

Caspian Tern Predation on Juvenile Salmonids in the Mid-Columbia River

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Abstract.—We used a bioenergetics approach to determine the magnitude of predation by Caspian terns *Sterna caspia* on juvenile salmonids *Oncorhynchus* spp. in the mid-Columbia River during 2000 and 2001. Caspian terns nesting on Crescent Island, Washington, located below the confluence of the Snake and Columbia rivers, consumed several hundred thousand juvenile salmonids each year of the study. Tern consumption of smolts was higher in 2001 (679,000 smolts; 95% confidence interval [CI]: 533,000–825,000 smolts) than in 2000 (465,000 smolts; 95% CI: 382,000–547,000 smolts) as a result of an increase in tern breeding pairs, fledging success, and percentage of salmonids in the diet. On-colony detection rates of passive integrated transponder tags from in-river migrating smolts were also higher in 2001 (0.90–12.40%) than in 2000 (0.03–1.60%); the higher predation rates in 2001 were probably caused by extreme drought conditions that resulted in reduced spill from hydroelectric dams, lower river flows, and increased travel times for in-river migrating smolts. Tern predation rates on juvenile steelhead *O. mykiss* were higher than those on yearling Chinook salmon *O. tshawytscha* in both years. The impacts of tern predation on steelhead smolts and yearling Chinook salmon from the Snake River were slight after accounting for the high proportion of smolts collected for transportation above Crescent Island. Survival of steelhead smolts from the upper Columbia River that are not transported above Crescent Island may be significantly affected by tern predation, particularly in low-flow years. Appreciably higher predation rates on salmonids by Crescent Island terns than those observed in 2001 are unlikely considering the constraints on tern colony expansion, limited capacity for increased per capita smolt consumption by terns, and current high transportation rates for Snake River smolts.

The decline of anadromous salmonids *Oncorhynchus* spp. in the Columbia River basin over the last century and a half has prompted state, federal, and tribal resource managers to investigate a multitude of strategies for promoting salmon recovery (NRC 1996; Lichatowich 1999). More than half of the 20 evolutionarily significant units (ESUs) of salmonids in the basin are currently listed under the U.S. Endangered Species Act (ESA; NMFS 2002), and all other ESUs have experienced declines. While much of the focus of salmon resto-

ration has been on the “four Hs” (improvement of freshwater and estuarine *habitat*, increasing survival through the *hydrosystem*, regulating human *harvest*, and modifying *hatchery* rearing practices; Federal Caucus 1999), reducing the impacts of predation by marine mammals, fish, and birds on salmon survival have also been considered important restoration strategies (NMFS 1995, 2000). In the Columbia River, predation on juvenile salmonids by piscivorous fishes has been investigated in detail (Rieman et al. 1991) and has resulted in an extensive management program to control losses of smolts to predation by northern pikeminnow *Ptychocheilus oregonensis* (Beamesderfer et al. 1996; Friesen and Ward 1999).

Avian predation on juvenile salmonids in the Columbia River basin has also been investigated (Ruggerone 1986; York et al. 2000; Collis et al. 2001, 2002; Roby et al. 2003; Ryan et al. 2003)

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¹ The Unit is supported jointly by the U.S. Geological Survey, Oregon Department of Fish and Wildlife, and Oregon State University.

Received March 9, 2004; accepted September 28, 2004
Published online April 15, 2005

and managed (Steuber et al. 1993; Pochop et al. 1998, 2001; Roby et al. 2002). Evidence of juvenile salmonid consumption by ring-billed gulls *Larus delawarensis* at Wanapum Dam (Ruggerone 1986) and Priest Rapids Dam (York et al. 2000) prompted the elimination of a gull colony on Cabin Island, Washington (Pochop et al. 1998), and the initiation of a management program to reduce numbers of gulls *Larus* spp. foraging at mid-Columbia River dams (USDA 2003). In the Columbia River estuary, evidence of predation on threatened and endangered salmonid ESUs by piscivorous birds prompted federal agencies to support a comprehensive assessment of avian predation on out-migrating juvenile salmonids (NMFS 1995). Caspian terns *Sterna caspia* breeding in the Columbia River estuary were of particular concern because of their growing numbers and the large proportion of juvenile salmonids in their diet (Collis et al. 2002). During the 1998 out-migration, Caspian terns consumed an estimated 9.1–15.7 million juvenile salmonids in the Columbia River estuary (approximately 13% of the number of juvenile salmonids to reach the estuary; Roby et al. 2003) and prompted the decision to manage this tern population to reduce its impact on the survival of juvenile salmonids (USACE 1999; Roby et al. 2002).

While detailed studies of Caspian tern predation on juvenile salmonids have been conducted in the Columbia River estuary since 1997 (Collis et al. 2001, 2002; Roby et al. 2002, 2003), levels of predation by Caspian terns breeding at colonies in the mid-Columbia River have not yet been quantified. These colonies are of concern to fisheries managers because data collected in 1997 and 1998 suggested that terns nesting on islands in the mid-Columbia River, like their counterparts in the Columbia River estuary, foraged primarily on juvenile salmonids (Collis et al. 2002). This study focused on juvenile salmonid predation by Caspian terns nesting on Crescent Island (510 river kilometers [rkm] from the mouth of the Columbia River), Washington, which is where the vast majority of Caspian terns nesting on the mid-Columbia River bred during the study period. Caspian terns also nested (approximately 275 pairs) on the mid-Columbia River at Three Mile Canyon Island (rkm 414); however, terns abandoned this colony midway through the 2000 breeding season because of nest predation by mink *Mustela vison* and did not recolonize the site in 2001 (Antolos 2003). Small numbers of Caspian terns also nested on Miller Rocks (rkm 333) on the mid-Columbia River during 2001, but the size of this colony probably did

not exceed 20 pairs (D. P. Craig, Willamette University, personal communication).

We estimated salmonid consumption by Caspian terns nesting at Crescent Island using a bioenergetics approach. Bioenergetics modeling was first used by Wiens and Scott (1975) to estimate prey consumption by piscivorous birds and has since been used with a variety of avian species in both freshwater and marine systems (e.g., Furness 1978; Glahn and Brugger 1995; Madenjian and Gabrey 1995; Derby and Lovvorn 1997). The technique combines data on energy requirements of predator populations with information on energy contribution of prey types to generate estimates of prey consumption. This same approach has been used in the Columbia River estuary to develop estimates of juvenile salmonid consumption by Caspian terns (Roby et al. 2003).

