AN ABSTRACT OF THE DISSERTATION OF

Donald E. Lyons for the degree of Doctor of Philosophy in Wildlife Science presented on April 27, 2010.
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Abstract approved:

Daniel D. Roby

This dissertation focuses on the predator-prey relationship between two species of avian predators, Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*), and one of their important prey types, juvenile salmonids (*Oncorhynchus* spp.), in the Columbia River estuary of Oregon and Washington states during the period 1998 – 2007. I used a data-rich bioenergetics framework to estimate juvenile salmonid consumption by these two avian predators, assessed impacts to at-risk salmonid populations by estimating salmonid mortality rates due to avian predation, and estimated potential demographic benefits to salmonids if avian predation were reduced. The managed relocation of the Caspian tern colony from Rice Island to East Sand Island, lower in the Columbia River estuary, reduced tern predation on salmonids from over 11 million smolts consumed annually to 4 – 7 million, but those benefits accrued primarily to sub-yearling Chinook salmon (*O. tshawytscha*). Combined consumption of juvenile salmonids by Caspian terns and double-crested cormorants in the Columbia River estuary was ca. 7 – 15 million smolts per year during 2006-2007, causing an 8 – 17% mortality rate among smolts

migrating through the estuary, with higher mortality rates for steelhead (*O. mykiss*) and coho salmon (*O. kisutch*). Under a potential management scenario to reduce avian predation by both species, improvements in the average annual population growth rate (λ) of salmonids ranged from 0.4% for sub-yearling Chinook to 3.1% for coho. These improvements are generally less than what is possible from altered hydropower system operation within the Columbia Basin for salmonid populations that are more severely affected by dams. For a few salmonid populations, reduced avian predation might contribute to stabilizing the population ($\lambda = 1$), but would need to be part of a broader recovery strategy to ensure population growth and recovery ($\lambda > 1$).

Climate was an important factor modulating Caspian tern predation on salmonids, with greater consumption of smolts occurring in years of cooler ocean conditions and higher Columbia River flows. Climate did not contribute to variation in consumption of salmonids by cormorants, perhaps due to the larger effect of growth in the size of the cormorant colony during the study period. Due to current trends in colony size (terns: stable, cormorants: increasing) and the planned dispersal of a portion of the tern population, cormorant predation will likely be a more significant mortality factor for Columbia Basin salmonids in the future than will tern predation. A critical unknown factor remains; that is the degree to which reductions in avian predation on salmonids might be compensated for by other salmonid mortality factors.

Bioenergetics-based Predator-prey Relationships Between Piscivorous Birds and Juvenile Salmonids in the Columbia River Estuary

by
Donald E. Lyons

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APPROVED:

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Donald E. Lyons, Author

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CONTRIBUTION OF AUTHORS

Dr. Dan Roby contributed to all aspects of each chapter included herein. Dr. G. Henk Visser provided assistance in chapter 3 with study design and conducted all doubly-labeled water lab analyses in his lab at the Centre for Isotope Research. For chapters 4 and 5, Jessica Adkins, Chris Couch, Karen Courtot, Allen Evans, Anne Mary Myers, Lauren Reinalda, and Yasuko Suzuki supervised field data collection and laboratory analyses. Ken Collis assisted with study design and project administration in chapters 4-6. Dr. David Kuligowski provided genetic species identification of salmonids recovered from the stomachs of cormorants in chapter 5. Drs. Laurie Weitkamp and Robert Emmett generously shared fish data from the Columbia River estuary and plume for inclusion in chapter 6.

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DEDICATION

To my brother John, who has taught me so much.

Bioenergetics-based Predator-prey Relationships Between Piscivorous Birds and Juvenile Salmonids in the Columbia River Estuary

Chapter 1

GENERAL INTRODUCTION

Donald E. Lyons

Many salmonid (*Oncorhynchus* spp.) populations in the U.S. Pacific Northwest have been in decline for over a century (Lichatowich 1999). In the Columbia River basin 13 of 20 evolutionarily significant units (ESUs) of salmonids are listed under the U.S. Endangered Species Act (ESA) as threatened or endangered (Good et al. 2005). Many recovery actions have recently focused on mitigating impacts of hydropower, hatcheries, harvest, and degraded freshwater habitat (Federal Caucus 2000); however, resource managers have also considered predators as a possible factor inhibiting recovery (NMFS 1995, 2000).

In the Columbia River basin, populations of colonial nesting piscivorous waterbirds have increased substantially in the last 30 years (Collis et al. 2002). Despite no records of Caspian terns (*Hydroprogne caspia*) nesting in the Columbia River estuary prior to 1984 (Gill and Mewaldt 1983, Suryan et al. 2004), by 1998 the largest known Caspian tern colony in the world, about 8,800 breeding pairs, existed at Rice Island, 34 km upstream from the river mouth (Wires and Cuthbert 2000). Similarly, double-crested cormorant (*Phalacrocorax auritus*) populations in the estuary increased from 131 breeding pairs in 1980 (Carter et al. 1995), to a total estuary breeding population in excess of 10,000 breeding pairs by 2003, the largest nesting concentration of this species on the Pacific Coast (Anderson et al. 2004) and perhaps in all of North America (Wires et al. 2001).

Piscivorous birds have often been cited as important predators on commercial fish species in other systems (Mace 1983, Wood 1987, Blackwell 1996, Rudstam et al. 2004). In 1997 and 1998, studies indicated that Caspian terns nesting at Rice Island in the Columbia River estuary relied upon juvenile salmonids for 73-77% of their diet (Collis et al. 2002). Using a bioenergetics approach, it was estimated that this single tern colony consumed 12.4 million juvenile salmonids (95% CI: 9.1-15.7 million) in 1998 (Roby et al. 2003). This consumption was estimated to represent up to 15% of some stocks of salmonids that reached the estuary (Collis et al. 2001b, Roby et al. 2003). Double-crested cormorants nesting in the estuary relied upon juvenile salmonids less than terns in 1997-1998, but salmonids were still an appreciable proportion of the diet (46% for cormorants nesting on Rice Island and 16% for cormorants nesting on East Sand Island, at river kilometer 8; Collis et al. 2002). Salmonid consumption by cormorants is not yet precisely understood, but recent large increases in the cormorant breeding population and their relatively large daily energy requirements suggest that salmonid consumption by cormorants may equal or exceed that by Caspian terns, despite the cormorants more diverse diet.

Other predators also consume large numbers of juvenile salmonids in the Columbia River basin. Annually, an estimated 16 million juvenile salmonids were consumed throughout the basin by a native fish predator, northern pikeminnow (*Ptychocheilus oregonensis*), in the early 1990s (Ward et al. 1995; Beamesderfer et al. 1996). This consumption estimate led to large scale management activities, such as the establishment of bounty fisheries to reduce the number of predatory-sized pikeminnow and reconfiguration of dam outflows to reduce predation rates. 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 a million juvenile salmonids per year (D.E. Lyons, 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 on smolts 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).

In recent decades, management of native predators has sometimes been proposed or pursued to benefit threatened or endangered wildlife populations (Goodrich and Buskirk 1995, Koenen et al. 1996, Mitchell et al. 1999, Kinley and Apps 2001, Schroeder and Baydack 2001, Yodzis 2001, Engeman et al. 2002, Ernest et al. 2002, Larson et al. 2002). In particular, anthropogenically enhanced populations of predators have sometimes been seen to pose risks for declining prey populations (Kress 1983, Guillemette and Brousseau 2001, Boarman 2003). "Spillover predation" (Schneider 2001) occurs when these abundant predators incidentally prey on rare species that contribute little to sustaining the predator population but nonetheless may be significantly affected by the predation. In this context, expanding populations of piscivorous birds in the Columbia River basin appear to be benefiting from both anthropogenic nesting habitat (e.g., dredged material disposal sites; Antolos et al. 2004, Suryan et al. 2004) and from artificially reared juvenile salmonids intended primarily for human harvest (> 100 million hatchery-reared smolts are released into the Columbia River annually; Collis et al. 2001b). Spillover predation occurs when terns, cormorants, gulls, etc., in addition to consuming non-listed hatchery-reared smolts, incidentally consume smolts from ESA-listed populations (Levin and Williams 2002), often taking the same proportion of these stocks as they do of the more abundant hatchery-reared stocks (Collis et al. 2001b).

Anthropogenic habitat changes that have occurred in the Columbia River basin over the last century may make modern cohorts of juvenile salmonids more susceptible to predation than during previous river conditions. The mainstem Columbia River migration corridor has been altered by the construction of dams and implementation of channelization practices (dredging, construction of dikes and jetties, etc.) for the purposes of power generation, flood control, safe and reliable navigation, irrigation, and use of the floodplain for agriculture or urban purposes (Lichatowich 1999). Degradation of smolt habitat quality or diminished smolt body condition due to habitat conditions has sometimes made smolts more vulnerable to predation (Mesa et al. 1994, Schneider 2001). In the Columbia River, stress associated with passage through the mainstem dams has made smolts more vulnerable to piscine predators in the immediate vicinity of the dams (Rieman et al. 1991, Mesa 1994, Mesa and Warren 1997). It is also hypothesized that non-lethal stress experienced by smolts during passage through the dams may lead to delayed mortality in the estuary or ocean, where avian predation could be one proximate cause of mortality (Schaller et al. 1999, Budy et al. 2002). Additionally, some smolts that are captured and transported around the dams as a mitigation measure may be stressed by this process and consequently more vulnerable to predation (Congleton et al. 2000).

Mortality rates of juvenile salmonids due to other factors are sometimes comparable to, but sometimes greatly exceed, documented predation rates, depending on where in the basin stocks originate. Direct mortality rates associated with passage through mainstem dams depend on flow conditions, route through the dam (spillway, turbine, or bypass facility), and configuration of each dam, but may sometimes approach 10% per dam (Muir et al. 2001). Columbia River salmonids may navigate anywhere from zero to nine mainstem dams during their out-migration and must survive hazards in the slackwater reaches associated with each dam (e.g., exotic predators, etc.), so out-migration mortality rates may accumulate. In-river out-migration mortality for perhaps the worst case ESU, Snake River spring/summer Chinook (migrating through eight dams and the associated reaches), has been estimated at up to 80% (Kareiva et al. 2000). To mitigate for this high mortality rate, much of this ESU is transported around the dams in barges or trucks (Kareiva et al. 2000, Antolos et al. 2005). Mortality rates in the nearshore ocean environment, due to competition, predation, or other factors, are poorly known but may greatly influence later recruitment rates. A strong relationship between decadal-scale climate regimes throughout the Northeast Pacific Ocean and salmonid recruitment rates has been shown for periods prior to the late 1990s (Pearcy 1992, Mantua et al. 1997, Hare and Mantua 2000, McFarlane et al. 2000), and a climate regime shift observed in 1998 (Chavez et al. 2003, Peterson and Schwing 2003) appears to be largely responsible for improvement in juvenile salmonid abundance and condition in the nearshore environment (Beamish et al. 2004b) and for increased recruitment beginning in 2000 (Beamish et al. 2004a).

Based on the above and other data, regional resource managers concluded that avian predation could be a potential contributing factor limiting recovery of imperiled Columbia River salmonid runs (NMFS 2000). Management of Caspian terns has been ongoing since a pilot study was initiated in 1999 to investigate if relocating terns to East Sand Island, in the marine portion of the estuary, might cause terns to forage more on marine forage fish and reduce the reliance of terns on salmonids (USACE 1999). Over the course of three years (1999 – 2001), the entire Caspian tern colony was relocated to East Sand Island using a combination of attraction at East Sand Island and passive habitat restrictions at Rice Island (Roby et al. 2002). Juvenile salmonids made up a significantly smaller proportion of the tern diet at East Sand Island (Roby et al. 2002), and preliminary calculations suggest millions fewer smolts were consumed by terns in each year since the relocation (D.E. Lyons, unpublished data). Resource managers have concluded that smolt consumption by estuary Caspian terns still poses a risk to listed salmonid populations, particularly steelhead (*O. mykiss*) ESUs, so management to disperse some Caspian terns to sites outside the Columbia River estuary is being implemented (USFWS 2005).

No management of the double-crested cormorant colony on East Sand Island has yet occurred, although resource managers are calling for further investigation of the impacts of cormorant predation on juvenile salmonid survival in the Columbia River estuary (NOAA 2004). Elsewhere in North America, double-crested cormorant populations are currently being managed to reduce conflicts with fisheries resources (USFWS 2003). In the Columbia River estuary, management of Caspian terns resulted in the displacement of a large cormorant colony (ca. 1000 breeding pairs) from Rice Island in the upper estuary (Collis et al. 1999). Efforts have also been made to prevent cormorants from roosting on pile dikes throughout the estuary (Collis et al. 2001a).

In addition to juvenile salmonids, Caspian terns and double-crested cormorants nesting in the Columbia River estuary consume significant numbers of other forage fishes, such as northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasi*), and Pacific sardine (*Sardinops sagax*). Populations of these marine fishes are known to track environmental fluctuations on the scale of years or decades (McFarlane and Beamish 2001, Chavez et al. 2003), though monitoring is sometimes difficult. It is likely that climate conditions affecting these alternative prey may ultimately play a role in modulating predation by piscivorous waterbirds on juvenile salmonids in the estuary.

This dissertation seeks to enhance our understanding of the predator-prey relationship between piscivorous waterbirds and juvenile salmonids (and other prey species) in the Columbia River estuary. Bioenergetics modeling is a suitable approach for studying the interactions of piscivorous birds and prey resources (Wiens and Scott 1975, Furness 1978). Precise measurements of predator energy requirements and prey energy content were collected to support this approach, and bioenergetics modeling was thus the primary methodology employed in the following studies. Chapters 2 and

3 fill in critical information gaps on the energy requirements of both Caspian terns (chicks) and double-crested cormorants (adults). Chapter 4 provides an assessment of the relationship between Caspian terns and Columbia River salmonids following management initiated in 1999, utilizing a bioenergetics model representing a substantial improvement and extension over previous efforts (i.e., Roby et al. 2003). Chapter 5 presents the first bioenergetics-based quantification of impacts on juvenile salmonids from predation by double-crested cormorants in the Columbia River estuary. The modulating influence of climate on Caspian tern consumption of juvenile salmonids in the Columbia River estuary is studied in chapter 6; chapter 7 provides an overall synopsis of this dissertation research. As a whole, this dissertation provides a model for comprehensively studying predator-prey interactions involving multiple predators and an entire prey community, with the focus on impacts to a particular threatened prey group - juvenile salmonids. It is my hope that these studies contribute to the regional dialogue on salmon and steelhead recovery in the U.S. Pacific Northwest and serve as an example of rigorous science for other contentious resource management issues, especially those involving piscivorous waterbirds and their prey.

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Chapter 2

VALIDATING GROWTH AND DEVELOPMENT OF A SEABIRD AS AN INDICATOR OF FOOD AVAILABILITY: CAPTIVE-REARED CASPIAN TERN CHICKS FED *AD LIBITUM* AND RESTRICTED DIETS

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ABSTRACT

For seabirds raising young under conditions of limited food availability, reducing food provisioning rates to the young is a primary means available to avoid an abandonment of the breeding effort. To identify chick characteristics indicative of limited food availability, we examined the growth and development of captive-reared Caspian tern (*Hydroprogne caspia*) chicks fed *ad libitum* and restricted (ca. one-third lower caloric intake) diets. *Ad libitum* fed chicks grew at similar rates and achieved similar size at fledging to that documented in the wild and had energetic demands that closely matched allometric predictions. We identified three general characteristics of food-restricted Caspian tern chicks compared to *ad libitum* chicks: (1) lower age-specific body mass, (2) lower age-specific skeletal and feather size, such as wing chord length, and (3) heightened levels of corticosterone in blood, both for baseline levels and levels in response to acute stress. Effects of diet restriction on feather growth were much less pronounced than effects on body mass and structural growth, apparently due to preferential allocation of food resources to maintain plumage growth. Measurements of chick body mass and feather development (e.g., wing chord length or primary length) or measurement of corticosterone levels in blood would allow useful evaluation of the nutritional status of chicks reared in the wild, and indications of the ecological conditions within the foraging range of parent seabirds. These measures would allow such an evaluation even in situations where a breeding colony was visited

only once during late chick-rearing and when the age of chicks was imprecisely known.

INTRODUCTION

Characteristics of avian growth and development are useful as indicators of ecological conditions (e.g., Cairns 1987), as predictors for the future survival and performance of individual birds (Lindstrom 1999, Metcalfe and Monaghan 2001), and to categorize species in an evolutionary context (Starck and Ricklefs 1998a).

For breeding birds, variable ecological conditions such as a limited food supply may induce any of several responses: clutch size reduction, brood size reduction, reduced chick provisioning rate, and/or abandonment of the clutch or brood. For short-lived species with high potential reproductive output, clutch and brood size variability, achieved through a variety of physiological and behavioral mechanisms, allow parents a great deal of flexibility to continue the breeding effort (Gill 1995). In long-lived species with low reproductive output (e.g., seabirds having a small or single-egg clutch), reduced chick provisioning rates and the resultant lower chick growth rates are the primary means available to avoid an abandonment of the breeding effort in times of limited food availability. Thus, in at least some cases, chick growth rates may be a highly sensitive indicator of environmental fluctuation (Cairns 1987, Harding et al. 2003, Einoder 2009). Similarly, other physiological effects of food limitation in chicks, such as a modified corticosterone response of the endocrine system, may also serve as an indication of ecological conditions (Nunez-de la Mora et al. 1996, Kitaysky et al. 1999, Kitaysky et al. 2001, Kitaysky et al. 2007, Benowitz-Fredericks et al. 2008).

Conditions during chick-rearing may have profound effects on individuals later in life, influencing post-fledging survival (Magrath 1991, Gaston 1997, Sagar and Horning Jr. 1998, Naef-Daenzer et al. 2001, Monros et al. 2002, Stienen and Brenninkmeijer 2002, Suedkamp Wells et al. 2007), recruitment (Both et al. 1999, Perrins and McCleery 2001, Van de Pol et al. 2006), age at first breeding (Blount et al. 2006), cognitive ability (Kitaysky et al. 2003), adult size (Searcy et al. 2004), clutch size (Perrins and McCleery 2001), competitive ability to secure optimal nesting habitat (Perrins and McCleery 2001, Van de Pol et al. 2006), and lifetime reproductive success (Van de Pol et al. 2006). During periods or in locations where food availability is not directly monitored, measures of chick growth and condition might allow projection of the future success of a cohort and provide a mechanistic understanding of demographic trends.

In an evolutionary context, measures such as growth rates, age at fledging, and fledging mass are important characteristics of particular life history types, as well as characters that allow placement of species into the framework of an altricial-precocial spectrum (Starck and Ricklefs 1998b). Energy requirements during growth, such as the maximum daily energy requirement prior to fledging and the total energy requirement to fledge, can be useful when considering energy demands placed on parent birds (Weathers 1992, Visser 2001). Similarly, the plasticity of development in response to varying ecological conditions is often an important indication of evolutionary adaptations in avian growth (Schew and Ricklefs 1998). The response of individuals' growth to food restriction has been a common technique applied to examine developmental plasticity, with different rates of growth in distinct body components usually interpreted to reflect optimal energy allocation to maximize short term survival (Oyan and Anker-Nilssen 1996, Kitaysky 1999, Dahdul and Horn 2003, Takenaka et al. 2005, Benowitz-Fredericks et al. 2006, Sears and Hatch 2008).

In these contexts, we examined the growth and development of Caspian terns (*Hydroprogne caspia*) using captive-reared chicks. Caspian terns are a relatively long-lived species with a moderate clutch size (1-3 eggs) and semi-precocial chicks that fledge around 35 days after hatch (Cuthbert and Wires 1999). Our specific aims were to (1) determine the effects of food restriction on Caspian tern chicks and identify how chicks with limited food intake allocate energy to growth of various body components, (2) establish baseline datasets of Caspian tern chick growth and development in chicks fed ample and restricted diets for future comparisons to wild chicks, ultimately to allow evaluation of foraging conditions near breeding colonies and allow assessment of potential future performance of individual chicks and/or cohorts, and (3) place Caspian terns in an evolutionary context among other seabirds using measures of energetic requirement for pre-fledged young.

METHODS

We collected 20 Caspian tern chicks from a colony on East Sand Island in the Columbia River Estuary, Oregon during the early chick-rearing period (28 May, 2001). The oldest chick was selected from each of 20 nests containing multiple chicks or 1-2 chick(s) and an egg. Using body mass at capture and information from Schew et al. (1994), chick age at capture was estimated for all chicks and ranged from 1-5 days post-hatch. Chicks were transported to a rearing facility on the day of capture and most chicks accepted food offerings within hours of initial capture. The rearing facility was an enclosed, unheated building in Chinook, WA, approximately 2 km from the East Sand Island colony. We initially housed chicks in groups of 10 in plastic wading pools with a 2-5 cm layer of sand as a substrate and at 10 days post-hatch chicks were moved to individual plastic tubs, again with a sand substrate. Wading pools were equiped with 3 heat lamps to simulate warmer conditions chicks would normally experience when brooded; chicks could position themselves directly under a heat lamp or up to 1 m away as desired. Once moved to individual plastic tubs, chicks experienced similar ambient temperatures to those at the East Sand Island colony, although were not exposed to precipitation or winds.

Chicks were fed Atlantic silversides (*Menidia menidia*) through day 10 post-capture, when the diet was switched to Pacific herring (*Clupea pallasi*). Initially, all chicks were fed an *ad libitum* diet, with food offered eight times daily (the initial offering at 0600 and the final at 2200 hours). After five days post-capture, the frequency of food offerings was reduced to six times daily (initially at 0600 and concluding at 2100 hours). Between food offerings, food was always available on trays for *ad libitum* fed chicks (see below). Silversides were obtained from the Oregon Coast Aquarium, Newport, OR (Bryant Tarr) and herring from Xanadu Seafoods, Inc., Lynnwood, WA. Both fish were obtained and stored frozen and partially thawed immediately prior to feeding. In addition to this frozen fish diet, terns received a broad spectrum vitamin supplement (Sea Tabs, Pacific Research Laboratories, Inc., San Diego, CA) daily during the rearing period. The vitamin tablet was inserted into the mouth of the first fish offered each tern at the beginning of each day. Terns did not have access to water during rearing; adequate hydration was achieved by injecting the abdominal cavity of fish with water using a syringe prior to offering fish to chicks.

Energy content of silversides and herring were determined using proximate composition analysis (Reynolds and Kunz 2001) of fish sampled from packages used throughout the rearing period. Individual fish were first weighed freshly thawed and then dried to constant mass in a convection oven to determine water content. Lipid was extracted from dried, ground fish samples using hexane – isopropyl alcohol (7:2 vol/vol) in a Soxhlet apparatus. Lean dry samples were then combusted in a muffle furnace to determine ash-free lean dry mass (94% protein, Montevecchi et al. 1984) by subtraction. The resulting energy content of both fish types was then calculated from proximate composition (water, lipid, ash-free lean dry matter, and ash content) using published (Schmidt-Nielsen 1997) energy equivalents of these fractions (lipid = 39.4 kJ/g and protein = 17.8 kJ/g).

Up to 10 days post-hatch, all chicks were fed an *ad libitum* diet. Diet treatments began at day 11 post-hatch for each chick. Chicks were randomly assigned to one of two groups of 10 chicks each: the "ad lib" group was continued on the *ad libitum* diet for the duration of the experiment; the "restricted" group was fed a restricted diet beginning on day 11 post-hatch, consisting of approximately two-thirds of the food consumed by birds in the ad lib group. Species and biomass of fish consumed were recorded separately for each chick throughout the rearing period.

Several morphological measurements were taken on all tern chicks approximately daily during the rearing period. Mass (± 1 g), wing chord length (± 1 mm), head + bill length (± 0.1 mm), culmen length (± 0.1 mm), and tarsus length (± 0.1 mm) were measured beginning the day of capture and 10th primary and scapular feather lengths beginning within three days of emergence. Growth rate curves for body mass were described for individual chicks from the day of capture until day 35 post-hatch using a three-parameter logistic growth rate function, and fitted parameter values for each diet treatment group were compared using the Wilcoxon rank-sum test. Unlike body mass, bone and feather growth data were adequately fit by a linear growth model (i.e., residuals were unbiased) so, for these parameters, the Wilcoxon rank-sum test was used to compare linear growth rates for each diet treatment, across the treatment period (day 10 – 35).

Apparent metabolizable energy coefficients (MEC) were measured for each chick at ages ranging from 27 to 30 days post-hatch. The sand substrate lining in individual tubs was replaced with Dry Dek (Kendall Products, Naples, FL) and all excreta was collected over a 24-hour period beginning at 0600 hours, following the overnight fast. Excreta was frozen for storage and total energy content was later determined using bomb calorimetry on dried samples (three 1-g aliquots per chick). Apparent MEC was calculated as the energy retained in the chick (energy consumed minus energy excreted) divided by the total energy consumed during the 24 hour period.

The total metabolizable energy requirement (TMER) of ad lib chicks from hatch to the nominal fledging age of 35 days post-hatch (Cuthbert and Wires 1999) was calculated by multiplying daily caloric intake by the measured apparent MEC and summing across the rearing period. This measured TMER was compared to an allometric prediction based on other birds after Weathers (1992), assuming a fledging body mass of 535 g. The peak daily metabolizable energy requirement (peak DMER) of ad lib chicks was compared to a similar allometric prediction (Weathers 1992).

We examined the effects of food restriction on the endocrine stress response of chicks by quantifying plasma corticosterone concentrations. Baseline corticosterone levels were measured by drawing blood five times across the rearing period, once prior to the food restriction period at 10 days post-hatch, and four times during the treatment period at an average age of 19, 25, 31, and 39 days post-hatch. (Individual chick ages on days when bleeding occurred varied up to ± 2 days from the average age.) Baseline blood draws occurred between 0500 and 0700 prior to the first feeding session of the day. Each draw consisted of ~ 0.5 ml taken from either brachial vein, and blood was collected within 3 min of taking the chick from its container. The temporal response to sustained stress (initial handling followed by restraint in a cotton bag) was measured at 39 days post-hatch by drawing blood within 3 min of the initial acute stress (baseline level), and again after 10, 30, and 50 min of sustained stress. Blood was refrigerated (~ 4ºC) and stored in 0.5 ml vials until centrifuged and plasma drawn off into separate vials (within 4 h of blood draws). Plasma was stored frozen at ~ -20ºC prior to laboratory analyses. Radioimmunoassay analyses were performed in the laboratory of A.S. Kitaysky, University of Alaska Fairbanks, Fairbanks, AK using the methodology of Wingfield & Farner (1975), Wingfield et al. (1992), and Kitaysky et al. (2005). Repeated measures ANOVA was used to test for significant differences resulting from diet treatment and age on baseline corticosterone levels and from diet treatment on the stress response series.

After 38 days of captive rearing, at an average age of 41 days post-hatch, eight chicks were randomly selected and euthanized for body composition analysis, four from each diet treatment group. Whole carcasses were frozen for later dissection and analysis. At the time of analysis, carcasses were thawed and dissected to examine the effects of diet treatment on feather mass, body composition, and the sizes of various internal organs (primarily gastro-intestinal), including the mass of liver, gallbladder, esophagus, proventriculus, ventriculus, pancreas, small intestine, and large intestine. Additionally, the internal surface areas of the proventriculus and ventriculus were compared, as were the lengths of each small and large intestines. Following dissections, body components were dried and whole body composition (excluding feathers) was determined using proximate composition analysis (Reynolds and Kunz

2001). The proximate composition methodology was similar to that for the fish fed to terns, outlined above, with the exception that petroleum ether was used as the lipid extraction solvent. Petroleum ether efficiently extracts storage fats (triacylglycerols), but not more polar lipids (e.g., cell membrane associated lipids, phospholipids), so the resulting estimated lipid content is a good measure of lipid reserves that are, for example, available to buffer chicks from short term periods of poor food availability. Tern body composition was partitioned between water, storage lipids, and lean dry matter (including polar [structural] lipids, protein, carbohydrates, and ash). Wilcoxon rank-sum tests were used to make all comparisons of body composition between diet groups.

Allocation of energy to different body components was examined using the mass-specific approach of Benowitz-Fredericks et al. (2006). For external morphology measures, we regressed log-transformed mean values against log-transformed mean mass at specific ages, for both diet treatment groups. We restricted data for this analysis to the period from just prior to the beginning of the treatment period (day 10) until mass growth began to depart from the linear phase of growth for the *ad libitum* fed chicks (day 24). If diet treatment was a significant term in the regression (after consideration of total body mass), we interpreted this as preferential allocation of energy to the particular morphological character. Log-transformed internal anatomical measurements and whole body fat content were regressed against log-transformed mass for individuals from each treatment group. Again, if diet treatment was significant after consideration of body mass, we interpreted this as preferential allocation. If diet treatment was not significant, then we interpreted differences in morphology or body composition between treatments to be a result of differences in overall body size alone.

All procedures and protocols involving live Caspian terns were approved by the Institutional Animal Care and Use Committee at Oregon State University. Scientific collection permits were obtained for all procedures involving handling or collection of terns from the U.S. Fish and Wildlife Service (Migratory Birds and Habitats, Region 1, Portland, OR) and the Oregon Department of Fish and Wildlife (Salem, OR).

RESULTS

All tern chicks survived in apparent good health throughout the rearing period. Chicks fed the restricted diet consumed an average of 65% of the total biomass that ad lib fed chicks consumed during the treatment period, days 11 – 35 post-hatch. Including the initial acclimation period up to day 10 post-hatch, when all birds were fed an *ad libitum* diet, restricted diet birds consumed approximately 69% of the biomass that ad lib birds did during days 1-35 post-hatch. At the beginning of the treatment period (day 10), body mass was similar between terns in the ad lib (218.3 ± 4.4 (SE) g) and restricted diet treatment birds (208.8 ± 3.0 (SE) g; $Z = 1.10$, $P = 0.27$).

Silversides had a higher energy density (5.80 kJ/g wet mass, SD = 0.47, n = 40) than did herring (4.78 kJ/g, SD = 1.06, n = 41). The total metabolizable energy requirement (TMER) of ad lib chicks from hatch to the nominal fledging age of 35 days post-hatch (Cuthbert and Wires 1999) was 18.8 MJ (SD = 1.1 MJ, n = 10). This measured TMER was 6.5% greater than an allometric prediction based on other birds, assuming a fledging body mass of 535 g (17.5 MJ; Weathers 1992). The peak daily metabolizable energy requirement (peak DMER) of ad lib chicks occurred on day 20 post-hatch and averaged 760 kJ/day (SD = 98, n = 10), just 1.4% below the allometric prediction (770 kJ/day; Weathers 1992).

As expected, chicks fed *ad libitum* were larger at fledging age (35 days post-hatch) than chicks fed a restricted diet (Table 2.1). The proportional difference in external morphological measurements seen in total body mass was 23.5%, with differences in wing chord, tarsus, and feather lengths from 8 – 11%.

Logistic model parameters for mass growth indicated significant differences in growth parameters between chicks from the two diet treatments. The fitted asymptotic mass of ad lib chicks was greater, and growth rate inflection points occurred at a later age, compared to chicks on the restricted diet (Table 2.2, Figure 2.1). A small difference in exponential growth rate constant between chicks in the two diet treatment groups was, however, only marginally significant ($P = 0.09$). Parameters of linear growth in bone, bill, and feathers were also significantly different between diet treatments (Table 2.2, Figure 2.2). In ad lib chicks, growth rates of feather-dominated measures were 10-12% greater and growth rates of bone- and bill-dominated measures were 37-52% greater than in chicks on the restricted diet.

Apparent MEC values were 0.799 (SE = 0.0071) for chicks on the ad lib diet treatment and 0.811 (SE = 0.0080) for those on the restricted diet treatment, not significantly different ($Z = 0.91$, $P = 0.36$).

Higher baseline plasma corticosterone concentrations were observed in chicks on the restricted diet (repeated-measures ANOVA: $F_{1,18} = 4.56$, $P = 0.05$; Figure 2.3A). A trend toward higher baseline corticosterone with age was suggested in restricted diet chicks ($P = 0.13$). At 39 days post-hatch, restricted diet chicks also had a much greater corticosterone response to sustained stress ($F_{1,18} = 18.19$, $P = 0.0005$; Figure 2.3B).

Feather mass was 13% greater in ad lib chicks (46.0 g ± 1.3 (SE), n = 4) compared to chicks on the restricted diet (39.8 g ± 1.8 (SE), n = 4) at ~ 41 days post hatch ($Z = 1.88$, $P = 0.03$). Of the chicks euthanized for body composition analysis, total body mass was 18.4% greater in ad lib chicks; liver mass and especially gallbladder mass reflected this difference (13.5% and 39.8% greater, respectively). Other internal organs, however, were not significantly different in size or mass between treatment groups (Table 2.3), indicating that other body components (i.e., structural size, muscle mass, fat deposits) were more responsible for the differences in total body mass between chicks in the two diet treatments. Ad lib chicks had a significantly higher storage lipid content (8.9% of wet mass ± 1.2 (SE), n = 4) than did restricted diet chicks (5.2% ± 0.6 (SE), n = 4; $Z = 2.16$, $P = 0.03$). This higher storage lipid content was balanced by a marginally significant trend towards lower water content in ad lib chicks (62.3% of wet mass ± 1.2 (SE), n = 4) than in restricted diet chicks (66.5% ± 1.1 (SE), n = 4; $Z = 1.88$, $P = 0.06$). The proportion of other components (lean dry matter) in the body was similar between diet treatments (28.8% of wet mass ± 0.7 (SE), n = 4, and 28.3% ± 1.3 (SE), n = 4, for ad lib and restricted diet chicks, respectively; $Z = 0.14$, $P = 0.99$).

Mass-specific allocation of energy to the various body components was similar between the two diet treatment groups, with the exception of feathers (Figure 2.4). Chicks on the restricted diet had greater feather mass and development for a given total body mass, as indicated by measurements of both flight feathers (lengths of wing chord and 10th primary) and non-flight feathers (scapular length). There was the suggestion that diet treatment produced differences in allocation to structural growth ($P = 0.07 – 0.10$ for skeletal measures); however, differences were not consistent across all measures. Differences between internal organs ($P = 0.16 – 0.97$) and storage lipid content ($P = 0.80$) were apparently a function of differences in body size alone.

DISCUSSION

We found that energy demands of captive-reared, *ad libitum* fed Caspian tern chicks were similar to allometric predictions based on asymptotic body mass and fledging age, derived from other (mostly wild-reared) birds (Weathers 1992). The growth parameters of these captive-reared ad lib chicks were within the reported range for wild Caspian tern chicks (Schew et al. 1994, Barlow and Dowding 2002); thus, we presume that their energy demands were similar to those of wild chicks. By falling so close to allometric predictions for both total metabolizable energy requirement and peak daily metabolizable energy requirement, Caspian terns appear to represent an intermediate position on the avian development rate spectrum described by Weathers (1992) and expanded upon by Starck, Ricklefs, and others (1998a). Similarly, among terns (Subfamily: Sterninae) Caspian terns appear to represent an intermediate developmental strategy, approximately mid-way between a quickly developing species such as the high latitude Arctic tern (*Sterna paradisaea*, peak DMER 65% greater than allometric prediction; Klaassen et al. 1989), and a slowly developing tropical species such as the sooty tern (*Sterna fuscata*, peak DMER 45% lower than prediction; Ricklefs and White 1981). Presumably, this reflects the ecological conditions Caspian terns evolved within, lacking the particularly short but intense seasonal burst of productivity at high latitudes, but greater and more seasonal productivity than in the tropics.

At the level of food restriction applied in this study, all external morphological measures were significantly different between the ad lib and restricted diet chicks by the nominal fledging age. Some characteristics of the growth and development of the chicks fed restricted diets were undoubtedly related to the age at which we began the food restriction treatment (day 11). Impacts to mass growth were immediate upon food restriction, as evidenced by the earlier and immediate onset of the fitted growth curve inflection point (at 10.5 days post-hatch in food restricted chicks vs. 12.3 days post-hatch for ad lib chicks). Only a small, non-significant difference in the fitted exponential growth constant was observed as chicks had entered the linear growth phase by approximately day 6 post-hatch, prior to initiation of food restriction. For all external morphology measures, we saw larger differences between diet treatment groups in absolute size at fledging than for growth rates during the treatment period, reflecting the initial 10 day period of normal growth without food restriction for all chicks. We also observed larger differences between diet treatment groups in the size at nominal fledging age of (non-feather) linear measures that experienced the greatest portion of their growth during the treatment period. For example, our food restriction regimen produced only a small reduction in tarsus length (8.5%) relative to head-bill and culmen length differences (15.1% and 26.2%, respectively). This reflects a greater portion of tarsus growth occurring prior to the onset of food restriction (the tarsus of ad lib chicks was 75% of fledging age length at day 10, head-bill and culmen sizes were 63% and 52% of fledging age length at day 10, respectively). The relative diminishment in size of the various body components in food restricted chicks may provide insight into the timing of the onset of food restriction for wild chicks.

Of the linear measurements, feather-based characters differed less between diet treatment groups and the mass-specific growth rate of feathers was greater for chicks on the restricted diet. Both of these observations indicate that developing Caspian terns have the ability to shift their energy allocation under conditions of food-energy limitation to preferentially promote feather growth. This preferential feather growth is consistent with many other bird species and presumably reflects the short term survival benefit of early flight capability (Lack 1968). Interestingly, growth of non-flight feathers (scapulars) was also preferentially maintained, suggesting that independent control of growth in distinct feather groups is beyond the physiological capability of terns. Other studies have demonstrated preferential allocation toward skeletal growth in alcids (Benowitz-Fredericks et al. 2006, Sears and Hatch 2008); however, our study only suggested this result ($P = 0.07 – 0.10$). Given the nesting ecology of terns, where flightless chicks sometimes escape predators by running or swimming, it is somewhat surprising that we did not find greater evidence of preferential allocation to tarsal growth, although it should be noted that most (75%) tarsal growth in Caspian terns occurs prior to our initiation of food restriction. Preferential allocation for skull growth has been observed in Atlantic puffins (*Fratercula arctica*) and interpreted to indicate the importance of the development of the brain and central nervous system (Oyan and Anker-Nilssen 1996). We did not measure skull size directly, but the mass-specific growth of an approximate measure of skull size, head-bill length minus culmen length (Oyan and Anker-Nilssen 1996), did suggest a small but highly significant difference in allocation between our ad lib and restricted diet groups (~ 6% difference in slope of the regression between non-transformed values, $P = 0.000001$). Further investigation into skeletal growth of terns under different feeding regimes might clarify some of these suggested effects.

The internal organ characters that we measured were in general similar between diet treatments, with the exception of liver and gallbladder masses, and the suggestion of small differences in intestinal size ($P = 0.07$; larger in ad lib chicks). Mass-specific analysis indicated that most differences between internal organs in these fledging aged chicks (41 days post-hatch) were a function of differences in body mass alone and did not reflect differential allocation. By 41 days post-hatch, growth of the ad lib chicks had reached a plateau and restricted diet chicks had caught up to a degree.

In Caspian terns, as in some other larids (Kitaysky et al. 1999, Kitaysky et al. 2001), nutritional stress induced both a heightened baseline corticosterone level and an amplified acute corticosterone stress response. This heightened hypothalamus – pituitary – adrenal activity in response to chronic food restriction in terns is consistent with Kitaysky's (2003) ecological hypothesis to explain inter-specific differences in stress response among seabirds. Adult Caspian terns provision chicks with single fish multiple times per day. This meal delivery rate is more frequent than many other species of seabirds and may allow greater parental buffering of chicks from variable availability of food resources than is possible in some other species, particularly those with less frequent meal delivery rates. Caspian tern chicks could potentially benefit more from heightened corticosterone levels, inducing greater begging from parents and more aggressive competition with siblings, than could chicks of a species that feeds its young infrequently and whose maximum clutch size is one egg (Kitaysky et al. 2003). In species where chicks receive a single food delivery each day (or less), a heightened corticosterone response in nutritionally challenged chicks would presumably be less beneficial (e.g., Kitaysky et al. 2005).

In this study we identified three general characteristics of food restricted Caspian tern chicks compared to well fed chicks: (1) lower structural growth rates, lower body mass, and smaller skeletal size for chicks at a particular age, (2) greater relative size of feather measurements, such as wing chord, for chicks of the same body mass as well fed chicks, and (3) heightened baseline and stress series corticosterone levels. Particular measures within any of these three categories would allow useful evaluation of the nutritional status of chicks raised in the wild, and serve as an indicator of the ecological conditions within the foraging range of parent terns. Measuring mass and wing chord, and/or sampling blood to measure corticosterone levels would allow such an evaluation even in situations where a breeding colony was visited only once late in the chick-rearing period and when the age of chicks was imprecisely known.

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Table 2.1. Mean (± SE) external morphological measures of approximately fledging-aged (35 days post-hatch) Caspian tern (*Hydroprogne caspia*) chicks fed *ad libitum* (ad lib; n = 10) and restricted (n = 10) diets. Wilcoxon rank-sum tests were used to test for differences between diet treatments.

	Total Body Mass (g)	Wing Chord (mm)	Tarsus (mm)	Head + Bill (mm)	Culmen (mm)	P10 (mm)	Scapular (mm)
Ad lib Diet	534.9 (11.9)	276.3 (2.0)	47.3 (0.5)	113 (1.1)	28.0 (0.3)	138.7 (1.8)	96.4 (2.9)
Restricted Diet	409.1 (5.2)	253.9 (2.7)	43.2 (0.6)	96.4 (0.6)	20.6 (0.2)	123.8 (1.8)	87.5 (2.6)
% Difference	23.5	8.1	8.5	15.1	26.2	10.7	9.2
Z-value	3.74	3.75	3.33	3.74	3.74	3.45	1.89
P	0.0002	0.0002	0.0009	0.0002	0.0002	0.0002	0.06

Table 2.2. Mean (± SE) logistic (mass) and linear (bone, bill, and feather) growth model parameters for Caspian tern (*Hydroprogne caspia*) chicks fed *ad libitum* (ad lib; n = 10) and restricted (n = 10) diets. Mass growth was characterized from the day of capture (1 – 5 days post-hatch) until 35 days post-hatch, fitting the asymptote (A), exponential growth rate constant (K), and inflection point (t_i). Bone and feather growth were fitted from the beginning of the diet treatment period (day 11 post-hatch) through day 35. Wilcoxon rank-sum tests were used to test for differences between diet treatments.

