

ARTICLE

Potential Effects of Management on Caspian Tern *Hydroprogne caspia* Predation on Juvenile Salmonids at a Colony in San Francisco Bay, California

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Abstract

San Francisco Bay is a proposed relocation site for some of the Caspian terns *Hydroprogne caspia* currently nesting at the world's largest colony for the species in the Columbia River estuary and consuming salmonids listed under the U.S. Endangered Species Act (ESA). However, several runs of salmonids listed under the ESA occur in San Francisco Bay and managers are concerned that increased Caspian tern predation may pose a threat to the recovery of these fish. We used a bioenergetics modeling approach, employing estimates of tern energy requirements and proportions of energy supplied by various prey types, to estimate the consumption of juvenile salmonids by Caspian terns nesting on Brooks Island in central San Francisco Bay during 2008 and 2009. Estimated salmonid consumption was ~205,000 smolts (95% confidence interval, 175,000–245,000 smolts) in 2008 and ~167,000 smolts (144,000–191,000 smolts) in 2009. The interannual difference in smolt consumption was due to the smaller size of the tern colony and lower nesting success in 2009. Estimated predation rates on ESA-listed Central Valley spring-run Chinook salmon *Oncorhynchus tshawytscha* (0.1%) were lower than those on unlisted fall-run Chinook salmon (1.0%). Continuation of the current downward trend in the number of Caspian terns nesting on Brooks Island and the resulting reductions in salmonid predation would not be sufficient to reverse salmonid declines in San Francisco Bay. The proposed enhancement of the Brooks Island Caspian tern colony to 3,000 individuals would at most cause declines in annual population growth rates of 0.28% for fall-run Chinook salmon and 0.02% for threatened spring-run Chinook salmon, assuming that the mortality from tern predation is 100% additive.

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Brooks Island, located near Richmond, California, is one of three sites in San Francisco Bay proposed as an alternative colony location in the 2006 Records of Decision for "Caspian Tern Management to Reduce Predation on Juvenile Salmonids in the Columbia River Estuary" (USFWS 2006). The intent of resource managers responsible for implementing the plan was to provide additional Caspian tern *Hydroprogne caspia* nesting habitat on Brooks Island so as to accommodate up to 1,500 breeding pairs of Caspian terns, including some displaced from the Columbia River estuary. However, the alternative colony site on Brooks Island was of particular concern because it is the site nearest the Sacramento River delta, where several U.S. Endangered Species Act (ESA)-listed salmonid runs enter San Francisco Bay (McEwan 2001; Good et al. 2005). Monitoring of Caspian tern diet at the Brooks Island colony, which occurred during 2003–2005 and resumed in 2008–2009, demonstrated that salmonids were a small part of the diet (5.3% of prey items; Collis et al. 2012). In 2008, salmonids in the diet were identified to species and evolutionarily significant unit (ESU) based on smolt coded wire tags (CWTs) recovered on the tern colony (Evans et al. 2011). Recovered CWTs indicated that the vast majority of the salmonid smolts consumed were from the unlisted Central Valley fall-run Chinook salmon *Oncorhynchus tshawytscha* ESU. The fall-run Chinook salmon ESU is the predominant salmonid run in the Bay Area, and several hatchery release sites for this ESU are located within 20 km of Brooks Island (FFC 2008, 2009).

Fish populations in the San Francisco Bay estuary have undergone serious declines since the 1970s (Meng et al. 1994) that have been attributed to both anthropogenic and climatic factors (Feyrer et al. 2007; Lindley et al. 2009). Historically, salmonid populations were prolific in the Sacramento and San Joaquin River drainages, with Chinook salmon and steelhead (anadromous rainbow trout) *O. mykiss* runs both estimated to have consisted of 1–2 million spawning adults (Yoshiyama et al. 1998; McEwan 2001). Two out of four runs of Chinook salmon in the Bay Area are now listed under the ESA; the Sacramento River winter-run Chinook salmon ESU is currently listed as endangered, and the Central Valley spring-run Chinook salmon ESU is listed as threatened. Both of these ESUs are currently estimated to consist of less than 10,000 spawning adults (Good et al. 2005). Although the Central Valley fall-run Chinook salmon ESU is not listed under the ESA, low spawning returns of this unit prompted the Pacific Fisheries Management Council to adopt a complete closure of commercial and recreational Chinook salmon fisheries off the coast of California and part of Oregon in 2008 and 2009 (NOAA 2008, 2009b). Naturally spawned California Central Coast coho salmon *O. kisutch* are listed as endangered; however, they have not been detected in stream surveys of the river basins in the San Francisco Bay area since 1995 and are considered extirpated from the area (NOAA 2005). The Central Valley steelhead ESU has been listed as threatened under the ESA since 1998 (NOAA 1998), and although the Central California Coast steelhead ESU is also listed as threatened,

there is no consensus as to whether it still survives in tributaries of San Francisco Bay (Good et al. 2005).

Caspian terns were first recorded nesting in San Francisco Bay in 1916 (Grinnell and Miller 1944). In 2009, nearly a century later, there were six breeding colonies of Caspian terns in the Bay Area, with a total breeding population of approximately 830 pairs (Collis et al. 2012). The largest of these colonies was located on a sandy spit of dredged material extending from Brooks Island, where more than 80% of the breeding population in the Bay Area nested. The size of this Caspian tern colony is limited by the availability of bare sand, their preferred nesting substrate. Encroaching vegetation and the erosion of nesting substrate are the factors that apparently constrain the size of this colony, and predation from western gulls *Larus occidentalis* and California gulls *L. californicus* nesting immediately adjacent to the tern colony further limits its size and productivity (Collis et al. 2012). Other available nesting habitat for Caspian terns in the Bay Area consists mostly of small islands located in former salt evaporation ponds. Many of these ponds are slated for inclusion in tidal salt marsh restoration projects, and the continued availability of nesting habitat for Caspian terns in the Bay Area is uncertain (Seto et al. 2003).

The National Marine Fisheries Service (NMFS) has management authority for all anadromous salmonids listed under the ESA. In 2006, the NMFS prepared a Biological Opinion stating that the creation of alternative Caspian tern nesting habitat on Brooks Island would probably not jeopardize the salmonid stocks in the San Francisco Bay area that are listed under the ESA (NOAA 2006). However, at that time accurate estimates of salmonid consumption rates by Caspian terns from the existing colony (or a colony of increased size) were not available.

Bioenergetics modeling combines data on the energy requirements of a predator, the number of predators present in a system, and the composition of prey in the diet of the predator to calculate prey consumption. Use of this method was pioneered by Wiens and Scott (1975) to estimate prey consumption by several seabird species. Subsequently, bioenergetics modeling has been used to estimate the consumption of fish by various piscivorous waterbird species in both freshwater and marine food webs (Furness 1978; Glahn and Brugger 1995; Madenjian and Gabrey 1995; Phillips et al. 1999). For Caspian terns, this method has previously been used to calculate juvenile salmonid consumption in the Columbia River estuary and along the mid-Columbia River (Roby et al. 2003; Antolos et al. 2005).

