avian predation demonstrated in the present study, support the hypothesis that avian predators disproportionately consume smolts that are less likely to survive to adulthood, indicating that smolt mortality from avian predation is partly compensatory.

Individual fish characteristics, including FL and rearing type (hatchery versus wild), were also related to differences in steelhead susceptibility to avian predation. The size of individual prey and the relationship between individual prey size and the size distribution of the prey population at large can have a major influence on survival probability (Rice et al. 1993; Sogard 1997). One of the most prevalent theories regarding the influence of juvenile fish size on susceptibility to predation is the "bigger is better" theory (Sogard 1997), which predicts that larger prey will have a survival advantage over smaller prey. However, our results support an alternative hypothesis—that predators select intermediate-sized prey to optimize their energy intake (MacArthur and Pianka 1966; Rice et al. 1997). Susceptibility to Caspian tern predation was highest for steelhead with FLs around 202 mm and was lower for larger or smaller steelhead. Evidence that salmonid susceptibility to predation by Caspian terns may be positively related to salmonid smolt FL was previously presented by Collis et al. (2001) and Ryan et al. (2003). Those authors noted that the relative susceptibility of various salmonid species to Caspian tern predation in the Columbia River estuary was correlated with fish size, as juvenile Chinook salmon and coho salmon *O. kisutch* were less susceptible than juvenile steelhead, which are generally larger. Caspian terns nesting on Crescent Island in McNary Pool were also found to disproportionately consume steelhead in comparison with relatively smaller Chinook salmon (Antolos et al. 2005; Evans et al. 2012). Size-dependent susceptibility of steelhead to Caspian tern predation in the present study provides strong empirical evidence in support of the hypothesis that relative size differences among salmonid ESUs are responsible, at least in part, for ESU-specific differences in predation rates by Caspian terns (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012).

A growing body of evidence suggests that the behavioral and physical traits associated with hatchery-raised salmonids enhance their susceptibility to predation (Olla and Davis 1989; Johnsson and Abrahams 1991; Álvarez and Nicieza 2003; Fritts et al. 2007). Several studies in the Columbia River estuary have noted that hatchery-reared salmonids were more susceptible to avian predation than their wild counterparts (Collis et al. 2001; Ryan et al. 2003; Kennedy et al. 2007). Our results indicate that hatchery-reared steelhead were more susceptible to some avian predators in freshwater systems: double-crested cormorants disproportionately consumed hatchery-reared steelhead relative to wild-origin steelhead, but this was not the case for Caspian terns. Although the mechanisms associated with increased susceptibility of hatchery-reared salmonids to avian predation have not been completely elucidated, numerous traits could play a role in the higher susceptibility of hatchery-reared salmonids to double-crested cormorant predation. Such traits include a lack of innate and learned predator avoidance behaviors (Olla and Davis 1989; Berejikian 1995), greater surface orientation (Mason et al. 1967), and increased stress levels associated with handling (Schreck 1981; Olla and Davis 1989).

Environmental factors have been shown to alter salmonid susceptibility to predation in both field and laboratory settings (Raymond 1979; Gregory 1993; Gregory and Levings 1998; Korstrom and Birtwell 2006). For instance, Antolos et al. (2005) suggested that low river flows and reduced in-river salmonid abundance were associated with increased predation rates on salmonids by Caspian terns nesting on Crescent Island. In our study, decreased discharge was strongly associated with increased steelhead susceptibility to Caspian tern predation. Discharge, which is correlated with water velocity, is a key factor determining the rate at which juvenile salmonids migrate through reservoirs (Berggren and Filardo 1993) and beyond the foraging range of central-place-foraging predators, such as colonial piscivorous waterbirds. However, this relationship was not consistent between the two predator species we examined, as steelhead susceptibility to double-crested cormorant predation was not significantly related to discharge.