	Mass Growth (Logistic Model)			Bone, Bill, and Feather Growth (Linear Model)					
	A (g)	K (day^{-1})	t_i (days)	Wing Chord (mm/day)	Tarsus (mm/day)	Head + Bill (mm/day)	Culmen (mm/day)	P10 (mm/day)	Scapular (mm/day)
Ad lib Diet	548.3 (10.4)	0.190 (0.004)	12.3 (0.21)	9.01 (0.02)	0.37 (0.005)	1.57 (0.007)	0.53 (0.002)	5.60 (0.01)	3.52 (0.03)
Restricted Diet	405.8 (5.1)	0.179 (0.003)	10.5 (0.18)	7.98 (0.03)	0.23 (0.004)	0.99 (0.006)	0.25 (0.002)	4.97 (0.02)	3.16 (0.03)
% Difference	26.0	5.5	14.9	11.5	39.0	36.9	51.9	11.3	10.4
Z-value	3.74	1.66	3.63	3.74	3.53	3.74	3.74	3.74	2.15
P	0.0002	0.09	0.0003	0.0002	0.0004	0.0002	0.0002	0.0002	0.03

Table 2.3. Mean (± SE) internal anatomical measurements of Caspian tern (*Hydroprogne caspia*) chicks at ca. 41 days post-hatching that were fed *ad libitum* (ad lib, n = 4) and restricted (n = 4) diets. Wilcoxon rank-sum tests were used to test for differences between diet treatments.

	Mass (g) Measures									Area (mm^2) Measures		Length (cm) Measures	
	Total Body Mass	Liver	Gallbladder	Esophagus	Proventriculus	Ventriculus	Pancreas	Small Intestine	Large Intestine	Proventriculus	Ventriculus	Small Intestine	Large Intestine
Ad lib Diet	505.2 (26.7)	16.4 (1.4)	0.81 (0.12)	4.97 (0.40)	1.54 (0.07)	5.50 (0.52)	1.42 (0.08)	11.1 (0.70)	0.93 (0.14)	617.0 (46.8)	1498.5 (111.8)	70.2 (1.5)	63.2 (4.1)
Restricted Diet	412.2 (9.6)	12.6 (0.7)	0.49 (0.09)	4.61 (0.22)	1.35 (0.18)	5.47 (0.44)	1.19 (0.28)	10.3 (0.49)	0.81 (0.09)	652.7 (30.4)	1649.8 (66.86)	68.4 (2.2)	53.7 (3.0)
% Difference	18.4	13.5	39.8	7.3	12.6	0.6	16.7	6.6	12.6	-5.8	-10.1	2.5	15.0
Z-value	2.17	1.88	1.75	0.43	0.43	-0.14	0.14	1.01	0.72	0.58	1.01	-0.53	1.45
P	0.02	0.03	0.04	0.33	0.33	0.56	0.44	0.31	0.23	0.56	0.31	0.30	0.07

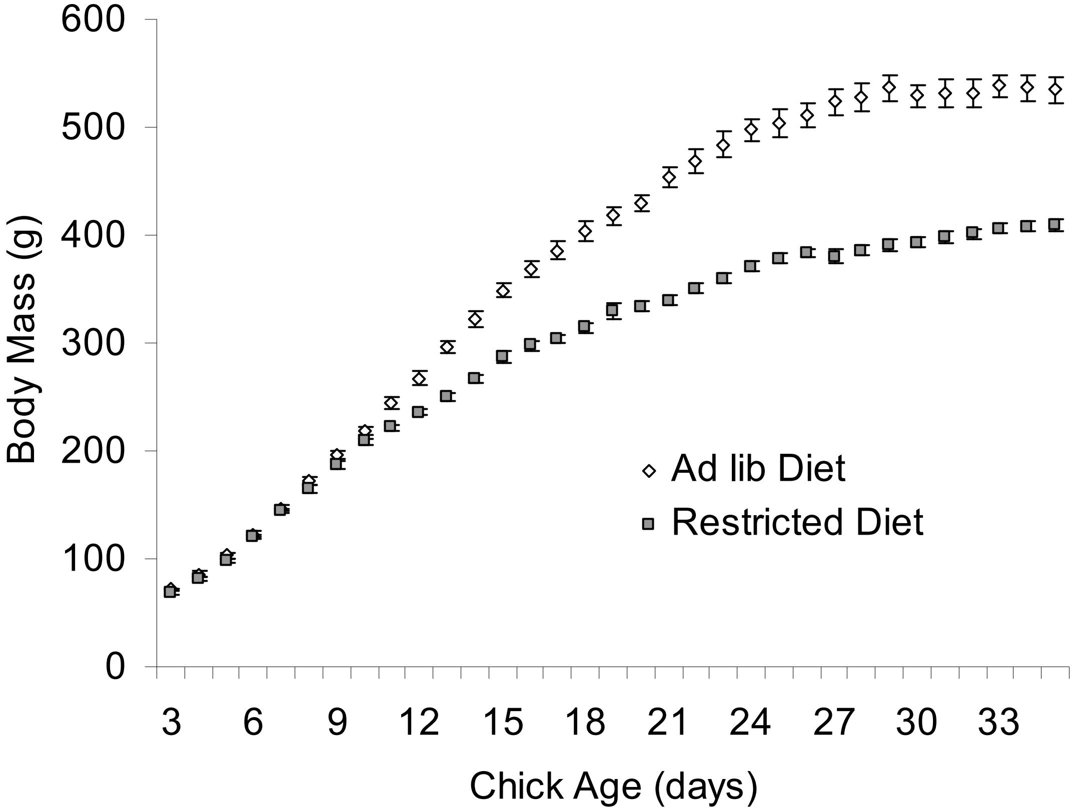


Figure 2.1. Growth in total body mass as a function of age for captive-reared Caspian tern (*Hydroprogne caspia*) chicks fed *ad libitum* (ad lib; n = 10) and restricted (n = 10) diets.

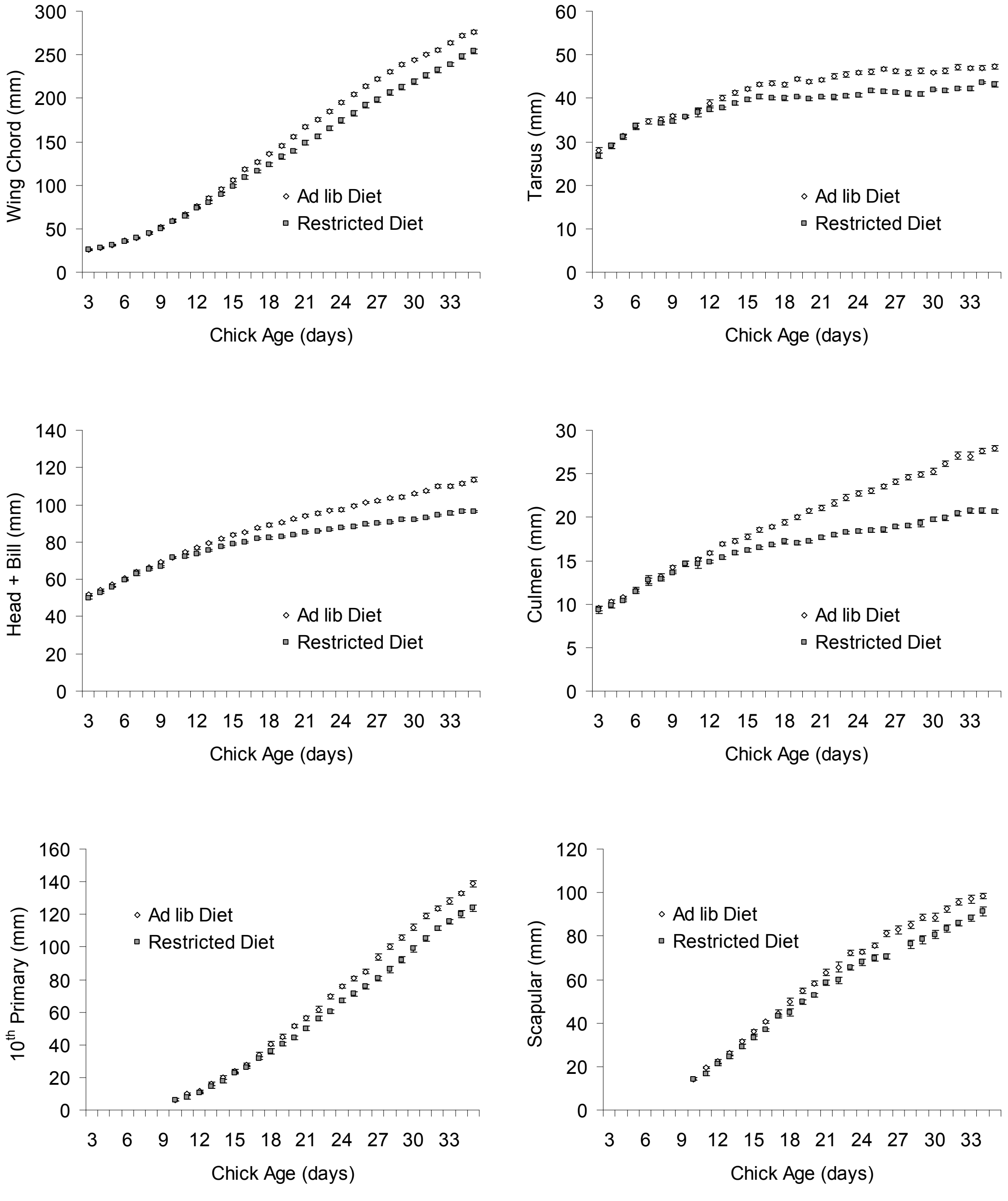
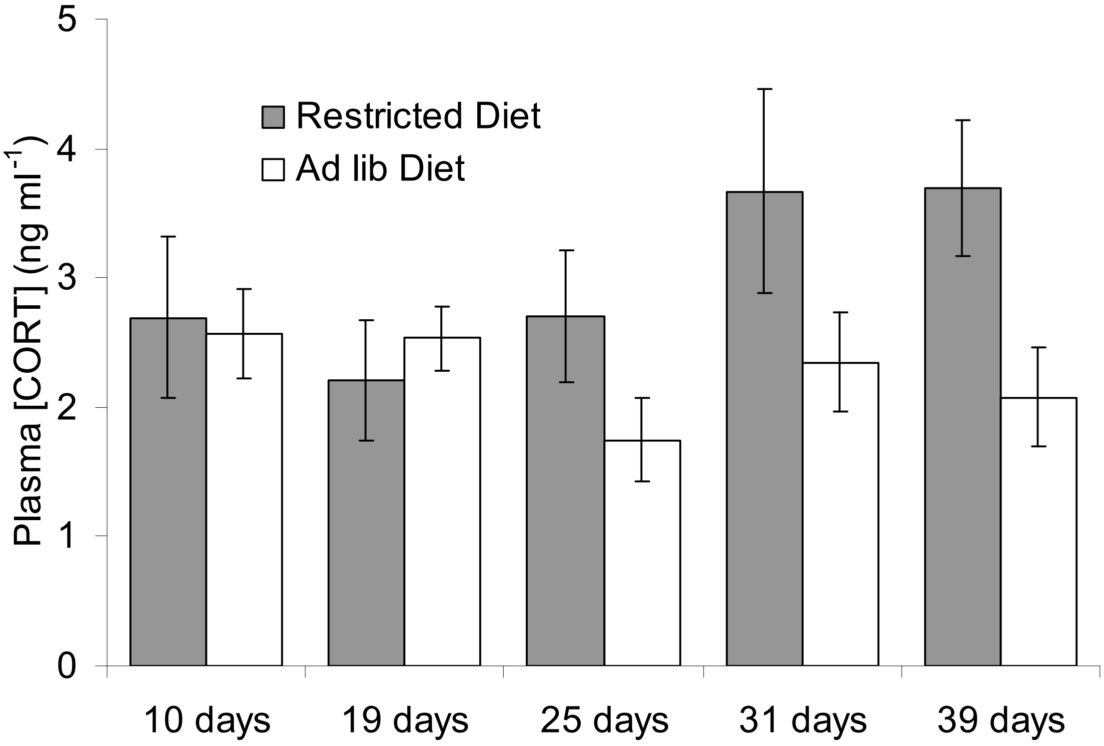


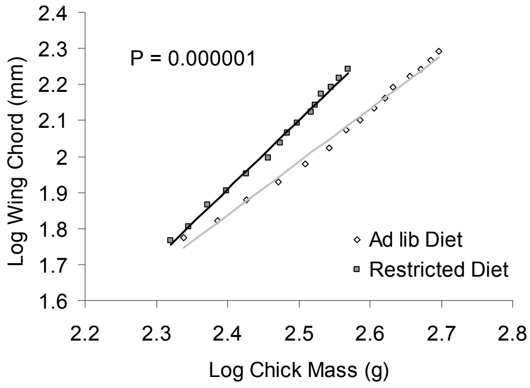
Figure 2.2. Growth in length of wing chord, tarsus, head + bill, culmen, 10th primary, and scapular feathers as a function of age in captive-reared Caspian tern (*Hydroprogne caspia*) chicks fed *ad libitum* (ad lib; n = 10) and restricted (n = 10) diets.

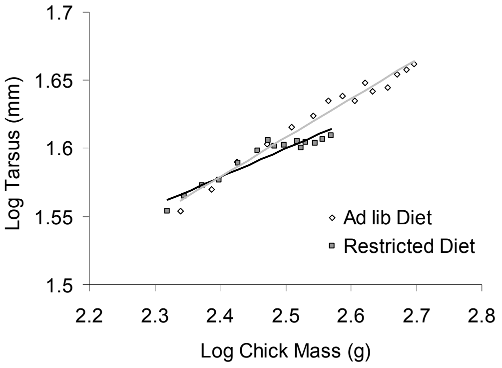
Figure 2.3. Plasma corticosterone (CORT) concentrations (± 1 SE) in captive-reared Caspian tern (*Hydroprogne caspia*) chicks fed *ad libitum* (ad lib; n = 10) and restricted (n = 10) diets: (A) baseline levels across the chick-rearing period and (B) a temporal response to sustained stress at 39 days post-hatch.

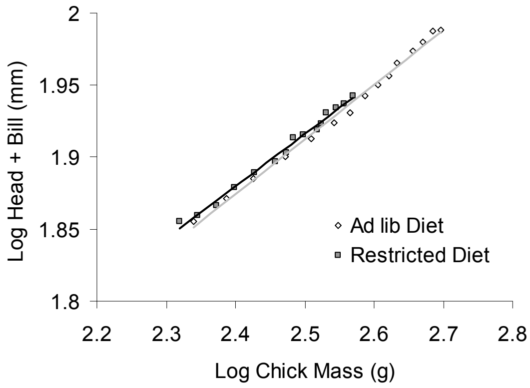

5
4
3
2
1
0
Plasma [CORT] (ng ml^{-1})
Restricted Diet
Ad lib Diet
10 days
19 days
25 days
31 days
39 days

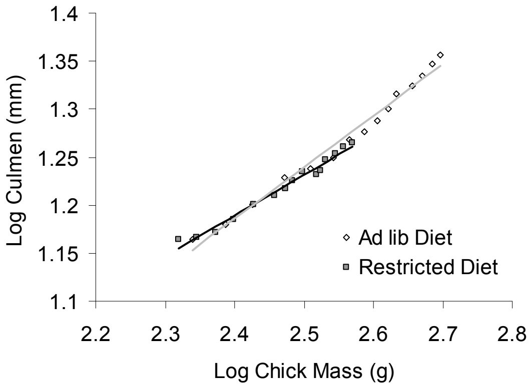

35
30
25
20
15
10
5
0
Plasma [CORT] (ng ml^{-1})
Restricted Diet
Ad lib Diet
0
10
20
30
40
50
Minutes After Initial Stress

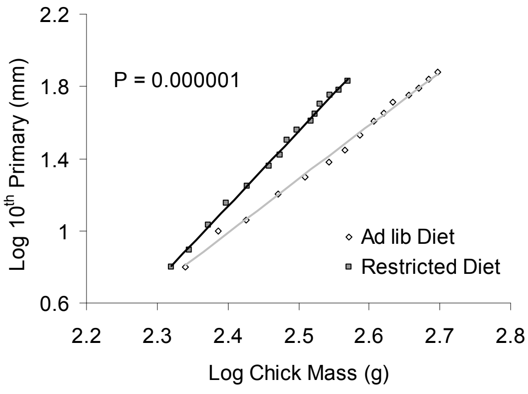
Figure 2.4. Growth in length of wing chord, tarsus, head + bill, culmen, 10th primary, and scapular feathers as a function of body mass in captive-reared Caspian tern (*Hydroprogne caspia*) chicks raised on either an *ad libitum* (ad lib; n =10) diet or a restricted intake (n = 10) diet. Each data point represents the mean length at a given age. Steeper slopes for restricted diet chicks indicate preferential allocation of resources to a given body component for a given body mass. For significant differences in size as a function of total body mass between diet treatment groups, *P* values are indicated.

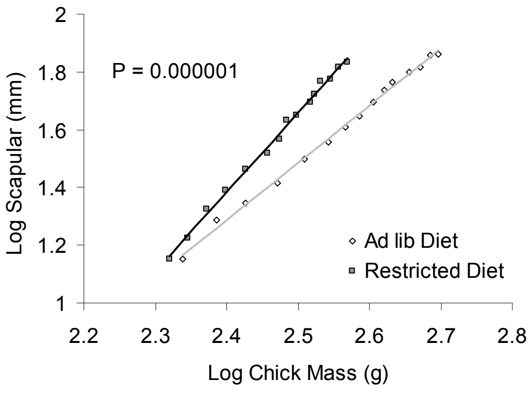

P = 0.000001
Log Wing Chord (mm)
2.4
2.3
2.2
2.1
2
1.9
1.8
1.7
1.6
◇ Ad lib Diet
■ Restricted Diet
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log Chick Mass (g)


Log Tarsus (mm)
1.7
1.65
1.6
1.55
1.5
◇ Ad lib Diet
■ Restricted Diet
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log Chick Mass (g)


Log Head + Bill (mm)
2
1.95
1.9
1.85
1.8
◇ Ad lib Diet
■ Restricted Diet
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log Chick Mass (g)


Log Culmen (mm)
1.4
1.35
1.3
1.25
1.2
1.15
1.1
◇ Ad lib Diet
■ Restricted Diet
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log Chick Mass (g)


P = 0.000001
Log 10th Primary (mm)
2.2
1.8
1.4
1
0.6
◇ Ad lib Diet
■ Restricted Diet
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log Chick Mass (g)


P = 0.000001
Log Scapular (mm)
2
1.8
1.6
1.4
1.2
1
◇ Ad lib Diet
■ Restricted Diet
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log Chick Mass (g)

Chapter 3

FIELD METABOLIC RATES OF BREEDING DOUBLE-CRESTED CORMORANTS (*Phalacrocorax auritus*) MEASURED USING THE DOUBLY-LABELED WATER TECHNIQUE

Donald E. Lyons, Daniel D. Roby, G. Henk Visser

ABSTRACT

We measured field metabolic rates (FMRs) of breeding double-crested cormorants (*Phalacrocorax auritus*) nesting near the mouth of the Columbia River, Oregon, USA using the doubly-labeled water technique. This study was intended to assist in the evaluation of predation rates by double-crested cormorants on juvenile salmonids in the Columbia River estuary, and more broadly for assessment of cormorant – fisheries conflicts across North America. The average FMR of breeding double-crested cormorants, measured during the chick-rearing period, was 3,571 kJ bird^{-1} day^{-1} (SD = 689.7, n = 7 males and 3 females). Assuming a 1:1 sex ratio in the breeding population, the estimated average FMR for all breeding adults was 3,423 kJ bird^{-1} day^{-1}. This estimate is 34% higher than the value predicted for double-crested cormorants using allometric equations for breeding seabirds, but only 5% higher than the allometric prediction based on FMR measured on other species in the Order Pelecaniformes. Estimates of food consumption rates ranged from 746 – 1295 g bird^{-1} day^{-1}, or 31 – 50% of average adult body mass. Possible reasons for measured FMR values that exceeded allometric predictions based on other seabirds may include the larger brood size (measured individuals in this study averaged 3 chicks per brood) and higher chick growth rates of double-crested cormorants compared to most other seabird species where FMR has been measured.

INTRODUCTION

Cormorants (*Phalacrocorax* spp.) are increasingly perceived to be in conflict with commercial and sport fisheries world-wide, particularly the great cormorant (*P. carbo*) in Europe (Carss 2003) and the double-crested cormorant (*P. auritus*) across North America (USFWS 2003). In the United States and Canada, double-crested cormorant populations have significantly increased from lows in the 1970s, with recovery due to reductions in environmental contaminants, greater legal protections, and in some cases, enhanced food supplies, such as increased aquaculture in certain wintering areas (Hatch and Weseloh 1999). These recent trends in cormorant population levels have resulted in greater predation on fishery stocks (e.g., Krohn et al. 1995, Derby and Lovvorn 1997, Rudstam et al. 2004, Diana et al. 2006, Dalton et al. 2009) and increased depredation at aquaculture facilities (Glahn and Brugger 1995), as well as predation on threatened and endangered fish species (Collis et al. 2001, Collis et al. 2002). Increasing predation by cormorants has usually occurred in the context of anthropogenic habitat alteration, stocking of hatchery-reared fish, introduction of exotic fish species, and/or competition with human fishers. Consequently, it has been difficult to reach consensus on efforts to assess impacts of cormorants on fish populations and to identify broadly acceptable policy options for cormorant management (USFWS 2003).

One common approach for assessing impacts of cormorants on prey species has been to estimate consumption, in terms of biomass or numbers consumed, using bioenergetic-based calculations (Glahn and Brugger 1995, Madenjian and Gabrey 1995, Derby and Lovvorn 1997, Seefelt and Gillingham 2008, Dalton et al. 2009, Chapter 5). A parameter central to these calculations is the field metabolic rate (FMR) of breeding adults, which has not been previously measured in double-crested cormorants. Most cormorant bioenergetic studies have relied thus far on either (1) allometric predictions of daily energy expenditure (DEE) based on measurements in other birds, (2) combinations of time-activity budgets and estimates of activity-specific energy expenditure rates, or (3) estimates of food biomass consumption (which often do not consider variations among prey types in quality i.e., lipid content and energy density). The doubly-labeled water (DLW) technique is a method commonly used to estimate field metabolic rates of free-ranging birds by measuring the amount of CO_2 respired over specific measurement intervals of several hours to several days. Consequently, this method allows measurements of CO_2 respiration rate during periods of normal activity unconstrained by laboratory conditions (Lifson and McClintock 1966, Nagy 1980).

In the Pacific Northwest region of the United States, double-crested cormorant populations have rebounded from earlier lows and now the largest colony in this region (ca. 12,000 pairs) exists at the mouth of the Columbia River between Oregon and Washington (Anderson et al. 2004). An iconic suite of fish species in this region, anadromous Pacific salmon (*Oncorhynchus* spp.), has suffered orders of magnitude decline from historical levels beginning in the late 1800s (Lichatowich 1999). Many populations of salmonids that spawn in the region are currently listed as threatened or endangered under the U.S. Endangered Species Act (Good et al. 2005). Juvenile salmonids make up a portion of the cormorant diet in this region (Collis et al. 2001, Collis et al. 2002) and fisheries managers are concerned that cormorants might limit the recovery of certain populations of Columbia Basin salmonids (NOAA 2008). As in the case of most seabird-fisheries controversies, cormorant predation on Columbia River salmonids exists in the context of other anthropogenic effects on salmonid populations: freshwater habitat loss and degradation due to human land use and the installation of dams, historically high harvest levels, and annual infusions of large numbers of hatchery-reared juveniles into the Columbia River system (Lichatowich 1999, Federal Caucus 2000). Bioenergetics-based estimates of cormorant consumption of juvenile salmonids will be an important contribution to an assessment of cormorant impacts on listed populations (Chapter 5) and allow an assessment of their overall impact in the context of other factors affecting salmonid populations.

To assist in the evaluation of double-crested cormorant predation on juvenile salmonids in the Columbia River estuary, and more broadly for assessment of cormorant – fisheries conflicts across North America, we sought to measure field metabolic rates of breeding cormorants nesting near the mouth of the Columbia River using the DLW technique.

METHODS

Field metabolic rates (FMR) of free-ranging, breeding adult double-crested cormorants (kJ bird^{-1} day^{-1}) was measured during the second or third week of chick-rearing at East Sand Island in 2001 (n = 7), or at Rice Island in 2003 (n = 2) and in 2006 (n = 1; Figure 3.1). All individuals measured were raising broods that included 2 – 4 nestlings (average = 3.0 nestlings). Individuals were captured at night, either by spotlighting or using noose poles extended from the windows of blinds to nearby nests. Following DLW injection, equilibration, and initial blood sampling, individuals were released prior to dawn at or near the colony and nest attendance and behavior was monitored during the following daylight period. Prior efforts to recapture injected cormorants proved unsuccessful, so individuals in this study were lethally collected at their respective colony using .22 caliber rifles during the 2nd day (or for 2 individuals, the 3rd day) following initial blood sampling, and a final blood sample was then obtained. A range of 27 – 54 hours elapsed between initial and final blood sampling. Because of the level of disturbance associated with lethal collection of adults at the colonies, our sample size was unavoidably small.

Captured adults were injected intraperitoneally with doubly-labeled water containing 9.75 atom % ^{18}O and 4.6 atom % ^{2}H, with a target DLW dose of 5.68 g per kg body mass. Following injection, adults were banded and held for 1.5 hours to allow isotopically-labeled water to equilibrate with body water. Then an initial blood sample of about 3-4 ml was obtained by puncturing the brachial or tarsal vein and collecting blood using a butterfly needle and syringe. Blood samples were also collected from un-injected adult cormorants for measurement of background levels of the two isotopes. The final blood sample, at collection, was drawn from veins with needle and syringe, if possible, or obtained directly from the heart and/or body cavity. Blood samples were held on ice in the field, usually < 8 hours following sample collection, before centrifugation to separate plasma for freezing and later analysis.

Frozen plasma was stored in glass vials until isotope analysis was performed in the lab of G.H.V. at the Centre for Isotope Research, University of Groningen, The Netherlands. Using the CO_2 equilibration technique, $^{18}O/^{16}O$ ratios in plasma were assigned by isotope ratio mass spectrometry, as were $^{2}H/^{1}H$ ratios in H_2 gas generated from water samples using a uranium oven at 800°C (following Visser et al. 2000). Isotope analyses were run in triplicate to assure accurate measurements 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 respired, appropriate for a protein-rich diet (Gessaman and Nagy 1988). Total body water (% of initial body mass) was calculated on the basis of ^{18}O dilution, using the plateau method (following Visser et al. 2000, equation 2).

To estimate daily prey consumption in units of biomass we assumed a metabolizable energy coefficient of 0.773 (Brugger 1993) and an average prey energy density of 4.6 kJ/g, typical for cormorants in the Columbia River estuary (Chapter 5).

All procedures and protocols involving live double-crested cormorants were approved by the Institutional Animal Care and Use Committee at Oregon State University. Scientific collection permits were obtained for all procedures involving handling or collection of cormorants from the U.S. Fish and Wildlife Service

(Migratory Birds and Habitats, Region 1, Portland, OR), the U.S. Geological Service (Bird Banding Lab, Patuxent, MD), and the Oregon Department of Fish and Wildlife (Salem, OR).

RESULTS

Captured individuals began returning to nests within several hours of release following injection with DLW, equilibration, and collection of the initial blood sample. Following return to the colony, nest attendance and chick provisioning rates were similar in DLW birds to those of control individuals also monitored.

Field metabolic rates (FMR) of adult double-crested cormorants measured during the chick-rearing period using the DLW technique averaged 3,571 kJ bird^{-1} day^{-1} (SD = 689.7, n = 10) and ranged from 2,653 to 4,606 kJ bird^{-1} day^{-1} (Table 3.1). The average FMR for the three individuals at Rice Island (3,384 kJ bird^{-1} day^{-1}) was very close to the average for the seven individuals at East Sand Island (3,650 kJ bird^{-1} day^{-1}). The range of FMRs for males was greater and reached much higher values (2653 – 4606 kJ bird^{-1} day^{-1}) than for females (3042 – 3068 kJ bird^{-1} day^{-1}). Males in the study were larger, however (males averaged 2,490 g and females 2,070 g), and mass-specific FMR values were similar between sexes (Wilcoxon rank-sum test P = 0.83; Table 3.1). The resulting population average FMR of 3,423 kJ bird^{-1} day^{-1}, assuming a 1:1 sex ratio, is 34% higher than the value predicted using allometric equations (Ellis and Gabrielsen 2001) based on field metabolic rates of all measured seabirds (2,558 kJ $bird^{-1}$ day^{-1} for a 2,275 g cormorant), but is only 5% higher than the allometric prediction based on other measured members of the Order Pelecaniformes (3,367 kJ $bird^{-1}$ day^{-1}, n = 4; Ellis and Gabrielsen 2001). Estimates of daily food consumption ranged from 746 – 1295 g $bird^{-1}$ day^{-1}, or 31 – 50% of body mass.

DISCUSSION

Prior to this study, daily field metabolic rates (FMR) of free-ranging, breeding double-crested cormorants, or their European ecological analog, the great cormorant, had not been measured using the doubly-labeled water technique. These FMR measurements provide an important advance in accuracy and validation for using bioenergetics methods to estimate impacts of cormorants on prey populations (e.g., Chapter 5).

Our measured values of energy expenditure rates using the doubly-labeled water technique exceed other estimated values for breeding cormorants using alternative approaches: allometric predictions based on other seabirds (Nagy 1987, Birt-Friesen et al. 1989, Ellis and Gabrielsen 2001), estimates based on combining activity-specific metabolic rates with time-activity budget data (Gremillet et al. 1995, Gremillet et al. 2000), and estimates based on the mass of food in stomach contents of birds returning to their nests (Gremillet et al. 1996, Gremillet et al. 2000) or based on using stomach temperature measurements to estimate meal size (Gremillet and Plos 1994, Gremillet et al. 2000). Our measured values also exceed those from studies that estimated field metabolic rates based on combinations of these methods (Glahn and Brugger 1995, Derby and Lovvorn 1997), or based on assumed values for daily food intake as a fixed percentage of cormorant body mass (e.g., Rudstam et al. 2004).

One potential reason that our measured FMR values exceeded allometric predictions based on all available measurements of FMR in other seabirds is that estimates of energy expenditure rates using allometric equations that are based on other measured seabird or waterbird species may be taxonomically biased towards species rearing a single, slow-growing chick (Visser 2001). The average clutch size of species included in allometric equations of seabird FMR (e.g., Ellis and Gabrielsen 2001) was 1.4 eggs (range = 1 to 3), whereas the clutch size of double-crested cormorants averages 3-4 eggs and ranges up to 7 (Hatch and Weseloh 1999, authors' unpublished data). The cormorants measured in our study were rearing an average of 3.0 nestlings (range: 2 – 4 nestlings) per brood, aged between 10 and 21 days post-hatch. Effects of larger broods have been investigated within at least one seabird species having multiple-chick broods, the black legged kittiwake (*Rissa tridactyla*), and larger broods were associated with significantly higher adult FMR (Fyhn et al. 2001, Jodice et al. 2006). Another factor suggesting high relative energy demands on cormorant parents during chick-rearing is the high growth rate of developing cormorant nestlings compared to other seabird young (Dunn 1975, Leger and McNeil 1987, Starck and Ricklefs 1998). Among similar-sized seabirds, the cormorant chick-rearing period is shorter and requires higher provisioning rates to sustain high nestling growth rates. This likely translates into greater peak energy demands on breeding adult cormorants, but would play out over a shorter portion of the annual cycle.

An additional factor that may also contribute to cormorant FMR values exceeding allometric predictions based on other seabirds is the greater thermoregulatory costs associated with the uniquely wettable plumage in cormorants. Cormorants likely experience greater heat loss while swimming at the surface, diving, and drying their plumage following foraging than would other pursuit-diving seabirds of a similar size (Gremillet et al. 1995), and it is unclear if locomotory energy savings while foraging due to less positive buoyancy (less air trapped within the plumage) compensates for greater thermoregulatory costs.

Our measured FMR values are consistent with those of other studies of FMR using the doubly-labeled water technique in species belonging to the Order Pelecaniformes. Our average measurement is within 5% of an allometric prediction based on four other species of pelecaniforms (Ellis and Gabrielsen 2001) measured while breeding, although none of those species were from family Phalacrocoracidae (cormorants and shags) or their closest relatives, the Pelecanidae (pelicans). Also, interestingly, measurements of FMR for wintering great cormorants using the doubly-labeled water technique were well predicted by allometric equations based on breeding seabirds (Keller and Visser 1999); perhaps energy demands for this species during the chick-rearing period are also significantly higher than currently available allometric predictions, as we have found for double-crested cormorants.

Given the somewhat higher than predicted field metabolic rates found in this study, our relatively small sample size (n = 10), and the direct relationship between FMR and prey consumption, additional measurements of FMR using the doubly-labeled water technique in free-ranging cormorants at other locations would enhance future studies of cormorant-fisheries interactions.

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Table 3.1. Field metabolic rate (FMR), mass-specific FMR (= FMR/initial body mass), and daily prey consumption of double-crested cormorants (*Phalacrocorax auritus*) nesting on Rice Island (RI) and East Sand Island (ESI) in the Columbia River estuary.

Individual/ Group	Date	Colony	Sex	Brood Size	Initial Body Mass	Total Body Water	Measurement Duration	Δ Body Mass	FMR	Mass Specific FMR	Prey Consumption[1]	
					(g)	(%)	(h)	(g)	(kJ day^{-1})	(kJ day^{-1} g^{-1})	(g day^{-1})	(% of body mass day^{-1})
1	6/29/2001	ESI	M	4	2580	67.2	52.1	-200	3065	1.188	862	33
2	6/30/2001	ESI	M	3	2335	65.4	29.6	-35	4171	1.786	1173	50
3	7/6/2001	ESI	F	3	1996	68.2	31.0	104	3042	1.524	855	43
4	7/6/2001	ESI	M	2	2696	61.7	30.3	329	4606	1.708	1295	48
5	7/6/2001	ESI	F	2	2095	68.9	27.5	-195	3068	1.464	863	41
6	7/7/2001	ESI	M	3	2545	62.4	28.1	-245	3604	1.416	1014	40
7	7/9/2001	ESI	M	4	2316	67.1	27.5	44	3998	1.726	1124	49
8	7/16/2003	RI	F	3	2118	76.9	31.8	157	3053	1.441	858	41
9	7/16/2003	RI	M	3	2376	77.4	54.1	-51	2653	1.117	746	31
10	7/13/2006	RI	M	3	2565	72.5	36.0	85	4447	1.734	1251	49
All males (n = 7)					2488				3792	1.525	1066	43
All females (n = 3)					2070				3054	1.477	859	42
Population[2]					2279				3423	1.501	963	42

[1] Assuming a metabolizable energy coefficient of 0.773 and average prey energy density of 4.6 kJ/g (Chapter 5)

[2] Based on a 1:1 sex ratio

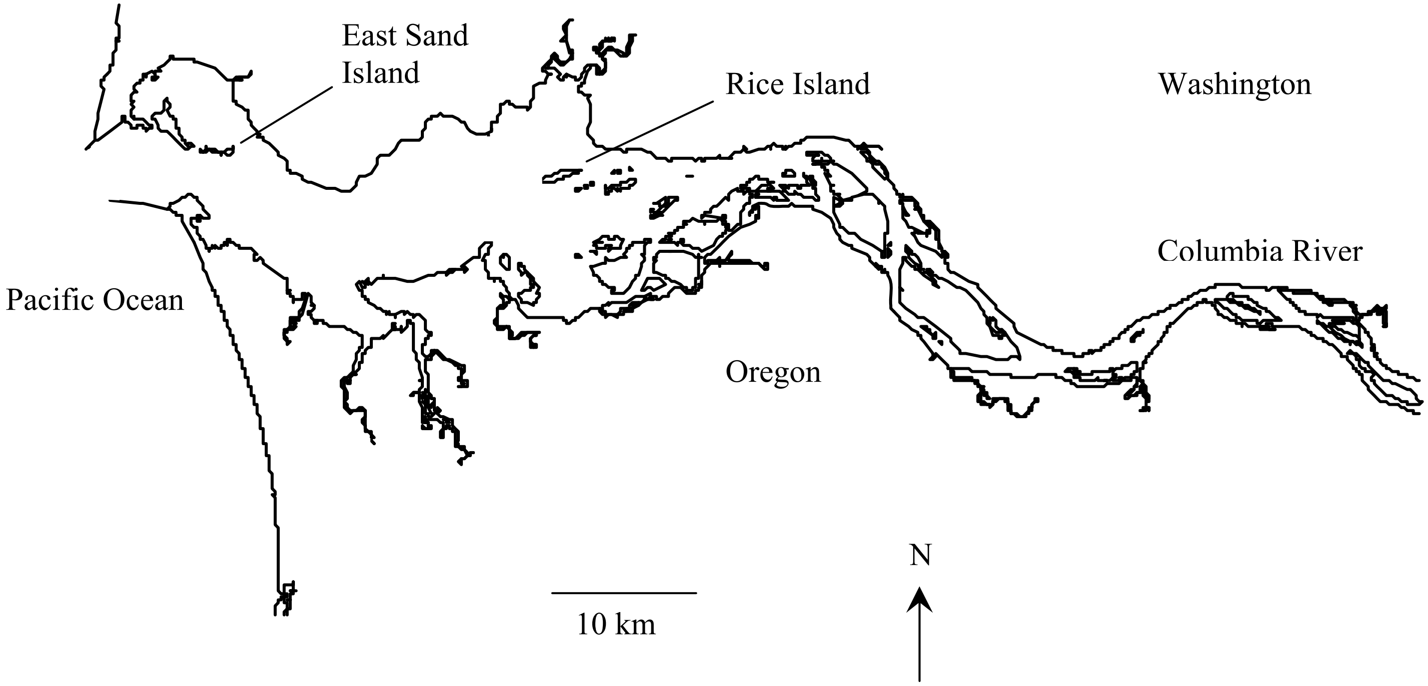

Figure 3.1. The Columbia River estuary. Field metabolic rates were measured for double-crested cormorants (*Phalacrocorax auritus*) nesting at colonies on Rice Island (river km 34) and on East Sand Island (river km 8).

Chapter 4

EVALUATING MANAGEMENT OF AVIAN PREDATON ON THREATENED AND ENDANGERED SALMONIDS

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ABSTRACT

We used demand-based bioenergetics methods to estimate consumption of juvenile salmonids (*Oncorhynchus* spp.) by Caspian terns (*Hydroprogne caspia*) nesting in the Columbia River estuary (Oregon, U.S.A) during 1997-2006, and to assess impacts of this predation on Columbia River salmonid populations. Thirteen of 20 anadromous salmonid evolutionarily significant units (ESUs) within the Columbia River basin are listed as threatened or endangered under the U.S. Endangered Species Act, and the possibility that predators might limit recovery is of concern. Point estimates of annual smolt consumption by terns in the estuary ranged from 12.1 million (95% CI: 10.1 – 14.1 million) in 1999 to 3.9 million (95% CI: 3.4 – 4.4 million) in 2005. Consumption of sub-yearling Chinook (*O. tshawytscha*) dropped abruptly with the managed relocation of the tern colony from Rice Island (river km 34) to East Sand Island (river km 8) over the course of three years (1999 – 2001). Consumption of coho salmon (*O. kisutch*) was also lower in years following relocation; however, the decrease was not as abrupt. Using an age-structured deterministic matrix population model and assuming an intermediate level of compensatory mortality (50%) following reductions in tern predation, we estimated that the average annual population growth rate (λ) may have increased 0.9% and 1.2% for sub-yearling Chinook and coho, respectively, following relocation of the tern colony. A planned dispersal of a portion (~ 60%) of the tern colony to outside the Columbia River basin could achieve benefits for several salmonid species/types ($\Delta\lambda$ =

1.1% for coho, 1.1% for sockeye salmon [*O. nerka*], 0.7% for steelhead [*O. mykiss*], and 0.4% for yearling Chinook, assuming 50% compensatory mortality). Applying these realized or expected benefits derived for each salmonid species/type to particular listed Columbia River ESUs would not move any salmonid population into a stable recovery (λ » 1), but some benefits approach, or occasionally exceed, improvements anticipated from planned hydropower system changes ($\Delta\lambda = 0 – 9\%$ for various ESUs, median = 2%). A comprehensive strategy, including a suite of recovery actions (e.g., changes in the hydropower system, restoration of freshwater/estuarine habitat, reform of hatchery practices, reductions in avian predation, etc.), would likely provide the best chance to fully restore Columbia River salmonid populations.

INTRODUCTION

In the modern era of extinction, conservation biologists usually focus research and management efforts on anthropogenic factors hindering the robustness of populations of threatened and endangered species. Emphasis is often placed upon identifying and reversing factors that likely caused population decline: degradation, fragmentation, and loss of habitat; effects of introduced species or pollutants; excessive human harvest or depredation; and more recently, effects of human-induced changes in climate (Caughley 1994, Groom et al. 2006). In the case of severely depressed populations and limited conservation resources, recovery actions focused on reversing long-term, usually ultimate, effects must sometimes be balanced against actions focused on short-term, sometimes merely proximate, effects. Likewise, when several factors act simultaneously to threaten species persistence, recovery plans should address these multiple factors in parallel. Species recovery may often rely on the summed or synergistic effects of many actions, any of which would be insufficient to accomplish recovery if performed in isolation.

