Avian Predation on Juvenile Salmonids in the Lower Columbia River

1997 Annual Report

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EXECUTIVE SUMMARY

Virtually every evolutionarily significant unit (ESU) of anadromous salmonid (*Oncorhynchus* spp.) in the Columbia River Basin is currently or soon will be listed under the Endangered Species Act of 1973. Colonial waterbirds (i.e., terns, cormorants, and gulls) may be important predators on juvenile salmonids in the lower Columbia River. Consequently, we initiated a study in 1997 to assess the impacts of fish-eating birds on the survival of juvenile salmonids during the out-migration. The objectives of this study were to (1) estimate the size of fish-eating waterbird colonies in the lower Columbia River and determine population trends, (2) estimate the number of juvenile salmonids consumed by these populations, (3) identify the factors that influence avian predation rates on smolts, and (4) recommend ways to reduce avian predation on smolts, if warranted by the study results.

There were nine major colonies of fish-eating birds that nested on islands in the lower Columbia River and estuary in 1997. Most of these islands are unnatural, created by either the dumping of dredge material or rising water levels associated with mainstem dam impoundments. Population censuses indicated that the number of fish-eating colonial waterbirds totaled roughly 170,000 individuals, a substantial increase over previous estimates. Rice Island, a dredge material disposal island in the Columbia River estuary, supported the largest known Caspian tern (*Sterna caspia*) colony in North America (over 16,000 birds in 1997), which had grown by over 600% since the colony originated in 1987. Two colonies of double-crested cormorants (*Phalacrocorax auritus*) in the estuary were the first and second largest on the entire Pacific coast of the U.S. and Canada. The nesting period for these colonies (mid-April to mid-July) generally coincided with the period of smolt out-migration. Nesting success at the Rice Island Caspian tern colony was low (ca. 5% of breeding pairs successfully raised a chick), due mostly to predation on eggs and chicks by glaucous-winged/western gulls (*Larus glaucescens* X *L. occidentalis*). Nesting success of double-crested cormorants, in contrast, was over 50%.

Diet analysis indicated that juvenile salmonids were an important part of the diet of some fish-eating waterbirds nesting in the Columbia River estuary. Caspian terns appeared to be most dependent on salmonids (roughly 75% of the diet), followed by double-crested cormorants (roughly 24% of the diet) and glaucous-winged/western gull hybrids (roughly 11% of the diet). The large California and ring-billed gull (*Larus californicus* and *L. delawarensis*) colonies up-river relied less on juvenile salmonids as a food source compared to fish-eating waterbirds in the estuary, perhaps due to high flows in 1997 and measures implemented at Columbia River dams to reduce bird predation. Juvenile salmonids were especially prevalent in the diets of fish-eating waterbirds in the estuary during May. Steelhead smolts were most prevalent in Caspian tern diets during early May, followed by coho smolts in late May - early June, and then chinook smolts in late June - late July.

Over a thousand salmonid smolt PIT tags were found on the Rice Island Caspian tern colony and we estimated that over 30,000 PIT tags have been deposited there over the last nine years. The recovered PIT tags indicate that steelhead smolts were consumed in greater proportion to availability than other salmonid species, and that juvenile salmonids of hatchery origin were consumed in greater proportion to availability than wild fish.

We estimate that 6 - 25 million juvenile salmonids were consumed by Caspian terns nesting on Rice Island in 1997, or approximately 6 - 25 % of the estimated 100 million out-migrating smolts that reach the estuary. We lack sufficient data to estimate the number of juvenile salmonids lost to cormorants and gulls in the estuary (collection of these data is proposed in 1998), but preliminary data suggest it is in the millions. Various management alternatives to reduce predation by Caspian terns on juvenile salmonids are discussed, including translocating the colony to a previous colony site on East Sand Island where a greater diversity of non-salmonid prey is available.

INTRODUCTION

Published research suggests that avian predation can be a substantial source of mortality for juvenile salmonids. Mace (1983) estimated that 10.4 - 31.7 % of hatchery-released chinook salmon smolts (*Oncorhynchus tshawytscha*) in the Big Qualicum River on Vancouver Island succumbed to avian predation within just two km of the hatchery. A subsequent study on the same river estimated that predation by merganser broods alone accounted for 24 - 65 % of smolt production (Wood 1987). Feltham (1995) estimated that mergansers removed 3 - 16 % of smolt production on two Scottish rivers. In a three year study on the Penobscot River in Maine, predation by double-crested cormorants (*Phalacrocorax auritus*) on hatchery-reared Atlantic salmon (*Salmo salar*) accounted for 7.5 - 9.2 % of the run (Krohn and Blackwell 1996; Blackwell 1995). Perhaps most impressive is the estimate by Kennedy and Greer (1988) that 51 - 66% of smolts from a wild run in an Irish river were lost to cormorant (*P. carbo*) predation.

Aggregations of piscivorous birds have been observed on the Columbia River near dams (Steuber et al. 1993; Jones et al. 1996), at hatchery (Schaeffer 1991, 1992) and barge release points (K. Collis, CRITFC, pers. obs.), and in the estuary (Bevan et al. 1994) near the large waterbird breeding colonies at Rice and East Sand islands. Ruggerone (1986) estimated that 2 % of the juvenile salmonids passing Wanapum Dam during the spring were eaten by gulls (primarily ring-billed gulls [*Larus delawarensis*]) foraging in the tailrace below the powerhouse. This estimate did not include juvenile salmonids lost to avian predators in the forebay or in the tailrace below the spillway. Avian predation on radio-tagged chinook smolts has been documented in the tailraces below The Dalles and John Day dams and in the Columbia River estuary (C. Schreck, OSU, pers. comm.). In 1995, 11.3 % (11/97) of radio-tagged yearlings and 5.7 % (4/71) of subyearlings fell prey to gulls below The Dalles Dam (J. Snelling, OSU, pers. comm.). In 1996, between 5 % and 38 % of radio-tagged chinook yearlings that resided in the Columbia River estuary were consumed by terns and cormorants nesting in that area (C. Schreck, OSU, pers. comm.). Given that these bird populations represent a small percentage of the total number of fish-eating birds nesting in the lower Columbia River, system-wide losses of juvenile salmonids to avian predators are probably high.

Gulls (*Larus* spp.) appear to be one of the most prevalent predators on juvenile salmonids throughout the Columbia River Basin, particularly on the lower Columbia River above Bonneville Dam (Jones et al. 1996; Ruggerone 1986; Thompson and Tabor 1981). Two islands created by The Dalles Dam impoundment (Little Memaloose Island and Miller Rocks) support ca. 1,500-2,000 breeding pairs of California and ring-billed gulls (*Larus californicus* and *L. delawarensis*, respectively; Thompson and Tabor 1981), which are known to forage intensively on juvenile salmonids at The Dalles and John Day dams (J. Snelling, OSU, pers. comm.). Three Mile Canyon Island, created by the John Day Dam impoundment, supported a large gull colony of approximately 4,500 breeding pairs in 1978 (Thompson and Tabor 1981), but current status of this colony is unknown. Dramatic increases at other large gull colonies near the confluence of the Snake and Columbia rivers have been reported by the U.S. Fish and Wildlife Service (E. Nelson, USFWS, pers. comm.).

Large breeding colonies of glaucous-winged/western gull hybrids (*Larus glaucescens* X *L. occidentalis*) are located on three islands in the Columbia River estuary (A. Clark, USFWS, pers. comm.). Although little is known about predation by glaucous-winged/western gulls on juvenile salmonids in the Columbia River Basin, they are opportunistic feeders and known to forage on smolts when they are locally abundant (Mossman 1959, Vermeer 1982).

Double-crested cormorants are a common piscivore in the lower Columbia River and estuary. Two large cormorant colonies have been reported on Rice and East Sand islands in the estuary. Together these two colonies, plus associated breeding pairs on nearby pilings and channel markers, support a population of approximately 4,500 breeding pairs (A. Clark, USFWS, pers. comm.). Annual aerial surveys conducted by the U.S. Fish and Wildlife Service since 1991 indicated that this breeding population is increasing in size. This is consistent with continent-wide growth in double-crested cormorant populations and increasing frequency of conflicts with salmonid and other fisheries (Nettleship and Duffy 1995; Derby and Lovvorn 1997).

Caspian terns (*Sterna caspia*) are another potentially important predator of juvenile salmonids in the Columbia River Basin. Caspian terns are strictly piscivorous and the largest of the North American terns. A large colony consisting of c. 5,000 breeding pairs has become established on Rice Island, a dredge material disposal island, in the Columbia River estuary (A. Clark, USFWS, pers. comm.). Two smaller Caspian tern colonies have become established above Bonneville Dam on Three Mile Canyon Island and Crescent Island, and appear to be increasing (E. Nelson, USFWS, pers. comm.). Other new breeding colonies of this species on the lower Columbia River may have gone undetected, as this species is known for abrupt shifts between breeding sites (Gill and Mewaldt 1983).

Given the numbers, population trajectories, species diversity, and wide distribution of avian predators on the lower Columbia River, total losses of juvenile salmonids to birds may now comprise a substantial proportion of each run. An extensive and comprehensive study will be necessary to determine the full extent of avian predation on Columbia and Snake river salmonids.

Regional plans for Snake River salmon recovery have recommended that avian predation be thoroughly investigated (NPPC 1994; NMFS 1995; CRITFC 1995). Available data suggest that predation is a major source of mortality for juvenile salmonids migrating through the mainstem Columbia and Snake rivers (Ruggerone 1986; Bevan et al. 1994). Anthropogenic perturbations to the Columbia River System have exacerbated predation-related mortality (Rieman et al. 1991; Li et al. 1987), and contributed to increases in populations of some predators (Beamesderfer and Rieman 1991; Gill and Mewaldt 1983). California and ring-billed gull numbers have increased dramatically, likely associated with expanding irrigation-based agricultural development in the Columbia River Basin. New islands created by dredging and impounding the Columbia River have provided safe nest sites and attracted gulls and other colonial waterbirds to breed. The breeding season of these piscivorous birds coincides with the period of out-migration of salmon smolts, potentially resulting in predation pressure in the vicinity of larger colonies. The chick-rearing period is the stage of the annual cycle when population energy requirements are greatest due to rapid growth in nestlings and intense foraging activity by breeding adults.