We used a bioenergetics model to estimate the consumption of juvenile salmonids and other prey types by Caspian terns nesting at the Brooks Island colony. We collected Caspian tern diet composition information at the Brooks Island colony in 2008 and 2009 and estimated predation on individual forage fish species. The specific objectives of this study were to (1) estimate the per capita consumption of juvenile salmonids by Caspian terns nesting on Brooks Island as well as total smolt consumption by all terns at the colony, (2) determine whether

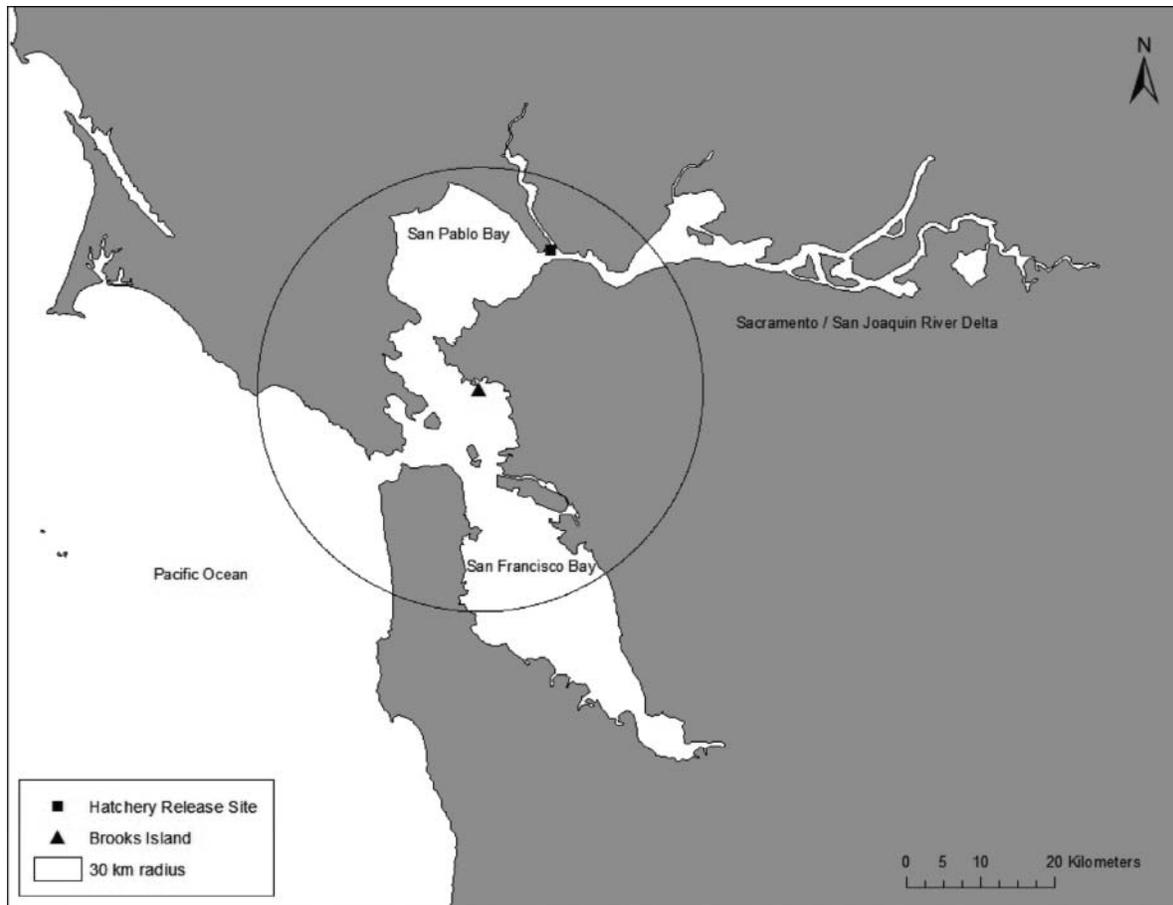


FIGURE 1. Map of the study area in San Francisco Bay showing the location of Brooks Island and the hatchery-raised salmon release site along with a 30 km radius circle that captures 90% of foraging activity of radio tagged Caspian terns nesting on Brooks Island.

this Caspian tern colony, the largest in the San Francisco Bay area, poses a significant threat to the recovery of any ESA-listed ESU of salmonid, and (3) assess whether a near doubling in the size of the Brooks Island Caspian tern colony would pose a considerable source of mortality for any salmonid ESU in the Bay Area. All animal handling protocols were approved by the Oregon State University Institutional Animal Care and Use Committee (Protocol 3722).

STUDY SITE

Brooks Island ($37^{\circ}53'59''\text{N}$, $122^{\circ}21'39''\text{W}$) is located in central San Francisco Bay within Contra Costa County, California (Figure 1). It is a natural island situated 2 km to the south of the Port of Richmond and has been augmented with dredged material that forms a sandy spit extending to the northwest of the island. Brooks Island is owned by the City of Richmond and managed by the East Bay Regional Parks District. Breeding by Caspian terns on this island was first documented in 1988 (Strong et al. 2004). A high count of Caspian terns nesting on Brooks Island was recorded in 2004, when an estimated 1,040

breeding pairs nested on the island. Since then, the colony has steadily decreased in size (Collis et al. 2012).

METHODS

Bioenergetics Model Structure

We used a bioenergetics model based largely on that used by Roby et al. (2003; Figure 2), with some improvements. This model employed estimates of individual Caspian tern energy requirements, the number of terns present, diet composition, and prey energy content to calculate the total numbers of each prey type consumed by Caspian terns nesting at Brooks Island in 2008 and 2009.

Input parameters for the model were measured directly at the Caspian tern nesting colony on Brooks Island, and samples of prey species consumed at this colony were collected in San Francisco Bay, when possible. Parameters that could not be measured during 2008 and 2009 at Brooks Island or in San Francisco Bay were estimated based on previously published studies from San Francisco Bay or the Columbia River estuary. Tern bioenergetics calculations were based on 11 2-week time

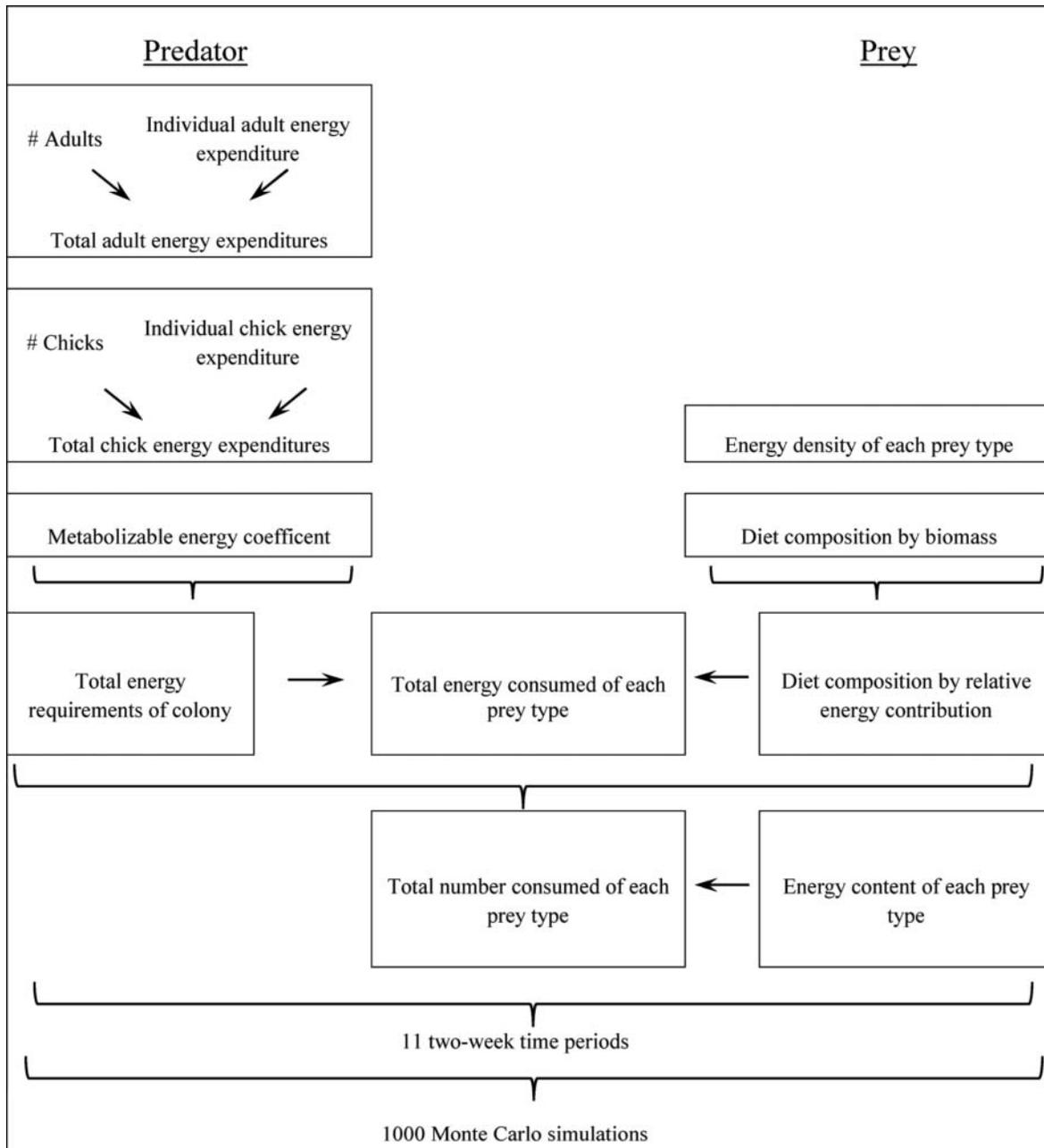


FIGURE 2. Bioenergetics model schematic used to estimate fish consumption by Caspian terns nesting at Brooks Island in San Francisco Bay, California.

periods (March 13–August 13) in 2008 and 2009 to account for seasonal and annual differences in some input parameters to the model (e.g., colony size, diet composition). The time periods spanned the dates when Caspian terns were present at the Brooks Island colony in those 2 years. These results were summed across the entire breeding season to obtain total estimated forage fish consumption. Per capita consumption of juvenile salmonids was calculated in 2008 and 2009 by dividing the total numbers of juvenile salmonids consumed by the number of Caspian terns breeding at Brooks Island in each year.

