Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary

Daniel D. Roby, Donald E. Lyons, David P. Craig, Ken Collis, and G. Henk Visser

Abstract: We estimated the consumption of juvenile salmonids (*Oncorhynchus* spp.) and other forage fishes by Caspian terns (*Sterna caspia*) nesting on Rice Island in the Columbia River estuary in 1997 and 1998 using a bioenergetics modeling approach. The study was prompted by concern that Caspian tern predation might be a substantial source of mortality to out-migrating juvenile salmonids from throughout the Columbia River basin, many populations of which are listed as threatened or endangered under the U.S. Endangered Species Act. The bioenergetics model used estimates of the energy requirements of the tern population and the proportion of tern energy requirements met by various prey types. The resulting estimate of the number of juvenile salmonids consumed by Rice Island Caspian terns was 8.1 million (5.9–10.4 million) in 1997 and 12.4 million (9.1–15.7 million) in 1998. Tern predation rates on juvenile salmonids were substantial, representing up to 15% of the juveniles to reach the estuary from some listed populations. Nevertheless, based on simple age-structured models of salmonid populations, it appears unlikely that management of Caspian tern predation alone would reverse salmonid declines. Management to reduce tern predation could, however, contribute to a comprehensive strategy to recover imperiled salmonid populations in the Columbia River basin.

Résumé : Nous avons utilisé une approche de modélisation bioénergétique pour estimer l'importance de la consommation de jeunes salmonidés (*Oncorhynchus* spp.) et d'autres poissons proies par des sternes caspiennes (*Sterna caspia*) pendant la période de nidification à l'île Rice, dans l'estuaire du Columbia, en 1997 et 1998. Ce projet a été conçu en réaction à la crainte que la prédation par la sterne caspienne soit une importante cause de mortalité des salmonidés juvéniles au cours de leur migration vers la mer dans l'ensemble du bassin du Columbia, dont plusieurs des populations sont menacées ou en danger selon la loi sur les espèces menacées (Endangered Species Act) des États-Unis. Le modèle bioénergétique utilise des estimations des besoins énergétiques de la population de sternes et de la proportion de ces besoins qui peut être comblée par chacun des types de proies. Le nombre estimé de jeunes salmonidés consommés par les sternes de l'île Rice a été de 8,1 (5,9–10,4) millions en 1997 et de 12,4 (9,1–15,7) millions en 1998. Le taux de la prédation exercée par les sternes sur les jeunes salmonidés s'est avéré élevé, représentant jusqu'à 15 % des jeunes poissons qui ont atteint l'estuaire dans certaines populations. Néanmoins, d'après des modèles simples de populations de salmonidés structurés selon l'âge, il semble peu probable que la gestion de la prédation par les sternes caspiennes puisse à elle seule renverser la tendance au déclin des salmonidés. Une gestion visant à la réduction de la prédation par les sternes pourrait cependant contribuer à une stratégie globale de récupération des populations de salmonidés du bassin du Columbia.

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Introduction

A critical step for the recovery of threatened and endangered species is identifying factors that cause populations to decline or prevent their recovery (Caughley 1994). Species on the edge of extinction can ill afford losses from any cause, even factors that were not responsible for the species' initial decline. Natural predation can limit prey populations

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D.D. Roby, D.E. Lyons,[1] and D.P. Craig.[2] U.S. Geological Survey – Oregon Cooperative Fish and Wildlife Research Unit,[3] Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, U.S.A.
K. Collis.[4] Columbia River Inter-Tribal Fish Commission, 729 NE Oregon, Suite 200, Portland, OR 97232, U.S.A.
G.H. Visser. Centre for Isotope Research, University of Groningen, and Zoological Laboratory, P.O. Box 14, 9750 AA Haren, Netherlands.

[1] Corresponding author (e-mail: lyonsd@ucs.orst.edu).
[2] Present address: Willamette University, Department of Biology, Salem, OR 97301, U.S.A.
[3] Supported jointly by the United States Geological Survey, Oregon Department of Fish and Wildlife, and Oregon State University.
[4] Present address: Real Time Research, 201 Yellowtail Hawk Avenue, Bend, OR 97701, U.S.A.

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when predation is not density-dependent (e.g., resulting from time lags and (or) prey switching), and other factors (e.g., habitat degradation, overharvesting) reduce the population to low levels. Consequently, conservation biologists have at times found themselves in the uncomfortable position of advocating management of native predators to protect endangered prey (Goodrich and Buskirk 1995; e.g., great horned owls preying on peregrine falcons (Redig and Tordoff 1988), mountain lions preying on bighorn sheep (United States Fish and Wildlife Service (USFWS) 2000)). Before implementing predator management in the name of threatened species restoration, however, it is desirable to quantify losses to predators and the impact of these losses on demography of the prey.

Nearly all wild stocks of salmonids (*Oncorhynchus* spp.) in the Columbia River basin have experienced major declines over the last century. Twelve of 20 recognized distinct population segments or evolutionarily significant units (ESUs) (Waples 1995) of anadromous salmonids that spawn in the basin have been listed as threatened or endangered under the U.S. Endangered Species Act (ESA) (National Marine Fisheries Service (NMFS) 2000*b*). The decline of wild salmonids in the Columbia River basin has been attributed to overharvesting, habitat degradation, hydroelectric dams, and reliance on hatcheries to mitigate for lost production (Lichatowich 1999). Predation may also be a limiting factor on severely depressed wild stocks in the Columbia River basin (Beamesderfer et al. 1996), particularly if predator populations are enhanced by the annual availability of hatchery-reared juvenile salmonids. The impact on wild smolt survival resulting from the functional and numerical response of predators to hatchery-raised smolts may be greatest in the Columbia River estuary, because all smolts produced in the Columbia River basin must pass through the estuary before entering the ocean.

Numbers of piscivorous (fish-eating) colonial waterbirds nesting on the lower Columbia River and estuary have more than doubled to >80 000 individuals over the last 20 years (Collis et al. 2002). The primary waterbird taxa include several species of gulls (*Larus* spp.), Caspian terns (*Sterna caspia*), and double-crested cormorants (*Phalacrocorax auritus*). These species are all native to the Pacific Northwest, and all are protected under the Migratory Bird Treaty Act of 1918. The recent increase in waterbird populations has, however, caused some salmon managers to speculate that the magnitude of avian predation on juvenile salmonids might be sufficient to inhibit recovery of some Columbia River basin salmonid stocks in serious decline.

At one of the larger colonies of piscivorous waterbirds in the lower Columbia River, Rice Island, the diet of nesting Caspian terns in 1997–1998 was 73–77% juvenile salmonids (Collis et al. 2002). Rice Island is a large dredged material disposal island in the Columbia River estuary near Astoria, Oreg., which in the 1990s was home to a large and increasing Caspian tern breeding colony. Caspian terns are nearly cosmopolitan in distribution, but worldwide numbers probably do not exceed 250 000 (Cramp 1985; Wires and Cuthbert 2000). Nesting by Caspian terns was first recorded on Rice Island in 1986, when about 1000 pairs nested on the west end of the island (United States Army Corps of Engineers (USACE) 2000). Only 2 years earlier, the first nesting by Caspian terns in the Columbia River estuary was recorded at East Sand Island. During the late 1980s and early 1990s, the Rice Island tern colony grew rapidly (USFWS, unpublished data), and by 1998, the colony consisted of nearly 8700 pairs (Roby et al. 2002), the largest Caspian tern colony in North America (Cuthbert and Wires 1999) and apparently in the world. Although Caspian terns were not known to be significant predators on juvenile salmonids, other piscivorous waterbirds have been shown to be under certain circumstances (Mace 1983; Wood 1987; Kennedy and Greer 1988; Blackwell 1995; Feltham 1995). Given the unprecedented size of the Rice Island tern colony, the preponderance of salmonids in the diet, and with most Columbia River salmonid populations listed as threatened or endangered (NMFS 2000*b*), investigation of consumption levels seemed warranted.

Bioenergetics models have previously been used to estimate consumption levels of piscivorous waterbirds, beginning with the pioneering work of Wiens and Scott (1975). These models calculate the amount of prey consumed in either biomass or numbers, based on diet composition, energy content of prey, energy requirements of individual consumers, and the number of individual consumers present (adults and juveniles). Estimating consumption using bioenergetics models avoids problems associated with using food capture rates to estimate consumption, which are potentially biased by selection of foraging sites or observation periods. Unlike biomass-based models, bioenergetics models take into account potential differences in prey quality (energy density). Previous applications of bioenergetic models have focused on predation on naturally reproducing fisheries of commercial or sportfishing interest (Furness 1978; Nagy et al. 1984; Guillet and Furness 1985; Cairns et al. 1990; Madenjian and Gabrey 1995) or on artificially propagated and stocked fisheries (Mace 1983; Wood 1987; Kennedy and Greer 1988; Glahn and Brugger 1995; Derby and Lovvorn 1997). In this study we apply bioenergetics modeling to estimate predation by an avian piscivore on valuable fish populations that are in decline.

