

## ECOSYSTEM-BASED MANAGEMENT OF PREDATOR–PREY RELATIONSHIPS: PISCIVOROUS BIRDS AND SALMONIDS

FRANCIS K. WIESE,<sup>1,3</sup> JULIA K. PARRISH,<sup>1,2</sup> CHRISTOPHER W. THOMPSON,<sup>1</sup> AND CHRISTINA MARANTO<sup>2</sup>

<sup>1</sup>*School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195 USA*

<sup>2</sup>*Biology Department, University of Washington, Seattle, Washington 98195 USA*

**Abstract.** Predator–prey relationships are often altered as a result of human activities. Where prey are legally protected, conservation action may include lethal predator control. In the Columbia River basin (Pacific Northwest, USA and Canada), piscivorous predators have been implicated in contributing to a lack of recovery of several endangered anadromous salmonids (*Oncorhynchus* spp.), and lethal and nonlethal control programs have been instituted against both piscine and avian species. To determine the consequences of avian predation, we used a bioenergetics approach to estimate the consumption of salmonid smolts by waterbirds (Common Merganser, California and Ring-billed Gull, Caspian Tern, Double-crested Cormorant) found in the mid-Columbia River from April through August, 2002–2004. We used our model to explore several predator–prey scenarios, including the impact of historical bird abundance, and the effect of preserving vs. removing birds, on smolt abundance. Each year, <1% of the estimated available salmonid smolts (interannual range: 44 830–109 209; 95% CI = 38 000–137 000) were consumed, 85–98% away from dams. Current diet data combined with historical gull abundance at dams suggests that past smolt consumption may have been 1.5–3 times current numbers, depending on the assumed distribution of gulls along the reaches. After the majority (80%) of salmonid smolts have left the study area, birds switch their diet to predominantly juvenile northern pikeminnow (*Ptychocheilus oregonensis*), which as adults are significant native salmonid predators in the Columbia River. Our models suggest that one consequence of removing birds from the system may be increased pikeminnow abundance, which—even assuming 80% compensatory mortality in juvenile pikeminnow survival—would theoretically result in an annual average savings of just over 180 000 smolts, calculated over a decade. Practically, this suggests that smolt survival could be maximized by deterring birds from the river when smolts are present, allowing bird presence after the diet switch to act as a tool for salmonid–predator control, and conducting adult-pikeminnow control throughout. Our analysis demonstrates that identifying the strength of ecosystem interactions represents a top priority when attempting to manage the abundance of a particular ecosystem constituent, and that the consequences of a single-species view may be counterintuitive, and potentially counterproductive.

**Key words:** avian predators; bioenergetics modeling; Columbia River; dams; larids; mergansers; northern pikeminnow; *Oncorhynchus* spp.; predator control; *Ptychocheilus oregonensis*; salmonids.

### INTRODUCTION

Knowledge of the strength of predator–prey relationships is a necessary pre-condition for effective ecosystem-based management. In cases where prey are rare, threatened, or endangered, conservation actions can include predator control, even if the original cause of prey population decline was not predation (Goodrich and Buskirk 1995). For instance, raven (*Corvus corax*) populations have been culled to benefit desert tortoises (*Xerobates agassizii*; Boarman 2003); coyotes (*Canis latrans*) have been reduced to minimize their impact on

San Joaquin kit foxes (*Vulpes macrotis mutica*; Cypher and Scrivener 1992); Great Black-backed and Herring Gull (*Larus marinus* and *L. argentatus*) populations have been culled to accommodate breeding of endangered Piping Plovers (*Charadrius melodus*; Olijnyk and Brown 1999); and California sea lions (*Zalophus californianus*) have been selectively taken because of their predation on salmonids (DeMaster and Sisson 1992).

In aquatic systems, control programs have been instituted for piscine and avian predators that consume commercially or recreationally important fish (Beamesderfer et al. 1996, Wright 2003), and/or threatened or endangered species (Winfield et al. 2003). Unlike terrestrial systems in which public opinion often turns against predator removal (Goodrich and Buskirk 1995), fishery interest-driven predator control in aquatic systems is often backed by public opinion (Wickens et al. 1992, Kirby et al. 1996). In fact, predator control

Manuscript received 1 November 2006; revised 25 June 2007; accepted 24 September 2007; final version received 24 October 2007. Corresponding Editor: P. S. Levin.

<sup>3</sup> Present address: North Pacific Research Board, 1007 W. 3rd Avenue, Suite 100, Anchorage, Alaska 99501 USA. E-mail: Francis.Wiese@nprb.org

has been permitted without evidence of significant impact to prey populations. For instance, Wright (2003) found no impact of an increasing cormorant (*Phalacrocorax carbo*) population on the fishable population of brown trout (*Salmo trutta*) in a Scottish lake, either before, or after annual culling of these seabirds.

In the John Day reservoir in the Columbia River (boundary between Washington and Oregon, USA), Harvey and Kareiva (2005) concluded that removal of nonindigenous fish species thought to prey upon, or compete against, native salmonids, were partly or totally offset by indirect food-web interactions. Beamesderfer et al. (1996) suggested that 10–20% of the northern pikeminnow (*Ptychocheilus oregonensis*) population continue to be removed annually from the Columbia River, even though this source of smolt mortality is inconsequential relative to harvest and hydropower impacts (McClure et al. 2003). Thus, although predator–prey interactions are often important in regulating prey populations, other factors operating in the system may be more significant, and/or nonlinear and indirect effects mediated through the food web may negate the desired effects of select predator removal, as classically described by Leopold (1949).

Since 1991 the National Oceanic and Atmospheric Administration Fisheries (NOAA-Fisheries) has listed 12 anadromous “evolutionarily significant units,” or ESUs (Waples 1991) of Columbia River Basin salmon and steelhead as threatened or endangered under the Endangered Species Act (McClure et al. 2003). The Columbia River Basin spans over 640 000 km<sup>2</sup> and once supported one of the most productive salmon fisheries in the world, with an estimated 7–15 million anadromous fish returning to spawn each year (McClure et al. 2003).

Overharvest, hydroelectric dams, habitat alteration, hatcheries, climate variability, and piscivorous predators have all been implicated in their decline or lack of recovery (e.g., Beamesderfer et al. 1996, Lichatowich 1999, Kareiva et al. 2000, Roby et al. 2003). To offset cumulative losses, between 150 and 200 million hatchery-raised salmonid smolts are added to the Basin every year (Fish Passage Center web site),<sup>4</sup> so that hatchery-to-wild ratios are now skewed to predominantly hatchery fish (>70%; NRC 1996).

In response to the listing of spring chinook, (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in the mid-Columbia River, a 50-year habitat-conservation plan (HCP; Anadromous Fish Agreement and Habitat Conservation Plan, Rocky Reach Hydroelectric Project, FERC license number 2145, 26 March 2002; *available online* at the Chelan County Public Utility District [PUD] web site)<sup>5</sup> guaranteeing that stock-specific survival rates of juvenile salmonids (including hatchery fish) as they pass through each of the three mid-

Columbia River dams and their associated reservoirs that Chelan and Douglas County are responsible for (Rock Island, Rocky Reach, and Wells), will be 93% or higher (*available online*).<sup>5</sup> Given these legally imposed limits to overall project (dam and reservoir) mortality, predator effects may still be deemed relevant to resource management even if a predator population does not impact the salmonid population demographically (i.e., depresses  $\lambda$ ) or only preys upon currently non-listed stocks.

Piscine predators in the Columbia River basin, exemplified by northern pikeminnow (Zimmerman and Ward 1999), and a suite of avian predators including gulls (*Larus* spp.), terns (*Sterninae* spp.; York et al. 2000, Collis et al. 2001), Double-crested Cormorants (*Phalacrocorax auritus*; Collis et al. 2002), and Common Mergansers (*Mergus merganser*) are known or thought to consume a nontrivial fraction of the outmigrating salmonid smolts. For example, pikeminnow consumption is estimated at 8% of total basin production (Beamesderfer et al. 1996), and Caspian Terns (*Hydroprogne caspia*) in the lower Columbia River removed an estimated 15% of juvenile salmonids that reached the estuary in 1997 and 1998 (Roby et al. 2003). Local populations of all predator species have increased in size as an indirect consequence of human alterations of the ecological landscape, including prey concentration at dams and creation of nesting habitat (Conover 1983, Beamesderfer et al. 1996, Wires and Cuthbert 2000).

In an attempt to meet the Habitat Conservation Plan goals, Public Utility Districts (PUDs) along the mid-Columbia River have incorporated avian predator control as one of several tools to reduce smolt mortality (*available online*).<sup>5</sup> Although lethal and nonlethal controls have been implemented at many dams in the mid-Columbia River (USDA 2003), it remains unclear (1) to what degree birds in this portion of the river select salmonid smolts as prey, and impact out-migrating stocks, (2) where the majority of avian predation takes place on the river, (3) whether the adopted predator-control regimes are effective in reducing salmonid smolt mortality, and (4) how removal of these birds affects the ecology of the system.

In this paper we use a bioenergetics approach to model the consumption of salmonid smolts by resident and migrant waterbirds found in the mid-Columbia River in Chelan County between Wells and Rock Island dam. To determine the management and conservation consequences of avian predation, we use our model to explore several predator–prey scenarios, including a comparison of contemporary vs. historic avian predation, as well as the ecological efficacy of the current lethal-control regime on smolt abundance. These values are calculated within a simple predator–prey (bird–salmon) framework, as well as within a larger ecosystem context, specifically the inclusion of northern pikeminnow. We suggest that a modeling approach that links bioenergetics to population dynamics may be

<sup>4</sup> ([http://www.fpc.org/hatchery\\_home.html](http://www.fpc.org/hatchery_home.html))

<sup>5</sup> ([www.chelanpud.org/HCP](http://www.chelanpud.org/HCP))

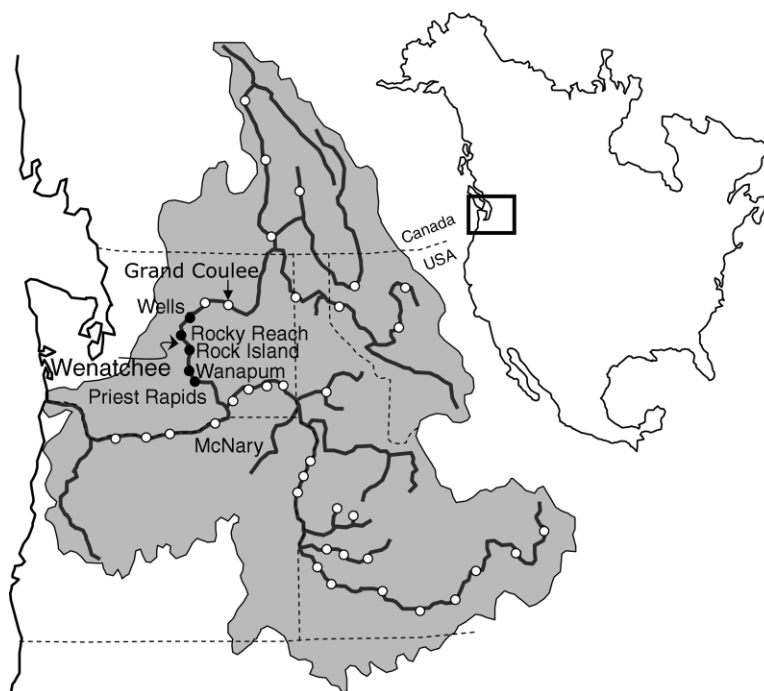


FIG. 1. Map of the Columbia River drainage (shaded area) with all major dams (circles) indicated. The five mid-Columbia dams are indicated with solid circles. The nearest major town, Wenatchee, is indicated by the arrow. Jurisdictional boundaries (state, federal) are shown by dashed lines.

useful in exploring the consequences of management decisions in systems in which species have been accorded differential value without regard to the larger roles they may play within the ecosystem.

#### METHODS

##### *Study area and species management*

Our study areas was located in the state of Washington, USA, along the mid-Columbia River, defined here as between Grand Coulee and McNary dams (Fig. 1). Effort was concentrated at Rock Island and Rocky Reach dams, 18 km and 6.5 km south and north of Wenatchee, Washington, USA, respectively, and their associated reaches (stretch of river between dams; 32.0 and 67.7 km long, respectively). Both hydroelectric projects (dams and associated reaches) are administered by the Chelan County Public Utility District (PUD).

The Columbia River Basin provides habitat for five species of anadromous salmonids: chinook, steelhead, coho (*Oncorhynchus kisutch*), sockeye (*O. nerka*), and chum (*O. keta*), of which the first four are found in the mid-Columbia, and specifically in our study area. During late March and April the bulk of hatchery chinook, coho and steelhead are released into the upper and mid Columbia River (FPC 2004). Daily surveys at the Rock Island Dam bypass trap indicate that most smolts (hatchery and wild) have left the system by mid-June (FPC 2004). Thus, although salmonids are present in our study area throughout the summer, their numbers

are vastly reduced relative to the spring peak (Fig. 2). Therefore, we divided our study into two periods: *early* (25 March through 15 June), when 80% of the salmonid smolts released from hatcheries above Rock Island Dam are still above McNary Dam, and *late* (16 June to 31 August). The start and stop dates were predetermined according to the historic period of lethal control of avian predators in Chelan County (Todd West [Chelan County PUD], *personal communication*).