Current management practices on the Columbia and Snake rivers offer many opportunities for predators to exploit salmon as a food source. Hydroelectric dams create "bottlenecks" to salmon migration and often injure or disorient out-migrating juvenile salmonids, increasing their vulnerability to avian predators. Hatchery and juvenile transportation practices that release salmonids *en mass* offer avian predators additional opportunities to exploit concentrated and vulnerable prey. Although extensive research has been conducted on the effects of piscivorous fishes on the survival of juvenile salmonids in the mainstem Columbia and Snake rivers (Rieman et al. 1991), no comprehensive study of avian predation on juvenile salmonids has been undertaken.

This project was designed to assess the impacts of avian predation on survival of juvenile salmonids. We sought to estimate the number of juvenile salmonids eaten by avian predators in the lower Columbia River (from the estuary to the head of McNary Pool), identify conditions under which predation is most prevalent, determine predator population trajectories, and provide recommendations to reduce predation by fish-eating birds, if warranted by the results. Our goal was to collect data that would improve our understanding of the factors affecting survival of salmonid smolts in the Columbia River Basin and provide managers with information important in decisions regarding salmon restoration.

Our specific objectives in the first year of this project were to; (1) identify the location, size, and population trajectories of piscivorous waterbird breeding colonies, (2) determine breeding chronology and productivity of piscivorous waterbird colonies, (3) determine diet composition of fish-eating birds, including taxonomic composition and energy content of various prey types, (4) estimate forage fish consumption rates, with special emphasis on juvenile salmonids, by breeding adults, (5) identify factors that influence the foraging success of piscivorous waterbirds, (6) recover salmon PIT tags from piscivorous waterbird colonies and relate to availability of PIT-tagged smolts in the river, and (7) compile information regarding alternatives for managing avian predation on juvenile salmonids.

METHODS

Study Site

We studied nine piscivorous waterbird breeding colonies on the lower Columbia River in 1997 (Figure 1). Three islands in the Columbia River estuary: East Sand Island, Miller Sands, and Rice Island (Figure 2, Clatsop County, Oregon) were intensively monitored. Six up-river islands (Miller Rocks and Little Memaloose Island, Klickitat County, WA; Three Mile Canyon Island, Gilliam County, OR; and Crescent Island, Richland Island, and Island # 18, Benton County, WA) were censused and were visited biweekly to collect data.

Population Census

In 1996 and 1997, piscivorous waterbirds were censused using direct counts from aerial photographs, which is the best option for estimating population size of ground-nesting colonial waterbirds (Bibby et al. 1993). We censused all known large colonies (>50 nesting pairs) on the lower Columbia River, from the Columbia River estuary to the head of McNary Pool (see Figure 1). Prior to the photo census, reference points that could be detected on aerial photographs were laid out at each colony to establish an accurate scale. Aerial photographs were taken by Bergman Photographic Services Inc. (Portland, Oregon), using a high resolution (1:1200), large format camera (Zeiss RMK Top 30). Overlapping color exposures were taken of each colony from a fixed-wing aircraft flying at low altitude (approx. 350 m) and slow air speed (approx. 125 km/h). The photo census was conducted during late incubation (as determined by ground-based surveys conducted at each colony), when maximum colony attendance was assumed (Bullock and Gomersal 1981; Gaston and Smith 1984). Total population size can be estimated by doubling the number of birds counted on photographs of each colony, but the number of individuals on the photographs over-estimates the number of active nesting pairs, as some individuals on the colony are non-breeders, failed breeders, and off-duty active breeders. Up-river colonies were photographed on 5 June between 0800 and 1000 PDT in 1996, and on 20 May between 1115 and 1315 PDT in 1997. Estuary colonies were photographed on 12 June between 1000 and 1100 PDT in 1996, and on 2 June between 1745 and 1830 PDT in 1997.

Analysis of photographs to estimate population size for each colony was carried out by the Survey, Mapping, and Photogrammetry Department at the Bonneville Power Administration (Portland, Oregon). Overlapping diapositive emulsions of each colony were analyzed using a Zeiss P-1 Stereoplotter. Counting and classifying birds by species, mapping of natural and cultural features, and outlining vegetation areas were accomplished using Zeiss PHOCUS software. Areas (m^2) occupied by nesting and loafing birds were calculated using Plus3 TerraModel software. Because the aerial photos were taken in color and at a large scale, individual nests and birds of different species were readily identified, with the exception of gulls (*Larus* spp.), which could not be distinguished. Birds were enumerated from the digitized photos and their location, along with the locations of other features (e.g., vegetation), were plotted on a map of desired scale. Direct counts of individuals on the ground within the area where nests were found were considered an index to total population size. Population indices were compared between years and among colonies.

In 1997, we tested the assumption that each bird counted on the colony from aerial photos represents one breeding pair for Caspian terns and double-crested cormorants nesting on Rice Island. Plots laid out on digitized maps of tern and cormorant colonies on Rice Island were reexamined to count the number of unattended nests, nests with one bird in attendance, and nests with two birds in attendance. In addition, ground counts were conducted of Caspian terns on the colony from an observation blind. On four days surrounding the day aerial photos were taken, the number of incubating and standing Caspian terns were counted in six different plots. Standing birds were assumed to be non-breeders or the off-duty mate of an incubating bird. These measures were used to interpret results from the aerial photo census and to adjust estimates of breeding population size based on direct counts of terns and cormorants on Rice Island.

Nesting Chronology, Productivity, and Chick Growth

Productivity and nesting chronology of Caspian terns breeding on Rice Island were determined by monitoring nests that were individually marked by numbered wooden stakes. We determined hatching chronology, clutch size, and hatching success by visiting marked nests once a week from 5 April through 5 July. Marked nests were also monitored from blinds. Overall nesting success was estimated by counting the number of young that reached fledging age as a proportion of the estimated number of breeding pairs, based on the photo census. After chicks left the nest (approximately one week after hatching), growth was monitored by measuring a random sample of young that were captured by driving crèches of chicks into temporary enclosures. Causes of individual nest failure were difficult to determine, but direct observations from blinds allowed general causes of nest failure to be documented for the Rice Island colony. Nesting success and chick growth of Caspian terns at up-river colonies were not monitored.

Productivity and nesting chronology of double-crested cormorants breeding in the estuary were sampled by monitoring nests (n = 64) located on channel markers in the vicinity of Rice Island. We determined hatching chronology, clutch size, hatching success, nestling survival rate, brood size at fledging, and overall nesting success by visiting each nest once a week from 5 April through 20 August. Causes of nest failure were difficult to determine in most cases, but available evidence was used to infer individual fates of nests (i.e., abandoned or depredated) on channel markers. At East Sand Island, collection of nesting chronology data was limited to observations made from the edges of the colony during the incubation and early chick-rearing phases. On-colony visits to the Rice Island and East Sand Island cormorant colonies were precluded by the risk of catastrophic nest failure due to disturbance of attending adults and resultant gull predation on eggs and/or chicks. Average brood size at the East Sand Island colony was estimated by counting the number of chicks in a random sample of 50 active nests.

Breeding chronology of gulls (glaucous-winged/western, California, and ring-billed) was described by walking transects through colonies every two weeks. The number of eggs and or chicks in at least 20 nests was recorded during each of these visits. Gull nests were not individually marked, nesting productivity was not monitored, and nestling growth rates were not measured. No effort was made to determine causes of individual nest failure, but notes were recorded regarding factors causing extensive failures of subsections of individual colonies (e.g. flooding, disease).

Growth rates of Caspian tern chicks were initially based on measuring wing length (± 1 mm) and body mass (± 1 g) of chicks that were individually marked (US Fish and Wildlife Service stainless steel leg bands) and restrained in fenced plots. Fencing chicks appeared to alter normal provisioning behavior of adults, so we removed the fences, resulting in chicks moving away from their original nest scrape. Because hatch dates of individual Caspian tern chicks outside the fenced plots were not known, growth in body mass was plotted as a function of wing length, using wing length as a surrogate for age. Transformation of the two variables (square root of body mass, square root of the natural log of wing length) produced a linear relationship with homogeneous variance. The slope of the simple linear regression was then used as an index to growth performance. Ages were also assigned to unknown-aged chicks, based on their wing length, and plots of body mass as a function of estimated age were used to determine the linear phase of body mass growth and estimate the slope of body mass growth (g/day) during the linear phase.

Growth rates of body mass (± 1 g) and wing length (± 1 mm) for double-crested cormorant nestlings were determined for marked individuals in all channel marker nests that hatched young and were safely accessible (n = 47 nests). Although cormorant nests on channel markers were only checked every five days, ages for marked nestlings could be assigned with accuracy of ± 2 days. Growth in body mass and wing length were plotted as a function of age (days post-hatching) so that the linear phase of growth for both these parameters could be determined. Growth in body mass as a function of wing length was also determined for comparison with other cormorant nestling growth data where age was not known.

Diet Composition

Terns, gulls, and cormorants feed their young at the nesting colony until nestlings are full-grown and capable of foraging on their own. The transport and delivery of meals by breeding adults to chicks at the colony provides an opportunity to determine the taxonomic composition and energy content of the diet. In cormorants and gulls, chick meals are delivered in the foregut (esophagus, proventriculus, and gizzard) of adult birds, so chick diet samples consist of semi-digested food. In terns, chick meals consist of single, whole fish that are transported in the bill. In all three taxa of fish-eating birds, diet samples can be collected non-destructively when chicks regurgitate during routine banding and measuring.

Because terns transport whole fish in their bills to their mates (courtship meals) and young (chick meals), considerable information on taxonomic composition of the diet can be obtained by direct observation of adults as they return to the colony with fish. Observation blinds were set up at the periphery of the colony prior to the onset of egg laying so that prey items could be identified with the aid of binoculars and spotting scopes.

Additionally, destructive sampling techniques were necessary to assess the diet composition of adult birds when non-destructive methods were inadequate (e.g., to sample diet outside the chick-rearing period or to assess relative proportions of various salmonid species in the diet of terns). The best method to obtain a random sample of the diet was to shoot adult birds en route to or on the colony. A shotgun was used to collect adults as they commuted back to the colony, and an air rifle was used to collect adults on the colony when collecting birds in flight was not feasible.

Chick Regurgitations

Sampling sites: Chick regurgitations were collected at all breeding colonies in the lower Columbia River (Figure 1), except for the Crescent Island gull and tern colonies. Chick regurgitations were not collected at Crescent Island to avoid disturbing a small nesting colony of white pelicans (*Pelecanus erythrorhynchos*), a protected species in the State of Washington.