We have presented information on the size and diet composition of the Rice Island Caspian tern colony elsewhere (Collis et al. 2002; Roby et al. 2002). Here we present estimates of prey consumption by this colony derived from a bioenergetics model based on those colony size and diet data and additional measures of prey size and energy content, average adult daily energy expenditure, seasonal trends in tern colony size, and estimated chick energy requirements. Our specific objectives in this paper are to (*i*) estimate the total number of juvenile salmonids and other prey types consumed by the Rice Island Caspian tern colony in 1997 and 1998; (*ii*) estimate the consumption of particular salmonid species and describe the trends in prey consumption throughout the tern breeding season; (*iii*) analyze the sensitivity of model estimates of salmonids consumed by terns to different input parameters and thereby assess which parameters contribute the most to model uncertainty; and (*iv*) develop a framework to quantitatively assess the impact of tern predation on population trends of ESA-listed salmonids.

Methods

We studied Caspian terns nesting at Rice Island in the

Columbia River estuary during 1997 and 1998. Rice Island is an artificial island consisting of sandy, dredged material and is located at river kilometre 34, near the maximum salt-water intrusion into the estuary (Fox et al. 1984). The nearby (<10 km) foraging environment is thus primarily fresh water, although tidally influenced, and marine forage fishes do not generally enter the estuary as far as Rice Island in appreciable numbers (Hinton et al. 1995). Purse-seine catches in the vicinity of Rice Island during spring have consisted primarily of juvenile salmonids and suggest that peak out-migration occurs in May (Hinton et al. 1995). Caspian terns have been described as generalist feeders (Cuthbert and Wires 1999), and in the foraging environment near Rice Island, juvenile salmonids may be the most readily available prey for most, if not all, of the nesting season (Collis et al. 2002).

Tern colony size

In both 1997 and 1998, the number of breeding adults at the colony at the time of peak colony attendance (late May, corresponding to the late incubation period) was estimated using high-resolution aerial photographs (see Collis et al. (2002) for details). Averages of three counts of birds in each year's photograph were converted into estimates of the number of breeding birds using ground counts of terns in each of eight representative 10 × 10 m census plots at the time that the aerial photographs were taken. The number of active breeding pairs at this point in each year was estimated by multiplying the average number of adult terns counted on the colony in the aerial photographs by the fraction of birds in plots that were sitting on a nest at the time that the photographs were taken.

To assess changes in the number of adult terns present in the estuary across the breeding season, a measure of colony size was obtained by censusing birds at the colony at least twice per week from blinds. Early and late in the season, when less than 2500 terns were on the colony, direct counts of all adults on the colony were used to estimate colony size. When more than 2500 terns were present, a subsampling technique was used whereby all terns were counted within 12 10 × 10 m stratified plots and the resultant bird density applied across the area of the entire colony. These ground-based counts were corrected for potential systematic error (problematic in ground-based counts of thousands of birds) and converted from counts of individuals into numbers of breeding pairs by multiplying by the ratio of the number of breeding pairs derived from the aerial photographs to a ground-based count of all adults that was performed at the time that the photographs were taken. In 1997, the frequency of census-taking was too low to adequately describe the seasonal trend in attendance, so the 1998 relative trend data were used for that year as well, but scaled to the number of breeding pairs present in the May 1997 aerial photograph.

We assumed that the number of nonbreeders or floaters present in the Columbia River estuary at the time of the aerial photograph (late incubation) was negligible compared with the size of the Rice Island breeding colony. This assumption was based on high nest attendance of birds present at the colony during that time (≥70% of adults present were sitting on nests) and aerial surveys of tern numbers throughout the estuary (excluding Rice Island) that did not exceed 25% of the estimated number of breeders (D.E. Lyons, unpublished data). Consequently, the number of terns counted away from the colony was consistent with the number of off-duty breeders not present at the colony. Also, only very rarely did we observe individual terns in subadult plumage at Rice Island or anywhere in the estuary. Nonbreeding terns present in the estuary at other times during the season (e.g., failed breeders) were included in our calculations if they roosted at the colony and were therefore included in our ground-based counts of all adults.

The number of chicks on the colony was estimated twice during the brood-rearing period: within 1–5 days after the median hatching date (first week of June) and about 1 week before the median fledging date (second week of July). The estimate in early chick-rearing was derived by multiplying the average number of young hatched per active nest by the number of adult pairs that had active nests during late incubation. The average number of young hatched per nest was determined by averaging counts of the number of young hatched per nest in the 12 10 × 10 m plots (N = 152 and 94 nests in 1997 and 1998, respectively). The estimate of young near the time of fledging was made using direct counts from blinds and counts of young captured during fledgling banding activities. For purposes of the bioenergetics modeling, the number of chicks was assumed to decline exponentially from the early estimate to the estimate near fledging, with chicks hatching in perfect synchrony on the observed median hatch date. Chicks were assumed to remain in the estuary for 1 week beyond the average fledging age of 37 days, consistent with our first observations (during twice weekly foraging site surveys) of fledglings outside the estuary occurring about 1 week after the first observations of fledglings flying at the colony.

Tern diet composition

In 1997, tern diet was assessed from foregut (i.e., esophagus, proventriculus, and gizzard) contents of adult terns collected (using a shotgun) upon their return to the colony with fish in their bill (Caspian terns provision mates and chicks by delivering whole fish carried in their bill; Collis et al. 2002). Whole fish carried in the bill ("bill-load fish") were also retrieved for each collected bird. For salmonids specifically, foregut contents were used to identify percent biomass of the diet to the level of family (Salmonidae). Identification of bill-load fish collected throughout the season was then used to subdivide the salmonid portion of the diet to species (chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), sockeye salmon (*Oncorhynchus nerka*), steelhead (*Oncorhynchus mykiss*)). Chinook salmon were further separated into spring–summer (yearling) and fall (sub-yearling) groupings using date-specific fork length criteria based on the bimodal fork length distribution observed in chinook salmon seined in five consecutive years from the Columbia River estuary during out-migration (Dawley et al. 1985). Collected bill-loads were found to be similar in taxonomic composition and size to foregut contents of adults returning to this colony (Collis et al. 2002).

In 1998, we assessed tern diet by visually identifying, from blinds adjacent to the colony, prey items brought to the colony by breeding terns (Collis et al. 2002). Bill-loads were identified with the aid of binoculars and spotting scopes, but in most cases were identifiable only to family. To identify prey items to species and to collect data on average mass and energy content of prey types, it was again necessary to collect adult foregut contents and bill-load fish as in 1997. The resulting bill-load diet composition by frequency was converted to diet composition by biomass using averaged mass measurements of collected bill-load fish of each respective prey type.

Fish mass and energy content

Mean prey mass for each prey type was determined by averaging the mass of whole fish from diet samples. The mean energy density of each prey type was based on proximate analysis of whole fish (see Anthony et al. (2000) for details) kept frozen until analysis. Individual fish were weighed fresh and dried to constant mass in a convection oven to determine water content. Lipid was extracted from dried samples using hexane – isopropyl alcohol (7:2 vol/vol) in a soxhlet apparatus. Lean dry samples were then ashed in a muffle furnace to determine ash-free lean dry mass (94% protein (Montevecchi et al. 1984)) by subtraction. Energy content of prey items was calculated from proximate composition (water, lipid, ash-free lean dry matter, and ash content) of diet samples, along with published (Schmidt-Nielsen 1997) energy equivalents of these fractions (lipid = 39.4 kJ/g and protein = 17.8 kJ/g for uricotelic vertebrates).

Daily energy consumption

Daily energy expenditure (DEE, kJ/day) of free-ranging breeding Caspian terns was measured directly using the doubly labeled water method (Lifson and McClintock 1966; Nagy 1980; Visser 2001). Adult terns nesting at Rice Island were captured in noose mats during the pipped egg stage of incubation or the first few days after hatching (when chicks were brooded continuously by parents). Captured adults were injected intraperitoneally with 0.9 mL of water containing ^{18}O and ^{2}H (62.1 and 35.7 atom %, respectively). Following injection, adults were weighed (±0.1 g), measured, banded, and held in cotton bags for 1 h after injection to allow isotopically labeled water to equilibrate with body water. An initial blood sample of about 80 μL was then obtained by puncturing the brachial vein and collecting blood in non-heparinized microhematocrit tubes. After blood sample collection, adults were dyed on the head and neck plumage with a unique pattern using rhodamine and were immediately released at the breeding colony. Injected adults were recaptured or lethally collected 24–48 h after injection and a second blood sample was collected. Blood samples were also collected from uninjected adult Caspian terns for measurement of background levels of the two isotopes. Tubes with blood were flame-sealed in the field and stored at about 5°C to prevent fermentation. All isotope analyses were conducted in the lab of G.H. Visser at the Centre for Isotope Research, University of Groningen, Netherlands. Using the CO_2 equilibration technique, ^{18}O:^{16}O ratios in blood were assigned by isotope ratio mass spectrometry, as were ^{2}H:^{1}H ratios in H_2 gas generated from water samples using an uranium oven at 800°C (following Visser et al. 2000). Isotope analyses were run in triplicate to assure accurate estimates of CO_2 production. Water flux rates and CO_2 production rates were calculated using standardized equations (Nagy 1980), assuming an energetic equivalent of 27.33 kJ/L CO_2, appropriate for a protein-rich diet (Gessaman and Nagy 1988). Total body water (percent of initial body mass) was calculated on the basis of ^{18}O dilution, using the plateau method (following Visser et al. 2000, eq. 2). All procedures and protocols involving live Caspian terns were reviewed and approved by the Institutional Animal Care and Use Committee at Oregon State University.