In human-altered ecosystems, the effects of predation on threatened and endangered species is often cited as a potential limiting factor for recovery and the management of predation is increasingly cited as a necessary short-term (or longer) action (Stancyk 1982, Garrott et al. 1993, Goodrich and Buskirk 1995, Hecht and Nickerson 1999). Numerous examples exist of exotic predators decimating naïve prey populations (e.g., Goldschmidt 1996, Fritts and Rodda 1999, Ruzycki et al. 2003); however, human activities can have the unanticipated effect of destabilizing the dynamic between even co-evolved predators and prey by rendering the prey more vulnerable or concentrating the predators at unusual densities. Prey can, for example, be made more vulnerable by the degradation of habitat, exposure to pollutants and parasites, or the elimination of refuge habitat (Macdonald et al. 1999, Schneider 2001, Evans 2004, Sinclair et al. 2005). Native predator populations can be subsidized (enhanced and/or locally concentrated) by the supplementation of food supplies (Price and Nickum 1995, Belant 1997, Smith and Engeman 2002, Boarman 2003), or experience ecological release from other limiting factors (e.g., elimination of or isolation from their own predators; Rogers and Caro 1998, Crooks and Soulé 1999, Elmhagen and Rushton 2007).

Over the last century, in the Pacific Northwest region of the United States, anadromous salmonids have suffered orders of magnitude decline from historical levels, resulting in more than half the identified evolutionarily significant units (ESUs) being extirpated or listed as threatened or endangered under the U.S. Endangered Species Act (Good et al. 2005, Gustafson et al. 2007). Within the Columbia River basin, the largest basin in the region, 13 of 20 remaining identifiable ESUs are listed (Good et al. 2005). The federal agencies involved in restoration of Columbia River salmonid populations organize the perceived problems for wild salmonids into four major categories: excessive harvest; competition and maladaptive interbreeding with large numbers of hatchery-reared fish; degradation of freshwater spawning, rearing, and migratory habitat; and direct and indirect mortality associated with fish passage through dams constructed for power generation, flood control, and irrigation purposes, including loss of habitat above dams constructed with no means of fish passage (Federal Caucus 2000). In addition to these factors, variable climate conditions in the ocean environment are now recognized to exert a strong density-independent effect on salmonid populations (Pearcy 1992, Mantua et al. 1997, Hare and Mantua 2000), and concern is growing over potential negative impacts of long term climate change (Mote et al. 2003, ISAB 2007).

Within this context, the effects of predators on Columbia River salmonids have been examined for more than two decades. In the freshwater environment, native fish (i.e., northern pikeminnow, *Ptychocheilus oregonensis*; Beamesderfer et al. 1990, Ward et al. 1995), exotic fishes (principally smallmouth bass, *Micropterus dolomieu*, and walleye, *Stizostedion vitreum*; Rieman et al. 1991, Zimmerman 1999), and a variety of bird species (gulls, *Larus* spp., Caspian terns, *Hydroprogne caspia*, double-crested cormorants, *Phalacrocorax auritus*, common mergansers, *Mergus merganser*, and others; Ruggerone 1986, Collis et al. 2002, Roby et al. 2002, Roby et al. 2003, Ryan et al. 2003, Antolos et al. 2005, Good et al. 2007, Wiese et al. 2008) have been documented to prey on juvenile salmonids. In addition, pinnipeds (harbor seals, *Phoca vitulina*, and sea lions, *Zalophus californianus* and *Eumetopias jubatus*; NMFS 1997, Laake et al. 2002, Tackley et al. 2008, Stansell et al. 2009) prey on both juveniles and adults. Similarly, in the ocean environment numerous bird (e.g., common murre, *Uria aalge*; Matthews 1983), fish (e.g., Pacific hake, *Merluccius productus*, and jack mackerel, *Trachurus symmetricus*; Emmett and Krutzikowsky 2008), and pinniped predators are also known to consume salmonids at various stages in their life histories.

Management of several of these predators has been proposed or implemented based on the perceived anthropogenic alteration of the predator-prey dynamic. For example, populations of northern pikeminnow, a piscivorous fish native to the Columbia River that preys on juvenile salmonids, have increased substantially in the warmer, slackwater reservoirs behind mainstem dams. Consumption of juvenile salmonids by pikeminnow was inferred to be substantially higher than historical levels and a reward fishery has been conducted since the early 1990s (Beamesderfer et al. 1990, Ward et al. 1995). Success of the program has regularly been evaluated in terms of predators removed from the system, but ultimate benefits to salmonid population trends have been difficult to assess (Beamesderfer et al. 1996).

Substantial avian predation on juvenile salmonids in the Columbia River has been documented as well, with the most significant occurring in the estuary, where in 1997 and 1998 Caspian terns were estimated to consume 8 – 12 million smolts annually (Roby et al. 2003). Terns nested on an island created from sand deposits dredged from the Columbia River shipping channel and by 1998 had grown to the largest colony of this species ever documented (Cuthbert and Wires 1999, Suryan et al. 2004). This creation of secure nesting habitat (isolated from mammalian predators) and the perceived food subsidy of millions of predator-naïve hatchery-reared smolts could be interpreted as an anthropogenic alteration of the predator – prey dynamic. A managed relocation of the tern colony occurred during 1999-2001 to an island lower in the estuary, where tern diet composition included significantly fewer salmonids and greater marine forage fish (USACE 1999, 2000, Roby et al. 2002). In 2006, a management plan was finalized to disperse a portion of the Caspian tern colony in the Columbia River estuary to sites elsewhere in Oregon and California, to further reduce predation impacts on juvenile salmonids (USFWS 2005, 2006).

Our primary goal in this paper is to critically evaluate management of Caspian terns, a native predator on threatened and endangered juvenile salmonids, both in terms of number of prey consumed and, to the extent possible, ultimate impacts to the demography of the prey. Our specific objectives are:

1. Estimate juvenile salmonid consumption by Caspian terns nesting in the Columbia River estuary following the managed 1999-2001 relocation of the colony within the estuary and compare to pre-management levels.
2. Estimate salmonid mortality rates due to Caspian tern predation and potential improvements in salmonid population trajectories due to the 1999-2001 colony relocation.
3. Investigate potential changes in abundance of adult salmonids concurrent with reductions in tern predation on juveniles, where data exist.
4. Estimate potential improvements in mortality rates and salmonid population trajectories due to the proposed dispersal of most of the Caspian terns currently nesting in the estuary.

METHODS

Study Area

We estimated prey consumption by Caspian terns nesting in the Columbia River estuary at Rice and East Sand islands from 1997 to 2006 (Figure 4.1). Rice Island (river km 34) is a completely artificial island created by disposal of sand dredged from the shipping channel of the Columbia River. East Sand Island (river km 8) is a natural island but with extensive anthropogenic alterations, including rip-rap stabilization, occasional dredge disposal, and historical construction activities (USACE 2000). At its position in the upper estuary, Rice Island is surrounded by primarily fresh water, whereas East Sand Island is surrounded by more brackish, marine waters. The fish communities present in close proximity (< 10 km) to each island reflect this salinity difference, with numerous marine forage fishes present near East Sand Island and largely absent near Rice Island (Bottom and Jones 1990, Hinton et al. 1995, Hinton and Emmett 2000).

Prey Consumption Estimation

Prey consumption was estimated using a revision of bioenergetics techniques used in Roby et al. (2003). A brief overview of the technique and data organization is presented here, but the reader is referred to that work for additional detail. Improvements in methodology and data quality over Roby et al. (2003) include measured chick energy requirements, measured assimilation efficiency, and more intensive sampling of several parameters: tern population size across the breeding season, tern diet composition, and mass and energy content of the various prey types. To allow consistent comparisons of prey consumption by terns nesting at Rice Island in 1997 and 1998 (first presented in Roby et al. 2003) to the subsequent years that make up the primary focus of this study, consumption estimates for the Rice Island tern colony during 1997-1998 were recalculated using the revised methodology and are included here.

Data requirements for the bioenergetics calculations fall into four categories: number of terns present (adults and chicks), tern diet composition (by relative frequency), tern energy requirements (adults and chicks), and prey energy content (a combination of prey mass and energy density for each prey type). Data were collected on the abundance and diet composition of terns across the breeding season for each colony in all years (late March until all terns had left the colony, usually by late August). Energy requirements were assumed to be the same for adults across season, year, and colony. Chick energy requirements increased with age within a season, but were assumed to be the same across year and colony. Distinct energy densities were obtained for each prey type, and were assumed constant across season, year, and colony. Similarly, distinct masses of the various individual prey types were obtained and assumed constant across season and colony, but were varied across years as data were available and significant differences observed.

Estimates of prey consumption (number of each prey type consumed) were calculated for discrete 2-week periods across the tern breeding season for each colony and year. A 2-week time increment was considered a prudent compromise for calculations based on the high sampling frequency (~ daily) of some important input parameters (e.g., estimates of the number of terns present, diet composition to family) and lower sampling frequency (4-week periods, annually, etc. as noted) of other parameters (e.g., diet composition to salmonid species, prey energy content, adult tern energy expenditure, etc.). Calculations were performed using a routine written in Visual Basic 6.0 (Microsoft Corporation, Redmond, WA). A Monte Carlo calculation technique was used to obtain confidence intervals for consumption estimates (Furness 1978). Each input parameter was assumed to be normally distributed with the measured (or assumed, where noted) mean and SE. Sampling errors in the input parameters were assumed to be uncorrelated. Calculations were performed 1000 times, with every run using independent, randomly drawn values for each of the input parameters. Calculations were performed for each 2-week period and summed to get annual totals for each colony and year.

Tern colony size: The number of adults breeding at each colony during late incubation (usually the 3rd or 4th week of May) was estimated using high-resolution aerial photographs (see Collis et al. 2002 for details). Counts of individuals in aerial photographs were converted to the number of breeding pairs using ratios of terns on nests to all terns present in sample plots observed from blinds at the edges of the colony at the time the aerial photography was taken. At other times during the season (approximately daily), the number of adults on colony was estimated by counting all terns visible from a blind. The ratio of each daily blind-based count to a similar count on the day of the late incubation aerial photography was multiplied by the estimate of breeding pairs from the aerial photograph to estimate the number of breeding pairs present daily throughout the season. We assumed that the number of non-breeding terns present in the estuary was negligible compared to the number of breeding terns present (Roby et al. 2003).

The number of tern chicks present at the colony was represented as an estimate of the number hatching, considered to occur on the median hatching date in the bioenergetics calculations, and an estimate of the number fledging, with an exponential decline (i.e., decay) in between. The number of chicks successfully hatching was estimated by multiplying the average number of young hatched per nest in sample plots by the estimated number of breeding pairs during late incubation. The number of chicks fledging was estimated by counting all chicks present on the colony 7-10 days following the initial observation of any chicks flying at each colony in each year. This count of all chicks present was performed using a second set of aerial photographs where the total number of terns counted in the photographs (adults and chicks could not reliably be distinguished) was multiplied by the ratio of chicks to all terns present (chicks + adults) in sample plots (n = 12) observed from blinds at the time of the photography. The exponential decline in the number of chicks between the median hatch date and the approximate median fledging date was fit to the trend in daily counts of chicks present in the sample plots. Chicks were assumed to be capable of flight around 37 days post-hatch (Cuthbert and Wires 1999) and to leave the colony and the Columbia River estuary at 42 days post-hatch (Roby et al. 2003).

Tern diet composition: Tern diet was quantified by prey type frequency identified to the level of family. Prey were identified to family as they were carried back to the colony by adult terns in their bill (“bill-load fish”), with the aid of binoculars or spotting scopes from blinds, approximately daily. In order to identify salmonids to species, a sample of adult terns was collected each year (except in 1999 at East Sand Island and in 2000 at Rice Island) to obtain bill-load fish and foregut contents for finer resolution analysis of diet composition. Sampling occurred across the breeding season and averaged 10 bill-load fish per week. Collected bill-load salmonids were identified to species using external morphology and Chinook salmon were further identified to age class (yearling or sub-yearling, a designation of streamor ocean-type juvenile life histories; Healey 1991) using date-specific length criteria (R. Emmett, NOAA Fisheries, personal communication). Soft tissue samples obtained from foreguts and identifiable as salmonids were identified to species by T. Robinson, Oregon State University, using PCR-based genetic techniques developed by Greig et al. (2002).

Species breakdowns for salmonids from both bill-load fish and foregut samples were pooled for 4-week sampling periods across the breeding season (4/10-5/7, 5/8-6/4, 6/5-7/2, and 7/3-7/30). Within each time period and for each colony, counts of salmonids by species (and age class, for Chinook) were pooled. For each colony, each year's breakdown was compared to the pooled totals from other years at that colony using Fischer's Exact Test. If a significant difference between a given year and the other years' pooled totals was detected, then the particular year's data alone was used in the subsequent bioenergetics calculations. If no significant difference was detected, then the pooled total (all years) for that colony was used. Comparisons between terns nesting at Rice Island and East Sand Island were made for each time period within the season (years pooled), also using Fischer's Exact Test.

Clupeids (Pacific herring, *Clupea pallasi*; Pacific sardine, *Sardinops sagax*; and American shad, *Alosa sapidissima*) in the tern diet collected as bill-load fish or from foregut samples were opportunistically identified to species as well. Identified clupeid sample sizes were smaller than for salmonids and statistical comparisons between colonies and years were not possible. Species breakdowns of clupeids were pooled across years for each colony separately, except for 4-week time periods when modest sample sizes ($n \geq 10$) indicated a strong dependence (≥ 90% of samples) on a single clupeid species (at East Sand Island, sardine: 4/10-5/7, 2004 and 2005, 5/8-6/4, 2001; herring: 6/5-7/2 and 7/3-7/30, 2000, and 5/8-6/4, 6/5-7/2 and 7/3-7/30, 2002; strong dependence on a single clupeid species did not occur at Rice Island).

Tern energy requirements: Daily energy expenditure of breeding Caspian terns was assumed to be 1040 kJ/day, as measured using the doubly-labeled water technique on terns nesting at Rice Island in 1997 and 1998 (Roby et al. 2003). We converted this energy expenditure into energy required using an assimilation efficiency of 0.80, as measured in developing Caspian tern chicks (D. Lyons, unpublished data) and seen in other species of terns (Drent et al. 1992, Klaassen et al. 1992, Chavez 1997, Visser 2001). Assimilation efficiency is not the true metabolizable energy coefficient, but bioenergetic studies typically use these values as reasonable approximations (Miller and Reinecke 1984).

Energy requirements of developing Caspian tern chicks were determined by captive rearing recently hatched chicks obtained from the East Sand Island colony in 2001 and quantifying the amount of food consumed by chicks fed *ad libitum* diets. The peak daily metabolizable energy requirements were 760 kJ/day and the total metabolizable energy required to fledging age was 18.8 MJ (Chapter 2), both consistent with allometric predictions (Weathers 1992).

Prey energy content: Mean fresh mass of each prey type was obtained from collected bill-load fish. Differences in average mass across years were tested for each prey type using Kruskal-Wallace one-way ANOVA on ranks. For prey types where significant annual differences were indicated, average mass was varied between years; otherwise, samples from all years were pooled and a single mean body mass was used. Energy density of each prey type was measured using proximate composition analysis (Reynolds and Kunz 2001, Roby et al. 2003) and assumed to be constant for each prey type across season and year.

Predation Rate Estimation

Numbers of smolts reaching the Columbia River estuary and potentially subject to tern predation were estimated using a process developed in collaboration with D. Marsh, NOAA Fisheries, Seattle, WA. Smolt availability was estimated to be the sum of:

1. Hatchery smolt production below Bonneville Dam (river km 235; lowest mainstem dam on the Columbia River). Data on annual hatchery releases were obtained from the website of the Fish Passage Center (www.fpc.org).
2. Wild smolt production below Bonneville Dam. Annual indices of wild smolt production from selected spawning streams (derived from counts of spawning adults) were scaled to the amount of spawning habitat estimated to exist below Bonneville Dam (D. Marsh, NOAA Fisheries, unpublished data).
3. Hatchery and wild smolts produced above Bonneville Dam, captured at an upriver dam, transported in a barge or truck, and released just below Bonneville Dam. Data on releases of transported smolts were obtained from the website of the Fish Passage Center (www.fpc.org).

4. Hatchery and wild smolts produced above Bonneville Dam and allowed to migrate in-river downstream through Bonneville Dam. First, counts of smolts observed at the juvenile bypass facility at Bonneville Dam were obtained from the website of the Fish Passage Center (www.fpc.org). Only a portion of smolts migrating in-river traverse Bonneville Dam through the juvenile bypass route, however – others pass through the turbines or over the spillway. To correct for these unobserved smolts, we divided the count of all smolts observed at the bypass facility by the detection probability at the bypass facility of smolts tagged with passive integrated transponder (PIT) tags (the proportion of all tagged smolts that were known to pass through Bonneville Dam that were detected at the bypass facility). Detection probability values were obtained from mark-recapture survival studies of tagged smolts conducted by NOAA Fisheries, Seattle, WA. (Hockersmith et al. 1999, Smith et al. 2000a, Smith et al. 2000b, Zabel et al. 2001, Zabel et al. 2002, Muir et al. 2003, Smith et al. 2004, Smith et al. 2005, 2006, Faulkner et al. 2007).

All of the above four groups of smolts were assumed to experience negligible mortality from the point of enumeration (Bonneville Dam or downstream rearing/release location) to the upper estuary (ca. river km 75). This is consistent with observations of relatively high survival through this stretch of river for radio-tagged smolts released just below Bonneville Dam (Schreck et al. 2006).

Detection probability data at Bonneville Dam were available for yearling Chinook in 1999-2006 and for steelhead in 1998-2003 and 2006. For each species, detection probability was regressed against average flow through Bonneville Dam in the month of May, when both species experience their peak out-migration through that dam (for yearling Chinook: $P = 0.11$, $R^2 = 0.36$; for steelhead: $P = 0.002$, $R^2 = 0.88$). Detection probabilities for years where data were lacking were obtained using these regressions. Detection probabilities were not available for sub-yearling Chinook, coho, or sockeye, and values for yearling Chinook were used instead.

Data on wild production below Bonneville Dam were available only in some years (yearling Chinook: 2000-2006; sub-yearling Chinook: 2000, 2003, 2005-2006; coho: 2005, steelhead: 1999-2000, 2004-2006; no sockeye salmon spawn below Bonneville Dam). In years when no data were available, smolts produced were assumed to be an average of smolts produced in years where data were available. Wild-spawned smolts from below Bonneville Dam were a minority of all smolts produced (23% of yearling Chinook, 21% of sub-yearling Chinook, 6% of coho, 4% of steelhead, and 0% of sockeye).

Predation rates were calculated for each species/type as the estimated number of smolts consumed divided by estimated number of smolts that reached the estuary, and expressed as a percentage. Rates were estimated for each of the 1000 Monte Carlo estimates of prey consumption, with the availability of each salmonid species/type drawn from a normal distribution with mean as estimated above and SE assumed to be 20% of the mean (consistent with uncertainty levels of component parameters, e.g., Piper et al. 1982, Faulkner et al. 2007).

Use of the various salmonid species/types by terns versus availability (abundance in estuary) of each salmonid type was determined by calculating Manly – Chesson preference index values (Chesson 1978, Manly et al. 1993):

$$P_i = \frac{d_i / N_i}{\sum_{j=1}^{k} (d_j / N_j)},$$

where d_i is the proportion of prey (salmonid) species/type i in the diet, N_i is the proportion of prey type i in the environment (proportion of all smolts that arrive in the estuary that are of species/type i), k is the number of species/types considered, and P_i is the calculated preference index value for species/type i. Sockeye were omitted from this analysis due to methodological limitations (consumption estimates were based on small samples; availability estimates were constrained by limited data). Preference for a given prey type is indicated when the index value is greater than 1 / k, or in this case, 1 / 4 = 0.25.

Explanatory Factors Analysis

To investigate the impact of management of the Caspian tern colony on the number of smolts consumed and the proportion of available smolts that were taken by terns, annual consumption totals and proportions of available smolts taken were compared for years when the tern colony was primarily or solely at Rice Island (1997-1999) and years when the colony was primarily or solely at East Sand Island (2000-2006) using Wilcoxon rank-sum tests. To further test whether potential differences between the two time periods (1997-1999 and 2000-2006) occurred as a result of management, 95% confidence intervals in consumption and proportion taken for the last year when the majority of terns nested at Rice Island (1999) and the first year when the majority nested at East Sand Island (2000) were examined for degree of overlap. If no overlap in confidence interval existed, this was taken as strong evidence that the abrupt relocation of terns from one island to the other was a more significant factor in changing tern predation than potential (possibly unrelated) temporal trends over the entire time period.

The possible effects of river flow on tern predation were investigated using single-variable correlations between estimated consumption and flows measured at the Beaver Army Terminal near Quincy, Oregon (river km 86; U.S. Geological Survey, Water Resource Data site number 14246900, data available at waterdata.usgs.gov, accessed 30 June 2007). Annual explanatory variables investigated were May flows (corresponding to peak out-migration period for yearling Chinook and steelhead), July flows (corresponding to peak arrival of sub-yearling Chinook to the estuary), and average flows across April to July (representing the nesting season for the majority of terns). Responses examined were the numbers consumed of each species/type of juvenile salmonid, along with all salmonid species/types together, and proportion of available smolts taken for each species/type separately and taken together.

Similarly, the potential effect of juvenile salmonid availability was assessed using correlations between estimated numbers arriving in the estuary and estimated numbers consumed by terns.

Demographic Model Analysis

For species and types of salmonids where significant reductions in predation were observed following relocation of the tern colony, the benefit to salmonid populations was assessed by estimating the change in the average annual population growth rate (λ) using the analytical framework of a simple deterministic, age-structured, matrix population growth model (Kareiva et al. 2000, McClure et al. 2000, Caswell 2001, McClure et al. 2003). The percent change in λ attributable to an increase in survival at a particular life history stage can be calculated (McClure et al. 2000, Caswell 2001) as a function of the initial survival rate (S_i), the survival rate following the change (S_f), and the average generational time (G):

$$\Delta\lambda = [(\frac{S_f}{S_i})^{1/G} - 1] \cdot 100\% .$$

This change in λ has been used to compare the efficacy of various actual and potential management actions intended to help recover Columbia River salmonid populations (McClure et al. 2003). Important assumptions of this approach are that increases in survival at a particular life-history stage are density-independent and independent of changes in survival elsewhere in the life history.

Mortality due to particular predators may be additive or, if reduced, may be compensated for by other mortality factors (e.g., other predators) later in the prey species' life history (Errington 1967). It is unknown to what degree reductions in tern predation may be compensated for by other predators, such as other piscivorous birds, mammals, or fish (or other mortality factors, e.g., competition). If tern predation is to some degree compensatory, then changes in λ calculated as above would be overestimated. To understand the effects of potential levels of compensation, changes in λ were calculated for a range of compensation by reducing the improvement in survival used to estimate Δλ (Roby et al. 2003):

$$\frac{S_f}{S_i} = \frac{(100 - \%\,\text{Compensation})}{100} \cdot \frac{S_{f_{\text{terns}}}}{S_{i_{\text{terns}}}},$$

Where $S_{i_{\text{terns}}}$ and $S_{f_{\text{terns}}}$ are initial and final survival of tern predation (i.e., 1 - predation rate). The case of 100% compensation results in no actual improvement in survival or λ.

Potential benefits of further management of the tern population, such as dispersal of some portion of the colony away from the Columbia River estuary (USFWS 2005, 2006) were considered using the same analytical framework. Possible improvements in salmonid λ values were estimated given a range of reductions in tern colony size, using the same range of assumptions on the degree of compensatory mortality as above, and the assumption that tern foraging behavior (i.e., diet composition) was not a function of tern density.

Relationship to Adult Returns

Finally, we used single-variable correlations to investigate the relationship between tern predation on coho salmon smolts in the estuary and estimated returns of adult coho to the Columbia River one year later. Coho is the most straightforward salmonid species for which to undertake this investigation, as they have a less variable life history than the other species, most individuals generally return to freshwater to spawn after only one year in the ocean environment, and adult abundance is relatively well monitored.

Estimates of the number of adult coho returning to the Columbia River are made annually to assess harvest regulations and track population status (PFMC 2007). These estimates are a sum of the lower river (below Bonneville Dam) commercial and recreational harvests, escapement to lower river hatcheries and tributary dams, and counts of adult coho migrating through Bonneville Dam. These numbers of adults entering the Columbia River can be further corrected using estimates of ocean exploitation rates by troll and sport fisheries to estimate the number of Columbia River coho that reached adult (or at least harvestable) size (PFMC 2007). This measure of adult abundance was used as the response variable for each correlation.

The relationship between adult coho abundance and four independent variables (from the year prior to the measures of adult abundance) were then investigated: (1) number of coho smolts consumed by terns, (2) proportion of available coho smolts consumed by terns, (3) number of coho smolts estimated to reach the estuary, and (4) the number of coho smolts that reached the estuary and did not succumb to tern predation (i.e., 3 minus 1).

All statistical tests were interpreted as significant at the $\alpha = 0.5$ level unless otherwise noted. Scientific collection permits were granted by the U.S. Fish and Wildlife Service (Region 1 Migratory Bird Office, Portland, OR) and the Oregon Department of Fish and Wildlife (Salem, OR). All animal handling and collection protocols were approved by the Oregon State University Institutional Animal Care and Use Committee.

RESULTS

The size of the nesting population of Caspian terns in the Columbia River estuary ranged from a low of 7,134 breeding pairs (95% CI: 5,834 – 8,434) in 1997 to a high of 9,933 breeding pairs (95% CI: 9,551 – 10,314) in 2002 (Table 4.1). Particularly from 1998 onward, the size of the Caspian tern breeding population has remained relatively stable. Productivity varied greatly over the course of the study, however, from a low of 0.06 fledglings/breeding pair in 1997 to a high of 1.39 in 2001 (Table 4.1). The proportion of salmonids in the tern diet was lower for terns nesting at East Sand Island (46 – 47%) than for terns nesting at Rice Island (77 – 90%; Table 4.1, Figure 4.2) during the two years when terns nested on both islands (1999 – 2000). In addition, the salmonid proportion of the diet at East Sand Island in all years (1999 – 2006: 17 – 47%) never reached that observed at Rice Island in earlier years (1997 – 2000: 73 – 90%; Table 4.1, Figure 4.2). Other major prey types were northern anchovy (*Engraulis mordax*), Pacific herring, Pacific sardine, American shad, shiner surfperch (*Cymatogaster aggregata*), surf smelt (*Hypomesus pretiosus*), and peamouth (*Mylocheilus caurinus*; Figure 4.2).

Breakdowns of salmonid species in tern diets differed between Rice Island in 1997 – 2000 and East Sand Island in 2000 – 2006 for each time period within the tern breeding season (4/10 – 5/7, *P* = 0.01; 5/8 – 6/4, *P* = 0.01; 6/5 – 7/2, *P* = 0.001; 7/3 – 7/30, *P* = 0.02; Table 4.2). Sub-yearling Chinook made up a larger proportion of salmonids in tern diets for all time periods during the season at Rice Island than compared to East Sand Island; conversely, yearling Chinook made up a larger portion of the salmonids identified in diets of East Sand Island terns. Incorporation of steelhead and coho in tern diets peaked earlier in the season at Rice Island and were utilized into July at East Sand Island. Sockeye were only a small component of all salmonids identified from either location. Chum salmon and cutthroat trout were not observed in the diet of terns. Chum were not a measurable portion of the tern diet, presumably due to their small size and early out-migration relative to the tern breeding season. Passive integrated transponder (PIT) tags implanted in sea-run cutthroat trout have been recovered on the East Sand Island tern colony (A. Evans and S. Sebring, Pacific States Marine Fisheries Commission, Hammond, OR., unpublished data), so terns consume this species; likely in small numbers, however, as evidenced by the lack of this species in bill-load samples.

Significant differences in mean fresh mass were indicated for several prey species across colonies and years: sub-yearling Chinook, coho, northern anchovy, Pacific herring, Pacific sardine, and smelt (Table 4.3). Energy density of the various prey types varied from 3.45 kJ/g (95% CI: 3.27 – 3.63) for Pacific tomcod (*Microgadus proximus*) to 5.70 kJ/g (95% CI: 5.33 – 6.07) for lamprey (*Lampetra* spp.). The resulting energy content per prey item ranged from 5.0 kJ/fish (95% CI:

3.63 – 6.34) for threespine stickleback (*Gasterosteus aculeatus*) to 280.8 kJ/fish (95% CI: 247.9 – 313.7) for steelhead.

Estimated prey consumption by Caspian terns ranged from 10.6 million fish (95% CI: 8.0 – 13.2 million) in 1997 to 23.1 million fish (95% CI: 19.5 – 26.6 million) in 2004 (Table 4.4). Consumption of juvenile salmonids ranged from 3.9 million smolts (95% CI: 3.4 – 4.4 million) in 2005 to 12.1 million smolts (95% CI: 10.1 – 14.1 million) in 1999 (Table 4.4). In most years, coho was the most frequently consumed smolt species; however, in 1998 and 1999 more than five million sub-yearling Chinook smolts were consumed by terns.

Annual estimates of smolt availability in the estuary ranged from 113 million (95% CI: 97 – 129 million) in 2001 to 153 million (95% CI: 130-176 million) in 1997 (Figure 4.3), with sub-yearling Chinook smolts being most numerous. The resulting proportion of available smolts taken by terns was lowest in 2003 at 3.2% of all juvenile salmonids that reached the estuary (95% CI: 2.6 – 3.8%) and highest in 1999 at 10.3% (95% CI: 8.1 – 12.5%; Figure 4.4A). Sockeye, coho, and steelhead had the highest mortality rates due to tern predation, followed by yearling Chinook and sub-yearling Chinook (Figure 4.4B-F).

Significantly fewer total salmonids ($Z = 2.28$, $P = 0.02$), sub-yearling Chinook ($Z = 2.28$, $P = 0.02$), and coho ($Z = 2.28$, $P = 0.02$) were consumed by terns during the years when the majority or all terns nested at East Sand Island (2000 – 2006) than when terns nested primarily or wholly at Rice Island (1997 – 1999). No significant differences between colony sites were seen for consumption of yearling Chinook, sockeye, or steelhead. The proportion of available sub-yearling Chinook ($Z = 2.28$, $P = 0.02$) and coho ($Z = 2.28$, $P = 0.02$) smolts taken was significantly lower for terns at East Sand Island; however, this was not true for yearling Chinook, sockeye, and steelhead, and only suggestive for all salmonids grouped together ($Z = 1.59$, $P = 0.11$). Confidence intervals for numbers of total salmonids and sub-yearling Chinook consumed by terns in 1999 and 2000 did not overlap (all salmonids: 10.1 – 14.1 million in 1999 and 5.6 – 7.7 million in 2000; sub-yearling Chinook: 5.4 – 7.6 million in 1999 and 0.8 – 1.2 million in 2000), indicating that a large reduction in consumption rate of sub-yearling Chinook occurred coincident with relocation of the colony. Similarly, confidence intervals for the proportion of available total salmonids and sub-yearling Chinook taken also did not overlap between 1999 and 2000 (all salmonids: 8.1 – 12.5% in 1999 and 4.3 – 6.7% in 2000; sub-yearling Chinook: 7.7 – 14.2% in 1999 and 1.2 – 2.2% in 2000). For coho, however, confidence intervals for both the number of smolts consumed and the proportion of available smolts consumed overlapped between 1999 and 2000, indicating that there was no abrupt change in coho consumption by terns associated with the colony relocation, despite a decrease over the longer term.

In most or all years at Rice Island (Figure 4.5A) and in all years at East Sand Island (Figure 4.5B), coho and steelhead were selected by terns, whereas sub-yearling and yearling Chinook were taken in lower proportion than their availability alone would have suggested. Correlations between availability and consumption of smolts were non-significant over the 10 years of this study (all P values ≥ 0.17). There was, however, a positive relationship between steelhead availability and number of steelhead consumed by terns when only the years terns nested primarily at East Sand Island (2000-2006) were examined ($P = 0.02$, $R^2 = 0.66$). A similar, but non-significant, relationship for coho was also suggested ($P = 0.09$, $R^2 = 0.48$) for this time period.

A weak, non-significant positive relationship between July river flow and number of sub-yearling Chinook smolts consumed was observed ($P = 0.08$, $R^2 = 0.33$). The relationship between July flow and the proportion of sub-yearling Chinook smolts consumed was weaker ($P = 0.12$, $R^2 = 0.27$). All other relationships between flow and consumption variables were non-significant ($P \geq 0.10$).

As indicated above, a higher proportion of sub-yearling Chinook survived tern predation in the estuary during the 2000-2006 period (98.9% survival), when terns primarily or wholly nested at East Sand Island, than survived the 1997-1999 period (92.7%) when terns primarily or wholly nested at Rice Island. Coho survival was also greater in later years (90.4% vs. 84.0% earlier). These increases in survival correspond to a range of increases in average annual population growth rate (λ) of 0 – 1.8% for sub-yearling Chinook and 0 – 2.5% for coho, depending on the degree of compensatory mortality (Figure 4.6). A reasonable estimate of 50% compensatory mortality would correspond to an increase in λ of 0.9% and 1.2% for sub-yearling Chinook and coho, respectively.

Potential improvements to the population growth rates of various salmonids after dispersing some or all terns away from the estuary varied significantly by species and run-type. The maximum potential improvement in λ, assuming no compensatory mortality whatsoever and complete dispersal of all terns out of the Columbia River estuary, ranged from 0.3% for sub-yearling Chinook to 3.4% for coho and sockeye (Figure 4.7). The potential improvement in λ, assuming compensatory mortality at 50% and complete dispersal of terns, was 0.1% for sub-yearling Chinook, 0.6% for yearling Chinook, 1.7% for coho, 1.8% for sockeye, and 1.1% for steelhead. For the scenario of 50% compensatory mortality and the planned dispersal of ~ 60% of the tern colony (USFWS 2006), estimated improvements in λ were 0.1% for sub-yearling Chinook, 0.4% for yearling Chinook, 1.1% for coho, 1.1% for sockeye, and 0.7% for steelhead.

Abundance of adult coho was not directly correlated to the number of coho smolts consumed by terns one year earlier ($P = 0.98$) nor to the proportion of available coho smolts taken by terns ($P = 0.54$). However, adult coho abundance was correlated to the number of smolts estimated to reach the estuary a year earlier ($P = 0.03$, $R^2 = 0.51$), and subtracting the estimated number of coho smolts consumed by terns a year earlier improved this correlation ($P = 0.008$, $R^2 = 0.65$).

DISCUSSION

This study demonstrates that salmonid consumption by Caspian terns significantly changed with the managed relocation of the tern colony from Rice Island in the upper estuary to East Sand Island in the lower estuary. In particular, consumption of sub-yearling Chinook dropped abruptly, concurrent with the relocation. Consumption of coho smolts was also lower following relocation, although no abrupt drop in coho consumption coincident with the relocation was not observed. Perhaps our methods were not sufficiently sensitive to detect an abrupt change in coho consumption or perhaps other temporal factors, such as improving near-shore ocean conditions (e.g., Emmett 2003), contributed to the longer-term decrease in coho consumption by terns. Improving ocean conditions were associated with higher abundance and, presumably, availability of marine forage fish to terns post-relocation. Consumption and survival of yearling Chinook, sockeye, and steelhead did not appear to be affected by relocating the tern colony.

Assessing the impacts of tern predation on salmonid populations first requires estimating predation rates or conversely, salmonid smolt survival. Our estimates of predation rates used estimates of salmonid smolts arriving in the estuary that relied on numerous assumptions to fill particular data gaps. Despite the limitations in methodology, however, these estimates of salmonid availability are consistent with several factors known to be associated with salmonid production and survival in the Columbia River basin. For example, the estimated number of smolts arriving in the estuary was highest in 1997, when river flows were significantly higher than any other year (at river km 86 the USGS Water Resources station reported 507 kcfs of flow in May, 1997; the range in May flows in all other years during the study period was 175 – 389 kcfs), measured survival of in-river migrants was among the highest recorded (Faulkner et al. 2007), and hatchery releases below Bonneville Dam were greatest.

The lowest estimate of arriving smolts was in 2001, when river flow (175 kcfs in May) and in-river survival were the lowest seen during the study period (Faulkner et al. 2007). We assumed negligible mortality between the point of enumeration and the upper reaches of the foraging area of terns (ca. river km 75). While studies of radio-tagged smolts migrating from Bonneville Dam to this area indicated a relatively low mortality rate (Schreck et al. 2006), significant mortality may occur for some groups of fish, such as via predation by northern pikeminnow (Ward et al. 1995). If such mortality occurred prior to arrival of smolts to tern foraging areas, our estimates of predation rates by terns would be underestimates.

The resolution of our analysis was at the level of prey species, or in the case of Chinook salmon, age class. This study could not resolve differences in predation between salmonid populations (ESUs) that are listed under the U.S. Endangered Species Act (ESA) and those not listed, nor between smolt groups that were reared in the wild vs. reared in a hatchery environment. Estimates of tern predation rates on wild and hatchery reared smolts implanted with passive integrated transponder (PIT) tags have suggested that sometimes, but not always, hatchery smolts are more susceptible to tern predation than are wild smolts (Collis et al. 2001, Ryan et al. 2003). Given that PIT tag-based predation rates on hatchery and wild smolts have consistently been of the same order of magnitude, however, the pooled results of this study serve as a useful indicator of impacts to wild stocks, most of which are ESA-listed. Additionally, several listed ESUs now include hatchery-reared smolts (e.g., Snake River sockeye).

Predation rates were highest (≥ 10% in a majority of years) for sockeye, coho, steelhead, and before tern colony relocation, sub-yearling Chinook. The incidence of sockeye smolts in the tern diet was low, but when extrapolated across the entire tern colony became significant for this low-abundance species. Estimated predation rates on sockeye were quite variable across the 10 years of our study (2 – 39%), in part due to methodological limitations (consumption estimates based on small sample sizes, availability estimates constrained by limited data), but also due to highly variable sockeye production within the basin. Counts of sockeye smolts at the Bonneville Dam bypass facility ranged across two orders of magnitude during this study, from 5,774 in 1997 to 487,183 in 2003 (Fish Passage Center 2007). Minimum predation rates on sockeye estimated from recoveries on the tern colony of PIT tags implanted in out-migrating smolts have generally been substantially lower than what we have derived here (< 5%, Collis et al. 2001, Ryan et al. 2003); further investigation seems warranted.

Steelhead have been shown to be highly susceptable to predation from piscivorous birds throughout the Columbia River basin (Collis et al. 2001, Roby et al. 2003, Ryan et al. 2003, Antolos et al. 2005, Good et al. 2007). Our results here confirm that this is still the case in the estuary, even following the tern colony relocation to East Sand Island. Our estimates of coho predation rates (6.1 – 19.6%) exceeded PIT tag-based results (< 5%, Collis et al. 2001, Ryan et al. 2003), but not as much as for sockeye. Available estimates of tern predation rates on coho based on PIT tags are for coho detected passing Bonneville Dam, whereas the majority of coho in the estuary (76% of the estimated available coho smolts, averaged across the 10 years of this study) are released from hatcheries below Bonneville Dam. The higher coho predation rates in this study may in some part reflect high susceptability of hatchery smolts not culled by the hazards of migration above Bonneville Dam. Additionally, published estimates of predation rates based on PIT tags recovered on bird breeding colonies are minimum estimates, due to imperfect tag recovery on colonies, so estimates of predation rates based on bioenergetics estimates of tern consumption would be expected to exceed those based on PIT tags.

The indications of tern preference among salmonid species/types presented here are a function of both the foraging ecology of terns and the extent of overlap in time and space between terns and the various salmonid species/types in the estuary. For example, sub-yearling (ocean-type) Chinook do not begin to arrive in the estuary in large numbers until late June or July, when the majority of terns are completing their breeding effort and are beginning to leave the estuary. Additionally, many sub-yearling Chinook may reside in the fresher, upper portion of the estuary for an extended period (weeks or even months, Bottom et al. 2005), consequently not occurring in large numbers close to East Sand Island in the lower estuary. These factors likely explain the low preference index values for sub-yearling Chinook for terns nesting at Rice Island and the even lower value for terns at East Sand Island.

Selection for steelhead and coho over yearling Chinook cannot be explained by temporal issues, however, as the outmigration of all three species overlap with the tern breeding season and each species apparently follows directed migration through the estuary without extended residence time in the freshwater portion of the estuary (Schreck and Stahl 1998, Bottom et al. 2005, Schreck et al. 2006); however, there is growing evidence that some fraction of coho smolts may reside in the estuary for at least brief periods (D. Bottom, NOAA Fisheries, pers. comm.). Due to their large average size relative to other salmonid smolts, steelhead have the highest average energy content per fish (Table 4.3) and selection for steelhead by terns may be based primarily on nutritional value, although behavioral differences (surface orientation) may contribute to higher susceptability to tern predation as well. Coho smolts also have higher average energy content than yearling or sub-yearling Chinook and, particularly at East Sand Island, remain a significant fraction of the salmonid portion of the tern diet into June and July, after steelhead and yearling Chinook have become minor components of the diet (Table 4.2). Additionally, of all the species/types, coho had the highest proportion of available smolts that were hatchery-reared and released below Bonneville (76%, compared to 48%, 36%, and 29% for sub-yearling Chinook, yearling Chinook, and steelhead, respectively). Preference for coho by terns may reflect (1) selection for them when they are the most energetically advantageous salmonid available (i.e., after steelhead have migrated through the estuary), (2) a longer estuary residency and thus exposure time to predation by terns, or (3) higher susceptability of hatchery smolts not vetted by the hazards of migration above Bonneville Dam.

