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Colonial Waterbird Predation on Juvenile Salmonids Tagged with Passive Integrated Transponders in the Columbia River Estuary: Vulnerability of Different Salmonid Species, Stocks, and Rearing Types

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Abstract.—Passive integrated transponder (PIT) tags implanted in Columbia River basin juvenile salmonids *Oncorhyncus* spp. were recovered from breeding colonies of Caspian terns *Sterna caspia* and double-crested cormorants *Phalacrocorax auritus* on Rice Island, a dredge spoil island in the Columbia River estuary. Tags were recovered to assess the relative vulnerability of different salmonid species, stocks, and rearing types to avian predators. We detected 50,221 PIT tags at the two bird colonies, mostly from juvenile chinook salmon *O. tshawytscha* and steelhead *O. mykiss* raised in hatcheries; 72% of the total tags were from the tern colony and 28% from the cormorant colony. Tagged steelhead smolts were more vulnerable to predation by both bird species than were yearling chinook salmon. More than 15% of PIT tags from steelhead smolts that were available in the estuary in 1998 were detected at the bird colonies compared with 2% of PIT tags from yearling chinook salmon. The greater vulnerability of steelhead may reflect size-dependent selection by avian predators. Salmonids listed under the Endangered Species Act and unlisted salmonids were equally vulnerable to predation by both terns and cormorants. Hatchery-raised yearling chinook salmon were more vulnerable than their wild counterparts to predation by terns, a surface-feeding species; however, hatchery-raised and wild yearling chinook salmon were equally vulnerable to predation by cormorants, a diving species. These results suggest that hatchery-raised yearling chinook salmon, and hatchery-raised steelhead in some years, are more vulnerable to tern predation than wild fish because they have a greater tendency to reside near the water surface where terns forage.

The conservation status of anadromous salmonids *Oncorhyncus* spp. in the Columbia River basin is a source of growing concern for a wide range of resource management agencies and publics in the Pacific Northwest, USA. Most of the 20 evolutionarily significant units (ESUs; the conservation unit) of anadromous salmonids in the Columbia River basin have been listed under the U.S. Endangered Species Act (ESA; NMFS 2000a). Eight ESUs are not currently listed, but the National Marine Fisheries Service (NMFS), the agency responsible for recovery of listed anadromous salmonids, has proposed one of these for listing in the near future, another is under review, and two are rapidly declining (H. Pollard, NMFS, personal communication). The risk of extinction for these ESUs has prompted a major allocation of resources toward restoring freshwater habitats, en-

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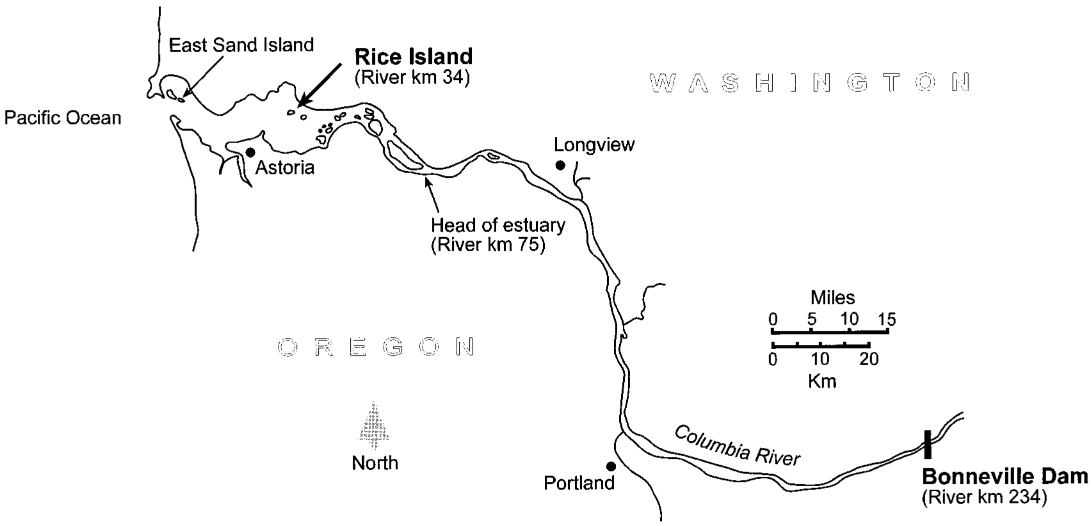

FIGURE 1.—The lower Columbia River and estuary from Bonneville Dam (the furthest downstream dam and the lowest fixed in-river detection point for juvenile salmonids tagged with passive integrated transponders on the Columbia River) to the river mouth. Base map courtesy of Schreck et al. 1997.

hancing passage through the hydrosystem (dams), restricting harvest, and improving hatchery production—the so-called ''four H's'' of salmon restoration.