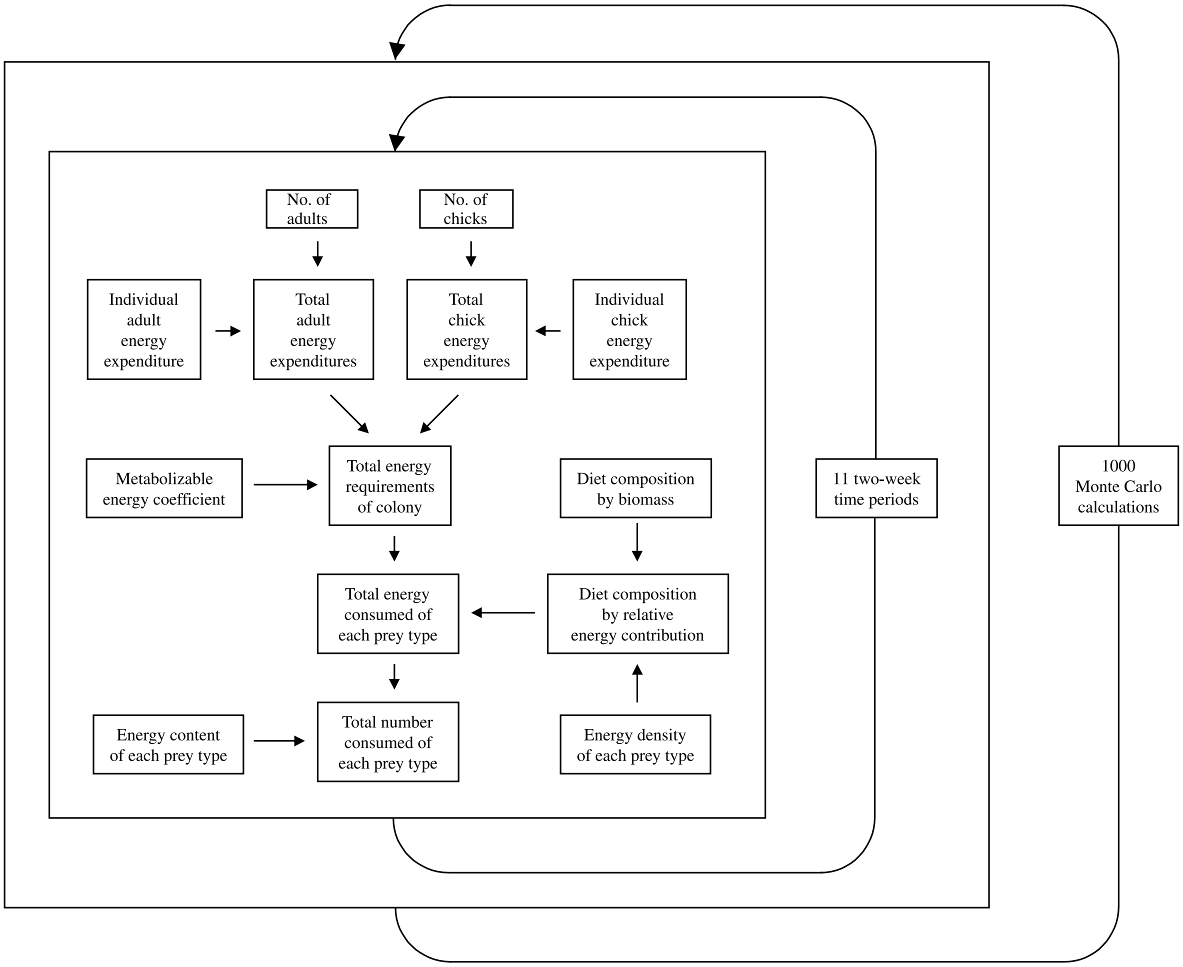
Energy expenditure rates of developing Caspian tern chicks have not been measured. Instead, we developed a simple model to estimate daily metabolizable energy requirements across the period of time that chicks were present in the estuary. Maintenance energy requirements of chicks were calculated as a function of chick age by using allometric equations relating postnatal resting metabolic rate (RMR) to chick body mass (Weathers and Siegel 1995), coupled with published mass-at-age data for Caspian tern chicks from colonies elsewhere on the Pacific coast (Schew et al. 1994). The additional energetic requirements for growth were modeled based on studies of developing common terns (*Sterna hirundo*; Ricklefs and White 1981). We assumed a peak energy allocation to growth of 85% of RMR at the time of maximum growth rate and an exponential (normal) decline in energy allocated to growth both before and after this time. Thermoregulatory costs of developing common terns in the Netherlands have been shown to be about 5% of the total postnatal energy budget (Klaassen 1994), so this value was used in our model. Activity costs of developing terns were modeled as increasing linearly beginning at day 10, up to 65% of RMR at day 37, following trends observed in common terns (Klaassen 1994). The total of these estimated daily metabolizable energy requirements (from hatch to fledge) was then compared with an allometrically derived total energy requirement for chicks based on fledging mass and age (Weathers 1992) to verify the adequacy of the model. Because the allometrically derived total energy requirement required fewer detailed assumptions, daily energy requirements were rescaled to sum to the allometrically derived value for total energy requirements. Finally, daily energy requirements of chicks during the first week after fledging (when chicks were capable of flight but assumed to be still resident in the estuary) were assumed to equal the requirements at fledging age (day 37).

Assimilation efficiency of a variety of seabirds, including terns, feeding on a variety of fish prey have been shown to range from 0.69 to 0.85 (Castro et al. 1989; Karasov 1990; Klaassen et al. 1992; Brugger 1993; Brekke and Gabrielsen 1994; Chavez 1997). Although assimilation efficiency is not the true metabolizable energy coefficient, bioenergetic studies have typically used these values as reasonable approximations (Miller and Reinecke 1984). Consistent with more comprehensive reviews of assimilation efficiency (Castro et al. 1989; Karasov 1990), we assumed the metabolizable energy coefficient to be 0.75 with a standard error (SE) of 0.025. Daily energy consumption was calculated as DEE divided by the metabolizable energy coefficient.

Bioenergetics model structure

A bioenergetics model was constructed in Visual Basic 6.0 to obtain reliable estimates of the number of juvenile salmonids and other prey types consumed by the tern popu-

Fig 1. Bioenergetics model structure for Caspian terns (*Sterna caspia*).



lation (Glahn and Brugger 1995; Madenjian and Gabrey 1995; Derby and Lovvorn 1997; Fig. 1). The model begins with estimates of the energy expenditure rates of individual birds, expanded by the estimated number of birds present at the colony. Dividing by the metabolizable energy coefficient produced the total energy requirements of the colony. Estimates of the numbers of juvenile salmonids and other prey types consumed to meet energy demands of the tern colony were then derived from measurements of the proportion (percent biomass) of salmonids and other prey categories in the diet, the mean mass of individual prey items in each prey category, and the mean energy density of items in each prey category.

The length of the breeding season (tern presence in the estuary, 27 March – 27 August) was broken into 11 two-week time periods, for each of which salmonid consumption was calculated. Data on the number of adults present, the number of chicks present, diet composition, and chick energy requirements were compiled separately for each two-week time period. In time periods 1 (27 March – 9 April), 10 (31 July – 13 August), and 11 (14–27 August), during which time no diet information was collected, the diet was assumed to be the same as that of the adjacent time period when diet composition was measured. Adult energy requirements and the average size and energy density of fish were assumed to be constant across the entire season.

To obtain confidence intervals (CIs) for the output estimates from the model, a Monte Carlo simulation technique was used (Furness 1978). Each input parameter was assumed to follow a normal distribution with the measured (or assumed, where noted) mean and SE (see Results). Sampling errors in the input parameters were assumed to be uncorrelated. The Monte Carlo analysis comprised 1000 runs of the model for each year, each run using a different set of randomly generated parameter values. In this manner, biomass and number of fish consumed were calculated for each prey type.

We investigated the sensitivity of the calculated number of salmonids consumed (for 1998 only) to any errors in the measurement of the input parameters by perturbing mean values of particular input parameters ±10% and calculating the corresponding shift in output values, leaving all other parameter values fixed at their nominal values. For purposes of perturbing diet composition data, the percentage of salmonids in the diet was perturbed (for all time periods simultaneously), with the contribution from other diet components increased or decreased a corresponding amount. In this case, the contributions to the diet of other prey types were held constant relative to each other. This individual parameter perturbation (IPP) approach gives an intuitive feel for sensitivity of the model to input parameters (Wiens and Innis 1974; Madenjian and Gabrey 1995), although it can sometimes lead to inap-

Fig. 2. Seasonal trend in attendance by adult Caspian terns at the Rice Island breeding colony in 1998. Values are means of all ground count estimates of individual adults within the 2-week time period starting with given date.