Mandated by NOAA-Fisheries to implement a bird-control program, mid-Columbia PUDs have contracted the USDA Wildlife Services since 1997 to control the number and behavior of piscivorous birds in the vicinity of five of the mid-Columbia dams (Wells, Rocky Reach, Rock Island, Wanapum, and Priest Rapids) using nonlethal (hazing) and lethal (shooting) control (USDA 2003). In Chelan County, control efforts have generally been limited to the area immediately surrounding each dam (within 1 km), as required by U.S. Fish and Wildlife Service permits (Paul Fielder [Chelan County PUD], *personal communication*), and based on the assumption that dams facilitate predator access to out-migrating smolts.

##### *Bioenergetics approach*

We constructed a time-dependent (week) bioenergetics model to estimate the number of juvenile salmonids consumed by avian predators along the Columbia River in Chelan County covering 25 March–31 August 2002–2004. Salmonid consumption (as well as that of all other

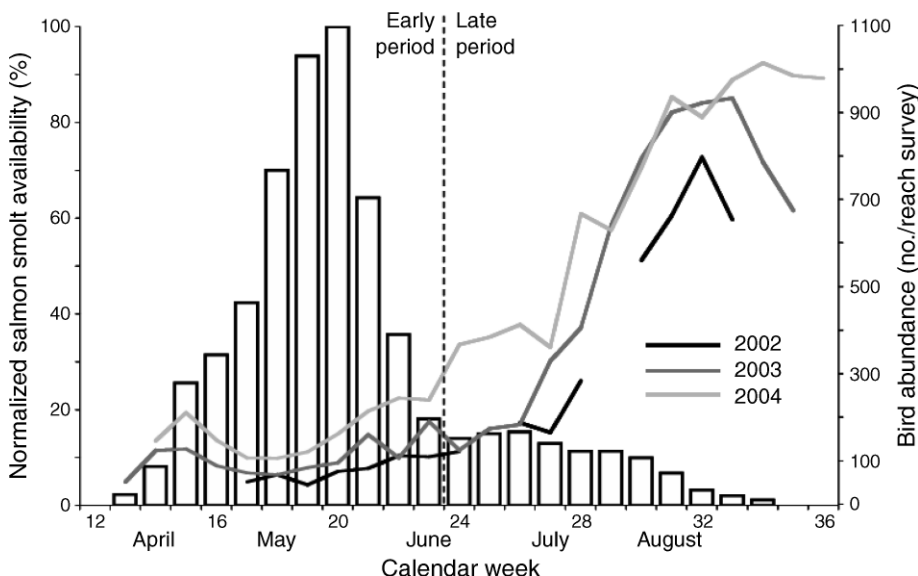


FIG. 2. Salmonid smolt availability index from daily counts of smolts out-migrating past Rock Island Dam, summed to weekly values, averaged over years (2002–2004), and normalized to percentage of maximum week (bars); and weekly bird abundance (summed over all species; see Fig. 3 for species list) from reach surveys between Rock Island and Wells dams (100 linear kilometers), 2002–2004 (lines). Months are listed below each starting calendar week (e.g., April starts in calendar week 14).

fish species consumed) was calculated by (1) defining the daily energy consumption of each bird predator (Table 1: Eq. 1), (2) calculating the proportion of this energy need covered by each prey fish species, based on diet samples (Table 1: Eq. 2), and (3) translating the energy contributed by each fish species back into actual numbers of fish consumed throughout the season based on week-specific bird abundance (Table 1: Eq. 3). The overall model was built stochastically. Unless otherwise indicated we calculated confidence intervals by drawing all measured parameters, and those taken from the literature where available, from a normal distribution based on the mean and standard error and by running each simulation 10 000 times. All calculations were performed for each bird species and age class.

*Daily energy consumption.*—Field metabolic rates (FMR, in kilojoules per day), also called “daily energy expenditure” (DEE), were calculated based on the

allometric relationship between field metabolism and body mass developed by Birt-Friesen et al. (1989; Eq. 4), and Nagy (1987; Eq. 5):

$$\log y = 2.99(\pm 0.04) + 0.727(\pm 0.039)\log x \quad (4)$$

$$\log y = 0.904(\pm 0.187) + 0.704(\pm 0.061)\log(x \times 1000) \quad (5)$$

where  $y$  is FMR and  $x$  is mass in kilograms. Although other equations for the calculation of FMR are available, and direct measurements for some of our study species have been made, we preferred using these more general equations, given the variability associated with measured energy expenditure due to environmental variables, predominantly temperature. Estimated values from these equations approximated (2–9% less) measurements of DEE from field studies using doubly labeled water (e.g., Roby et al. 2003) and results from

TABLE 1. Equations used in the bioenergetic calculations of the number of salmonids consumed by avian predators.

| Equation  | Parameters  |
|---|---|
| 1) $E_c = DEE \times mef \times E_r / ae$   | DEE = daily energy expenditure (kJ/d)†<br>$E_r$ = proportion of the energy demand contributed by fish‡§<br>mef = molt energy factor†§<br>ae = assimilation efficiency†  |
| 2) $pE_{sp} = p_{nsp} \times m_{sp} \times E_{sp} / \sum (P_{nsp} \times m_{sp} \times E_{sp})$ | $p_{nsp}$ = proportion (by number, $n$ ) of each fish species in fish portion of diet‡<br>$m_{sp}$ = mean mass (g) of each fish species in diet‡<br>$E_{sp}$ = mean energy density (kJ/wet mass) per fish in species in diet‡ |
| 3) $Sp_c = \sum (E_c \times pE_{sp} \times N_w \times 7) / E_{sp} \times m_{sp}$                | $x$ = number of weeks (w)<br>$N_w$ = number of birds per weekly survey‡<br>7 = no. days per week  |

† Based on Eqs. 4 and 5, taken from the literature.  
 ‡ Values were calculated from data collected in this study.  
 § Calculated for gulls only.

consumption rate studies of captive birds (Wood and Hand 1985, Hatch and Weseloh 1999). We used both equations to provide variability in the final estimate and to examine the elasticity of the model to this input parameter.

We used the seasonal average of body mass for all bird predators (Appendix A), except as follows. Significant differences in body mass among weeks were only observed in after-hatch-year Ring-billed and California Gulls ( $\chi^2 = 72.68$  and  $72.67$ , respectively,  $df = 17$ ,  $P < 0.0001$ ) so we applied weekly means and standard errors. Because Common Mergansers breed within the study area, hatch-year birds were observed well before they fledged. Therefore, we estimated a chick-to-adult ratio in body size throughout the summer based on contemporaneously collected visual information (J. Smith, *unpublished data*).

Daily energy expenditure for gulls was modified by three additional terms, accounting for non-fish diet items, molt, and assimilation efficiency. Because gulls do not exclusively feed on fish, we discounted their energy contribution from the non-fish component in their diet. To this end, we calculated the percentage volume of fish items in the stomach (proventriculus and gizzard; see *Diet*, below), and converted this percentage based on the average energy density of fish (4.6 kJ/g wet mass) and non-fish (2.6 kJ/g wet mass, Petersen and Ward 1999). This resulted in  $65.2\% \pm 7.8\%$  and  $68.0\% \pm 7.6\%$ , respectively, of California and Ring-billed Gull energy requirements being met by fish.

Because gulls undergo a body- and flight-feather molt throughout the summer (Ryder 1993, Winkler 1996), we added a "molt energy factor" of 10–15% of DEE to gull-specific calculations (Thompson and Boag 1976, Murphy and King 1992), taking into consideration the proportion of the population that was molting in any given week (C. Thompson, *unpublished data*).

Published values for assimilation efficiency vary greatly (Castro et al. 1989, Karasov 1990, Brugger 1993, Chavez 1997), and are dependent on the type of prey consumed (Brugger 1993). Although using 0.75 has been suggested (e.g., Castro et al. 1989, Karasov 1990, Roby et al. 2003), we found no empirical data to support this specific value for the bird and prey species investigated in this study. Thus, we conservatively drew random values from a uniform distribution of the published range (0.69–0.85).

*Diet.*—In all years, USDA Wildlife Services personnel were stationed within 1 km downstream of the tailrace of Rock Island Dam between early April and the end of August, as part of a preexisting avian predator lethal control program. Although birds may have been drawn to the dam for foraging opportunities, individuals were not shot while feeding. Instead, birds were taken as they transited the collection site. We assumed that the diet of birds collected by USDA Wildlife Service was representative of all birds found within the study area; and even

though most birds were shot between 06:30 and 14:00 hours, we assumed that gut contents were representative of diel diet. The shooting schedule followed a "week on-week off" pattern. As a result, this level of lethal-control effort was up to 80% lower than in 2001, the last year of continuous daily lethal control, and the year previous to the onset of this study. Maximum sizes of samples taken every two weeks (set at 10 birds) were not achieved for all species, dependent on time of season and species' use of the river (e.g., hatch year gulls were never present early in the season). All carcasses recovered from the river were provisionally identified, individually bagged, and immediately stored in compartmentalized coolers lined with dry ice, one bird per compartment, and transferred to  $-20^\circ\text{C}$  freezers daily. Carcasses were subsequently thawed, (re)identified, aged to hatch year (HY) and after-hatch year (AHY, sub-adult and adult), weighed, measured, and necropsies were conducted to determine sex and to collect the entire gastrointestinal tract. Unless examined immediately, the latter was refrozen and  $-20^\circ\text{C}$ .

Thawed gut contents were sorted into fish (whole and partial fish, otoliths, and bones) and non-fish food items (insects, plant material, non-fish vertebrates, and anthropogenic sources such as french fries and hot dogs), and the percentage volume of each component in each gut was visually estimated by 5% increments. We used volume for this initial division, rather than the more traditional mass, because a nontrivial number of gull stomachs contained a slurry of digested material largely but not entirely composed of starch (later identified as processed potato). Because the slurry could not be separated into individual pieces or portions for easy weighing, we adopted a volumetric approach in order not to discount this food source. We used the percent volume of non-fish to scale DEE (see *Daily energy consumption*, above).

Many previous bioenergetics studies have focused sample collection at colony sites, and, specifically, on birds returning with fish. This approach greatly facilitates the use of whole fish in dietary analysis. Because birds in our study were not collected during or immediately after foraging bouts, the number of whole fish recovered was small (294) even given our large sample size (1685 birds processed). Therefore, we chose to include identifiable partial fish (643 additional identified diet items), and otoliths (5972 identified items), greatly augmenting our sample, with the caveat that this may have introduced bias against small or more easily digestible food items (although a large number of small stickleback otoliths were identified).

Whole and partial fish were identified to species whenever possible. Otoliths were identified to the lowest taxonomic level possible, usually to species. Verification of otolith identification was assured by blind testing with "dummy samples" constructed from a reference collec-

tion. Of 64 dummy samples, 96% were identified to species correctly.

Whole fish recovered from guts were identified and weighed, and standard length (SL) was taken. In addition, we created the measurement "dorsal standard length" (DSL), defined as the perpendicular distance between two parallel lines intersecting: (1) the insertion of the posterior-most dorsal fin (excluding the adipose fin) and (2) the posterior-most point on the hypural plate. The ratio DSL:SL was used to create standard curves to estimate the length of fish that had been partially digested by birds. DSL conversions were only used when the fit of DSL:SL exceeded  $R = 0.95$ .

To help establish reliable length-to-mass relationships and energy densities of all relevant fish prey, and to create an otolith reference collection, we extensively expanded our fish samples retrieved from guts by conducting direct collections of fish at the dams and on the reaches. From 2002 through 2004, Chelan County PUD personnel and Washington Department of Fish and Wildlife personnel stationed at the dams collected fish for this study. In 2004 additional fish were collected from the river via minnow trapping, angling, beach seining, and electro-shocking. Species not listed under the U.S. Endangered Species Act were taken as needed. Listed fish were collected only if mortally wounded. Chinook, coho, and steelhead smolts were also provided by local hatcheries (Lake Wenatchee, Simalkameen Ponds, Winthrop, Leavenworth, Chiwawa Ponds, Turtle Rock, and Chelan). In total, 2100 fish of 33 species were collected. Specimens were identified, individually bagged, frozen on dry ice, and transferred to  $-20^{\circ}\text{C}$  freezers daily. Reference fish were subsequently thawed, and length (SL, DSL) and mass were measured. Freshly measured samples vs. frozen, thawed, and re-measured samples varied by less than 3%. Saccular, utricular, and/or lagenar otoliths (depending on family) were removed from individuals of known length (Parrish et al. 2006). Otolith length and height were measured and used to generate otolith length to fish length curves (minimum acceptable correlation for use of  $R = 0.9$ ).