We assessed stock-specific tern predation rates using salmonid tags recovered at the Crescent Island colony based on methods from a separate study conducted by NOAA Fisheries (Ryan et al. 2001a, 2001b, 2003; Glabek et al. 2003). Each year millions of juvenile salmonids in the Columbia River basin are implanted with passive integrated transponder (PIT) tags to gather information on downstream survival and behavior. Thousands of these tagged fish are consumed annually by avian predators and deposited on nesting colonies throughout the Columbia River basin (Collis et al. 2001; Ryan et al. 2001a, 2003). On-colony recoveries of PIT tags as well as detections of PIT-tagged smolts migrating in-river can be used to estimate minimum stock-specific predation rates and relative vulnerability of salmonid stocks to avian predators (Collis et al. 2001; Glabek et al. 2003; Roby et al. 2003; Ryan et al. 2003). In the Columbia River estuary, these results have been used to (1) evaluate the magnitude of Caspian tern predation on juvenile salmonids relative to other sources of smolt mortality (Roby et al. 2003), and (2) suggest potential methods for reducing the impact of terns on survival of juvenile salmonids (e.g., colony relocation: see Roby et al. 2002).

To evaluate the potential benefits of managing Crescent Island Caspian terns to reduce predation on salmonid stocks, we used an approach recently promulgated by NOAA Fisheries. Kareiva et al. (2000) used a deterministic population matrix modeling framework to assess the average annual population growth rate (λ) for threatened and endangered ESUs of salmonids from the Columbia River basin and compared the relative improvements in λ that could result from various recovery

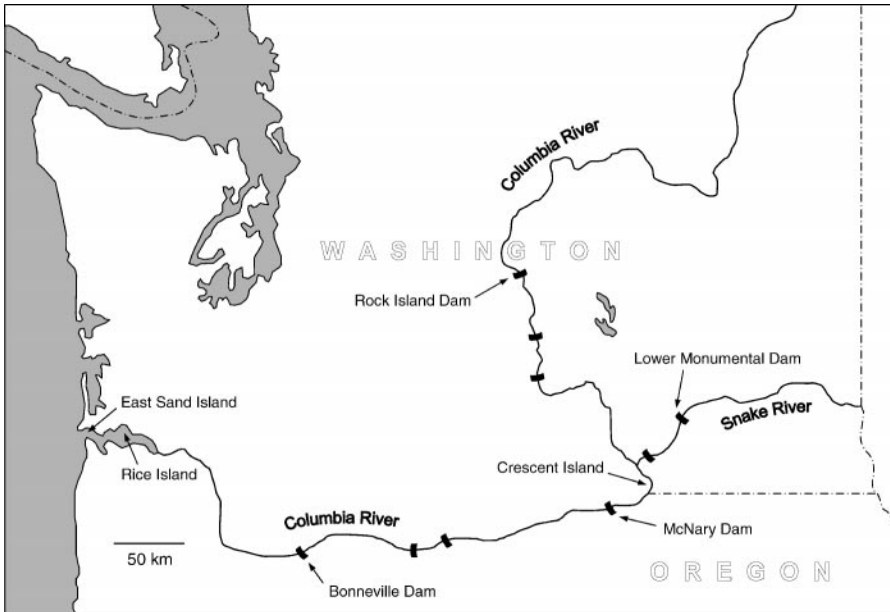


FIGURE 1.—Map of the study area showing the location of the Caspian tern colony that was the focus of this study (Crescent Island), current and recent Caspian tern colony sites in the Columbia River estuary, and hydropower dams mentioned in the text.

activities (McClure et al. 2003). Listed ESUs subject to Crescent Island tern predation appear to require at least 1–15% increases in λ to produce positive population trajectories (i.e., $\lambda > 1.00$; McClure et al. 2003). While estimating λ with precision is somewhat problematic (Kareiva et al. 2000, 2001; Dambacher et al. 2001; McClure et al. 2003), this modeling approach may be useful when comparing the potential efficacy of alternative recovery actions by evaluating the potential increases in λ ($\Delta\lambda$) for the respective actions. This approach has already been used to assess the efficacy of managing Caspian tern predation in the Columbia River estuary (Roby et al. 2003).

The overall objectives of this study were (1) to estimate juvenile salmonid consumption by Caspian terns nesting on Crescent Island, (2) to determine tern predation rates on specific salmonid stocks in the Snake and Columbia rivers to assess their relative impacts, and (3) to calculate the potential for salmonid stock recovery based on a possible management strategy of reducing predation by Crescent Island Caspian terns.

Study Area

Our research efforts focused on the Caspian tern colony on Crescent Island (46.094°N, 118.929°W), Washington, the largest colony for this species in

interior Washington and Oregon during the study period (Antolos 2003). Crescent Island is a dredge-spoil island of 3.2 ha located in the McNary Dam impoundment of the Columbia River, approximately 510 rkm upstream from the mouth of the Columbia River (Figure 1). Caspian terns colonized the island soon after its creation in 1985 (Ackerman 1994) and nest in association with a larger colony of California gulls *L. californicus* (Collis et al. 2002).

Methods

Bioenergetics Approach

The bioenergetics approach used to estimate fish consumption in this study was based largely on that used to estimate fish consumption by Caspian terns nesting in the Columbia River estuary (Roby et al. 2003). We directly measured input parameters for terns nesting on Crescent Island (i.e., number of breeding adults and their young, duration of the breeding season, diet composition, average mass and energy density of prey items), while other parameters were from previous studies (i.e., daily energy expenditure and metabolic efficiency of adult terns, energy requirements of young terns; see Roby et al. 2003). To account for seasonal and annual differences in the input parameters, calculations of consumption were performed sepa-

rately for each of eight 2-week periods in 2000 (3 April–23 July) and nine 2-week periods in 2001 (2 April–5 August), which reflected when terns were present at the Crescent Island colony during those years. The number of breeding adults, the number and energy requirements of their young (chicks), and diet composition varied across these 2-week periods; other parameters were assumed to be consistent across the entire breeding season. Output parameters of interest, such as estimates of biomass and numbers of prey consumed, were summed from all 2-week periods to get yearly totals.

Confidence intervals (CIs) for output estimates were obtained by means of a Monte Carlo calculation technique (Furness 1978) following Roby et al. (2003). We performed 1,000 calculations to estimate total consumption for each 2-week time period within each year. For each calculation, a value was randomly selected from the distribution of each input parameter (all assumed to follow a normal distribution and were described by a mean and standard error), and output values were calculated and summed to provide yearly totals. These 1,000 yearly output totals were then averaged to provide final estimates and their respective CIs were defined as the range that encompassed 95% of all output totals from the 1,000 sets of calculations.

The general formulae used to generate consumption estimates in a 2-week time period, i , for a specific prey type, k , in units of biomass, (B_{ki} ; metric tons) or numbers of fish (N_{ki}), were

$$B_{ki} = ER_{Ci} \cdot EC_{ki} \cdot \frac{1}{ED_k}, \text{ and}$$

$$N_{ki} = ER_{Ci} \cdot EC_{ki} \cdot \frac{1}{ED_k} \cdot \frac{1}{M_k},$$

where ER_{Ci} is the total energy requirements of the Crescent Island colony during time period i , ER_{ki} is the proportion of energy contributed by prey type k during time period i , and ED_k is the average energy density and M_k is average mass of prey type k (see following sections for parameter definitions and calculations).