In addition to these measures, increasing attention has focused on losses of emigrating smolts to predators: fish such as the northern pikeminnow *Ptychocheilus oregonensis,* walleye *Stizostedion vitreum,* and smallmouth bass *Micropterus dolomieu* (Rieman et al. 1991; Ward et al. 1995) and piscivorous waterbirds such as gulls *Larus* spp., terns *Sterna* spp., and cormorants *Phalacrocorax* spp. (Ruggerone 1986; Schreck et al. 1997; Schreck and Stahl 1998; Roby et al. 1998; Collis et al. 1999). Schreck et al. (1997) and Schreck and Shahl (1998) placed radio tags in hatchery-raised, yearling chinook salmon *O. tshawytscha* to monitor survival in the lower Columbia River and estuary. Detections of radio tags at colonies of piscivorous birds suggested that avian predation might be a major source of mortality, causing losses of 5–29% of the radio-tagged smolts that survived to the estuary (Schreck and Stahl 1998). In the mid-1990s, NMFS biologists became especially concerned about increasing populations of colonial piscivorous birds in the Columbia River estuary and in March 1995 formalized their concern in a Biological Opinion issued on the Operation of the Federal Columbia River Power System (NMFS 1995). That biological opinion directed the U.S. Army Corps of Engineers (USACE) to study the impact on juvenile salmonid survival of one waterbird colony in particular, the growing Caspian tern *S. caspia* colony on Rice Island, an artificial island created by the disposal of dredge material.

Rice Island is located in the Columbia River estuary, 34 km from the river mouth (Figure 1). During 1996–1998, this island was the site of the largest Caspian tern breeding colony in North America (14,000–16,000 breeding birds; Collis et al.1999; Cuthbert and Wires 1999), and probably in the world (authors' unpublished data). About 75% of prey items identified at the Rice Island Caspian tern colony in 1997 and 1998 were juvenile salmonids (Roby et al. 1998; Collis et al. 1999). In both years, estimates of the number of juvenile salmonids consumed by terns nesting at Rice Island were in the millions (Roby et al. 1998; Collis et al. 1999). This is the only Caspian tern colony that is known to rely primarily on salmonids as a food source (Cuthbert and Wires 1999).

In addition, Rice Island during 1996–1998 supported the second-largest breeding colony of double-crested cormorants *Phalacrocorax auritus* on the Pacific Coast of the United States and Canada: 1,200–2,400 breeding birds (Carter et al. 1995; Roby et al. 1998; Collis et al. 1999). Although cormorants nesting on Rice Island did not specialize in feeding on juvenile salmonids to the same extent as did Caspian terns, salmonid smolts composed 30% of identifiable cormorant prey items in 1997 and 53% in 1998 (Roby et al. 1998; Collis et al. 1999). Differences in diet between these two piscivorous waterbirds are expected because terns capture their prey at or near the surface (Cuthbert and Wires 1999), whereas cormorants are accomplished divers that capture prey throughout the water column down to depths of at least 22 m (Lewis 1929; Ainley et al. 1981).

Caspian terns first nested on Rice Island in 1986, when about 1,000 breeding pairs were counted (G. Dorsey, USACE, personal communication); double-crested cormorants first colonized the island 2 years later (Carter et al. 1995). The tern colony subsequently increased by over 600% in the next decade (Roby et al. 1998), apparently at the expense of other Caspian tern colonies formerly located along the coast of Washington in Grays Harbor, Willapa Bay, and northern Puget Sound, as well as East Sand Island, which is located in the Columbia River estuary near the Pacific Ocean (Figure 1; Roby et al. 1998).

Beginning in 1987, significant numbers of emigrating juvenile salmonids (wild and hatchery origin) in the Columbia River basin were tagged with passive integrated transponder (PIT) tags. A PIT tag is a microchip attached to a copper coil antenna encased in a glass capsule that is implanted with large-gauge needles into the abdominal cavity of juvenile salmonids. The tag is about 12 mm long by 2 mm in diameter and transmits a unique code whenever the tag is excited by a magnetic field, which is the basis for a variety of detection devices. The unique code enables individual or group indentifications.

The use of PIT tags to monitor smolt survival during emigration and subsequent return rates of adults has grown dramatically; currently about 1 million juvenile salmonids are PIT-tagged annually (PSMFC 2000). PIT tags are detected at juvenile bypass systems and fish ladders at the mainstem dams, and other in-river locations.

Beginning in 1996, we recovered PIT tags from the Rice Island bird colonies following the breeding season. PIT-tag collections were part of a larger study to assess the impact of tern and cormorant predation on survival of juvenile salmonids in the Columbia River estuary. We reasoned that numbers of PIT tags on bird colonies would provide some indication of the magnitude of avian predation and which salmonid stocks were most vulnerable to piscivorous waterbirds.

Results from our early PIT-tag recovery efforts indicated that there were tens of thousands of PIT tags from juvenile salmonids on the Caspian tern colony at Rice Island (Roby et al. 1998). These recoveries, when compared to in-river availability of various PIT-tagged stocks, provided minimum estimates of the proportion of certain salmonid stocks that succumbed to predation by terns or cormorants nesting at Rice Island. Estimates of the magnitude of avian predation based on these PIT-tag detections were minimal because (1) an unknown proportion of all PIT tags consumed by birds nesting on the colony are either regurgitated or defecated off-colony, (2) wind and water erosion removes an unknown number of tags from the colony, and (3) some PIT tags are damaged before or after they are deposited on the colony, rendering them unreadable with electronic equipment.