Predator- and prey-specific length:mass conversions were created from three prioritized data sources: (1) whole and partial fish extracted from bird butts; (2) otoliths from bird guts, where clearly eroded/digested samples were excluded (sensu Derby and Lovvorn 1997:549–553); (3) published allometric relationships (available online).<sup>6</sup>

Energy density of whole fish prey (kJ/g wet mass) was determined via bomb calorimetry. For each fish species identified in bird stomachs (proventriculus and gizzard), we thawed six fish collected through the study area as described above, and measured, weighed, and dried them at  $60^{\circ}\text{C}$  until daily mass changes remained below

0.1 g. Dried fish were ground into a fine, homogeneous powder and allowed to dry overnight ( $60^{\circ}\text{C}$ ). Ground samples were made into pellets ( $<0.2$  g) using a Parr Pellet Press (Parr Instrument Company, Moline, Illinois, USA). Three pellets per fish were combusted in a Parr 1425 Semimicro Calorimeter (Parr Instrument Company), and gross heat (kJ/g) values determined. Samples were available for 24 of the 26 fish species identified across all bird stomachs. Energy contents of species for which we did not have any samples were assigned an average of known values within the same family (Appendix B).

*Predator abundance.*—Abundance of piscivorous birds along the two reaches between Rock Island and Wells dams was determined from a total of 14 weekly boat surveys conducted between 23 April and 13 August 2002; 23 weekly boat surveys between 25 March and 26 August 2003; and 24 weekly boat surveys between 30 March and 30 August 2004. All surveys were completed in a single day beginning at 30 min after sunrise and ending by 18:00 hours, following a standard survey track, and covering the entirety of both reaches. All birds were counted and identified to species and age class (hatch year, HY; sub-adult and adult = after-hatch-year, AHY) whenever possible with the aid of handheld  $10 \times 42$  Swarovski binoculars. Because the total number of birds did not fluctuate wildly from week to week, we assumed our surveys to be representative of daily abundances within a week.

Abundance of cormorants, which were almost exclusively observed roosting on towers adjacent to Rock Island Dam (and out of sight of reach survey effort), was determined through reach surveys as well as 3–4 daily systematic instantaneous scans of 3–4 sectors immediately upstream (forebay) and downstream (tailrace) of the dams, encompassing a total of  $0.78 \text{ km}^2$  at Rock Island and  $0.45 \text{ km}^2$  at Rocky Reach. Effort in different sectors was kept equal throughout the day and season.

In order to compare the three years we expanded our 2002 abundance estimates to match the 2003–2004 sample periods. For this, we assumed all four weeks previous to the onset of observations in 2002 to be equal to the mean of the first three weeks of observation, and the two weeks after the last observations to be equal to the mean of the last two weeks of data.

#### *Dam vs. reach predation*

The estimates of salmonid consumption derived from Eq. 3 (see Table 1) encompass the entire study area, including the dams. Conventional wisdom, avian predator control strategies, and legal mandates all implicitly indicate that the majority of avian predation on salmonid smolts in dammed-river systems occurs at the dams (Ruggerone 1986; available online).<sup>5</sup> To test this assumption, we focused on behavioral observations at dams and estimated what proportion of all salmonids consumed in the study area was taken there. We estimated the number of successful attacks on salmonids

<sup>6</sup> ([www.fishbase.org/home.htm](http://www.fishbase.org/home.htm))

by birds (species specific and age-class specific) observed at dams as

$$S_c(\text{dam}) = \sum_{w=1}^x (A \times p_a \times p_d) \quad (6)$$

where  $S_c$  is salmonid consumption,  $x$  is the number of weeks ( $w$ ),  $A$  is the estimated total number of attacks ( $A$ ) at dams per week (from attack scans),  $p_a$  is the proportion of successful attacks at dams per week (from focal bird observations), and  $p_d$  is the proportion of diet (by number) composed of salmonids (from diet analysis).

Behavioral observations to collect these data were as follows. In the 15 minutes between instantaneous scans we recorded the total number of attacks on fish, for all birds, where attacks were operationally defined as diving from an aerial or surface position (attack scans). Identification to species and age class was made with handheld  $10 \times 42$  Swarovski binoculars and a tripod-mounted  $20\text{--}60\times$  Swarovski spotting scope. When California and Ring-billed Gulls could not be identified to species, they were recorded as gulls. Average daily attack rates, defined as “the number of dives per hour per bird species  $\times$  age class,” were calculated for each week by binning data into three time-of-day categories (morning, midday, afternoon), calculating bin averages, and summing over the appropriate number of hours. We assumed only diurnal attacks. In total, 11 397 attack scans (2849 hours) were performed in 2002–2004 at Rock Island and Rocky Reach Dams.

Focal bird observations were used to determine species- and age-class-specific foraging efficiency at the dams. Birds for focal observations were chosen based on a randomly generated table. Attacks were labeled “successful” if a fish was seen in the bill, or in the case of the Double-crested Cormorants and Common Mergansers, if the bird appeared to swallow upon surfacing. We conservatively assumed that only one fish was caught per dive in the absence of specific information to the contrary. Seasonal (early and late) success rates were determined on the basis of dives with known outcomes, where the minimum sample size (number of attacks of known outcome) was 10. In total, 2761 focal observations (1982 hours) were performed to determine foraging success of birds at dams.

We assumed that birds only foraged during daylight hours (total daylight over the study period ranged from 12.5 to 15.6 h). We subtracted estimated salmonid consumption at the dams from total salmonid consumed (via the bioenergetics model) to obtain estimated number of salmonids captured by avian predators on the reaches.

### Statistics

Differences in the number of attacks, foraging success, and diet composition among bird species and age classes estimated above were analyzed using a general linear model (GLM) framework (SAS 2003), where the

response was treated as continuous and using a normal link function. As a result, chi-square values are presented instead of the usual  $F$  for ANOVA/ANCOVA designs. In all instances a full model, including interactions, was built to investigate differences. Where interactions were insignificant ( $P > 0.05$ ), they were dropped and only a main effects model was considered, e.g., for diet:

$$p(\text{salmonid}) = \beta_0 + \beta_1 \text{year} + \beta_2 \text{species} + \beta_3 \text{age} + \beta_4 \text{time period} \quad (7)$$

where the proportion ( $p$ ) of salmonids in the diet was first transformed (arcsine of the square root of the proportion) to conform to normality assumptions. Significant differences were determined at  $P < 0.05$ , means are presented as  $\pm 1$  SE, and all tests are two tailed.

We also conducted an elasticity analysis to determine the most influential input parameters on salmonids-consumption estimates in our bioenergetics model. To this end we conducted individual-parameter perturbations of 10% of the value of each parameter and determined the corresponding change in the output. Elasticity ( $E$ ) of each parameter was then calculated as

$$E = \frac{\Delta S_c / \Delta f}{S_c / f} \quad (8)$$

where  $S_c$  is the estimated salmonid consumption and  $f$  is any of the given parameters investigated. We report elasticities for chinook salmon consumption of adult birds in 2004; all other bird–fish combinations yielded similar results. We chose to integrate individual parameter uncertainty into the model design as described above and thus did not perform a parameter uncertainty analysis.

### Management scenario models

We used the structure of the bioenergetics model to investigate a set of plausible alternative predator-abundance scenarios and the implications for predator-control efficacy, given current management goals and practices. We also used this structure to investigate the importance and implications of including additional ecological interactions, namely the relationships among birds, salmonids, and northern pikeminnows.

Rather than randomly changing observed avian predator abundance to examine its effects on salmonids-predation levels, we first calculated how many additional smolts might have been consumed had no lethal control efforts taken place during the course of this study. To this end we added all known shot birds back into the week-specific reach-survey abundances, and assumed all birds stayed in the system for the remainder of the summer. In a second alternative predator abundance scenario we attempted to determine the level of avian predation of salmonid smolts from the past, prior to the initiation of any predator control

efforts. Historic data on avian predator abundance in this system are scarce. However, we found annual reports from 1979 to 1982 with graphical data on the average number of gulls (not identified to species; no variance data, no data on other species were available) in the tailrace of Rock Island and Rocky Reach Dams on a daily basis (Committee on Fishery Operations 1980, 1981, 1982, 1985). Original data on gull abundance were collected by PUD personnel as a proxy of smolt abundance at the dams, and were apparently used to regulate the amount of water discharged to facilitate smolt out-migration. Up to three counts were made daily (morning, noon, afternoon). We recreated the average daily data set, per dam per year, from graphs, and calculated weekly averages to match the temporal specificity of the contemporary reach surveys.

To examine the importance and influence of other ecosystem interactions in the system, we explored the relationship between bird consumption of salmonid smolts and juvenile pikeminnow, vs. adult pikeminnow consumption of smolts. Here we asked a theoretical question: What is the difference in total smolt consumption if birds remain or are removed from the system if we also take into account this additional predator-prey interaction? Because birds eat both salmonids and juvenile pikeminnow, the full effect of removing birds from the system may not be felt for several years (i.e., until the juvenile pikeminnow that birds would have consumed, had they not been removed, grow into salmonid predators themselves).

For this purpose we constructed a simple stochastic coupled predation-population matrix model for pikeminnow, following fish that would have survived had birds not consumed them. The model was populated with data from this study: salmonid consumption by birds (Table 2), number and size (a proxy for age) of pikeminnow consumed by birds (Appendix B), as well as data from the literature (age and predation rate of pikeminnow on salmonids, pikeminnow survival and longevity). Pikeminnow are considered major salmonid predators once they reach lengths  $>210$  mm, and then, depending on the study, show a predation rate of 0.13–0.69 salmon per predator per day (Vigg et al. 1991, Beamesderfer et al. 1996). At a length of 210 mm, pikeminnow are about 3 years old (Wydoski and Whitney 2003). In our study, the average age (approximated by size) of pikeminnow consumed varied among bird species, representing 2-year-olds for gulls, 2.2 years for terns, 1.5 years for mergansers, and 2.4 years for cormorants (Appendix B). Survival of juvenile ( $<3$  years old) pikeminnow that would have been consumed by each bird species was iterated monthly until age 3, using a monthly survival value of 0.944 and an error of 0.005 (Beamesderfer et al. 1996). Adult ( $\geq 3$  years) survival values in the literature range between 0.70 and 0.88 (Rieman and Beamesderfer 1990, Parker et al. 1995). We iterated adult survival annually using the lower value in the range, rather than drawing from a distribution of

unknown shape. Likewise, we were also conservative (i.e., generating the lowest salmonids-consumption value by pikeminnow) by setting the predation rate of adult fish at the lower end of the published range (0.13 salmon per predator per day) as well as by only assuming a three-month (120-d) window of salmon availability per year.

Pikeminnow live to  $\sim 13$  years (Wydoski and Whitney 2003). Therefore, we ran our model over 11 years (because the juveniles entering the model in the first year were already 1.5–2.4 years old; see above), allowing the first cohort of pikeminnow to live out their lives, thus assuming no additional pikeminnow control. For ease of calculation, the model was run without explicit fecundity, although in subsequent years “new” pikeminnow were allowed to populate the system to the extent that the bird diets specified. Thus, over each successive year, additional pikeminnow (those released by bird predation), all starting as juveniles, entered our model. For each of the 11 years, we calculated: (1) the number of smolts consumed by this increasing number of northern pikeminnow, and (2) the number of smolts bird predators would have consumed had they remained in the system (i.e., our study values). Because bird abundance and diet varied among years in our study, we ran a mixed-year model, i.e., using the mean of 2002–2004. Output was the cumulative number of salmonids consumed by the pikeminnow, minus the number of salmonids consumed by the birds. A negative value would indicate that birds have a larger effect than pikeminnow. A positive value would indicate the reverse. To generate a distribution of model output, the model was run 100 000 times. Having no information on system carrying capacity or population-density control for pikeminnow, we did not include density dependence in the northern pikeminnow model. However, because removal of a predator rarely results in a direct increase in prey abundance (Goodrich and Buskirk 1995), we investigated predator compensation scenarios for the mortality of juvenile pikeminnow in the absence of predation by birds of 0%, 30%, 50%, and 80%.