Decreased water clarity (i.e., increased turbidity) can decrease the susceptibility of fish prey to predation by piscivorous fishes due to a potential reduction in predator–prey encounter rates (Gregory 1993; Gregory and Levings 1998; De Robertis et al. 2003). Strod et al. (2008) found that increased turbidity reduced fish prey detection and predation by the great cormorant *Phalacrocorax carbo sinensis*, a pursuit-diving species similar to the double-crested cormorant. Similarly, we found that steelhead susceptibility to double-crested cormorant predation decreased with increasing turbidity, indicating a decreasing probability that a steelhead would be consumed by a double-crested cormorant as turbidity increased. Unlike susceptibility to double-crested cormorant predation, the susceptibility of steelhead to Caspian tern predation was positively related to turbidity. Differences between Caspian terns and double-crested cormorants in terms of the influence of turbidity on steelhead susceptibility to predation are likely due to variation in foraging behavior between the two avian predators. The reduction in steelhead susceptibility to double-crested cormorant predation as turbidity increased may have been due to a decrease in encounter rates that would affect a pursuit-diving predator (Strod et al. 2008). However, decreased reaction times and reduced use of cover by salmonids in more-turbid water (Gregory 1993; Gregory and Levings 1998; Korstrom and Birtwell 2006) may increase steelhead susceptibility to plunge-diving predators like Caspian terns.

The presence of large numbers of prey can swamp the short-term capacity of predators to attack, handle, and consume them, which in turn can improve an individual prey's chances of survival (Ims 1990). Consistent with the predator-swamping hypothesis, an increased abundance of in-river steelhead was associated with a decreased susceptibility of individual steelhead to predation by Caspian terns. Ryan et al. (2003) noted a similar relationship between increased salmonid abundance and reduced susceptibility to avian predation in the Columbia River estuary, attributing this relationship to a greater potential for predator satiation and an improved ability of schooling fish to avoid predation. The association between in-river steelhead abundance and susceptibility to avian predation in the present study was, however, specific to Caspian terns. The lack of a relationship between in-river steelhead abundance and susceptibility to double-crested cormorant predation was likely due to the strong correlation between peak steelhead abundance and peak double-crested cormorant abundance (Figure 2C, E). The increased food demands associated with more breeding pairs and chicks in the double-crested cormorant colony along with the greater metabolic requirements of double-crested cormorants relative to Caspian terns (Roby et al. 2003; Lyons 2010) may have superseded any influence that steelhead abundance would have had on their susceptibility to predation by double-crested cormorants.

Prey often live in communities that include several predator species. However, the majority of studies have only examined predation impacts associated with one predator species (Sih et al. 1998). In the Columbia River basin, Caspian terns and double-crested cormorants are responsible for the majority of smolt losses due to avian predation (Collis et al. 2002; Evans et al. 2012). Predator-specific differences in foraging behavior, size, and gape width (Cuthbert and Wires 1999; Hatch 1999) suggest that the functional roles of these top avian predator species may be different, and thus their impacts on prey populations (e.g., salmonids) may also differ. The influences of individual fish characteristics and river conditions on steelhead susceptibility to avian predation in this study were often predator specific, further demonstrating the need to evaluate predator-specific impacts. Information on the predator-specific impacts from multiple predators will improve top-down ecosystem management (i.e., predator management) to recover fish populations of conservation concern where such actions are warranted and applicable.

The efficacy of predator control efforts for restoring prey populations of conservation concern depends on whether reductions in mortality due to predation are compensated for by other mortality factors. Separating the ultimate causes of mortality (e.g., degraded fish condition) from the proximate causes (e.g., avian predation on fish in degraded condition) can provide valuable insight into complex predator–prey interactions. For instance, if most of the juvenile salmonids that are consumed by avian predators would have died from other causes, then reductions in avian predation will not result in commensurate increases in the number of returning adult salmonids (i.e., smolt-to-adult survival; Schreck et al. 2006). Our results suggest that the efficacy of management actions to reduce avian predation may be somewhat discounted by the disproportionate predation on steelhead in degraded condition. However, the low prevalence of externally degraded steelhead smolts observed in this study (see Table 1) and the on-colony recovery of PIT tags from steelhead that were apparently in good condition suggest that some proportion, perhaps substantial, of smolt mortality due to avian predation is additive. At this time, studies that quantify the level of compensatory mortality associated with avian predation in the Columbia River basin have yet to be published. Further, it appears that hydrosystem operations and river conditions (e.g., discharge and water clarity) can also influence the susceptibility of steelhead to avian predation. Identification of individual smolt characteristics and hydrosystem practices that affect smolt survival and susceptibility to predation will aid in the development of management strategies that contribute to the recovery of ESA-listed salmonid stocks in the Columbia River basin.