Improvements to the methods of Roby et al. (2003) included the use of recently measured energy requirements of Caspian tern chicks instead of allometric equations as well as a measured assimilation efficiency value that was not previously available (Lyons and Roby 2011).

A Monte Carlo simulation was used to estimate the confidence intervals (CIs) of each output parameter (Furness 1978) following Roby et al. (2003). This technique uses a randomly selected set of values for the input parameters for each simulation run of the model. All input parameters were assumed

to originate from a normal distribution, and 1,000 simulations of the model were completed for each year of the study. The 1,000 output values were averaged to obtain final estimates and 95% CIs. Differences in output parameters were interpreted as significant at the 0.05 level if the 95% CIs did not overlap.

Bioenergetics Model Input Parameters

Colony size and number of young.—The size of the Caspian tern colony at the peak of each breeding season was estimated using averages taken from three independent counts of high-resolution aerial photography (Collis et al. 2002). The average of the total number of adult Caspian terns on-colony was converted to an estimate of the total number of breeding pairs using ground counts of sitting and standing adult terns that were made at the same time as the aerial photography from an observation blind adjacent to the tern colony. Sitting terns were assumed to be attending a nest. Because the bioenergetics model is based on 2-week intervals, additional estimates of colony size were needed for each 2-week period over the course of the entire breeding season. Consequently, the numbers of adults present on the breeding colony were counted from observation blinds several times per week. The highest count per day was averaged over the 2-week period and used to estimate colony size during each 2-week interval.

The numbers of young Caspian terns on the colony during the 2008 and 2009 breeding seasons were estimated once during the early chick-rearing stage and again close to fledging to account for the change in the energy needs of chicks as they grow. A sample of active nests was monitored from the observation blind several times per week. The presence and number of eggs and/or chicks in each nest in the sample were recorded and used to obtain an average number of chicks hatched per nesting attempt. This average was then multiplied by the number of active nests on the colony during late incubation to produce an estimate of chicks present during early chick-rearing. The total number of fledglings produced at the colony in each year was estimated using counts of the number of chicks on the colony conducted 7–10 d after the first fledgling was observed or counts of chicks that were captured and banded on the colony during this time period in both years of the study (Roby et al. 2003). For any areas of the colony where chicks were not captured, we counted the number of chicks that could be seen from a boat in the water or from the observation blind and used this as the number of fledglings present. Although some chicks will have already left the colony at this time, there are some chicks that will not survive all the way to fledging, so that conducting our count at this time gives a reasonable estimate of the number of large chicks that were fed on the colony during the season.

Caspian tern energy expenditure.—To estimate the daily energy expenditure (DEE; kJ/d) for adult Caspian terns nesting at the Brooks Island colony in 2008 and 2009, we used the DEE of adult breeding Caspian terns measured at a colony on Rice Island in the Columbia River estuary during 1997 and 1998 (Roby et al. 2003). Briefly, Roby et al. (2003) used the doubly labeled

water technique (Lifson and McClintock 1966; Nagy 1980) to measure the field metabolic rates of adult Caspian terns (males and females) captured near the end of the incubation period or very early in chick-rearing. We assumed that the DEE of Caspian terns nesting at Brooks Island was the same as that of Caspian terns nesting on Rice Island and that the DEE of terns late in incubation or early in chick-rearing was representative of the average DEE over the course of the breeding season. While DEE does vary across the breeding season, the values measured during late incubation and early chick-rearing are a reasonable estimate of average DEE across the season (Roby et al. 2003).

The daily energy expenditure of Caspian tern chicks at Brooks Island in 2008 and 2009 was estimated using the DEE of captive Caspian tern chicks that were collected from the East Sand Island colony in the Columbia River estuary in 2001 (Lyons and Roby 2011). Briefly, young chicks ($n = 10$) were raised in captivity and fed ad libitum diets in order to quantify the daily energetic requirements of chicks from hatching to fledging age (~42 d) using the balance technique. The mean total metabolizable energy (TME) was then calculated across all 10 chicks and daily requirements were calculated for the 42-d chick-rearing period. We assumed that the energy requirements of Caspian tern chicks at Brooks Island were the same as those of the captive-raised chicks.

Diet composition.—To determine diet composition, observations of prey items transported by adult Caspian terns in their bills to the Brooks Island colony were collected from the observation blind over the course of the breeding season. Each bill-load prey item was identified to the lowest possible taxon using binoculars and spotting scopes (Collis et al. 2002). Diet composition was then calculated for each 2-week period for input to the bioenergetics model. During 2008 and 2009, no diet data were collected at the colony during the earliest 2-week time period, so diet composition was assumed to be the same as during the subsequent 2-week period. In 2009 very few diet data were collected during 2-week time period 10, and none were collected during 2-week time period 11. For both of these periods we added the diet data from time period 9 ($n = 381$ identified prey items) to those from time period 10 ($n = 9$ prey items) and calculated diet composition using that combined data set. The number of identified prey items per 2-week period was greater than 300 in 7 of the 11 time periods in 2008, with a range of 23–788 identified items. In 2009, the number of identified prey items was greater than 300 for 9 of the 11 time periods, ranging from 128 to 733.

In both years we identified juvenile salmonids in tern bill-loads as either “steelhead and trout” (steelhead or rainbow trout) or “Chinook salmon.” Rainbow trout and steelhead are difficult to distinguish from one another at a distance using only binoculars. There are several reservoirs <15 km from Brooks Island where rainbow trout are stocked (CDFG 2009), and juvenile steelhead migrating from spawning areas in the Sacramento and San Joaquin River drainages to the Pacific Ocean must pass through central San Francisco Bay near Brooks Island. During

a radio-tracking study of the Caspian terns nesting at Brooks Island, two aerial telemetry detections of Caspian terns were made at a stocked reservoir (Adrean 2011). Consequently, it is possible that the Caspian terns from Brooks Island consumed both resident rainbow trout and anadromous steelhead.

Average mass of prey items.—Along with identification to taxon, the total length of each tern prey item was estimated as a multiple of the average Caspian tern bill length (7.0 cm; Quinn 1990). These methods followed Antolos et al. (2005), who found an observer error range of 1% overestimation to 4% underestimation. Length-to-mass regression equations were generated for the most prevalent prey types in the diet of which we were able to collect samples. Total length and mass measurements of two silverside species (jacksmelt *Atherinopsis californiensis* and topsmelt *Atherinops affinis*) and shiner perch *Cymatogaster aggregata* were obtained from live fish at the Marine Science Institute in Redwood City, California, that were caught in otter trawls conducted in San Francisco Bay. Total length measurements were taken in millimeters and fish were weighed to the nearest 0.001 g using a digital top-loading balance. Northern anchovy *Engraulis mordax* ($n = 7$) and Pacific staghorn sculpin *Leptocottus armatus* ($n = 7$) samples were obtained from trawls conducted by the California Department of Fish and Game in San Francisco Bay during 2004 and 2005. Of clupeids (Pacific herring *Clupea pallasii* and Pacific sardine *Sardinops sagax*), only Pacific sardines caught in 2009 by commercial fishermen in central San Francisco Bay near Sausalito were measured ($n = 11$). Chinook salmon fork length and body mass measurements from both the Sacramento River delta and the mouth of San Francisco Bay were based on a 10-year data set collected during 1995–2005 (MacFarlane 2010). To convert fork length to total length we applied a ratio of 1.085, which was obtained from a regression equation of fork length on total length from measurements of 28 juvenile fall-run Chinook salmon smolts from the Coleman National Fish Hatchery in 2009.