Energy Requirements of the Colony (ER_{Ci})

Total energy requirements of the colony (ER_{Ci}) for a given 2-week time period, i , were the sum of adult energy requirements (ER_{Ai}) and chick energy requirements (ER_{Yi}), namely,

$$ER_{Ci} = ER_{Ai} + ER_{Yi}.$$

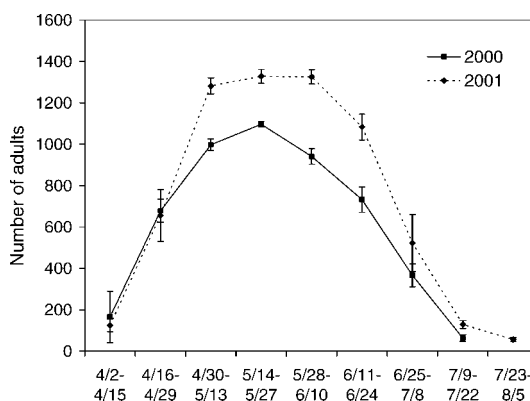


FIGURE 2.—Estimated numbers of adult Caspian terns associated with the colony at Crescent Island during each 2-week period of the breeding season in 2000 (3 April–23 July) and 2001 (2 April–5 August). Error bars represent standard errors of the means.

*Energy requirements of adults (ER_{Ai}).—*Daily energy expenditure, DEE_A (kJ/d), of Caspian terns nesting on Crescent Island was assumed to be the same as that of Caspian terns breeding at a colony in the Columbia River estuary. Using the doubly labeled water technique (Lifson and McClintock 1966; Speakman 1997), average DEE_A of free-ranging adult Caspian terns was measured as 1,040 kJ/d (SD = 209; $n = 24$) in the Columbia River estuary (Roby et al. 2003). We assumed that the metabolizable energy coefficient, MEC, of adult terns (the proportion of energy available from food that is incorporated into metabolic pathways) was 0.75 (SE = 0.025; Roby et al. 2003) based on estimates of assimilation efficiency in birds (the proportion of energy available from food that is absorbed by the digestive tract; see Roby et al. 2003 for details). While not a true measure of the metabolizable energy coefficient, assimilation efficiency has been commonly used in bioenergetic studies as a reasonable approximation (Miller and Reinecke 1984).

The number of breeding adults associated with the Crescent Island Caspian tern colony was estimated for each 2-week period of the 2000 and 2001 breeding seasons. The number of adults attending the colony (i.e., not away from the colony foraging or roosting, or otherwise absent) was counted 2–8 times/2-week period and averaged over the period. These counts were converted to estimates of the total number of adults associated with the colony for each time period, A_i (Figure 2) by multiplying (1) by the ratio of the number of nests present to the number of adults attending

during the late incubation period (when maximum colony attendance was assumed; Bullock and Gomersal 1981; Gaston and Smith 1984) and (2) by a factor of 2 (to incorporate both of the adults associated with each nest), as in the following equation:

$$A_i = 2 \cdot \left(\frac{\text{number of nests}}{\text{number adults attending}} \right)_{\text{late incubation}} \times (\text{number adults attending})_i.$$

The total energy requirements of adult Caspian terns breeding at Crescent Island during the 2-week time period, i , were thus calculated as

$$ER_{A_i} = \frac{DEE_A}{MEC} \cdot 14 \text{ d } A_i.$$

*Energy requirements of young (ER_{Y_i}).—*Estimation of chick energy requirements followed procedures described in Roby et al. (2003). The total metabolizable energy requirements of a Caspian tern chick from hatching to departure from the colony were estimated as 19.2 MJ (SE = 10.5; see Roby et al. 2003) and were partitioned into daily metabolizable energy requirements (MER_{Y_d}) by chick age, d , using a growth model based on similar tern species (see Roby et al. 2003 for details).

For simplicity in our calculations, we treated all Crescent Island chicks as hatching on the observed median hatching date and departing the colony on the observed median departure date. The number of Caspian tern chicks on the Crescent Island colony was estimated for each day, Y_d , between these dates. We assumed that chicks departed from the colony 1 week after the typical fledgling age of 37 d (d_F ; Cuthbert and Wires 1999), so in our calculations chicks were present for three of the 2-week time periods into which we partitioned the season. By observing the nest contents from a blind for a randomly selected subset of nests, the number of hatchlings, H , was determined by multiplying the number of nests counted during late incubation by an estimate of the number of chicks per nest at hatching. The number of fledglings, F , was estimated by averaging a series of counts of the number of chicks present on-colony spanning 2 weeks around the median fledgling date. We assumed an exponential decline in the number of chicks present and alive, Y_d , between these two estimates, namely,

$$Y_d = He^{rd},$$

where the rate of decline, r , was estimated as

$$r = \frac{\log_d \left(\frac{F}{H} \right)}{d_F}.$$

The energy requirements of chicks (ER_{Y_i}) for each 2-week time period, i , were then calculated as

$$ER_{Y_i} = \sum_d \frac{MER_{Y_d}}{MEC} \cdot Y_d,$$

where

$d = 1, \dots, 14$ for the first 2-week period after hatch;

$d = 15, \dots, 28$ for the second 2-week period after hatch; and

$d = 29, \dots, 42$ for the third 2-week period after hatch.

Proportion of Energy Contributed by Prey Type (EC_{k_i})

For each 2-week time period, i , the proportion of the total energy consumed by the Crescent Island Caspian tern colony that was contributed by prey type k was calculated as

$$EC_{k_i} = \frac{NP_{k_i} \cdot M_k \cdot ED_k}{\sum_{k=1}^{13} (NP_{k_i} \cdot M_k \cdot ED_k)},$$

where NP_{k_i} is the number of prey identified as type k of 13 prey types identified during time period i .

Prey identification.—Bill loads carried by adult Caspian terns (fish held crosswise in the bill) to the Crescent Island colony were observed and identified from an observation blind adjacent to the colony. Caspian terns plunge-dive for prey and transport whole fish in their bills to the colony site to feed mates and young (and allows prey items to be identified from a remote vantage point). Each prey item was visually identified to the lowest distinguishable taxon using binoculars and spotting scopes (see Collis et al. 2002). We assumed that prey items brought back to the colony by breeding adults represented the overall diet of Caspian terns nesting at this site, an assumption supported by observations in the Columbia River estuary that prey composition in gut contents did not differ significantly from prey composition of bill loads (Collis et al. 2002). The number of identified bill loads per 2-week time period was usually about 250 fish, but ranged between 11 and 391 fish.

In 2001 we made a concerted effort to identify prey to species, where possible, and to identify

salmonids as either steelhead *O. mykiss* or "other salmonids" (i.e., Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, or sockeye salmon *O. nerka*) so that differences in prey species' average mass, energy density, or both could be accounted for in our analysis. Steelhead were distinguished from other salmonids by the shape of the anal and caudal fins, coloration and speckling patterns, shape of parr marks, or a combination of these characteristics.