Sample Collection: Chick regurgitations were collected from 31 May through 4 August between 0645 and 2300 PDT. Chick diet samples were obtained by collecting spontaneous regurgitations from chicks, caused either by handling or stress associated with investigator intrusion in the colony. Samples were stored in labeled whirl-pak bags, weighed on an Ohaus battery-powered top-loading balance (± 0.1 g), and stored in a cooler on ice until they were placed in a freezer at the end of the day. The samples were kept frozen at -20^{o}C until laboratory analysis. All relevant field data (i.e., sample number, date, time, species, colony location, and field identification of prey item) were recorded and subsequently entered into a database.

Adult Stomach Contents

Sampling sites: Adult stomach contents were collected from adult birds shot en route to or on the colonies listed in Figure 1. Generally, birds were collected at or near the colony. Birds collected away from the immediate vicinity of a colony were presumed to be from the waterbird colony nearest to the collection site.

Sample Collection: Sampling was conducted from 8 April through 29 July from 0830 to 1955 PDT. Each week approximately five samples per species were collected from each colony in the estuary. Three to five samples per species were collected from each up-river colony biweekly. Body mass and wing length of each adult bird collected were recorded prior to dissection. Immediately after collections, the abdominal cavity was opened, the foregut (esophagus, proventriculus, and gizzard) removed, and the contents emptied into a whirl-pak bag. Each sample was weighed, stored, and frozen as described above. All relevant data on collected adults (i.e., sample number, date, time, species, age, sex, body mass, wing chord, colony location, bird activity, commuting direction, and field identification of prey items) were recorded and subsequently entered into a database.

The U. S. Department of Agriculture, Wildlife Services has been charged with implementing avian predation abatement measures at lower Columbia River Dams. We worked with Wildlife Services and the Corps to collect birds shot as part of this program for the purpose of determining diet of adult birds foraging at the dams. Birds were shot at or near The Dalles and John Day dams from 4 April through 12 May from 0605 to 2120 PDT. Wildlife Services provided the following data for each bird collected: species, date, time, location, and activity. All birds collected by Wildlife Services were stored in a freezer located at The Dalles Dam until laboratory analysis. Birds collected by Wildlife Services were analyzed separately from diet samples collected at the colonies and comparisons were made between the two sample groups.

Dropped Fish

Sampling sites: Caspian terns returning to the Rice Island colony were shot to retrieve whole fish carried in their bills and for adult stomach content analysis (described above). Most birds were shot as they were flying westward along the southern shoreline of Rice Island. Birds were shot at a location roughly 0.4 km east of the colony, a location far enough removed so as not to noticeably disturb the terns on the colony.

Data Collection: Dropped fish were collected from 1 May through 29 July from 0915 to 1750 PDT. Dropped fish samples were particularly important in determining the proportion of various salmonid species in the diet. Birds were shot over land so that dropped fish could be easily retrieved. Samples were handled and data collected as described above.

Colony-Based Diet Observations

Sampling sites: Colony-based diet observations were conducted at the Rice Island Caspian tern colony. Observations of the taxomonic composition of prey items brought to the colony by breeding terns were recorded from blinds located at the periphery of the colony.

Data Collection: Observations (total hours = 66.75; total days = 11) were conducted from 6 June to 15 July between 0600 and 2000 PDT. Prey items were identified to the lowest discernible taxon using either binoculars or spotting scopes. We were confident in our ability to discern salmonids from non-salmonids based on direct observations from blinds, but were less confident in our ability to differentiate between the different salmonid species, necessitating the collection of adult stomach contents from terns. Prey length was estimated by a visual size comparison of the prey item relative to bill length (approximately 8.5 cm) for Caspian terns. Prey taxon, length, meal type (courtship or chick meal), date, and time of delivery were recorded.

Laboratory Analysis of Diet Samples

Sub-sampling: Adult stomach contents, chick regurgitations, and dropped fish were sorted and grouped by predator species, location, and sampling week. Because cormorants and gulls feed chicks by regurgitation of their foregut contents, it was assumed that the taxonomic composition of adult stomach contents and chick regurgitations were similar and therefore could be pooled with samples collected during the same time period and for the same species. Caspian terns, on the other hand, feed chicks whole fish carried in their bill (or occasionally in the throat), suggesting that prey items fed to chicks could differ from those consumed by adults. Furthermore, dropped fish could be part of the adult diet (i.e., if a courtship meal) or the chick diet (i.e., if a chick meal). Hence, each diet sample type for terns (i.e., adult stomach contents, chick regurgitations, and dropped fish) was analyzed separately and only results from adult stomach content analysis were used to compare tern diet with diet of other piscivorous waterbirds.

When we collected more samples than were needed for diet analysis were collected, we sub-sampled for laboratory analysis. For estuary colonies, five samples from each sampling week were selected for laboratory analysis. When fewer than five samples were available for a given week, additional samples were chosen from the nearest possible week. Samples of the best relative quality and freshness were selected for analysis. Good quality samples were those in which individual prey items were intact and not in an advanced stage of digestion. Due to smaller sample sizes, all samples collected from up-river gull colonies and all dropped fish collected from terns were analyzed.

Analysis: Adult stomach contents, chick regurgitations, and dropped fish were analyzed to determine taxonomic composition of the diet at the Oregon Department of Fish and Wildlife (ODFW) laboratory in Clackamas, OR. Samples were partially thawed, removed from whirl-pak bags, and re-weighed. Samples were separated into major food categories: fish, crustaceans, mollusks, insects, non-fish vertebrates, plant material, and refuse. Fish were further identified to genus and species, whenever possible. Items from each taxonomic category were weighed and enumerated. Whole or nearly intact fish were individually weighed, measured for fork length, and refrozen for proximate analysis to determine energy content. Semi-digested fish matter was not always clearly identifiable. Unidentifiable fish samples were artificially digested according to the methods of Peterson et al. (1990, 1991). Once digested, diagnostic bones (i.e., cleithra, dentaries, pharyngeal arches, and opercles) were removed from the sample and identified to species using a dissecting microscope (Hansel et al. 1988). Unidentified fish samples that did not contain diagnostic bones were classified as unknown fish. The taxonomic composition of waterbird diets was expressed as % of total biomass and % of total prey items.

PIT Tag Recovery

In 1996 and 1997, we recovered salmon PIT (Passive Integrated Transponder) tags from the Rice Island Caspian tern colony in the Columbia River estuary. This colony was well-suited for recovery of PIT tags due to its large size, the prevalence of salmonids in the diet of Caspian terns, and colony substrate conditions conducive to PIT tag detection and recovery.

The colony was searched for tags when the birds had left the colony following the breeding season (24 - 27 September 1996 and 18 - 22 August 1997). Non-systematic sampling was used to maximize the number of PIT tags recovered from the colony. Non-systematic sampling involved visually searching for tags on the surface of the colony in areas having high nesting densities of Caspian terns. The relative numbers of PIT tags recovered on Rice Island from each salmonid species and rearing type were compared to what might be expected based on their relative availability. Relative availability was estimated to be the proportion of each salmonid species or rearing type of (1) the total PIT-tagged fish released (PITAGIS 1997) and (2) the total PIT-tagged fish detected in-river in the estuary (Ledgerwood et al. 1997). Statistical comparisons are by Chi-squared tests for independence (Siegel 1988).

Stratified systematic sampling was used to estimate the total number of PIT tags on the colony. Meter-square quadrats were located at the intersection of transect lines laid out on the colony so as to cover it with a grid of 20 m X 20 m squares. Sampling strata were delineated from high-resolution aerial photographs taken during the latter part of the incubation period. The two sampling strata were areas where nests were located and areas outside where nest scrapes occurred, but where adults and young sometimes roosted. The sandy substrate within each quadrat was excavated down to a depth where fish bones were no longer detected (usually < 5 cm), then run through a set of soil sieves to recover all tags in the quadrat.

Bioenergetics Model Construction and Components

We constructed a bioenergetics model to obtain supportable estimates of the number of juvenile salmonids consumed by piscivorous waterbirds (Madenjian and Gabrey 1995; Glahn and Brugger 1995; Derby and Lovvorn 1997; Figure 3). The model starts with estimates of the energy expenditure rates of individual birds, expanded by the estimated number of birds in the population and the average duration of their residence in the estuary (based on counts of nesting and roosting birds at the colony) in order to derive an estimate of the energy demands of the population for the entire season. Estimates of the numbers of juvenile salmonids and other prey types consumed to meet population energy demands were derived from measurements of the proportion (% biomass) of salmonids and other prey categories in the diet, the mean mass of individual prey items in each prey category, and the mean energy density of items in each prey category. The conceptual model that forms the basis for the bioenergetics calculations is shown in Figure 3. For each input variable in the bioenergetics model, we used a range of values that were designed to produce minimum, maximum, and "best guess" estimates for the number of juvenile salmonids consumed by the bird population. We used empirical data, collected in 1997, for all input variables except daily energy expenditure and energy assimilation efficiency. Values for these parameters were based on published studies of seabird energetics (Birt-Friesen et al. 1989; Glahn and Brugger 1995; Jackson and Cooper, In press).

Daily energy expenditure (kJ bird^{-1} day^{-1}) of adult Caspian terns during the breeding season has not been previously measured. Therefore, we estimated daily energy expenditure (DEE) from published, empirically-derived allometric equations predicting field metabolic rates of seabirds as a function of total body mass. The empirical data used to generate these prediction equations were obtained by using the doubly-labeled water method to measure CO_2 production in free-ranging seabirds during the breeding season, especially the chick-rearing period (Birt-Friesen et al. 1989). The range of estimated DEEs used in the bioenergetics model for Caspian terns was based on average adult body mass measured on terns nesting at Rice Island in the Columbia River estuary (654 g, SD = 68.2, n = 121) and three different allometric equations presented in Birt-Friesen et al. (1989). The allometric prediction for seabirds not using flapping flight (736 kJ/day) was used for the minimum estimate of DEE, the allometric prediction for seabirds using flapping flight (1,138 kJ/day) was used as the maximum estimate, and the allometric prediction for all seabirds (907 kJ/day) was considered the best estimate of DEE for adult Caspian terns.

In addition, we attempted to use the doubly-labeled water method (Lifson and McClintock 1966) to directly measure the daily energy expenditure of adult Caspian terns nesting at the Rice Island colony. During the second and third weeks of the chick-rearing period, we captured adults in walk-in traps and noose mats placed around chicks that were tethered to stakes. Captured adults were injected intraperitoneally with 0.9 ml of doubly-labeled water ($D_2{}^{18}O$). Following injection, adults were weighed (± 0.1 g), measured (wing length ± 1 mm, culmen ± 0.1 mm, and tarsus ± 0.1 mm) and banded with USFWS stainless steel leg bands. The plumage of each adult was also dyed with rhodamine in a unique pattern so that injected adults could be easily recognized in the colony. Injected adults were held in cotton bags for one hour post-injection to allow isotopically labeled water to equilibrate with body water. Then an initial blood sample of about 80 ul was obtained by puncturing the brachial vein and collecting blood in nonheparinized microhematocrit tubes. Adults were then released at the breeding colony. Injected adults were recaptured the day following injection and a second blood sample was taken. Blood samples were also collected from uninjected adult Caspian terns for measurement of background levels of the two isotopes. Tubes with blood were flame-sealed in the field and stored at about 5^o C.