Energy density of prey types.—We used the samples collected as described above to estimate average total energy content (kJ/fish) and average energy density (kJ/g wet mass) of the various prey types that comprised at least 1.0% of the prey items in the Caspian tern diet. After samples were collected and measured, they were frozen until laboratory analysis. We conducted proximate-composition analysis (Reynolds and Kunz 2001) to determine the percent water, lipid, ash-free lean dry matter (AFLDM), and ash of prey samples using methods described in detail by Anthony et al. (2000). Briefly, samples were thawed and weighed to determine wet mass, then dried to a constant mass in a convection oven at 60°C to determine dry mass. Each fish was then homogenized using a mortar and pestle and total lipids were extracted using a Soxhlet apparatus and a solvent system of 7:2 hexane : isopropyl alcohol (volume basis). Lean dry samples were then incinerated in a muffle furnace at 600°C for 12 h to determine ash content. We estimated protein content from the AFLDM, which consisted of 94% protein (Montevecchi and Piatt 1984). We calculated energy content and

average energy density for each prey type using the published energy equivalents of 17.8 kJ/g for protein and 39.3 kJ/g for lipid (Schmidt-Nielsen 1997).

Pacific tomcod *Microgadus proximus* ($n = 12$), leopard shark *Triakis semifasciata* ($n = 1$), and plainfin midshipman *Porichthys notatus* ($n = 1$) were also collected from trawls conducted by the California Department of Fish and Game in San Francisco Bay during 2004 and 2005 and subjected to the proximate analysis method. Because only one specimen each of leopard shark and plainfin midshipman were analyzed, the resulting energy content and energy density from each specimen were used as inputs into the bioenergetics model. In these two cases, we used an estimate of uncertainty for energy density and mass that was 20% of the single measured value.

The average energy density of Chinook salmon smolts was based on a 10-year data set collected during 1995–2001 and 2003–2005, using Chinook salmon smolts collected from both the Sacramento River delta and the mouth of San Francisco Bay. Total lipids were extracted from these samples using a chloroform–methanol biphasic procedure, and total protein was measured by the Lowry method (MacFarlane 2010).

When specimens of marine fish prey types from San Francisco Bay were not available for proximate composition analysis, we used measurements obtained by Roby et al. (2003) from the Columbia River estuary. These included the following prey types: steelhead, flatfish (Pleuronectidae), Pacific sand lance *Ammodytes hexapterus*, and smelts (Osmeridae). Freshwater sunfishes *Lepomis* spp. and basses *Micropterus* spp. were pooled into one prey category (centrarchids) and estimates of average energy density from Antolos et al. (2005) were used, as data were not available from San Francisco Bay.

There were some cases in both years of the study when prey items could only be identified as nonsalmonids. For these cases we used a weighted average based on the relative proportions of nonsalmonid prey types identified during each 2-week time period to estimate an average energy density and average mass for this prey category. For prey types totaling <1.0% of identifiable prey items in each year and for which no energy density information was available, the prey items were pooled together into an “other” category and assigned the average energy density of all known prey types. The following prey types were included in this category: Pacific pompano *Peprilus simillimus*, kelpfish (Clinidae), shrimp (Caridea), Pacific saury *Cololabis saira*, striped bass *Morone saxatilis*, and white croaker *Genyonemus lineatus*.

Predation Rate Estimation

In 2008, salmonid consumption estimates were converted into predation rate estimates (number consumed/number available) to investigate the effect of the Brooks Island Caspian tern colony on annual population growth rates of two Chinook salmon stocks that originate in the Central Valley of California: spring-run and fall-run Chinook salmon. The availability of spring- and fall-run Chinook salmon to tern predation was

based on the total number released into San Pablo Bay in 2008, which was obtained from the Regional Mark Information System Database maintained by the Pacific Fisheries Management Council (RMPC 1977). Previous research indicated that the vast majority (99.7%) of the Chinook salmon consumed by the Caspian terns nesting on Brooks Island were hatchery-raised Chinook salmon released directly into San Pablo Bay (Evans et al. 2011) and that the release locations in San Pablo Bay are well within the foraging range of the Caspian terns nesting on Brooks Island (Figure 1; Adrean 2011). Bay-released fish were therefore used as the best measure of juvenile salmon availability to terns nesting on Brooks Island. This assumption results in predation rate estimates that are biased upwards because of the exclusion of an unknown number of smolts released in-river that survived to the bay and were therefore available to terns. Based on Evans et al. (2011), 99.5% and 0.5% of the Chinook salmon consumed in 2008 were from the fall and spring runs, respectively. These percentages were multiplied by the total number of Chinook salmon consumed by terns in 2008 to estimate the number of fall- and spring-run Chinook salmon consumed during that year. Average predation rates, expressed as percentages, were calculated as the estimated number of smolts from each salmonid run consumed by Brooks Island Caspian terns divided by the estimated number of smolts from that run that were available to foraging terns.

We also estimated predation rates for a scenario in which the Brooks Island Caspian tern colony increased to 1,500 breeding pairs (3,000 individuals), as proposed by the U.S. Fish and Wildlife Service and the U.S. Army Corps of Engineers in their respective Records of Decision (USFWS 2006; USACE 2006). To do this, the estimate of per capita salmon consumption by Brooks Island terns in 2008 was multiplied by the proposed number of Caspian terns to obtain an estimate of salmonid consumption. We followed the same methods as described above to obtain estimates of the predation rate for each salmonid run.

Change to Salmonid Population Growth Rates

We calculated the change in the annual population growth rate (λ) for spring- and fall-run Chinook salmon in the event of a hypothetical elimination of the Caspian tern breeding colony on Brooks Island in order to evaluate the impact of tern predation at the levels measured in 2008. We also estimated the predation rates on spring- and fall-run Chinook salmon by the Caspian terns nesting on Brooks Island assuming an increase to 3,000 nesting individuals (1,500 pairs) and used these estimates to calculate the change in λ for spring- and fall-run Chinook salmon. Initial estimates of λ for the Chinook salmon runs most consumed by Brooks Island Caspian terns were calculated from the following equation for the population growth rate from Lindley et al. (2007):

$$\begin{aligned} &\text{population growth rate (\% per year)} \\ &= (\text{slope of } \log_e S_t \text{ versus time}) \times 100, \end{aligned}$$

where S_t is the annual spawning run estimate. We obtained spawning run estimates for 2001–2010 from the California Department of Fish and Game GrandTab database (CDFG 2011). Estimates of λ for salmonids are difficult to calculate with precision (McClure et al. 2003), so our initial estimates were used to provide a platform for our results of the percent change in λ only. The percent change in λ of salmon runs following elimination or enhancement of the Brooks Island tern colony was calculated as

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

where S_f is the salmon survival rate due to tern predation following either elimination or enhancement of the tern colony, S_i is the initial survival rate, and G is the average salmon generational time (McClure et al. 2003; Good et al. 2007).

Predator control to enhance prey populations can be justified if predators affect prey abundance (Gasaway et al. 1992), but it may be necessary to determine what portion of the mortality attributable to predation is additive (as opposed to compensatory) in order to estimate the effect of mortality due to predation on prey abundance (Errington 1967). It is not known what proportion of smolt mortality caused by Caspian tern predation is additive, but it is certainly less than 100%. A study relating the health status of steelhead to smolt susceptibility to avian predation found that steelhead in compromised health were more susceptible to Caspian tern predation, an indication that smolt mortality from Caspian tern predation is at least partly compensatory (Hostetter 2009). Consequently, we have calculated the percent change in λ for salmonid runs from tern predation under the assumptions of 100, 75, 50, and 25% additive mortality. The proportion of additive mortality was then applied to the variable S_f in the equation listed above for percent change in λ as follows:

$$\begin{aligned} &1 - [(S_i - S_f) \times \% \text{ additive mortality}] + \text{salmonid predation rate} \\ &= S_f \text{ including additive mortality level.} \end{aligned}$$

RESULTS

Bioenergetics Model Input

Colony size and numbers of young.—The peak size of the Caspian tern breeding colony at Brooks Island in 2008 was 812 breeding pairs (95% CI, 776–844; SE = 17; $n = 3$ counts). In 2009 colony size was significantly lower at 681 breeding pairs (95% CI, 655–707; SE = 13; $n = 3$ counts).