We conducted trials before and after the 2001 breeding season to assess our accuracy in distinguishing steelhead from other salmonid species by using samples of juvenile salmonids collected in the Columbia River estuary. In two double-blind trials, 25 randomly selected juvenile salmonid samples were presented to the primary fish identification technician for the 2001 season at distances of 10–40 m; this approximated the range of distances at which Caspian tern bill loads would be identified from an observation blind at the Crescent Island colony. Fish were presented for a brief interval (<1 min) and identified by the technician as either steelhead or other salmonid with binoculars. Each fish was presented five times in a randomly selected order of 125 presentations, and accuracy was determined as the proportion of presentations a fish was accurately identified. The average of these percentages, or the overall accuracy of the trials, was 91% in the preseason trial and 95% in the postseason trial. We were not able to distinguish the other salmonid, so these species were grouped in our analysis.

In 2000, when prey items were only identified to the family level, the species composition of prey was assumed to be the same as in 2001 during the corresponding time period. When we were only able to identify prey items as nonsalmonids (less prevalent in 2001 because of increased familiarity with prey types), we used a weighted average to estimate energy density and average mass of this category based on the relative proportions of all identified nonsalmonid prey types in the corresponding 2-week time period.

Average mass of prey items (M_k).—We calculated the average mass of prey by estimating the lengths of fish delivered to the tern colony by breeding adults and incorporating these data into allometric relationships of fresh mass (g) versus length (cm) for each prey type. Length estimation was based on relating the length of the fish to the average length of a Caspian tern bill from the gape to the tip (8.5 cm). Because salmonids comprised a large proportion of tern diets, the accuracy of

our length estimation for salmonids was also assessed by conducting trials with samples of juvenile salmonids collected in the Columbia River estuary. Again, two double-blind trials were performed, where 25 randomly selected juvenile salmonid samples were presented five times each in a randomly selected order (at distances of 10–40 m for <1 min). Length was estimated by the primary fish identification technician in a similar manner to that conducted in the field (i.e., by estimating in relation to a known length; in this case the index finger of the presenter, which also measured 8.5 cm). The difference between the estimated and actual length was then divided by the actual length to obtain the percent error for each presentation. This percentage was averaged for each fish and then for all five presentations. Overall, salmonid lengths were overestimated by 1% in the preseason trial and underestimated by an average of 4% in the postseason trial.

Allometric equations of length and mass (length–mass regressions) were developed for prey types observed in the diet of Crescent Island Caspian terns by collecting fish samples in the mid-Columbia River. The majority of samples were obtained during 30 May–13 June 2001 between rkm 439 and rkm 536 of the Columbia River in conjunction with a study conducted by the Oregon Department of Fish and Wildlife. Fish were captured at night with an electrofishing boat and placed in a holding tank on the vessel until processed. Samples were measured for total length (± 1 mm) and weighed using a spring-loaded Pesola scale (Baar, Switzerland; ± 0.5 g for fish <60 g and ± 1 g for larger fish) and either released or collected for analysis of energy content. Additional samples were collected by hook and line at known tern foraging sites near Crescent Island. Estimated lengths of prey items from tern bill load observations were entered into the appropriate equations, and the estimated mass of each fish observed was calculated. These masses were then averaged by prey type.

Juvenile salmonids were not collected as part of this study because of the potential impacts to threatened and endangered stocks. Instead, we used the lengths and masses of juvenile salmonid samples obtained by lethally collecting adult Caspian terns that had fish in their bills in the Columbia River estuary during 2000 and 2001 (D. D. Roby, unpublished data) to develop length–mass regressions for steelhead and other salmonid species. Only intact fish collected as dropped bill loads from adult terns were used in this analysis.

The regression for other salmonid species was based on pooled samples of coho and Chinook salmon (slopes of regression lines after log transformation did not differ significantly; $P = 0.39$). Sockeye salmon were not included in this regression because this species did not appear in bill loads collected from Caspian terns in the estuary in 2000 or 2001, presumably because they do not comprise a substantial portion of tern diets (Collis et al. 2001). In cases where we were not able to collect adequate samples of nonsalmonid prey types to develop accurate length–mass regressions (i.e., peamouths *Mylocheilus caurinus* and lampreys [family Petromyzontidae]), we incorporated length and mass data from samples collected in the Columbia River estuary.

Energy density of prey (ED_k).—We analyzed whole fish (collected by the methods described above) in the laboratory to determine mean energy density (KJ/g wet mass) of each prey type. Energy density of individual fish was estimated based on biochemical composition as determined by proximate composition analysis (see Anthony et al. 2000 for detailed methods) and then averaged by prey type. Fish were weighed fresh on an electronic balance (± 0.01 g) after collection and kept frozen until proximate analysis could be conducted. To determine water content of fish, the fish were partially thawed in the laboratory, weighed again to verify accuracy of initial wet mass, then dried in a convection oven at 60°C to constant mass (± 0.001 g). A Soxhlet apparatus was used to extract lipids from dried samples using a hexane:isopropyl alcohol (7:2 on a volume basis) solvent system so that lipid content of dried samples could be determined. Lean, dry samples were placed in a muffle furnace and ashed at 600°C for 12 h to determine ash-free lean dry mass (94% protein; Montevecchi et al. 1984). Published energy equivalents of lipid (39.4 kJ/g) and protein (17.8 kJ/g for uricotelic vertebrates; Schmidt-Nielsen 1997) were then used to determine energy density of fish.

Because juvenile salmonids were not collected near Crescent Island, we used energy densities derived from salmonids collected in the Columbia River estuary (Roby et al. 2003). Energy densities of coho and Chinook salmon were averaged together to determine mean energy density of other salmonid species. In addition, we included energy density data from fish collected in the Columbia River estuary (Roby et al. 2003) to determine mean energy densities for peamouths and lampreys because we were not able to collect sufficient samples of these prey types near Crescent Island.

Tern Predation Rates

We used on-colony detections of PIT tags from juvenile salmonids and estimates of in-river availability of PIT-tagged smolts to estimate tern predation rates on steelhead and yearling Chinook salmon. The methods for recovering PIT tags on Crescent Island are presented in Ryan et al. (2001a and 2003) and are only briefly summarized here. NOAA Fisheries systematically scanned the Crescent Island tern nesting site for PIT tags using a flat-plate detector mounted to a four-wheel-drive vehicle, and a hand-held, pole-mounted transceiver to detect tags in areas inaccessible to the flat-plate detector. Detection efforts were conducted in both 2000 and 2001, approximately 60 d after the completion of tern nesting activities. The entire colony site was passed over three times in three different orientations, until close to 500 unique tags were detected on the last pass. Tag recoveries at Crescent Island are minimum estimates because (1) an unknown proportion of consumed tags are deposited off-colony, (2) wind and water erosion remove an unknown number of tags from the colony, and (3) detection efficiency, though not precisely known, is probably less than 100% (Ryan et al. 2003). NOAA Fisheries PIT tag recovery data, along with tagging and in-river detection information, reside in a centralized database maintained by the Pacific States Marine Fisheries Commission (PSMFC 2003) and are available to the public.