## RESULTS

### Diet

A total of 30 different species of fish were found in stomachs (proventriculus and gizzard) of birds shot below Rock Island Dam (mid-Columbia River, Washington, USA) (Appendix B), including four anadromous salmonid species. The mean aggregate fresh mass of fish consumed often varied among bird species and age classes, and was often larger for mergansers and cormorants. Trends in the proportion of the diet (as fresh mass) composed of salmonids differed among bird species ( $\chi^2 = 17.7$ ,  $df = 1$ ,  $P < 0.0001$ ) and time-periods ( $\chi^2 = 40.14$ ,  $df = 1$ ,  $P < 0.0001$ , Table 3). As expected, there was a large (30–49%) drop in the percentage of the diet composed of salmonids between the period of high (early) and low (late) salmonid abundance across all bird



TABLE 2. Estimated number of anadromous salmonids and percentage of total consumed by avian predators on the mid-Columbia River in Chelan County, Washington, USA, 25 March–31 August 2002–2004.

| Period      | Predator species† | Age‡  | Salmon species |               |               |               | Salmonid total (%) |                          |
|-------------|-------------------|-------|----------------|---------------|---------------|---------------|--------------------|--------------------------|
|             |                   |       | Chinook        | Coho          | Sockeye       | Steelhead     |                    |                          |
| 2002        |                   |       |                |               |               |               |                    |                          |
| Early       | CAGU              | AHY   | 390            | 53            | 319           | 0             | 763 (2.2)          |                          |
|             | CATE              | AHY   | 56             | 167           | 0             | 56            | 279 (0.8)          |                          |
|             | COME              | HY    | 32             | 0             | 293           | 0             | 325 (0.9)          |                          |
|             |                   | AHY   | 2123           | 0             | 19 190        | 0             | 21 313 (60.3)      |                          |
|             | DCCO              | AHY   | 202            | 0             | 202           | 0             | 404 (1.1)          |                          |
|             | RBGU              | AHY   | 1932           | 429           | 9660          | 215           | 12 236 (34.6)      |                          |
|             | Total             |       | 4735 (13.4)    | 649 (1.8)     | 29 664 (84.0) | 271 (0.8)     | 35 319 (58.9)      |                          |
| Late        | CAGU              | HY    | 1208           | 0             | 0             | 0             | 1208 (4.9)         |                          |
|             |                   | AHY   | 451            | 150           | 150           | 0             | 751 (3.1)          |                          |
|             | CATE              | HY    | 22             | 2             | 8             | 0             | 32 (0.1)           |                          |
|             |                   | AHY   | 640            | 58            | 233           | 0             | 931 (3.8)          |                          |
|             | COME              | HY    | 2602           | 0             | 0             | 0             | 2602 (10.6)        |                          |
|             |                   | AHY   | 3120           | 0             | 0             | 0             | 3120 (12.7)        |                          |
|             | DCCO              | HY    |                |               |               |               |                    |                          |
|             |                   | AHY   | 2475           | 0             | 225           | 0             | 2700 (11.0)        |                          |
|             | RBGU              | HY    | 850            | 0             | 565           | 0             | 1415 (5.8)         |                          |
|             |                   | AHY   | 10 153         | 0             | 1696          | 0             | 11 849 (48.2)      |                          |
|             |                   | Total |                | 21 521 (87.2) | 210 (0.9)     | 2877 (11.7)   | 0                  | 24 608 (41.1)            |
|             | Grand total       |       |                | 26 256 (43.8) | 859 (1.4)     | 32 541 (54.3) | 271 (0.5)          | 59 927 (49 586–72 354)   |
| 2003        |                   |       |                |               |               |               |                    |                          |
| Early       | CAGU              | AHY   | 342            | 114           | 285           | 0             | 741 (2.7)          |                          |
|             | CATE              | AHY   | 240            | 120           | 96            | 0             | 456 (1.7)          |                          |
|             | COME              | HY    | 274            | 82            | 110           | 82            | 548 (2.0)          |                          |
|             |                   | AHY   | 8417           | 2523          | 3372          | 2523          | 16 835 (61.3)      |                          |
|             | DCCO              | AHY   | 1257           | 0             | 180           | 0             | 1437 (5.2)         |                          |
|             | RBGU              | AHY   | 6346           | 0             | 1120          | 0             | 7466 (27.2)        |                          |
|             | Total             |       | 16 876 (61.4)  | 2839 (10.3)   | 5163 (18.8)   | 2605 (9.5)    | 27 483 (61.3)      |                          |
| Late        | CAGU              | HY    |                |               |               |               |                    |                          |
|             |                   | AHY   | 572            | 0             | 0             | 0             | 572 (3.3)          |                          |
|             | CATE              | HY    | 73             | 3             | 3             | 3             | 82 (0.5)           |                          |
|             |                   | AHY   | 1197           | 46            | 46            | 46            | 1335 (7.7)         |                          |
|             | COME              | HY    | 3062           | 0             | 0             | 0             | 3062 (17.7)        |                          |
|             |                   | AHY   | 3760           | 0             | 0             | 0             | 3760 (21.7)        |                          |
|             | DCCO              | HY    |                |               |               |               |                    |                          |
|             |                   | AHY   | 3073           | 0             | 346           | 346           | 3765 (21.7)        |                          |
|             | RBGU              | HY    | 0              | 0             | 1561          | 0             | 1561 (9.0)         |                          |
|             |                   | AHY   | 1605           | 0             | 1605          | 0             | 3210 (18.5)        |                          |
|             |                   | Total |                | 13 342 (76.9) | 49 (0.3)      | 3561 (20.5)   | 395 (2.3)          | 17 347 (38.9)            |
|             | Grand total       |       |                | 30 218 (67.4) | 2888 (6.4)    | 8697 (19.4)   | 3000 (6.7)         | 44 830 (37 197–54 882)   |
| 2004        |                   |       |                |               |               |               |                    |                          |
| Early       | CAGU              | HY    | 138            | 0             | 113           | 0             | 251 (0.4)          |                          |
|             |                   | AHY   | 1779           | 0             | 1455          | 0             | 3234 (4.6)         |                          |
|             | CATE              | AHY   | 102            | 204           | 0             | 0             | 306 (0.4)          |                          |
|             | COME              | HY    | 289            | 0             | 948           | 145           | 1382 (1.9)         |                          |
|             |                   | AHY   | 9589           | 0             | 31 430        | 4794          | 45 813 (64.6)      |                          |
|             | DCCO              | HY    | 216            | 31            | 21            | 41            | 309 (0.4)          |                          |
|             |                   | AHY   | 4859           | 695           | 462           | 925           | 6941 (9.8)         |                          |
|             | RBGU              | AHY   | 6529           | 407           | 4080          | 1632          | 12 648 (17.8)      |                          |
|             |                   | Total |                | 23 501 (33.2) | 1337 (1.9)    | 38 509 (54.3) | 7537 (10.6)        | 70 884 (64.9)            |
|             | Late              | CAGU  | HY             | 389           | 0             | 0             | 389                | 778 (2.0)                |
|             |                   |       | AHY            | 9783          | 0             | 0             | 0                  | 9783 (25.5)              |
|             |                   | CATE  | HY             | 179           | 6             | 0             | 0                  | 185 (0.5)                |
|             |                   | AHY   | 1974           | 64            | 0             | 0             | 2038 (5.3)         |                          |
| COME        |                   | HY    | 4342           | 0             | 0             | 0             | 4342 (11.3)        |                          |
|             |                   | AHY   | 4610           | 0             | 4610          | 0             | 9220 (24.1)        |                          |
| DCCO        |                   | HY    | 0              | 0             | 0             | 0             | 0                  |                          |
|             |                   | AHY   | 4514           | 0             | 0             | 970           | 5484 (14.3)        |                          |
| RBGU        |                   | HY    | 0              | 0             | 0             | 0             | 0                  |                          |
|             |                   | AHY   | 6495           | 0             | 0             | 0             | 6495 (16.9)        |                          |
|             |                   | Total |                | 32 286 (84.2) | 70 (0.2)      | 4610 (12.0)   | 1359 (3.5)         | 38 325 (35.1)            |
| Grand total |                   |       |                | 55 787 (51.1) | 1407 (1.3)    | 43 119 (39.5) | 8896 (8.1)         | 109 209 (90 984–136 794) |

Notes: Confidence intervals of 95% are given for total salmonids consumed across all bird species (Grand total). Results shown are those derived from Eq. 4 (Birt-Friesen et al. 1989). Blank cells indicate that no birds of a given species × age class were present.

† Avian-predator key: CAGU, California Gull; CATE, Caspian Tern; COME, Common Merganser; DCCO, Double-crested Cormorant; RBGU, Ring-billed Gull.

‡ Key to abbreviations: HY, hatch-year bird; AHY, after-hatch-year bird (i.e., sub-adults and adults).

TABLE 3. Mean aggregate percentage fresh mass of salmonids found in bird stomachs collected on the Columbia River in Chelan County, Washington, USA, summer 2002–2004.

| Avian predator species† | Age‡ | 2002      |           | 2003      |          | 2004      |           |
|-------------------------|------|-----------|-----------|-----------|----------|-----------|-----------|
|                         |      | Early     | Late      | Early     | Late     | Early     | Late      |
| CAGU                    | HY   |           | 4.5 (10)  |           | 0.0 (17) |           | 0.0 (24)  |
|                         | AHY  | 50.8 (22) | 6.8 (28)  | 41.9 (17) | 2.1 (20) | 47.3 (20) | 15.9 (19) |
| CATE                    | HY   |           | §         |           | N/A      |           | §         |
|                         | AHY  | 99.4 (8)  | 5.4 (56)  | 62.5 (12) | 9.7 (43) | 36.6 (11) | 19.3 (37) |
| COME                    | HY   |           | N/A       |           | §        |           | 19.7 (17) |
|                         | AHY  | 12.8 (7)  | 2.6 (5)   | 16.5 (21) | 9.7 (10) | 40.9 (31) | 2.3 (19)  |
| DCCO                    | HY   |           | 5.5 (44)  |           | 6.4 (52) |           | 0.0 (14)  |
|                         | AHY  | §         | 4.0 (28)  | 7.7 (9)   | 2.1 (22) | 23.5 (36) | 7.4 (32)  |
| RBGU                    | HY   |           | 3.6 (26)  |           | 3.5 (16) |           | 0.0 (17)  |
|                         | AHY  | 61.5 (25) | 14.3 (34) | 50.2 (26) | 3.0 (35) | 62.6 (23) | 7.1 (28)  |

Notes: Early period = 25 March to 15 June; late period = 16 June to 31 August. Samples sizes of birds with fish or otoliths in their stomachs are shown in parentheses (see *Methods: Bioenergetics approaches: Diet* for details). Blank cells indicate that no birds of a given species × age class were present.

† Species key: CAGU, California Gull; CATE, Caspian Tern; COME, Common Merganser; DCCO, Double-crested Cormorant; RBGU, Ring-billed Gull.

‡ Key to abbreviations: HY, hatch-year bird; AHY, after-hatch-year bird (i.e., subadults and adults).

§ Sample size <5.

species ( $\chi^2 = 21.21$ ,  $df = 1$ ,  $P < 0.0001$ ). During the peak in bird abundance (late), salmonids never exceeded 20% of fresh mass diet, and was <10% for the majority of bird species and age classes (Table 3). Relative to terns and gulls, mergansers and cormorants had significantly lower salmonid fresh mass in their diets, especially during the early period (post-hoc test:  $\chi^2 = 9.6$ ,  $df = 1$ ,  $P < 0.005$ ).

#### Bird abundance along reaches

The absolute number of terns, gulls, cormorants, and mergansers along the roughly 100 km of the Columbia River between Wells Dam and Rock Island Dam, and the changes in these numbers across the season from late March through August were remarkably similar among years (Fig. 2). Overall, bird abundance was low from late March through June (calendar weeks 12–26), with a weekly average of only 142 birds. However, bird numbers increased rapidly from early July to peak at >1000 birds per reach survey by August before decreasing. Common Mergansers dominated the species assemblage until mid-July, comprising, on average, 55% of all birds seen (Fig. 3A). After July, Ring-billed Gulls became the most abundant species (45% of total). This latter peak included breeders and hatch-year birds invading the River after the breeding season. Caspian Terns and Double-crested Cormorants were consistently minor players, comprising ~10% of total birds (Fig. 3B). In sum, this stretch of the mid-Columbia River appears to be dominated by resident Common Mergansers, and seasonally visited by Ring-billed and California Gulls after the close of the breeding season. Total birds seen over the season may vary, although the seasonal pattern of appearance appears to be persistent across years.

#### Bioenergetic model

Using Eq. 4, piscivorous birds on the Columbia River in the vicinity of Chelan County consumed between

747 000 and 2.5 million fish annually between 25 March and 31 August 2002–2004. The great majority (34–83%) of these, especially in 2004, were sticklebacks (*Gasterosteus aculeatus*). Of the totals, only 4.4–6.0% (44 830–109 209) were salmonids (not including mountain whitefish; Table 3). In all years, about 60% of salmonids were consumed during the early period (Table 3), a result of the sequential seasonal interaction between salmonid availability (high, low) and number of avian predators (low, high). With the exception of 2003, sockeye dominated the salmonid portion of the avian diet during the early period. Chinook, presumably sub-yearling chinook, dominated the late period in all years (>76%). We could not directly distinguish between spring chinook (the listed ESU [evolutionarily significant unit]) and other chinook (e.g., summer, fall) from our diet samples. Hatchery-release data, however, indicate that about 85–96% of chinook released in the early season above Rock Island Dam are spring chinook, whereas practically none of the chinook released late are springs (FPC 2004). Applying these proportions to the model output suggests that the majority of chinook consumed by birds were not spring chinook.