Estimating the improvement in the average annual population growth rate due to reductions in tern predation, while not a direct measure of the potential benefits of tern management, does allow comparisons to other salmonid recovery actions in the Columbia River basin (Roby et al. 2003, Good et al. 2007). Given the likelihood of at least some level of compensatory mortality following reductions in tern predation (e.g., Schreck et al. 2006), a prudent approach is to compare other recovery actions to improvements in λ from reduced tern predation assuming some intermediate level of compensation. If a 50% level of compensation is assumed, improvements in λ over the timeframe of this study due to relocation of the tern colony would have been 0.9% for sub-yearling Chinook, and 1.2% for coho. For comparison, possible improvements in λ due to anticipated (in the year 2000) improvements to the hydropower system range from 0 – 9% (median = 2%) across the various evolutionarily significant units (ESUs) of salmonids throughout the Columbia River basin (McClure et al. 2003). Recent estimates of λ for listed Columbia River salmonid ESUs were 1.01 – 1.03 for coho (range of subpopulation values for the Lower Columbia ESU), 0.85 – 0.99 for Chinook (range of values for all Chinook ESUs, regardless of age at outmigration), and 0.93 – 1.00 for steelhead (range of values for all steelhead ESUs; McClure et al. 2003, Good et al. 2005). Improvements in λ due to the managed tern relocation were, therefore, unlikely to shift populations to a state of recovery (λ >> 1), but approached the benefits from anticipated changes in the mainstem hydropower system, or even exceeded those for some listed ESUs (e.g., Willamette River sub-basin ESUs).

The estimated potential benefits from future management of Caspian terns in the Columbia River estuary, specifically the federal agencies' plan to disperse more than half of the tern population away from the estuary, in some cases exceed benefits already obtained via the managed relocation of the tern colony within the estuary. Specifically, sockeye (Δλ = 1.1%), steelhead (Δλ = 0.7%), and to a lesser degree yearling Chinook (Δλ = 0.4%) could benefit from such management (assuming 50% compensatory mortality and 60% dispersal of terns), whereas there is no evidence that these species/types benefited from the initial tern colony relocation. Coho would likely benefit a similar amount (Δλ = 1.1%) to estimated improvements due to the first relocation, but sub-yearling Chinook would presumably benefit little (Δλ = 0.1%) from additional tern management. Our estimates of the potential benefits of additional tern management for salmonid populations are generally comparable to those ESU-specific estimates produced for steelhead based on the recovery of PIT tags at the East Sand Island tern colony (Δλ = 0.5 – 0.9%, assuming a 60% reduction in tern colony size and 50% compensatory mortality; Good et al. 2007).

Few data exist to examine the degree to which other salmonid mortality factors may compensate for reductions in avian predation. However, in one study on the Oregon coast, adult returns of hatchery-reared coho smolts were compared between those released in estuaries and those transported 6 – 32 km offshore before release, with the intent that those released offshore would be much less susceptable to near-shore (primarily avian) predators, such as common murres (McNeil et al. 1991, Pearcy 1992). For most paired releases, results were equivocal; however, this may have been associated with the negative effects of barge or on-deck tank transport and abrupt release into saltwater. In paired comparisons of estuary releases and smolts transported offshore in net pens, where a more gradual freshwater to saltwater transition occurred, offshore released fish returned as adults significantly more often in 4 of 5 cases. This qualified result would be consistent with estuary or near-shore avian predation being to some degree additive. Similarly, elsewhere in the Columbia River, management to reduce predation on juvenile salmonids by northern pikeminnow has apparently not resulted in compensatory increased consumption of salmonids by another piscivorous fish, smallmouth bass (Ward and Zimmerman 1999). Finally, in the Columbia River estuary, we have seen no evidence of a compensatory functional response by double-crested cormorants (i.e., salmonids have not become a larger portion of the cormorant diet) during the period that tern predation on salmonids has decreased, although cormorant colony size has increased (authors' unpublished data).

Documenting the direct effects of predator management on prey population abundance is often difficult and a number of factors make this problematic for Columbia River salmonid populations. Numerous recovery actions are occurring simultaneously within the basin, all seeking to improve salmonid survival. It can be unclear how to distinguish the effects of one action from any number of other coincident actions. Additionally, salmonid survival to sexual maturity is a strong function of the highly variable ocean environment (Pearcy 1992, Mantua et al. 1997, Hare and Mantua 2000). Changes in tern predation due to the 1999-2001 colony relocation are somewhat confounded by concurrent strongly signaled shifts in the physical (Pacific Decadal Oscillation) and biological (prey, competitor, and predator communities) ocean environment that resulted in higher 2001 adult return rates than seen in decades for some Columbia River populations (Schwing et al. 2002, Peterson and Schwing 2003, Beamish et al. 2004, Scheuerell and Williams 2005, Emmett et al. 2006). Finally, because of the size of the basin and the number of salmonid populations within it, data collection to provide highly precise population parameters is difficult. For example, even the maximum potential improvements to λ from complete elimination of tern predation and no compensatory mortality (0.3 – 3.4%) are generally smaller than the standard error associated with the point estimates of λ (0.1 – 20.2%, median = 12.8%, of the point estimate). Measuring a significant response in λ due to the management of tern predation seems unlikely, if not impossible.

Our estimates of coho smolt production in the basin (i.e., the number of smolts that reached the estuary) explained 51% of the variability in adult coho abundance over the decade of this study. Many types of fisheries management practices presume that production of juveniles can be a useful predictor of adult abundance. In recent decades, however, it has been shown that variability in the ocean environment can have a strong density-independent effect on adult salmonid abundance (Pearcy 1992, Mantua et al. 1997). Smolt production would presumably explain less variation in adult return levels over a longer time frame than the present study, when a greater range of ocean conditions would occur.

Despite no direct relationship between the number of coho smolts consumed by terns and subsequent adult abundance, we found that incorporating the number of smolts consumed by terns into the relationship between smolt production and eventual adult abundance did improve that correlation. Two interpretations of this result are possible: (1) tern predation on smolts could be acting to some degree in an additive manner to other sources of coho mortality and be a causal (albeit secondary) factor limiting adult abundance, or (2) tern predation and adult abundance could both be related to a third variable, such as near-shore ocean conditions (e.g., primary productivity or forage fish densities). In years of poor ocean conditions, terns might rely more on salmonids migrating down the river than on marine forage fish (e.g., anchovy, herring, and sardine), and similarly, smolts that enter the ocean may experience lower survival due to increased competition for limited food (Fisher and Pearcy 1988) or increased predation resulting from fewer alternative (marine origin) prey for marine predators (e.g., Pacific hake and jack mackerel; Pearcy 1992, Emmett et al. 2006). Under this latter scenario, the numbers of smolts consumed by terns could be an indication of conditions that smolts will encounter in the near-shore environment and an important anticipator of subsequent smolt survival during the early ocean critical period.

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Table 4.1. Annual Caspian tern (*Hydroprogne caspia*) breeding and diet parameters used to estimate salmonid (*Oncorhynchus* spp.) smolt consumption by terns nesting on Rice Island (RI) and East Sand Island (ESI) in the Columbia River estuary.

	1997	1998	1999		2000		2001	2002	2003	2004	2005	2006
	RI	RI	RI	ESI	RI	ESI	ESI	ESI	ESI	ESI	ESI	ESI
Breeding pairs	7,134	8,766	8,328	547	588	8,513	8,982	9,933	8,325	9,502	8,822	8,929
Fledglings per pair	0.06	0.45	0.55	1.20	0.15	0.57	1.39	1.08	1.08	0.92	0.37	0.72
Salmonid portion of diet*	85%	73%	77%	46%	90%	47%	33%	31%	24%	17%	23%	31%

* Percent of total prey items consumed.

Table 4.2. Taxonomic composition (percent frequency) of juvenile salmonids (*Oncorhynchus* spp.) in bill-loads of collected Caspian terns (*Hydroprogne caspia*) by nesting island and time period within season, pooled over years.

	Rice Island, 1997-2000				East Sand Island, 1999-2006			
Classification	4/10-5/7	5/8-6/4	6/5-7/2	7/3-7/30	4/10-5/7	5/8-6/4	6/5-7/2	7/3-7/30
Chinook salmon, sub-yearling	4.9	7.9	54.6	89.3	1.8	5.6	29.2	66.3
Chinook salmon, yearling	23.3	16.4	5.2	2.7	39.3	22.9	21.5	4.6
Coho salmon	23.3	60.5	29.9	6.7	25.2	45.9	41.5	26.1
Sockeye salmon	0.0	0.0	1.0	1.3	0.0	0.8	1.5	0.0
Steelhead	48.5	15.1	9.3	0.0	33.7	24.8	6.2	3.0
n	103	152	97	75	163	244	65	28

Table 4.3. Mean fresh mass and energy content of prey types for Caspian terns (*Hydroprogne caspia*) nesting in the Columbia River estuary. Where significant differences were seen in average mass of prey types between colonies and years (see text for tests of significance), different values for mass were used for each colony-year consumption calculation and the range in annual mass and energy content values is given. A single value of energy density was used for each prey type for all colony-years, with sample size for proximate composition analysis indicated in parentheses. Energy density values for yearling and sub-yearling Chinook were not significantly different and were pooled.

Prey family	Species/type	Mass (g)	Energy density (*n*) (kJ/g)	Energy content (kJ/fish)
Salmonidae	Chinook, sub-yearling	7.7 – 16.8	3.98 (12)	30.6 – 66.9
	Chinook, yearling	32.5	3.98 (12)	129.4
	Coho	24.0 – 39.7	5.04 (12)	121.0 – 200.1
	Sockeye	19.3	4.83 (3)	93.2
	Steelhead	60.9	4.61 (12)	280.8
Engraulidae	Anchovy	11.2 – 27.2	5.37 (14)	60.1 – 146.1
Clupeidae	Herring	21.0 – 48.5	4.90 (10)	102.9 – 237.6
	Sardine	11.8 – 48.3	4.51 (10)	53.2 – 217.8
	Shad	30.0	5.61 (7)	168.3
Cyprinidae	Peamouth, N. Pikeminnow	40.1	5.66 (12)	227.0
Petromyzontidae	Lamprey	5.8	5.70 (6)	33.1
Pleuronectidae	Flounder	23.3	4.19 (12)	97.6
Ammodytidae	Sandlance	5.3	5.61 (6)	29.7
Cottidae	Sculpin	20.3	3.83 (12)	77.7
Osmeridae	Smelt	15.6 – 32.5	5.02 (12)	78.3 – 163.1
Gasterosteidae	Stickleback	1.4	3.62 (7)	5.0
Catostomidae	Sucker	62.5	4.45 (6)	278.1
Embioticidae	Surfperch	25.6	4.16 (13)	106.5
Gadidae	Cod	33.8	3.45 (13)	116.6
Pholidae	Gunnel	4.7	4.39 (1)	20.6

Table 4.4. Estimated number of prey consumed by Caspian terns (*Hydroprogne caspia*) nesting in the Columbia River estuary, 1997 – 2006. Numbers are mean estimates of prey consumed with 95% confidence intervals, in millions of fish.

	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
All Prey Items	10.6 (8.0-13.2)	15.5 (11.9-19.0)	20.9 (17.9-24.0)	13.5 (11.3-15.7)	17.1 (15.0-19.1)	18.1 (16.0-20.2)	16.6 (14.7-18.5)	23.1 (19.5-26.6)	17.3 (15.0-19.7)	20.6 (17.5-23.7)
All Salmonids	7.3 (5.5-9.1)	11.4 (8.8-14.0)	12.1 (10.1-14.1)	6.7 (5.6-7.7)	5.6 (4.9-6.3)	5.9 (5.2-6.5)	4.1 (3.6-4.6)	4.0 (3.4-4.6)	3.9 (3.4-4.4)	5.4 (4.6-6.1)
Sub-yearling Chinook	2.3 (1.7-3.0)	5.1 (3.9-6.4)	6.5 (5.4-7.6)	1.0 (0.8-1.2)	0.9 (0.7-1.0)	0.7 (0.6-0.8)	0.5 (0.4-0.6)	0.5 (0.4-0.6)	0.4 (0.3-0.4)	0.8 (0.6-0.9)
Yearling Chinook	0.9 (0.6-1.2)	1.1 (0.8-1.4)	1.3 (1.0-1.7)	1.6 (1.3-1.9)	1.4 (1.2-1.6)	1.3 (1.2-1.5)	1.5 (1.3-1.7)	0.8 (0.6-0.9)	1.2 (1.0-1.3)	1.6 (1.4-1.9)
Coho	3.0 (2.2-3.8)	3.9 (3.0-4.8)	2.9 (2.3-3.4)	2.6 (2.2-3.0)	2.2 (1.9-2.5)	2.6 (2.3-2.9)	1.3 (1.1-1.4)	1.3 (1.1-1.5)	1.2 (1.0-1.3)	1.9 (1.6-2.2)
Sockeye	0.04 (0.02-0.05)	0.08 (0.06-0.10)	0.10 (0.07-0.14)	0.05 (0.04-0.06)	0.05 (0.04-0.06)	0.03 (0.03-0.04)	0.05 (0.04-0.06)	0.07 (0.05-0.08)	0.02 (0.02-0.02)	0.03 (0.03-0.04)
Steelhead	1.0 (0.6-1.4)	1.3 (0.8-1.7)	1.3 (1.0-1.6)	1.4 (1.2-1.7)	1.1 (0.9-1.2)	1.2 (1.0-1.3)	0.8 (0.7-0.9)	1.3 (1.1-1.5)	1.2 (1.0-1.4)	1.0 (0.8-1.1)

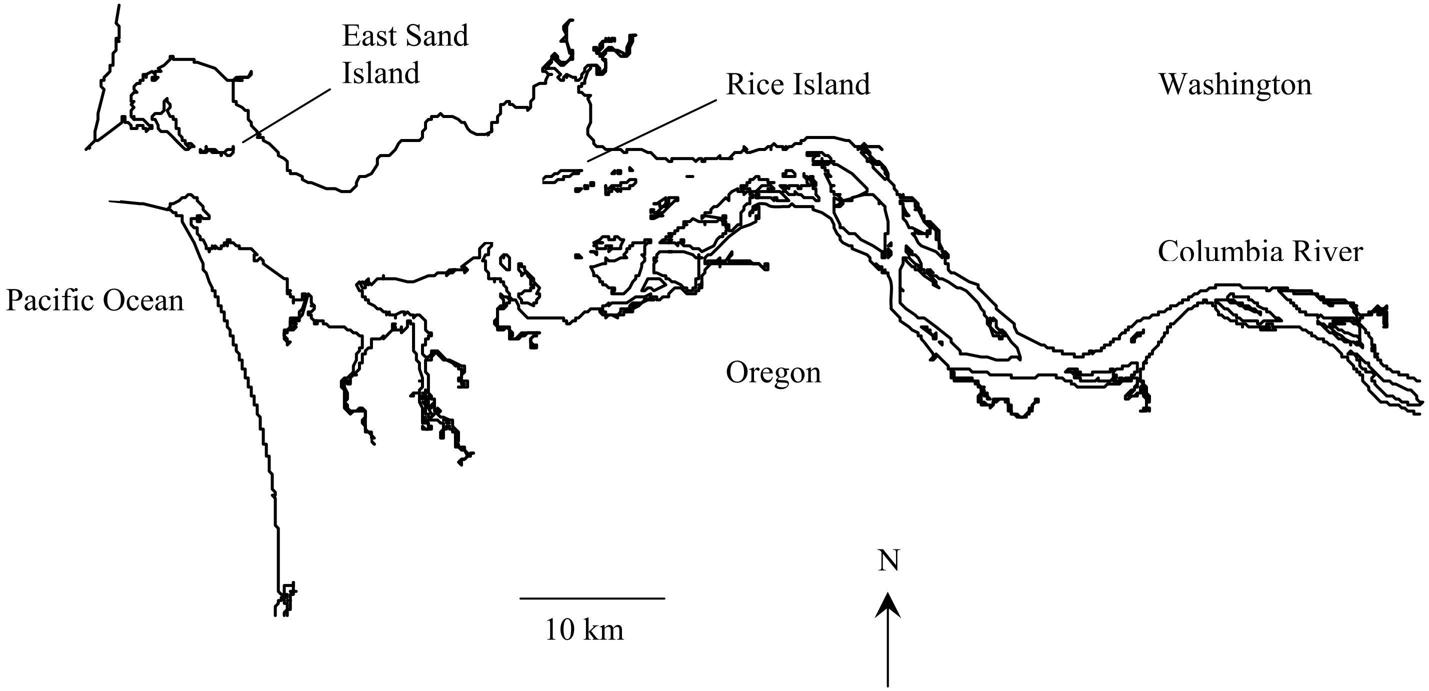


Figure 4.1. The Columbia River estuary. Caspian tern (*Hydroprogne caspia*) colonies existed on Rice Island (river km 34) during 1997-2000 and on East Sand Island (river km 8) during 1999-2006.

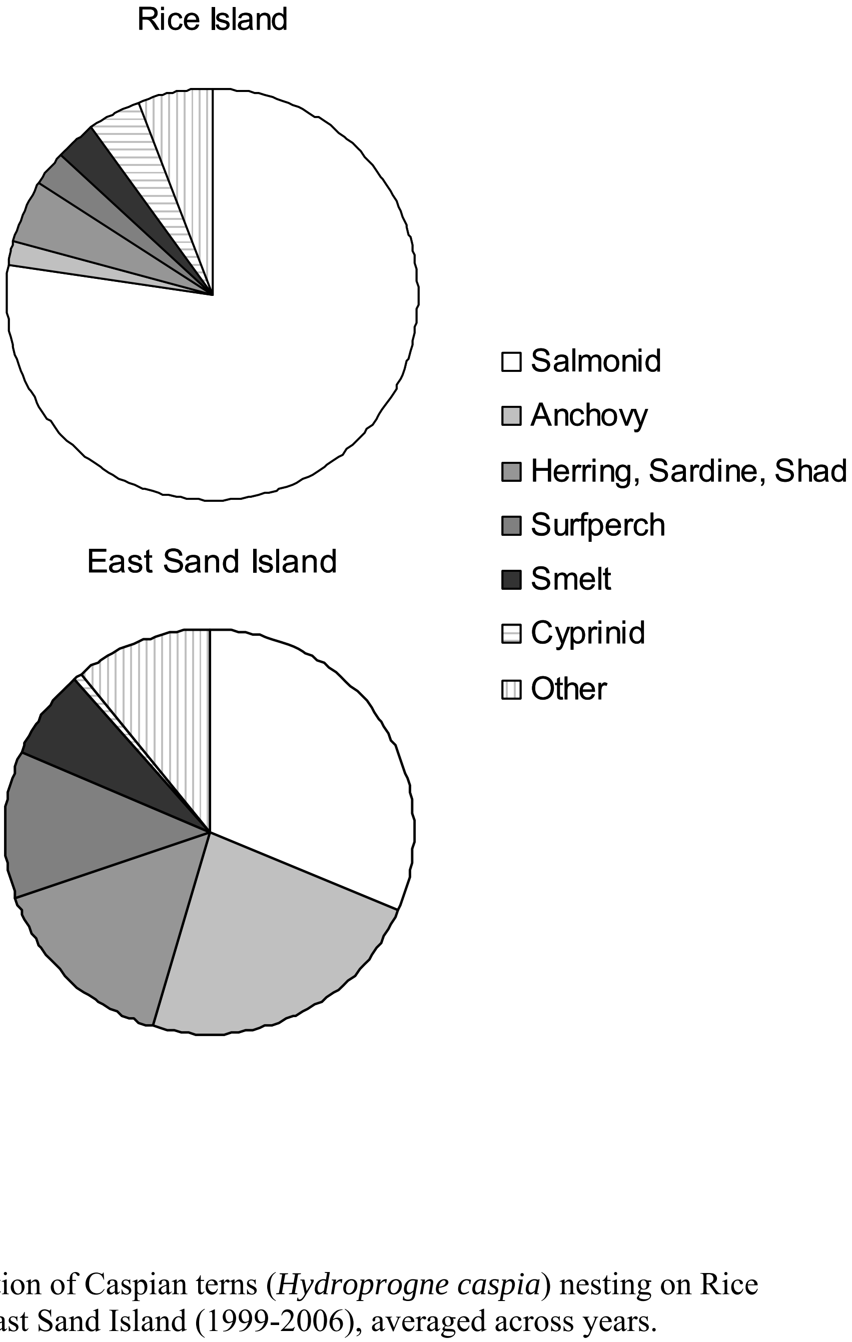


Figure 4.2. Diet composition of Caspian terns (*Hydroprogne caspia*) nesting on Rice Island (1997-2000) and East Sand Island (1999-2006), averaged across years.

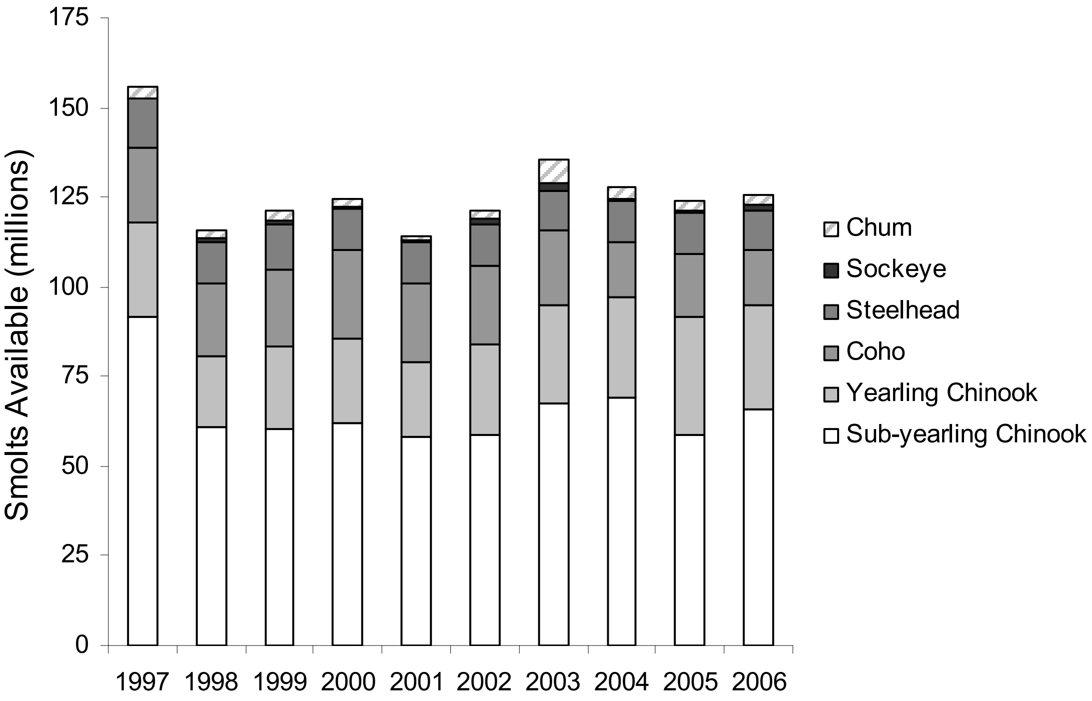


Figure 4.3. Estimated availability of juvenile salmonids (*Oncorhynchus* spp.) in the Columbia River estuary during 1997-2006. Estimates were derived in collaboration with D. Marsh, NOAA Fisheries, Seattle, WA.

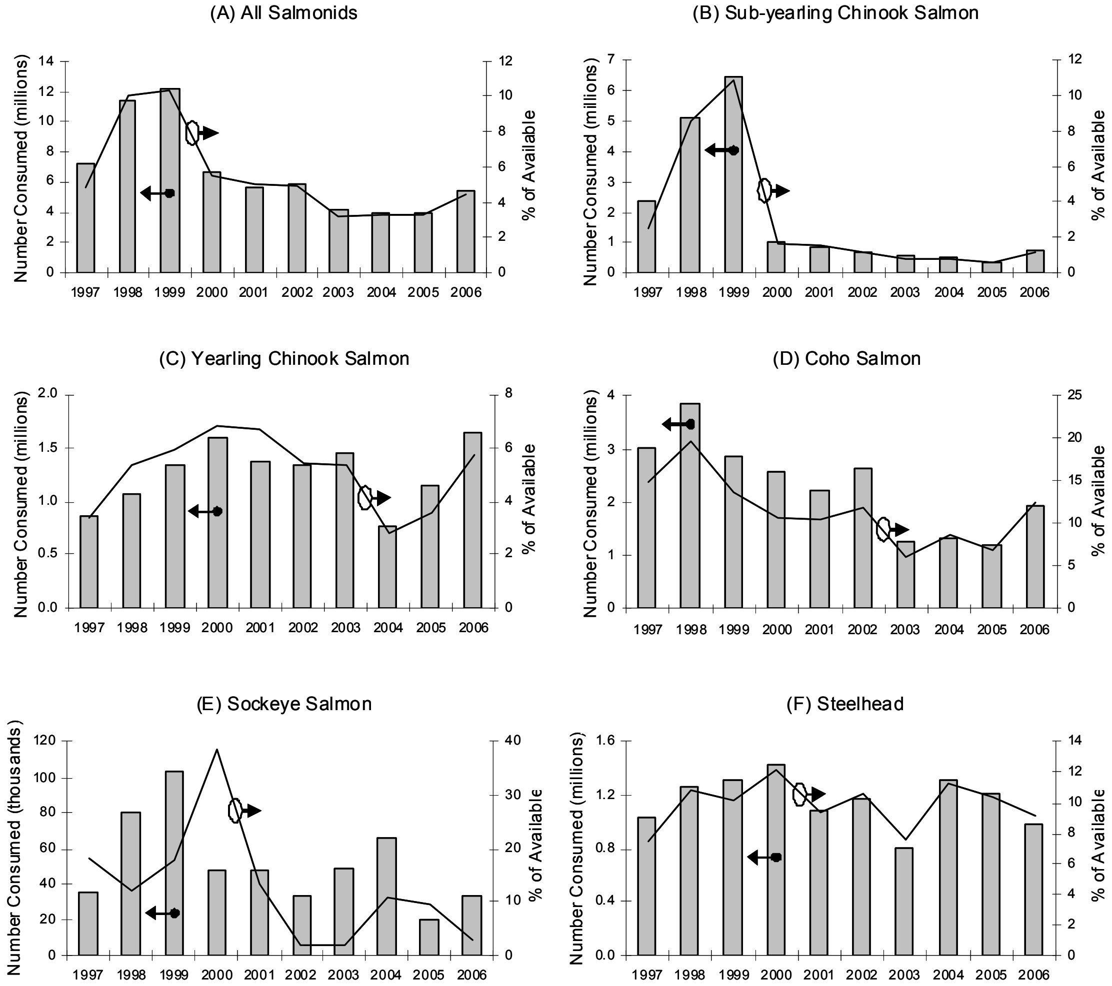


Figure 4.4. Estimated smolt consumption (bars, left axis) and proportion of available smolts taken (lines, right axis) by Caspian terns (*Hydroprogne caspia*) of (A) all juvenile salmonids (*Oncorhynchus* spp.), (B) sub-yearling Chinook salmon (*O. tshawytscha*), (C) yearling Chinook salmon, (D) coho salmon (*O. kisutch*), (E) sockeye salmon (*O. nerka*), and (F) steelhead (*O. mykiss*).

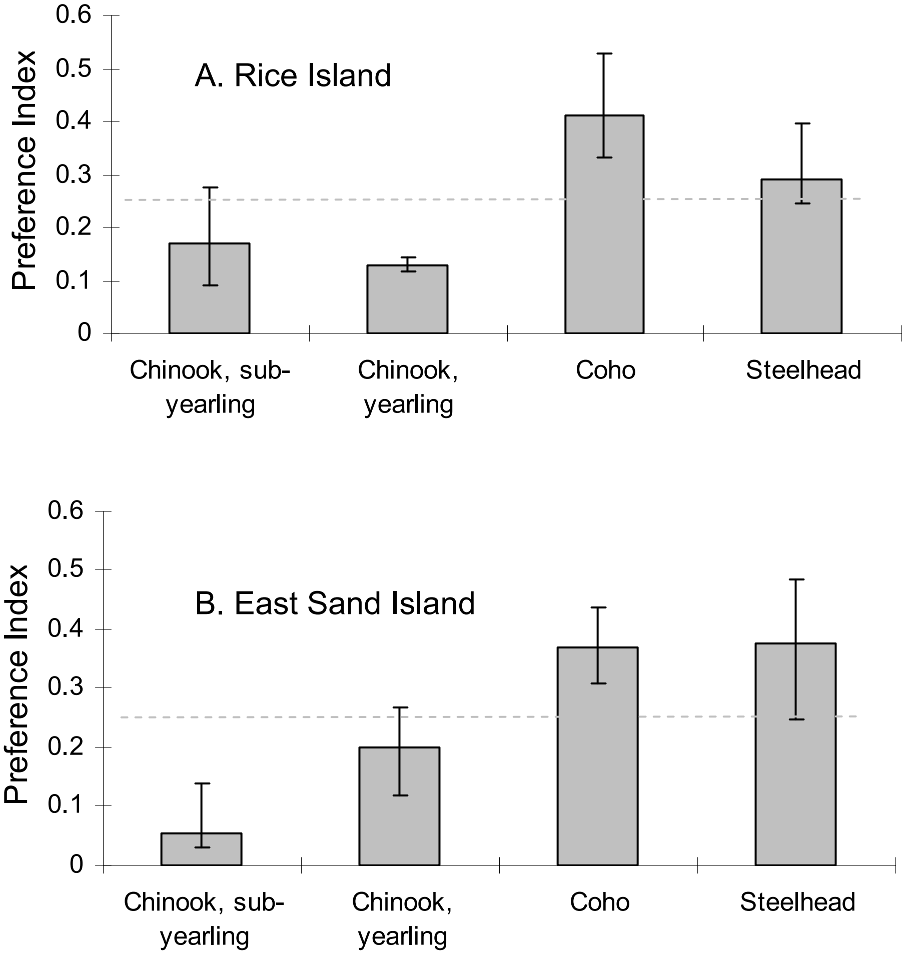


Figure 4.5. Manly – Chesson preference indices for juvenile salmonids (*Oncorhynchus* spp.) consumed by Caspian terns (*Hydroprogne caspia*) nesting on (A) Rice Island (1997-2000) and (B) East Sand Island (1999-2006). Bars indicate the mean across years for each island and whiskers represent the range in annual values. Values greater than 0.25 (1 / number of species) indicate preference; values below 0.25 indicate avoidance.

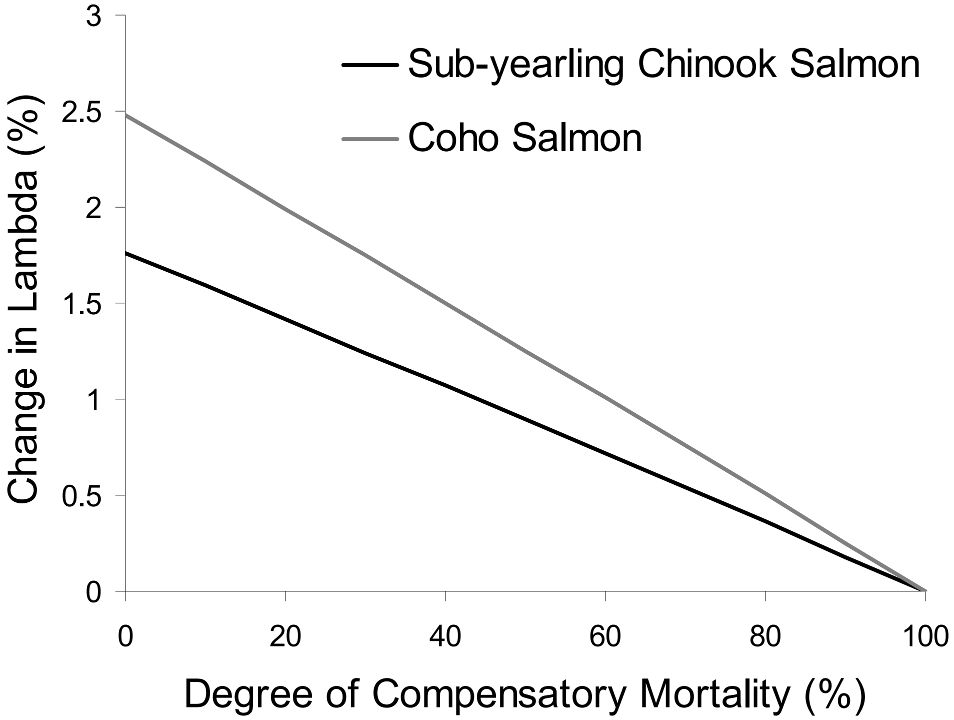
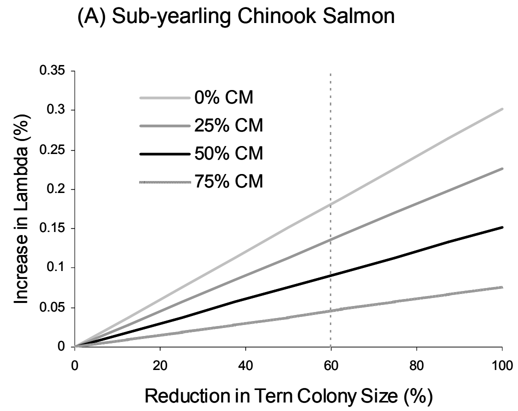
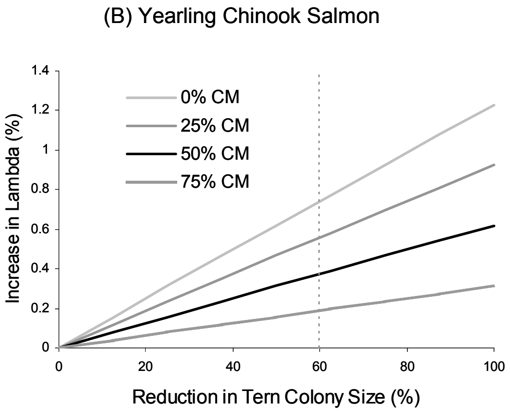
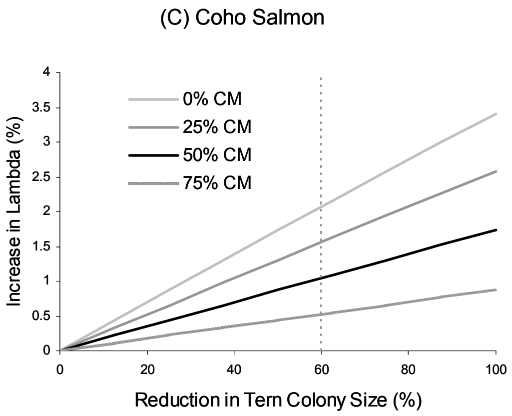


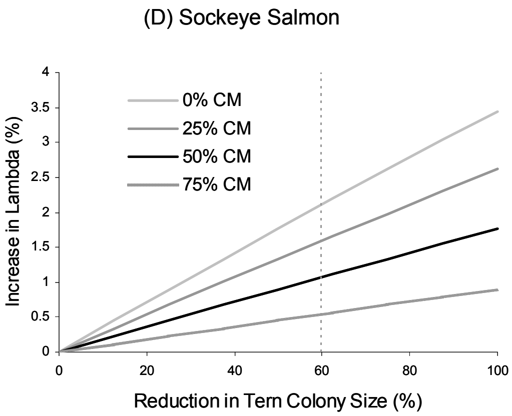
Figure 4.6. Increases in the average annual population growth rate (λ) of sub-yearling Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) corresponding to changes in survival during 1997-1999, when most or all Caspian terns (*Hydroprogne caspia*) nested at Rice Island, compared to 2000-2006, when most or all Caspian terns nested at East Sand Island. The degree of compensatory mortality for reductions in tern predation is unknown; hence, a range is presented.

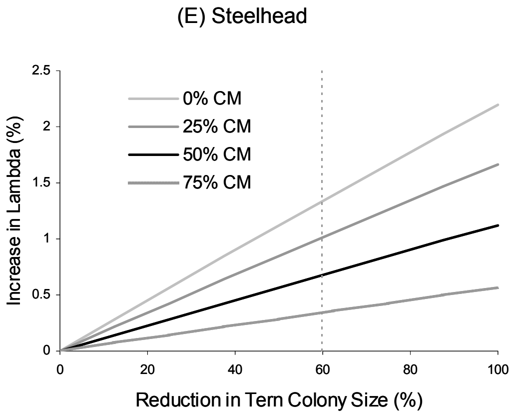
Figure 4.7. Required reductions in the size of the Caspian tern (*Hydroprogne caspia*) colony on East Sand Island in the Columbia River estuary in order to achieve potential increases in the average annual population growth rate (λ) of five species/types of Columbia River salmonids (*Oncorhynchus* spp.). For each species/type of salmonid, the separate lines represent four levels of potential compensatory mortality (CM) for reductions in tern predation (0%, 25%, 50%, and 75%). It is assumed that terns would not change their foraging behavior (i.e., diet composition) as a function of their own density. The vertical dashed line corresponds to a 60% reduction in the size of the tern colony, the proposed management target (USFWS 2005, 2006).


(A) Sub-yearling Chinook Salmon


(B) Yearling Chinook Salmon


(C) Coho Salmon


(D) Sockeye Salmon


(E) Steelhead

Chapter 5

DOUBLE-CRESTED CORMORANT PREDATION ON JUVENILE SALMONIDS IN THE COLUMBIA RIVER ESTUARY: IMPLICATIONS FOR THREATENED AND ENDANGERED SALMONID POPULATIONS

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ABSTRACT

Expanding predator populations are increasingly hypothesized to limit recovery of depleted populations of Pacific salmon (*Oncorhynchus* spp.) in the Pacific Northwest region of the U.S. and elsewhere. We utilized bioenergetic techniques to estimate consumption of juvenile salmonids by one such predator, double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary during 1998 – 2007. These results were used to estimate smolt mortality rates due to cormorant predation and potential improvements in population growth rates (λ) of salmonids if cormorant predation rates were reduced. Cormorants annually consumed from 2.4 million smolts (95% CI: 1.1 – 3.7 million) to 15.0 million smolts (95% CI: 8.0 – 22.0 million) during the decade-long study. Sub-yearling Chinook salmon (*O. tshawytscha*) was the most frequently consumed smolt species/type, followed by coho salmon (*O. kisutch*), steelhead (*O. mykiss*), yearling Chinook salmon, and sockeye salmon (*O. nerka*). A reduction in cormorant predation to 50% of 2006 – 2007 levels would be expected to achieve 0.3% increases in λ for sockeye and yearling and sub-yearling Chinook, a 1.0% increase for steelhead, and a 2.0% increase for coho, assuming that 50% of mortality due to cormorant predation is compensatory. Management to reduce cormorant predation would, by itself, be unlikely to shift any evolutionarily significant unit (ESU) of Columbia River salmonids to a state of recovery ($\lambda > 1$), and would be less beneficial than planned improvements in the Columbia River hydropower system for ESUs most negatively affected by the

hydropower system. Cormorant management in the Columbia River estuary could, however, provide modest benefits to salmonid ESUs throughout the basin, particularly for coho salmon and steelhead. The magnitude of these benefits would be dependent on (1) the nesting location and future population size of double-crested cormorants within the estuary, (2) river flows, ocean conditions, and other factors that influence the relative availability of alternative prey, (3) smolt condition and naïveté regarding predators, and (4) the degree to which smolt mortality from cormorant predation is additive.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) have suffered orders of magnitude decline from historical levels in the Pacific Northwest region of the United States (Lichatowich 1999). More than half of the identified evolutionarily significant units (ESUs) of salmonids that spawn in the region have been extirpated or listed as threatened or endangered under the U.S. Endangered Species Act (Good et al. 2005, Gustafson et al. 2007). Within the Columbia River basin, the largest basin in the region, 13 of 20 remaining ESUs are listed (Good et al. 2005). Anthropogenic limiting factors for wild salmonids have been grouped into four major categories: (1) excessive harvest; (2) degradation of freshwater spawning, rearing, and migratory habitat; (3) competition and maladaptive interbreeding with large numbers of hatchery-reared fish; and (4) direct and indirect mortality associated with fish passage through dams constructed for power generation, flood control, and irrigation purposes, including loss of habitat above dams constructed with no means of fish passage (Federal Caucus 2000). Variable climate conditions in the ocean environment are an increasingly recognized density-independent effect on salmonid populations as well (Pearcy 1992, Mantua et al. 1997, Hare and Mantua 2000), and potential negative impacts of long-term climate warming are an emergent concern (Mote et al. 2003, ISAB 2007).

Predation has long been studied as a potential regulating factor for prey populations (e.g., Errington 1967). Over the past three decades, many native and non-native predators of Columbia River salmonids have been investigated as potential constraints on salmon recovery. In the freshwater environment, native fish (i.e., northern pikeminnow [*Ptychocheilus oregonensis*]; Beamesderfer et al. 1990, Ward et al. 1995), exotic fishes (principally smallmouth bass [*Micropterus dolomieu*] and walleye [*Stizostedion vitreum*]; Rieman et al. 1991, Zimmerman 1999), and a variety of native bird species (gulls [*Larus* spp.], Caspian terns [*Hydroprogne caspia*], double-crested cormorants [*Phalacrocorax auritus*], common mergansers [*Mergus merganser*], and others; Ruggerone 1986, Collis et al. 2002, Roby et al. 2002, Roby et al. 2003, Ryan et al. 2003, Antolos et al. 2005, Good et al. 2007, Wiese et al. 2008) have been documented to prey on juvenile salmonids. In addition, pinnipeds (harbor seals [*Phoca vitulina*] and sea lions [*Zalophus californianus* and *Eumetopias jubatus*]; NMFS 1997, Laake et al. 2002) prey on both juveniles and adults. Similarly, in the marine environment numerous seabird (e.g., common murre [*Uria aalge*]; Matthews

1983), fish (e.g., Pacific hake [*Merluccius productus*] and jack mackerel [*Trachurus symmetricus*]; Emmett and Krutzikowsky 2008), pinniped, and cetacean (e.g., killer whales [*Orcinus orca*]; Ford and Ellis 2006) predators are also known to consume salmonids at various stages in their life histories.