We assessed on-colony detection rates of PIT tags on the Crescent Island tern colony separately for Snake River and upper Columbia River salmonid stocks in 2000 and 2001. For Snake River stocks, PIT tags used in analyses were from steelhead and yearling Chinook salmon smolts that had been tagged and released into the river between 1 March and 3 July and interrogated passing Lower Monumental Dam (lowest PIT tag interrogation point on the Snake River). Similarly, for upper Columbia River stocks, PIT tags were from smolts that had been interrogated or tagged at Rock Island Dam (lowest PIT tag interrogation point on the Columbia River above Crescent Island). On-colony detection rates were calculated by simply dividing the total number of interrogated PIT-tagged fish (by location and species) by the total number of those tags subsequently detected on the Crescent Island tern colony. These predation rates represent minimum estimates because (1) they do not account for mortality of PIT-tagged fish from Lower Monumental Dam or Rock Island Dam to the

vicinity of Crescent Island, and (2) an unknown number of deposited tags are not detected by NOAA Fisheries.

To more accurately assess the impact of Crescent Island terns on salmonid stocks from the Snake River, tern predation rates were corrected to account for the proportion of those stocks that were collected for transportation and bypassed the federal hydrosystem in barges or trucks (NMFS 2000). These transported fish were not available as prey for Crescent Island terns. This correction was not necessary for upper Columbia River stocks because there was no smolt transportation program at Columbia River dams above Crescent Island (i.e., all upper Columbia River smolts must migrate in-river past Crescent Island).

Impact of Tern Predation on Salmonid Populations

We estimated potential improvements in λ from tern management for four ESA-listed ESUs of salmonids whose entire geographic spawning and presmolt rearing ranges exist upriver from Crescent Island. After Kareiva et al. (2000) and McClure et al. (2003), we used the analytical framework of an age-structured population matrix model to calculate the percentage increase in λ for each salmonid ESU attributable to an increase in survival at a particular life history stage by using the following equation:

$$\Delta\lambda = \left[\left(\frac{S_f}{S_i} \right)^{1/G} - 1 \right] \times 100\%,$$

where S_i is the initial survival rate before recovery action, S_f is the survival rate after the recovery action, and G is the average generation time (McClure et al. 2003). Generation times vary among and within species (across ESUs); for the five Columbia River steelhead ESUs, values range from 4.27 to 4.85 (McClure et al. 2003). This change in λ , assuming it is density independent and independent of changes in survival elsewhere in the life history cycle of the organism, can then be used to compare the efficacy of various potential recovery actions.

Within the population modeling framework, we considered passage through the reach near Crescent Island as a distinct life history stage with initial survival rates, S_i , equal to $(1 - [\text{tern predation rate}])$ and the final survival rates, S_f , equal to 1 by using average generational times, G , for each ESU from NOAA (2000). This allowed calculation of the change in λ that would be expected

for each ESU in the event that all predation by Crescent Island Caspian terns was eliminated and all mortality as a result of tern predation was additive (no other mortality factors will compensate for reductions in tern predation). For each ESU, tern predation rates were based on on-colony detections of PIT tags, including both smolts that were members of the ESU and nonlisted hatchery smolts from the same geographic area of the same species and run type. Previous comparisons of susceptibility to tern predation for listed versus nonlisted smolts of the same species have not indicated significant differences (Collis et al. 2001; Ryan et al. 2003). Estimated tern predation rates for each ESU were based on transportation-adjusted PIT tag recoveries on the Crescent Island tern colony, and predation rates from 2000 and 2001 were averaged with equal weighting.

Results

Energy Requirements of the Colony

The average number of Caspian tern nests counted during late incubation at Crescent Island increased 21% from 548 (SD = 7.41; $n = 4$) in 2000 to 664 (SD = 20.60; $n = 3$) in 2001. Overall attendance patterns were similar in both years (Figure 2). In 2000 the average number of chicks per nest at hatching was 1.5 (SD = 0.82; $n = 166$) and the estimated number of fledglings in the colony was 356 (SD = 124; $n = 7$). In 2001 the number of chicks per nest at hatching averaged 1.9 (SD = 0.74; $n = 181$) and the estimated number of fledglings was 637 (SD = 127; $n = 5$). Average fledgling success increased 48% from 0.65 fledglings/nest in 2000 to 0.96 fledglings/nest in 2001. Estimated total energy requirements of the Caspian tern colony at Crescent Island was 112×10^3 MJ in 2000 and 150×10^3 MJ in 2001 (Table 1). Energy requirements of the chick population constituted 12.4% of total colony requirements in 2000 and 16.2% in 2001.

Energy Contributions of Prey

From bill load observations, salmonids were the predominant prey type in the diet of Caspian terns nesting at Crescent Island (mean \pm SE, $64 \pm 1.1\%$ in 2000 and $69 \pm 1.0\%$ in 2001). Of the salmonid portion of the diet, other salmonids (i.e., Chinook, coho, and sockeye salmon combined) made up a greater proportion of the diet by number and energy contributed than did steelhead alone (Table 1; Figure 3).

Mean energy densities of prey types determined from proximate composition analysis ranged from

TABLE 1.—Total energy requirements of the Caspian tern colony at Crescent Island in 2000 and 2001 and the percent energy contributed by prey type, as determined from a bioenergetics model. Energy requirement data are means, with SDs in parentheses.

Energy requirement and contribution of prey	2000	2001
Energy requirements (10 ³ MJ)		
Total	111.7 (9.86)	150.3 (15.70)
Adults	97.8 (6.28)	125.9 (8.80)
Young	13.9 (7.45)	24.4 (12.30)
Energy contribution of prey (%)		
All salmonids	71.2	76.0
Steelhead	29.1	29.9
Other salmonids	42.1	46.1
Bass <i>Micropterus</i> spp.	4.4	4.5
Bluegill <i>Lepomis macrochirus</i>	4.3	3.8
Chiselmouth <i>Acrocheilus alutaceus</i>	0.8	0.9
Northern pikeminnow	0.1	0.1
Peamouth	2.3	4.5
Catfish (Ictaluridae)	2.0	2.5
Lamprey (Petromyzontidae)	0.1	0.1
Sculpin (Cottidae)	0.3	1.3
Sucker (Catostomidae)	0.6	2.0
Yellow perch <i>Perca flavescens</i>	1.1	1.2
Unidentified nonsalmonids	12.8	3.1

3.40 to 8.75 kJ/g wet mass (Table 2). Steelhead had the greatest average mass per fish (61.1 g) but only the second highest energy content per fish (281.7 kJ). Catfish had the greatest average energy content per fish in 2001 (352.6 kJ) because of a high average mass (40.3 g) and the highest mean energy density (8.75 kJ/g) of all prey types analyzed in this study. In 2000 the average mass of catfish brought back to the Crescent Island tern colony was lower (23.9 g), so average energy content of individual catfish in that year (209.1 kJ) was not as high as that of steelhead.