In 2008, the average number of chicks hatched per nesting attempt was 1.29 (95% CI, 1.09–1.49; SE = 0.1; $n = 31$), and the estimated number of fledglings produced at the colony was 341. In 2009, the average number of chicks hatched per nesting attempt was not significantly different at 0.94 chicks (95% CI, 0.76–1.12; SE = 0.09; $n = 77$), but the estimated total number of fledglings produced at the colony was just 97.

Caspian tern energy expenditure.—The average energy expenditure rate of adult Caspian terns nesting at Brooks Island was assumed to be the same as that of Caspian terns nesting on Rice Island in the Columbia River estuary, or 1,040 kJ/d (SD = 209; $n = 24$; Roby et al. 2003). The average energy consumption of Caspian tern chicks at Brooks Island was assumed to be the same as that of captive-raised Caspian tern chicks collected from the East Sand Island colony in the Columbia River estuary (Lyons and Roby 2011). The daily metabolizable energy requirements for captive-reared Caspian tern chicks peaked at 760 kJ/d. The mean TME required by tern chicks from hatching to fledging was 18,769 kJ (Lyons and Roby 2011).

Estimates of the total energy requirements of the Caspian tern colony at Brooks Island were calculated separately for the 2008 and 2009 nesting seasons (Table 1). Total energy requirements in 2009 were 28.3% lower than in 2008, likely due to the smaller tern colony size and productivity in 2009. The energy requirements of chicks accounted for 6.8% and 3.5% of total colony energy requirements in 2008 and 2009, respectively. These proportions are similar to those reported for the Rice Island (Roby et al. 2003) and the East Sand Island Caspian

TABLE 1. Energy requirements of the Caspian terns nesting at Brooks Island in 2008 and 2009 and the percentage of total energy consumption by the tern colony that was derived from each prey type. Mean energy requirements are reported, with standard deviations in parentheses.

Species	2008	2009
Energy consumption (10^4 MJ)		
Adult terns	17.3 (1.1)	14.0 (0.9)
Juvenile terns	1.3 (0.1)	0.5 (0.1)
Total	18.6 (1.1)	14.5 (0.9)
Energy contribution by prey type (%)		
Steelhead/trout	0.6	0.6
Chinook salmon	5.1	4.2
Total salmonids	5.7	4.8
Clupeids (herrings and sardines)	28.6	18.5
Northern anchovy	22.3	8.1
Shiner surfperch	14.8	22.1
Goby	9.1	4.8
Silversides	8.8	22.7
Smelt	3.4	7.2
Pacific staghorn sculpin	2.5	1.8
Centrarchids	1.6	3.4
Plainfin midshipman	0.3	1.0
Flatfishes	0.2	0.9
Leopard shark	0.1	0.3
Pacific sand lance	<0.1	<0.1
Pacific tomcod	<0.1	0.5
Other	0.3	0.8
Unidentified nonsalmonids	2.2	3.3

TABLE 2. Diet composition (% of prey items) of Caspian terns nesting at Brooks Island in 2008 and 2009.

Prey type	2008	2009
Steelhead/trout	0.3	0.2
Chinook salmon	9.9	7.8
Total salmonids	10.2	8.0
Clupeids (herrings and sardines)	14.4	9.4
Northern anchovy	29.1	11.3
Shiner surfperch	19.9	32.3
Goby	9.7	5.9
Silversides	5.4	14.3
Smelt	2.3	5.5
Pacific staghorn sculpin	4.4	3.3
Centrarchids	1.2	2.5
Plainfin midshipman	0.4	1.7
Flatfishes	0.2	1.0
Leopard shark	0.1	0.1
Pacific sand lance	<0.1	0.1
Pacific tomcod	<0.1	0.4
Other	0.2	0.7
Unidentified nonsalmonids	2.5	3.1

tern colonies (Lyons 2010), indicating similar ratios of adults to chicks.

Diet composition.—In 2008, the most prevalent prey type in the tern diet was northern anchovy (29% of prey items), followed by shiner surfperch (20% of prey items). In 2009, the most prevalent prey type was shiner surfperch (32% of prey items), while northern anchovy accounted for only 11% of prey items. Juvenile salmonids were the 4th and 5th most prevalent prey type in the diet and accounted for 10% and 8% of identified prey items in 2008 and 2009, respectively. The following prey types accounted for less than 5% of tern diet composition in both years: Pacific staghorn sculpin, centrarchids, plainfin midshipman, juvenile Pacific tomcod, flatfishes, Pacific sand lance, and juvenile leopard shark (Table 2).

Average mass and energy density of prey types.—The average total length of each prey type in the tern diet was estimated from observations of bill load fish delivered to the breeding colony by adults in each study year and input into the corresponding length–mass regression equation to estimate the average mass of each prey type (Table A.1 in the appendix).

The prey types with the lowest energy density were plainfin midshipman and Pacific tomcod, at 3.4 kJ/g wet mass, while Pacific sand lance had the highest energy density at 5.6 kJ/g wet mass (Table A.1). Marine forage fishes generally had energy densities in excess of 5.0 kJ/g wet mass. The average energy density of Chinook salmon smolts was 4.8 kJ/g wet mass and that of steelhead smolts was 4.6 kJ/g wet mass, lower than that of marine forage fishes but similar to that of estuarine prey types, such as shiner surfperch and silversides. The estimated average

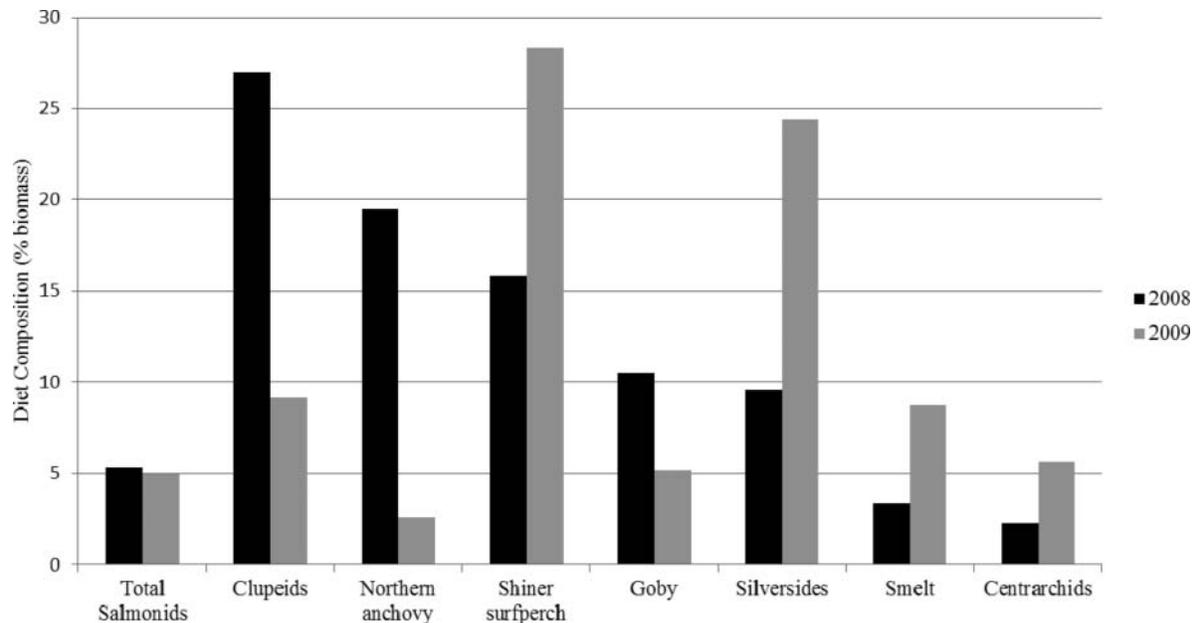


FIGURE 3. Caspian tern diet composition (% biomass of primary prey types) at the Brooks Island breeding colony in central San Francisco Bay, California during 2008 and 2009.

energy density of the “other” prey category was 4.5 kJ/g wet mass.