Here, we examine our use of the PIT tags recovered from the Caspian tern and double-crested cormorant colonies on Rice Island in 1996–1998 to address five questions. (1) Are the various species of juvenile salmonids found in the Columbia River estuary equally vulnerable to bird predation? (2) Are listed and unlisted salmonid ESUs equally vulnerable to bird predation? (3) Are juvenile salmonids raised in hatcheries more vulnerable than wild fish to bird predation? (4) Are the relative vulnerabilities of various species, stocks, and rearing types to tern predation similar to those for cormorant predation? (5) What factors contribute to the vulnerability of juvenile salmonids to bird predation in the estuary?

Methods

During 1996–1998, PIT tags were recovered or detected (in situ) on Rice Island after the Caspian tern and double-crested cormorant colonies had dispersed after the breeding season (August–October). Tags were recovered from the Rice Island colonies by visually searching for PIT tags on the surface of the colony and by using a set of soil sieves to separate buried PIT tags from the finer grained substrate. Recovered PIT tags were removed from the colony and later read with hand-held PIT tag readers (Avid, Datamars, Destron). Tags were also detected and read in situ using hand-held electronic PIT tag readers and a large flat-plate PIT-tag detector and reader, specially designed for PIT-tag interrogation at bird colonies (Ryan et al. in press). The tag reading efficiency of the flat plate detector was 97% at depths up to 2.5 cm (Ryan et al. in press), where most PIT tags were located based on our sampling using soil sieves (K. Collis, personal observation).

PIT-tagged juvenile salmonids have been released since 1987 from numerous locations throughout the Columbia River basin upstream from Bonneville Dam. Fixed receiving stations have been installed at Columbia and Snake river dams and in-river (e.g., fish traps) to monitor both downstream and upstream passage of juvenile and adult salmonids, respectively. Tagging, release, and dam and in-river passage information on all PIT-tagged salmonids are available in a centralized database managed by the Pacific States Marine Fisheries Commission. We used this database, the Passive Integrated Transponder Tag Information System (PSMFC 2000), to obtain information from tag recoveries from the Caspian tern and double-crested cormorant colonies on Rice Island: migration year (i.e., 1987–1998), species (i.e., chinook salmon, coho salmon *O. kisutch*, sockeye salmon *O. nerka*, or steelhead *O. mykiss*), stock (i.e., fall, winter, spring, or summer runs), tag and release location (i.e., Snake River basin, Columbia River basin above the Snake River confluence, or Columbia River basin below the Snake River confluence), rearing type (i.e., hatchery-raised or wild), and fork length. Fall chinook salmon and spring and summer chinook salmon are classified here as subyearling and yearling chinook salmon, respectively. Additionally, we assigned all PIT-tagged juvenile salmonids that were detected at Bonneville Dam in 1998 to one of the following groups: listed ESU (i.e., listed under the Endangered Species Act), unlisted ESU, or unknown listing status. These determinations were based on the ESA listing status of Columbia River basin salmonids in April 2000 (NMFS 2000a; M. Delarm, NMFS, personal communication). Listing status was unknown if the fish was captured and PIT-tagged at an in-river location (i.e., main-stem dam or fish trap) where both listed and unlisted ESUs of the same species were present.

We used passage information gathered at Bonneville Dam, the furthest downstream dam and lowest fixed PIT-tag detection point on the Columbia River (Figure 1), to examine the relative abundance of different PIT-tagged salmonid species, stocks, and rearing types and assess their availability to Caspian terns and double-crested cormorants nesting on Rice Island. Previous research has shown minimal mortality of radio-tagged yearling chinook salmon migrating downstream from Bonneville Dam (river kilometer [rkm] 234) to the head of the Columbia River estuary (rkm 75; C. Schreck et al. 1997; Schreck and Stahl 1998), despite the presence of piscivorous northern pikeminnow in that reach (Ward et al. 1995). For purposes of this study, we assumed that the negligible mortality rates of radio-tagged yearling chinook salmon also applied to PIT-tagged individuals of other species and stocks in this reach.

Descriptive statistics were used to analyze all PIT tags recovered from the bird colonies (e.g., tags from fish emigrating in 1987–1998). Additionally, PIT-tag recoveries from the 1997 and 1998 migration years were analyzed to determine the relative vulnerability of various salmonid groups (i.e., species, stocks, ESUs, and rearing types) to predation by Caspian terns and double-crested cormorants nesting on Rice Island. Differences among salmonids in their vulnerability to bird predation were based on comparisons of the relative proportion of PIT tags from various salmonid groups emigrating in those years and subsequently found at the bird colonies.

To account for differences in the availability (in-river) and detectability (at the dam) between groups of fish, only PIT-tagged juvenile salmonids detected at Bonneville Dam and subsequently recovered on the Rice Island tern or cormorant colonies were used in the analysis. Tagged juvenile salmonids that were transported by barge or truck around the lower Columbia and Snake river dams were not included in the analyses presented here. For comparisons of relative vulnerability of steelhead smolts and yearling chinook salmon of hatchery and wild origin, the sample of PIT-tagged fish detected at Bonneville Dam was limited to that period when both groups of fish being compared were passing Bonneville Dam (i.e., >50 detections·group^{-1}·week^{-1}). In all other comparisons, the sample of PIT-tagged juvenile salmonids available for birds to prey upon included all those detected at Bonneville Dam between 1 April and 1 August (the nesting season for terns and cormorants in the estuary) in 1997 and 1998.