Across much of North America, populations of double-crested cormorants have rebounded over the past several decades from levels suppressed by contaminant exposure and persecution (Krohn et al. 1995, Weseloh et al. 1995, Hatch and Weseloh 1999, Wires et al. 2001, Wires and Cuthbert 2006). Growing cormorant populations have frequently come into at least perceived conflict with aquaculture (e.g., Glahn and Brugger 1995, Mott and Boyd 1995, Price and Nickum 1995, USFWS 2003) or fisheries (e.g., Madenjian and Gabrey 1995, Rudstam et al. 2004, Diana et al. 2006, Seefelt and Gillingham 2008), including salmonid fisheries (Kennedy and Greer 1988, Krohn et al. 1995, Blackwell et al. 1997, Derby and Lovvorn 1997). Potential impacts of cormorants on aquaculture and fisheries contributed to the issuance of a Public Resource Depredation Order by the U.S. Fish and Wildlife Service, allowing local wildlife agencies in 24 states to lethally control cormorants to protect public resources (USFWS 2003).

Population levels of double-crested cormorants along the Pacific coast of North America have, however, been relatively stable over the last two decades, with the exception of the Columbia River estuary, where a nascent colony in 1989 (< 100 pairs) has grown by more than two orders of magnitude into one of the largest colonies in North America (> 10,000 pairs; Collis et al. 2002, Anderson et al. 2004, this study).

Initial studies of diet composition suggested that cormorants residing in the Columbia River estuary rely significantly on juvenile salmonids (Collis et al. 2001, Collis et al. 2002, Ryan et al. 2003). Additionally, substantial predation (millions of juveniles consumed annually) by another avian predator in the basin, Caspian terns, has been documented in the estuary and the mid-Columbia River (Roby et al. 2003, Antolos et al. 2005, Chapter 4).

When impacts of predation on salmonids have been found to be significant, management of predators in the Columbia River basin has been proposed or implemented based on the perceived anthropogenic destabilization of the predator-prey dynamic. These predators may benefit from the food subsidy of millions of predator-naïve, hatchery-reared smolts, as well as short-term or lingering physiological effects to smolts from passage through dams and slack water reservoirs (Schreck et al. 2006). One native, piscivorous fish, northern pikeminnow, has seen substantial population increases in the warmer, slackwater reservoirs behind mainstem dams (Beamesderfer et al. 1996). Consumption of juvenile salmonids by pikeminnow was inferred to be substantially higher than historical levels, and a reward fishery has been conducted since the early 1990s (Beamesderfer et al. 1990, Ward et al. 1995). An avian piscivore, the Caspian tern, has similarly benefited from the creation of preferred nesting habitat on dredged material disposal sites (sandy areas on islands isolated from mammalian predators). The managed relocation of a Caspian tern colony to reduce predation on juvenile salmonids has occurred (USACE 1999, 2000, Roby et al. 2002), and additional tern relocations are planned to further reduce impacts from this predator (USFWS 2005, 2006).

Our objectives in this study are to estimate consumption of juvenile salmonids by double-crested cormorants nesting in the Columbia River estuary over the 10-year period 1998 – 2007, and to put this into the context of salmonid life histories by estimating smolt mortality rates and the potential benefits to salmonid populations if cormorant predation was reduced. Additionally, we analyze a limited set of associated factors (river flow, smolt abundance) to potentially identify variables that may explain some of the annual variability in smolt consumption by cormorants.

METHODS

We estimated prey consumption by double-crested cormorants nesting in the Columbia River estuary on Rice and East Sand islands (Figure 5.1) from 1998 to 2007. Rice Island (river km 34) is a completely artificial island created by disposal of sand dredged from the shipping channel of the Columbia River. East Sand Island (river km 8) is a natural island but with extensive anthropogenic alterations, including rip-rap stabilization, occasional dredged material disposal, and historical construction activities (USACE 2000). At its position in the upper estuary, Rice Island is surrounded by primarily fresh water, whereas East Sand Island is surrounded by more brackish, marine waters. The fish communities present in close proximity (< 10 km) to each island reflect this salinity difference, with numerous marine forage fishes present near East Sand Island and largely absent near Rice Island (Bottom and Jones 1990, Hinton et al. 1995, Hinton and Emmett 2000).

All procedures and protocols involving double-crested cormorants were reviewed and approved by the Institutional Animal Care and Use Committee at Oregon State University. Scientific collection permits were obtained for all procedures involving handling or collection of cormorants from the U.S. Fish and Wildlife Service (Migratory Birds and Habitats, Region 1, Portland, OR), the U.S. Geological Survey (Bird Banding Lab, Patuxent, MD), and the Oregon Department of Fish and Wildlife (Salem, OR).

Prey Consumption Estimation

Prey consumption was estimated using a revision of bioenergetics techniques used in Roby et al. (2003) and Lyons et al. (Chapter 4) to estimate prey consumption by Caspian terns in this system. A brief overview of the technique and data organization is presented here, but the reader is referred to those works for additional detail. Data requirements for bioenergetics calculations fall into four categories: number of cormorants present (adults and chicks), cormorant diet composition (relative biomass of prey types), cormorant energy requirements (adults and chicks), and prey energy content (a combination of average prey mass and energy density for each prey type).

Data were collected on the abundance of cormorants across the breeding season for each colony in all years (generally late March until all cormorants had quit roosting at the colony in late summer or early fall), and diet composition data were collected from the latter half of April until the end of July. Adult energy expenditures were measured using the doubly-labeled water technique during chick-rearing (Chapter 3) and chick energy requirements were derived from published valued for cormorants and other birds. Prey energy densities were obtained from a parallel study on the bioenergetics of Caspian terns in the Columbia River estuary (Chapter 4), where energy densities were measured using proximate composition analysis (Reynolds and Kunz 2001). Prey mass data were obtained from whole fish captured by terns (Chapter 4) and, for larger prey types, from minimally digested samples removed from the stomachs of collected cormorants.

Estimates of prey consumption were calculated for discrete 2-week periods across the cormorant breeding season for each colony and year. Calculations were performed using a routine written in Visual Basic 6.0 (Microsoft Corporation, Redmond, WA). A Monte Carlo calculation technique was used to obtain confidence intervals for consumption estimates (Furness 1978). Each input parameter was assumed to be normally distributed with the measured (or assumed, where noted) mean and standard error (SE). Sampling errors in the input parameters were assumed to be uncorrelated. Calculations were performed 1000 times, with every run using independent, randomly drawn values for each of the input parameters. Calculations performed for each 2-week period were summed to get annual totals for each colony and year.

Cormorant colony size: The number of adults breeding at each colony during late incubation (usually the 4th week of May or 1st week of June) was precisely estimated using high-resolution aerial photographs (see Collis et al. 2002 for details). Counts of occupied nests in aerial photographs were interpreted as the peak number of breeding pairs for a given colony in a given year. Multiple counts of occupied nests by independent observers varied with a SE ≤ 3% of the mean count.

At times during the season other than late incubation, the numbers of adult cormorants associated with the colony were opportunistically estimated as a proportion of the late incubation colony size. Three different techniques were used to obtain proportional colony size, involving observations from either blinds within the colony or from boats just offshore of the island: (1) direct counts of all adults present, used during early and late periods each breeding season when ≲ 3,000 individuals were present; (2) the ratio of occupied colony area at a given time to the occupied area during late incubation, used during periods of colony formation and breakup but when ≳ 3,000 individuals were present; and (3) the ratio of active nests present in plots at a given time to the number of active nests present in those plots during late incubation, used during the incubation and early-chick rearing periods, when nest territories are defended and distinct. The variability of estimates (coefficient of variation) obtained using methods (1) and (2) were up to 20% between observers, where as method (3) varied up to 10%. The sample size of these opportunistically obtained estimates of proportional colony size varied across years (n = 12 – 53) and were used to categorize the seasonal attendance patterns for each year of the study for three distinct portions of the breeding season. Colony size during arrival and colony establishment (period 1; 27 March – 21 May) was classified as either early or late; colony size during late incubation and early chick-rearing (period 2; 22 May – 2 July) was classified as either sustained or peaked; and colony size during late chick-rearing and post-fledging (period 3; 3 July – 5 November) was classified as either early departure, normal departure, or a protracted stay. The uncertainty in colony size was set to the variability in estimation seen in the predominant estimation method for a given period (either 20% or 10%, as above). In a few cases (1998-1999, 2002-2003), when the sample size of observations was ≤ 5 for a given period, the uncertainty in colony size was assumed to be 10 percentage points higher (either 30% or 20%, depending on measurement method).

During the post-fledging period at each colony it became difficult to distinguish between adults and juveniles when observing from any distance (i.e. > 50 m). At these times, we developed ratios of juveniles to adults from areas we could observe well enough to distinguish, and applied these ratios to our estimates of all cormorants present to determine the numbers of adults and juveniles present.

Small numbers of cormorants nested elsewhere in the Columbia River estuary during our study: on navigational markers (all years), pilings on Desdemona Sands (2000), the Astoria – Megler Bridge (beginning in 2004), and upper estuary islands (including small colonies at Rice Island in 2001 – 2003 and again in 2006 and at Miller Sands Spit in 2006 - 2007). In all years these nesting efforts consisted of < 5% of the number of cormorants nesting on East Sand Island or, for 1998, East Sand and

Rice islands combined. Because we lacked diet information for birds nesting at these smaller colonies and given they were a small portion of the estuary population (< 5%), we did not include them in our analysis.

We also had little information regarding the number of non-breeding cormorants present in the Columbia River estuary during the breeding season or their diet, so none are included in our analysis. Our estimate of the peak numbers of cormorants breeding during late incubation does not include any birds present, but not breeding at that time; however, we did not see significant nest initiation (> 5% of late incubation nest count) in any year following aerial photography during late incubation. Our estimates of cormorants present at the breeding colonies prior to the incubation period and following early chick-rearing include all cormorants present on the nesting islands, and so would include any birds that had not yet initiated nesting or that had completed or aborted their nesting attempt, but were using the nesting island as a roost site.

The number of cormorant chicks present at the colony was estimated using observations of focal nests at representative plots within the colony. For focal nests we determined the number of chicks hatched and estimated productivity (number of chicks per nesting attempt) at 28 days post-hatch (after 28 days chicks frequently left their nests, making it difficult or impossible to obtain per-nest productivity). For the purposes of consumption calculations, the colony was considered to be completely synchronous, with all chicks hatching on the same day (5 June) and, for those chicks surviving, becoming completely independent from parents eight weeks later. We estimated the total number of chicks surviving on each day of the chick-rearing period by fitting a negative logarithmic function to the average initial number hatching per nest (multiplied by the late incubation nest count) and the day 28 productivity measure (again multiplied by the late incubation nest count), and extrapolating this function onward to day 56 for the latter half of the chick-rearing period. This function matched our observations that most chick mortality occurred early in the chick rearing period, as seen by others (e.g., Leger and McNeil 1987). After day 56, estimates of the number of juvenile cormorants still present were determined as part of the adult census process outlined above.

Cormorant diet composition: Cormorant diet data were obtained from stomach contents of cormorants collected during the breeding season (late April until the end of July, ca.10 individuals per week) at each colony in each year (see Collis et al. 2002 for additional information on diet methodology). Diet composition, in percent biomass, was taken from the identification to prey family (or genus and species, when possible) of all undigested soft tissue present in the fore-gut. Stomachs lacking any soft tissue (but possibly containing bones), and portions of gastro-intestinal tracts lacking any undigested soft tissue (e.g., bones in intestines), were excluded from the quantitative diet composition analysis. Soft tissue was identified to family using external features when possible or, when necessary, once artificially digested to reveal diagnostic bones. Unidentifiable soft tissue lacking diagnostic bones was excluded from analysis. For calculations, diet composition data were pooled over 4-week periods within each year (4/10 – 5/7, 5/8 – 6/4, 6/5 – 7/2, and 7/3 – 7/30), with the sampling unit being each individual fore-gut sample.

Salmonids (Chinook [*Oncorhynchus tshawytscha*], coho [*O. kisutch*], chum [*O. keta*], and sockeye salmon [*O. nerka*]; steelhead [*O. mykiss*] and cutthroat [*O. clarki clarki*] trout) in the cormorant diet were identified to species using morphology of external soft tissue morphology when possible or, more frequently, using genetic techniques. Selected soft tissue samples identifiable as salmonids from collections during 1998 – 2005 were identified to species by T. Robinson, Oregon State University, using PCR-based genetic techniques developed by Greig et al. (2002). Beginning with samples from the 2006 breeding season, salmonids in fore-gut samples were identified to species using PCR amplified genetic material (extracted from intact soft tissue or bone) in the lab of D.R.K. following procedures outlined in Purcell et al. (2004). Salmonids identified as Chinook salmon up through 2005 were classified as either yearling or sub-yearlings, depending on the date of sample collection: Chinook found in the diet of cormorants prior to 5 June were presumed to be yearlings; Chinook collected after 5 June were presumed to be sub-yearlings. For Chinook samples collected in 2006 – 2007, it was possible to identify stock of origin, using the Columbia River Basin portion of the Chinook salmon microsatellite DNA baseline (after Seeb et al. 2007), and also including data for additional baseline populations in the lower Columbia and Willamette rivers. Yearling or sub-yearling classification of those Chinook smolts was inferred from the adult run timing of the identified stock. For diet composition analysis and prey consumption calculations, salmonids identified to species were grouped into 4-week periods across the season (as above) and, due to small sample sizes for most years, within those periods were pooled across all years and colonies of the study.

Daily Energy Consumption: To estimate adult energy requirements during the chick-rearing period we used values of daily energy expenditure measured using the doubly-labeled water technique (Chapter 3). Because chick-rearing is usually the most energetically demanding period within the breeding season for cormorants (e.g., Gremillet et al. 1995), energy demands during pre-laying, incubation, and the post-breeding period were scaled from the measured value during chick-rearing using a process modeled after the work of Gremillet and colleagues for great cormorants (*Phalacrocorax carbo carbo*) in Normandy (Gremillet et al. 2000, Gremillet et al. 2003). Scaling factors were derived by combining time-activity budgets (portion of time spent resting/roosting, incubating/brooding, in flight, or foraging/swimming) from cormorants in the Columbia River estuary (D.E.L. unpublished data) with estimated relative energy expenditures of each activity (after Gremillet et al. 2000), and comparing between the periods of pre-laying, incubation, chick-rearing, and post-breeding.

Energy or food requirements of captive or semi-captive double-crested cormorant chicks have been measured on at least two occasions (Dunn 1975, Cummings 1987); however, both studies were conducted on populations whose adult body mass and chick mass at fledging were lower than those observed in the Columbia River estuary. We instead used allometric predictions of total metabolizable energy requirements from hatching to fledging (Weathers 1992) and partitioned this total energy requirement into daily metabolizable energy requirements using the trend in daily requirements observed by Dunn (1975) for double-creseted cormorants. We assumed a fledgling mass of 2150 g, approximately 5% lower than the observed average adult mass of 2275 g, consistent with observations elsewhere (Dunn 1975, Leger and McNeil 1987), and a fledging age of 46 days post-hatch (Dunn 1975, Leger and McNeil 1987, Hatch and Weseloh 1999). Juvenile cormorants were assumed to be fed by adults following fledging (capability of flight) at 46 days until day 56, Energy requirements were assumed equal from day 46 through day 56, after which juveniles were considered to be completely self sufficient and undertaking the necessary flight and foraging activity to provision themselves. At this point, their energy requirements were assumed to be equal to post-breeding adults, less 5% for the lower body mass presumably maintained for some time following fledging (Hatch and Weseloh 1999). Adult energy expenditure rates were lowered from levels during chick-rearing to post-breeding levels (determined as above) at 56 days post-hatch.

Assimilation efficiency (AE) or the true metabolizable energy coefficient (MEC; Miller and Reinecke 1984), which considers endogenous energy losses, have been measured on multiple occasions for double-crested cormorants consuming a variety of fish: chicks fed pollock (*Pollachius virens*, AE = 79.9 - 88.1%; Dunn 1975), yearlings consuming Atlantic herring (*Clupea harengus*, AE = 72.9%; Cummings 1987), and adults consuming channel catfish (*Ictalurus punctatus*, MEC = 79%), gizzard shad (*Dorosoma cepedianum*, MEC = 78%), and bluegill (*Lepomis* *macrochirus*, MEC = 75%; Brugger 1993). Consistent with comprehensive reviews of assimilation efficiency in seabirds consuming fish (Castro et al. 1989; Karasov 1990), we used a value of 77.3% (standard error = 2.5%) for the metabolizable energy coefficient, equal to the average MEC measured on adults feeding on different prey after Brugger (1993). Daily energy consumption was calculated as daily energy expenditure divided by the metabolizable energy coefficient (expressed as a proportion).

Prey energy content: Prey energy densities and some prey mass data were obtained from a parallel study on the bioenergetics of Caspian terns in the Columbia River estuary (Chapter 4), where energy densities were measured using proximate composition analysis (Reynolds and Kunz 2001) and mass data were obtained from whole fish captured by terns. Distinct energy densities were obtained for each prey type (to the taxonomic resolution of our identification, as outlined above), and were assumed constant across season, year, and colony. Similarly, distinct masses of the various individual prey types were obtained and assumed constant across season and colony, but were varied across years as data were available and significant differences were observed using Kruskal-Wallace one-way ANOVA on ranks. Masses of prey types where there was evidence that cormorants sometimes consumed much larger individuals than terns did, or were even capable of handling (i.e., peamouth [*Mylocheilus caurinus*], sculpin [Cottidae], flounder [Pleuronectidae], Pacific herring [*Clupea pallasi*], and suckers [Catostomidae]), were taken instead from minimally digested specimens removed from the stomachs of collected cormorants.

Sensitivity Analysis: We investigated the sensitivity of the bioenergetics model structure (for 2007 only) to variability in the input parameters by perturbing nominal values of particular input parameters 10% and calculating the elasticity in the number of salmonids consumed (Caswell 2001). To assess the relative contributions of the observed variability in input parameters to the uncertainty in the output, linear multiple regression was performed (again, for 2007 only), with number of salmonids consumed as the dependent variable using all 1000 simulation runs (Swartzman and Kaluzny 1987). To indicate which input variables contributed most 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 other parameters. This allows an assessment of which parameters, in this model structure, contributed 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).

Predation Rate Estimation

Numbers of smolts reaching the estuary and potentially subject to cormorant predation were estimated using a process developed in collaboration with D. Marsh, NOAA Fisheries, Seattle, WA. The details of these estimates are provided elsewhere (Chapter 4) and the reader is referred there for more details. In brief, the numbers of smolts available were calculated to be a sum of (1) hatchery smolt production below Bonneville Dam (the lowest mainstem dam in the Columbia Basin), (2) estimated wild smolt production below Bonneville Dam, (3) hatchery and wild smolts produced above Bonneville Dam, captured at an up-river dam, transported in a barge or truck, and released just below Bonneville Dam, and (4) hatchery and wild smolts produced above Bonneville Dam and allowed to migrate in-river down through Bonneville Dam. Few if any data exist to evaluate any differential mortality of these groups from their points of enumeration (Bonneville Dam or downstream rearing/release locations) to the upper estuary (ca. river km 75). Consequently, all four groups of smolts were assumed to experience negligible mortality through this river reach. This is consistent with at least one study where relatively high survival was observed through this stretch of river for radio-tagged smolts released just below Bonneville Dam (Schreck et al. 2006).

Predation rates were calculated for each species/type as the estimated number of smolts consumed, divided by estimated number of smolts that reached the estuary, and expressed as a percentage. Rates were estimated for each of the 1000 Monte Carlo estimates of prey consumption, with the availability of each salmonid species/type drawn from a normal distribution with mean as estimated above and SE assumed to be 20% of the mean.

Use of the various salmonid species/types by cormorants versus availability (abundance in estuary) of each salmonid type was investigated by calculating Manly – Chesson preference index values (Chesson 1978, Manly et al. 1993):

$$P_i = \frac{d_i / N_i}{\sum_{j=1}^{k} (d_j / N_j)},$$

where d_i is the proportion of prey (salmonid) species/type i in the diet, N_i is the proportion of prey type i in the environment (proportion of all smolts that arrive in the estuary that are of species/type i), k is the number of species/types considered, and P_i is the calculated preference index value for species/type i. Sockeye were omitted from this analysis due to methodological limitations in some years (consumption estimates based on small samples, availability estimates constrained by few data). Preference for a given prey type is indicated when the index value is greater than 1 / k or, in this case, 1 / 4 = 0.25.

Explanatory Factors Analysis

The possible effects of river flow on cormorant predation were investigated using single-variable correlations between estimated consumption and flows measured at the Beaver Army Terminal near Quincy, Oregon (Rkm 86; U.S. Geological Survey, Water Resource Data site number 14246900, data available at waterdata.usgs.gov; accessed 30 June 2007). Annual explanatory variables investigated were May flows (corresponding to peak out-migration period for yearling Chinook, coho, and steelhead), July flows (corresponding to peak arrival of sub-yearling Chinook to the estuary), and average flows across April to July (representing the cormorant nesting season). Responses examined were the numbers consumed of each species/type of juvenile salmonid, along with all salmonid species/types together, and proportion of available smolts taken for each species/type separately and taken together.

Similarly, the potential effect of juvenile salmonid availability was assessed using correlations between estimated numbers arriving in the estuary and estimated numbers consumed by cormorants.

Demographic Model Analysis

The potential benefit to salmonid populations from a reduction in cormorant predation was assessed by estimating the change in the average annual population growth rate (λ) using the analytical framework of a simple deterministic, age-structured, matrix population growth model (Kareiva et al. 2000, McClure et al. 2000, Caswell 2001, McClure et al. 2003, Roby et al. 2003, Good et al. 2007, Chapter 4). The percent change in λ attributable to an increase in survival at a particular life history stage can be calculated (McClure et al. 2000, Caswell 2001) as a function of the initial survival rate (S_i), the survival rate following the change (S_f), and the average generational time (G, in years):

$$\Delta\lambda = [(\frac{S_f}{S_i})^{1/G} - 1] \cdot 100\%.$$

This change in λ has been used to compare the efficacy of various actual and potential management actions intended to help recover Columbia River salmonid populations (McClure et al. 2003, Roby et al. 2003, Good et al. 2007, Chapter 4). Important assumptions of this approach are that increases in survival at a particular life-history stage are density-independent and independent of changes in survival elsewhere in the life history.

Mortality due to particular predators may be additive or, if reduced, may be compensated for by other mortality factors (e.g., other predators) later in the prey species' life history (Errington 1967). It is unknown to what degree reductions in cormorant predation may be compensated for by other predators, such as other piscivorous birds, mammals, or fish (or other mortality factors, e.g., competition). If mortality due to cormorant predation is to some degree compensatory, then changes in λ calculated as above would be overestimated. To understand the effects of potential levels of compensation, changes in λ were calculated for a range of compensation by reducing the improvement in survival used to estimate Δλ (Roby et al. 2003):

$$\frac{S_f}{S_i} = \frac{(100 - \%\ \text{Compensation})}{100} \cdot \frac{S_{f_{\text{cormorants}}}}{S_{i_{\text{cormorants}}}},$$

where $S_{i_{\text{cormorants}}}$ and $S_{f_{\text{cormorants}}}$ are initial and final survival of cormorant predation (i.e., 1 - predation rate). The case of 100% compensation results in no actual improvement in survival or λ. In these analyses, we used the estimated smolt mortality due to cormorant predation in 2006 – 2007 (averaged across years for each species/type) to calculate initial survival, so as to represent recent trends in consumption (i.e., reflect the current colony size and diet composition).

RESULTS

The number of double-crested cormorants nesting on Rice and East Sand islands in the Columbia River estuary roughly doubled during the course of this study, from an estimated 7,080 breeding pairs in 1998 (95% CI: 6,695 – 7,463) to 13,771 pairs in 2007 (95% CI: 12,945 – 14,597; Table 5.1). Cormorants typically began arriving at nesting sites in early to mid-April and the last birds departed anywhere between early September and early November, depending on year. Productivity (measured at 28 days post-hatch) varied greatly over the course of the study, from a low of 0.55 fledglings/breeding pair (95% CI: 0.40 – 0.70) at Rice Island in 1998 to a high of 2.78 (95% CI: 2.66 – 2.90) at East Sand Island in 2007 (Table 5.1).

Cormorant diets were diverse, consisting of fishes from at least 14 families and also occasionally including invertebrates (shrimp). At Rice Island in 1998, salmonids constituted about half of the cormorant diet (Table 5.1, Figure 5.2). Salmonids were less prevalent in the diet of cormorants nesting at East Sand Island, but were still the most abundant prey type during 1998 – 2000. During 2001 – 2007 northern anchovy (*Engraulis mordax*) replaced salmonids as the most prevalent prey type. Other important prey for cormorants nesting at East Sand Island included clupeids (Pacific herring, Pacific sardine [*Sardinops sagax*], and American shad [*Alosa sapidissima*]), flounder, and sculpins (Figure 5.2).

The salmonid species breakdown in cormorant diets differed across the season, with coho salmon and steelhead more prevalent in April and May and sub-yearling Chinook salmon dominant in June and July (Table 5.2). Passive integrated transponder (PIT) tags implanted in sea-run cutthroat trout have been recovered on the East Sand Island cormorant colony (A.F.E. and S. Sebring, Pacific States Marine Fisheries Commission, Hammond, OR; unpublished data), revealing that cormorants consume this salmonid species as well. Only two fish in cormorant stomach contents were identified as cutthroat trout in this study, so consumption of this species is likely much less than for other salmonids; consequently, we did not distinguish cutthroat from steelhead in our calculations. Despite a small spawning population in the lower Columbia River, no chum salmon were observed in diet samples, so this salmonid was excluded from our calculations.

Significant differences across years in mean fresh mass of individuals were indicated for several prey types: sub-yearling Chinook, coho, anchovy, clupeids, and smelt (Table 5.3). Energy density of the various prey types varied from 3.45 kJ/g (95% CI: 3.27 – 3.63) for Pacific tomcod (*Microgadus proximus*) to 5.70 kJ/g (95% CI: 5.33 – 6.07) for lamprey (*Lampetra* spp.). The resulting average energy content per prey item ranged from 5.0 kJ/fish (95% CI: 3.63 – 6.34) for threespine stickleback (*Gasterosteus aculeatus*) to 840 kJ/fish (95% CI: 583 – 1021) for suckers.

Daily energy expenditure (DEE) of adult double-crested cormorants measured with the doubly-labeled water technique averaged 3,423 kJ/day (SD = 689.7, n = 10) and ranged from 2,653 to 4,606 kJ/day (Chapter 3). Estimated energy expenditure rates during pre-laying and incubation (2,944 kJ/day; 86% of value during chick-rearing) and during post-fledging (2,702 kJ/day; 79% of the chick-rearing value) reflected lower demands on adults when they were not provisioning young.

The total metabolizable energy requirement (TMER) of individual chicks (from hatching to fledging) derived using allometric equations (Weathers 1992) was 69.6 MJ (fledging mass = 2,150 g, fledging age = 46 days), 44% of the cumulative requirements for an individual adult over the same time period (3,423 kJ/day over 46 days). The daily metabolizable energy requirements increased from 66 kJ chick^{-1} day^{-1} on the first day post-hatch to 2,298 kJ chick^{-1} day^{-1} at the time of peak energy demand (day 28) and decreased to 1,952 kJ chick^{-1} day^{-1} at fledging. The maximum daily energy requirement for chicks was 67% of adult DEE, consistent with typical measured values for other seabirds (Visser 2001). Once chicks were self sufficient (after day 56), their metabolizable energy requirements were estimated at 2,567 kJ/day.

Estimated prey consumption by double-crested cormorants nesting in the Columbia River estuary ranged from 70.8 million fish (95% CI: 30.3 – 119 million) in 1999 to 449 million fish (95% CI: 123 – 774 million) in 2006 (Table 5.4). Estimated consumption of juvenile salmonids ranged from 2.4 million smolts (95% CI: 1.1 – 3.7 million) in 2005 to 15 million (95% CI: 8 – 22 million) in 1998 (Table 5.4; Figure 5.3). Sub-yearling Chinook salmon was the most frequently consumed smolt species/type when years were pooled, followed by coho salmon, steelhead, yearling Chinook salmon, and sockeye salmon.

Elasticity analysis of the bioenergetics model structure revealed that, for comparable percentage variation (+/- 10% of nominal value), changes in diet composition (% of diet that was salmonids), seasonal colony attendance pattern, peak numbers of breeding pairs, adult daily energy expenditure, and the metabolizable energy coefficient would produce the greatest changes in the estimated salmonid consumption by cormorants (Table 5.5). Regression analysis using relative partial sum of squares, incorporating both model structure and actual measured variability in input parameters, indicated that the uncertainty in (1) the seasonal colony attendance pattern of cormorants in the estuary and (2) in the proportion of the diet that was salmonids contributed more to the uncertainty in the estimated number of salmonids consumed than did uncertainty in other input variables (Figure 5.4). Other major contributing factors to output uncertainty were the total metabolizable energy requirement of chicks, the energy density of non-salmonid prey types, and the average mass of salmonid prey species/types.

The proportion of all available smolts in the estuary that were taken by cormorants was greatest in 1998 and 1999, but was highest for spring migrating smolts (yearling Chinook, coho, and steelhead) in 2006 and 2007 (Figure 5.3). The proportion of sub-yearling Chinook consumed by cormorants, which was high in 1998 and 1999, declined in 2000 and remained low subsequently. Sub-yearling Chinook, coho, and steelhead had the highest average annual mortality rates due to cormorant predation (7.6 – 8.0%) and yearling Chinook the lowest (2.9%). In all years at East Sand Island and in 1998 at Rice Island, yearling Chinook were taken in lower proportion to their relative availability (Figure 5.5). Sub-yearling Chinook, coho, and steelhead were sometimes, but not consistently, taken in somewhat greater proportion to their availability. Correlations between availability and consumption of smolts of all species/types were non-significant over the 10 years of this study (all P values $\geq$ 0.19).

Correlations suggested a positive relationship between average annual river flow in May and the absolute number of spring migrating smolts (yearling Chinook, coho, sockeye, and steelhead) consumed by cormorants ($P = 0.05 – 0.06$, $R^2 = 0.37 – 0.39$). No relationship between cormorant consumption of sub-yearling Chinook and river flows during any period was indicated ($P > 0.27$). Correlations between May flows and the proportion of smolts taken by cormorants were weaker but still suggestive for yearling Chinook, coho, and steelhead ($P = 0.09 – 0.10$). All other relationships between flow and cormorant consumption variables were non-significant ($P \geq 0.10$).

Potential improvements to salmonid population growth rates (λ) from eliminating some or all cormorant predation in the estuary varied significantly by salmonid species. The maximum potential improvement in λ, assuming no compensatory mortality whatsoever and complete elimination of cormorant predation in the estuary, ranged from 1.2 – 1.3% for sockeye and yearling and sub-yearling Chinook to 3.9% for steelhead and 7.7% for coho (Figure 5.6). The potential improvement in λ, assuming complete elimination of cormorant predation and compensatory mortality of 50%, ranged from 0.6 – 0.7% for sockeye and yearling and sub-yearling Chinook to 2.0% for steelhead and 4.0% for coho. Fifty percent reductions in cormorant predation, and assuming 50% compensatory mortality, might achieve increases in λ ranging from 0.3% for sockeye and yearling and sub-yearling Chinook to 1.0% for steelhead and 2.0% for coho.

DISCUSSION

Double-crested cormorants consumed millions of juvenile salmonids annually in the Columbia River estuary, corresponding to a 3 – 8% smolt mortality rate, depending on salmonid species/type, averaged across all the years of this study. These mortality rates are comparable to those induced by other major predators of juvenile salmonids, including northern pikeminnows (Ward et al. 1995, Beamesderfer et al. 1996) and Caspian terns (Roby et al. 2003, Chapter 4). Our estimates of cormorant predation, combined with those by Caspian terns, which also nest in the estuary, indicate that 6 – 26 million smolts per year (5 – 23% of those available) may have fallen victim to avian predators during the period 1998 – 2007. This combined avian predation in the estuary may be the single greatest source of mortality for Columbia Basin salmonids during their out-migration to the ocean during some years; although other factors replicated within the basin (e.g., mainstem hydropower dams) presumably cause greater cumulative smolt mortality (Kareiva et al. 2000, McClure et al. 2003, Welch et al. 2008).

In 1998, the only year of this study when a large colony of cormorants existed at both Rice Island, in the upper estuary, as well as at East Sand Island in the lower estuary, we saw significantly higher per capita smolt consumption by cormorants nesting at Rice Island (2900 smolts consumed per breeding pair at Rice Island vs. ca. 2000 smolts per pair at East Sand Island). In the years since, comparisons of PIT tag recoveries between East Sand Island and small cormorant nesting colonies in the upper estuary (e.g., Miller Sands Spit) have consistently indicated greater per capita smolt consumption by cormorants nesting in the upper estuary (A.F.E., unpublished data). Presumably, this difference is due to greater exposure of cormorants nesting in the lower estuary to alternative prey of marine origin, such as anchovy and clupeids.

Over the entire 10-year study period, sub-yearling Chinook salmon was the salmonid most frequently consumed by cormorants, although similar proportions of available coho salmon and steelhead were taken compared to sub-yearling Chinook. While sub-yearling Chinook had a lower energy content than most other prey, they typically reside in the estuary for an extended period (weeks or months; Bottom et al. 2005) and thus have a significantly longer exposure to cormorant predation than other salmonid species/types. We saw the highest estimated annual consumption of spring migrants (steelhead, coho, and yearling Chinook) during 2006 – 2007. This increase in consumption of spring migrants reflected a greater incorporation of salmonids in the cormorant diet during late April and May and also the expanding size of the cormorant colony.

The bioenergetics consumption estimates were calculated for entire species of salmonid, and for Chinook salmon divided by age class/life history type. A majority of smolts produced in the Columbia Basin are of hatchery origin; unfortunately, we had no reliable method to discern rearing type for the salmonids recovered from cormorant digestive tracts. Thus, attributing portions of the estimated consumption to hatchery-reared and wild groups was not possible. Studies comparing the relative susceptibilities of hatchery-reared and wild salmonids to cormorant predation (using passive integrated transponders [PIT] tags implanted in smolts and later detected and/or recovered at bird colonies) have, however, generally found no consistent difference (Collis et al. 2001, Ryan et al. 2003). Consequently, our results appear equally applicable to salmonids of either hatchery or wild origin. Similarly, due to limited sample sizes and limited ability to discern evolutionarily significant units (ESUs) of salmonids recovered from cormorant stomachs, estimates of ESU-specific consumption were also not possible. Representative PIT-tagged samples of all the various salmonid ESUs from the Columbia River basin have not been established; however, in studies comparing the relative susceptabilities of ad hoc groups of smolts belonging to different ESUs, somewhat different susceptibilities to predation by Caspian terns nesting in the Columbia River estuary have been noted (Good et al. 2007). Given current data limitations, we investigated potential benefits for Columbia Basin salmonids from possible reductions in cormorant predation at the species/type level, rather than for individual ESUs.

Comparisons between salmonid mortality rates due to cormorant predation in the Columbia River estuary derived from bioenergetic methods and those based on PIT tag recoveries are not straightforward, but mortality rates are in general agreement (Table 5.6). Bioenergetics-based estimates of mortality rates generated in this study apply to entire species/type groups produced in the Basin, whereas PIT tag-derived estimates have typically been for ad hoc tagged samples of Basin populations. Additionally, estimates of mortality rates derived from PIT tag recoveries are minimum estimates because tag detection efforts have sometimes not corrected for incomplete electronic detection at bird colonies (Collis et al. 2001, Ryan et al. 2001, Ryan et al. 2003), and, for cormorants, have never been corrected for the < 100% deposition rate of ingested tags onto colonies (i.e., some unknown portion of tags ingested by cormorants are regurgitated or defecated away from the colony). Nonetheless, comparisons of recent (2006 – 2007) salmonid mortality rates between this study and those derived for PIT-tagged smolts detected migrating in-river through the juvenile bypass facility at Bonneville Dam (Ryan et al. 2007, Roby et al. 2008, Sebring et al. 2008) found the methodologies in reasonable agreement (Table 5.6).

Bioenergetics estimates for coho and steelhead mortality rates due to cormorant predation are much higher than for PIT tag-based rates. For coho salmon at least, this may reflect the inclusion of predation on hatchery-reared smolts released below Bonneville Dam in the bioenergetics estimates. A majority of all the coho produced in the Basin are from hatcheries below Bonneville Dam (76% of the estimated available coho smolts, averaged across the 10 years of this study), and few of these smolts are PIT-tagged. The smolts from these hatchery releases in the lower river are quickly exposed to cormorant predation, whereas fish detected at Bonneville Dam and used in the PIT tag-based estimates have already survived the rigors of a portion of their out-migration and may be less vulnerable to cormorant predation. Some hatchery-reared sub-yearling Chinook released below Bonneville Dam have displayed much higher susceptibility to cormorant predation than sub-yearlings detected passing through Bonneville Dam, supporting this hypothesis (Ryan et al. 2007, Sebring et al. 2008). Steelhead released below Bonneville Dam, however, have not demonstrated a greater susceptibility to cormorant predation (Ryan et al. 2007, Sebring et al. 2008).

Estimating the improvement in the average annual population growth rate (λ) due to reductions in cormorant predation, while not a direct measure of the potential increases in adult salmonid abundance, does allow comparisons to other salmonid recovery actions in the Columbia River basin (Roby et al. 2003, Good et al. 2007). Possible improvements in λ due to anticipated (in the year 2000) improvements to the hydropower system ranged from 0 – 9% (median = 2%) across the ESUs of salmonids throughout the Columbia River basin, with greatest benefit for Snake River Chinook (1 – 9%), Snake River steelhead (2 – 4%), Upper Columbia River Chinook (4 – 5%), and Upper Columbia River steelhead (2 – 4%) ESUs (potential benefits for coho and sockeye were not estimated; McClure et al. 2003). The likely maximum benefit for Chinook and steelhead from potential reductions in cormorant predation, associated with complete elimination of cormorant predation and assuming this predation was 100% additive, would result in improvements in λ of 1.3% for Chinook and 3.9% for steelhead.

Given the likelihood of at least some level of compensatory mortality following reductions in cormorant predation (e.g., Schreck et al. 2006), a prudent approach is to compare other recovery actions to improvements in λ from reduced cormorant predation assuming some intermediate level of compensation (Roby et al. 2003, Chapter 4). Additionally, prior predator management policies in the Columbia River basin designed to assist in salmon recovery have had partial reductions in predation as goals, not complete extirpation of native predators (Beamesderfer et al. 1996, USACE 1999, 2000, USFWS 2005). Assuming a 50% level of compensation by other mortality factors, the achievement of a 50% reduction in cormorant predation would produce an estimated 0.3% and 1.0% improvement in λ for Chinook (yearlings and sub-yearlings) and steelhead, respectively. Recent estimates of λ for listed Columbia Basin salmonid ESUs were 1.01 – 1.03 for coho (range of subpopulation values for the Lower Columbia ESU), 0.85 – 0.99 for Chinook (range of values for all Chinook ESUs, regardless of age at out-migration), and 0.93 – 1.00 for steelhead (range of all steelhead ESU values; McClure et al. 2003, Good et al. 2005). Thus, management to reduce cormorant predation would be unlikely to shift salmonid populations to a state of recovery ($\lambda > 1$) and would be less beneficial than the planned improvements in hydropower system operation for the ESUs most negatively affected by the hydropower system. Reductions in cormorant predation rates in the Columbia River estuary might, however, provide some benefit to ESUs from throughout the basin, including those that are not directly affected by proposed operational changes in the mainstem hydropower system (e.g., Lower Columbia River and Upper Willamette River ESUs).

The magnitude of benefits to Columbia Basin salmonid populations from potential management to reduce cormorant predation in the estuary would be dependent on several factors, only some of which might be managed directly: (1) the nesting location and future population size of double-crested cormorants within the estuary, (2) river flows, ocean conditions, and other factors that influence the relative availability of alternative prey, (3) smolt condition and naïveté regarding predators, and (4) the degree to which smolt mortality from cormorant predation is additive.

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Table 5.1. Colony size, productivity, and diet parameters used to estimate salmonid (*Oncorhynchus* spp.) smolt consumption by double-crested cormorants (*Phalacrocorax auritus*) nesting on Rice Island (RI) and East Sand Island (ESI) in the Columbia River estuary.

	1998		1999	2000	2001	2002	2003	2004	2005	2006	2007
	RI	ESI	ESI	ESI	ESI	ESI	ESI	ESI	ESI	ESI	ESI
Breeding pairs	795	6,285	6,561	7,162	8,120	10,230	10,646	12,480	12,287	13,738	13,771
Fledglings per pair	0.55	1.35	1.42	1.04	1.93	1.75	2.30	2.11	1.38	1.92	2.78
Salmonid portion of diet*	51.8%	15.3%	27.9%	16.8%	9.4%	5.1%	7.5%	5.9%	1.7%	14.0%	10.6%

* Percent of total biomass consumed.

Table 5.2. Taxonomic composition (percent of identifiable salmonid prey items) of juvenile salmonids (*Oncorhynchus* spp.) in stomachs of collected double-crested cormorants (*Phalacrocorax auritus*) by time period within season, pooled across colonies and years (1998-2007).