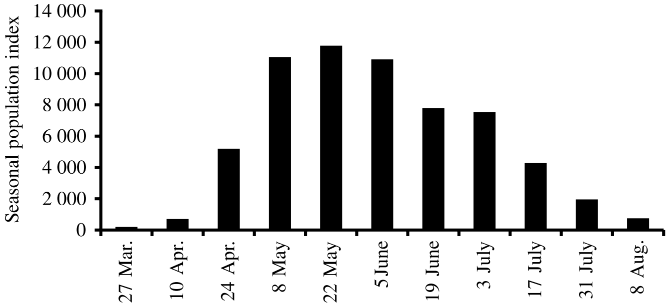
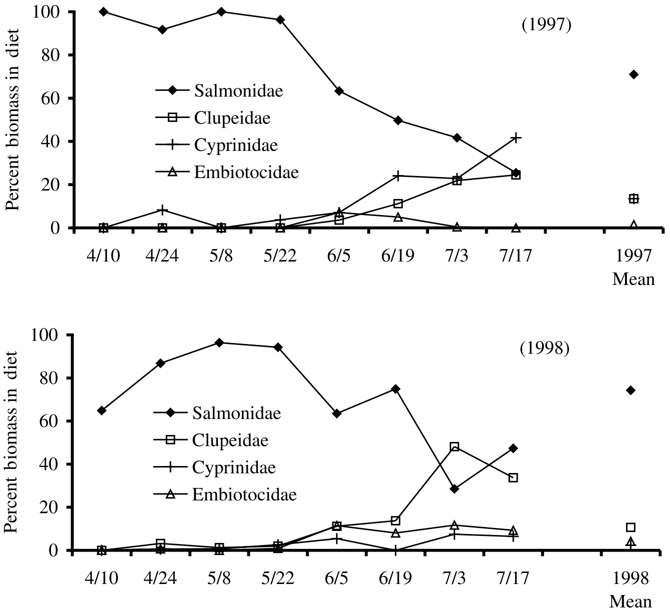


Fig. 3. Seasonal trends in diet composition (percent biomass) for major prey types of Caspian terns nesting at Rice Island in 1997 and 1998. Further information on diet composition can be found in Collis et al. (2002). Dates are expressed as month/day.



propriate conclusions if used to rank the relative contributions of each input parameter to the output variability (Gardner et al. 1981).

To assess the relative contributions of input parameters to the uncertainty in the output, multiple regression was performed (again, for 1998 only) with number of salmonids consumed as the dependent variable using all 1000 simulation runs (Swartzman and Kaluzny 1987). To indicate which input variables made the largest contribution to the total variation in number of salmonids consumed, parameters were ranked by their associated relative partial sums of squares (RPSS), which removes the effects of all other parameters. This allows an assessment of which parameters, in this model structure, contribute the most uncertainty to the output and provide the most opportunity for improving the output precision by further refinement in data collection (Derby and Lovvorn 1997).

Results

Bioenergetics model input

The estimated number of Caspian terns nesting on Rice Island increased from 7134 breeding pairs in 1997 to 8766 pairs in 1998, a difference of 22.9%. Productivity of fledglings was quite low in 1997 (an estimated 0.05 fledglings raised per pair), but higher in 1998 (0.44 fledglings per pair), although not as high as reported productivity elsewhere (Cuthbert and Wires 1999; Roby et al. 2002). The number of terns attending the colony increased rapidly through April and reached a maximum in late May, during the late incubation period (Fig. 2). Most terns departed the colony when breeding activities were completed (because of either nest failure or fledging of young), and nearly all terns had left the estuary by mid- to late August.

Salmonids (salmon and steelhead) made up most of the tern diet for most of the breeding period (71.0% of biomass in 1997 (Appendix A) and 74.3% in 1998 (Appendix B)). Other major prey types consumed were Pacific herring (Clupeidae, *Clupea pallasi*), peamouth (Cyprinidae, *Mylocheilus caurinus*), smelts (Osmeridae), and surfperches (Embiotocidae). Salmonids were frequently >90% of the diet early in the breeding season but were gradually replaced by alternative prey during the brood-rearing period (Fig. 3). Steelhead made up the highest proportion of diet biomass during April, coho salmon in May and early June, and chinook salmon (sub-yearlings) in late June and July (Table 1).

Measured energy densities of prey items ranged from 3.96 to 6.16 kJ/g wet mass of prey (Table 2). Smelt, herring, lamprey (*Lampetra* spp.), and peamouth were the prey types with the highest average energy density (kJ/g wet mass). Salmonids were not among the higher energy density prey types, averaging only 4–5 kJ/g. Suckers (Catostomidae), steelhead, and peamouth were the most profitable prey items in terms of energy per fish, primarily because of their large size (Table 2).

DEE of adult Caspian terns measured with doubly labeled water averaged 1040 kJ/day (standard deviation (SD) = 209.1, n = 24) and ranged from 632 to 1539 kJ/day. We measured adults during late incubation (n = 4), during the first week of chick-rearing (n = 6), and at the transition between these periods (nests containing both eggs and chicks; n = 14). Twenty-two of these measurements were made during the 1998 breeding season, whereas the other two measurements were made in 1997. The average DEE from the two measurements from 1997 (1044.4 kJ/day) was very close to the average for the entire sample. This measured value is 15% higher than the value predicted based on allometric equations (from Birt-Friesen et al. 1989) for the field metabolic rate of seabirds in general (902 kJ/day for a 650-g tern) but is 8% less than the allometric prediction for seabirds using flapping flight (1132 kJ/day).

The total metabolizable energy requirement (TMER) of individual chicks (from hatch to fledging) derived using allometric equations (Weathers 1992) was 19.2 MJ (fledging mass = 570 g, fledging age = 37 days), 50% of the cumulative requirements for individual adults over the same time period (1040 kJ/day over 37 days). Chick TMER estimated by totaling the modeled daily metabolizable energy requirements of chicks across the 37-day prefledging period was

Table 1. Taxonomic composition (percent biomass) of salmonids in bill-loads of collected Caspian terns (*Sterna caspia*) by time periods.

	1997				1998			
Classification	4/10 to 5/7	5/8 to 6/4	6/5 to 7/2	7/3 to 7/30	4/10 to 5/7	5/8 to 6/4	6/5 to 7/2	7/3 to 7/30
Chinook salmon, sub-yearling	2.2	2.6	48.6	55.2	1.4	3.6	24.5	76.0
Chinook salmon, yearling	3.0	4.8	0	0	19.0	9.8	0	8.6
Coho salmon	10.8	63.8	37.0	44.8	20.4	56.9	54.4	15.4
Steelhead	84.0	28.9	14.4	0	59.3	29.7	21.1	0
N	23	42	22	12	21	41	23	27

Note: Dates are expressed as month/day. Chinook salmon were classified as yearling or sub-yearling using the criteria in Dawley et al. (1985).

Table 2. Average prey mass (g) and average energy densities (kJ/g wet mass) of fish in bill-loads of collected terns measured using proximate composition analysis.

	Fish mass			Fish energy density			
Prey type	Mass (g)	SD	*N*	Energy density (kJ/g)	SD	*N*	Fish energy content (mass × energy density, kJ)
Chinook salmon, sub-yearling (Salmonidae)	12.0	8.6	40	3.98[a]	0.57	12	47.8
Chinook salmon, yearling (Salmonidae)	25.7	9.0	10	3.98[a]	0.57	12	102.3
Coho salmon (Salmonidae)	29.1	14.6	43	5.04	0.90	12	146.7
Steelhead (Salmonidae)	59.6	14.0	18	4.61	0.86	12	274.8
Herring (Clupeidae)	22.6	13.5	87	5.78	0.86	9	130.6
Peamouth, pikeminnow (Cyprinidae)	38.6	22.9	45	5.69	1.41	12	219.6
Lamprey (Petromyzontidae)	6.5	5.1	7	5.70	0.45	6	37.0
Flounder (Pleuronectidae)	18.1	11.8	22	4.17	0.29	6	75.5
Sculpin (Cottidae)	20.9	12.5	24	3.96	0.75	11	82.8
Smelt (Osmeridae)	23.5	14.3	33	6.16	1.29	11	144.8
Stickleback (Gasterosteidae)	1.3	0.7	70	4.90	1.04	3	9.1
Sucker (Catostomidae)	60.8	2.5	2	4.66	0.57	5	283.3
Surfperch (Embiotocidae)	21.3	8.5	29	4.16	0.78	13	88.6

[a] There were no significant differences between yearling and sub-yearling chinook energy density values measured using proximate analysis, so values were pooled for bioenergetics calculations.

Table 3. Major input parameters for the Caspian tern bioenergetics model.

	Mean	CV (%)	*N*
Demographic parameters			
Breeding pairs, 1997	7134	20.3	12
Breeding pairs, 1998	8766	20.0	12
Hatchlings/nest, 1997	1.39	38.1	152
Hatchlings/nest, 1998	1.58	39.2	94
Fledglings, 1997	400	12.5	1
Fledglings, 1998	3900	12.5	1
Energetic parameters			
Adult DEE (kJ/day)	1040	20.1	24
Chick TMER (MJ)	19.2	54.5	1
Metabolizable energy coefficient	0.75	3.3	1

Note: CV, coefficients of variance; DEE, daily energy expenditure; TMER, total metabolizable energy requirement.