Bioenergetics Model Output

Marine and estuarine forage fish species accounted for approximately 86% of the identified Caspian tern prey biomass at the Brooks Island colony in 2008 and for 78% in 2009 (Figure 3). For each prey type, the mean energy density was combined with the proportion of biomass consumed for that prey type to estimate the percent of energy required by the tern colony that was provided by each prey type. In 2008, clupeids and northern anchovy supplied the highest proportions of total required energy (28.6% and 22.3%, respectively). In 2009, silversides and shiner surfperch supplied the highest proportions of total required energy (22.7% and 22.1%, respectively). Juvenile salmonids contributed <6.0% of the total energy required by the Brooks Island Caspian tern colony in both years of the study (Table 1).

We estimated the total number of fish consumed to be about 1.91 million (95% CI, 1.64–2.18 million) in 2008 and about 1.70 million (95% CI, 1.47–1.92 million) in 2009 (Table 3). The 95% confidence intervals for these estimates do overlap, suggesting that the difference between the 2 years in the total number of fish consumed was not significant. The estimated total number of juvenile salmonids consumed by Brooks Island Caspian terns in 2008 was 204,911 (95% CI, 175,292–234,530), which included approximately 200,685 fish in the “Chinook salmon” category and 4,226 fish in the “steelhead or trout” category. In 2009, the estimated total number of juvenile salmonids consumed was 167,383 (95% CI, 143,600–191,167).

This total was comprised of 163,258 Chinook salmon and 4,125 steelhead or trout. As with the total amount of fish consumed, these estimates suggest a lower number of salmon consumed in 2009 than in 2008; however, the overlap in the 95% confidence intervals indicates that the difference is not statistically significant.

The average per capita predation on all juvenile salmonids by adult Caspian terns nesting on Brooks Island in 2008 was 126 fish (95% CI, 108–145), and the per capita predation on juvenile Chinook salmon was 124 smolts (95% CI, 106–142). The average per capita predation on all juvenile salmonids by adult Caspian terns in 2009 was 123 fish (95% CI, 105–140), and the per capita predation on juvenile Chinook salmon was 120 smolts (95% CI, 103–137). Overlapping 95% confidence intervals suggest that there were no significant differences between years in the per capita predation by terns on all salmonids or on Chinook salmon alone.

Predation Rate Estimates and Changes to Salmonid Population Growth Rates

Approximately 21.1 million Chinook salmon were released into San Pablo Bay during 2008, of which 94% (~19.9 million) and 6% (~1.2 million) were from the fall and spring runs, respectively. Based on our consumption estimates and the relative susceptibility of each Chinook salmon run-type to tern predation derived from Evans et al. (2011), we estimated that in 2008 the Caspian tern colony on Brooks Island consumed approximately 200,000 fall-run Chinook salmon and approximately 1,000 spring-run Chinook salmon, equivalent to predation rates of 1.0% and 0.1%, respectively. For fall-run Chinook salmon,

TABLE 3. Mean prey consumption and 95% confidence intervals (total numbers of fish) by Caspian terns nesting at Brooks Island in 2008 and 2009; all values are in thousands.

Prey type	2008		2009	
	Mean	95% CI	Mean	95% CI
Steelhead/trout	4.2	3.4–5.1	4.1	3.1–5.1
Chinook salmon	200.7	171.6–229.8	163.3	140.0–186.5
Total salmonids	204.9	175.3–234.5	167.4	143.6–191.2
Clupeids	277.7	238.0–317.3	176.4	152.2–200.6
Northern anchovy	559.9	479.4–640.3	193.9	166.7–221.1
Shiner surfperch	364.2	312.6–415.9	515.3	446.5–584.0
Goby	200.1	169.3–230.9	98.9	84.6–113.3
Silversides	94.4	80.6–108.1	229.8	198.2–261.4
Smelt	51.3	43.6–59.0	108.6	93.5–123.6
Pacific staghorn sculpin	76.1	64.6–87.5	50.8	43.7–57.9
Centrarchids	19.6	16.4–22.8	40.5	35.0–46.0
Plainfin midshipman	7.8	6.6–9.0	22.8	19.3–26.3
Flatfishes	3.0	2.5–3.4	15.9	13.7–18.1
Leopard shark	1.2	1.0–1.3	2.5	2.1–2.9
Pacific sand lance	0.9	0.8–1.1	2.2	1.9–2.5
Pacific tomcod	0.3	0.2–0.4	7.6	6.5–8.8
Other	4.2	3.5–4.8	12.2	10.5–13.8
Unidentified nonsalmonids	45.3	38.1–52.5	53.7	46.4–61.0
Total	1,910.7	1,643.1–2,178.4	1,698.4	1,473.3–1,923.6

the initial population growth rate calculated from a 10-year regression was 0.7165. Eliminating the mortality from predation by Brooks Island terns (assuming that this mortality was 25, 50, 75, or 100% additive) would result in increases in λ of 0.08, 0.17, 0.25, and 0.34%, respectively. For spring-run Chinook salmon the initial λ calculated from a 10-year regression was 0.8074. Eliminating the mortality from predation by Brooks Island terns would result in increases in λ of 0.01, 0.01, 0.02, and 0.03%, respectively (Table 4).

We also estimated Chinook salmon smolt consumption for a hypothetical increase in the number of breeding Caspian terns on Brooks Island to 1,500 pairs, based on the per capita esti-

mate of 124 Chinook salmon smolts consumed by the colony in 2008. A colony this size would be expected to consume approximately 372,000 Chinook salmon smolts in one breeding season, consisting of about 370,000 fall-run Chinook salmon and 1,900 spring-run Chinook salmon. This level of consumption is equivalent to predation rates of 1.9% for fall-run Chinook salmon and 0.2% for spring-run Chinook salmon smolts. At the assumed additive mortality levels of 25, 50, 75, and 100%, these predation rates would result in declines in λ of 0.07, 0.14, 0.22, and 0.28%, respectively, for fall-run Chinook salmon and 0.01, 0.01, 0.02, and 0.02%, respectively, for spring-run Chinook salmon (Table 4).

TABLE 4. Potential changes to annual population growth rates (λ) of Central Valley spring-run (threatened) and fall-run (species of concern) Chinook salmon under two management scenarios for Brooks Island Caspian terns over a range of levels of additive mortality from Caspian tern predation. The percent changes to the initial values of λ are given in parentheses.

Salmon stock	Initial λ	0 Caspian tern breeding pairs				1,500 Caspian tern breeding pairs			
		25% additive mortality	50% additive mortality	75% additive mortality	100% additive mortality	25% additive mortality	50% additive mortality	75% additive mortality	100% additive mortality
Spring-run Chinook salmon	0.8074	0.8075 (+0.01%)	0.8075 (+0.01%)	0.8076 (+0.02%)	0.8077 (+0.03%)	0.8073 (-0.01%)	0.8073 (-0.01%)	0.8072 (-0.02%)	0.8072 (-0.02%)
Fall-run Chinook salmon	0.7165	0.7173 (+0.08%)	0.7182 (+0.17%)	0.7190 (+0.25%)	0.7199 (+0.34%)	0.7158 (-0.07%)	0.7151 (-0.14%)	0.7143 (-0.22%)	0.7136 (-0.28%)

DISCUSSION

Impact of Caspian Tern Predation on Salmonids

The main objectives of this study were to estimate the consumption of juvenile salmonids by the Caspian terns nesting on Brooks Island and determine whether the tern colony at its current size or at a proposed enhanced size poses a significant mortality risk for ESA-listed salmonids. Central Valley fall-run Chinook salmon were by far the most susceptible to predation by Caspian terns from this colony. Although this Chinook salmon ESU is not listed under the ESA, it is of conservation concern and poor adult returns from this ESU resulted in the closure of commercial and recreational salmon fishing along the coast of California in 2008 and 2009 (NOAA 2008, 2009b). This resulted in considerable regionwide economic hardship; US\$170 million in disaster relief was distributed over the course of 2008 and 2009 by the Pacific Fisheries Management Council to individuals and businesses dependent on salmon fishing (NOAA 2009a).