Classification	4/10-5/7	5/8-6/4	6/5-7/2	7/3-7/30
Chinook salmon, sub-yearling	4.7	3.8	73.7	100.0
Chinook salmon, yearling	12.8	23.7	0.0	0.0
Coho salmon	50.8	30.3	10.5	0.0
Sockeye salmon	0.0	0.5	0.0	0.0
Steelhead	31.8	41.7	15.8	0.0
N	59	39	19	27

Table 5.3. Mean fresh mass and energy content of double-crested cormorant (*Phalacrocorax auritus*) prey types. Where significant differences were seen in prey type mass between colonies and years (see text for tests of significance), different values for mass were used for each colony-year consumption calculation, and the range in average annual mass and energy content values is given. A single value for energy density was used for each prey type for all colony-years, with sample size for proximate composition analysis indicated in parentheses. Energy density values for yearling and sub-yearling Chinook were not significantly different and were pooled.

Prey family	Species/type	Mass (g)	Energy density (N) (kJ/g)	Energy content (kJ/fish)
Salmonidae	Chinook salmon, sub-yearling	7.7 – 16.8	3.98 (12)	30.6 – 66.9
	Chinook salmon, yearling	32.5	3.98 (12)	129.4
	Coho salmon	24.0 – 39.7	5.04 (12)	121.0 – 200.1
	Sockeye salmon	19.3	4.83 (3)	93.2
	Steelhead	60.9	4.61 (12)	280.8
Engraulidae	Anchovy	11.2 – 27.2	5.37 (14)	60.1 – 146.1
Clupeidae	Herring, Sardine, Shad	17.5 – 73.4	4.94 (27)	86.4 – 362.6
Cyprinidae	Peamouth, N. Pikeminnow	60.0	5.66 (12)	339.8
Petromyzontidae	Lamprey	5.8	5.70 (6)	33.1
Pleuronectidae	Flounder	29.7	4.19 (12)	124.4
Ammodytidae	Sandlance	5.3	5.61 (6)	29.7
Cottidae	Sculpin	27.1	3.83 (12)	103.8
Osmeridae	Smelt	15.6 – 32.5	5.02 (12)	78.3 – 163.1
Gasterosteidae	Stickleback	1.4	3.62 (7)	5.0
Catostomidae	Sucker	188.8	4.45 (6)	840.2
Embiotocidae	Surfperch	25.6	4.16 (13)	106.5
Gadidae	Cod	33.8	3.45 (13)	116.6
Pholidae	Gunnel	4.7	4.39 (1)	20.6

Table 5.4. Estimated number of prey consumed by double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary, 1998 – 2007. Numbers are mean estimates of prey consumed with 95% confidence intervals in parentheses, in millions of fish.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
All Prey Types	89.6 (42-139)	70.8 (30-119)	104.6 (45-164)	123.6 (52-195)	109.0 (39-179)	165.5 (70-261)	276.4 (115-438)	252.3 (109-396)	448.7 (123-774)	335.3 (125-545)
All Salmonids	15.0 (8.0-22.0)	12.4 (5.9-18.8)	7.9 (3.8-12.0)	6.8 (3.2-10.3)	4.6 (2.0-7.3)	3.4 (1.5-5.3)	7.3 (3.5-11.2)	2.4 (1.1-3.7)	9.1 (4.1-14.2)	9.2 (4.3-14.0)
Sub-yearling Chinook salmon	12.1 (6.0-18.2)	8.6 (4.0-13.2)	4.6 (2.1-7.0)	5.0 (2.3-7.7)	4.1 (1.7-6.5)	1.0 (0.4-1.5)	5.2 (2.4-8.1)	1.9 (0.8-3.0)	1.9 (0.9-3.0)	4.1 (1.8-6.3)
Yearling Chinook salmon	0.7 (0.3-1.0)	0.9 (0.3-1.6)	0.9 (0.3-1.4)	0.4 (0.2-0.7)	0.1 (0.0-0.2)	0.7 (0.2-1.2)	0.5 (0.2-0.8)	0.1 (0.0-0.1)	1.7 (0.7-2.8)	1.1 (0.4-1.7)
Coho salmon	1.4 (0.7-2.0)	1.7 (0.6-2.9)	1.4 (0.6-2.2)	0.8 (0.3-1.3)	0.3 (0.1-0.6)	1.0 (0.4-1.6)	1.0 (0.4-1.6)	0.3 (0.1-0.4)	3.6 (1.4-5.7)	2.7 (1.0-4.3)
Sockeye salmon	0.02 (0.01-0.04)	0.03 (0.00-0.06)	0.03 (0.00-0.06)	0.01 (0.00-0.03)	< 0.01	0.03 (0.00-0.05)	0.02 (0.00-0.03)	< 0.01	0.05 (0.00-0.10)	0.02 (0.00-0.05)
Steelhead	0.8 (0.4-1.2)	1.1 (0.4-1.8)	1.0 (0.4-1.5)	0.5 (0.2-0.8)	0.1 (0.0-0.2)	0.7 (0.2-1.1)	0.6 (0.2-1.0)	0.2 (0.1-0.3)	1.8 (0.8-2.9)	1.3 (0.5-2.1)

Table 5.5. Elasticity associated with major input parameters and the estimated number of salmonids (*Oncorhynchus* spp.) consumed by double-crested cormorants (*Phalacrocorax auritus*) in 2007. Input parameters were perturbed 10% from nominal values and elasticity values estimated using the Monte Carlo calculation process for salmonid consumption (incorporating 1000 iterations).

Parameter		Elasticity
Adult daily energy expenditure		0.98
Chick total metabolizeable energy		0.15
Peak breeding pairs		1.14
Seasonal trend in cormorant population		1.18
Metabolizeable energy coefficient		-0.85
Number of chicks hatched		0.05
Number of chicks fledged		0.35
% of diet that was salmonids		1.20
Prey mass (salmonids)	Sub-yearling Chinook	-0.36
	Yearling Chinook	-0.01
	Coho	-0.08
	Sockeye	0.01
	Steelhead	-0.23
Prey mass (non-salmonids)	Anchovy	0.01
	Clupeids	0.01
	Flounder	0.06
	Sculpin	-0.03
Energy density (salmonids)	Sub-yearling Chinook	0.00
	Yearling Chinook	0.01
	Coho	0.02
	Sockeye	-0.03
	Steelhead	-0.04
Energy density (non-salmonids)	Anchovy	-0.40
	Clupeids	-0.05
	Flounder	-0.13
	Sculpin	-0.15

Table 5.6. Comparison of double-crested cormorant (*Phalacrocorax auritus*) predation rates (number taken / number available, expressed as a percentage) on various species/types of juvenile salmonids (*Oncorhynchus* spp.) in the Columbia River estuary during 2006 – 2007. Predation rates based on recoveries of passive integrated transponder (PIT) tags are taken from Ryan et al. (2007), Roby et al. (2008), and Sebring et al. (2008), and are percentages taken by cormorants of PIT-tagged smolts that had been previously detected passing through the Bonneville Dam juvenile bypass facility. Additionally, PIT tag-based predation rates are not corrected for the < 100% deposition rate of ingested tags onto colonies (i.e. some unknown portion of tags ingested by cormorants are regurgitated or defecated away from the colony), and thus are minimum estimates.

Salmonid Species/Type	Predation Rate Estimate (%)	
	Bioenergetics	PIT tag recoveries
Sub-yearling Chinook salmon	4.7	3.3
Yearling Chinook salmon	5.4	4.1
Coho salmon	19.9	6.0
Sockeye salmon	4.5	7.3
Steelhead	16.7	8.1

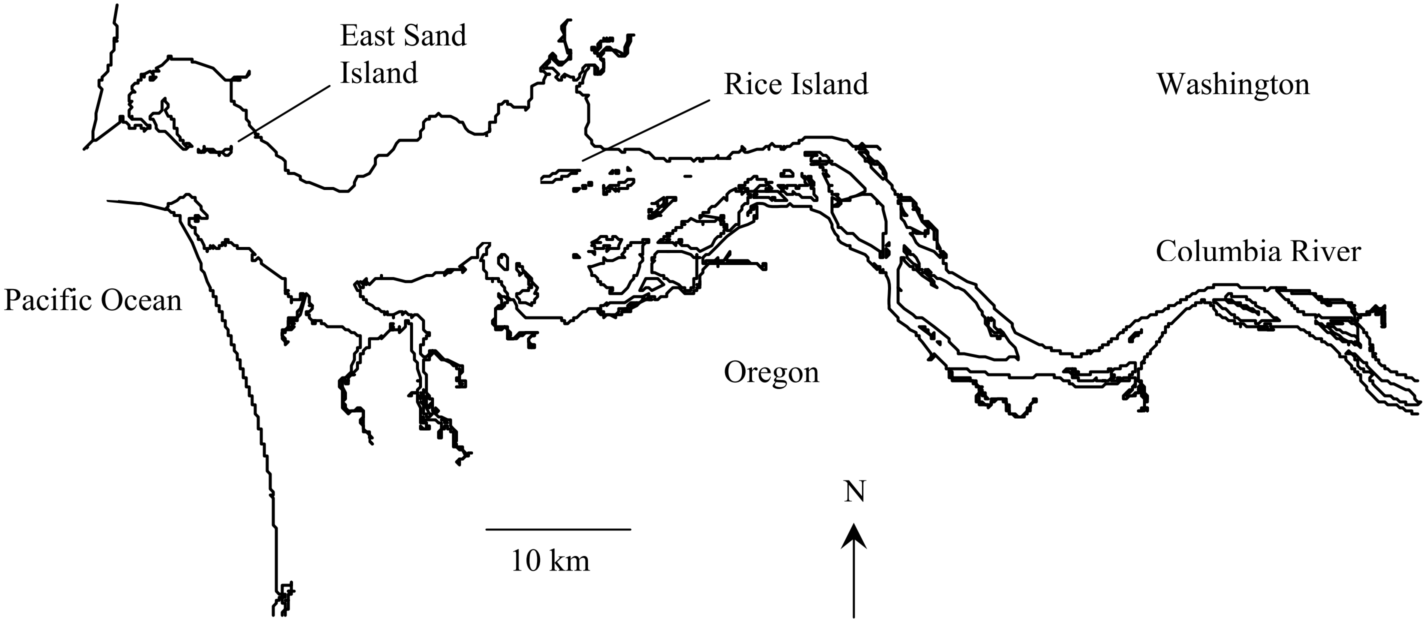


Figure 5.1. The Columbia River estuary. Prey consumption was estimated for double-crested cormorants (*Phalacrocorax auritus*) nesting at a colony on Rice Island (river km 34) in 1998 and at a colony on East Sand Island (river km 8) during 1998-2007.

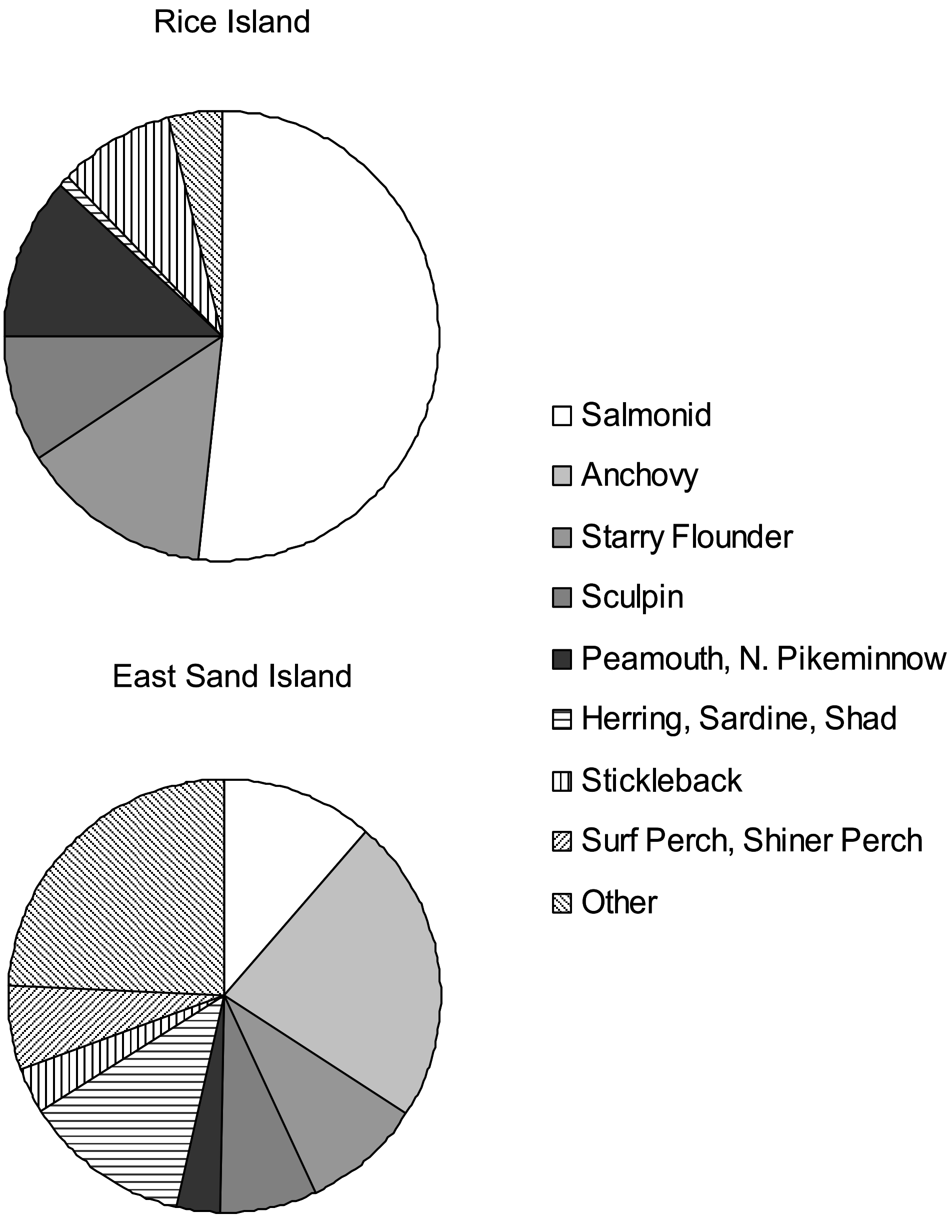


Figure 5.2. Diet composition (% biomass) of double-crested cormorants (*Phalacrocorax auritus*) nesting on Rice Island (1998) and on East Sand Island (1998-2007, averaged across years).

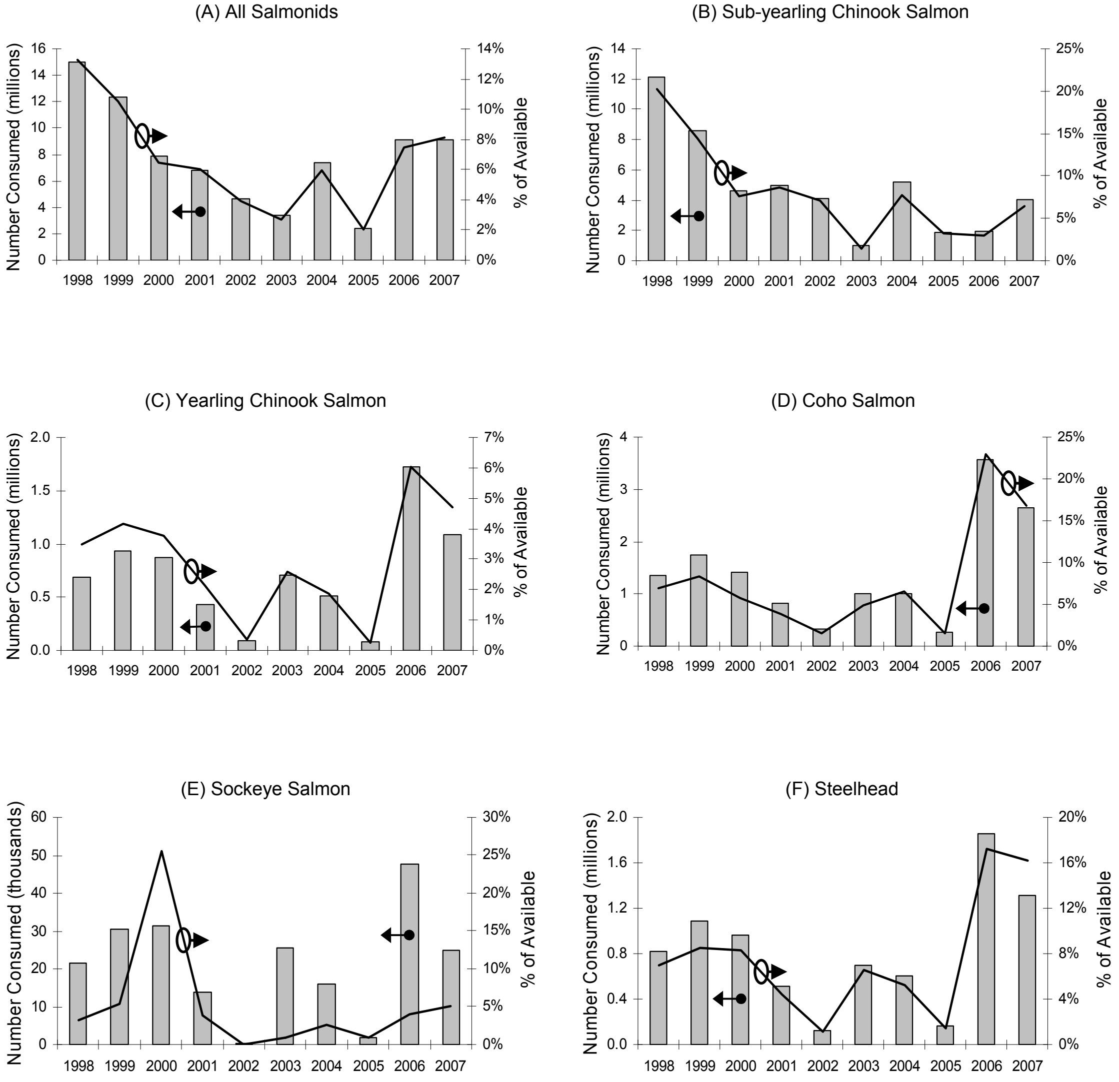


Figure 5.3. Estimated consumption of smolts (bars, left axis) and proportion of available smolts taken (lines, right axis) by double-crested cormorants (*Phalacrocorax auritus*) of (A) all juvenile salmonids (*Oncorhynchus* spp.), (B) sub-yearling Chinook salmon (*O. tshawytscha*), (C) yearling Chinook salmon, (D) coho salmon (*O. kisutch*), (E) sockeye salmon (*O. nerka*), and (F) steelhead (*O. mykiss*).

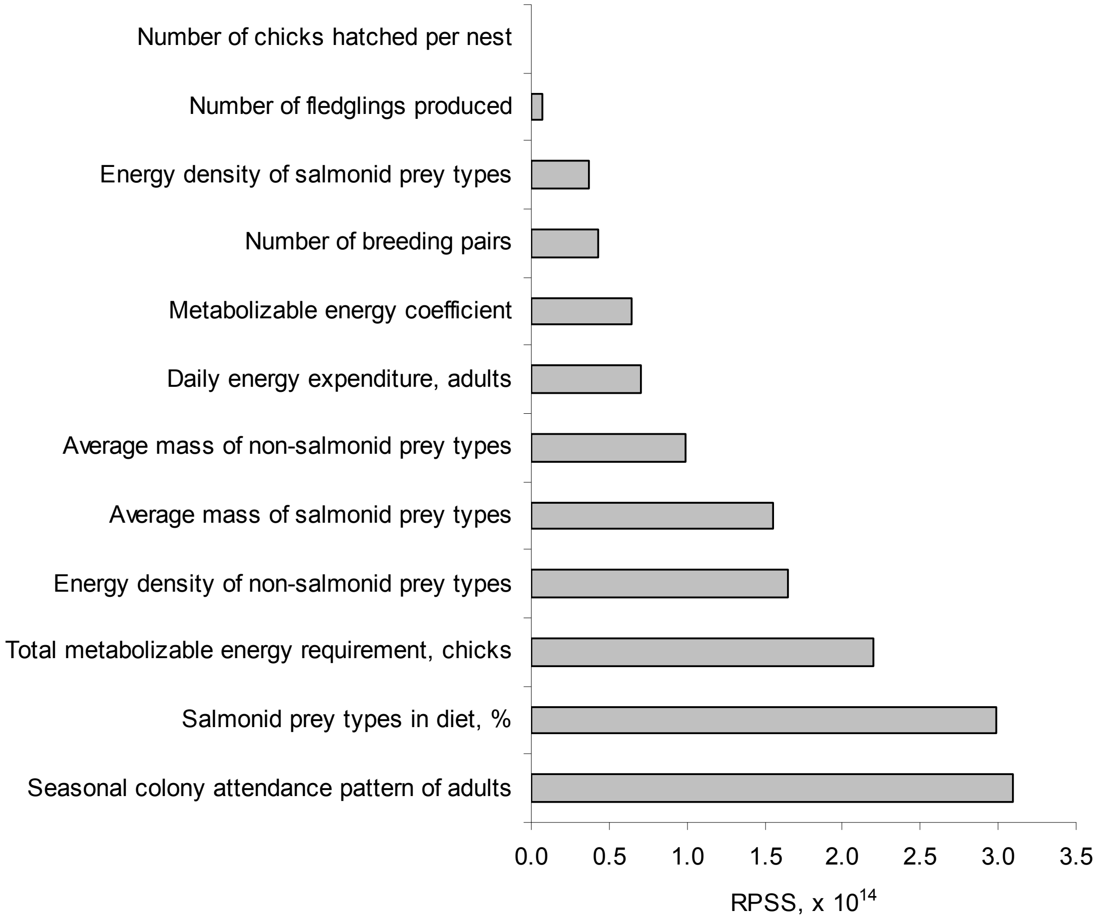


Figure 5.4. Relative partial sum of squares (RPSS) values from regression of bioenergetics input variables on total salmonids (*Oncorhynchus* spp.) consumed by double-crested cormorants (*Phalacrocorax auritus*) nesting on East Sand Island in 2007. Input variables having the largest RPSS contributed most to the uncertainty in the estimate of salmonids consumed.

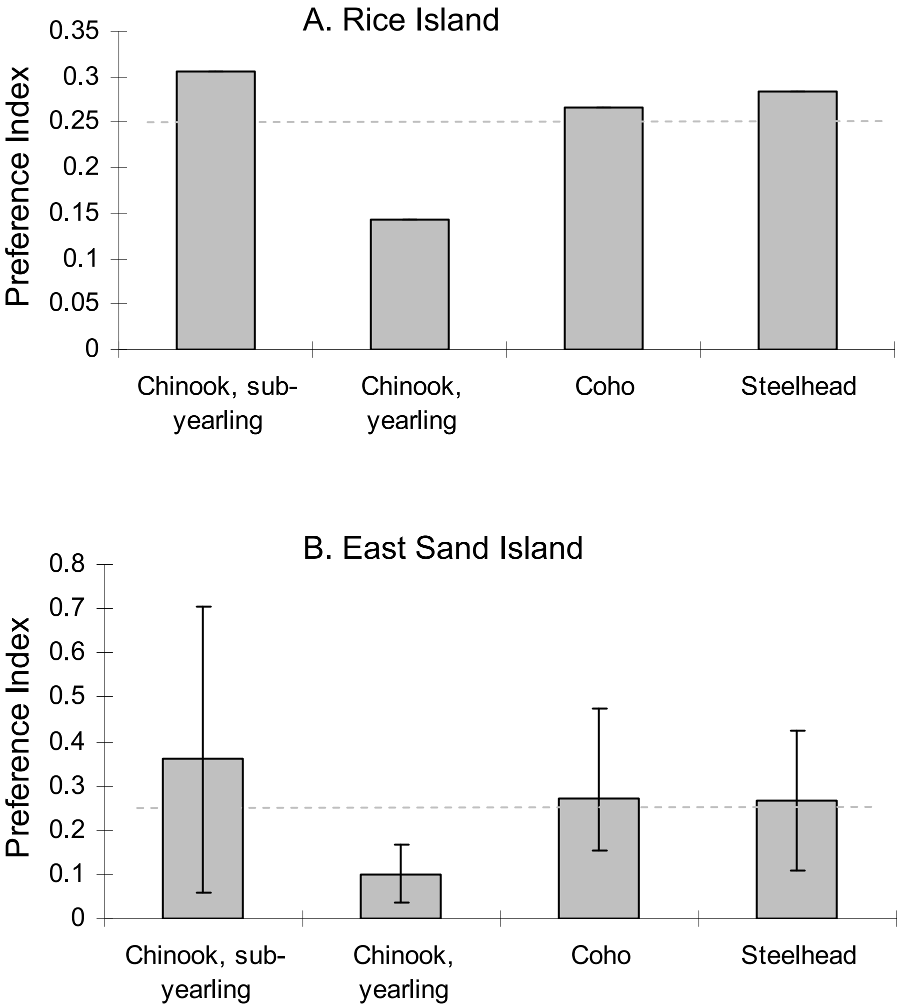
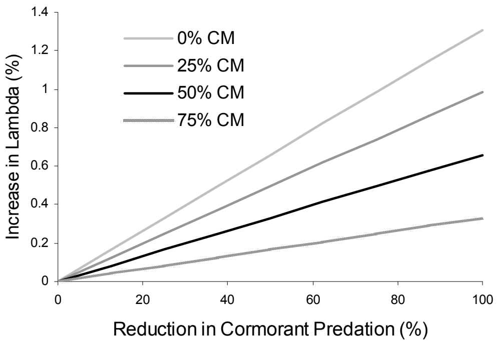


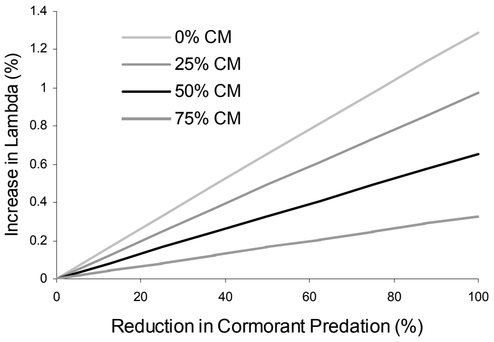
Figure 5.5. Manly – Chesson preference indices for juvenile salmonids (*Oncorhynchus* spp.) consumed by double-crested cormorants (*Phalacrocorax auritus*) nesting on (A) Rice Island (1998) and (B) East Sand Island (1998-2007). Bars indicate the mean across years for East Sand Island and whiskers represent the range in annual values. Values greater than 0.25 (1 / number of species) indicate preference; values below 0.25 indicate avoidance.

Figure 5.6. Required reductions in size of the double-crested cormorant (*Phalacrocorax auritus*) colony on East Sand Island in the Columbia River estuary in order to achieve potential increases in the average annual population growth rate (λ) of five species/types of Columbia River salmonids (*Oncorhynchus* spp.). For each species/type of salmonid, the separate lines represent four levels of potential compensatory mortality (CM) for reductions in cormorant predation (0%, 25%, 50%, and 75%; there is not an effect on λ if mortality is 100% compensatory). These predictions assume that cormorants would not change their foraging behavior (i.e., diet composition) as a function of their own density.

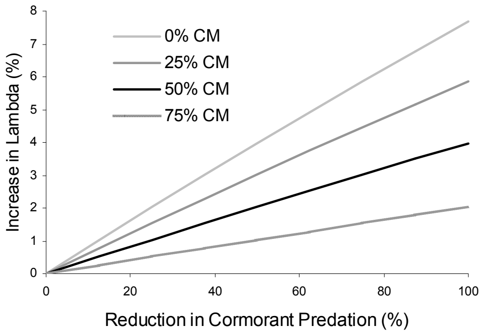
(A) Sub-yearling Chinook Salmon



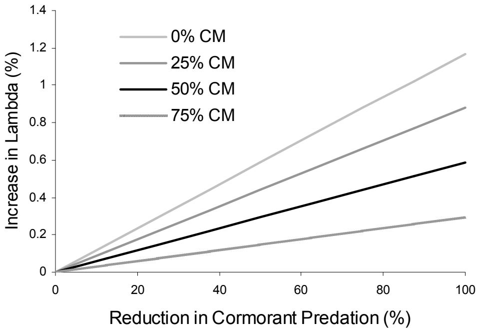
(B) Yearling Chinook Salmon



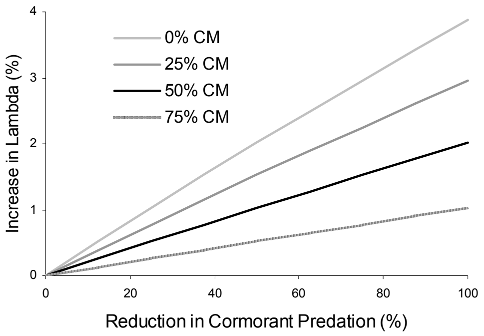
(C) Coho Salmon



(D) Sockeye Salmon



(E) Steelhead



Chapter 6

EFFECTS OF ANNUAL CLIMATE VARIABILITY ON JUVENILE SALMONID CONSUMPTION BY AN ESTUARINE-BASED AVIAN PREDATOR

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ABSTRACT

Understanding the effects of current climate variability on biotic interactions may benefit conservation efforts and prioritization of future risks. We examined the relationship between annual changes in climate conditions and the predator-prey interaction of Caspian terns (*Hydroprogne caspia*) and juvenile salmonids (*Oncorhynchus* spp.). We focused on the Columbia River estuary on the Pacific Coast of North America, where 13 of 20 evolutionarily significant units of salmonids are listed under the U.S. Endangered Species Act and where the largest Caspian tern colony in the world is located. We found that the Pacific Decadal Oscillation, the El Niño/Southern Oscillation, and regional sea surface temperatures were all related to the annual consumption of salmonids by terns. In general, fewer salmonids were consumed in years of warmer conditions. Warmer conditions corresponded to both a numerical response by terns (i.e., smaller tern colony size), and a functional response (less dietary reliance on salmonids and more on marine forage fishes). Also, lower Columbia River flows following winters of light snowpack were associated with less reliance on and consumption of salmonids by terns, as marine forage fish were more available in the estuary. Reduced levels of tern predation on salmonids in years of warmer conditions and lighter snowpack suggests that tern predation will not add to other negative effects of future climate warming on Columbia Basin salmonids.

INTRODUCTION

Increasing awareness of global climate change (IPCC 2007) has generated great interest within the biological sciences community in understanding the sensitivity of populations, species, and ecosystems to climate variability. Most investigations searching for fingerprints of climate change in animal populations have focused on changes in phenology or species range (Root et al. 2003), although there is a growing awareness of the potential impact of climate change on biotic interactions (Durant et al. 2007, Sutherst et al. 2007). Predicting biotic interactions under future climate regimes is problematic because of the complexity of most climate and ecological systems; however, understanding the effects of current climate variation on biotic interactions may allow a prioritization of risks for sensitive species (Sutherst et al. 2007). Periods falling in the warmer portion of the current distribution of climate conditions may be the best available surrogate for future average conditions (e.g., Mote et al. 2003).

Our understanding of how climate-driven ocean conditions can affect populations of diverse marine taxa along the Pacific coast of North America, such as salmonids (*Oncorhynchus* spp.; Pearcy 1992, Beamish and Bouillon 1993, Mantua et al. 1997, Logerwell et al. 2003, Scheuerell and Williams 2005, Zabel et al. 2006), Dungeness crab (*Cancer magister*; Shanks and Roegner 2007), and phytoplankton and rocky intertidal communities (Menge et al. 2009) has expanded rapidly in recent years. Populations of anadromous salmonids along the Pacific Coast are of particular conservation concern, where orders of magnitude declines have occurred over the last century (Lichatowich 1999, Gustafson et al. 2007). In the Columbia River basin, the largest basin in the region, 13 of 20 extant evolutionarily significant units (ESUs) are listed under the U.S. Endangered Species Act (Good et al. 2005). For these salmonids, the juvenile life history stage during the estuarine and early ocean period has been identified as a critical period for survival and recruitment of individuals into the adult breeding population (Pearcy 1992, Kareiva et al. 2000, Beamish and Mahnken 2001). Survival during this life history stage has been linked to climatic variation (e.g., Logerwell et al. 2003, Scheuerell and Williams 2005, Zabel et al. 2006), although precise mechanisms of variable mortality after ocean entry have been difficult to document (but see Emmett 2006, Emmett and Sampson 2007).

In the estuary of the Columbia River, predation by Caspian terns (*Hydroprogne caspia*) has been documented to be a significant mortality factor for juvenile salmonids migrating to the ocean, with millions of smolts consumed by terns on an annual basis (Collis et al. 2001, Roby et al. 2003, Chapter 4). Due to a consistent preponderance of hatchery-reared smolts released throughout the basin (> 100 million smolts annually, Fish Passage Center 2007) and barge transport of large numbers of smolts through the river system to the estuary, the aggregate availability of juvenile salmonids to predators in the Columbia River estuary is a relatively weak function of climate. In contrast, however, the regional abundance of potentially important alternative prey for estuarine piscivorous predators, notably northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasi*), and Pacific sardine

(*Sardinops sagax*), has been documented to vary with climate at multiple temporal scales (Baumgartner et al. 1992, Francis et al. 1998, Chavez et al. 2003, Emmett 2003).

Examining the relationship between climate and consumption of juvenile salmonids by Caspian terns could benefit current efforts to predict abundance of adult salmonids and to design appropriate conservation and harvest strategies, as well as inform prioritization of future risks to salmonid populations from global climate change. Our specific objectives in this study were to (1) investigate the possible effects of short-term (e.g., annual) changes in climate conditions on consumption of juvenile salmonids by Caspian terns nesting in the Columbia River estuary, (2) decompose the variability in Caspian tern predation into potential numerical (local tern abundance) and functional (dietary) responses to climate variation, and, if a functional response is evident, (3) examine whether the functional response by Caspian terns is consistent with independent measures of forage fish availability. This examination of climate effects on the Caspian tern – salmonid predator-prey relationship could also serve as a template for other situations where biotic interactions may play an important role in the persistence of imperiled species under future climate regimes.

METHODS

We examined the relationship between climate and annual consumption of juvenile salmonids by Caspian terns nesting in the Columbia River estuary at East

Sand Island during 2000 – 2008. East Sand Island (river km 8) is a natural island with extensive anthropogenic alterations, including rip-rap stabilization, occasional dredged material disposal, and historical construction activities (USACE 2000), and is surrounded by brackish, marine waters. The Caspian tern colony on East Sand Island, consisting of about 10,000 breeding pairs, is the largest of its kind in the world (Wires and Cuthbert 2000, Suryan et al. 2004). Terns have access to a diverse forage fish community within the estuary, where freshwater species are available in the upper estuary and brackish water and marine species are present lower in the estuary, closer to East Sand Island (Bottom and Jones 1990, Hinton et al. 1995, Hinton and Emmett 2000).

Climate Measures

We related tern consumption of salmonids to two indices of climate at the Pacific Basin scale: the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and the Multivariate El Niño/Southern Oscillation (ENSO) Index (MEI; Wolter and Timlin 1993, 1998). Monthly index values of the PDO were obtained from the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/pdo). We used sliding bi-monthly values (12 per year) of the MEI obtained from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory at http://www.cdc.noaa.gov.

At a more regional or local scale we used three measures of climate conditions: upwelling along the Oregon and Washington coast, local sea surface temperature

(SST), and Columbia River flows. Daily upwelling indices were downloaded from NOAA's Pacific Fisheries Environmental Laboratory at http://www.pfeg.noaa.gov and converted into two annual measures of upwelling. The first measure was the date of the annual spring transition of the California Current into an upwelling domain (Huyer et al. 1979). Timing of spring transition was estimated using the daily upwelling indices at 42º, 45º, and 48º north latitude averaged together, with high frequency oscillations in daily upwelling strength removed by calculating a 45-day moving average for the daily time series. The spring transition was considered to have occurred when the moving average of the upwelling index equaled 15 or greater. The second measure of upwelling was the strength of summer upwelling, defined as the average of daily values from June 1st to July 31st, which roughly corresponds to the chick-rearing portion of the terns' annual breeding cycle.

SST data were obtained from two sources. First, optimal interpolation SST values (Reynolds and Smith 1994, Reynolds et al. 2002) for 46º N, 124º W (just off the mouth of the Columbia River) were derived from satellite measurements in conjunction with in situ data collected at nearby buoys and ships by NOAA's National Centers for Environmental Prediction (available at http://www.ncep.noaa.gov). Second, in situ SST data from the buoy nearest to the Columbia River mouth having a complete data series during 2000 – 2008 (44.64º N, 124.5º W; buoy 46050, 156 km from East Sand Island) were obtained from NOAA's National Data Buoy Center at http://www.ndbc.noaa.gov.

Daily measurements of river flow (kcfs) recorded at the Beaver Army Terminal near Quincy, Oregon (river km 86) were obtained from the U.S. Geological Survey at waterdata.usgs.gov (site number 14246900). This location was downstream from the confluences with all major tributaries in the Columbia Basin. Daily river flows were averaged across April – July to provide a single annual measure of flow during the Caspian tern nesting season.

Salmonid Consumption

Consumption of juvenile salmonids by Caspian terns was estimated using a bioenergetics modeling technique described in detail elsewhere (Chapter 4). Briefly, bioenergetics calculations relied on four major categories of empirical data: (1) tern abundance (adults and chicks), (2) energy requirements of individual adult and juvenile terns, (3) tern diet composition (proportion of various prey types in the diet), and (4) energy content of the various tern prey types. Both individual tern energy requirements and prey energy content were assumed constant across years, so the proximate source of annual variability in estimated salmonid consumption was changes in tern abundance and/or tern diet composition.

The abundance of adult Caspian terns residing in the Columbia River estuary each year was quantified by estimating the size of the breeding colony on East Sand Island using high resolution aerial photography during late incubation (usually the 3rd or 4th week of May, see Collis et al. 2002 for details). To convert the counts of individuals in aerial photography to the number of breeding pairs present we used ratios of terns on nests to all terns present in sample plots (n = 12) observable from blinds at the edges of the colony. We assumed that the number of non-breeding terns present in the estuary was negligible compared to the number of breeding terns (Roby et al. 2003). Production of fledgling terns was estimated using a second set of aerial photography during the late chick-rearing period (usually the 1st or 2nd week of July). Counts of all individuals (adults plus chicks) in aerial photography of the colony were corrected to estimate fledgling abundance using counts of adults and chicks in sample plots on the colony, recorded by observers in blinds at the edge of the colony (see Roby et al. 2002).

The taxonomic composition of tern diets was quantified based on the frequency of prey types identified as they were brought back to the colony by adult terns. Caspian terns transport whole prey items back to the breeding colony in their bills, and these prey can be identified to the level of family by trained observers in blinds located at the edge of the tern colony, with the aid of binoculars or spotting scopes. Diet composition data were collected approximately daily each year across the tern breeding season, with 25 fish identified during daytime high and low tide periods.

Statistical Relationships

Correlations between time series can be confounded due to autocorrelation in one or both series, which can result in inflated variances and unexpectedly high Type I error rates. Low-frequency correlation, or multi-year covariation in annual time series, can be removed using the process of first differencing, i.e., performing correlations between the annual changes in time series data. However, first difference correlations may have the problem of lower power to detect significant covariation (or increased Type II error rates; Pyper and Peterman 1998). We opted to conservatively investigate potential relationships between annual salmonid consumption and climatic indices by calculating Pearson correlation coefficients on first differenced quantities. Our time series were relatively short (nine years), so we did not examine multiple explanatory variables simultaneously. We reported a relationship as significant when P values were ≤ 0.10.

When a significant trend between a particular climate measure and salmonid consumption by terns was indicated, we dissected the relationship into numerical versus functional responses by terns to climate conditions. To evaluate a potential numerical response on the part of terns, we used the relationship between significant climate measures and tern colony size. This measure incoporated the effects of annual mortality, recruitment of sub-adult terns into the breeding population (Caspian terns demonstrate delayed maturation, breeding first at 3-5 years of age; Cuthbert and Wires 1999), immigration and emigration to and from the East Sand Island colony, and the terns propensity to breed in a given year. To evaluate a functional response we we used the relationship between climate and tern diet composition. We considered using per capita consumption of juvenile salmonids by terns as a measure of functional response but this variable was highly correlated with diet composition measures [$R^2 = 0.94$, $P < 0.001$]. Diet composition measures were considered to be more indicative of potential underlying mechanisms and so were used instead. For diet composition measures, we used the salmonid proportion of the diet (% of total prey items) and, the approximate converse, the schooling marine forage fish proportion of the diet (MFF; i.e., anchovy, herring, or sardine). Salmonids and MFF proportions of the diet were not mutually independent quantities (R = 0.87), but each represents distinct mechanisms for how climate could influence salmonid consumption, so we report relationships between climate and both measures of tern diet composition. On an annual basis, salmonids and MFF combined to constitute 57 – 75 % (average = 66%) of the tern diet.

For the large-scale climate measures (PDO and MEI), and also the SST measures, we calculated averages over four periods of the year to investigate the possibility of a critical period of climate conditions that might more strongly relate to subsequent tern predation on salmonids. We examined relationships based on conditions (1) during the tern breeding season (April – July), (2) the winter and early spring immediately preceding the tern breeding season (January – April), (3) the fall and early winter preceding the tern breeding season (October – December of the previous calendar year), and (4) the fall, winter, and spring preceding the tern breeding season (October of the previous year through the April immediately preceding the tern breeding season, or periods 2 and 3 combined). Data were unavailable during multiple winters for buoy SST; consequently, relationships between salmonid consumption and time period 3 were not possible and the buoy SST value for April alone was substituted for period 2 (January – April). The relative strength of relationships between salmonid consumption by terns and climate during these various temporal periods was evaluated by comparing how much of the variability in smolt consumption (i.e., R^2 values) was explained by each period.

Forage Fish Availability

We examined two measures of MFF availability from two studies conducted by NOAA Fisheries, one in the Columbia River estuary and one in the near-shore environment just off the Oregon and Washington coast, to better understand mechanisms behind potential trends in the MFF component of Caspian tern diets relative to climate variables.