18.3 MJ, only 4.7% less than the allometrically derived value. The modeled daily metabolizable energy requirements (after rescaling to the allometrically derived TMER) increased from 192 kJ per chick per day on the first day after hatching to 707 kJ per chick per day at the time of fledging. The modeled maximum daily energy requirement for chicks was 68% of adult DEE, consistent with typical measured values for other seabirds (Visser 2001). Demographic and energetic input parameters to the bioenergetics model are summarized in Table 3.

Bioenergetics model output

Our estimate of total energy requirement for the Rice Island Caspian tern colony was 1.52 × 10^6 MJ in 1997 (95% CI, 1.16–1.88 × 10^6 MJ) and 1.96 × 10^6 MJ (95% CI, 1.48–2.44 × 10^6 MJ) in 1998, a difference of 29% (Table 4). The higher energy consumption in 1998 is attributable to an increase in the adult population size and more chicks surviving to fledge. Nevertheless, total energy consumption by prefledging terns was approximately an order of magnitude lower than total energy consumption by adults: 3.9% of adult consumption in 1997 and 9.2% in 1998, primarily because of the unusually low survival of chicks in both years. Juvenile salmonids provided 67.3 and 72.0% of the tern population energy requirements in 1997 and 1998, respectively, with most of this provided by coho salmon and steelhead smolts in both years (Table 4).

This energy consumption translated into an estimated biomass consumption of 307.8 tonnes (metric tons (t)) (95% CI, 231.4–384.1 t) in 1997 and 407.7 t (95% CI, 302.9–512.6 t) in 1998 (Table 5). The estimates of tern consumption of juvenile salmonids were 216.8 t (95% CI, 160.4–273.2 t) in 1997 and 304.7 t (95% CI, 225.0–384.3 t) in 1998. The higher estimate in 1998 is a result of the higher tern population energy requirements and a slightly higher energy contri-

Table 4. Energy consumption by adult and juvenile Caspian terns in 1997 and 1998 and percent of total energy consumed by the tern population contributed by each prey type.

	1997	1998
Energy consumption (× 10^6 MJ)		
Adult population	1.46 (0.18)	1.78 (0.22)
Juvenile population	0.06 (0.03)	0.18 (0.09)
Entire population	1.52 (0.18)	1.96 (0.24)
Energy contribution by prey type (%)		
All Juvenile salmonids (Salmonidae)	67.3	72.0
Chinook salmon, sub-yearling	8.9	13.2
Chinook salmon, yearling	1.9	3.7
Coho salmon	38.0	35.9
Steelhead	18.5	19.2
Herring (Clupeidae)	8.4	13.6
Peamouth, pikeminnow (Cyprinidae)	14.7	3.8
Lamprey (Petromyzontidae)	0.8	0.4
Flounder (Pleuronectidae)	1.0	<0.1
Sculpin (Cottidae)	0.6	0.9
Smelt (Osmeridae)	2.0	3.4
Stickleback (Gasterosteidae)	<0.1	<0.1
Sucker (Catostomidae)	0.7	0.0
Surfperch (Embiotocidae)	1.7	5.2
Other non-salmonids	2.7	0.5

Note: Consumption estimates given are mean with standard deviation in parentheses.

bution by juvenile salmonids in that year. Biomass consumption estimates of herring (Clupeidae) and peamouth (Cyprinidae) exceeded 10 t in both years, as did surfperches (Embiotocidae) and smelts (Osmeridae) in 1998. Estimates of consumption of all other prey types were <10 t in both years (Table 5).

This biomass consumption translated into estimates of 11.6 million fish (95% CI, 8.7–14.7 million) consumed by the tern colony in 1997 and 17.0 million fish (95% CI, 12.4–21.5 million) consumed in 1998 (Table 5). An estimated 8.1 million juvenile salmonids (95% CI, 5.9–10.4 million) were consumed in 1997 and 12.4 million (9.1–15.7 million) in 1998. The difference between years is attributable to higher biomass of salmonids consumed in 1998 and a higher proportion of sub-yearling chinook (a prey type of relatively low energy content) in the salmonid portion of the 1998 tern diet (Tables 2 and 5). In 1997, coho salmon were the most numerous prey taken, followed by sub-yearling chinook salmon. In 1998, sub-yearling chinook salmon were taken more often, followed by coho salmon (Table 5).

Our estimates of the number of fish consumed peaked in June of both years, with 5.9 million fish consumed during the time period from 5 June to 2 July 1998 (Fig. 4). Even though biomass consumption was relatively constant during May and June, the number of fish consumed increased in June because of a transition in diet composition from high energy steelhead to lower energy fish, such as sub-yearling chinook salmon.

Uncertainty in model output

Sensitivity analysis using the IPP approach resulted in changes in the estimate of juvenile salmonid consumption that ranged from no discernable difference up to an 11.8% difference when individual input parameters were perturbed ±10% (Table 6). Parameters fell roughly into three categories: (1) those in which the best estimate of juvenile salmonid consumption changed roughly in proportion to the parameter perturbation (e.g., number of breeding pairs, adult DEE, metabolizable energy coefficient, percent of salmonids in the diet); (2) those that had a measurable but smaller impact than the 10% perturbation (e.g., the various chick parameters, percent of sub-yearling chinook salmon in diet, the energy densities and average masses of the more frequent prey types, such as sub-yearling chinook salmon, coho salmon, steelhead, and herring); and (3) those that had no measurable (≤1%) impact on juvenile salmonids consumption for the 10% perturbation performed (e.g., energy densities and average masses of the less frequent prey types, such as yearling chinook salmon, lamprey, flounder, sculpin, etc., not shown in Table 6).

Regression analysis of the model results indicated that our estimate of the number of tern breeding pairs contributed most to the uncertainty in the number of salmonids consumed, based on the relative partial sum of squares (Fig. 5). The next most significant factors contributing to uncertainty were the TMERs of developing chicks and the seasonal attendance patterns of adults in the estuary. Other strong factors were average DEE of adults, average mass of the salmonid prey consumed, metabolizable energy coefficient of terns, and the energy density of salmonids. Uncertainty in other factors contributed little to the eventual uncertainty calculated for the number of salmonids consumed (Fig. 5).

Discussion

Bioenergetics modeling results

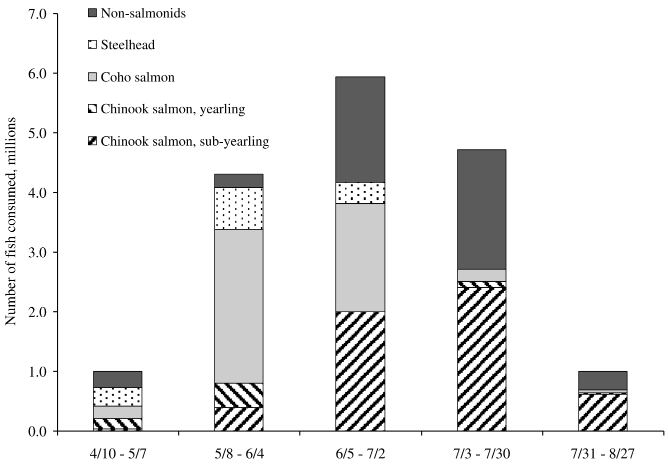
The accuracy of bioenergetic estimates of prey consumption depends on both model structure and input data. Our model to estimate prey consumption by the Rice Island Caspian tern colony benefited from direct measurements of colony size, diet composition, prey energy content, and adult DEE. In particular, directly measuring adult DEE allowed us to use a simpler model structure than alternative approaches, such as combining time–activity budgets, allometrically derived estimates of basal metabolic rate, and estimates of activity-specific energy expenditure multipliers (Wiens and Innis 1974; Furness 1978; Guillet and Furness 1985; Glahn and Brugger 1995; Derby and Lovvorn 1997). DEE measurements also provided greater accuracy in our consumption estimates than would allometric predictions of field metabolic rate. Combining energy requirements of terns with measurements of energy density and average mass of various prey types allowed us to avoid estimating daily food intake, which can be problematic (Feltham and Davies 1996). Thirteen prey types were included in the diet composition and energy content components of the model. Additionally, seasonal data on colony attendance and diet composition allowed us to partition the model temporally into 11 two-week periods to better reflect dramatic seasonal trends in population size and diet. As far as we are aware, these data are generally more extensive than previous population bioenergetics modeling efforts for piscivorous waterbirds.

Table 5. Calculated mean prey consumption by Caspian terns in 1997 and 1998 in biomass and numbers of prey consumed.