The proposed increase in the size of the Caspian tern colony on Brooks Island to 1,500 breeding pairs would lead to an estimated reduction in the population growth rate of the fall-run Chinook salmon ESU of up to 0.28%, assuming 100% additive mortality. The assumption of 100% additive mortality from Caspian tern predation is the worst-case scenario for the Chinook salmon ESU because it assumes that none of the mortality from tern predation is compensatory. The assumption of 100% additive mortality from Caspian tern predation is now known to be unrealistic (Hostetter 2009), but in the absence of an actual measure of percent additive mortality, this assumption errs on the side of the fish population of conservation concern. If the number of breeding pairs of Caspian terns nesting on Brooks Island fell to zero, the annual population growth rate of the fall-run Chinook salmon ESU would be expected to increase by 0.34% (again, assuming 100% additive mortality; Table 4).

Spring-run Chinook salmon, which are listed under the ESA, were far less susceptible to predation by Brooks Island Caspian terns than unlisted fall-run Chinook salmon. A near doubling of the Caspian tern colony size at Brooks Island would lead to a decrease in the annual population growth rate of spring-run Chinook salmon of 0.02% (assuming 100% additive mortality). This level of reduction in population growth rate is even lower than the amount calculated and found to be acceptable by the National Marine Fisheries Service for predation by Caspian terns on this ESA-listed salmon run ($\Delta\lambda = 0.05\%$; NOAA 2006). If the Caspian tern colony on Brooks Island were to disappear altogether, this would lead to an expected increase in the population growth rate for the spring-run Chinook salmon ESU of 0.03% (assuming 100% additive mortality; Table 4). By comparison, management actions at East Sand Island in the Columbia River estuary to reduce the size of the Caspian tern colony there are expected to result in increases in λ of over 1% for some ESA-listed salmonid stocks (Good et al. 2007; Lyons 2010).

The Sacramento River winter-run Chinook salmon ESU is currently listed as endangered under the ESA. No fish from this run were released into San Pablo Bay, and although 96% of the approximately 70,000 winter-run Chinook salmon that were released in-river were coded-wire-tagged, none of these tags were recovered on Brooks Island in 2008 (Evans et al. 2011). We therefore assume that predation by the Caspian terns nesting on Brooks Island is not a significant source of mortality for this ESA-listed run.

We were not able to evaluate the impact of tern predation on juvenile steelhead because estimates of the numbers of steelhead smolts out-migrating through San Francisco Bay are not available. No hatchery-raised juvenile steelhead were released into San Pablo Bay in 2008, and none of the hatchery-raised fish released in-river were marked with CWTs (RMPC 1977). The consumption of rainbow trout and steelhead was almost two orders of magnitude less than the consumption of Chinook salmon, but further study is needed to determine what proportion of *O. mykiss* consumed by Brooks Island Caspian terns are stocked rainbow trout as opposed to ESA-listed steelhead smolts.

The number and relative composition of hatchery-raised salmonid smolts released into San Pablo Bay influenced the subsequent predation rates by the Caspian terns nesting on Brooks Island. Evans et al. (2011) demonstrated that the vast majority (99.7%) of coded-wire-tagged salmonid smolts consumed by Brooks Island terns in 2008 were from fish released en masse into San Pablo Bay via net-pens. By comparison, the consumption of in-river (volitional out-migrant) Chinook smolts by Brooks Island Caspian terns in 2008 was extremely low (0.3%) despite the fact that similar numbers of tagged Chinook salmon were released in the river (~5.7 million) and in the bay (~6.3 million). Additionally, the proportion of the diet of Caspian terns nesting on Brooks Island that was juvenile salmonids was two- to threefold higher in 2008–2009 (~8–10% of prey items) than in 2003–2005 (~3–4% of prey items; author's unpublished data). The greater percentage of juvenile salmonids in the diet of Brooks Island terns in 2008–2009 coincided with the release en masse of more hatchery-reared juvenile salmonids in San Pablo Bay (RMPC 1977). Given this, substantial changes to the number or run-type composition (spring, fall, or winter) of Chinook salmon smolts released into San Pablo Bay in the future will likely influence Caspian tern predation rates and the risks and benefits of Caspian tern management initiatives on Brooks Island.

We are unable to predict how the Caspian tern diet composition would change if the colony were to double in size. It is possible that a particular food source could become limiting in the future, causing a shift to greater reliance on juvenile salmonids. However, during our study Caspian terns increased their reliance on estuarine fish during 2009—a year of lower marine forage fish availability (PFMC 2010) relative to 2008—but did not significantly change their reliance on juvenile salmonids (Figure 3).

Salmonid Consumption by Brooks Island Caspian Terns

The Caspian terns nesting on Brooks Island consumed about 205,000 juvenile salmonids in 2008 alone. Salmonid consumption by the Caspian terns nesting on East Sand Island in the Columbia River estuary can help put these results into context. Total smolt consumption by East Sand Island terns was estimated at 3.9–5.9 million smolts/year during 2001–2006 (Lyons 2010), and this level was determined to be high enough to warrant management actions to reduce the size of the colony (USFWS 2006). This is equivalent to an average consumption rate of 265 smolts per adult Caspian tern per year, more than double the amount consumed by individual Brooks Island Caspian terns in 2008 or 2009. Furthermore, the vast majority (98%) of the juvenile salmonids consumed by Brooks Island Caspian terns were from the hatchery-reared, unlisted fall-run Chinook salmon ESU (Evans et al. 2011), while the Caspian terns in the Columbia River estuary have substantial impacts on juvenile salmonids from multiple ESA-listed ESUs (Collis et al. 2001; Ryan et al. 2003). Management to reduce the size of the Caspian tern colony at East Sand Island is expected to improve λ by at least 1.1% for some ESA-listed ESUs, assuming a moderate (50%) level of additive mortality (Lyons 2010). By comparison, if the Caspian tern colony at Brooks Island increased to the proposed size of 3,000 individuals, the greatest expected declines in λ would be 0.28% for the unlisted fall-run Chinook salmon ESU and 0.02% for the threatened spring-run Chinook salmon ESU (assuming 100% additive mortality).

Our estimates of Caspian tern predation rates on salmonids based on bioenergetics model outputs were somewhat higher (by 28–29%) than those calculated using CWT recoveries on the tern colony at Brooks Island. However, the predation rates calculated using CWT recoveries were minimum estimates due to the likely deposition of some CWT tags ingested by Caspian terns in loafing and foraging areas away from the colony (Evans et al. 2011).

There were several factors that contributed to the estimated lower consumption of salmonids by Brooks Island terns in 2009 than in 2008. The number of breeding pairs of Caspian terns at the Brooks Island colony, as well as the number of young terns raised to fledging age, was lower in 2009. This resulted in a lower total energy requirement for the colony in 2009. The number of Caspian terns nesting at the Brooks Island colony has declined 35% since 2004, likely the result of limiting factors such as vegetation encroachment on tern nesting habitat and competition from the California gull and western gull colonies that are also present on the island (Collis et al. 2012). If the size of the Caspian tern colony on Brooks Island continues to decline, the total number of juvenile salmonids consumed by the colony per year will also likely decline.

Although salmonid smolt consumption was lower in 2009, the per capita predation rate of juvenile salmonids by adult Caspian terns did not differ appreciably between 2008 and 2009. The number of juvenile salmonids released via net-pen into eastern San Pablo Bay (approximately 20 km from Brooks Island)

was 31% lower in 2009 (~13.8 million salmonid smolts) than in 2008 (~20.0 million smolts; FFC 2008, 2009), but the lower number of salmon released in eastern San Pablo Bay during 2009 was not reflected in lower per capita predation rates on juvenile salmonids by Caspian terns. The high use of San Pablo Bay by foraging Caspian terns (Adrean 2011) is likely due to the high availability of forage fish following releases of hatchery-raised salmon from the net-pens. Hatchery-raised salmonids can be more susceptible to avian predation due to behavioral deficits, such as the lack of predator avoidance and tendency to feed at the water's surface (Olla et al. 1994; Collis et al. 2001). Hatchery releases in eastern San Pablo Bay occurred around midday (FFC 2008, 2009), when Caspian terns are most active (Cuthbert and Wires 1999), and regardless of tide stage. Juvenile salmonids released from the net-pens were allowed to acclimate in the pens for as little as 1 h prior to release (FFC 2008). Because of the predictability of smolt releases and the short period of acclimation, the released smolts were highly susceptible to a variety of predators, including Caspian terns. Individual piscivorous waterbirds are attracted to foraging flocks of conspecifics (Krebs 1974; Silverman et al. 2004), so the prerelease acclimation period in the net-pens allowed Caspian terns to gather at the location of the release. A study of Caspian tern foraging behavior in San Francisco Bay using radiotelemetry also suggested that individual terns learned the location and timing of net-pen releases and repeatedly returned to forage on recently released smolts (Adrean 2011), indicating that modifications to hatchery release practices may reduce the predation-related mortality of these fish.