Isotope concentrations in distilled water from blood samples were measured in the lab of G. H. Visser, Centre for Isotope Research, University of Groningen, The Netherlands. Using the CO_2 equilibration technique, ${}^{18}O/{}^{16}O$ ratios in blood were assigned by isotope ratio mass spectrometry, as were ${}^{2}H/{}^{1}H$ ratios in H_2 gas generated from water samples using zinc as a catalyst. Isotope analyses were run in triplicate to assure accuracy of estimates of CO_2 production. Water flux rates and CO_2 production rates were calculated on the basis of equations in Nagy (1980), using an energetic equivalent of 27.33 kJ/l CO_2, 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 (i.e., no extrapolation).

We also collected time-activity data on adult Caspian terns, both at the colony on Rice Island and at foraging sites. These data will be used to construct time-energy budgets and, in concert with measurements of DEE using doubly-labeled water, will be used to estimate field metabolic rates of terns during various stages of the nesting cycle (Weathers and Nagy 1980; Weathers et al. 1984; Goldstein 1988). Time-activity budgets were measured using the instantaneous scan method (Altmann 1974). The percent time spent in different activities (i.e., roosting, preening, walking, sitting, courtship feeding, copulating, incubating, chick feeding, aggression, flapping flight, hovering flight, gliding flight, plunge diving) were determined and will be used in conjunction with activity-specific metabolic rates to estimate daily energy expenditure rates during each phase of the nesting cycle. Approximately 71 hours of time-activity budget data were collected, but will not be used to estimate time-energy budgets until additional measurements of DEE are made using the doubly-labeled water method (planned for FY 98).

Energy assimilation efficiencies for a variety of seabirds feeding on a variety of prey have been shown to average 0.75, but ranged from about 0.70 to 0.80 (Jackson and Cooper, In press). Consequently, we used 0.75 as our best estimate, 0.80 as the minimum estimate (high energy assimilation efficiencies yield low food consumption rates), and 0.70 as the maximum estimate. Daily energy consumption was calculated from daily energy expenditure divided by assimilation efficiencies (Figure 3). Seasonal energy consumption was the product of daily energy consumption and mean duration of individual residency in the estuary in days. The latter was estimated to be 80 days at a minimum (ca. April 26 to July 14), 100 days at a maximum (ca. April 16 to July 24), and 90 days as the "best" estimate (April 19 to July 20). Caspian terns were regularly observed in the Columbia River estuary from as early as April 1 to as late as August 31, a period of over 150 days. But relatively small numbers of terns were present in the estuary prior to the middle of April or after the latter part of July. Peak numbers of terns were present on the colony late in incubation, when the aerial photos were taken, but these numbers were not present throughout the nesting season. Colony attendance was noticeably reduced by late June, when many nesting pairs had already failed.

Total population energy consumption for Caspian terns was the product of seasonal energy consumption and estimated population size (from aerial photo census). The minimum estimate for population size (13,746 individuals) was derived from twice the estimate of actively incubating or brooding adults on the colony at the time of the aerial photo census, based on counts of representative plots on the colony. The maximum population estimate (18,830 individuals) was twice the number of terns counted on the aerial photos. The best estimate of population size (16,034 individuals) was based on the total count of terns from the aerial photos, corrected for the number of nest scrapes (which were discernible in the aerial photographs) and the proportion of nest scrapes where both members of the pair were present. No attempt was made to explicitly census the nonbreeding portion of the population, but nonbreeders were normally present on the colony and thus were included in population estimates based on aerial photos. No attempt was made to incorporate the energy consumption of nestling Caspian terns in the bioenergetics model. Hatching success and nestling survival were so low at the Rice Island Caspian tern colony in 1997 that adding in estimates of energy consumption by chicks produced trivial changes in total population energy consumption. Only 400 chicks survived until fledging, with most chick mortality taking place during age 3 - 8 days when chicks weighed only 50 - 100 g and consumed few fish compared to fledglings.

The mean energy densities of each category of prey (Figure 3) were based on lab analyses of whole fish selected from diet samples. Derby and Lovvorn (1997) have shown through uncertainty analyses that energy content of fish can be a very important source of variation in bioenergetics estimates of fish consumed by avian predators. Fish were kept frozen until proximate analysis was conducted in the lab. Individual fish were weighed fresh and dried to constant mass in a convection oven at 60°C to determine water content. Lipid content of dried samples was determined by solvent extraction using a soxhlet apparatus and the solvent system 7:2 hexane/isopropyl alcohol (v:v). Lean dry samples were then ashed in a muffle furnace at 550°C in order to determine ash-free lean dry mass (>95% protein). Energy content of prey items was calculated from proximate composition (water, lipid, ash-free lean dry matter, and ash content) of diet samples, along with published energy equivalents of these fractions (lipid = 39.4 kJ/g, protein = 17.8 kJ/g; Schmidt-Nielsen 1990:171).

The relative proportions of each prey category in the diet (% wet biomass) and the corresponding specific mean energy density (kJ/g wet mass) were multiplied to calculate the percent total energy consumption by prey category. The percent total energy consumption by prey category and the total population energy consumption were multiplied to estimate the total energy contribution by each prey category. The mean energy density of each prey category was also multiplied by the mean mass of individual prey items in the corresponding prey category in order to estimate the mean energy content of individual prey in each category. Finally, the latter values were then divided into the total energy contribution for the corresponding prey category in order to yield the number of prey in each category consumed by the bird population during the entire breeding season. The number of juvenile salmonids consumed by the bird population was one output variable from the calculations.

Sensitivity analysis determines which input variables can potentially contribute to the greatest error in model output (i.e., number of salmonids consumed). This analysis will be included as part of the bioenergetics results in FY 98.

Foraging Ecology

The scope of our investigations into piscivorous waterbird foraging ecology in 1997 was limited mostly to qualitative observations within the estuary and to data collected on-colony at Rice Island. The locations, times, and numbers of foraging double-crested cormorants or Caspian terns were recorded whenever aggregations of one or both species were observed in the estuary. Caspian tern chick provisioning rates were recorded by monitoring active nests on Rice Island throughout daylight hours. We used the delivery rates of fish to young on the colony as an indirect measure of feeding activity in the estuary. The relationships between delivery rates of fish to the Rice Island colony and both local time and tidal stage were explored using correlation analysis. A more detailed study of the foraging ecology of piscivorous waterbird populations in the estuary is planned for the 1998 breeding season.

RESULTS

Population Census

Population indices for piscivorous waterbirds nesting in the lower Columbia River are listed in Table 1. In 1997, population indices for all but one colony (Island #18 gull colony) increased from the previous year (Table 1). The largest increases were for the up-river Caspian tern colonies, equaling 200 % and 106 % for the Crescent Island and Three Mile Canyon Island colonies, respectively. The number of gulls nesting on Miller Rocks in 1997 also increased substantially from the previous year (126 %; Table 1). It appears that the gull and cormorant colonies on East Sand Island are relatively stable, growing by 5 % or less from 1996 to 1997. Although the gull colony at Island #18 showed a reduction in the number of nesting birds from 1996 to 1997, we believe that the actual number of nests initiated in 1997 may have been greater than the previous year. More than 15 % of the nests initiated on Island #18 in 1997 were flooded by high water prior to the photo census and therefore were not counted.

Longer term population trajectories for piscivorous waterbird colonies were determined by comparing the 1997 census results with the first known population estimate for each colony (Table 2). All colonies except the cormorant colony on Rice Island have increased substantially since the year of first census. The most notable population increase has been the Caspian tern colony on Rice Island, increasing at an average rate of about 21 % per year since the colony was first established in 1987. Up-river gull colonies have also increased on average from between 4 and 8 % per year, depending on location. The cormorant colony at East Sand Island has increased by an average of 17 % per year, while the colony at Rice Island has remained stable as compared to the first census.

Ground surveys and reexaminations of digitized photos indicate that there was not a one-to-one correspondence between the number of birds counted on photos and the number of active breeding pairs or active nests on the Rice Island Caspian tern colony at the time of the photo. Ground counts of Caspian terns conducted around the time that the photos were taken indicated that 73 % of the birds counted on the Rice Island colony were on nests (6,873 birds), indicating about 13,746 breeding adults at the time the aerial photos were taken. Also, digitized photos of the Rice Island tern colony were examined to determine the number of nest scrapes on the colony and the number of terns associated with each nest scrape. These results indicate that of the total nest scrapes counted, 77 % were attended by one adult, 21 % were attended by two adults, and 2 % were unattended. Based on these percentages, we estimate that there were a total of 8,017 nest scrapes (7,825 nest scrapes attended by one or two birds and 192 unattended nests) on the colony at the time the photo was taken. This represents our best estimate of the number of pairs attempting to nest on the Rice Island Caspian tern colony in 1997. Because Caspian terns normally attempt to breed for the first time at age three (Cuthbert and Wires, In press), and because one- and two-year-old subadults rarely are found on the breeding grounds (L. Wires and F. Cuthbert, pers. comm.), our best estimate of the Caspian tern population size in the Columbia River estuary was 16,034 individuals, double the count from aerial photos of nest scrapes on the colony.

For double-crested cormorants nesting on Rice Island there was nearly a one-to-one correspondence between adults counted on the colony and the number of active nests (i.e., nesting pairs). Of the total nests counted, 93 % were attended by one adult, 7 % were attended by two adults, and 0 % were unattended. These results suggest that there were about 1,178 breeding pairs on the Rice Island colony at the time the photographs were taken. If the same correction factor is used for the East Sand Island colony, there were about 4,926 breeding pairs there.

Nesting Chronology, Productivity, and Chick Growth

Breeding chronology was determined for each piscivorous waterbird colony on the lower Columbia River (Figures 4a, b). Median laying and hatching dates were determined for Caspian terns and double-crested cormorants nesting on Rice Island and the channel markers, respectively (Figures 4a, b) for use in the bioenergetics model to estimate consumption rates of juvenile salmonids. In general, the nesting cycles of piscivorous waterbirds in the estuary were roughly one week behind those populations nesting up-river (Figure 4a, b). Also, there were interspecific differences in nesting chronology among species nesting in the estuary, with glaucous-winged/western gull hybrids being roughly 2 - 4 weeks behind Caspian terns and double-crested cormorants.