	1997			1998		
		Number of prey			Number of prey	
Prey type	Biomass mean (t)	Mean ($\times 10^6$)	95% CI ($\times 10^6$)	Biomass mean (t)	Mean ($\times 10^6$)	95% CI ($\times 10^6$)
All prey items	307.8	11.6	8.7–14.7	407.7	17.0	12.4–21.5
All juvenile salmonids (Salmonidae)	216.8	8.1	5.9–10.4	304.7	12.4	9.1–15.7
Chinook salmon, sub-yearling	34.0	2.9	1.8–4.0	65.1	5.5	3.9–7.0
Chinook salmon, yearling	7.2	0.3	0.1–0.4	18.0	0.7	0.4–1.0
Coho salmon	114.5	4.0	2.8–5.1	140.2	4.9	3.5–6.2
Steelhead	61.1	1.0	0.5–1.5	81.4	1.4	0.9–1.9
Herring (Clupeidae)	22.2	1.0	0.6–1.3	46.0	2.0	1.5–2.6
Peamouth, pikeminnow (Cyprinidae)	39.6	1.0	0.7–1.4	13.3	0.3	0.2–0.4
Lamprey (Petromyzontidae)	2.2	0.3	0.2–0.5	1.3	0.2	0.1–0.3
Flounder (Pleuronectidae)	3.7	0.2	0.1–0.3	0.4	<0.1	<0.1
Sculpin (Cottidae)	2.5	0.1	0.1–0.2	4.7	0.2	0.2–0.3
Smelt (Osmeridae)	5.0	0.2	0.1–0.3	10.8	0.5	0.2–0.7
Stickleback (Gasterosteidae)	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Sucker (Catostomidae)	2.2	<0.1	<0.1	0	0	0
Surfperch (Embiotocidae)	6.4	0.3	0.2–0.4	24.7	1.2	0.8–1.5
Other non-salmonids	7.2	0.2	0.1–0.3	1.9	<0.1	<0.1

Note: For numbers of prey consumed, 95% confidence intervals (CI) are given.

Fig. 4. Estimated numerical consumption of fish by Caspian terns nesting at Rice Island during 1998, broken down into 4-week time periods. Dates are expressed as month/day.



Our model relied on several simplifying assumptions, however. We assumed that average adult DEE measured during the transition between incubation and brood-rearing was representative of average adult DEE throughout the breeding period, whereas presumably adult energy expenditure may vary with breeding stage or other factors. A number of assumptions were made to develop a model of energy requirements for chicks, and uncertainty analysis suggested that the confidence interval for our estimate of the number of juvenile salmonids consumed could be narrowed if a more precise measure of chick energy needs was obtained. Our estimates of the TMERs of chicks using two independent techniques were in good agreement, however, so using the parameter uncertainty from one of these techniques (the allometric prediction; Weathers 1992) was perhaps unduly conservative. An additional, important assumption regarded our treatment of potential nonbreeding adult terns in the estuary. Consistency between the number of terns seen away from Rice Island (D.E. Lyons, unpublished data) and number of off-duty breeding adults not present at the colony led us to believe that the number of nonbreeders or floaters was negligible compared with the size of the Rice Island breeding colony. We suspect that this abnormally large Caspian tern colony may be a strong attractant for any breeding-age tern that passes through the estuary.

The sensitivity analysis using individual parameter perturbation indicated that the estimated number of salmonids consumed could change significantly if some input parameter values changed, such as the number of breeding pairs, adult DEE, metabolizable energy coefficient, or percent salmonids in the diet. Our estimates of metabolizable energy coefficient (from the literature) or percent salmonids in the diet (measured directly) had relatively small coefficients of variation compared with other parameters, however, so they contributed little to the uncertainty in the output, as indicated by the regression uncertainty analysis. Our estimates appear to be most contingent on our ability to estimate the number of terns that attempted to breed at the Rice Island colony and their attendance patterns through the breeding season. Aerial photographs of the colony enhanced the precision of counts of individuals on the colony, but translating this into the number of breeding pairs introduces some uncertainty. Ground counts of large groups of terns on-colony, such as we made at other times during the season to monitor seasonal attendance, are by their nature imprecise. Future versions of the bioenergetics model would be improved by better measurements of tern numbers throughout the breeding season.

Other predators on juvenile salmonids

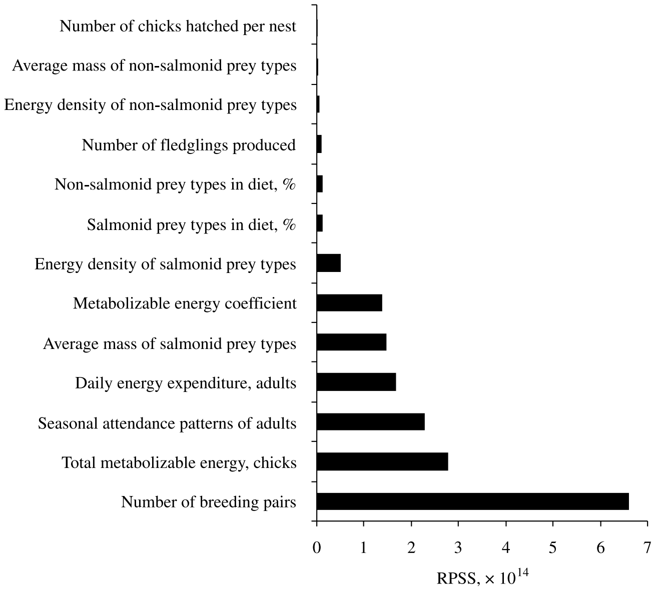
Our bioenergetics approach yielded the estimates that Caspian terns consumed between 5.9 and 10.4 million juvenile salmonids in 1997 and between 9.1 and 15.7 million in 1998. Although this level of predation is substantial, Caspian

Table 6. Results of the individual parameter perturbation (IPP) sensitivity analysis for the Caspian tern bioenergetics model in 1998.

Input parameter	SE (% of mean)	Change in salmonid consumption for a +10% input perturbation (%)	Change in salmonid consumption for a –10% input perturbation (%)
Number of breeding pairs	5.3	8.6	–9.3
Daily energy expenditure, adults	4.1	8.4	–9.2
Metabolizable energy coefficient	3.3	–9.5	11
Total metabolizable energy requirements, chicks	54.5	0.2	–1.5
Salmonids in diet (%)	2.1	9.9	–11.8
Sub-yearling chinook proportion of salmonids (%)	12.7	2.4	–3.3
Steelhead proportion of salmonids (%)	19.5	–1.3	0.1
Energy density of prey			
Chinook salmon, sub-yearling	5.2	–2.2	1
Coho salmon	5.2	–3.9	3.3
Steelhead	5.4	–2.5	2.1
Clupeidae	5	–2.1	1.2
Average mass of prey			
Chinook salmon, sub-yearling	10.6	–2.2	1.9
Coho salmon	8.8	–3.6	3.3
Steelhead	5.5	–2.1	1.2
Clupeidae	7.1	–2.1	1.3

Note: Percent changes in the estimated total number of salmonids consumed are given for ±10% perturbations of input parameters. For context, the standard error (SE) as a percentage of the mean of each input parameter is also given. Parameters having no measurable impact (<1%) when perturbed were omitted from table.

Fig. 5. Relative partial sums of squares (RPSS) from regression uncertainty analysis for parameters used to estimate numbers of salmonids consumed by Caspian terns nesting on Rice Island in 1998. Input variables for the bioenergetics model having the largest RPSS contributed most to the uncertainty in the estimated number of salmonids consumed.



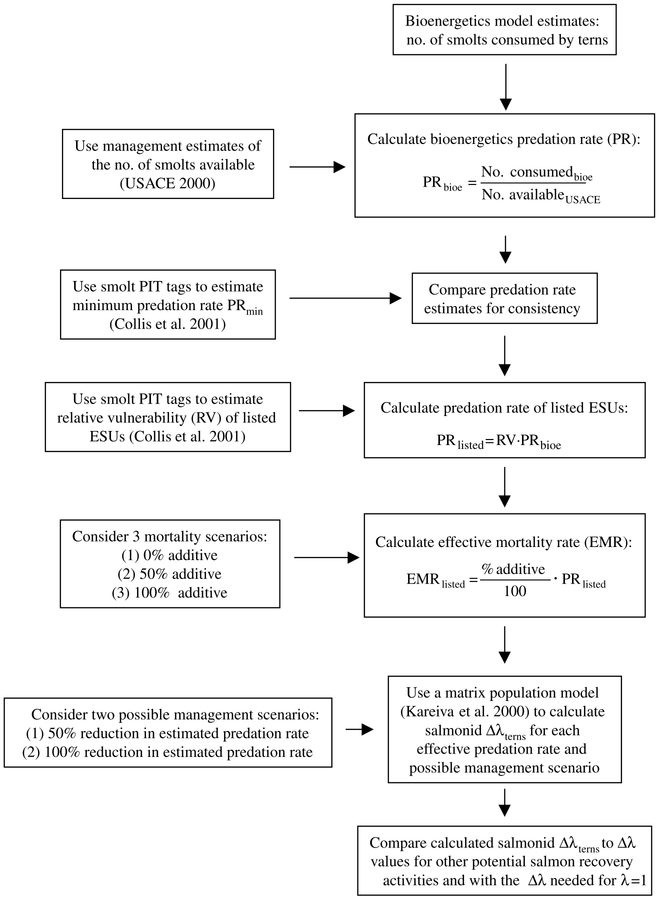
terns may not be the most frequent predator of juvenile salmonids in the Columbia River basin. An estimated 16 million juvenile salmonids were consumed annually by northern pikeminnow (*Ptychocheilus oregonensis*) in the entire lower Columbia and Snake rivers (Ward et al. 1995; Beamesderfer et al. 1996); this estimate led to large-scale management activities, such as the establishment of fisheries to reduce the number of predatory-sized pikeminnow, reconfiguration of dam outflows to reduce predation rates, etc. Because northern pikeminnow occur in main-stem river habitat throughout the basin, pikeminnow predation occurs on smolts earlier in their out-migration and may occur on earlier salmonid life history stages, compared with tern predation. In either case, individual salmonids consumed by pikeminnow may have a lower reproductive value to their respective populations than smolts consumed by terns in the estuary just before completing their migration to the ocean.