Proportion tests (Z; Siegel 1994) and Student's t-tests (t; Snedecor and Cochran 1980) were used for statistical comparisons at $\alpha = 0.05$. Means are expressed as $x \pm$ SE.

Results

A total of 50,221 PIT tags from juvenile salmonids tagged and released in the Columbia River basin from 1987 to 1998 were detected at Caspian tern and double-crested cormorant colonies on the Rice Island. The great majority (>90%) of detected tags were detected in situ using the flat-plate PIT-tag detector (Ryan et al. in press). A total of 36,221 (72.1%) tags were recovered from the tern colony and 14,000 (27.9%) from the cormorant colony. Tags from juvenile salmonids tagged in every migration year beginning with 1987 were

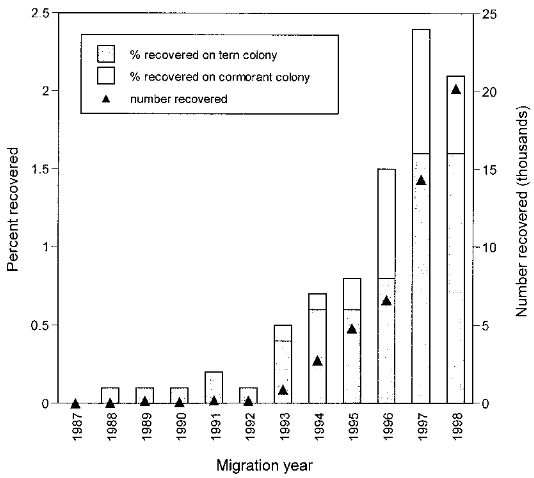

FIGURE 2.—Number of passive integrated transponder tags from juvenile salmonids that were subsequently detected at the Rice Island (lower Columbia River) Caspian tern and double-crested cormorant colonies, as well as percentages of tags recovered (based on number of tagged juveniles released) at the tern and cormorant colonies. Data are presented by migration years 1987–1998.

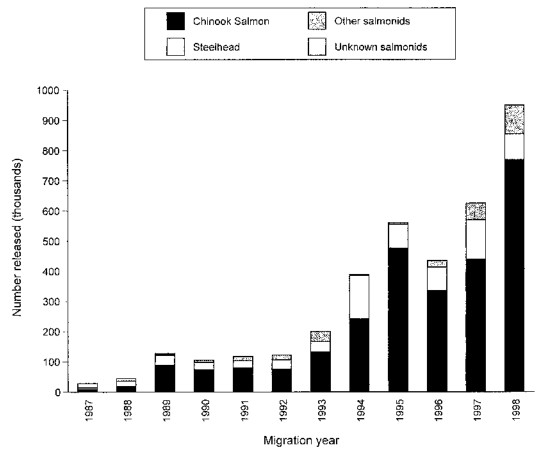

FIGURE 3.—Number of juvenile salmonids tagged with passive integrated transponders released annually in the Columbia River basin, 1987–1998. ‘‘Other salmonids’’ includes coho and sockeye salmon; ‘‘unknown salmonids’’ represents juvenile salmonids that were not identified to species.

detected on Rice Island (Figure 2), but the majority (34,521 or 68.7%) came from the 1997 and 1998 migration years. This is primarily a reflection of the dramatic increase in numbers of juvenile salmonids PIT-tagged and released in the Columbia River basin from 1987 to 1998 (Figure 3).

Of all the PIT tags recovered from both Rice Island bird colonies, most were from chinook salmon (25,474 or 50.7%), followed by steelhead (19,376 or 38.6%), coho salmon (5,107 or 10.2%), sockeye salmon (259 or 0.5%), and unidentified salmonid species (5 or $<$ 0.001%). These differences partially reflect species disparity in the number of tagged juvenile salmonids released in the Columbia River Basin (Figure 3). More tags from juvenile salmonids raised in hatcheries (38,682 or 77.0%) were recovered at the two bird colonies than from salmonids of wild (3,936 or 7.8%) or unknown (7,603 or 15.1%) origin. Again, these differences largely reflect differences in numbers of hatchery-raised versus wild juveniles tagged; of all the juvenile salmonids PIT-tagged in 1997 and 1998, 74.9% were hatchery-raised, 7.6% were wild, and 17.5% were of unknown rearing type.

A total of 67,475 PIT tags from juvenile salmonids were detected at Bonneville Dam between 1 April and 1 August in 1997 and 1998 (25,033 and 42,442, respectively). Of these, 912 (3.6%) of the 1997 tags and 1,502 (3.5%) of the 1998 tags were subsequently found at the Rice Island tern colony and for the cormorant colony, 411 (1.6%) for 1997 and 413 (1.0%) for 1998.

Tag recoveries at the Rice Island bird colonies suggest that terns and cormorants did not consume the various salmonid species, rearing types, and stocks in proportion to availability. Of the total number of PIT-tagged steelhead smolts detected at Bonneville Dam in 1997 (7,597) and 1998 (6,032), 6.5% (497) and 13.3% (803) were subsequently found on the Rice Island tern colony, proportions that were much greater than for the other salmonid species (Figure 4). Similarly, the proportions of PIT tags from steelhead smolts detected at the Rice Island cormorant colony (2.7% in 1997 and 2.3% in 1998) were also greater than for the other salmonid species (Figure 4). Combining PIT tags detected at the tern and cormorant colonies, minimums of 9.2% of the steelhead detected at Bonneville Dam in 1997 and 15.6% in 1998 were subsequently consumed by birds nesting on Rice Island (Figure 4).