Model Biases

There are some potential biases in our fish consumption estimates that must be considered before these results are used to inform management of the Brooks Island Caspian tern colony. Estimates of smolt consumption have been shown to be sensitive to the energy expenditure rate of Caspian tern adults and the total metabolizable energy requirements of juvenile Caspian terns (Roby et al. 2003). Our measurements of the energy expenditure rate in adult Caspian terns were taken from wild, free-ranging birds nesting at Rice Island in the Columbia River estuary. Climate differences may be a confounding factor that could cause a difference in the adult energy expenditure rate for Caspian terns nesting at these two locations. Energy demand is closely related to ambient temperature (Kendeigh 1969); an inverse relationship between DEE and temperature would cause our prey consumption estimates to be biased upward somewhat. However, the mean temperatures during the breeding season are only 3–4°C lower in the Columbia River estuary than in the San Francisco Bay area, so we would not expect a major difference in energy demand between the two sites.

We used the TME measured for captive-reared Caspian tern chicks raised under ambient temperatures near the Columbia River estuary to estimate the energy requirements of juvenile terns at Brooks Island. It is not known how close this estimate is

to that of chicks raised on Brooks Island, so there may be some bias associated with this measurement. Daily energy expenditure has only varied slightly with latitude for chicks of other tern species (Arctic tern *Sterna paradisaea*, Antarctic tern *S. vittata*, and common tern *S. hirundo*; Klaassen 1994); consequently, we do not expect that this was a significant source of error in our model.

Our observations of fish delivered to the colony, which were used to estimate Caspian tern diet composition, may contribute to bias in model outputs if Caspian terns engage in selective foraging behavior. Studies of several seabird species have shown that adults forage farther from the colony to meet their own energy requirements with higher-quality prey items and closer to the colony to provision chicks with lower-quality but more accessible prey items (Weimerskirch et al. 1997; Weimerskirch 1998). Radiotelemetry studies conducted on Caspian terns have not suggested this pattern of foraging behavior (Lyons et al. 2005, 2007; Anderson et al. 2007; Adrean 2011), but radiotelemetry tracking may not provide sufficient sensitivity to examine this question. However, the bioenergetics model input parameter of the proportion of each prey type in the diet appears to contribute little to the uncertainty of model output, according to a sensitivity analysis (Roby et al. 2003).

Kleptoparasitism of prey items from Caspian terns by gulls is not accounted for in our model. California and western gulls nest in close proximity to Caspian terns on Brooks Island and are often observed stealing fish as the terns return to the colony to feed a mate or chicks. These events occurred at a rate of about 7.5% of fish delivery attempts by terns nesting at Brooks Island in both 2008 and 2009 (L. J. Adrean, unpublished). If the Caspian terns from Brooks Island are taking more fish than required for their own energetic needs to compensate for gull kleptoparasitism, our estimate of total predation on all prey types may be biased slightly downward.

A sensitivity analysis on bioenergetics model input parameters completed by Roby et al. (2003) indicated that uncertainty in model results is most affected by the estimate of the number of breeding pairs at the colony. However, the Caspian tern colonies at Brooks Island are linear in shape and highly visible from the observation blind or a boat in the water, making ground counts of sitting and standing terns quite accurate. The Brooks Island tern colony is also small and relatively easy to count using aerial photography; our resulting standard error for counts from photography was also very low. We believe that our estimates of breeding pairs at Brooks Island are reliable and contributed little to the uncertainty of our estimates of prey consumption from the bioenergetics model.

Conclusions

The net effect of the proposed increase in the number of Caspian terns nesting on Brooks Island and the reduction in the number of Caspian terns nesting in the Columbia River estuary would be beneficial to ESA-listed salmonid ESUs on the West Coast overall. If the Brooks Island Caspian tern colony increased to 1,500 breeding pairs, the enhanced predation pres-

sure would result in declines in salmonid population growth rates of at most fractions of 1%, whereas management to reduce the size of the Caspian tern colony in the Columbia River estuary is expected to yield increases in annual population growth rates for some salmonid ESUs of at least 1%. In particular, the proposed larger Brooks Island Caspian tern colony would be expected to negatively impact the annual population growth rate of ESA-listed spring-run Chinook salmon by 0.02% or less, an amount lower than that deemed acceptable for this stock by the National Marine Fisheries Service ($\Delta\lambda = 0.05\%$). The vast majority of juvenile salmonids that were consumed by Brooks Island Caspian terns were hatchery-reared smolts released from net-pens in San Pablo Bay. The per capita predation rate on juvenile salmonids by Caspian terns from this colony would likely decline appreciably if hatchery releases in San Pablo Bay were scheduled for late in the evening and on outgoing tides.

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APPENDIX: DETAILS OF CASPIAN TERN PREY

TABLE A.1. Length (L)–mass (M) regression equations, average prey mass, energy density, and energy content of major prey types identified in the diet of Caspian terns nesting at Brooks Island during 2008 and 2009; n.a. = not available.

Prey item	Length–mass regression			2008 prey mass (g)			2009 prey mass (g)			Energy density (kJ/g)			2008 energy content (kJ)	2009 energy content (kJ)
	Equation ($M =$)	R^2	N	Mean	SD	N	Mean	SD	N	Mean	SD	N		
Steelhead/trout	n.a.			61.2	16.3	231	61.2	16.3	231	4.6	0.9	12	282.1	282.1
Chinook salmon	$(L - 62.148)/4.058$	0.83	22	8.8	0.1	1	8.0	0.1	1	4.8	0.8	13	42.0	37.9
Clupeids	$(L - 110.180)/1.289$	0.79	14	37.0	0.2	1	16.2	0.1	1	5.3	1.2	11	197.5	86.6
Northern anchovy	$(L - 80.394)/3.107$	0.93	14	13.2	0.1	1	4.2	<0.1	1	5.1	1.5	7	68.1	21.4
Shiner surfperch	$(L - 48.451)/3.339$	0.94	33	16.5	0.1	1	17.2	0.1	1	4.7	0.8	7	77.5	80.5
Goby	$(L - 63.098)/3.813$	0.94	17	20.0	0.2	1	16.3	0.2	1	4.4	0.9	8	88.7	72.2
Silversides	$(L - 96.955)/2.016$	0.85	25	38.7	0.6	1	33.3	0.3	1	4.6	0.8	11	179.1	154.0
Smelt	n.a.			25.1	10.2	7	25.1	10.2	7	5.0	1.3	12	126.0	126.0
Pacific staghorn sculpin	$(L - 64.624)/3.040$	0.94	15	16.1	0.2	1	15.4	0.2	1	3.9	0.6	9	63.4	60.6
Centrarchids	n.a.			43.7	4.1	194	43.7	4.1	194	3.5	0.3	17	151.2	151.2
Plainfin midshipman	n.a.			23.9	4.8	1	23.9	4.8	1	3.4	0.7	1	80.3	80.3
Flatfishes	n.a.			23.3	16.6	25	23.3	16.6	25	4.2	0.4	12	97.6	97.6
Leopard shark	n.a.			52.9	10.6	1	52.9	10.6	1	3.8	0.8	1	199.4	199.4
Pacific sand lance	n.a.			5.6	2.9	38	5.6	2.9	38	5.6	0.5	6	31.5	31.5
Pacific tomcod	n.a.			33.9	10.7	4	33.9	10.7	4	3.4	0.3	13	117.0	117.0
Other	n.a.			25.0	5.0	1	25.0	5.0	1	4.5	0.9	1	112.5	112.5