We used both formulations for the calculations of daily energy expenditure (DEE) but present tabular results only for the more conservative approach (e.g., lower numbers of fish consumed, Table 2; Birt-Friesen et al. 1989; Eq.4). Using Eq. 5 (Nagy 1987) to determine DEE increased overall salmonid consumption by 54%; and DEE formulation, together with the number of birds in the system, was the largest contributing factor in the elasticity analysis (Table 4). Varying other critical input parameters by 10% of their value and comparing the impact on model output revealed that the proportion of salmonids in the diet ranked third, followed by bird mass. Fluctuations in mean mass and energy content of

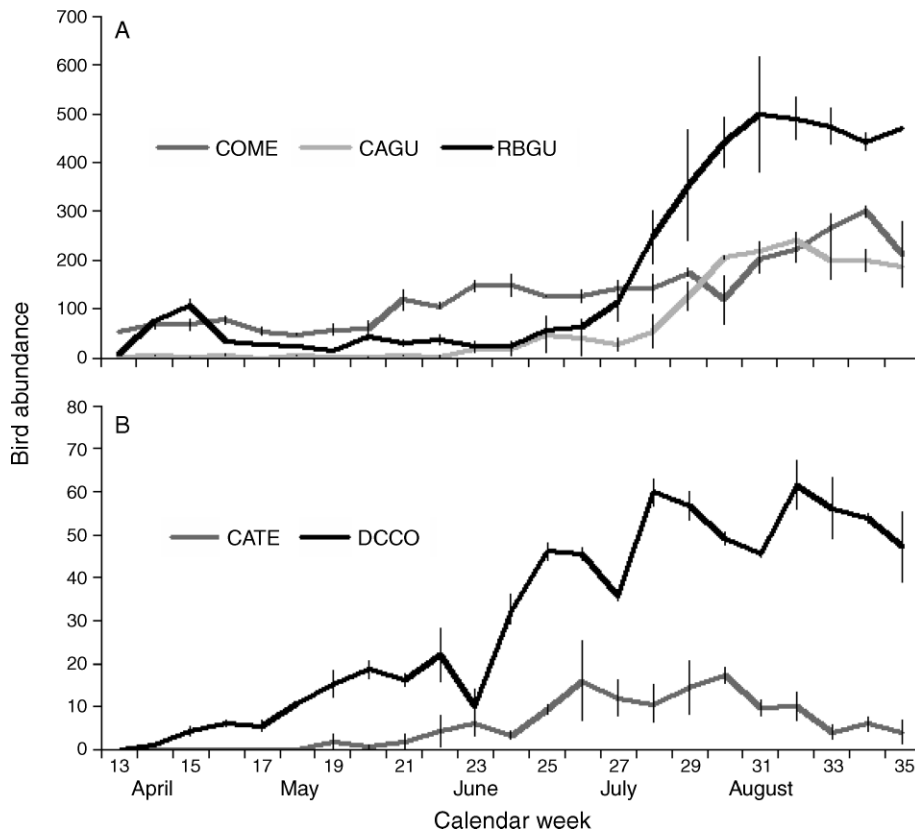


FIG. 3. Weekly abundance of five species of birds observed during reach surveys between Rock Island and Wells dams, Washington, USA, and at roosting areas immediately north of Rock Island Dam (cormorants only), 2002–2004: (A) Common Mergansers (COME), California Gulls (CAGU), and Ring-billed Gulls (RBGU); (B) Caspian Terns (CATE) and Double-crested Cormorants (DCCO). Data are means  $\pm$  SE.

fish consumed had low elasticities and contributed little to changes in the final consumption estimates.

*Percentage of smolt runs consumed by birds*

To estimate the percentage of each salmonid species taken by birds within the study area, we used the mean output of the bioenergetics model (Table 3) and a series of smolt availability estimates. For hatchery chinook, coho, and steelhead, we used release data (FPC 2004), and applied a distance-specific mortality rate of 0.0006% loss per kilometer traveled from release site to entry into the study area (from Muir et al. 2001: Fig. 6). We

estimated additional wild production from published species-specific hatchery-to-wild ratios: coho, 95% hatchery, chinook 75%, steelhead 70% (Columbia Basin Fish and Wildlife Authority 1990, cited in NRC [1996]). Because wild sockeye productivity is extremely variable from year to year, we used annual estimates of sockeye smolt production from the Lake Wenatchee system (I. Miller, unpublished data) and from acoustic surveys in Lake Osoyoos (Rankin et al. 2003, Hyatt and Rankin 2005), which collectively represent the majority of sockeye entering our study area. These estimates included the hatchery release data from the Okanagan

TABLE 4. Elasticities for 10% changes in input parameter values on chinook consumption (bioenergetic model output).

| Parameter                     | Avian predators† |       |       |       |       | Mean $\pm$ SD    |
|-------------------------------|------------------|-------|-------|-------|-------|------------------|
|                               | CAGU             | CATE  | COME  | DCCO  | RBGU  |                  |
| No. birds                     | 1.02             | 0.98  | 1.02  | 1.02  | 1.02  | 1.01 $\pm$ 0.02  |
| Daily energy expenditure, DEE | 1.00             | 0.99  | 1.01  | 1.04  | 1.00  | 1.01 $\pm$ 0.02  |
| Percentage chinook in diet    | 0.77             | 0.96  | 1.02  | 0.92  | 0.73  | 0.88 $\pm$ 0.13  |
| Bird mass                     | 0.75             | 0.72  | 0.75  | 0.76  | 0.75  | 0.75 $\pm$ 0.01  |
| Energy density of chinook     | -0.21            | -0.05 | -0.01 | -0.07 | -0.25 | -0.12 $\pm$ 0.11 |
| Mean mass of chinook          | -0.21            | -0.04 | -0.01 | -0.07 | -0.25 | -0.12 $\pm$ 0.11 |

Notes: Calculations are shown for adult birds in 2004. Patterns and values in other years and ages were similar.

† For key to avian predators, see Table 2.

TABLE 5. Estimates of percentage smolt mortality attributable to bird predation in Chelan County together with history of smolt availability.

| Salmonid species, by year | Hatchery release | Mortality before reaching Chelan County | Hatchery : wild ratio† | Total no. smolts |                         | Percentage of available smolts consumed |
|---------------------------|------------------|---|------------------------|------------------|-------------------------|---|
|                           |                  |   |                        | Available        | Taken by bird predation |   |
| 2002                      |                  |   |                        |                  |                         |   |
| Chinook                   | 6 502 212        | 328 487                                 | 0.75                   | 7 799 278        | 26 256                  | 0.34                                    |
| Coho                      | 1 182 134        | 35 339                                  | 0.95                   | 1 205 902        | 859                     | 0.07                                    |
| Steelhead                 | 877 386          | 48 534                                  | 0.7                    | 1 092 068        | 271                     | 0.02                                    |
| Sockeye                   | 3 656 716        | 277 480                                 | NA                     | 3 379 236        | 32 541                  | 0.96                                    |
| 2003                      |                  |   |                        |                  |                         |   |
| Chinook                   | 5 977 095        | 259 606                                 | 0.75                   | 7 211 763        | 30 218                  | 0.42                                    |
| Coho                      | 1 181 623        | 33 579                                  | 0.95                   | 1 207 125        | 2888                    | 0.24                                    |
| Steelhead                 | 882 558          | 50 219                                  | 0.7                    | 1 097 106        | 3000                    | 0.27                                    |
| Sockeye                   | 7 180 056        | 177 940                                 | NA                     | 7 002 116        | 8697                    | 0.12                                    |
| 2004                      |                  |   |                        |                  |                         |   |
| Chinook                   | 6 468 738        | 309 350                                 | 0.75                   | 7 776 573        | 55 787                  | 0.72                                    |
| Coho                      | 1 334 237        | 51 352                                  | 0.95                   | 1 349 597        | 1407                    | 0.10                                    |
| Steelhead                 | 853 405          | 55 025                                  | 0.7                    | 1 054 402        | 8896                    | 0.84                                    |
| Sockeye                   | 6 622 572        | 80 711                                  | NA                     | 6 541 861        | 43 119                  | 0.66                                    |

† NRC species-specific ratios are derived from Columbia Basin Fish and Wildlife Authority (1990), cited in NRC (1996).

and Wenatchee hatcheries above, so we discounted those numbers. Note that because we could not tell wild from hatchery smolts in the gut contents of birds taken in this study, we simply assumed a take in proportion to estimated occurrence in the river. From this process we inferred that the estimated take of salmonid smolts by all birds combined never exceeded 1%, and was most often less than 0.5% per species (Table 5). If these mortality estimates are doubled, to account for potential sources of error or variation (e.g., DEE: Eq. 5 vs. Eq. 4; longer predation season, etc.), and averaged over the three years of the study, consumption in all cases remained under 1.2% (chinook, 0.91%; coho, 0.27%; steelhead, 0.69%; sockeye, 1.16%).

#### *Dam predation vs. reach predation*

In our study system the number of attacks varied between dams and periods, and among species and age classes (Fig. 4). In all years, 95% of attacks were performed by the diving species, Common Mergansers and Double-crested Cormorants. Attacks by both species were significantly higher in the late season (mergersers:  $\chi^2 = 9.20$ ,  $df = 1$ ,  $P < 0.005$ ; cormorants,  $\chi^2 = 17.26$ ,  $df = 1$ ,  $P < 0.0001$ ), when the majority of the salmonid smolts had out-migrated. By contrast, both gull species concentrated their attack effort at the dam during the early (salmonid abundant) period, a trend that was significant for California Gulls ( $\chi^2 = 5.71$ ,  $df = 1$ ,  $P < 0.05$ ). As would be expected, after-hatch year birds carried out more attacks overall ( $\chi^2 = 35.82$ ,  $df = 1$ ,  $P < 0.0001$ ).

Foraging success also varied among species ( $\chi^2 = 24.16$ ,  $df = 1$ ,  $P < 0.001$ ) and period ( $\chi^2 = 29.82$ ,  $df = 1$ ,  $P < 0.0001$ ; Fig. 4). During the early period, nearly one in two attacks was successful across all species (species:  $\chi^2 = 8.85$ ,  $df = 1$ ,  $P > 0.05$ ), whereas late period success

rates were manifestly lower. Success rates of after-hatch year birds differed among species ( $\chi^2 = 15.75$ ,  $df = 1$ ,  $P < 0.005$ ) with gulls succeeding at 35% or more of their attempts, and cormorants a little over half of that (Fig. 4). Although foraging success for cormorants and mergansers may be biased low because they tend to swallow their prey under water, our observed values fall within the ranges in previous literature (Wood and Hand 1985, Hatch and Weseloh 1999).

Combining the data on attack and success rates allows an estimation of the total number of fish removed by each predator type at each dam. Assuming that bird diet did not differ between birds found at dams and those along the reaches, we partitioned predation on salmonids between dams and reaches, by subtracting those fish that must have been consumed at the dams from the total salmonid consumption estimated by the bioenergetics model. With the exception of adult cormorants (roosting at Rock Island Dam) and adult California Gulls in 2002, all species  $\times$  age class combinations consumed the majority of salmonids away from the dams (Table 6). In fact, we estimate that overall, 85–98% of the predation on salmonid smolts occurred away from dams, as did a majority of the predation on the other fish species.

#### *Management scenarios*

*Alternative predator abundance.*—To estimate what the total present-day impact of avian predators on salmonid smolts would be in the absence of lethal control, we added the birds that were shot by USDA Wildlife Services in 2002–2004 (total of 2316 or 8.8% of live birds counted in the system, and up to 60% of birds present in any given week) back into the system (predator-abundance parameter in the bioenergetics model), and conservatively assumed that they stayed

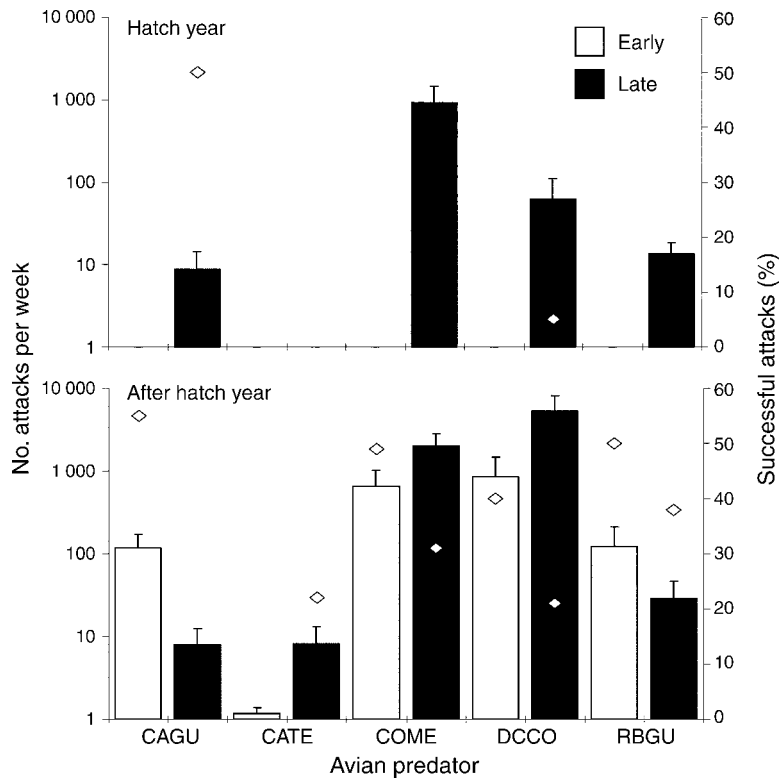


FIG. 4. Number of estimated attacks (bars) and success rates (diamonds) per week in the early (25 March–15 June) and late (16 June–31 August) periods 2002–2004 at Rock Island and Rocky Reach Dams by hatch-year and after-hatch-year birds. Data are means + SE. Lack of values indicates that a given species × age class made no attacks. For avian-predator codes, see Fig. 3.

for the remainder of the season. Thus, we calculate a worst-case present-day smolt-mortality scenario. This approach estimated that salmonid consumption would have been 2.32, 1.36, and 1.45 times higher in 2002, 2003, and 2004, respectively. The higher difference in 2002 is mostly due to the much higher number of birds

taken that year, especially during the early season (428 vs. 153 and 141 in 2003 and 2004, respectively).