Salmonids contributed the greatest percentage of the total amount of energy required by the Crescent Island colony (71.2% in 2000; 76.0% in 2001), while steelhead contributed a lower proportion than other salmonid species combined (roughly 30% less in both years; Table 1). In 2000, unidentified nonsalmonids contributed the next highest fraction (12.8%), followed by bass (4.4%) and bluegills (4.3%). In 2001, greater familiarity with prey types left fewer nonsalmonid prey items unidentified, and peamouths (4.5%) contributed the next highest percentage of total energy requirements for Crescent Island terns. Other prey types contributing at least 2% of energy requirements in 2001 were bass, bluegills, catfish, suckers, and unidentified nonsalmonids (Table 1).

Consumption Estimates

We estimated that Caspian terns breeding at Crescent Island consumed 25.0 metric tons (95%

CI, 20.3–29.6 metric tons) of fish biomass in 2000 and 33.4 metric tons (95% CI, 26.2–40.6 metric tons) in 2001 (Table 3). Juvenile salmonids comprised the majority of prey biomass consumed, and we estimated that tern consumption of juvenile salmonids was 17.4 metric tons (95% CI, 14.2–20.5 metric tons) in 2000 and 25.1 metric tons (95% CI, 19.6–30.6 metric tons) in 2001. Other prey types for which Crescent Island Caspian terns consumed more than 1.0 metric ton of fish biomass per year included bass, bluegills, peamouths, suckers, and unidentified nonsalmonids (Table 3).

We estimated that the total number of fish consumed by terns nesting at Crescent Island was 679,000 (95% CI, 552,000–806,000) in 2000 and 912,000 (95% CI, 718,000–1,104,000) in 2001 (Table 3). Crescent Island terns consumed an estimated 465,000 juvenile salmonids (95% CI, 382,000–547,000) during the 2000 breeding season and an estimated 679,000 juvenile salmonids (95% CI, 533,000–825,000) during the 2001 breeding season, approximately 46% higher than in 2000. Steelhead comprised 24.7% of total salmonids consumed by Caspian terns at Crescent Island in 2000 and 23.4% in 2001 (Table 3).

Discussion

Prey Consumption

Caspian terns nesting at Crescent Island consumed approximately 465,000 juvenile salmonids in 2000 and approximately 679,000 juvenile sal-

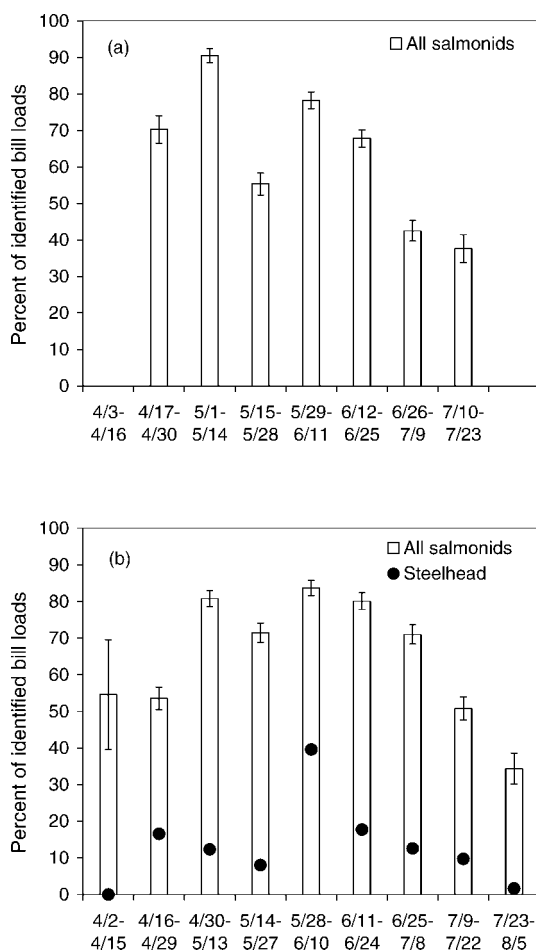


FIGURE 3.—Percent salmonids in the diet of Caspian terns based on bill load observations during each 2-week period of the breeding season at Crescent Island in (a) 2000 and (b) 2001. Error bars represent standard errors of the proportions.

monids in 2001. The 46% increase in the numbers of juvenile salmonids consumed in 2001 compared with 2000 resulted from an increase in the numbers of tern breeding pairs and chicks and a higher prevalence of salmonids in tern diets. Although smolt consumption at the Crescent Island Caspian tern colony increased from 2000 to 2001, the longer-term impacts on smolt survival of this subpopulation of Caspian terns (includes colonies at Crescent and Three Mile Canyon islands) have probably remained stable since 1996. Caspian terns, like many other tern species, have adapted to changes in the availability of suitable nesting habitat by readily shifting their nesting activities from one site to another (Cuthbert 1988; Cuthbert and Wires 1999; Wires and Cuthbert 2000; Collis et

al. 2002; Roby et al. 2002). The increase in size of the Crescent Island tern colony from 2000 to 2001 was probably caused by the failure of the Three Mile Canyon Island tern colony in 2000 and the immigration of some of those birds to the Crescent Island colony in 2001. Suitable nesting habitat for Caspian terns on Crescent Island is limited, however, and the size of the colony in 2002 was intermediate between the size in 2000 and 2001 (CBR 2003). Over the past five years, there has been no significant change in the total number of Caspian terns nesting on the mid-Columbia River (Antolos 2003) or the proportion of salmonids in the diet (Collis et al. 2002; Antolos 2003). Without sustained increases in one or both of these factors, substantial and long-term increases in smolt consumption by terns nesting on the mid-Columbia River are unlikely.

One source of uncertainty in our estimates of salmonid consumption by terns at Crescent Island is the effect of kleptoparasitism by gulls; California gulls nesting at Crescent Island frequently pirated Caspian tern bill loads (Antolos 2003). To compensate for this kleptoparasitism, Caspian terns nesting at Crescent Island may take more juvenile salmonids than are necessary to meet their own energetic requirements and those of their young. Our estimates of salmonid consumption are based on tern energy requirements and, thus, do not compensate for prey caught by terns that are subsequently pirated by gulls. This suggests that our estimates of smolt losses to terns based on the bioenergetics calculations may have been low.

Caspian terns nesting at Crescent Island consumed up to 25-fold fewer salmonids during the study period than did Caspian terns nesting on Rice Island in the Columbia River estuary during 1997 and 1998; Caspian terns consumed an estimated 8.1 million salmon smolts in 1997 and 12.4 million salmon smolts in 1998 (Roby et al. 2003). The large disparity in smolt consumption between the two tern colonies was primarily a result of the considerable difference in size of the colonies (there were between 7,000 and 9,000 Caspian tern breeding pairs on Rice Island in 1997 and 1998; Roby et al. 2003). Smolt consumption and predation rate estimates for the Rice Island tern colony (Collis et al. 2001; Roby et al. 2003; Ryan et al. 2003) led to a relocation of the colony 26 km downriver to a historic breeding site on East Sand Island, where terns were expected to consume fewer salmonids (USACE 1999; Roby et al. 2002). Management efforts to relocate the colony and reduce smolt consumption were successful; Caspian

TABLE 2.—Length–mass regressions (average mass [M ; g] = a ·total length [L ; cm] ^{b}), energy density, and average energy content (mass × energy density) of prey items found in the diet of Caspian terns breeding at Crescent Island in 2000 and 2001.