A larger proportion of PIT tags detected at the tern colony were from hatchery-raised yearling (in 1998) chinook salmon than from wild yearling chinook salmon (Table 1). Hatchery-raised steelhead released in 1997 were more vulnerable to tern predation compared to their wild counterparts, but not in 1998. For cormorant predation, however, tag recoveries suggest that hatchery-raised yearling chinook salmon and steelhead were as vulnerable as their wild counterparts. Regardless of rearing type, larger proportions of PIT tags from steelhead

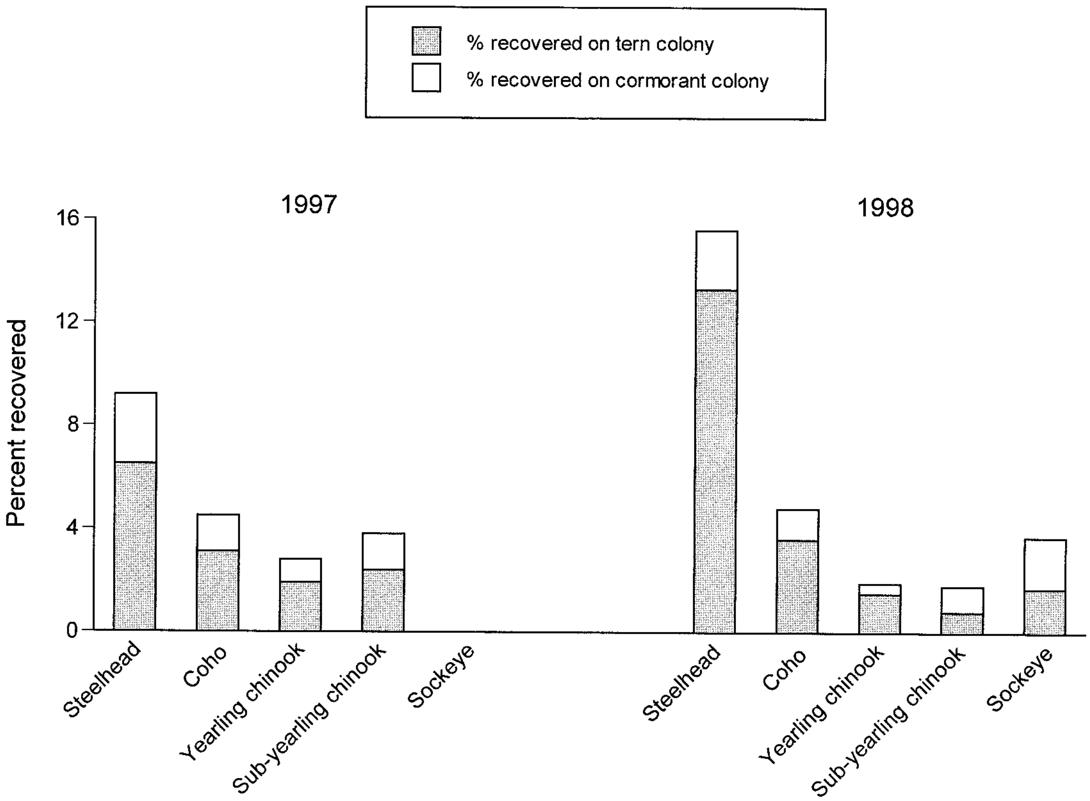

FIGURE 4.—Percent recovery of passive integrated transponder (PIT) tags at the Rice Island (Columbia River estuary) Caspian tern and double-crested cormorant colonies; tags were from juvenile salmonids that had been detected at Bonneville Dam in 1997 and 1998. The sample size of PIT-tagged sockeye salmon smolts detected at Bonneville Dam in 1997 was inadequate (<50 fish) to conduct the analysis.

TABLE 1.—Relative vulnerability of wild and hatchery-raised steelhead and yearling chinook salmon to predation by Caspian terns and double-crested cormorants nesting on Rice Island (Columbia River estuary) in 1997 and 1998. Only juvenile salmonids tagged with passive integrated transponders (PIT) that were detected at Bonneville Dam (N_d) and subsequently recovered at the Rice Island Caspian tern and double-crested cormorant colonies (N_c) were included in the analysis. The sample size of PIT-tagged wild yearling chinook salmon detected at Bonneville Dam in 1997 was inadequate to conduct the analysis.