The second predator-abundance scenario compared the present-day gull counts to historic gull counts (no historic data are available for other species) at Rock Island and Rocky Reach dams during the early season

TABLE 6. Of the number of salmonids consumed by birds, the estimated percentage consumed at the dams (Rock Island and Rocky Reach) in Chelan County, Washington, USA, 25 March–31 August 2002–2004.

| Species† | Age‡ | 2002  |       | 2003  |      | 2004  |      |
|----------|------|-------|-------|-------|------|-------|------|
|          |      | Early | Late  | Early | Late | Early | Late |
| RBGU     | AHY  | 18.9  | 0.6   | 0.1   | 0.1  | 3.1   | 0.0  |
|          | HY   |       | 0.3   |       | 0.5  |       | 0.0  |
| CAGU     | AHY  | 100.0 | 1.2   | 5.7   | 0.3  | 12.9  | 0.6  |
|          | HY   |       | 1.6   |       | 0.0  |       | 0.0  |
| COME     | AHY  | 1.6   | 7.7   | 14.3  | 10.2 | 0.6   | 0.7  |
|          | HY   |       | 0.0   |       | 0.0  |       | 0.0  |
| DCCO     | AHY  | 40.8  | 100.0 | 100.0 | 54.1 | 18.4  | 12.3 |
|          | HY   |       | 0.2   |       | 0.0  |       | 0.0  |
| CATE     | AHY  | 0.0   | 0.0   | 0.0   | 0.0  | 0.0   | 0.0  |
|          | HY   |       | 0.0   |       | 0.0  |       | 0.0  |
| Total    |      | 10.6  | 12.4  | 14.4  | 15.0 | 3.5   | 2.1  |

Notes: The remainder (i.e., 100% minus the table values) corresponds to salmonids that were consumed from along the reaches. Blank cells reflect the fact that HYs do not consume salmonids in the early season.

† For avian-predator species codes see Table 2.

‡ Key to abbreviations: HY, hatch-year bird; AHY, after-hatch-year bird (i.e., sub-adults and adults).

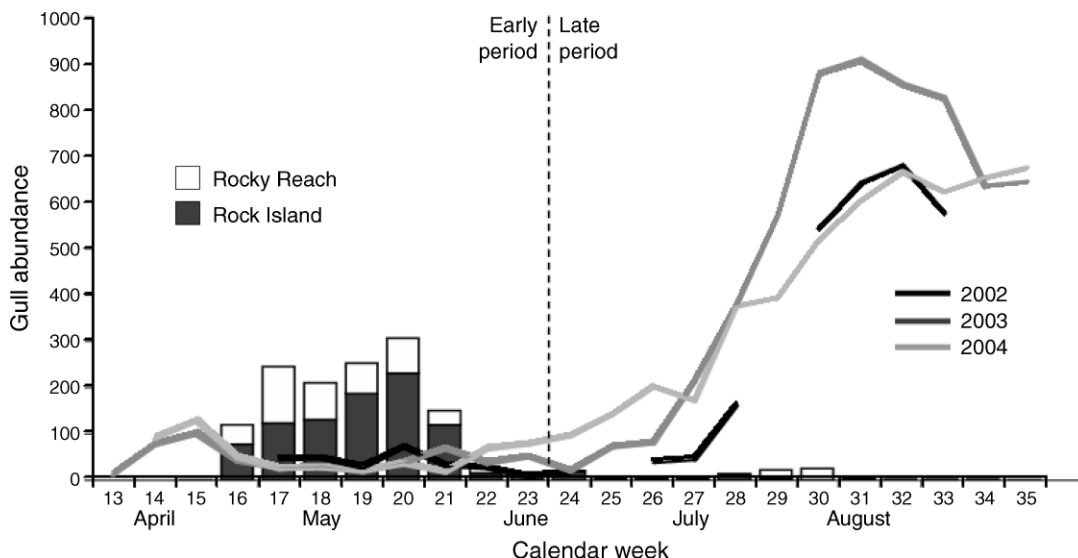


FIG. 5. Current (lines) and historic (bars) weekly average counts of gulls in Chelan County. Lines are 2002–2004 data from reach surveys; bars are 1979–1982 data from counts at dams.

of 1979–1983 (Fig. 5; COFO 1980, 1981, 1982, 1985). According to the historic data, gull visitation at dams during the peak salmonid out-migration period was higher than currently observed throughout the reaches (Fig. 5). Because there is no historic information on bird diet, or even the species of gulls, we ran this scenario assuming the maximum salmonid consumption diet observed in this study: Ring-billed Gulls during early season 2004. Calculating the past salmonid-consumption scenario for the early season only, we estimate that gulls congregating at dams may have consumed roughly 15 647 smolts per year (95% CI 13 226–18 387) during 1979–1983. By comparison, early period gulls during 2002–2004 consumed 8207 to 12 999 salmonid smolts per year.

#### Higher-order interactions

Finally, it is important to remember that all of the bird species consumed a wide variety of prey species, many of which interact with each other. The best example is northern pikeminnow, a well-known salmon smolt predator (Vigg et al. 1991, Beamesderfer et al. 1996). Avian predators, mostly mergansers and gulls, consumed 28 000–97 000 juvenile pikeminnow per year (Table 7), roughly equal to the number of salmonids taken in the two latter years. Between 72% and 82% of this predation occurred in the late period, when the majority of salmonids had left the system, forcing birds to turn to alternative prey.

We quantified the effects of this ecosystem interaction by comparing the total number of salmonid smolts eaten by the birds, iterated annually, to the total number of salmonid smolts pikeminnow would have eaten had (1) the birds been removed from the system, releasing the pikeminnow from predator control, and (2) some

percentage of the released pikeminnow been allowed to grow out to an age at which they would begin to consume salmonids (set at three years). Assuming no compensation, (i.e., that no other predator in the system would consume juvenile pikeminnow released by predation in the absence of birds), in the first year after pikeminnow reach 3 years of age, an additional  $447\,955 \pm 15\,230$  (mean  $\pm$  SE) salmonid smolts would have been consumed by these piscine predators. However, removal of predators from a system (in this case, the annual removal of bird predators) rarely translates into a concomitant increase in prey survival. It is likely that other predators would have consumed a fraction of the juvenile pikeminnow not eaten by the (removed) bird predators, i.e., there would be compensation. However, even with 80% of the juvenile pikeminnow cohort removed annually by other predators, keeping birds in the system (i.e., having no lethal control of birds) still resulted in an average net salmonid benefit in excess of  $2\,020\,000 \pm 57\,401$  fish (mean  $\pm$  SE) over the 11-year period we ran the model.

#### DISCUSSION

Bioenergetic approaches have been used in a variety of ecological, conservation, and management contexts, including assessment of the impacts of climate on consumption patterns (Petersen and Kitchell 2001, Humphries et al. 2002), input of fishery-derived food resources on predator populations (Arcos and Oro 2002), dynamics of an introduced predator (Kooi et al. 1999), foraging needs of listed species (Winship et al. 2002), and effects of predators on prey of commercial or conservation interest (Peer et al. 2003, Roby et al. 2003, Antolos et al. 2005, this study). Although input parameters to bioenergetic models are numerous,

TABLE 7. Estimated number of northern pikeminnow consumed by avian predators in the mid-Columbia River in Chelan County, 25 March–31 August 2002–2004.

| Avian predator                 |     | No. northern pikeminnow consumed |               |                 |
|--------------------------------|-----|----------------------------------|---------------|-----------------|
| Species                        | Age | 2002                             | 2003          | 2004            |
| Early period, 15 March–15 June |     |                                  |               |                 |
| RBGU                           | AHY | 394 ± 34                         | 521 ± 50      | 1806 ± 172      |
|                                | HY  |                                  |               |                 |
| CAGU                           | AHY | 35 ± 3                           | 141 ± 14      | 249 ± 23        |
|                                | HY  |                                  |               | 19 ± 2          |
| COME                           | AHY | 7097 ± 965                       | 8591 ± 1170   | 13 838 ± 1936   |
|                                | HY  | 108 ± 9                          | 280 ± 22      | 418 ± 37        |
| DCCO                           | AHY | 202 ± 15                         | 392 ± 30      | 1435 ± 125      |
|                                | HY  |                                  |               | 64 ± 6          |
| CATE                           | AHY | 0                                | 0             | 0               |
|                                | HY  |                                  |               |                 |
| Total                          |     | 7836 ± 1025                      | 9924 ± 1286   | 17 829 ± 2301   |
| Late period, 16 June–31 August |     |                                  |               |                 |
| RBGU                           | AHY | 11 102 ± 934                     | 18 500 ± 1550 | 30 592 ± 2723   |
|                                | HY  | 3959 ± 342                       | 5469 ± 472    | 5264 ± 497      |
| CAGU                           | AHY | 1052 ± 88                        | 2862 ± 241    | 7828 ± 682      |
|                                | HY  | 1691 ± 165                       | 3881 ± 357    | 2598 ± 245      |
| COME                           | AHY | 0                                | 2507 ± 334    | 27 830 ± 3 677  |
|                                | HY  | 0                                | 2041 ± 151    | 717 ± 55        |
| DCCO                           | AHY | 1589 ± 122                       | 4570 ± 364    | 3550 ± 275      |
|                                | HY  | 0                                | 0             | 30 ± 2          |
| CATE                           | AHY | 417 ± 34                         | 312 ± 26      | 494 ± 43        |
|                                | HY  | 14 ± 1                           | 19 ± 2        | 45 ± 5          |
| Total                          |     | 19 825 ± 1686                    | 40 161 ± 3496 | 78 948 ± 8205   |
| Grand total                    |     | 27 661 ± 2711                    | 50 085 ± 4782 | 96 777 ± 10 506 |

Note: Data are means ± SE. Results were derived from Eq. 4 (Birt-Friesen et al. 1989).

difficult to determine accurately, and require up-scaling of data obtained at the individual level to the population (Ney 1990), adequate dietary and predator distribution and abundance data allow using these models to explore a range of possible scenarios, facilitating proactive management decisions.

The results of the bioenergetic modeling effort of our study indicate that the predation pressure avian predators currently exert on out-migrating salmonid smolts within the Chelan County Public Utility District (PUD) study area of the mid-Columbia River is small, despite the fact that all birds were collected in the immediate vicinity of Rock Island Dam, which may have biased at least recently consumed prey towards adfluvial and actively migrating fish, i.e., salmonids. Across all salmonid species, total consumption during the five-month spring–summer period 2002–2004 ranged between 37 000 and 137 000 fish, depending on the year (Table 2). Had no lethal control been exercised during the tenure of the study, our most liberal estimates of total salmonid consumption (that is, assuming all of these individuals remained in the system from the day they were taken) are still quite low, with a potential maximum of just under 200 000 fish taken in 2004. Had we used the Nagy (1987) rather than the Birt-Friesen (1989) energetics formulation, smolt-consumption estimates would have increased by half again, but this still produces an absolute maximum of just over 300 000 smolts consumed per year, including those that would have been consumed by the shot birds. In fact, even

when we estimate historical predation rates by gulls counted at Rock Island and Rocky Reach Dams (Fig. 1), our estimate of smolt consumption by these predators (assuming current diets) is only an additional 15 647 salmonids.

In all cases, and even accounting for potential sources of error, the estimated percentage loss of salmonids due to birds was <1.2% per stock. Thus, at current predation levels, birds consume a small fraction of the allowable 7% per stock mortality ceiling set by the Habitat Conservation Plan in the studied section of the mid-Columbia River. In comparison, in the Columbia River estuary, Roby et al. (2003) estimated that approximately 8.1–12.4 million salmon, representing ~13% of the smolts reaching the estuary, were consumed by a single tern colony of approximately 15 000 birds. Similarly, terns nesting on Crescent Island (~1200 breeding birds), located in the mid-Columbia Basin just south of the confluence of the Snake River, were estimated to have removed 465 000–679 000 smolts per year (Antolos et al. 2005). The high numbers in both places are the result of large numbers of terns, spatiotemporal overlap of tern breeding and smolt out-migration, and specialist diets composed of ~70% salmonids (Roby et al. 2003, Antolos et al. 2005).