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APPENDIX: INDIVIDUAL VARIABLE RESULTS FROM LOGISTIC REGRESSION MODELS

TABLE A.1. Individual variable results from logistic regression models used to evaluate the susceptibility of juvenile steelhead to predation by Caspian terns (kcfs = kilo cubic feet per second; LMN = Lower Monumental Dam; ICH = Ice Harbor Dam). External condition characteristics are defined in Table 1.

Variable[a]	df	χ^2	*P*	Effect	Odds ratio	95% CI	*P*
				Individual characteristics			
Body injury	2	4.4	0.112	Moderate vs. absent	0.94	0.76–1.16	0.569
				Severe vs. absent	1.24	0.99–1.55	0.057
Descaling	2	4.9	0.086	5–20% vs. <5%	1.09	0.93–1.27	0.298
				>20% vs. <5%	1.40	1.02–1.92	0.035
Disease	2	2.9	0.232	Moderate vs. absent	1.55	0.86–2.77	0.145
				Severe vs. absent	1.25	0.78–2.00	0.353
Ectoparasites	2	4.5	0.105	Moderate vs. absent	1.56	1.02–2.37	0.039
				Severe vs. absent	0.79	0.28–2.22	0.660
Fin damage	2	3.2	0.198	Moderate vs. absent	0.87	0.74–1.03	0.115
				Severe vs. absent	0.98	0.80–1.21	0.855
Integrated condition	2	7.7	0.022	Fair vs. good	1.05	0.89–1.23	0.584
				Poor vs. good	1.31	1.08–1.58	0.006
Rearing type	1	3.7	0.053	Hatchery vs. wild	0.83	0.68–1.00	0.053
FL	1	111.8	<0.001	1-cm increase	0.90	0.88–0.91	<0.001
FL + FL^2	2	97.8	<0.001	NA			<0.001
				Environmental factors			
Discharge	1	2.8	0.093	10-kcfs increase	0.98	0.95–1.00	0.093
Water clarity	1	8.7	0.003	1-m increase in Secchi depth	0.66	0.50–0.87	0.003
Release location	1	4.8	0.028	LMN vs. ICH	1.32	1.03–1.69	0.028

[a] Associations were determined after controlling for detection efficiency, predator abundance, prey abundance, and migration year.

TABLE A.2. Individual variable results from logistic regression models used to evaluate the susceptibility of juvenile steelhead to predation by double-crested cormorants (kcfs = kilo cubic feet per second; LMN = Lower Monumental Dam; ICH = Ice Harbor Dam). External condition characteristics are defined in Table 1.

Variable[a]	df	χ^2	*P*	Effect	Odds ratio	95% CI	*P*
				Individual characteristics			
Body injury	2	6.0	0.050	Moderate vs. absent	1.19	0.91–1.57	0.200
				Severe vs. absent	1.42	1.05–1.93	0.025
Descaling	2	2.0	0.376	5–20% vs. <5%	1.15	0.95–1.39	0.164
				>20% vs. <5%	1.09	0.69–1.70	0.721
Disease	2	48.9	<0.001	Moderate vs. absent	2.69	1.61–4.50	<0.001
				Severe vs. absent	3.08	2.15–4.43	<0.001
Ectoparasites	2	0.2	0.917	Moderate vs. absent	0.86	0.43–1.75	0.680
				Severe vs. absent	NA[b]	NA[b]	0.958
Fin damage	2	8.8	0.012	Moderate vs. absent	1.17	0.91–1.49	0.218
				Severe vs. absent	1.49	1.13–1.96	0.005
Integrated condition	2	19.9	<0.001	Fair vs. good	1.20	0.97–1.48	0.092
				Poor vs. good	1.72	1.36–2.19	<0.001
Rearing type	1	9.4	0.002	Hatchery vs. wild	1.61	1.19–2.18	0.002
FL	1	0.5	0.482	1-cm increase	1.01	0.98–1.04	0.482
FL + FL^2	2	3.1	0.078	NA	–	–	0.078
				Environmental factors			
Discharge	1	0.0	0.959	10-kcfs increase	1.00	0.96–1.04	0.959
Water clarity	1	3.9	0.047	1-m increase in Secchi depth	1.44	1.00–2.07	0.047
Release location	1	34.9	<0.001	LMN vs. ICH	0.52	0.42–0.65	<0.001

[a] Associations were determined after controlling for detection efficiency, predator abundance, prey abundance, and migration year.

[b] No PIT tags from steelhead with severe ectoparasites were recovered on the double-crested cormorant colony.