The Rice Island Caspian tern colony experienced lower than expected reproductive success in 1997. Approximately 400 young were fledged from an estimated 8,017 nests initiated. The overwhelming cause of tern nest failure was predation on eggs and young by glaucous-winged/western gull hybrids. Only 26 % of the sample of initiated nests (n = 152) hatched young, and of these the average brood size at hatching was .39 ± 0.53 chicks/nest (Table 3). Most young that hatched from marked nest scrapes moved away from the scrapes between two and six days after hatching. Because Caspian tern chicks are highly nidifugous (leave the nest scrape soon after hatching), itwas impossible to monitor individual or average nest fates, but we directly observed from the blinds a high incidence of chick predation by gulls. Tern chicks appeared most vulnerable to gull predation from two to 10 days post-hatch (approx. 3 - 12 June). During this stage of development, chicks frequently moved a short distance from the nest scrape when the attending parents flushed from their scrape due to disturbance from bald eagles or humans. After a disturbance, parents immediately returned to the nest scrape. If the chick was still at the scrape it was usually safe, but if the chick had moved it was frequently depredated by gulls. In addition to capitalizing on disturbances, gulls constantly patrolled the colony to prey on chicks that were not guarded by a parent. Predation rates were greater at the edge of the colony as compared to the center.

Double-crested cormorants were moderately productive in 1997 (Table 4), fledging an average of 1.61 and 2.11 young per successful nest on East Sand Island and the channel markers, respectively. Mean clutch size on the channel markers was 4.2 ± 1.3 eggs. Only 56 % of eggs hatched (84 % of nests hatched at least one egg). Most eggs that failed to hatch appeared to have been abandoned, and abandoned clutches were typically small (1 - 3 eggs), suggesting that abandonment occurred during the laying period. The nests on channel markers did not appear to experience the high rates of gull predation that were observed at the East Sand Island colony. Cormorant nests on Rice Island were not monitored, but it was notable that cormorants were not as susceptible to disturbance from bald eagles as the nearby Caspian tern nests.

Growth rates for Caspian tern (Table 5) and double-crested cormorant chicks (Table 5, Figure 5) were measured and will be particularly useful for future inter-year and inter-colony comparisons of colony productivity as it relates to diet. These data will also be useful for comparisons to previously published data from other double-crested cormorant and Caspian tern colonies.

Diet Composition

We analyzed a total of 723 diet samples from piscivorous waterbirds. Of those, 257 samples were from Caspian terns (92 adult stomach contents, 46 chick regurgitations, 119 dropped fish), 154 were from double-crested cormorants (64 adult stomach contents, 90 chick regurgitations), 103 were from gull spp. nesting in the estuary (53 adult stomach contents, 50 chick regurgitations), and 234 were from gull spp. nesting up-river (150 adult stomach contents and 59 chick regurgitations from gulls at the colony, 25 adult stomach contents from gulls foraging at dams).

Diet composition varied by predator species, location (Table 6), and stage of the breeding season (Table 8). Caspian terns and double-crested cormorants are strictly piscivorous, whereas gulls consume a diverse array of food types (Table 6). Caspian tern diets contained the highest percentage of salmonids (74.5 % by mass), followed by double-crested cormorants (23.7 % by mass), and glaucous-winged/western gull hybrids nesting in the estuary (10.8 % by mass; Table 6). Gulls that nest up-river were less dependent on salmonids as a food source, with salmon showing up in the diets of gulls nesting at only one of the six up-river colonies (Little Memaloose Island: 16 % by mass, averaged over the entire nesting season; Table 7), and then only early in the nesting season. The diet of double-crested cormorants nesting in the estuary differed between nesting locations (Figure 6). Cormorants nesting on East Sand Island, located near the mouth of the Columbia River, had fewer salmonids in their diet (16 % by mass) as compared to cormorants nesting at locations farther up-river (Rice Island and nearby channel markers: 35 % by mass; Figure 6), but diet composition from East Sand Island was based on a small sample size. Because most stomach contents samples were collected in the Rice island area, the diet composition data for cormorants in the estuary is probably biased toward salmonids. There were also differences in the proportion of the diet that was salmonids depending on where adults were collected, specifically California gulls collected at dams (66 % by mass, n = 24) vs. at nearby colonies (43 % by mass, n = 25) during the same time period (14 April through 15 May).

The relative proportions of the different salmonid species in the diet of Caspian terns based on dropped fish are presented in Figure 7. Coho and chinook salmon made up the greatest percent of prey items in the diet of terns (36 % and 30 %, respectively), whereas steelhead smolts were the most prevalent prey type by mass (43 %; Figure 7). Salmonid consumption varied over time for piscivorous waterbirds nesting in the estuary (Table 8). In general, the percent (by mass) of the diet of piscivorous waterbirds that were salmonids was highest in April and especially May, and declined rapidly in June and July (Table 8). The period of highest incidence of salmonids in the diet generally coincides with the period of peak smolt out-migration in the estuary. Bi-weekly comparisons of the relative proportions of the different salmonid species in the diet of Caspian terns showed that early in the season the diet is comprised mostly of coho salmon and steelhead, and by chinook salmon later in the season (Figure 8). Colony-based observations of the Caspian tern diet during the chick-rearing period (i.e., June and July) differed in the percent of prey items that were salmonids (69 %) as compared to the dropped fish data for the same time period (81 %).

PIT Tag Recovery

A total of 1,001 salmon PIT tags were recovered from the Rice Island Caspian tern colony in 1996 and 1997. The majority (866 tags or 86.5 %) was recovered by visually searching the surface of the colony. By comparison, soil sieves and electronic PIT tag readers were less effective in recovering large numbers of PIT tags, with 119 (11.9 %) and 16 (1.6 %) tags recovered using these methods, respectively. Most tags (825 or 82.4 %) recovered were intact and their tag codes were read. PIT tags were recovered from every migration year beginning with 1989, with the majority (695 tags or 84.2 %) coming from migration years 1995 - 1997. All but 134 tags (16.2 %) were from fish known to be tagged and released in the Snake River Basin (691 tags or 83.8 %). Of all the tags recovered, most were from steelhead (395 tags or 47.9 %), followed by chinook salmon (385 tags or 46.7 %), coho salmon (43 tags or 5.2 %), and sockeye salmon (2 or 0.2 %). A greater number of PIT-tagged salmonids of hatchery origin (723 tags or 87.6%) were recovered on the Rice Island Caspian tern colony, as compared to salmonids of wild (40 tags or 4.8 %) or unknown (62 tags or 7.5 %) origin. Of the PIT tags recovered from the colony, 312 (37.8 %) were from fish that were not detected at mainstem dams following release, presumably because those fish passed dams by routes other than the juvenile by-pass system (i.e., via spill, turbines, etc.). The remainder (513 tags or 62.2 %), were from fish interrogated at at least one juvenile by-pass facility on the lower Columbia or Snake rivers and were either transported (88 tags or 17.2 %), by-passed (329 tags or 64.1 %), or their disposition was unknown (96 tags or 18.7 %).

We estimated that the total number of salmon PIT tags on the Rice Island Caspian tern colony was 33,801 (95 % confidence interval, 25,154 - 42,448). Of those, 12,362 tags (95 % confidence interval, 6,777 - 17,947) were estimated to be from the 1997 migration year, or 2.0 % of the total number of tags released in that year (621,861; Figure 9; PITAGIS 1997). Approximately 7 % of the total number of PIT-tagged steelhead released in 1997 were estimated to be on the Rice Island Caspian tern colony (see Figure 10 for the results for other salmonid species). The number of PIT tags on the colony is expected to be a minimum estimate of the PIT tags consumed by terns because not all PIT tags consumed by Caspian terns are deposited at the colony (i.e., could be excreted at roosting sites, foraging sites, etc.). PIT tag recoveries on the Rice Island colony suggest that Caspian terns are not consuming the various salmonid species and rearing types in proportion to their availability. Steelhead appeared to be preferred by terns compared to other salmonid species in both the 1996 (Table 9) and 1997 (Table 10) migration years. Alternatively, steelhead smolts may be more available than other species because they spend more time near the surface. Chinook salmon, the large majority of the PIT-tagged run (roughly 76%; PTAGIS 1997), were under-represented in the PIT tag sample from the colony compared to other salmonid species in 1996 (Table 11) and 1997 (Table 10). PIT-tagged salmonids of hatchery origin appeared on the colony in greater numbers than expected, based on the presumed ratio of PIT-tagged hatchery to PIT-tagged wild juvenile salmonids in the estuary in 1996 (Figure 11; Tables 12 and 13). Analysis of the PIT tag data is ongoing, and other results concerning how avian predation rates vary by salmonid species and size, migration year, rearing type, transportation and passage conditions, and colony location will be included in subsequent publications.

Bioenergetics Model Output

Bioenergetics modeling was used to estimate the total number of juvenile salmonids consumed by Caspian terns nesting on Rice Island during the 1997 breeding season. This estimate is particularly sensitive to errors in the estimation of daily energy expenditure, population size, the duration of the predation period (breeding season), and the proportion of juvenile salmonids in the diet (% diet biomass; Madenjian and Gabrey 1995).

Estimated daily energy expenditure (DEE) of Caspian terns (mean body mass = 654 g) based on allometric equations (Birt-Friesen et al. 1989) ranged from 736 to 1,138 kJ/day (Table 14). Adult Caspian terns proved difficult to catch once their chicks were more than a few days old and able to leave the nest scrape. Consequently, only three adults were injected with doubly-labeled water, and, of these, two were subsequently recaptured for collection of blood samples. These two adults yielded two estimates of daily energy expenditure: 848.9 kJ/day (initial body mass = 541.8 g, total body water = 62.2 %, water efflux = 186.6 g/day) and 1,239.8 kJ/day (initial body mass = 590.5 g, total body water = 64.4 %, water efflux = 196.1 g/day). The average DEE from this small sample was 1,044.4 kJ/day (SD = 276.4, n = 2), close to the maximum estimate, derived from allometric equations, that was used in the bioenergetics model. These few data suggest that daily energy expenditure of breeding Caspian terns during the chick-rearing period may be somewhat higher than predicted by allometric equations relating DEE to body mass in seabirds as a whole, and emphasizes the importance of obtaining additional measurements using the doubly-labeled water method in 1998.