Migration year and species	Wild			Hatchery-raised			Proportional test	
	N_d	N_c	%	N_d	N_c	%	Z	P
Caspian tern colony								
1997								
Steelhead	323	9	2.8	6,220	333	5.4	2.02	0.04
1998								
Steelhead	1,247	146	11.7	4,438	595	13.4	1.57	0.11
Yearling chinook salmon	2,124	11	0.5	17,650	286	1.6	3.95	<0.001
Double-crested cormorant colony								
1997								
Steelhead	323	12	3.7	6,220	163	2.6	−1.19	0.23
1998								
Steelhead	1,247	29	2.3	4,438	106	2.4	0.13	0.90
Yearling chinook salmon	2,124	8	0.4	17,650	72	0.4	0.21	0.83

TABLE 2.—Relative vulnerability of yearling chinook salmon and steelhead of wild and hatchery origin to predation by Caspian terns and double-crested cormorants nesting on Rice Island (Columbia River estuary) in 1997 and 1998. Only juvenile salmonids tagged with passive integrated transponders (PIT) that were detected at Bonneville Dam (N_d) and subsequently recovered at the Rice Island Caspian tern and double-crested cormorant colonies (N_c) were included in the analysis. The sample size of PIT-tagged wild yearling chinook salmon detected at Bonneville Dam in 1997 was inadequate to conduct the analysis.

Migration year and species	Yearling chinook salmon			Steelhead			Proportional test	
	N_d	N_c	%	N_d	N_c	%	Z	P
Caspian tern colony								
1997								
Hatchery-raised	3,767	90	2.4	6,940	452	6.5	9.30	<0.001
1998								
Wild	2,140	11	0.5	1,274	149	11.7	14.95	<0.001
Hatchery-raised	17,896	291	1.6	4,709	642	13.6	36.86	<0.001
Double-crested cormorant colony								
1997								
Hatchery-raised	3,767	62	1.6	6,940	188	2.7	3.48	<0.001
1998								
Wild	2,140	8	0.4	1,274	30	2.3	5.34	<0.001
Hatchery-raised	17,896	71	0.4	4,709	108	2.3	13.07	<0.001

smolts were detected at the tern and cormorant colonies than from yearling chinook salmon (Table 2).

Of those PIT-tagged juvenile salmonids detected in 1998 at Bonneville Dam, 4,423 (10.4%) were ESA-listed, 25,881 (61.0%) were unlisted, and 12,138 (28.6%) were of unknown listing status. Of all the listed salmonid species, steelhead and sockeye salmon experienced the highest predation rates by both terns and cormorants nesting on Rice Island (Table 3). In general, the proportions of PIT tags found at the bird colonies were similar for listed and unlisted ESUs of the same species, except for PIT-tagged sockeye salmon (but note small their small sample size).

Discussion

The PIT-tag data indicate that Caspian terns and double-crested cormorants nesting on Rice Island are not consuming the various species of juvenile salmonids in proportion to their availability in the estuary. Steelhead were more vulnerable to predation by both Caspian terns and double-crested cormorants than were yearling chinook salmon.

TABLE 3.—Relative vulnerability of listed (U.S. Endangered Species Act) and unlisted juvenile salmonids to predation by Caspian terns and double-crested cormorants nesting on Rice Island (Columbia River estuary) in 1998. The juvenile salmonids tagged with passive integrated transponders (PIT) were identified as listed or unlisted based on the listing status of Columbia River basin salmonid stocks in April 2000 (NMFS 2000; M. Delarm, National Marine Fisheries Service, personal communication). Only PIT-tagged juvenile salmonids detected at Bonneville Dam (N_d) and subsequently recovered at the Rice Island tern and cormorant colonies (N_c) were included in the analysis.

Species	Listed stocks			Unlisted stocks			Proportional test	
	N_d	N_c	%	N_d	N_c	%	Z	P
Caspian tern colony								
Steelhead	1,548	193	12.5	4,484	610	13.6	1.13	0.26
Chinook salmon	2,702	21	0.8	12,963	220	1.7	3.53	<0.001
Coho salmon[a]				8,251	298	3.6		
Sockeye salmon	173	6	3.5	183	0	0.0	−2.54	0.01
All salmonids	4,423	220	5.0	25,881	1,128	4.4	−1.84	0.07
Double-crested cormorant colony								
Steelhead	1,548	37	2.4	4,484	101	2.3	−0.31	0.75
Chinook salmon	2,702	18	0.7	12,963	98	0.8	0.50	0.62
Coho salmon[a]				8,251	96	1.2		
Sockeye salmon	173	5	2.9	183	2	1.1	−1.22	0.22
All salmonids	4,423	60	1.4	25,881	297	1.1	−1.19	0.23

[a] None of the PIT-tagged coho salmon released in the Columbia River basin in 1998 were listed under the U.S. Endangered Species Act.

Based on PIT tag recoveries, more than 15% of tagged steelhead smolts that reached the estuary in 1998 were consumed by piscivorous waterbirds nesting on Rice Island, whereas only 2% of yearling chinook salmon were consumed. These comparatively high rates of avian predation on steelhead smolts are of particular concern because they apply equally to both ESA-listed and unlisted steelhead stocks. Recent population viability models suggest that currently listed steelhead have the highest probability of extinction of all listed salmonid stocks from the Columbia River basin (NMFS 2000b). This is the first documentation of significant losses to predators of ESA-listed salmonid stocks from the Columbia River basin.