Above Priest Rapids Dam (Fig. 1), however, the lack of colonies and low tern numbers make conditions very different. The percentage of salmonids in the diet across all birds in the Chelan County study area was, at most, one tenth that of the lower-river breeding-colony sites

(4.5–7.7%, depending on the year). Moreover, the average number of avian predators we counted on reach surveys never exceeded 500 birds, and peaked at just below 1200, or 1.8–4.5% of the estuarine breeding population of all avian species (~26 440; Collis et al. 2002). Thus, although terns, gulls, and cormorants can be considered abundant vertebrates (sensu Goodrich and Buskirk 1995) in the lower Columbia River, more than doubling in population over the last two decades (Collis et al. 2002) and tern–salmon interactions can be considered an example of hyperpredation (e.g., unnaturally high levels of prey consumption, Smith and Quinn 1996, Gibson 2006), the same is clearly not true in the mid-Columbia River above Priest Rapids.

Whereas both the estuarine and marine phases of Columbia River salmon have been identified as critical stages (Pearcy 1992, Kareiva et al. 2000), no such link has been made to the relatively brief time period smolts spend further upriver (Bickford and Skalski 2000). Roby et al. (2003) modified the McClure et al. (2000) cumulative risk initiative (CRI) approach to assess the effect of a management action on the percentage increase in  $\lambda$  of a given salmon stock. Eliminating tern predation from the estuary and assuming that 50% of the smolt mortality was compensatory yielded only a 0.96% gain in the population growth rate for endangered steelhead (1–1.4 million consumed by estuarine terns; Roby et al. 2003). The current northern pikeminnow management program may increase  $\lambda$  by a maximum of 0.4–0.7% (Roby et al. 2003). Although pikeminnows overall consume more smolts than estuarine terns (~16 million annually throughout the lower Columbia and Snake Rivers; Ward et al. 1995, Beamesderfer et al. 1996), this predation occurs further upriver and thus earlier in the salmonid life history, when each smolt has a lower future reproductive value relative to the older individuals reaching the estuary. Given the low number of relatively early life history smolts consumed in the mid-Columbia Chelan County region by birds, salmonid population growth would be essentially unaffected by total removal of this particular predation source (parallel to investigations on the removal on non-indigenous species by Harvey and Kareiva [2005]), especially assuming likely predatory compensation by other in-river predators (e.g., pikeminnow). By contrast, much larger increases in  $\lambda$  (median, 7%; range, 1–62%) for several listed ESUs (evolutionarily significant units) have been calculated based on a variety of management actions ranging from dam passage improvements for both smolts and adults, to a no-harvest scenario (Kareiva et al. 2000, McClure et al. 2000, 2003).

#### *Ecology vs. policy*

Since 1997 an average of  $3360 \pm 1808$  (mean  $\pm$  SD) avian predators per year have been shot at the five mid-Columbia dams and two associated hatcheries, for a total of 16 800 birds from 1997 through 2001 (USDA 2003). Almost 90% of this take occurred at three dams:

Wanapum, Priest Rapids, and Rock Island. The vast majority have been Larids, principally Ring-billed and California Gulls (48% and 27% cumulative, respectively). The take of Caspian Terns was only 9%, Double-crested Cormorants 6%, and Common Mergansers 3%. Herons and miscellaneous/unidentified gulls made up the remainder of the total cumulative take. It is possible that the current low impact of bird predation on out-migrating salmonid smolts in the Chelan County PUD study area may be a result of the avian-predator management programs begun in the 1990s. Were these the correct predators to take?

Within the time frame of this study, Common Mergansers were clearly the most important salmonid smolt predator at the population level. Adults collectively consumed just over half of all smolts estimated to have been taken by birds in the study area (Table 2). Significant predation on smolts by mergansers has been documented in the Big Qualicum River on Vancouver Island, where they were responsible for 24–65% of smolt loss (Wood 1987), as well as in Scotland, where they consumed 3–16% of salmon smolts on two rivers (Feltham 1995). Given their overlap with peak smolt numbers in the mid-Columbia River, and the fact that mergansers raise large broods on the river, it is not surprising that their relative contribution to predation is high. However, the per capita impact of mergansers was low. Paradoxically, the least abundant avian predator in the system, Caspian Terns, represented the highest per capita impact. Per capita scoring allows for the possibility of proactive management strategies, as predators of high importance, either within or among salmonid species, are identified as those whose relative increase in the system would lead to the largest increase in the number of salmonids consumed. Thus, an increase in adult Caspian Terns would have a far greater effect than a similar numeric increase in mergansers. This result is not surprising, given their high consumption of salmonid smolts, particularly steelhead, in the mid and lower Columbia (Collis et al. 2001, Ryan et al. 2003, Antolos et al. 2005), and evidence of tern predation of salmon smolts elsewhere (Sweden, Soikkeli 1973; Grays Harbor, Washington, USA, Smith and Mudd 1978). However, tern visitation to this particular stretch of the river is infrequent (Fig. 3B); this species was consistently absent from the river during April and into May, when smolt numbers were high. In sum, to the extent that avian predation on smolts needs to be managed in this system, current management strategies should concentrate on Common Mergansers, followed by gulls, whereas future management strategies should be aimed at minimizing the relative increase in Caspian Terns.

The fact that overall impact of bird predators on salmonid smolt mortality is low seems inconsistent with situations in which birds are concentrated in space and time in highly visible locations such as dams. Early accounts of gull visitation to mid-Columbia River dams routinely mentioned “hundreds” of birds, although few



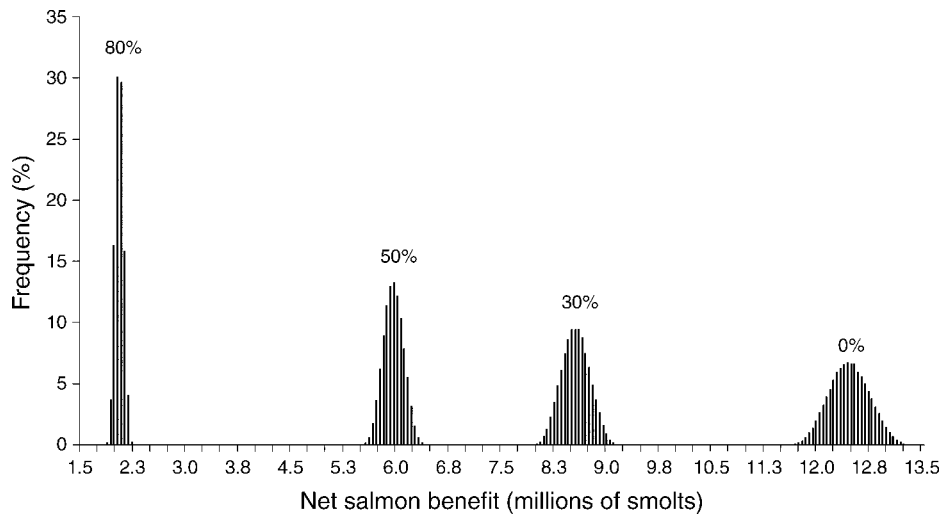


FIG. 6. Net salmonid benefit, or the number of salmonid smolts that would theoretically have been saved from predation in the Chelan County system, over an 11-year period, had birds not been removed. Data are output from a linked bioenergetics–population matrix model with 100 000 runs per scenario. No compensation (0%), and 30%, 50%, and 80% compensation scenarios for juvenile northern pikeminnow mortality in the absence of bird predation are shown.

verifiable data sets exist (e.g., Ruggerone 1986). Visible concentrations of avian predators preying on commercial or recreational fishery resources have been the impetus for hazing and lethal-control programs worldwide (Kirby et al. 1996, Frederiksen et al. 2001, Wright 2003). The historical data sets we recovered from Chelan County did, in fact, indicate significantly higher gull concentrations at the dams during the early season than those we witnessed during the three years of this study (Fig. 5). To our knowledge, there were never gull colonies in the vicinity of either dam. Changes in the timing of gull abundance may instead be a consequence of the imposition of control measures, including lethal control, hazing, and wires, all dissuading gulls from foraging in the tailrace, where the historical counts were taken. Late season gull abundance documented in this study was concentrated in the forebay (J. K. Parrish, unpublished data).

Are dams the correct location to curb avian predation? Skalski et al. (2001) estimated total project (that is, reach plus dam) survival of steelhead smolts for both Rocky Reach and Rock Island projects, using radio tags to monitor movement and loss rates of fish. Overall survival was quite high (96.58% and 99.83%, respectively), with reach-associated mortality (6.07% and 2.49%) significantly higher than dam-associated mortality (which in that study was essentially zero). Although the authors speculate that potential biases in release design may have artificially elevated reach-mortality estimates, a larger point is that the majority of mortality occurred away from dams. A later study on chinook smolt survival from Rocky Reach through Wanapum dams (Skalski et al. 2002) came to similar conclusions, namely that although project survival was quite high (93.91–94.76%), mortality along the reaches exceeded mortality due to passage

through the dams by 1% to almost 4%. Our observations of bird abundance and foraging effort at the dams support these findings in that the majority of bird predation seems to occur along the reaches. Thus, control strategies confined to the dams, although more easily implemented, are not maximally effective at deterring avian predation on salmonid smolts, given the current diversity, distribution, and abundance of birds.

#### *Ecosystem considerations*

Before adopting a specific management strategy it is important to determine the strength of predator–prey relationships (Wootton 1997, Steinmetz et al. 2003) and the likely community-level effects of weakening them (Kitchell et al. 2000). Our study underscores the crucial, and obvious, point that even highly managed systems such as the Columbia River are still complex ecosystems in which alterations can provoke direct and indirect ripple effects. A case in point is the dietary switch avian predators make from salmonids to pikeminnow across the season.

Linking our bioenergetics model to a simple stochastic model of a coupled predation–population matrix for pikeminnow created a specific “what if” tool allowing exploration of potential resource-management effects of increasing one predator over another. Broader food-web mass-balance approaches have often been used to simulate existing ecological data, allowing prediction of the relative strength of predator–prey connections (Bundy 2001, Bundy and Fanning 2005), identifying the importance of compensatory and depensatory feedbacks within fished systems (Walters and Kitchell 2001), and generating hypotheses about the consequences of discrete management actions (e.g., Kitchell et al. 2000, Harvey et al. 2003, Harvey and Kareiva 2005). Linking

more data-explicit bioenergetics models to predator–population models has allowed for post hoc explorations of the effects of predators in shaping communities (e.g., Williams et al. 2004). In our modeling scenarios, allowing birds to remain in the system rather than removing them, even at a relatively high level of predator compensation on juvenile pikeminnow (e.g., 80%), resulted in a large net savings of salmonid smolts (approximately 2 million smolts saved over the 11-year period; Fig. 6). In this ecosystem-based strategy, late-season birds actually become indirect tools of salmonid predator control instead of hyper-predators. Managing for minimal early-season bird abundance, via hazing and passive structures (e.g., wires at dams, caps on piling throughout the reaches; J. K. Parrish, *unpublished data*) would improve this approach. Of course, the simple solution is to also control pikeminnow, which is exactly the current management plan.

An ecosystem approach to fishery management has been put forward as a strategy to provide society with continued access to fishery resources while simultaneously preserving the structure and functions of a healthy ecosystem upon which resource production is based (Pikitch et al. 2004). In such an approach, maintenance of system goods goes hand-in-hand with a deepening in our understanding of the ecosystem relationships most likely to be affected by human interventions (e.g., Kitchell et al. 2000). Our analysis demonstrates that identifying the strength of ecosystem interactions (e.g., Essington and Hansson 2004) represents a top priority when attempting to manage the abundance of a particular ecosystem constituent—and that the consequences of a single-species view may be counterintuitive, and potentially counterproductive.

#### ACKNOWLEDGMENTS

We thank the Chelan County PUD, Joanna Smith, Kate Litle, Kristian Happa-Aho, Heather Ziel, Marlisa Walden, Marissa Stratton, Bill Walker, Spencer Smith, Jon Walsh, Liz Donelan, Colin French, and the 2002–2004 Wenatchee field crews. The manuscript was much improved thanks to three anonymous reviewers. Funding was provided by Chelan County PUD.