In the Columbia River estuary, NOAA (L.A. Weitkamp and R.L. Emmett) conducted purse seining during 2001-2003 and 2007-2008 primarily in deeper channel (≥ 5 m depth) sites in the lower, brackish-water portion of the estuary. All sites sampled were within 10 km of East Sand Island. Seining occurred throughout the spring and summer; however, sampling was greatest and most consistent across years in May and June, so data were restricted to that time period. This period corresponded to the portion of the tern breeding season when Caspian terns were most numerous at the breeding colony. Each year's measure consisted of pooled data from 4-5 days of sampling spread across May and June, with 2-16 (median 8) hauls per day. Seining was conducted on incoming or slackwater tides and only during daylight hours. Due to changes in site selection (sampling focused on a subset of sites in later years) and gear (nets having differing capture efficiency, etc.) over the course of this study, abundance of MFF was not estimated; rather, frequency of occurrence in hauls was viewed as a more consistent measure of potential availability of MFF to terns. In order to describe occurrence in quantities that would be associated with significant availability to terns, MFF were considered to occur in an individual haul if they were more than 5% of the total catch. Because seining occurred only in some years during the tern study period, only qualitative comparisons between MFF availability, tern diets, and climate indices were made.

In the near-shore environment, NOAA (R.L. Emmett) conducted surface trawls during 2000-2008 at stations 5 – 55 km off the mouth of the Columbia River and off the mouth of Willapa Bay, the next large estuary 45 km to the north (Emmett et al. 2006). Caspian terns seldom forage more than 1 km from shore in this region (Lyons et al. 2005, Anderson et al. 2007), so we restricted data to sampling stations 5 and 10 km from shore. Sampling occurred across spring and summer at approximately 10-day intervals; however, we restricted data to just those samples collected in May and June to more closely match the estuary seine data and the period of highest tern abundance. Trawling was conducted at night to take advantage of diel migrations to the surface and to minimize visual avoidance of the net. Densities of MFF were estimated by dividing catch estimates by the volume sampled by the net (fishing distance multiplied by the mouth area of the trawl, assuming a capture efficiency of 100%). MFF density estimates were first compared to the proportion of the tern diet that was MFF using first-difference correlation, and then compared to climate variables that were related to tern diet composition.

RESULTS

Indices of climate-driven ocean and river conditions varied considerably during 2000 – 2008 (Figure 6.1). Cooler conditions predominated across the Pacific Basin and locally during the early years of the study period (2000 – 2002). In 2003, basin-wide (PDO, MEI) and local SST measures indicated a significant warming that persisted at least through 2005. The latter three years of the study were quite variable, although all measures indicated significant cooling in 2008. The earliest and strongest upwelling occurred off the Oregon and Washington coasts in 2001. In 2005, the spring transition to upwelling was delayed and upwelling remained weak during the terns' breeding season. Columbia River flows were historically low in 2001 and high in 2002, 2006, and 2008. Flows in June and July of 2008 were particularly high.

Point estimates of the Caspian tern breeding population varied from 8,325 pairs in 2003 to 10,668 pairs in 2008 (Table 6.1), with no significant trend during the period. Salmonids were generally around a third of the tern diet on an annual basis, although greater reliance was seen in 2000, when salmonids made up 45% of the diet, and less reliance during 2003-2005. In 2004 only 18% of fish consumed by terns were salmonids. The proportion of the tern diet that was schooling marine forage fish (MFF) varied from 21% to 51%, with the highest proportions recorded during 2004 – 2005 and the lowest in 2000 and 2008. Fledgling production by terns was highest in 2001, and lowest in 2005. During the study period, estimated consumption of salmonids by Caspian terns peaked at 6.7 million smolts in 2000, and again in 2008, with no temporal trend indicated. In 2005, terns consumed only about 3.9 million smolts, the fewest of any year during the study period.

Significant relationships existed between each large scale climate index in the Pacific Basin (PDO and MEI) and annual salmonid consumption by Caspian terns (Table 6.2). For both these climate indices, the time period (October – April) preceeding the terns breeding season and the smolt out-migration explained much more of the variation in smolt consumption than did the period during which the predation was actually occurring. At a more regional or local scale, SST measures were also significantly related to salmonid consumption; however, a shorter time lag was indicated for the relationship between salmonid consumption and optimal interpolation SST and no lag at all for buoy SST values (Table 6.2). In all cases, cooler conditions corresponded to higher levels of salmonid consumption by terns. Neither upwelling measure was related to salmonid consumption, but greater salmonid consumption was seen in years with higher Columbia River flows (Table 6.2).

Of the two large-scale climate indices, the PDO had a substantially stronger relationship with salmonid consumption by Caspian terns than did the MEI (the best MEI model explained 53% of the variation in smolt consumption and the best PDO model explained 71%). Consequently, we focused on testing relationships between the PDO and tern population and diet parameters. Tern colony size was significantly negatively related to the PDO, with smaller colonies during shifts to warmer, positive PDO conditions; however, there was no relationship between the PDO and tern productivity (Table 6.3). First difference correlations between the PDO and the proportion of marine forage fish in the diet was marginally significant (*P* = 0.09), with greater reliance on MFF during shifts to warmer, positive PDO conditions. The corresponding first difference correlation between the PDO and the proportion of salmonids in the diet was not significant (*P* = 0.23). However, correlations between the PDO and diet measures without first differencing were significant for both MFF and salmonids (*P* = 0.01 and 0.02, respectively; Table 6.3), suggesting that there may be co-variation between the PDO and salmonids in the tern diet on a multi-year, rather than annual, basis.

Of the two regional/local measures of SST, the optimal interpolation SST had a somewhat stronger relationship with salmonid consumption than did buoy SST (buoy SST explained 45% of the variation in smolt consumption and optimal interpolation SST explained 55%), so we proceeded to examine relationships between just the optimal interpolation SST and tern diet and population parameters. We saw increases in the size of the tern colony when SST became cooler (Table 6.4); however, no relationship existed between SST and productivity or either diet variable.

Columbia River flows were not related to tern colony size or productivity; however, flows were related to both the proportion of salmonids in the tern diet (positively) as well as MFF in the tern diet (negatively, Table 6.5).

These results describe relationships between climate measures and tern consumption of all Columbia River salmonid species pooled together. Parallel analyses were separately performed for each of the major salmonid species in the

Columbia River (Chinook [*O. tshawytscha*], coho [*O. kisutch*], and steelhead [*O. mykiss*]) and similar results were obtained. Trends were always of similar direction and magnitude and relationships were generally significant between climate and coho and steelhead consumption, and sometimes, but less often so, for Chinook.

In general, terns relied more on MFF when MFF more frequently occurred in estuary seine sampling (Figure 6.2). In the high river flow year of 2008, MFF were less commonly encountered in seines and were also a smaller proportion of the tern diet. In other years, MFF were relatively frequently observed in seines and more heavily relied upon by terns. Annual changes in near-shore MFF densities did not relate to changes in tern diet composition when all years were considered ($R^2 = 0.09$, $P = 0.48$; Figure 6.2); however, if the outlier data point from 2004 was omitted, this relationship was significantly positive ($R^2 = 0.76$, $P = 0.01$, slope = 3.28E-5 [95% CI: 1.17E-5 to 5.39E-5]). Changes in MFF densities for all years were positively correlated to PDO changes ($R^2 = 0.62$, $P = 0.02$, slope = 3896 [95% CI: 870 to 6923]), but not to interpolated sea surface temperatures or Columbia River flow ($R^2 = 0.33$, $P = 0.14$ and $R^2 = 0.13$, $P = 0.38$, respectively).

DISCUSSION

Our results indicate that climate plays an important role in mediating the predator-prey relationship between Caspian terns and juvenile salmonids in the Columbia River estuary. Large scale climate indices, such as the Pacific Decadal

Oscillation and the Multivariate ENSO Index, explained significant amounts of the variation in salmonid consumption by terns, as did local SST and Columbia River flows, an integrated measure of climate conditions. Winter and early spring climate were generally more significantly related to salmonid consumption by terns than conditions during the spring/summer season, when the predation actually occurred.

Climate was associated with both numerical and functional responses in tern consumption of salmonids. Cool PDO and low local SST conditions prior to the tern breeding season were associated with larger tern colonies, presumably due to either increased winter survival or enhanced breeding propensity, or both. Cooler conditions in the California Current System along the North American Pacific Coast are generally associated with greater primary productivity and enhanced forage fish populations in the near shore environment (Francis et al. 1998). This may result in greater prey resources throughout the year for Pacific Coast Caspian terns, many of which winter in coastal areas of Guatemala, Mexico, and southern California and migrate to and from breeding sites along the Pacific Coast (Gill and Mewaldt 1983, Cuthbert and Wires 1999, Suryan et al. 2004). Enhanced prey resources may result in greater winter survival or improved physiological condition entering the breeding season, which likely would result in greater breeding propensity.

Cooler conditions and greater Columbia River flows were associated with a greater proportion of salmonids in tern diets, a functional response by terns to climate-induced changes in prey availability. Ocean climate conditions may affect availability of marine forage fish to Caspian terns in two somewhat different ways – affecting both the regional population size of these prey species, as well as their spatial distribution. For example, overall abundance of MFF in the near-shore environment tracked PDO conditions and in most years near-shore abundance also tracked the reliance of terns on these prey in the Columbia River estuary. However, in 2004 the MFF abundance in near-shore areas dropped precipitously from the levels of prior years, but terns relied more on these prey during that year than in any other year of the study, suggesting a redistribution of MFF into the Columbia River estuary in that year.

As evidenced by both tern diets and estuary purse seine sampling, high river flows seem to reduce availability of MFF to terns, perhaps by inhibiting entry of these fish into the estuary or perhaps reducing residence time after entry. High flows reduce saltwater intrusion into the estuary and presumably make it less hospitable for MFF. Columbia River summer flows are strongly dependent upon snow pack that develops the previous winter in the Cascade and Northern Rocky mountains and effectively integrate climate conditions over a similar timeframe to that which we found the PDO to be most strongly related to annual salmonid consumption by terns (Mote et al. 2003). Flows into the estuary were not well correlated to the PDO during the years of our study (first difference correlation: $R^2 = 0.30$, $P = 0.16$); however, such flows do not reflect true precipitation and runoff within the basin, as irrigation withdrawals and water storage practices vary somewhat among years. PDO and ENSO indices have been useful predictors of Columbia River flows over longer time frames (Hamlet and Lettenmaier 1999, Barton and Ramirez 2004).

Not all measures of climate were related to salmonid consumption by terns, particularly the two measures of upwelling that we examined, the spring transition and the average June and July strength of upwelling. Despite no apparent association with tern abundance or diet composition, upwelling did have other effects on Caspian terns. Tern productivity in the Columbia River estuary was strongly negatively related to the date of spring transition to upwelling (first difference correlation: $R^2 = 0.76$, $P = 0.005$). A particularly late spring transition in 2005 (May 31st; Kosro et al. 2006, Pierce et al. 2006) corresponded to the lowest productivity observed during this study (0.37 fledglings/pair; other years ranged from 0.57 to 1.39 fledglings/pair). Marine forage fish were prevalent in tern diets in 2005; anchovy made up a greater portion of the diet than in any other year of our study (35% versus 12 – 32% in other years). Average body masses of anchovy, sardine, and smelt caught by terns that year, however, were among the lowest seen during the study (authors unpublished data), presumably reflecting a poor food base for forage fish due to late upwelling.

During the course of our study, a large and growing colony of double-crested cormorants (*Phalacrocorax auritus*) also nested at East Sand Island in the Columbia River estuary and consumed millions of juvenile salmonids annually (Chapter 5). We performed parallel analyses to those presented here for Caspian terns but found little relationship between climate and salmonid consumption by cormorants, or with cormorant population or diet measures. Cormorants maintain a more diverse diet in the Columbia River estuary than do Caspian terns, with both salmonids and marine forage fish making up a smaller proportion of their annual diet (a combined 33 – 59%

of cormorant diet, as opposed to 57 – 75% of tern diets during the study period). Climate effects on cormorant predation may have been masked by the continual increase in cormorant population size, as the annual population growth rate (λ) for the colony averaged 1.07 from 2000 – 2008 (authors' unpublished data).

Long term regional Caspian tern population trends

The Pacific Coast Caspian tern population saw a large population and range expansion during the 1960s and 1970s (Gill and Mewaldt 1983). The population increased 70% over this time frame and shifted a majority of its breeding northward from California to Washington. Caspian terns colonized coastal Washington in 1957 (Alcorn 1958) and the population rapidly increased there (Penland 1982). Interestingly, this Pacific Coast population expansion was associated with a cool phase of the PDO from 1947 – 1976 (Mantua et al. 1997). In the 1980s and 1990s Caspian tern populations continued to increase (Suryan et al. 2004), despite predominantly warm PDO conditions during this period; however, major breeding sites shifted from coastal Washington to sites along the Columbia River in Oregon and interior Washington, where an abundance of hatchery-reared juvenile salmonids provided a predictable, reliable food source (> 100 million smolts annually, Fish Passage Center 2007). Over the past decade (1998 – 2008), PDO conditions have not been consistently warm or cool and Caspian tern populations have remained relatively stable, particularly at the population center in the Columbia River estuary. Caspian terns are relatively long-lived birds, with an estimated average life span of approximately 11 years (Gill and Mewaldt 1983, Suryan et al. 2004). It is plausible, therefore, that Caspian tern populations may track decadal-scale climate (PDO) conditions, presumably through the mechanism of bottom-up climate control over prey abundance. Population trends would also be influenced by the availability of nesting habitat and prey resources that are not strongly linked to climate, such as hatchery-reared salmonids.

Climate impacts on estuarine and ocean salmonid survival

Estuarine and early ocean survival of salmonids is believed to be a critical determinant of future adult returns to natal streams (Pearcy 1992). In the Columbia River and some other basins, long-term records are available of salmonid survival from juvenile downstream migration through the lowest point of enumeration (in the Columbia River, Bonneville Dam at river km 234) until the corresponding adult upstream migration past that point and have been analyzed for possible relationships to climate (e.g., Logerwell et al. 2003, Scheuerell and Williams 2005, Zabel et al. 2006). Generally, cooler ocean conditions (as described by the PDO, ENSO indices, or SST measures) and earlier and greater upwelling in the year of ocean entry have been associated with greater adult returns of Chinook and coho salmon, and presumably higher survival in the estuarine and first ocean year period. In contrast, our results indicate that in the Columbia River estuary, Caspian tern predation is greater in years of cooler ocean conditions and no relationship exists between tern predation and upwelling. Two important implications are suggested by these results.

First, for juvenile salmonids, climate conditions that promote survival at one life history stage (early ocean period) may depress survival at another life history stage (estuarine period). Second, because ocean conditions that increase tern predation on smolts are also associated with greater adult returns, it appears unlikely that tern predation is a strong regulatory factor for most Columbia River Chinook and coho salmonid populations, at least over the range of tern predation seen in this study. Conclusions for steelhead are less certain as tern impacts are quite significant (Collis et al. 2001, Antolos et al. 2005) and effects of climate on adult returns are less understood. In general, related analyses have suggested that reductions in tern predation associated with management may offer benefits to some Columbia River salmonid populations but are unlikely to reverse recent population declines (Roby et al. 2003, Good et al. 2007, Chapter 4).

Projecting impacts of future climate warming

Global circulation climate models still lack the necessary resolution to accurately predict future climate at smaller than continental scales, particularly for measures other than air temperature (IPCC 2007). One expected result, however, is the alteration of the Columbia River hydrological cycle, with greater flows during winter and reduced flows during summer (Mote et al. 2003, ISAB 2007). This condition might allow greater use of the estuary by marine forage fish during the late spring and summer and boost the buffering of predation on salmonids that these prey provide. In addition to projections for Columbia River flows, warmer conditions that have occurred during positive phases of the PDO have been proposed as a surrogate for future anthropogenic climate change (e.g., Mote et al. 2003). These conditions might induce lower over-winter survival and/or lower breeding propensity for Caspian terns and thus reduce the Pacific Northwest tern breeding population, which might reduce predation impacts. Warmer conditions might also shift the distribution of marine forage fish into the Columbia River estuary in some years, which would enhance their buffering of salmonids; however, average abundance of marine forage fish might also decrease during prolonged warmer conditions. Projections of lower tern predation on salmonids during warmer conditions suggest that tern predation will be a mortality factor of decreasing importance for Columbia River salmonids under likely future climate regimes.

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Table 6.1. Annual Caspian tern (*Hydroprogne caspia*) abundance, diet, and juvenile salmonid (*Oncorhynchus* spp.) consumption in the Columbia River estuary, 2000 - 2008. For further details, see Chapter 4.

	2000	2001	2002	2003	2004	2005	2006	2007	2008
Breeding pairs	9,101	8,982	9,933	8,325	9,502	8,822	8,929	9,623	10,668
Salmonid proportion of diet*	45%	32%	31%	25%	18%	23%	32%	30%	32%
Marine forage fish (MFF) proportion of diet*	21%	43%	30%	41%	51%	45%	36%	38%	26%
Fledglings per breeding pair	0.57	1.39	1.08	1.08	0.92	0.37	0.74	0.66	0.57
Salmonid consumption (millions)	6.7	5.6	5.9	4.1	4.0	3.9	5.4	5.5	6.7

* Percent of total prey items consumed.

Table 6.2. First difference correlations between climate variables and annual salmonid (*Oncorhynchus* spp.) consumption by Caspian terns (*Hydroprogne caspia*) in the Columbia River estuary.

Climate Measure	Time Period	Slope (95% CI)	R^2	*P*
PDO[1]	October – December	-0.63 (-1.01 to -0.26)	0.66	0.01
	January – April	-0.81 (-1.32 to -0.30)	0.63	0.02
	October – April	-0.80 (-1.22 to -0.38)	0.71	0.01
	April - July	-0.81 (-1.48 to -0.15)	0.50	0.05
MEI[2]	October – December	-0.62 (-1.12 to -0.13)	0.52	0.04
	January – April	-0.80 (-1.41 to -0.18)	0.53	0.04
	October – April	-0.72 (-1.28 to -0.17)	0.53	0.04
	April - July	-0.04 (-2.18 to 2.09)	< 0.01	0.97
Buoy SST[3]	October – December	-0.28 (-2.41 to 1.86)	0.01	0.80
	April	-0.92 (-1.84 to -0.004)	0.40	0.09
	April - July	-0.69 (-1.31 to -0.06)	0.45	0.07
Interpolated SST[3]	October – December	-0.46 (-2.60 to 1.67)	0.03	0.68
	January – April	-1.47 (-2.76 to -0.18)	0.55	0.03
	October – April	-1.10 (-1.91 to -0.29)	0.46	0.06
	April - July	-1.08 (-2.04 to -0.12)	0.46	0.06
Upwelling	Spring Transition	-9.21E-3 (-3.50E-2 to 1.65E-2)	0.08	0.50
	June – July	1.44E-4 (-3.04E-2 to 3.07E-2)	< 0.01	0.99
Columbia River Flow	April - July	7.88E-6 (5.69E-7 to 1.52E-5)	0.44	0.07

[1] Pacific Decadal Oscillation (Mantua et al. 1997)
[2] Multivariate El-Niño/Southern Oscillation Index (Wolter and Timlin 1993, 1998)
[3] Sea surface temperature

Table 6.3. Relationships between the Pacific Decadal Oscillation (PDO) and Caspian tern (*Hydroprogne caspia*) population and diet parameters. PDO values were averaged over October – April preceding each tern breeding season. Results of first difference correlations are presented for all parameters; for diet parameters correlation results without first differencing are also presented in brackets.

Parameter	Slope (95% CI)	R^2	*P*
Colony Size	-746 (-1131 to -361)	0.71	0.01
Productivity	0.15 (-0.14 to 0.44)	0.15	0.34
Salmonid Proportion of Diet	-0.032 (-0.081 to 0.016) [-0.068 (-0.116 to -0.020)]	0.24 [0.54]	0.23 [0.02]
Marine Forage Fish Proportion of Diet	0.072 (-0.00002 to 0.14) [0.91 (0.38 to 0.145)]	0.41 [0.63]	0.09 [0.01]

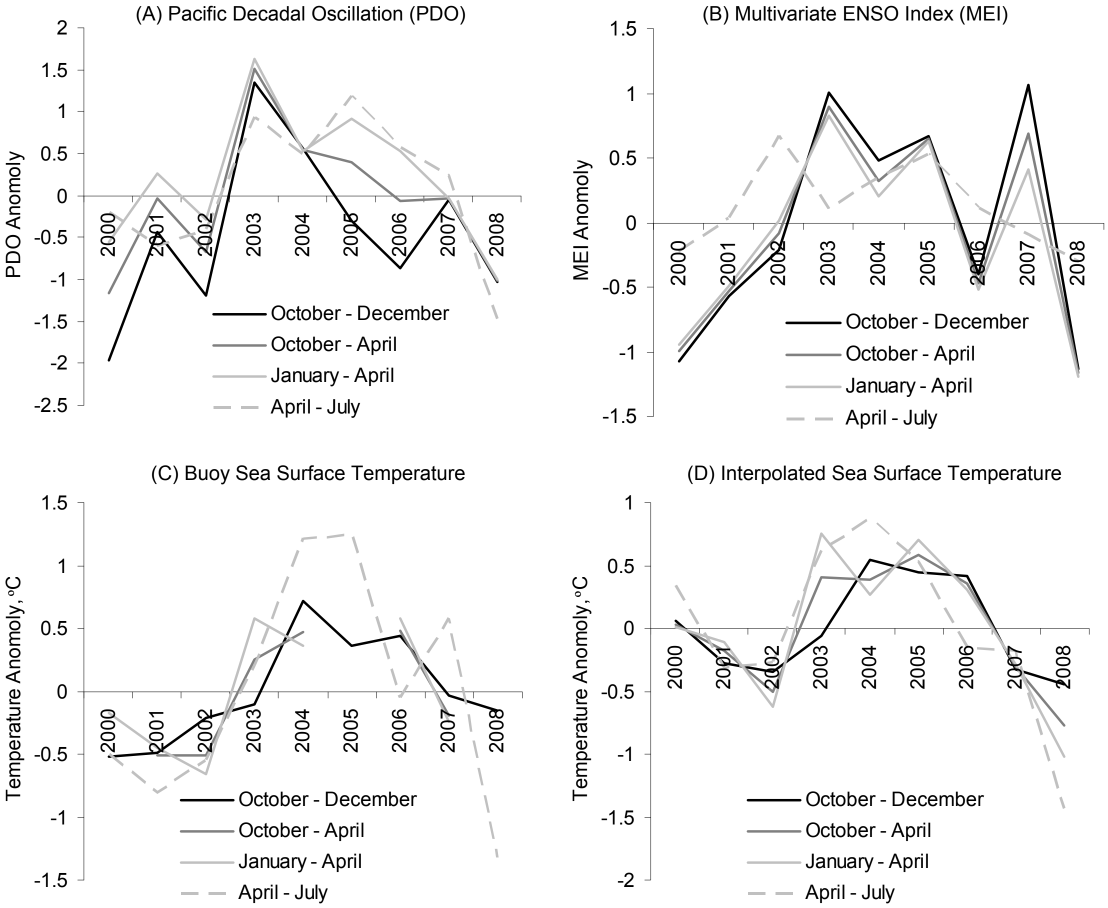
Table 6.4. Relationships between optimal interpolation sea surface temperature (SST) values (Reynolds and Smith 1994, Reynolds et al. 2002) for 46º N, 124º W (just off the mouth of the Columbia River) and Caspian tern (*Hydroprogne caspia*) population and diet parameters. SST values were averaged over January – April preceding each tern breeding season.

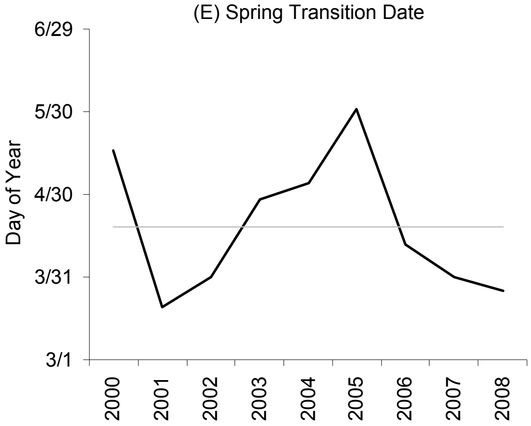
Parameter	Slope (95% CI)	R^2	*P*
Colony Size	-1298 (-1651 to -946)	0.90	0.0003
Productivity	-0.034 (-0.52 to 0.45)	< 0.01	0.89
Salmonid Proportion of Diet	-0.017 (-0.10 to 0.067)	0.03	0.70
Marine Forage Fish Proportion of Diet	0.061 (-0.073 to 0.19)	0.12	0.40

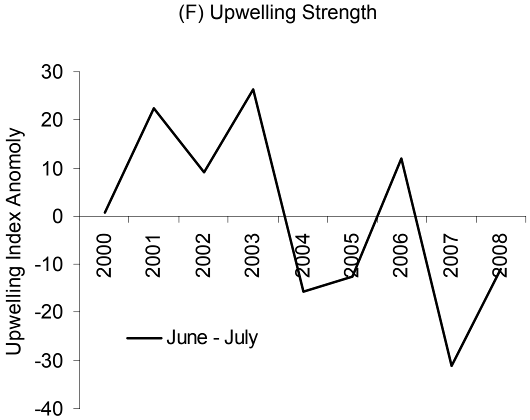
Table 6.5. Relationships between Columbia River flow and Caspian tern (*Hydroprogne caspia*) population and diet parameters. River flows were averaged over April – July for each tern breeding season.

Parameter	Slope (95% CI)	R^2	*P*
Colony Size	3.2E-3 (-5.4E-3 to 1.2E-2)	0.08	0.48
Productivity	-2.0E-6 (-5.5E-6 to 1.6E-6)	0.17	0.31
Salmonid Proportion of Diet	6.3E-7 (2.3E-7 to 1.1E-6)	0.56	0.03
Marine Forage Fish Proportion of Diet	-1.3E-6 (-1.8E-6 to -7.7E-7)	0.81	0.002

Figure 6.1. Trends in several climate indices for the Pacific Northwest Region of the U.S. during 2000 – 2008. See text for data sources.


(A) Pacific Decadal Oscillation (PDO)
PDO Anomoly
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
2000
2001
2002
2003
2004
2005
2006
2007
2008
October - December
October - April
January - April
April - July
(B) Multivariate ENSO Index (MEI)
MEI Anomoly
1.5
1
0.5
0
-0.5
-1
-1.5
(C) Buoy Sea Surface Temperature
Temperature Anomoly, °C
1.5
1
0.5
0
-0.5
-1
-1.5
(D) Interpolated Sea Surface Temperature
Temperature Anomoly, °C
1
0.5
0
-0.5
-1
-1.5
-2


(E) Spring Transition Date
Day of Year
6/29
5/30
4/30
3/31
3/1
2000
2001
2002
2003
2004
2005
2006
2007
2008


(F) Upwelling Strength
Upwelling Index Anomoly
30
20
10
0
-10
-20
-30
-40
2000
2001
2002
2003
2004
2005
2006
2007
2008
June - July

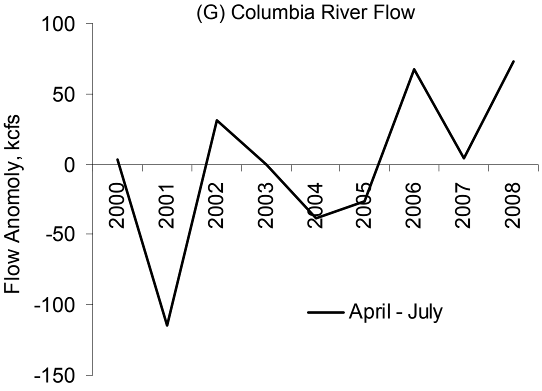
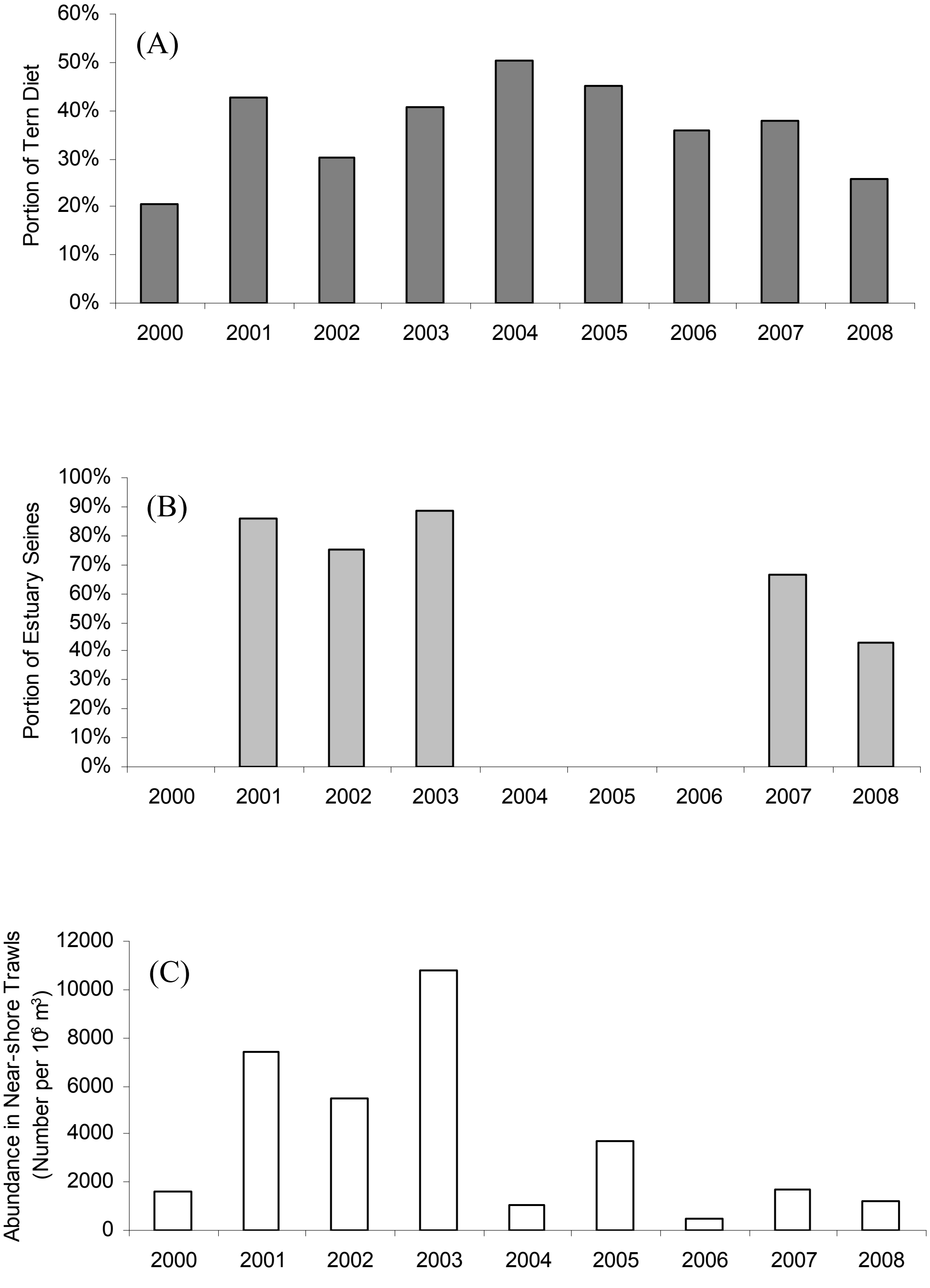

(G) Columbia River Flow
Flow Anomoly, kcfs
100
50
0
-50
-100
-150
2000
2001
2002
2003
2004
2005
2006
2007
2008
April - July

Figure 6.2. Marine forage fishes (northern anchovy [*Engraulis mordax*], Pacific herring [*Clupea pallasi*], and Pacific sardine [*Sardinops sagax*]) (A) in the diet of Columbia River estuary Caspian terns (*Hydroprogne caspia*), (B) their frequency of occurrence in seines conducted by NOAA Fisheries in the Columbia River estuary, and (C) their abundance in NOAA Fisheries surface trawls 5 – 10 km from shore off the mouth of the Columbia River and off Willapa Bay, the next large estuary to the north (Emmett 2006).


(A)
Portion of Tern Diet
60%
50%
40%
30%
20%
10%
0%
2000
2001
2002
2003
2004
2005
2006
2007
2008
(B)
Portion of Estuary Seines
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
2000
2001
2002
2003
2004
2005
2006
2007
2008
(C)
Abundance in Near-shore Trawls (Number per 10⁶ m³)
12000
10000
8000
6000
4000
2000
0
2000
2001
2002
2003
2004
2005
2006
2007
2008

Chapter 7

SYNOPSIS AND CONCLUSIONS

Donald E. Lyons

This dissertation focuses on the predator-prey relationships between two species of avian predators, Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*), and one of their important prey types, juvenile salmonids (*Oncorhynchus* spp.), in the Columbia River estuary of Oregon and Washington states. After over a century of decline (Lichatowich 1999), a majority of Columbia Basin salmonid populations are now listed under the U.S. Endangered Species Act (Good et al. 2005), and impacts of avian predators are considered a possible factor limiting recovery (NOAA 2008).

Potential impacts of avian predators are most significant in the estuary of the Columbia River, as opposed to elsewhere in the basin, for several reasons. First, the largest populations of piscivorous birds within the basin exist there and rely on salmonids for a significant portion of their diet (Collis et al. 2002). The Caspian tern and double-crested cormorant colonies on East Sand Island in the Columbia River estuary are in fact the largest colonies for each species currently known (Cuthbert and Wires 1999, Wires et al. 2001, Anderson et al. 2004). Secondly, all the evolutionarily significant units (ESUs) of salmonids within the Columbia Basin migrate through the estuary and are exposed to predation by birds present there, whereas smaller waterbird colonies spread throughout the basin have access to only one or a few ESUs (e.g., Antolos et al. 2005). Additionally, the juvenile salmonids that reach the estuary have the highest potential reproductive value to their respective populations of all the juveniles present in the Basin, as they are the survivors of two high mortality life-history stages, freshwater rearing and downstream freshwater migration.

Energy is a useful currency to quantify levels of predation and to more broadly understand ecological relationships between predators and prey. I used a data-rich bioenergetics framework to estimate prey consumption by Caspian terns and double-crested cormorants, and consumption of juvenile salmonids in particular. These bioenergetic-based prey consumption calculations required data input in four major categories: (1) predator energy requirements (adults and developing offspring), (2) energy content of all the various prey types, (3) predator abundance (again, both adults and developing offspring), and (4) predator diet composition.

Compared to other seabirds, Caspian terns appear to follow the ecological norm with respect to energy demands. Field metabolic rates (FMR) of breeding adult Caspian terns have been measured in this system and are 15% higher than allometric prediction based on seabirds in general but 8% less than predicted based on seabirds using flapping flight (Figure 7.1; Roby et al. 2003). The total metabolizeable energy requirement for a developing Caspian tern chick to fledge was just 6.5% higher than the allometric prediction (Chapter 2). Breeding adult double-crested cormorants exhibited unexpectedly high energy demands for their body mass compared to other seabirds, however, with average FMR 34% higher than predicted by allometric equations (Figure 7.1; Chapter 3). Possible reasons for greater than expected energy expenditure rates in cormorants may include larger brood size and higher chick growth rates (Dunn 1975) compared to most other seabird species where FMR has been measured (Visser 2001).

In terms of an energetic measure of prey quality, energy density (kJ per gram fresh mass), juvenile salmonids do not stand out from other members of the forage fish community present in the Columbia River estuary (Figure 7.2). For a given mass, marine forage fishes (Pacific sandlance [*Ammodytes hexapterus*], northern anchovy [*Engraulis mordax*], smelt [Osmeridae], and Pacific herring [*Clupea pallasi*]) were more energy-rich than most juvenile salmonids, and particularly more so than Chinook salmon (*O. tshawytscha*). Energy density is just one aspect of prey quality, however. Total energy content per fish is likely also an important selection criterion for avian predators, particularly Caspian terns, which carry a single whole fish back to their colonies in their bill to provision mates and chicks. In terms of this measure of prey quality, many juvenile salmonids rank higher than alternative prey, particularly steelhead (*O. mykiss*), which combine an intermediate energy density with nearly the largest average body mass of all the prey types consumed. Sub-yearling Chinook salmon are at the opposite extreme, ranking very low in energy content per fish based on low energy density and small size.

Energy demands of Caspian tern and double-crested cormorant chicks peak at around 3/5th of fledging age (~ 21 days post-hatch for Caspian terns [Chapter 2] and ~28 days post-hatch for double-crested cormorants [Dunn 1975]). The energy expenditure rates of parent terns and cormorants and the entire parent-offspring unit also peak at this time due to heightened foraging activity by parents to provision chicks. The pattern of energy demand for entire colonies of either species follows the energy demand curve for the family unit, but is modified by the synchrony of nesting and the rate of brood reduction, complete nest loss, and the timing of colony departure by adults and fledglings. Nesting synchrony and reproductive success varied considerably across the years of this study, but energy demand typically peaked in late May or early June for Caspian terns and in late June and early July for double-crested cormorants (Figure 7.4). Cormorants, particularly young of the year, extended their presence in the estuary into October in most years of the study; however, terns usually left the estuary within a week or two of completing nesting activities, with the colony largely empty by sometime in August. Total energy requirements were substantially greater for the cormorant colony, due to the larger body size of cormorants (2275 g vs. 650 g for terns), longer period of residency, and in the later years of this study, larger colony size.

The energy demands of these avian predators overlapped across the year with the timing of migration of most juvenile salmonids through the estuary. The migratory peak for spring migrating smolts (yearling Chinook and coho salmon and steelhead) generally occurred in mid-May (Fish Passage Center 2007), slightly prior to the peak Caspian tern energy demand and well in advance of the peak cormorant energy demand. Later migrating (June and July) sub-yearling Chinook salmon entered the estuary when energy requirements of the tern colony were declining but when cormorant requirements were still substantial.

Diet composition data collected each year across the season showed some similar trends between avian predator species, but greater reliance upon salmonids by Caspian terns than by double-crested cormorants (Figures 7.5A and 7.6A; Chapters 4 and 5). Once diet composition data are combined with data on average prey mass, energy density, and the seasonal attendance pattern for each bird species, it is possible to calculate the relative energetic contribution of each prey type to meeting the energy requirements of each colony (Figure 7.5B and 7.6B). For Caspian terns, salmonids actually made up a greater proportion of the energy acquired by the tern colony than the diet composition data alone would suggest. Conversely, salmonids are of lesser importance to the cormorant colony across the season than the diet composition data suggest. These species differences in part reflect a closer synchronization of peak energy demands and availability of higher quality salmonids (steelhead and coho) in terns than in cormorants.

Using the various input data described above, I employed a bioenergetics technique to estimate the numbers of prey consumed by terns and cormorants, and specifically the number of juvenile salmonids consumed (Figure 7.7). Between 7 and 15 million smolts have been consumed annually by these avian predators during the period 2000 – 2007. In recent years, the point estimates of salmonid consumption by cormorants have exceeded those of terns, although 95% confidence intervals still overlap. Given the upward trend in cormorant population size over the last decade and the relative stability of the tern population, it seems that double-crested cormorants are likely to pose greater impacts on salmonid populations in the Columbia Basin in the future, particularly once the majority of the tern colony is dispersed by managers to locations outside the basin (USFWS 2005).

These smolt consumption estimates, in combination with estimates of smolt availability in the Columbia River estuary, can be used to derive species-specific (and for Chinook, life history type-specific) mortality rates (Figure 7.8). The mortality rates of coho salmon and steelhead smolts due to combined predation by terns and cormorants averaged more than 15% of available smolts over the study, and were about 8% of available smolts for Chinook salmon. For salmonid stocks that originate above Bonneville Dam (the lowest mainstem dam in the Columbia Basin), mortality rates from smolt migration through Bonneville Dam until the return of these fish as adults (often discussed as "ocean mortality", but actually including estuarine mortality as well) are typically > 95%, with mortality for some cohorts exceeding 99% (Kareiva et al. 2000, Logerwell et al. 2003, Scheuerell and Williams 2005, Zabel et al. 2006). Mortality due to predation by terns and cormorants in the estuary, at ca. 7 – 15%, makes up a significant fraction of this loss. This level of mortality due to avian predation in the estuary is also comparable to mortality levels in a single reach of the Columbia River above Bonneville Dam (from one mainstem dam to the next mainstem dam below it), which ranges from about 5 to 15% (e.g., Faulkner et al. 2007).

The salmonid mortality rates due to avian predation can be put into the context of other salmonid recovery actions using the framework of an age-structured, deterministic population growth model (McClure et al. 2000, McClure et al. 2003, Roby et al. 2003, Good et al. 2007). Using this framework, I estimated the possible increase in the average annual population growth rate (λ) if avian predation by terns and cormorants were reduced. For this analysis, I used mortality rates due to cormorant predation averaged from 2006 – 2007 only, as these recent years were qualitatively and quantitatively different than earlier years. Mortality rates for terns were averaged across 2000 – 2007, the period during which tern nesting has occurred exclusively or primarily on East Sand Island. I assumed that tern predation would be reduced by 60%, consistent with the current management plan (USFWS 2005), and considered a hypothetical scenario where cormorant predation was reduced 50% (no cormorant management plan has yet been considered). Additionally, I assumed that other mortality factors would compensate for 50% of any reduction in avian predation. The actual degree of compensation that might occur is unknown, but is likely some intermediate level, rather than avian predation being completely additive or completely compensatory (Roby et al. 2003). Under this scenario, the potential improvement in λ for reductions in avian predation ranged from 0.4% for sub-yearling Chinook salmon to 3.1% for coho salmon (Figure 7.9).