Differences among forage fishes in their vulnerability to predation may be attributable to differences in fish behavior, physiology, condition, and size (Campbell 1979; Matkowski 1989; Mesa et al. 1994). Juvenile salmonids from the Columbia River basin differ in their (1) timing of migration through the estuary (Dawley et al. 1986; Martinson et al. 1999), (2) horizontal and vertical distribution in the river (Mains and Smith 1964; Smith 1974; Dawley et al. 1986; Dauble et al. 1989; Ledgerwood et al. 1991; Beeman et al. 2000), (3) degree of smoltification (physiological readiness to enter saltwater; Zaugg et al. 1985; Congleton et al. 2000), (3) stress levels (Congleton et al. 2000), (4) incidence of disease and trauma (Maule et al. 1997; Martinson et al. 1999), and (5) size (Martinson et al. 1999). All these factors may affect the relative vulnerability to avian predation of different groups of salmonids migrating through the Columbia River estuary.

We found little evidence to support the hypothesis that behavioral, physiological, or condition factors are responsible for steelhead smolts being more susceptible than yearling chinook salmon to bird predation. Emigrating yearling chinook salmon and steelhead smolts have similar migration timing (Martinson et al. 1999); because we restricted our analysis to a period when both species were passing Bonneville Dam in appreciable numbers, it is unlikely that differences in migration timing can explain the observed differences in susceptibility. Several studies (Dawley et al. 1986; Dauble et al. 1989; Ledgerwood et al. 1991), including a recent study using pressure-sensitive radio transmitters (Beeman et al. 2000), suggest there are no major differences in the in-river spatial distribution of emigrating steelhead smolts and yearling chinook salmon. Both species tend to migrate midriver (Dawley et al. 1986; Dauble et al. 1989; Ledgerwood et al. 1991) and at similar depths (2.4 m for yearling chinook salmon and 2.7 m for steelhead smolts were the median migration depths through McNary Pool; Beeman et al. 2000). Additional study is need to determine if the observed similarities in depth distribution between yearling chinook salmon and steelhead at up-river locations (Beeman et al. 2000) apply to Columbia River estuary and nearshore.

Both steelhead smolts and yearling chinook salmon move rapidly through the estuary to the ocean (Dawley et al. 1986), suggesting that the two species do not differ in physiological readiness to enter saltwater once they reach the estuary. Steelhead smolts examined at main-stem dams have a higher prevalence of gas bubble trauma (GBT) signs than do yearling chinook salmon (Maule et al. 1997; Martinson et al. 1999). This could render steelhead smolts more vulnerable than yearling chinook salmon to predation near dams; however, recovery from GBT is rapid and complete once the fish is exposed to equilibrated water (Meekin and Turner 1974; Hans et al. 1999). No data exist on the relative stress levels of steelhead versus yearling chinook salmon migrating inriver. However, measurements of cortisol levels in steelhead and yearling chinook salmon that are transported past dams in barges indicate that yearling chinook exhibit a higher stress response than do steelhead (Congleton et al. 2000), a species difference in stress response that may exist for inriver migrating fish.

The available evidence suggests that the most likely source of differences between steelhead and yearling chinook in vulnerability to predation by terns and cormorants is size-dependent selection by the birds. Steelhead are significantly larger than all other emigrating salmonid stocks in the Columbia basin (Martinson et al. 1999), suggesting that terns and cormorants may be selecting larger fish. Size-dependent selection by piscivorous waterbirds has been documented in several studies (Latta and Sharkey 1966; Kirkham et al. 1985; Wood and Hand 1985; Sjöberg 1988), including studies of Caspian and Forster’s terns *Sterna forsteri* (Baltz et al. 1979), roseate terns *S. dougallii* (Shealer 1998), and double-crested cormorants (Knopf and Kennedy 1981). Size-dependent selection might be expected if larger fish are more conspicuous and easier to capture or if birds preferentially feed on fish having higher energy content, as predicted by optimal foraging theory when large and small prey availability is similar (Stephens and Krebs 1986). Terns tend to feed their chicks fish of increasing size as the chick rearing period progresses, which supports the hypothesis of selection for larger prey by breeding Caspian terns (Wiggins and Morris 1987; Smith 1993; Parkin 1998; Shealer 1998).

Although vulnerability to predation by terns and cormorants nesting on Rice Island was similar between ESA-listed and unlisted steelhead, smolts of listed sockeye salmon did appear to be more vulnerable to bird predation than their unlisted counterparts. The significantly higher vulnerability of listed sockeye salmon to bird predation may also reflect size selection by Caspian terns, because listed Snake River sockeye salmon were significantly larger than unlisted sockeye from the mid and upper Columbia River at the time they were PIT-tagged; means ± SE were 142.1 ± 2.4 mm fork length (N =109) for listed and 102.6 ± 1.3 mm (N = 183) for unlisted (t = 15.6, $P < 0.001$).

The PIT-tag recoveries also indicate that hatchery-raised yearling chinook salmon and hatchery-raised steelhead in 1997 were more vulnerable than their wild counterparts to predation by terns, a surface-feeding species. However, vulnerability of hatchery-raised and wild yearling chinook salmon or steelhead to predation by cormorants, a diving species, was similar. These results suggest that hatchery-raised juvenile salmonids are more vulnerable than wild salmonids to tern predation because of the tendency of hatchery fish to migrate or forage nearer the surface of the water where terns feed.