Other predators on juvenile salmonids from the Columbia River basin include two large breeding colonies of double-crested cormorants (together consisting of several thousand breeding pairs) that existed in the estuary in 1997 and 1998 (Collis et al. 2002). Salmonids made up about half of the diet for those cormorants nesting on Rice Island, and total smolt consumption by cormorants may have been several million annually (Collis et al. 1999). Several gull species (*Larus* spp.) nest in large numbers in the Columbia River estuary and throughout the basin (Collis et al. 2002), and although salmonids generally make up only a small proportion of their diets on a population basis, combined predation may total nearly a million juvenile salmonids per year (authors, unpublished data). Marine mammals, particularly harbor seals (*Phoca vitulina*), have also been documented to be predators on juvenile salmonids in the Columbia River estuary (Riemer and Brown 1997). Although the level of predation by harbor seals has been difficult to quantify, it appears to be less than that of avian predators in the estuary (Laake et al. 2002).

Tern predation rates and salmon recovery

Although estimates of the number of prey consumed are useful for understanding the effects of predators on endangered species, further insight can be gained by estimating

Fig. 6. Framework for quantitatively assessing the impacts of Caspian tern predation on Columbia River basin salmonid evolutionarily significant units (ESUs) listed under the U.S. Endangered Species Act. Predation rates generated using bioenergetics estimates of consumption in combination with estimates of smolt availability (United States Army Corps of Engineers (USACE) 2000) are first compared with minimum predation rates obtained by analyzing smolt passive integrated transponder (PIT) tags found at the tern colony (Collis et al. 2001). Then predation rates for listed ESUs are calculated using relative vulnerability estimates for those ESUs generated from PIT tag analysis (Collis et al. 2001). Next, the effective mortality rate (EMR) of salmonids is calculated for different assumptions regarding the additive or compensatory nature of mortality from tern predation. Finally, the change in average annual population growth rate (λ) resulting from management of tern predation ($\triangle\lambda_{\text{terns}}$) is calculated using a matrix population model framework (Kareiva et al. 2000) and compared with improvements in λ from other potential salmon recovery actions and the improvement in λ needed to achieve $\lambda = 1$.



the predation rate (proportion of available prey taken by the predator) and the consequent impact on the prey population trajectory (λ, the average annual population growth rate, is a useful measure). In Fig. 6, we present a framework for quantitatively assessing the impacts of Caspian tern predation on ESA-listed Columbia River salmonids by using our estimates of the number of smolts consumed in combination with pertinent data published elsewhere. The rest of this discussion will use this framework to evaluate the impact of tern consumption levels (documented above) on trends in salmonid populations.

To estimate predation rates (PR; proportion of available juvenile salmonids taken by terns) from our consumption estimates, some information on availability of juvenile salmonids in the estuary is necessary. Direct measurements of the number of Columbia River basin juvenile salmonids that reach the estuary during out-migration do not exist. However, predictions before out-migration have been made based on planned hatchery releases, anticipated river flow conditions, and expected extent of smolt transport around dams (Schiewe 1998). In the absence of better information, these estimates have been incorporated into planning documents and used in management decision making (USACE 2000). In 1998, it was predicted that 96.6 million salmon smolts would reach the estuary during out-migration (Schiewe 1998; USACE 2000).

To estimate the predation rate by terns on juvenile salmonids, we assumed that the actual number of smolts to reach the estuary was between 77 and 116 million fish (96.6 million ± 20%). Values were drawn from a uniform distribution having these bounds and combined with the estimated smolt consumption for each of the 1000 Monte Carlo simulation runs of the bioenergetics model to generate an estimate of the 1998 predation rate (PR_{bioe}) with 95% CI. Using this approach, the estimated 12.4 million smolts consumed by the Rice Island Caspian tern colony make up 13.0% (95% CI, 9.1–16.9%) of the estimated total number of smolts to enter the estuary (Table 7). By salmonid species, the predation rate by terns ranged from 5.4% (3.0–7.8%) of sub-yearling chinook salmon to 25.2% (16.0–34.5%) of coho salmon. Steelhead, having the highest proportion of listed fish (18% of all the steelhead that entered the estuary), had an estimated tern predation rate of 15.1% (8.5–21.6%).

Predation rates estimated from the analysis of passive integrated transponder (PIT) tags contained in some smolts and deposited by terns on their colony after ingestion (Collis et al. 2001) are also presented in Table 7. In general, predation rates based on PIT tag recoveries should be minimum estimates (PR_{min}), given that some unknown proportion of consumed tags are deposited by terns in areas away from the colony, not all tags on the colony are detected, and some tags lose function after ingestion by terns. As expected, the predation rates estimated using our bioenergetics analysis and estimates of the number of smolts present in the estuary generally exceeded estimates from PIT tag recoveries. Predation rates for chinook salmon and particularly coho salmon were substantially higher using the bioenergetics approach; however, for steelhead the estimate of predation rate using the bioenergetics approach was only slightly higher than the estimate using PIT tag recoveries (15.1 vs. 13.3%). A likely explanation for the similarity in estimated tern predation rates on steelhead using the two methods might be an overestimation of the number of steelhead smolts that entered the estuary and were available to terns. Similarly, the large disparity in predation rates for coho and chinook salmon using the two methods may indicate that the numbers of these two taxa reaching the estuary may have been substantially underestimated.

Our estimates of predation rates are averages for all salmonids of each particular species (or age class for chi-

Table 7. Predicted number of total and U.S. Endangered Species Act (ESA) listed salmonid smolts (from United States Army Corps of Engineers (USACE) 2000) that entered the Columbia River estuary in 1998 and proportion consumed by the Rice Island Caspian tern colony based on the bioenergetics estimates of numbers of smolts consumed.

	Estimated number of smolts entering estuary		Predation rate (%) Estimates using bioenergetics estimates of tern consumption		Estimates using analysis of PIT tags found on the tern colony[a]	
	Total ($\times 10^6$)	ESA listed (%)	Estimate	95% CI	Estimate	95% CI
Chinook salmon, yearling	13.1	3.8	10.4	6.6–14.2	1.5	1.3–1.7
Chinook salmon, sub-yearling	53.2	0.04	5.4	3.0–7.8	0.8	0.6–1.1
Chum salmon	1	0	NA[b]	NA[b]	NA[d]	NA[d]
Coho salmon	19.5	0	25.2	16.0–34.5	3.6	3.2–4.0
Sockeye salmon	0.6	10	NA[c]	NA[c]	2.3	0.4–4.2
Steelhead	9.2	18	15.1	8.5–21.6	13.3	12.4–14.2
All salmonids	96.6	2.4	13	9.1–16.9	4.4	4.2–4.6

Note: For comparison, predation rates are also presented based on analysis of smolt passive integrated transponder (PIT) tags found at the Rice Island tern colony (Collis et al. 2001). CI, confidence interval; NA, not applicable.

[a] A minimum estimate of predation rate; see text for details.

[b] Chum salmon were not observed in collected tern bill-loads in 1997 or 1998 and therefore were excluded from the bioenergetics analysis.

[c] Only one sockeye salmon was observed in collected tern bill-loads (in 1998), and sockeye were therefore excluded from the bioenergetics analysis.

[d] Chum salmon were not PIT-tagged in 1998.

nook salmon), regardless of population status (listed as threatened or endangered under the U.S. ESA or not). PIT tag analysis has been used to assess the relative vulnerability (RV) of listed vs. unlisted stocks (Collis et al. 2001) and can be used to help apply the average predation rate that we have generated using the bioenergetics approach to the ESA-listed stocks. For PIT-tagged steelhead, there was no difference in relative vulnerability between listed and unlisted stocks, so the predation rate for the listed stocks ($\mathrm{PR}_{\mathrm{listed}}$) is approximately equal to the predation rate for steelhead in general ($\mathrm{PR}_{\mathrm{bioe}}$ or 15.1%). For chinook salmon, a significant difference existed in vulnerability to tern predation; listed PIT-tagged stocks were taken only about half (47%) as often as unlisted stocks. Less than 0.1% of the sub-yearling chinook smolts predicted to enter the estuary were listed in 1998, so the predation rate for unlisted stocks would be approximately equal to the average predation rate (5.4%). The predation rate for listed sub-yearling chinook stocks can be estimated as 47% of that rate, or approximately 2.5%. Using a similar approach for listed yearling chinook salmon yields an approximate predation rate of 4.9%. No Columbia River basin coho salmon are listed as threatened or endangered, so no further breakdown of predation rate was investigated for that species.