Two comparisons are helpful to put these potential demographic benefits to salmonids in context. First, Figure 7.10 presents a comparison of the above estimated potential improvement in λ on a species basis to published estimates of needed improvements in λ for the evolutionarily significant units of Chinook, coho, and steelhead listed under the U.S. Endangered Species Act (ESA). For most ESUs of Chinook and steelhead, the potential benefits of managing avian predation would not be sufficient to increase λ to a stable level (λ = 1). For a few ESUs, particularly for Lower Columbia River (LCR) coho, potential benefits from reductions in avian predation are of a similar magnitude to that which is needed to stabilize the population. Even for these ESUs, however, other recovery actions would be required to see population increases ($\lambda > 1$).

A second useful contextual comparison is between potential benefits of reduced avian predation and estimated benefits of other salmon recovery objectives. The best data available for such a comparison are for altered hydropower system operation (Figure 7.11; McClure et al. 2003). For Chinook salmon, potential benefits from improvements to hydropower system operation are more substantial than those from reductions in avian predation, with the exception of the Upper Willamette River (UWR) ESU, which accrues little benefit from altered operation of mainstem Columbia River dams, all of which exist above the confluence of the Columbia and Willamette rivers. For steelhead, benefits of reduced avian predation are comparable to those estimated for altered hydropower system operation for most ESUs, and benefits from reduced avian predation outweigh the negligible benefits from hydropower changes for the UWR ESU. Additional hydropower system changes have been proposed (NOAA 2008) since McClure et al. (2003) but for ESUs not as significantly affected by the hydropower system (i.e., Upper Willamette River, Lower Columbia River), reductions in avian predation may still provide comparable benefits.

Many factors have been shown to influence the susceptibility of individual juvenile salmonids to avian predation in the Columbia River, including size, rearing history, run timing, body condition, disease, and migration history (Collis et al. 2001, Ryan et al. 2003, Hostetter 2009). Climate-driven ocean conditions have also been implicated in salmonid survival (Logerwell et al. 2003, Scheuerell and Williams 2005, Zabel et al. 2006), but the specific effects of climate on mechanisms of mortality (e.g., predation) have not been easy to examine (but see Emmett 2006, Emmett and Sampson 2007).

Investigating the effects of climate on Caspian tern predation on juvenile salmonids (Chapter 6), I found that terns responded both numerically and functionally to large-scale climate indices such as the Pacific Decadal Oscillation (Mantua et al. 1997) and the El Niño/Southern Oscillation (Wolter and Timlin 1993, 1998). In years of cooler conditions, the East Sand Island tern colony was larger and alternative prey (marine forage fish) were a smaller proportion of tern diets, apparently because they were less likely to spend time in the Columbia River estuary. Both factors contributed to increased tern predation on salmonids in cool years. An additional climate-driven factor, Columbia River flow (driven primarily by winter snow pack in the mountains of the Columbia Basin), was related to tern predation on salmonids, with greater predation on salmonids in years of higher flow, apparently again due to the lower prevalence of marine forage fish in the estuary in those years. Interestingly, similar examinations of climate in relation to cormorant predation on juvenile salmonids did not identify any apparent relationships, perhaps due to the larger effect of cormorant colony growth during the study period.

Despite over a decade of study by scores of biologists, scientific uncertainty remains regarding the significance of avian predation on juvenile salmonids in the Columbia River estuary. We now know that millions of smolts are consumed by

Caspian terns and double-crested cormorants on an annual basis in the Columbia River estuary and that this predation constitutes a significant mortality rate: 7 – 15%, depending on species and life history type. This level of mortality is comparable or greater than the impacts of many other anthropogenic factors in the freshwater environment and is a significant proportion of the estuary/ocean mortality all anadromous salmonids endure. Determining the significance of this mortality at the juvenile life history stage on adult population size has remained problematic, however. Recent research on the differential susceptibility of smolts having differing health or body condition status has suggested that salmonid mortality due to avian predation may be at least partially compensated for by other mortality sources (Schreck et al. 2006, Hostetter 2009); however, the degree to which this compensation may occur is largely unknown. Perhaps the greatest contribution future studies of avian predation might make would be an enhanced understanding of the degree to which avian predation is additive or compensatory.

Given the remaining scientific uncertainties, an adaptive management approach to reducing avian predation on juvenile salmonids would appear to have obvious benefits. Any large reductions in predation, particularly on heavily depredated coho and steelhead, might provide the best opportunity to observe an effect on adult abundance and thus offer insight into the question of the additive vs. compensatory nature of smolt mortality due to avian predation. Unfortunately, detecting a change in adult abundance due solely to reductions in avian predation will always be unlikely, due to the myriad of other confounding factors, including natural environmental variation, directional climate change, an increasing human population within the Columbia Basin, and other salmon recovery activities. It seems prudent to design future management efforts to attempt to answer important questions, but to acknowledge the likely continued uncertainty on fundamental scientific issues. Given this likely future uncertainty, management approaches that reduce avian predation, but are also benign to regional populations of piscivorous birds, seem most likely to win broad support among diverse interest groups. One such management paradigm is the careful management of nesting habitat for piscivorous birds – preventing birds from nesting in areas where their impacts on salmonids will be pronounced, but providing suitable nesting habitat in areas where impacts on threatened fishes will be less problematic (Roby et al. 2002, Chapter 4). A distributed network of suitable nesting sites across western North America could minimize impacts to any particular fish population and avoid the elevation of risk for piscivorous bird populations when huge proportions of their populations are concentrated at a single nesting site.

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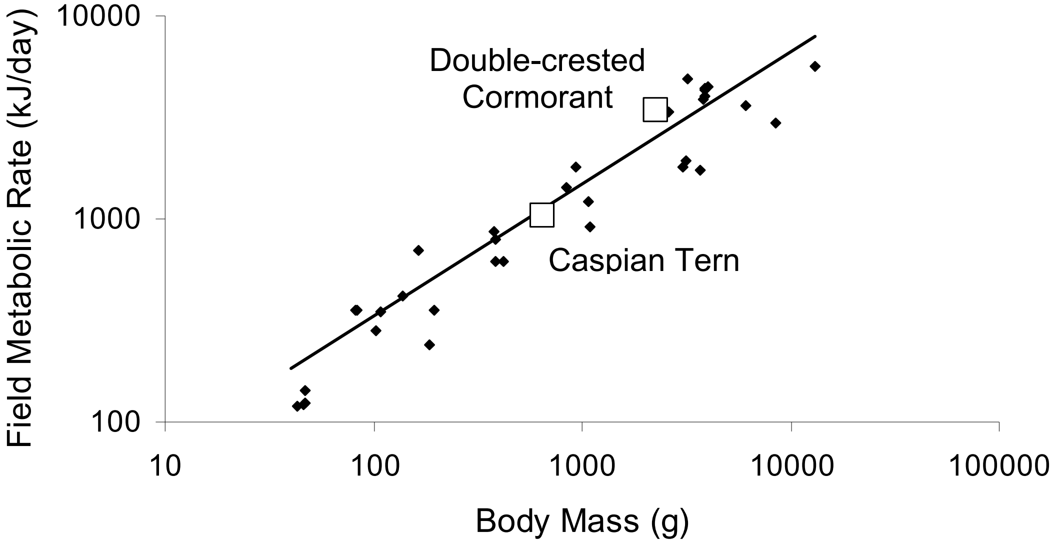


Figure 7.1. Field metabolic rates of breeding adult seabirds after Ellis and Gabrielsen (2001). Caspian tern (*Hydroprogne caspia*) metabolic rates are similar to the allometric prediction (Roby et al. 2003); however, double-crested cormorant (*Phalacrocorax auritus*) values exceed prediction by 34% (Chapter 3).

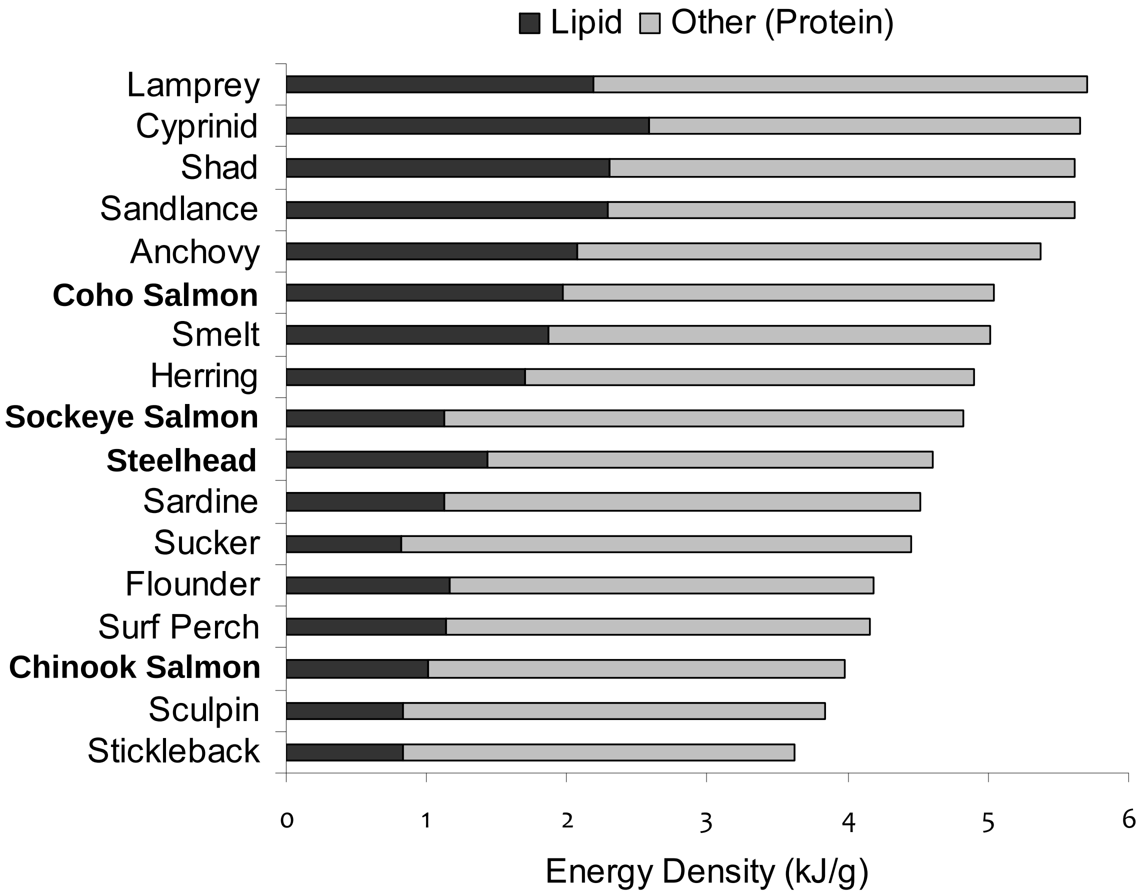


Figure 7.2. Energy density of forage fishes in the diet of Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary. Juvenile salmonids are highlighted in bold text.

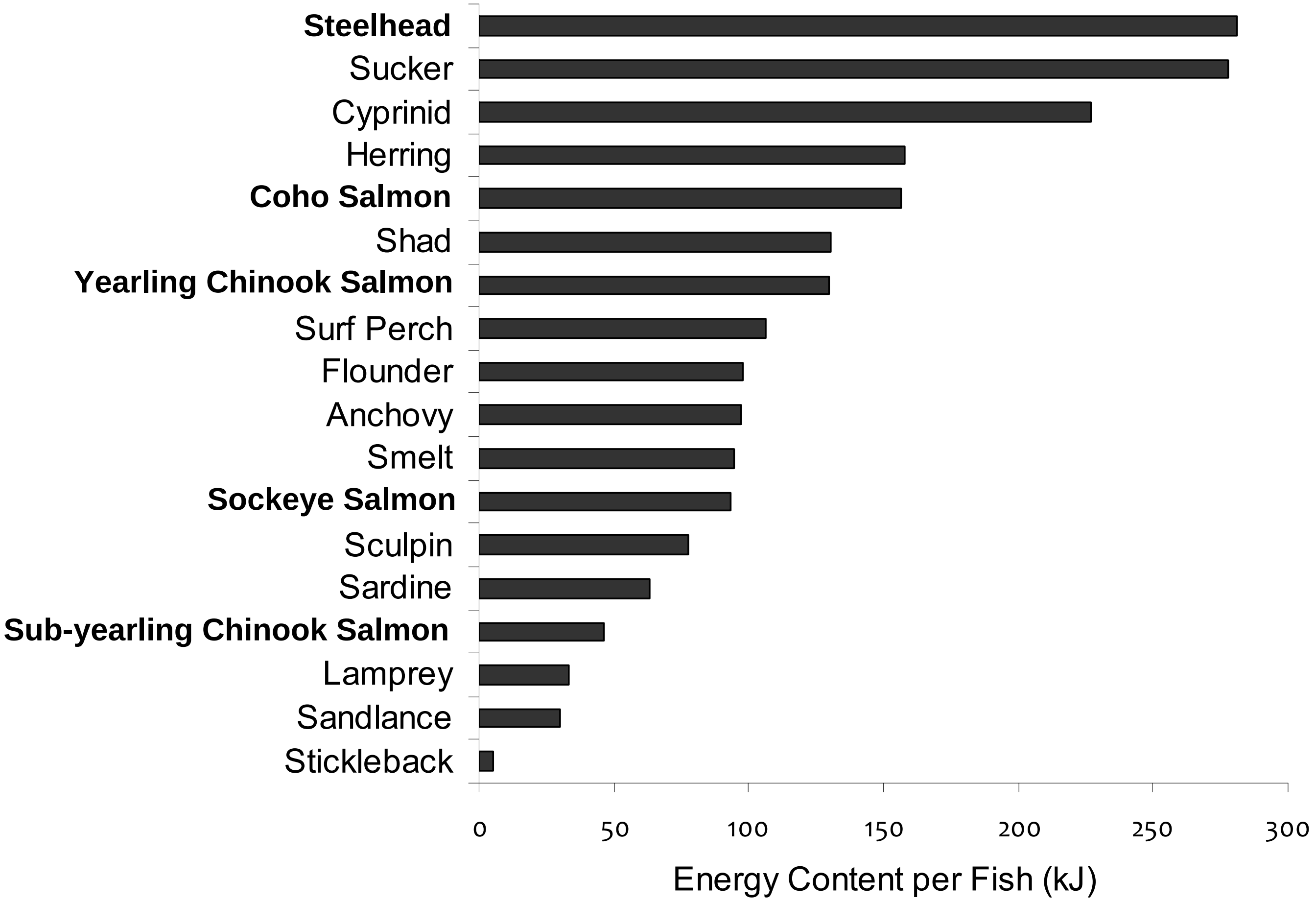


Figure 7.3. Energy content of common prey of Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary. Juvenile salmonids are highlighted in bold text.

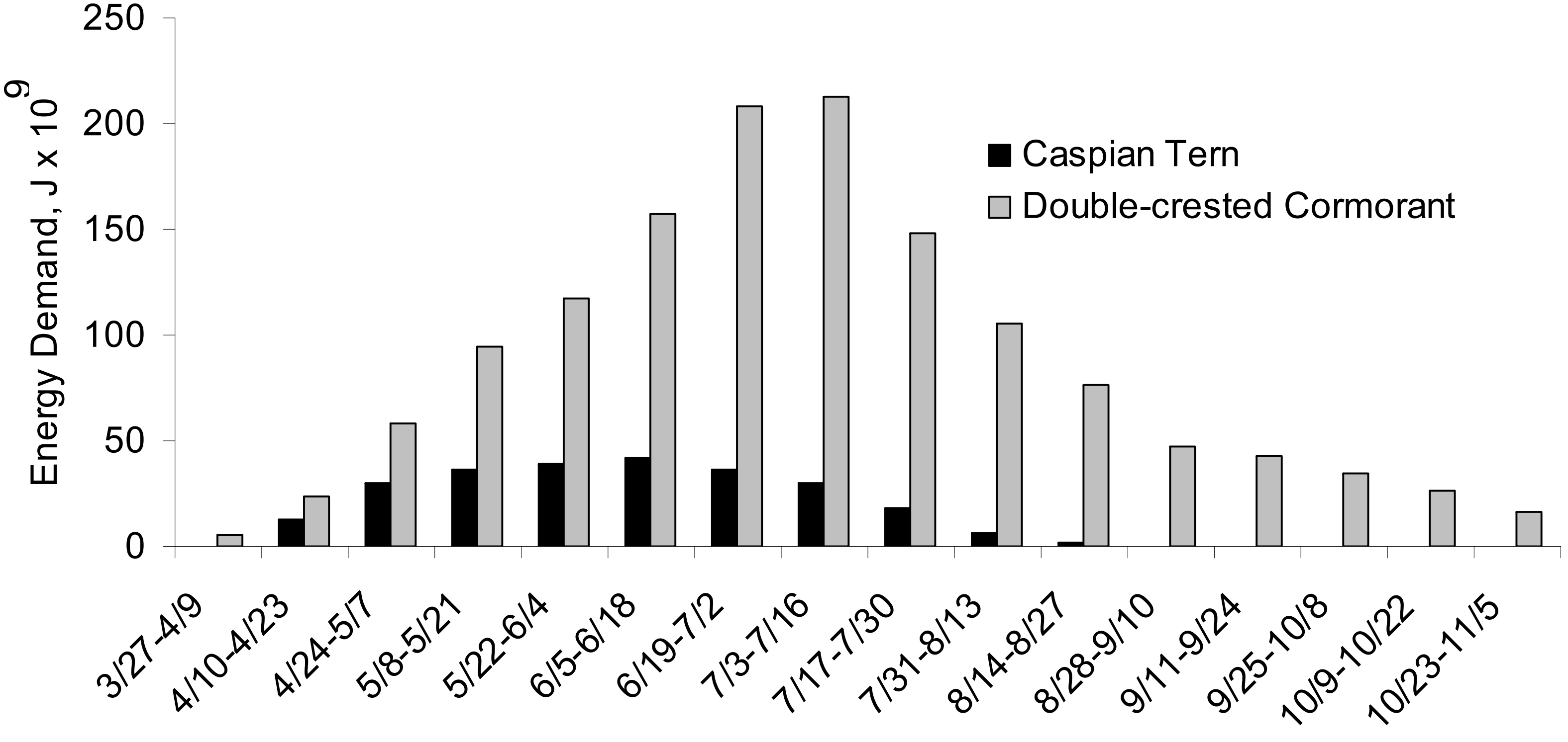


Figure 7.4. Typical energy demand for entire breeding colonies across the annual breeding cycle for Caspian tern (*Hydroprogne caspia*) and double-crested cormorant (*Phalacrocorax auritus*) colonies on East Sand Island in the Columbia River estuary.

Figure 7.5. Typical annual values of the (A) unweighted diet composition (by frequency) and (B) resulting prey energy contribution for the Caspian tern (*Hydroprogne caspia*) colony on East Sand Island in the Columbia River estuary.

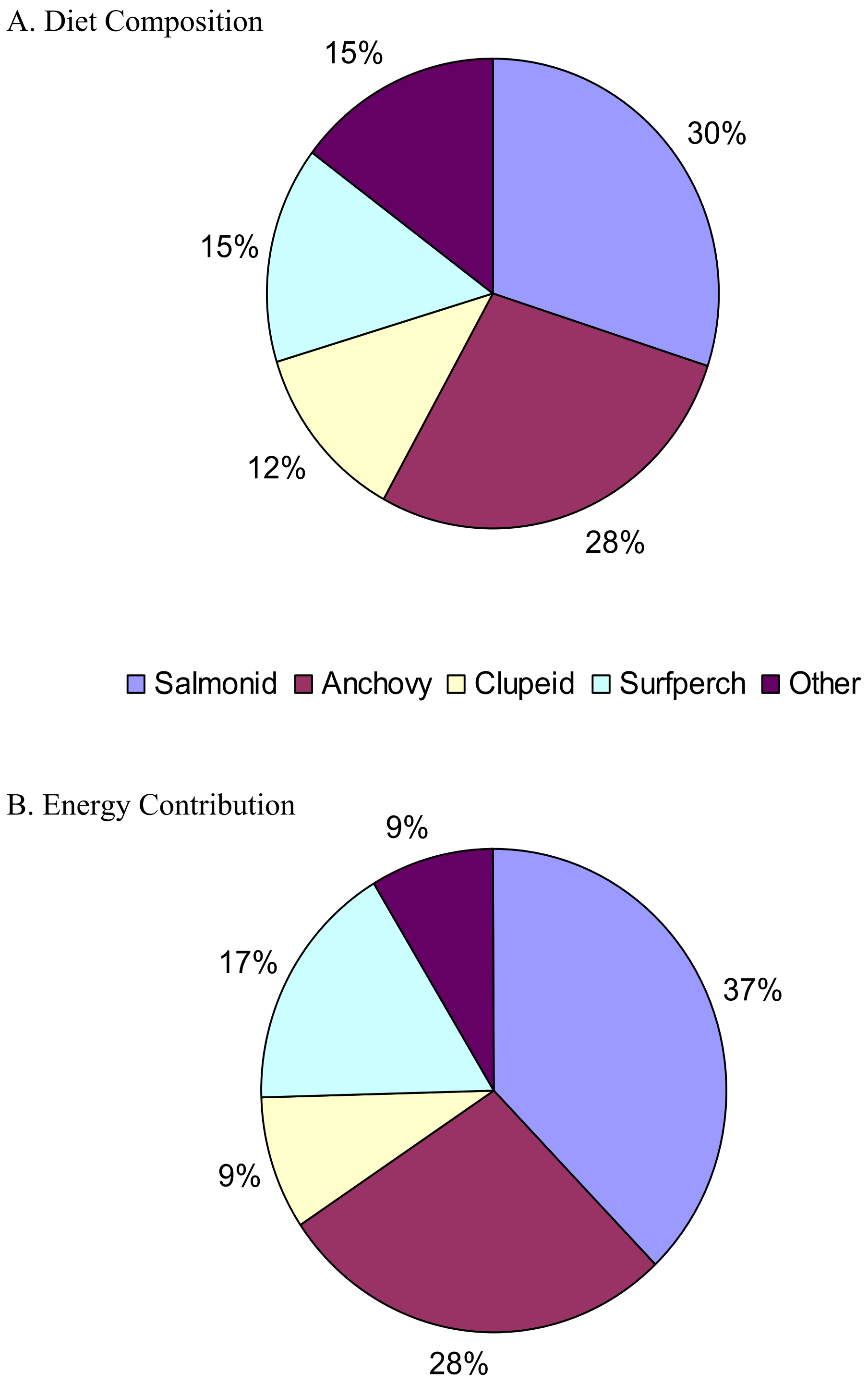
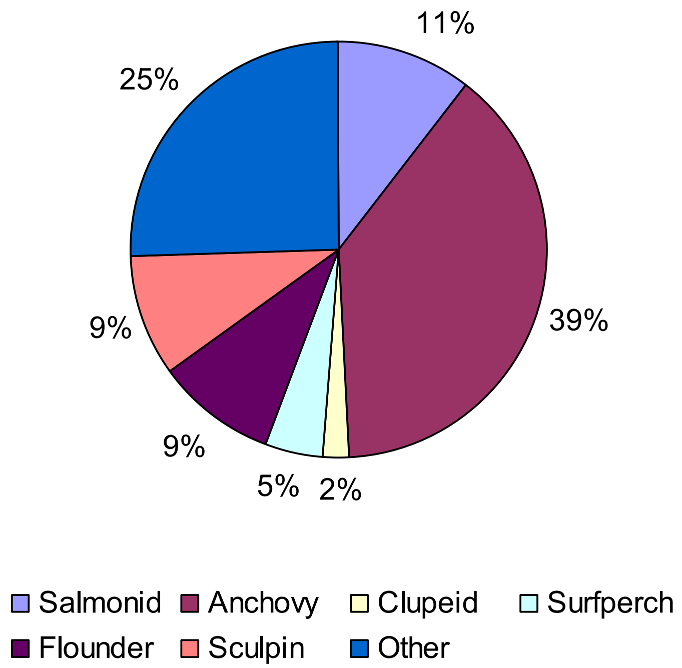
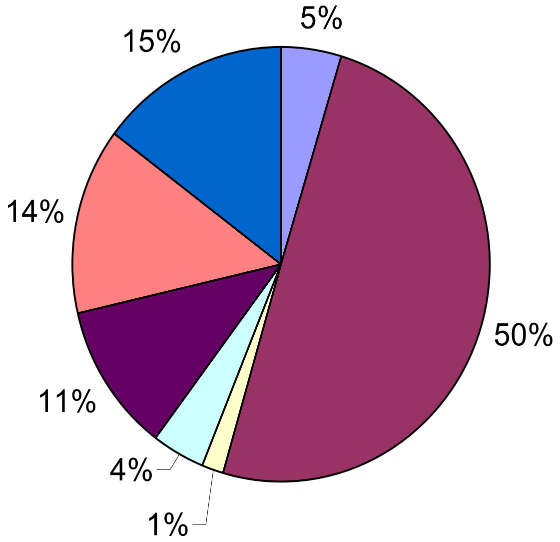

A. Diet Composition
15%
30%
15%
12%
28%
■ Salmonid ■ Anchovy ■ Clupeid ■ Surfperch ■ Other
B. Energy Contribution
9%
17%
37%
9%
28%

Figure 7.6. Typical annual values of the (A) unweighted diet composition (by biomass) and (B) resulting prey energy contribution for the double-crested cormorant (*Phalacrocorax auritus*) colony on East Sand Island in the Columbia River estuary.



A. Diet Composition



B. Energy Contribution

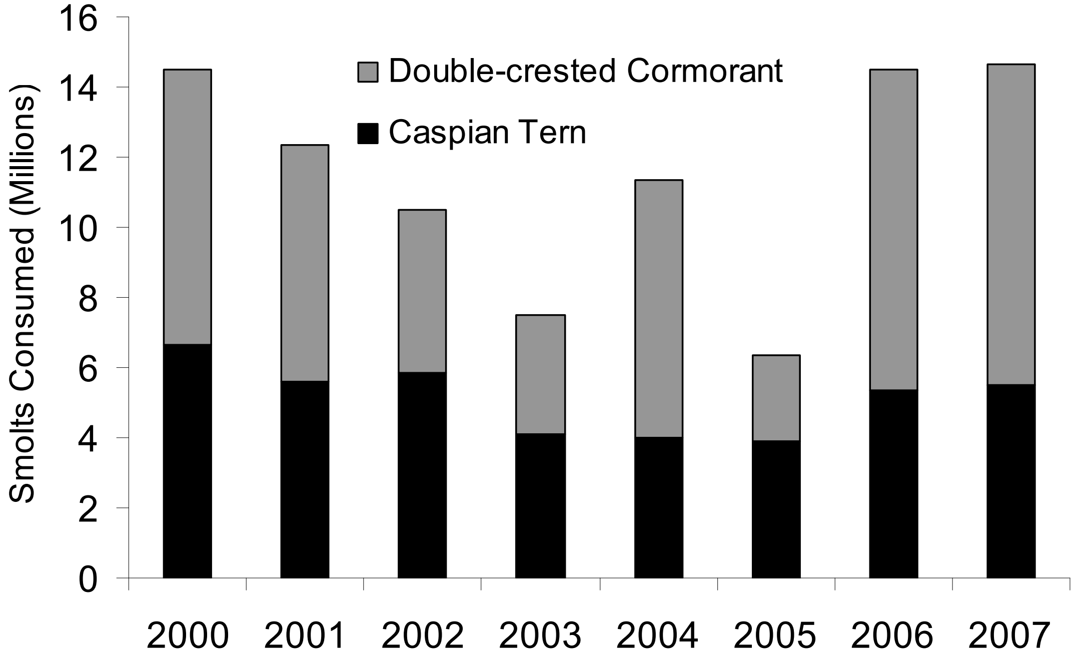
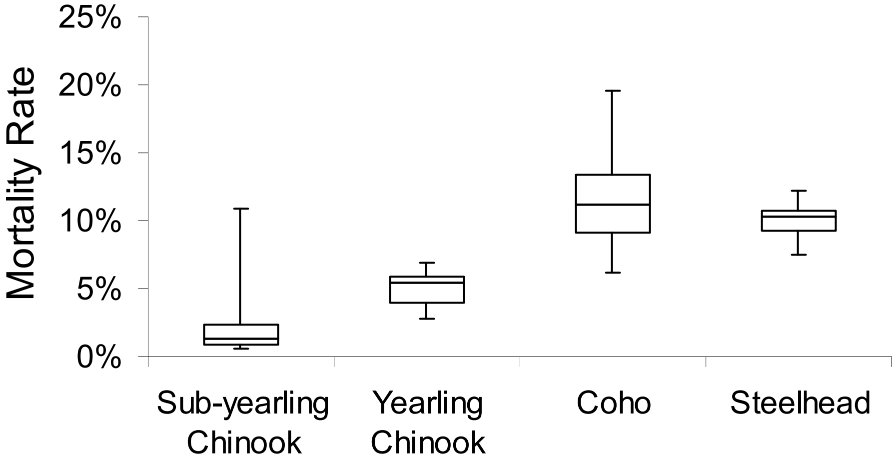


Figure 7.7. Annual consumption of juvenile salmonids (*Oncorhynchus* spp.) by Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) nesting at colonies on East Sand Island in the Columbia River estuary.

A. Caspian terns



B. Double-crested cormorants

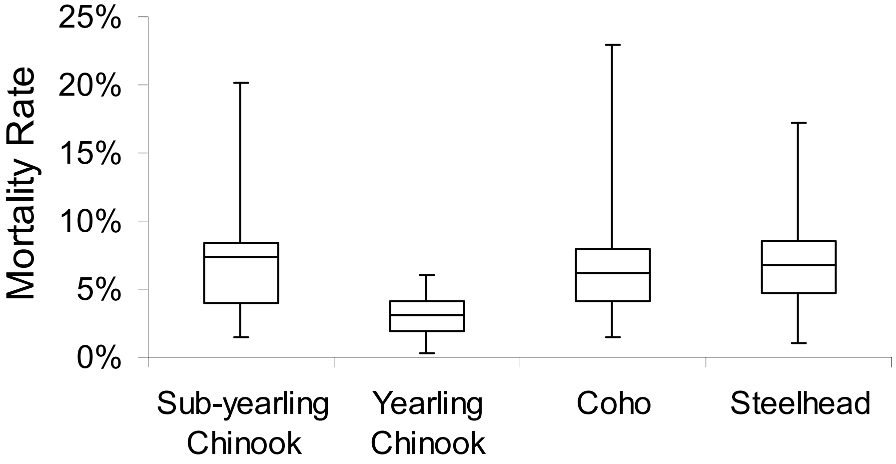


Figure 7.8. Salmonid (*Oncorhynchus* spp.) species-specific (and life history type-specific for Chinook salmon [*O. tshawytscha*]) mortality rates due to avian predation by (A) Caspian terns (*Hydroprogne caspia*) and (B) double-crested cormorants (*Phalacrocorax auritus*) nesting on East Sand Island in the Columbia River estuary. Boxplots depict the range in estimates of annual mortality rates.

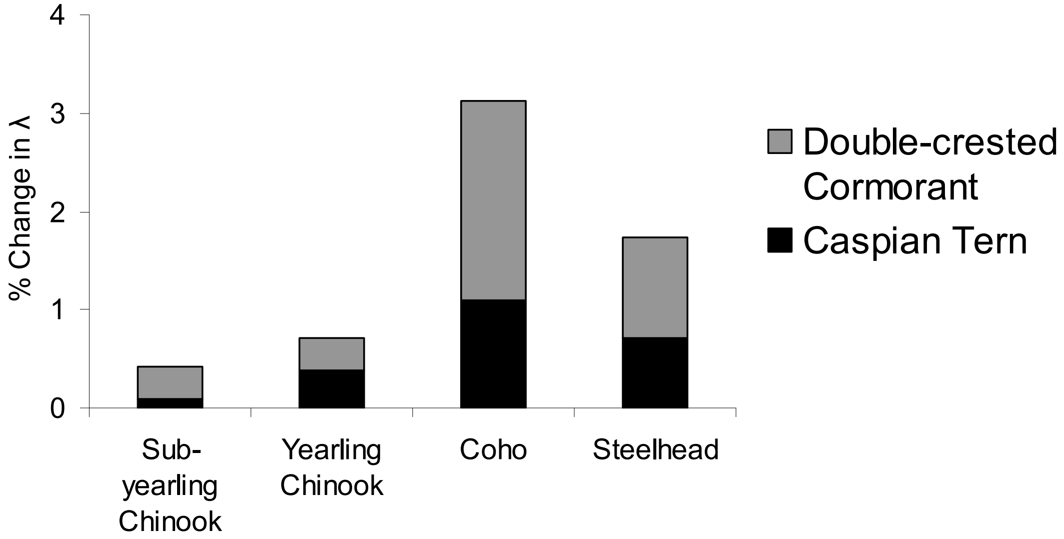


Figure 7.9. Potential improvements in the average annual population growth rate (λ) of Columbia Basin salmonids (*Oncorhynchus* spp.) if avian predation by Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) were reduced in the Columbia River estuary. A 60% reduction in tern predation, a 50% reduction in cormorant predation, and a 50% compensatory mortality rate in salmonids spared from avian predation were assumed.

Figure 7.10. Comparison of estimated improvements (% change) in the average annual population growth rate (λ) of Columbia Basin salmonids due to potential reductions in avian predation in the Columbia River estuary and the needed improvements in λ (% change) for the salmonid evolutionarily significant units listed under the U.S. Endangered Species Act to achieve a stable population growth rate (λ = 1). Needed improvements are drawn from McClure et al. (2003).

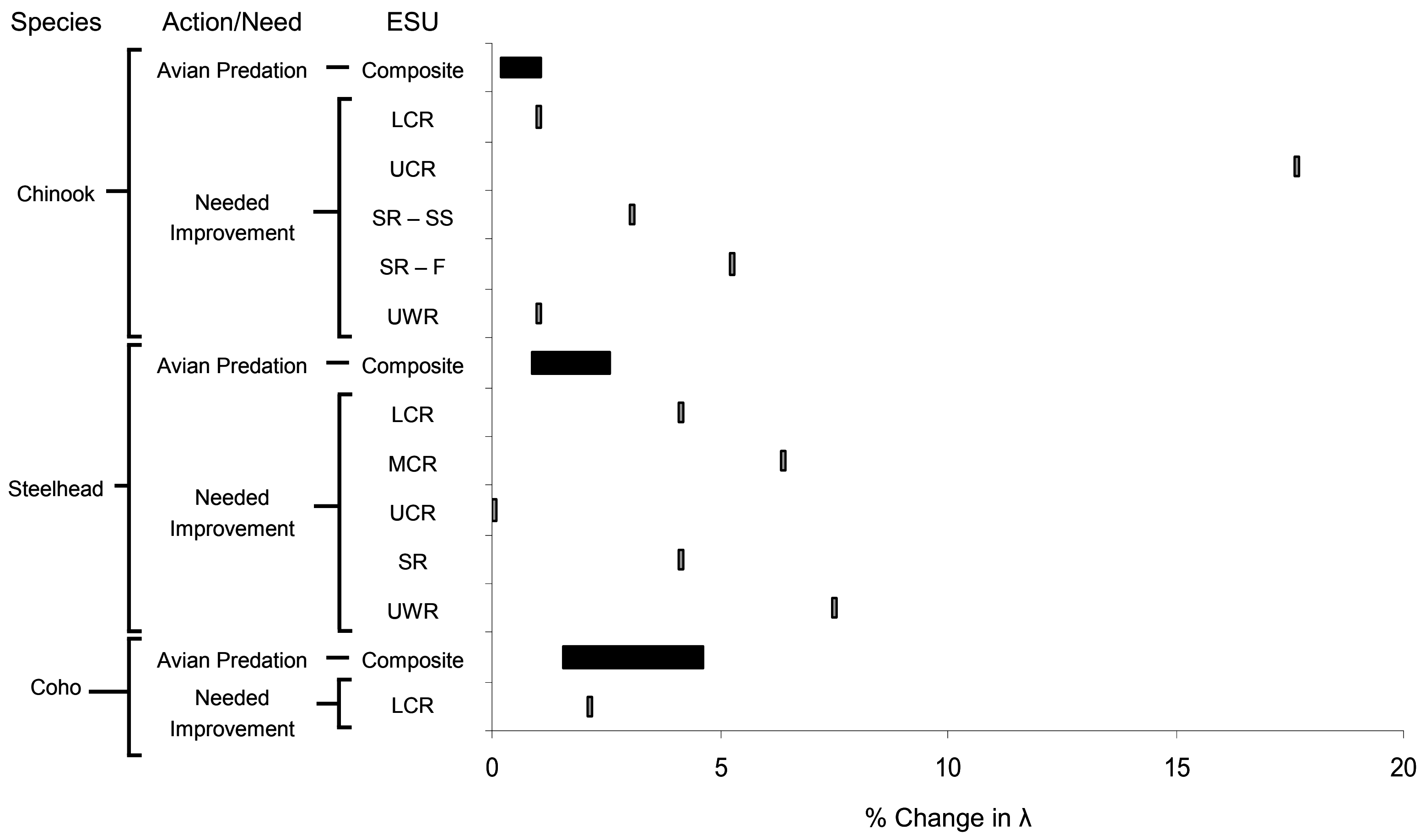
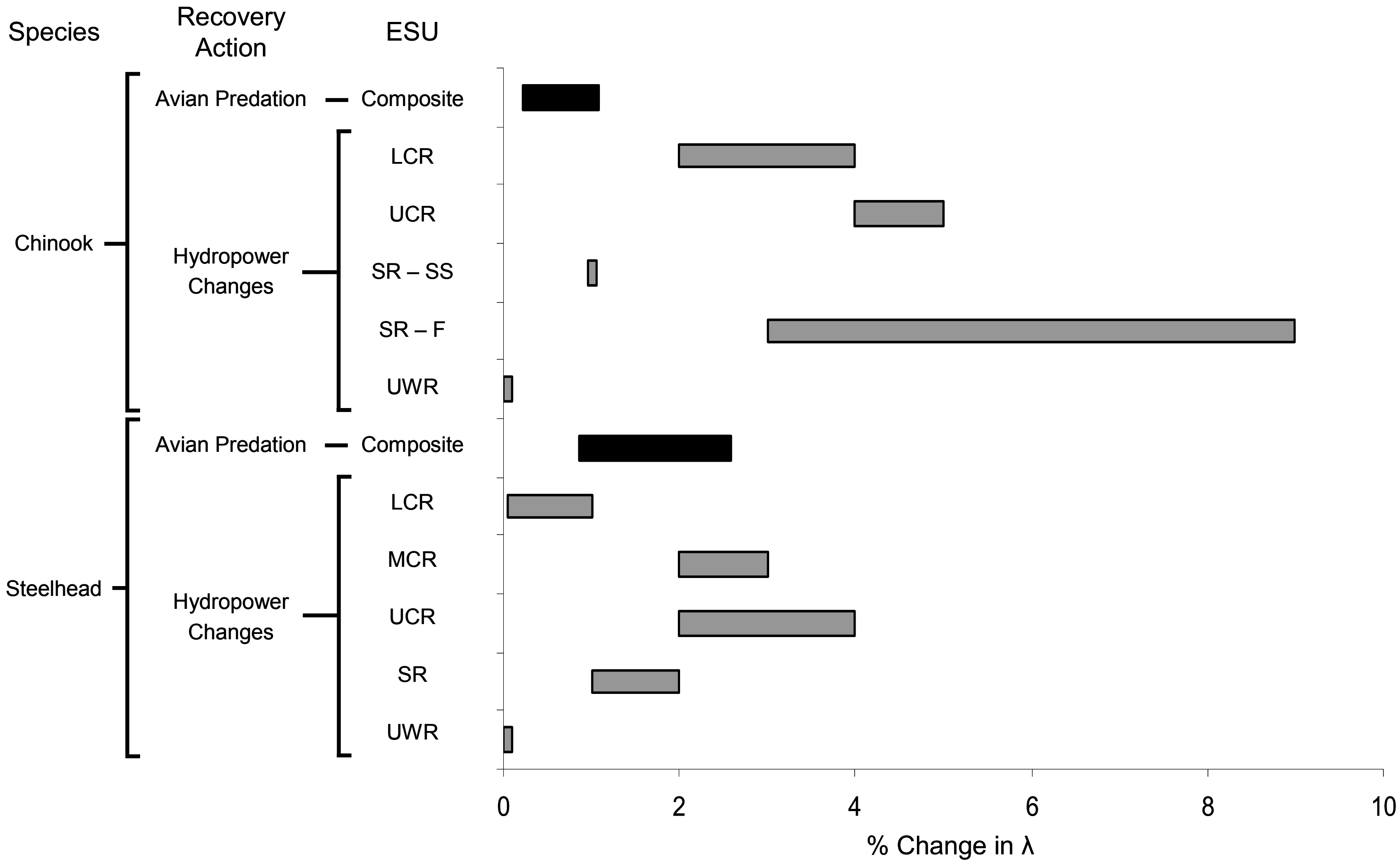

Species
Action/Need
ESU
Chinook
Avian Predation
Composite
Needed Improvement
LCR
UCR
SR – SS
SR – F
UWR
Steelhead
Avian Predation
Composite
Needed Improvement
LCR
MCR
UCR
SR
UWR
Coho
Avian Predation
Composite
Needed Improvement
LCR
0
5
10
15
20
% Change in λ

Figure 7.11. Comparison of potential improvements (% change) in the average annual population growth rate (λ) of Columbia Basin salmonids due to potential reductions in avian predation in the Columbia River estuary and due to altered management of the Federal Columbia River Hydropower System (McClure et al. 2003).


Species
Recovery Action
ESU
Chinook
Avian Predation
Composite
Hydropower Changes
LCR
UCR
SR – SS
SR – F
UWR
Steelhead
Avian Predation
Composite
Hydropower Changes
LCR
MCR
UCR
SR
UWR
0
2
4
6
8
10
% Change in λ

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