A large body of evidence suggests that hatchery-raised juvenile salmonids suffer greater mortality in the wild than do naturally produced smolts (Miller 1954; Wales 1954; Vincent 1960; Reisenbichler and McIntyre 1977; Raymond 1988). Lower survivorship of hatchery smolts can be partially attributed to behavioral and physical traits that render them more vulnerable to predation (Dickson and MacCrimmon 1982; Olla et al. 1990; Johnsson and Abrahams 1991; Berejikian 1995). Hatchery-raised juvenile salmonids, compared with wild fish, have elevated stress levels associated with handling (Schreck 1981; Olla and Davis 1989), lack both innate and learned predator avoidance behaviors (Olla and Davis 1989; Suboski and Templeton 1989; Berejikian 1995), and are more surface-oriented (Vincent 1960; Mason et al. 1967; Moyle 1969; Sosiak et al. 1979). All of these traits could contribute to the higher susceptibility of hatchery-raised juvenile salmonids to avian predation.

Our results suggest that the Rice Island Caspian tern colony had a greater impact on survival of juvenile salmonids than did the Rice Island double-crested cormorant colony. This difference was expected because during 1996–1998 the Rice Island Caspian tern colony numbered 14,000–16,000 breeding birds, whereas the Rice Island double-crested cormorant colony numbered only 1,200–2,400 breeding birds (Collis et al. 1999). However, the per capita impact of double-crested cormorants on smolt survival (1997 = 0.17 and 1998 = 0.26 PIT tags recovered per breeding cormorant) was about three times greater than for Caspian terns (1997 = 0.06 and 1998 = 0.09 PIT tags recovered per breeding tern), a difference largely attributable to the nearly four times greater body mass of double-crested cormorants (2,464.0 ± 17.9 g, N = 245) compared with Caspian terns (682.6 ± 5.0 g, N = 292). Also, not all double-crested cormorants that nested in the Columbia River estuary during 1996–1998 were at the Rice Island colony; most nested at the East Sand Island colony (Figure 1; Collis et al. 1999). Thus, the losses of smolts to cormorants nesting on Rice Island represent only a portion of the total losses to cormorants in the Columbia River estuary during those years.

Over the past decade, production of hatchery-raised juvenile salmonids in the Columbia River basin has been between 145 and 210 million fish annually (L. Basham, Fish Passage Center, personal communication; Figure 5). During the same

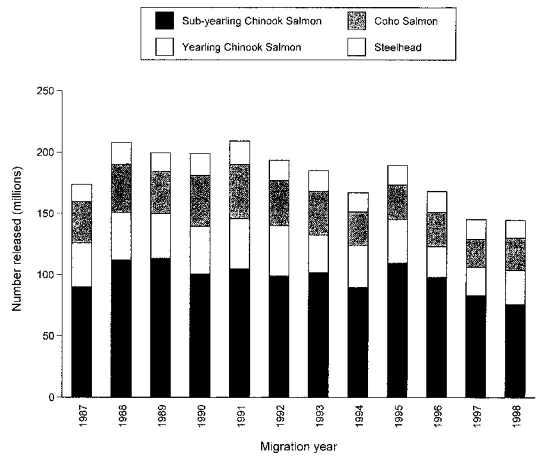

FIGURE 5.—Hatchery production of chinook salmon, coho salmon, and steelhead in the Columbia River basin, 1987–1998. The numbers of sockeye salmon, chum salmon, and sea-run cutthroat trout *O. clarki* released from Columbia River basin hatcheries are not shown because annual releases of each stock are less than 1 million fish.

period, the abundance and availability of marine forage fishes along the coasts of Oregon and Washington were in decline due to weak upwelling associated with the regime shift in the late 1970s and a series of unprecedented El Niño events. Species sensitive to coastal upwelling, such as northern anchovies *Engraulis mordax*, Pacific herring *Clupea pallasi*, Pacific sand lance *Ammodytes hexapterus*, and smelt (Osmeridae), declined substantially along the coast of the Pacific Northwest during the weak upwelling decades of the 1980s and, especially, the 1990s (Emmett and Brodeur, in press). Ainley et al. (1994) suggested that coastal areas influenced by the California Current, including Oregon and Washington, can no longer support the historical populations of natural avian predators. This evidence supports the hypothesis that the buildup of breeding colonies of piscivorous waterbirds in the Columbia River estuary was partially due to the greater relative abundance and reliability of food in the estuary compared with marine forage fishes along the coast. Other studies have suggested that the foraging and nesting distributions of piscivorous waterbirds may shift from marine habitats to estuarine or riverine habitats when ocean conditions are poor (Carter et al. 1995; Stenzel et al. 1995).

We suspect that the production and release of large numbers of hatchery-raised smolts attracted many piscivorous waterbirds to nest in the Columbia River estuary because the timing of the peak salmonid emigration generally coincides with the breeding season of colonial waterbirds. Additionally, the construction of islands in the estuary from dredged material coupled with the loss of breeding habitat and build up of predator populations at former waterbird colonies outside the estuary were contributing factors in the extraordinary increases in piscivorous waterbird populations in the Columbia River estuary during the last decade. As components of a comprehensive plan to restore salmonids throughout the Columbia River basin, management alternatives aimed at reducing or limiting the size of the Caspian tern and double-crested cormorant populations in the estuary are being considered, along with other means to reduce avian predation (e.g., modification of hatchery practices).

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