Daily energy consumption of adult Caspian terns, derived from DEE and energy assimilation efficiencies (range = 0.70 - 0.80), ranged from 920 to 1626 kJ $tern^{-1}$ day^{-1} (Table 14). Minimum average duration of residency in the estuary was estimated at 80 d, maximum average duration was estimated at 100 d, and the best estimate of average duration was 90 d. We are confident that at least 14,000 Caspian terns were using Rice Island as a nesting and/or roosting site for 80 - 100 days during the 1997 breeding season. A few hundred Caspian terns began roosting on Rice Island in the first week of April, with thousands arriving and initiating courtship in the second and third weeks of April. The majority of terns intending to breed on Rice Island were almost certainly foraging in the estuary and lower Columbia River for at least two weeks preceding egg-laying, which was initiated in the first week of May. Caspian tern numbers on the Rice Island colony peaked and remained high through late May and early June, but gradually declined following widespread nest failure early in the chick-rearing phase (mid June). The breeding season extended until the second week of July, when all tern chicks had either died or fledged. Thousands of terns, however, continued to roost on Rice Island during the night until the middle of August, which would argue for extending the maximum mean individual occupancy to 100 days for the purposes of the bioenergetics model.

Estimates of population size for the Rice Island Caspian tern colony were largely based on the aerial photo census, conducted at the end of the incubation stage of the nesting cycle (Table 14). The maximum population estimate for the bioenergetics model (18,830 individuals) was based on doubling the direct count from the aerial photographs of adult terns on the ground within the colony. We reasoned that at most each tern in the estuary was represented by 0.5 terns on the colony. This over-estimates the number of nesting pairs, because some nests were attended by both members of the pair at the time of photography, and some birds on the colony were failed breeders, nonbreeders, or subadults. Based on counts conducted from the blinds during the aerial photo census period, however, we documented that about 73 % of adults on the ground within the colony were brooding eggs or chicks. Consequently, the colony minimally included 6,873 nesting pairs, or 13,746 breeding adults, the minimum estimate of population size used in the bioenergetics model. The best estimate of population size (16,034 individuals) was derived from the ratio of nest scrapes to adults on the ground in representative plots on the colony. Estimated total population energy consumption for the Rice Island Caspian tern colony in 1997 ranged from 1.012×10^9 to 3.061×10^9 kJ (Table 14).

The mean energy densities measured for each prey category ranged from a low of 3.96 kJ/g wet mass for sculpins to a high of 6.36 kJ/g wet mass for herring (Table 15). Juvenile salmonids ranged from 3.98 kJ/g wet mass for chinook salmon smolts to 5.07 kJ/g wet mass for sockeye salmon smolts. Estimates of the relative contribution of juvenile salmonids to the total energy consumption of the tern population were somewhat different depending on whether fish transported in the bill (i.e., dropped fish) or adult stomach contents were used to estimate diet composition (Table 15). On the basis of bill loads, approximately 84 % of total energy consumption by the population was juvenile salmonids (Table 15). In comparison, the stomach samples indicated that about 76 % of total energy consumption was in the form of juvenile salmonids (Table 15). In both samples, however, steelhead smolts contributed about a third of total energy consumption. The relative contribution of chinook, coho, and sockeye smolts is more difficult to determine because the majority of salmonids from stomach samples could not be identified to species. Nevertheless, the small size of most unidentified salmonids in stomach samples suggests that most were chinook smolts, the most numerous salmonid species among the sample of fish from bill loads as well. On this basis, mean energy density for unidentified juvenile salmonids from stomach samples was estimated to be 4.0 kJ/g wet mass, the average energy density for chinook smolts analyzed in the lab (Table 15). If future analyses determine that the energy density of unidentified salmonids from stomach samples is actually higher, the bioenergetics model would indicate that the numbers of juvenile salmonids consumed by the tern population was slightly lower than estimated in Table 16.

Using the diet data from bill loads (i.e., dropped fish) and the range of estimated population energy consumption rates for the Rice Island Caspian tern colony, the estimated number of juvenile salmonids consumed in 1997 was between 6.6 and 20.2 million smolts, with a “best” estimate of 11.4 million (Table 16). By comparison, the adult Caspian tern stomach content analysis yielded an estimate of between 8.5 and 24.7 million smolts, with a “best” estimate of 14.5 million smolts (Table 16).

Better and more complete data on seasonal diets of double-crested cormorants nesting at the two colonies in the estuary are needed to confidently generate a range and best estimate for predation by this species on juvenile salmonids (Glahn and Brugger 1995). Nevertheless, using the same approach as in the Caspian tern bioenergetics model, it is likely that millions of smolts were consumed by double-crested cormorants in the estuary during the 1997 breeding season (Table 17). Estimates of energy consumption by cormorant broods were not included in these calculations because of the uncertainties involved in several input variables to the bioenergetics model for cormorants in the estuary, but adding this to the model will only increase the etimates of smolts consumed. The model output supports the hypothesis that cormorants in the estuary consumed the same order of magnitude of juvenile salmonids as did Caspian terns in 1997. The available data for gull consumption of juvenile salmonids in the estuary suggests it is in the hundred thousands, an order of magnitude lower than tern and cormorant consumption. Data on which to base better estimates of cormorant and gull predation on smolts in the estuary will be collected in 1998.

Foraging Ecology

Anecdotal evidence suggested that there may be a commensal relationship between Caspian terns and double-crested cormorants foraging in the Columbia River estuary. On at least 10 different occasions (mostly in May and June) aggregations of Caspian terns (20 to 250 individuals) were observed plunge-diving in the immediate vicinity of foraging flocks of double-crested cormorants (20 to 300 individuals). A reasonable inference is that the diving cormorants were driving fish to the surface, improving foraging opportunities for surface-feeding terns. Mixed-species foraging flocks were most often observed at the Tongue Point confluence of the John Day Channel and the primary shipping channel of the Columbia River. Mixed-species foraging flocks were also common along the shallow shelf at the confluence of Youngs Bay and the main channel. On two occasions, coincident with large smolt releases from net pens at the Youngs Bay Yacht Club (Clatsop County Economic Development Council), we observed terns and cormorants feeding for over three hours on what appeared to be salmon smolts. A major mixed foraging flock of over 100 terns and 150 cormorants was also noted in slough water in the South Channel southeast of Lois Island.

Individual terns commonly appeared to be commuting between Rice Island and Pt. Elice, WA (N. end of Astoria-Megler Bridge). From Pt. Elice it appeared terns either turned North to forage in Baker Bay or continued along the main channel to the mouth of the river. Smaller groups of terns were commonly recorded foraging in shallow lower-tidal water surrounding Desdemona Sands in the vicinity of the Astoria Bridge. The shallow channels that cut through Desdemona Sands and the extensive tidal flats of Baker Bay were another focal point of individual tern foraging activity. Individual and small aggregations of double-crested cormorants commonly foraged near pile dikes north and east of Miller Sands, as well as off the south side of East Sand Island. Cormorants were observed to sit on the pilings, dive in to catch a fish, and then pull out to rest on the pilings again. The turbulence and back eddies below pile dikes may disorient or concentrate fish, making them easy prey for avian predators.

A total of 36 Caspian tern broods were intensively monitored on seven different days to measure chick meal delivery rates. Chicks were observed for a total of 331 hours and the total number of feedings observed was 104. The weighted mean number of fish delivered was 0.314 fish chick^{-1} hour^{-1}, and the mean number of chick meals delivered per day was 4.4 (normalized to a 14-h day). Because variation about the mean cannot be calculated for the weighted mean, the mean of 0.337 meals chick^{-1} hour^{-1} was used to calculate variance and confidence intervals. Using this mean, an average of 4.71 fish were consumed by each chick per 14-hour day with a 95 % CI of 3.62 to 5.70 fish chick^{-1} day^{-1} (SE = 0.038, n=36, df = 35).

The number of fish delivered chick^{-1} hour^{-1} as a function of time of day seemed to have defined peaks in the early morning, late morning, and evening. When these data were separated by date and tide stage (Tongue Point, Astoria), however, these peaks coincided with the outgoing tide. Our analysis showed that the highest delivery rates of food to chicks occurred during ebb and low tide stages. High and flood tide stages had lower fish delivery rates. The weighted mean number of chick feeds per chick hour during each tide stage are: high - 0.178; flood - 0.229; ebb - 0.398; and low - 0.508. The calculations to provide weighted means do not allow for the calculation of variance or standard error. Unweighted mean fish delivery rates chick^{-1} hour^{-1} and confidence intervals (± 2 standard errors) for the four tide stages are: high - 0.161 (± 0.073, n=31); flood - 0.218 (± 0.097, n=30); ebb - 0.517 (± 0.236, n=26); and low - 0.482 (± 0.193, n=36).

We found no significant correlations between the number of fish delivered chick^{-1} hour^{-1} and a variety of other variables examined, including date, days past median hatching date (June 7), number of disturbances, and time of day. Tide stage was the only variable that suggested a negative correlation with chick feeds per hour.

DISCUSSION

Prior to this study the effects of avian predation on the survival of juvenile salmonids in the lower Columbia River were poorly understood. Recoveries of radio-tagged smolts at colonies of fish-eating birds suggested that avian predation might be a major source of smolt mortality, causing smolt losses in the range of 5 - 30% of those that reached the estuary, with some runs in some years experiencing as much as 40% mortality (Schreck et al., unpubl. data). The results of the first year of this investigation confirm that bird predation in the estuary is a source of considerable mortality to out-migrating smolts, within the range of estimates from radio-telemetry studies.

Population Census and Historical Trends

There are currently nine major colonies of fish-eating waterbirds located on the Columbia River from the mouth to the head of McNary Pool. The two largest waterbird colonies in the study area are gull colonies (mixed California and ring-billed gulls) in the Richland area, with a total number of ca. 70,000 individuals in both 1996 and 1997. Comparisons of aerial photo censuses of colonies from 1996 and 1997 suggest that almost all colonies of piscivorous birds in the study area increased substantially, particularly the Caspian tern colonies on Crescent and Three Mile Canyon islands, the mixed gull colony on Miller Rocks, and the double-crested cormorant colony at Rice Island. Comparison of 1997 aerial photo counts with previously published or unpublished estimates of colony size indicate that in the longer term (i.e., decadal scale) the Caspian tern colony on Rice Island, the cormorant colony on East Sand Island, and the gull colony on Richland Island have seen the most growth. Population increases of colonial waterbirds along the lower Columbia River may have resulted mostly from a variety of anthropogenic changes in the Columbia Basin, especially creation of new nesting habitat (islands) by impoundments and dumping of dredge material, irrigation-based agricultural development east of the Cascades, and hatchery production of 100 - 200 million salmonid smolts annually, which have become an important food source for some predator populations. The rapid expansion of colonial waterbird populations may result in increased avian predation rates on juvenile salmonids in the coming years.