Prey item	<i>L</i> – <i>M</i> regression			2001 prey mass (g)			Energy density (kJ/g)			Energy content (kJ)
	Equation	<i>r</i> ²	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	
Steelhead	0.0052· <i>L</i> ^{3.06}	0.64	39	61.1	18.1	233	4.61	0.86	12	281.7
Other salmonids	0.0248· <i>L</i> ^{2.55}	0.92	153	29.6	13.5	796	4.51	0.91	24	133.5
Bass	0.0109· <i>L</i> ^{3.05}	0.99	88	41.1	19.9	137	3.40	0.20	11	139.7
Bluegill	0.0046· <i>L</i> ^{3.60}	0.96	22	48.2	22.4	70	3.56	0.41	9	171.6
Chiselmouth	0.0094· <i>L</i> ^{2.98}	0.96	75	45.4	20.1	12	3.96	0.53	11	179.8
Northern pikeminnow	0.0043· <i>L</i> ^{3.22}	0.99	11	25.0	10.6	4	4.65	0.48	5	116.3
Peamouth	0.0082· <i>L</i> ^{2.99}	0.98	15	21.8	13.4	116	5.72	1.37	13	124.7
Catfish	0.0207· <i>L</i> ^{2.74}	0.97	10	40.3 ^a	13.4	25	8.75	0.89	4	352.6
Lamprey	0.0025· <i>L</i> ^{2.72}	0.77	11	5.5 ^a	3.3	14	5.86	0.59	7	31.9
Sculpin	0.0065· <i>L</i> ^{3.27}	0.98	47	47.4 ^a	14.5	24	3.74	0.55	12	177.3
Sucker	0.0097· <i>L</i> ^{3.02}	0.98	91	37.6 ^a	19.9	38	4.35	0.59	12	163.6
Yellow perch	0.0078· <i>L</i> ^{3.11}	0.98	46	32.5 ^a	15.6	21	4.38	0.37	12	142.4

^a Prey mass was calculated separately in 2000. In all other cases, 2001 prey mass was used for both years because species distinctions were not made in 2000 (length estimates by family did not differ statistically in 2000 and 2001).

terns switched to the East Sand Island colony site over a 3-year period and consumed about 50% fewer juvenile salmonids in 2001 (approximately 6 million; D. E. Lyons, D. D. Roby, K. Collis, unpublished data) than did terns at the former colony on Rice Island in 1998. Nevertheless, consumption of juvenile salmonids by terns nesting on East Sand Island in 2001 was still about an order of magnitude greater than that of terns nesting on Crescent Island.

Tern Predation Rates on Salmonid Populations

Analysis of PIT tag data from the Crescent Island tern colony in 2000 and 2001 revealed that, despite the much lower numbers of smolts con-

sumed by the Crescent Island tern colony compared with tern colonies in the Columbia River estuary, predation rates on some PIT-tagged stocks were surprisingly high (Table 4). For example, the predation rate by Crescent Island terns on in-river migrant Snake River steelhead was 12.4% in 2001, which was similar to tern predation rates on PIT-tagged steelhead in the Columbia River estuary (10–15%; Collis et al. 2001; Ryan et al. 2003).

The much higher predation rates by Crescent Island terns on in-river migrating steelhead compared with yearling Chinook salmon (Table 4) were consistent with results from the Columbia River estuary (Collis et al. 2001; Ryan et al. 2003). The greater vulnerability of steelhead, which have

TABLE 3.—Estimates of prey consumption by Caspian terns nesting at Crescent Island in 2000 and 2001 in terms of biomass and total numbers.

Prey item	2000			2001		
	Biomass (Mean metric tons)	Number (10 ³)		Biomass (Mean metric tons)	Number (10 ³)	
		Mean	95% CI		Mean	95% CI
All prey	25.0	679.0	552.0–806.0	33.4	912.0	718.0–1,104.0
All Salmonids	17.4	465.0	382.0–547.0	25.1	679.0	533.0–825.0
Steelhead	7.0	115.0	91.9–138.0	9.7	159.0	121.0–197.0
Other salmonids	10.3	350.0	289.0–410.0	15.4	520.0	410.0–629.0
Bass	1.4	34.6	25.2–44.0	2.0	47.8	35.7–59.9
Bluegill	1.4	28.2	23.1–33.3	1.6	33.7	27.0–40.3
Chiselmouth	0.2	4.7	3.1–6.4	0.3	7.6	4.9–10.3
Northern pikeminnow	<0.1	1.0	0.6–1.4	<0.1	1.6	0.9–2.3
Peamouth	0.4	20.6	15.5–25.7	1.2	54.5	43.8–65.2
Catfish	0.2	10.3	8.6–12.0	0.4	10.7	7.6–13.8
Lamprey	<0.1	4.3	3.2–5.4	<0.1	4.9	3.7–6.0
Sculpin	0.1	2.3	1.7–2.9	0.5	10.8	8.3–13.4
Sucker	1.6	3.9	2.9–4.9	0.7	18.6	13.9–23.3
Yellow perch	0.3	10.4	8.5–12.2	0.4	12.7	10.6–14.8
Unidentified nonsalmonids	3.3	94.0	74.3–114.0	1.0	29.5	24.3–34.7

TABLE 4.—On-colony detection rates of passive integrated transponder (PIT) tags on the Crescent Island Caspian tern colony in 2000 and 2001 (i.e., estimated tern predation rates on juvenile salmonids). Tags were from juvenile yearling Chinook salmon and steelhead that had been released in the Snake River and subsequently interrogated while passing the juvenile bypass facility at Lower Monumental Dam or that had been released in the upper Columbia River and subsequently interrogated or tagged at the juvenile collection facility at Rock Island Dam during 2000 and 2001. Predation rates on Snake River smolts were adjusted by accounting for the proportion of fish that were transported in fish barges or trucks prior to reaching Crescent Island (i.e., fish that were not available to Crescent Island terns). Out-migrating smolts from the upper Columbia River were not transported. Sample sizes used to derive predation rates ranged between 3,900 and 59,000 PIT-tagged fish; PIT tag detections on the Crescent Island tern colony were conducted by NOAA Fisheries as part of a separate study.

Species	Snake River stocks				Upper Columbia River stocks	
	2000		2001		2000	2001
	Predation rate	Adjusted rate ^a	Predation rate	Adjusted rate ^b	Predation rate	Predation rate
Steelhead	1.6%	0.30%	12.4%	0.17%	1.40%	6.7%
Yearling Chinook Salmon	0.3%	0.09%	3.9%	0.08%	0.03%	0.9%
Both species	1.1%	0.20%	5.5%	0.09%	0.20%	1.4%

^a Calculated by multiplying the PIT tag on-colony detection rate by the proportion of the run that migrated in-river (i.e., 29% for yearling Chinook salmon and 19% for steelhead; FPC 2001).