#### LITERATURE CITED

- Antolos, M., D. D. Roby, D. E. Lyons, K. Collis, A. F. Evans, M. Hawbecker, and B. A. Ryan. 2005. Caspian Tern predation on juvenile salmonids in the Mid-Columbia River. *Transactions of the American Fisheries Society* 134:466–480.
- Arcos, J. M., and D. Oro. 2002. Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater *Puffinus mauretanicus*. *Marine Ecology Progress Series* 239:209–220.
- Beamesderfer, R. C. P., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake Rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2898–2908.
- Bickford, S. A., and J. R. Skalski. 2000. Reanalysis and interpretation of 25 years of Snake–Columbia River juvenile salmonid survival studies. *North American Journal of Fisheries Management* 20:53–68.
- Birt-Friesen, V. L., W. A. Montevecchi, D. K. Cairns, and S. A. Macko. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* 70:357–367.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing common raven predation on desert tortoises. *Environmental Management* 32:205–217.
- Brugger, K. E. 1993. Digestibility of three fish species by Double-crested Cormorants. *The Condor* 95:25–32.
- Bundy, A. 2001. Fishing on ecosystems: the interplay of fishing and predation in Newfoundland–Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1153–1167.
- Bundy, A., and L. P. Fanning. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1474–1489.
- Castro, G., N. Stoyan, and J. P. Myers. 1989. Assimilation efficiency in birds: a function of taxon or food type? *Comparative Biochemistry and Physiology A* 92:271–278.
- Chavez, K. J. H. 1997. Gut passage time, energy assimilation efficiency and growth in captive chicks of two fish-eating seabirds: Caspian tern and elegant tern. Thesis. California State University, Long Beach, California, USA.
- COFO [Committee on Fishery Operations]. 1980. Annual Report of the Committee on Fishery Operations. Summary of 1979 special project operations. Chelan County Public Utility District, Wenatchee, Washington, USA.
- COFO [Committee on Fishery Operations]. 1981. Annual Report of the Committee on Fishery Operations. Summary of 1981 special project operations. Chelan County Public Utility District, Wenatchee, Washington, USA.
- COFO [Committee on Fishery Operations]. 1982. Annual Report of the Committee on Fishery Operations. Summary of 1982 special project operations. Chelan County Public Utility District, Wenatchee, Washington, USA.
- COFO [Committee on Fishery Operations]. 1985. Annual Report of the Committee on Fishery Operations. Summary of 1983 special project operations. Chelan County Public Utility District, Wenatchee, Washington, USA.
- Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the Lower Columbia River: implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537–550.
- Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, and R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. *Transactions of the American Fisheries Society* 130:385–396.
- Conover, M. R. 1983. Recent changes in Ring-billed and California Gull populations in the Western United States. *Wilson Bulletin* 95:362–383.
- Cypher, B. L., and J. H. Scrivener. 1992. Coyote control to protect endangered San Joaquin kit foxes at the Naval Petroleum Reserves, California. Pages 42–47 in *Proceedings of the 15th Vertebrate Pest Conference*. University of California, Davis, California, USA.
- DeMaster, D. P., and J. E. Sisson. 1992. Pros and cons of pinniped management along the North American coast to abet fish stocks. Pages 321–330 in D. R. McCuillough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Applied Science, New York, New York, USA.
- Essington, T. E., and S. Hansson. 2004. Predator-dependent functional responses and interaction strengths in a natural food web. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2215–2226.
- Feltham, M. J. 1995. Consumption of Atlantic salmon smolts and parr by goosanders: estimates from doubly-labeled water

- measurements of captive birds released on two Scottish rivers. *Journal of Fish Biology* 46:273–281.
- Frederiksen, M., J.-D. Lebreton, and T. Bregnballe. 2001. The interplay between culling and density-dependence in the great cormorant: a modelling approach. *Journal of Applied Ecology* 38:617–627.
- Gibson, L. 2006. The role of lethal control in managing the effects of apparent competition on endangered prey species. *Wildlife Society Bulletin* 34:1220–1224.
- Goodrich, J. M., and S. W. Buskirk. 1995. Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology* 9:1357–1364.
- Harvey, C. J., S. P. Cox, T. E. Essington, S. Hansson, and J. F. Kitchell. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES Journal of Marine Science* 60:939–950.
- Harvey, C. J., and P. M. Kareiva. 2005. Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia River reservoir. *Biological Invasions* 7:651–663.
- Hatch, J. J., and D. V. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). In A. Poole and F. Gill, editors. *The birds of North America*, number 441. The Birds of North America, Philadelphia, Pennsylvania, USA.
- Humphries, M. M., D. W. Thomas, and J. R. Speakman. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418:313–316.
- Hyatt, K. D., and D. P. Rankin. 2005. Fish and water management tools (FWMT) project assessments: Osoyoos Lake juvenile sockeye salmon (*Oncorhynchus nerka*) production associated with the 2001, 2002 and 2003 brood year returns of adults to the Okanagan R., British Columbia. Report to file: JSIDS-SRe2-05. Salmon and Freshwater Ecosystems Division, Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada.
- Karasov, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* 13:391–415.
- Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer chinook salmon in the Columbia River basin. *Science* 290:977–979.
- Kirby, J. S., J. S. Holmes, and R. M. Sellers. 1996. Cormorants *Phalacrocorax carbo* as fish predators: an appraisal of their conservation and management in Great Britain. *Biological Conservation* 75:191–199.
- Kitchell, J. F., et al. 2000. Sustainability of the Lake Superior fish community: Interactions in a food web context. *Ecosystems* 3:545–560.
- Kooi, B. W., M. P. Boer, and S. A. L. M. Kooijman. 1999. Resistance of a food chain to invasion by a top predator. *Mathematical Biosciences* 157(1–2):217–236.
- Leopold, A. 1949. Thinking like a mountain. Pages 129–133 in *A Sand County almanac*. Oxford University Press, New York, New York, USA.
- Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C., USA.
- McClure, M. M., E. E. Holmes, B. K. Sanderson, and C. E. Jordan. 2003. A large-scale multispecies status assessment: anadromous salmonids in the Columbia River basin. *Ecological Applications* 13:964–989.
- McClure, M., B. Sanderson, E. Holmes, C. Jordon, P. Kareiva, and P. Levin. 2000. A standardized quantitative analysis of risks faced by salmonids in the Columbia River basin. National Marine Fisheries Service, Seattle, Washington, USA.
- Muir, W. D., S. G. Smith, J. G. Williams, and E. E. Hockersmith. 2001. Survival estimates for migrant yearling chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia Rivers, 1993–1998. *North American Journal of Fisheries Management* 21:269–282.
- Murphy, M. E., and J. R. King. 1992. Energy and nutrient use during molt by the white-crowned sparrows *Zonotrichia leucophrys gambelii*. *Ornis Scandinavica* 23:304–313.
- Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57:111–128.
- Ney, J. J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* 2:55–81.
- NRC [National Research Council]. 1996. *Upstream: salmon and society in the Pacific Northwest*. National Academy Press, Washington, D.C., USA.
- Olijnyk, C. G., and K. M. Brown. 1999. Results of a seven year effort to reduce nesting by Herring and Great Black-backed Gulls. *Waterbirds* 22:285–289.
- Parker, R. M., M. P. Zimmerman, and D. L. Ward. 1995. Variability in biological characteristics of northern squawfish in the lower Columbia and Snake Rivers. *Transactions of the American Fisheries Society* 124:335–346.
- Parrish, J. K., K. Haapa-aho, W. Walker, M. Stratton, J. Walsh, and H. Ziel. 2006. Small-bodied and juvenile fishes of the Mid-Columbia Region including keys to diagnostic otoliths and cranial bones. 2006. University of Washington, Seattle, Washington, USA.
- Pearcy, W. G. 1992. *Ocean ecology of North Pacific salmonids*. Washington Sea Grant Program, University of Washington, Seattle, Washington, USA.
- Peer, B. D., H. J. Homan, G. M. Linz, and W. J. Bleier. 2003. Impact of blackbird damage to sunflower: bioenergetic and economic models. *Ecological Applications* 13:248–256.
- Petersen, J. H., and J. F. Kitchell. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1831–1841.
- Petersen, J. H., and D. L. Ward. 1999. Development and corroboration of a bioenergetics model for northern pike-minnow feeding on juvenile salmonids in the Columbia River. *Transactions of the American Fisheries Society* 128:784–801.
- Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. *Science* 305:346–347.
- Rankin, D. P., B. Hanslit, K. D. Hyatt, and H. Wright. 2003. Surveys to determine the status of *Mysis relicta*, juvenile “nerkids” along with associated physical and biological conditions in Osoyoos Lake during 2002. Report to file: JSIDS-SRe 06-2002. Salmon in Regional Ecosystems Section, Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada.
- Rieman, B. E., and R. C. Beamesderfer. 1990. Dynamics of a northern squawfish population and the potential to reduce predation on juvenile salmonids in a Columbia River reservoir. *North American Journal of Fisheries Management* 10:228–241.
- Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. *Canadian Journal of Zoology* 81:250–265.
- Ruggerone, G. T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Transactions of the American Fisheries Society* 115:736–742.
- Ryan, B. A., S. G. Smith, J. M. Butzerin, and J. W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary, 1998–2000. *Transactions of the American Fisheries Society* 132:275–288.
- Ryder, J. P. 1993. Ring-billed Gull (*Larus argentatus*). In A. Poole and F. Gill, editors. *The Birds of North America*, number 33. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists’ Union, Washington, D.C., USA.

- SAS. 2003. Version 8. SAS Institute, Cary, North Carolina, USA.
- Skalski, J. R., J. Lady, R. Townsend, A. E. Giorgi, J. R. Stevenson, C. M. Peven, and R. D. McDonald. 2001. Estimating in-river survival of migrating salmonid smolts using radiotelemetry. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1987–1997.
- Skalski, J. R., R. Townsend, J. Lady, A. E. Girogi, J. R. Stevenson, and R. D. McDonald. 2002. Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1385–1393.
- Smith, A. P., and D. G. Quinn. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77:243–267.
- Smith, J. L., and D. Mudd. 1978. Food of the Caspian tern in Grays Harbor, Washington. *Murrelet* 59:105–106.
- Soikkeli, M. 1973. Tagged salmon smolts in the diet of the Caspian tern. Report 3. Swedish Salmon Research Institute, Turku, Sweden.
- Steinmetz, J., S. L. Kohler, and D. A. Soluk. 2003. Birds are overlooked top predators in aquatic food webs. *Ecology* 84:1324–1328.
- Thompson, D. C., and D. A. Boag. 1976. Effect of molting on the energy requirements of Japanese Quail. *Condor* 78:249–252.
- USDA [U.S. Department of Agriculture]. 2003. Environmental assessment and finding of no significant impact on piscivorous bird damage management for the protection of juvenile salmonids on the mid-Columbia River. USDA, Olympia, Washington, USA.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:421–438.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 58:39–50.
- Waples, R. 1991. Definition of a “species” under the Endangered Species Act: application to Pacific salmon. NOAA Technical Memo. National Marine Fisheries Service F/NWC-194. National Marine Fisheries Service, Portland, Oregon, USA.
- Ward, D. L., J. H. Petersen, and J. J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. *Transactions of the American Fisheries Society* 124:321–334.
- Wickens, P. A., P. A. Shelton, J. H. M. David, J. G. Field, W. H. Oosthuizen, J.-P. Roux, and A. M. Starfield. 1992. A fur seal simulation model to explore alternative management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1396–1405.
- Williams, T. M., J. A. Ester, D. F. Doak, and A. M. Springer. 2004. Killer appetites: Assessing the role of predators in ecological communities. *Ecology* 85:3373–3384.
- Winfield, I. J., D. H. Crawshaw, and N. C. Durie. 2003. Management of the cormorant, *Phalacrocorax carbo*, and endangered whitefish, *Coregonus lavaretus*, populations of Hawswater, UK. Pages 335–344 in I. G. Cowx, editor. *Interactions between fish and birds: implications for management*. Fishing News Books, Blackwell Science, Oxford, UK.
- Winkler, D. W. 1996. California Gull (*Larus californicus*). In A. Poole and F. Gill, editors. *The Birds of North America*, number 259. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists’ Union, Washington, D.C., USA.
- Winship, A. J., A. W. Trites, and D. A. S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Stellar sea lions *Eumatopias jubatus* in Alaska, USA. *Marine Ecology Progress Series* 229:291–312.
- Wires, L. R., and F. J. Cuthbert. 2000. Trends in Caspian Tern numbers and distribution in North America: a review. *Waterbirds* 23:388–404.
- Wood, C. C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I. Predation during the seaward migration. *Canadian Journal of Fisheries and Aquatic Sciences* 44:941–949.
- Wood, C. C., and C. M. Hand. 1985. Food-searching behaviour of the common merganser (*Mergus merganser*). I. Functional responses to prey and predator density. *Canadian Journal of Zoology* 63:1260–1270.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* 67:45–64.
- Wright, G. A. 2003. Impact of cormorants on the Loch Leven trout fishery and the effectiveness of shooting as mitigation. Pages 288–297 in I. G. Cowx, editor. *Interactions between fish and birds: implications for management*. Fishing News Books, Blackwell Science, Oxford, UK.
- Wydoski, R. S., and R. R. Whitney. 2003. *Inland fishes of Washington*. University of Washington Press, Seattle, Washington, USA.
- York, D. L., J. L. Cummings, J. E. Steuber, P. A. Pochop, and C. A. Yoder. 2000. Importance of migrating salmon smolt in Ring-billed (*Larus delawarensis*) and California Gull (*L. californicus*) diets near Priest Rapids Dam, Washington. *Western North American Naturalist* 60:216–220.
- Zimmerman, M. P., and D. L. Ward. 1999. Index of predation on juvenile salmonids by northern pikeminnow in the lower Columbia River basin, 1994–1996. *Transactions of the American Fisheries Society* 128:995–1007.

#### APPENDIX A

A table showing mass of bird carcasses collected in Chelan County, Washington, USA, during the summers of 2002–2004 (*Ecological Archives* A018-022-A1).

#### APPENDIX B

A table showing mean mass and caloric density of prey species found in stomachs of birds shot at Rock Island Dam, Washington, USA, during the summers of 2002–2004 (*Ecological Archives* A018-022-A2).