The Caspian tern colony on Rice Island, a dredge material disposal island in the Columbia River estuary, is currently the largest in North America (over 16,000 individuals) and perhaps the world (Cuthbert and Wires, In press). This colony has increased by over 600 % since 1987, when it originated on Rice Island (G. Dorsey, USACE, pers. comm.). The colony has apparently expanded at the expense of other Caspian tern colonies formerly located in Grays Harbor, Willapa Bay, and near Everett, Washington. Prior to the mid-1950s, breeding Caspian terns in Washington and Oregon were known only from inland lakes and marshes. The first breeding record on the coast was a colony of 50 pairs on Goose Island, Grays Harbor, Washington in 1957 (Alcorn 1958). This colony peaked in 1970 and was abandoned by 1977 (Speich and Wahl 1989). Beginning in 1974, a Caspian tern colony became established on Whitcomb Island, also in Grays Harbor, that increased in size to roughly 1,000 pairs by 1976, but the colony was abandoned by 1981. Beginning in 1976 another island in Grays Harbor, Sand Island, was used by nesting Caspian terns. By 1981 over 2,000 pairs were nesting on Sand Island, one of the largest known colonies of the species anywhere along the Pacific coast of North America (Gill and Mewaldt 1983), but this colony in turn disappeared by the early 1990's (J. Smith, WDFW, pers. comm.). Since 1990 there has been no confirmed nesting by Caspian terns in Grays Harbor.

In 1981 over 500 pairs of Caspian terns were found nesting on Gunpowder Island in Willapa Bay, and by 1982 there were approximately 3,000 pairs nesting there (Speich and Wahl 1989). Two years later a smaller colony of about 1,000 pairs was noted breeding on East Sand Island in the Columbia River estuary (G. Dorsey, USACE, pers. comm.). This was apparently the first record of nesting Caspian terns in the Columbia River estuary. By 1987 this colony had moved to Rice Island, where the population increased rapidly from the initial estimate of 1,500 pairs to about 6,200 pairs in 1991 (A. Clark, USFWS, pers. comm.). The current estimate of over 8,000 pairs at the Rice Island colony is larger than the estimate of the entire Pacific Coast population 15 years ago (Gill and Mewaldt 1983). The initial rapid buildup of this colony in the late 1980s and early 1990s was apparently due mostly to shifting of breeding pairs from Sand Island in Grays Harbor, Gunpowder Island in Willapa Bay, and East Sand Island near the mouth of the Columbia River to the single large colony at Rice Island. There are currently no other known Caspian tern breeding colonies along the coasts of Washington and Oregon.

Some evidence from band returns supports our interpretation of the origin of the Rice Island Caspian tern colony. In 1997, three adults terns were collected as part of food habits studies that were banded as young chicks on the Sand Island colony in Grays Harbor in late May or early June of 1980, 1978, and 1976, making these adults 17, 19, and 21 years old, respectively. The number of banded adults (n = 3) in the sample of collected adults (n = 157) suggests that there were several hundred banded adults in the Rice Island colony in 1997. Most of these banded adults were probably banded as nestlings on Sand Island in Grays Harbor, where the Washington Department of Fish and Wildlife banded approximately 500-1,500 Caspian tern chicks annually during the late 1970s and early 1980s (Gill and Mewaldt 1983, J. Smith, WDFW, pers. comm.). In summary, the history of the Caspian tern breeding population along the Washington and Oregon coasts has been a short one (ca. 40 years) of rapid expansion, low philopatry, and large colony sizes compared with other areas of North America. This is part of a general trend for Pacific Coast Caspian terns of (1) shifting breeding colonies from inland, natural sites to coastal anthropogenic sites (dredge spoil islands), (2) shift from nesting in small groups within larger colonies of gulls to nesting in large, single-species colonies, (3) dramatic overall population increase, and (4) rapid northward range expansion (Gill and Mewaldt 1983; Cuthbert and Wires, In press).

The two smaller Caspian tern colonies in the up-river portion of the study area (Three Mile Canyon Island in John Day Pool and Crescent Island in McNary Pool) are also increasing. Between 1996 and 1997, there was a two-fold increase in numbers of Caspian terns at Three Mile Canyon Island and a three-fold increase at Crescent Island, suggesting that these two colonies may be undergoing very rapid expansion. These two inland colonies are ecologically more typical of Caspian tern colonies, in that nesting terns are mixed in with larger colonies of California and ring-billed gulls. Unlike the larger glaucous-winged/western gulls that nest around the Caspian tern colony on Rice Island, these two species of gulls are less prone to prey on Caspian tern eggs and chicks, nor are they as kleptoparasitic on Caspian terns. Although their nesting habitat was created by the hydrosystem, we do not know if the diet of Caspian terns nesting at these two inland colonies is as specialized on juvenile salmonids as is that of the Rice Island colony.

The current increase of double-crested cormorants nesting in the Columbia River estuary is also part of a continuing expansion of populations of this species along the Pacific coast of North America (recently reviewed by Carter et al. 1995). Unlike the historically unprecedented increase in Caspian tern populations along the Pacific Coast, it appears that double-crested cormorants are recovering from population declines all along the Pacific Coast that were suffered in the late 1800's and early 1900's owing to various human activities. Like Caspian terns, double-crested cormorants utilize artificial islands and structures (i.e., pilings and channel markers) in the Columbia River estuary to nest. Furthermore, their population expansion is relatively recent; the colony on East Sand Island was discovered in 1987-88 and the colony on Rice Island originated in 1988. Again, the rapid initial build-up of these breeding colonies indicates that breeders were recruited from other colonies. The double-crested cormorant colonies at East Sand Island (ca. 5,200 pairs) and Rice Island (ca. 1,200 pairs) are currently the two largest known colonies for this species on the Pacific coasts of the U.S. and Canada (Carter et al. 1995).

Nesting Success

The ca. 5% nesting success of Caspian terns breeding at Rice Island in 1997 was unexpected, given the large size of the colony and its rapid increase during the last decade. Observations from blinds left little doubt over the proximate cause of most nest failure (gull predation on eggs and chicks), but the ultimate cause of such high nest predation rates is more difficult to ascertain. Certainly the high frequency of bald eagle disturbance at the tern colony was a contributing factor. Most bald eagle nesting pairs in the Columbia River estuary failed in 1997, and failed breeders are known to wander more widely from nesting territories (R. G. Anthony, OSU, pers. comm.). This may have contributed to the high incidence of bald eagle disturbance observed at the Rice Island Caspian tern colony in 1997. The strong reaction of adult Caspian terns to proximity of bald eagles appeared justified from the signs of eagle predation on adult terns that were frequently found around the colony. Remains of plucked and decapitated Caspian terns were frequently encountered around the periphery of the colony at sites where eagles were known to perch. On two occasions bald eagles were observed from the blinds preying on adult terns in the colony. Disturbance from bald eagles also reduces nesting success of Caspian terns on Rice Island due to increased gull predation on eggs and chicks. Similarly, researchers working on the colony or moving to or from observation blinds also contributed to higher nest predation rates by gulls, at least locally. Despite the general prevalence of gull predation on nests, bald eagles and researchers played roles in the low nesting success of Caspian terns at Rice Island in 1997.

Both bald eagles and glaucous-winged/western gulls have apparently played roles in the previous demise of other Caspian tern colonies at Grays Harbor and Willapa Bay. The history of short-lived colonies and shifting breeding sites, plus observations of increasing gull and eagle disturbance (J. Smith, WDFW, pers. comm.) at former Caspian tern colonies suggests that low nest site fidelity may be related to the gradual build-up of predator populations once a colony is established.

Productivity of double-crested cormorants nesting in the estuary was considerably higher than that of Caspian terns. Most active nests on the channel markers near Rice Island successfully fledged young (73%), and the average number of young fledged per successful nest was 2.1. This nesting success suggests that the cormorant breeding population in the estuary is likely to expand again in 1998. Substantial increases in the East Sand Island and Rice Island colonies in 1998 are especially likely because of predicted high sea surface temperatures and poor upwelling along the Oregon and Washington coasts associated with El Niño. During previous El Niño years, double-crested cormorants nesting on islands off the coast have shifted inland in an apparent attempt to nest near areas of higher food availability (Carter et al. 1995).

Diet Composition

Juvenile salmonids were the most important component of the diet of Caspian terns nesting in the estuary, regardless of whether diet composition was expressed as a proportion of total prey items or as a proportion of total biomass consumed (Figure 7). The preponderance of salmonids in the diet of Rice Island Caspian terns was consistent among samples of adult stomach contents, bill loads (i.e., dropped fish), and visual identifications of prey delivered to the colony. At least during the 1997 breeding season, Caspian terns nesting at the Rice Island colony foraged primarily on juvenile salmonids. The proportion of salmonids in the diet declined as the breeding season progressed, so that by July salmonids no longer comprised the majority of biomass consumed, but still represented the majority of prey items consumed. These results reflect the generally poor availability of alternative fish prey in the area of Rice Island during spring. Hinton et al. (1995) reported that forage fish caught in purse seines near Miller Sands in May were 99.4 % juvenile salmonids (n = 696 fish). Peamouth and other alternative forage fishes for terns became more numerous in mid-summer trawls (Hinton et al. 1995).

By comparison, the diet of other piscivorous waterbirds was more varied. Double-crested cormorants consumed many smolts (30% of identifiable prey items in stomachs), especially in May (Figure 6), but in general cormorant diets were much more diverse than tern diets (Table 6). The large body size and high metabolic rates of double-crested cormorants, however, suggest that the lower proportion of salmonids in the diet may be compensated by higher food requirements, so that total consumption of juvenile salmonids by cormorants nesting in the estuary could be similar to numbers consumed by Caspian terns. Comparison of diet composition between cormorants nesting on Rice Island and East Sand Island revealed some interesting differences. Cormorants nesting on Rice Island (20 km farther from the ocean than East Sand Island) had more than twice the proportion of juvenile salmonids in the diet (35 % vs. 16%; see Figure 6), and also consumed more peamouth. These two important prey items for Rice Island cormorants were largely replaced by sculpin and shiner perch, forage fish with more marine affinities, in diets of cormorants from East Sand Island. The high proportion of salmonids in cormorant diets for May (95.3 %; see Table 8) was based on 15 stomach samples collected near Rice Island and four stomach samples collected near East Sand Island. Of the 63 identifiable prey items in the stomachs from the Rice Island area, all but one (98 %) were salmonids, whereas of the 10 identifiable prey items in the stomachs from the East Sand Island area only two (20 %) were salmonids. These large local differences in cormorant diets between colonies have been reported previously (Neuman et al. 1997). It will be necessary, therefore, to develop separate bioenergetics models for each of these colonies in order to accurately estimate predation on smolts by cormorants in the estuary as a whole. Such a sampling effort is planned for the 1998 season.