These unexpectedly high estimates of tern predation rates, especially for ESA-listed steelhead, suggest a lack of density dependence. The annual production and release of 150–200 million hatchery-raised salmonid smolts throughout the Columbia River basin (Fish Passage Center (FPC) 2002), however, provides a major food source for large numbers of avian predators in the Columbia River estuary (Collis et al. 2002). Smolt PIT tag returns on the Rice Island tern colony indicate that although over 80% of juvenile steelhead consumed by terns originated from hatcheries, wild smolts are consumed in proportion to their availability (Collis et al. 2001). Thus hatchery-raised smolts apparently provide avian predators with an alternative prey on which to switch as listed wild stocks continue to decline. Given that most salmonid stocks in the Columbia River basin have been listed as either threatened or endangered (NMFS 2000*b*), there is considerable interest in the potential impact of avian predators such as Caspian terns on salmonid populations. Management of the Caspian tern colony at Rice Island to reduce predation on juvenile salmonids could be considered a recovery action in this context (NMFS 2000*a*). Predation rates on juvenile salmonids cannot, however, be easily translated into effects on the number of returning spawning adults.

In the Columbia River basin, quantitative approaches to assessing the relative value of various potential salmon restoration options have been investigated for several years (Marmorek and Peters 1998). A recent approach promulgated by NMFS, called the Cumulative Risk Initiative (CRI), in part involves assessing the average annual population growth rate (λ) for threatened and endangered evolutionarily significant units (ESUs) of salmonids and comparing the relative improvements in λ that could result from undertaking various recovery activities (McClure et al. 2000; Kareiva et al. 2000). Although estimating λ with precision is somewhat problematic (Kareiva et al. 2000; Dambacher et al. 2001; Kareiva et al. 2001), most ESUs appear to require 5–15% increases in λ to change the population trajectory from negative to positive (i.e., $\lambda > 1$; McClure et al. 2000). The CRI approach may be most useful, however, when comparing the potential efficacy of alternative recovery actions by evaluating the potential increases in λ for the respective actions.

Using the analytical framework of an age-structured population matrix model, the percent increase in λ attributable to an increase in survival at a particular life history stage can be calculated as

$$\Delta\lambda = \left[\left(\frac{S_{\mathrm{f}}}{S_{\mathrm{i}}}\right)^{1/G} - 1\right] \times 100$$

where S_{i} is the initial survival rate before recovery action, S_{f} is the survival rate following the recovery action, and G is the average generational time (McClure et al. 2000). This change in λ, assuming that it is independent of density and of changes in survival elsewhere in the life history of the organism, can then be used to compare the efficacy of various potential recovery actions.

Several potential recovery actions have been considered under this framework. Altered management of the Columbia and Snake rivers hydropower system (the cumulative impact of over 100 specific actions) could potentially achieve 3–15% improvements in λ, depending on the salmonid ESU (NMFS 2000*a*). Breaching four dams on the Snake River might increase λ by 6–27% for the Snake River spring–summer chinook ESU, depending on assumptions regarding hydropower system induced mortality in smolts that occurs after they pass through the hydropower system (NMFS 2000*a*). Reductions in harvest of adult salmon could also increase λ. At most, complete elimination of harvest could increase λ by 4–12% for steelhead and 1–30% for chinook salmon (depending on ESU) when compared with harvest levels of the 1980s and early 1990s (McClure et al. 2000). The northern pikeminnow management program, which has resulted in an estimated reduction in predation of 3.8 million smolts per year (Friesen and Ward 1999), might produce increases of 0.4–0.7% in λ if this mortality is assumed to be completely additive. Other factors that might increase salmonid population growth rates, such as habitat improvement and modification of hatchery procedures, are currently being quantitatively assessed (M. McClure, personal communication).

The CRI framework also allows a relative assessment of impacts by Caspian tern predation on salmonids if the current survival rate of salmonids to tern predation (the compliment of the tern predation rate) can be estimated and an expected survival rate to tern predation can be hypothesized for management actions that might reduce the consumption of juvenile salmonids by terns. Various reductions in tern predation rates could be hypothesized given a range of possible management alternatives. One possible scenario for analysis might be the complete elimination of tern predation in the estuary, perhaps corresponding to a hypothetical situation of no terns nesting in the estuary. Another possible scenario is a 50% reduction in tern predation, perhaps corresponding to a relocation of terns to an island closer to the mouth of the river where salmonids may be a smaller proportion of tern diets (Collis et al. 2002; Roby et al. 2002). In both of these scenarios, a critical and unknown factor must be considered: to what extent will other predators or other forms of mortality compensate for any reduction in tern predation?

For informational purposes, we estimated the potential increase in λ ($\Delta\lambda_{\text{terns}}$) for three hypothetical scenarios: (1) tern predation eliminated and mortality from tern predation completely (100%) additive; (2) tern predation reduced 50% and mortality from tern predation 50% additive; and (3) mortality from tern predation completely compensatory. Because steelhead smolts make up the largest fraction of the listed juvenile salmonids that entered the estuary in 1998, predation rates for steelhead were used in this example, assuming a mean generation time of 4.53 years (mean of mean generation times for the five listed Columbia River basin ESUs (McClure et al. 2000)). The effective mortality rate ($\text{EMR}_{\text{listed}}$) for the calculation of Δλ is the predation rate of the listed ESU multiplied by the fraction of the mortality that is considered additive. The corresponding increases in λ for the three scenarios were 3.68, 0.96, and 0%, respectively.

During the years 1999–2001, management actions appear to have reduced overall tern predation rates on juvenile salmonids about 50% based on changes in diet composition (Roby et al. 2002). Our view is that tern predation is intermediate between completely additive and completely compensatory mortality, and perhaps 50% additive is a useful number to assume to allow comparative evaluations of the efficacy of tern management (i.e., scenario 2 above) in the context of other recovery activities for Columbia River basin listed salmonids. Thus the 0.96% gain in population growth rate for steelhead hypothesized in scenario 2 may be the most pertinent measure of the possible efficacy of tern management actions undertaken to date, given the uncertainty surrounding the additive or compensatory nature of tern predation on juvenile salmonids. Based on this conclusion, it appears that management of tern predation alone would not reverse salmonid (specifically steelhead) declines. Tern management could, however, be part of a broader comprehensive strategy combining several recovery actions to increase the annual population growth rate to a sustaining level (λ ≥ 1).

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Appendix A

Table A1. Percent biomass of prey items in the diet of Rice Island Caspian terns (*Sterna caspia*) during 1997.

Prey family	4/10 to 4/23	4/14 to 5/7	5/8 to 5/21	5/22 to 6/4	6/5 to 6/18	6/19 to 7/2	7/3 to 7/16	7/17 to 7/30	Seasonal weighted mean
Salmon, steelhead (Salmonidae)	100	91.7	100	96.3	63.3	49.7	41.7	25.5	71
Herring (Clupeidae)	0	0	0	0	3.6	11.2	21.9	24.5	13.5
Peamouth, pikeminnow (Cyprinidae)	0	8.3	0	3.7	7.1	24.1	22.8	41.7	13.5
Lamprey (Petromyzontidae)	0	0	0	0	3.6	0	0	0	0.4
Flounder (Pleuronectidae)	0	0	0	0	0	2.7	0	8.3	1.4
Sculpin (Cottidae)	0	0	0	0	1	0	5.2	0	0.8
Smelt (Osmeridae)	0	0	0	0	7.1	1.9	0	0	1.1
Stickleback (Gasterosteidae)	0	0	0	0	0	0	0	0	<0.1
Sucker (Catostomidae)	0	0	0	0	3.6	0	0	0	0.5
Surfperch (Embiotocidae)	0	0	0	0	7.1	5	0.4	0	1.5
Other non-salmonids	0	0	0	0	3.6	5.4	8	0	2.1
N	13	24	18	16	28	37	25	12	173

Note: Further information on diet composition can be found in (Collis et al. 2002). Dates are expressed as month/day.

Appendix B

Table B1. Percent biomass of prey items in the diet of Rice Island Caspian terns (*Sterna caspia*) during 1998.

Prey family	4/10 to 4/23	4/14 to 5/7	5/8 to 5/21	5/22 to 6/4	6/5 to 6/18	6/19 to 7/2	7/3 to 7/16	7/17 to 7/30	Seasonal weighted mean
Salmon, steelhead (Salmonidae)	64.9	86.8	96.4	94.2	63.5	74.9	28.5	47.4	74.3
Herring (Clupeidae)	0	3.2	1.2	2	11.2	13.8	48.1	33.7	10.7
Peamouth, pikeminnow (Cyprinidae)	0	0.6	0.8	2.6	5.4	0	7.5	6.5	2.4
Lamprey (Petromyzontidae)	0	0	0	0	0	0.7	0.6	1	0.2
Flounder (Pleuronectidae)	0	0.3	0	0	0	0	0.6	0	0.1
Sculpin (Cottidae)	0	0.3	0	0.3	1.1	1.8	2.9	2.2	0.8
Smelt (Osmeridae)	35.1	8.1	1.1	0	4.8	1.7	0	0	6.9
Stickleback (Gasterosteidae)	0	<0.1	0	0	0	0	<0.1	0	<0.1
Sucker (Catostomidae)	0	0	0	0	0	0	0	0	0
Surfperch (Embiotocidae)	0	0.7	0	0.9	11.5	8.1	11.7	9.3	4.2
Other non-salmonids	0	0	0.5	0	2.5	0	0	0	0.4
N	28	189	157	233	343	106	198	122	1374

Note: Diet composition by frequency was converted to composition by biomass using average prey mass data from Table 4. Further information on diet composition can be found in Collis et al. (2002). Dates are expressed as month/day.