^b Calculated by multiplying the PIT tag on-colony detection rate by the proportion of the run that migrated in-river (i.e., 2% for yearling Chinook salmon and 1.4% for steelhead; FPC 2002).

the greatest smolt mass and energy content of the salmonid species (Table 2), may reflect size-dependent selection by Caspian terns (Collis et al. 2001; Ryan et al. 2003). Steelhead may also have a greater tendency to reside near the water surface than do other salmonid species (R. Emmett, NOAA Fisheries, personal communication), making them more vulnerable to predation by plunge-diving terns that feed mostly in the top meter of the water column.

Large proportions of juvenile salmonids from the Snake River basin are transported each year by barge and truck and released below Bonneville Dam to improve smolt survival through the hydrosystem (NMFS 2000). The estimated proportion of steelhead and yearling Chinook salmon smolts from the Snake River that were transported was 81% and 71%, respectively, in 2000 (FPC 2001) and 99% and 98%, respectively, in 2001 (FPC 2002). Consequently, the overall impact of Crescent Island terns on Snake River steelhead (based on predation rates adjusted for the proportion of smolts transported) was far less than for steelhead from the upper Columbia River (Table 4). This difference was especially pronounced during 2001, when all but 1.4% of steelhead smolts from the Snake River basin were transported and, hence, unavailable to terns nesting at Crescent Island. After adjusting for the proportion of out-migrants that were transported past Crescent Island in 2001, the predation rate by Crescent Island terns on Snake River steelhead was only 0.17% (Table

4). In comparison, predation rates by Crescent Island terns on upper Columbia River steelhead were at least 6.7% (Table 4).

Extreme drought conditions in 2001 corresponded with much higher tern predation rates on in-river migrants in 2001 compared with 2000 (Table 4); these conditions were associated with reduced spill from hydroelectric dams, lower river flows, and higher water clarity in 2001 (FPC 2002). Travel times for in-river migrating smolts were also greater in 2001 compared with the previous 2–3 years (60% higher for yearling Chinook salmon and 150% higher for steelhead smolts in the mid-Columbia River; 50% higher for yearling Chinook salmon and 60% higher for steelhead smolts in the Snake River; FPC 2002). Thus, river conditions in 2001 likely resulted in increased exposure and, hence, greater vulnerability of in-river migrants to predation by Crescent Island terns. Our results suggest that there is a strong link between the impact of predation by Crescent Island terns on smolt survival and the operation of the Columbia River basin hydrosystem. Specifically, enhanced spill and transportation used to assist juvenile salmonids in their out-migration were associated with lower tern predation rates on salmonid stocks.

Effects of Tern Predation on Salmonid Populations

Demographic analysis using an age-structured matrix population modeling framework (Kareiva et al. 2000; NMFS 2000; McClure et al. 2003;

Roby et al. 2003) suggested that potential improvements in λ from management to completely eliminate predation by Crescent Island terns were quite small for three of the four salmonid ESUs investigated: 0.02% for the Snake River spring–summer Chinook salmon ESU, 0.05% for the Snake River steelhead ESU, and 0.01% for the upper Columbia River spring Chinook salmon ESU. For the upper Columbia River steelhead ESU, however, the estimated potential improvement in λ was 1.10%. The much higher potential benefit from tern management for upper Columbia River steelhead compared with the other three salmonid ESUs is probably because of the higher susceptibility of steelhead smolts to tern predation compared with yearling Chinook salmon smolts and the lack of smolt transportation for upper Columbia River stocks compared with Snake River stocks.

Because the estimated predation rates were based on on-colony detections of PIT tags, they are minimal estimates, whereas the estimated improvements in smolt survival from elimination of tern predation were based on the assumption of completely additive mortality and are, therefore, maximal estimates. Consequently, the calculated $\Delta\lambda$ represents a reasonable estimate of the potential benefit from hypothetical management to eliminate predation by the Crescent Island tern colony, given the limitations of available data.

Several other potential recovery actions have been considered within this modeling framework (NMFS 2000; McClure et al. 2003; Roby et al. 2003); the possible increases in λ from these actions provide context for the potential increase in λ from management of the Crescent Island tern colony. The northern pikeminnow management program, which has resulted in a reduction in predation of about 3.8 million juvenile salmonids/year (Friesen and Ward 1999), might produce increases of 0.4–0.7% in λ if this mortality is assumed to be completely additive (Roby et al. 2003). For ESUs above Crescent Island, complete elimination of adult salmonid harvest by humans could increase λ by 4.0–8.0% for steelhead and by 1.0–2.0% for yearling Chinook salmon, when compared with average harvest levels during 1980–1999 (McClure et al. 2003). Altered operation of the current hydropower system on the Columbia and Snake rivers (cumulative effect of over 100 specific actions) could potentially increase λ by 1.0–5.0% (McClure et al. 2003) for the four ESUs considered here.

Some benefit to the upper Columbia River steel-

head ESU might result from Crescent Island tern management to reduce predation. The estimated benefit from tern management would, however, be less than other proposed management activities (McClure et al. 2003; Roby et al. 2003) and would probably be insufficient to reverse the population decline if other recovery actions having greater impact are not also implemented. Current estimates of λ for upper Columbia River steelhead range from 0.69 to 1.00, given uncertainty regarding how many hatchery-reared fish contribute to reproduction in the wild (McClure et al. 2003), so a conservative recovery goal might exceed 5.0–10.0% improvement in λ to recover this ESU to sustaining levels (i.e., $\lambda \geq 1.00$). Further analyses to assess the potential benefits to upper Columbia River steelhead stocks from management of tern predation would be enhanced by data spanning additional years with representative river flows.

Acknowledgments

Bonneville Power Administration (BPA) and the Northwest Power and Conservation Council (NPCC) provided funding for this research. We thank W. Maslen of BPA and G. Bisbal of NPCC for their support of this work. We also thank the U.S. Fish and Wildlife Service's McNary National Wildlife Refuge, especially R. Chuck, for permission to work on Crescent Island. J. Adkins, N. Bargmann, B. Begay, C. Cardoni, C. Cowan, C. Couch, D. Craig, K. Gorman, A. M. Myers, L. Sheffield, and G. H. Visser provided invaluable field and laboratory assistance. E. Holsberry and R. Self provided logistical support for which we are grateful. We thank J. North and H. Tachata of the Oregon Department of Fish and Wildlife and the entire northern pikeminnow electrofishing crew for the opportunity to collect fish samples on the Columbia River. J. H. Glabek, E. P. Nunnallee, J. W. Ferguson, and R. D. Ledgerwood of NOAA Fisheries kindly granted permission to use their unpublished data on smolt PIT tags recovered from the Crescent Island tern colony. B. Mur, D. Yule, and an anonymous reviewer provided extensive helpful comments that improved earlier versions of this manuscript.

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