The limited data on diet composition of glaucous-winged/western gulls in the estuary suggest that juvenile salmonids are an appreciable proportion of the diet (11 % of stomach contents, Table 6). Most stomach contents samples were collected in the vicinity of Rice Island, however, where most of the juvenile salmonids in the diet of gulls may represent Caspian tern bill loads that were pirated by the gulls on or near the Rice Island tern colony. Also, most gulls that nest in the estuary breed at East Sand Island, a location where more alternative prey (i.e., marine invertebrates and fish) are available. Kleptoparasitism of Caspian terns by glaucous-winged/western gulls was very prevalent at the Rice Island colony. Gull diet samples for the month of May indicated an especially high proportion of juvenile salmonids in the diet (48.9 %, Table 8). But of the 16 gull stomach contents samples collected during May, all but one (94 %) were collected in the Rice Island area. Because the majority of glaucous-winged/western gulls in the estuary (71 %) nest on East Sand Island, basing total smolt losses to glaucous-winged/western gulls in the estuary on samples obtained from Rice Island may be in error.

There were small amounts of fish in general, and salmonids in particular, in the stomach contents of California and ring-billed gulls nesting at up-river colonies in 1997. These colonies had the most diverse diets of all the colonial waterbirds studied, to include insects, mollusks, plant material, and anthropogenic garbage (Table 7). The only up-river gull colony where juvenile salmonids were found in stomach contents was the California gull colony on Little Memaloose Island (16 % of total mass of stomach contents) in The Dalles pool. This colony is situated closer to a mainstem dam than any other up-river colony, and gulls from this colony are known to prey on juvenile salmonids in the tailrace of The Dalles Dam (J. Snelling, OSU, pers. comm.). Other gull colonies may opportunistically prey on juvenile salmonids when available, but the data collected in 1997 suggest they were a trivial part of the diet. Dams may be the focus of predation on juvenile salmonids by up-river gull colonies, and some of the smolts taken by gulls at the dams may be either dead of injured. Current efforts to control avian predation at the dams (bird wires, hazing, shooting) may be effective in minimizing gull predation as a source of smolt mortality.

Collection of fish transported in the bill by adult terns (“bill loads” or “dropped fish”) offers a special opportunity to identify Caspian tern prey down to the taxonomic level of species. The dropped fish sample indicated that steelhead smolts were most prevalent in the diet through early May, coho smolts were most common in the diet from late May to early June, while juvenile chinook salmon became an important part of the diet from late June to late July. The data on recovered smolt PIT tags at the Rice Island colony suggests that steelhead smolts were selected over coho smolts, which were selected over chinook smolts (Figure 10). This apparent preference for different species of smolts follows the trend in average size of these species, with steelhead smolts weighing on average over twice that of coho smolts, which averaged over twice the weight of chinook smolts (Table 15). The PIT tag data, coupled with the dropped fish sample, suggest that the availability of steelhead and coho smolts dropped off sharply by mid June, and remained low relative to the availability of chinook smolts for the remainder of the breeding season. There is a possibility that the fish transported in the bill by adult terns may not be representative of the fish consumed by those adults. Breeding adults might select especially large or lipid-rich fish to transport back to the colony, and consume the smaller and/or leaner prey themselves. We collected 30 adult terns during the 1997 breeding season that were transporting a fish in their bill and had fresh prey in their stomach. Of this sample, 19 terns (63 %) had the same type and size of prey in their stomach as the bill load fish, seven terns (23 %) had larger prey in the stomach than the bill load fish, and only four terns (13 %) had smaller prey in the stomach than the bill load fish. This limited sample suggests that the composition of fish from bill loads is similar to the composition of adult diets for Rice Island Caspian terns.

Systematic sampling for PIT tags on the Rice Island Caspian tern colony suggests that there have been over 33,000 smolt PIT tags deposited there. Based on the total number of smolts PIT-tagged in 1996 and 1997, and the proportion of those PIT tags that were estimated to be on the Rice Island colony, we estimated that the tern population consumed millions of smolts in both 1996 and 1997. The data on recovered PIT tags from the colony also indicated that hatchery-raised smolts were more vulnerable to Caspian tern predation than were wild smolts. This might be explained by differences between hatchery and wild stocks in (1) their vertical depth distribution (i.e., hatchery fish more surface oriented than wild fish), (2) stress or disease levels, (3) residence time in the estuary, and/or (4) differences in predator avoidance abilities. Further investigation of these and other factors in the 1998 field season may help explain differences in predation rates on various stocks, rearing types, and transported versus non-transported juvenile salmonids.

Estimated Number of Salmonids Consumed

Estimates of the numbers of juvenile salmonids consumed by the Rice Island Caspian tern colony during the 1997 breeding season are in the range of 6 to 25 million fish, based on bioenergetics calculations. The numbers consumed by this one waterbird colony could represent a significant proportion (ca. 6 - 25 %) of all out-migrating smolts that reached the estuary in 1997. The available data on cormorants diet in the estuary are insufficient to provide an estimate of numbers of smolts consumed in 1997, but the available data suggest that losses to cormorants were in the millions (Table 17). Estimates of smolt losses to birds in the range of 10 - 30 % of all smolts reaching the estuary in 1997 appear likely, confirming estimates based on predation of radio-tagged smolts (Schreck et al., unpubl. data). By comparison, an estimated 15.2 million juvenile salmonids have been consumed annually by northern pikeminnow in the entire lower Columbia and Snake rivers (Beamesderfer et al. 1996).

Foraging Behavior

No attempt was made to systematically collect data on the foraging behavior of terns, cormorants, or gulls during the 1997 breeding season. Anecdotal observations suggested that piscivorous waterbirds foraging in the estuary take advantage of tidal currents, obstructions in the river, strandings on tidal flats, and the foraging activities of conspecifics and other fish-eating birds to enhance their foraging efficiency on juvenile salmonids. Identifying those environmental factors that contribute to high predation rates by birds could potentially provide new and effective means of managing avian predation on smolts. We also lack information on the distribution of foraging piscivorous waterbirds in the estuary and the foraging ranges of terns, cormorants, and gulls with respect to their breeding colonies. Collection of these data is planned for the 1998 field season.

Limitations of the Data

Only one year of data from this study is available for drawing conclusions regarding the magnitude of avian predation on juvenile salmonids. Annual variation in weather and flow conditions and smolt behavior likely result in considerable variation in avian predation rates. Reliable estimates require multiple years of measurement to account for normal annual variation. The spring of 1997 was the highest run-off year on record for the Columbia River Basin. Coupled with high sea surface temperatures and poor up-welling in marine waters, it is not likely that 1997 was representative of "normal" avian predation rates on juvenile salmonids.

We currently lack the data necessary to calculate even crude estimates of the numbers of juvenile salmonids consumed by cormorants and gulls, or to refine estimates of the numbers of smolts consumed by Caspian terns. The only means of developing reliable estimates of numbers of juvenile salmonids consumed by birds is by using a bioenergetics modeling approach (Derby and Lovvorn 1997). Several crucial input variables for the bioenergetics calculations are imprecisely known or unknown, including estimates of numbers of nonbreeding adults that may spend little time at the breeding colony and the duration of their residence in the estuary, the average proportion of prey biomass represented by each salmonid species, and daily energy requirements of adults and their young. The first may be difficult to measure, but we should obtain a better sense of the numbers of nonbreeders that forage in the estuary but spend little time at the colony by monitoring numbers of adults at alternative roosting and loafing sites throughout the estuary. In 1998 we will initiate systematic surveys of the estuary that will help identify tern roosting areas where nonbreeders may rest. The second variable is difficult to measure without bias, even when stomach samples are collected from adults returning to the colony from foraging trips. A bias in where adults are collected can easily lead to a strongly biased diet sample if adults are commuting in a particular direction to forage on certain prey type(s). During the 1998 field season, we will attempt to reduce this bias in estimating the proportion of the diet that is juvenile salmonids. Estimating the third variable, adult daily energy requirements (DEE), requires further experimental work using the doubly-labeled water technique. The two measurements obtained for DEE of Caspian tern in 1997 using this technique suggest that predictions of DEE from the allometric equation for all seabirds (Birt-Friesen et al. 1989) may underestimate actual field metabolic rates, and thus underestimate the number of salmonids consumed based on the bioenergetics model.

We currently have two consecutive years of colonial waterbird census data, but determining current population trends of fish-eating bird colonies will require a minimum of three consecutive years of census data. We know very little about the foraging strategies of fish-eating birds and the factors that enhance or reduce their efficiency as predators on juvenile salmonids. Recommending alternatives for managing avian predation on smolts will be difficult without this information.

Using the smolt PIT tags recovered on the Rice Island Caspian tern colony to make inferences about relative vulnerability of smolt species and rearing types to tern predation is problematic without reliable data on the composition of smolts available in the estuary for terns to prey on. These data are potentially available from trawl surveys of PIT tagged smolts in the estuary (R. Ledgerwood, NMFS, pers. comm.).

Management Implications

One of the objectives of this research was to develop recommendations for managing avian predation on juvenile salmonids, if warranted by the study results. If current trends continue in 1998, management of avian predators in the estuary appears justified. The picture emerging after a year of study, with special emphasis on research in the estuary, is of a highly dynamic, nonequilibrium system with potentially unprecedented predation pressure on out-migrating salmonids from birds. The combination of new colonial waterbird nesting habitat in the form of expanding islands of dredge material, large and apparently unprecedented colonies of piscivorous waterbirds, and declining alternative forage fish resources for these avian predators, both in the estuary and the nearshore marine environment, may have resulted in these unexpectedly high losses of smolts to birds.

There is a growing body of evidence that the operation of the hydrosystem may be contributing to unexpectedly high avian predation rates on juvenile salmonids in the Columbia River estuary. Carl Schreck and co-workers have collected data that support the hypothesis that various efforts to reduce smolt mortality in-river (e.g., enhanced spill, barging) may cause hatchery-raised smolts to reach the estuary before they are fully smolted. Smolts that reach the estuary prematurely may be avoiding seawater by remaining in the freshwater lens at the surface where they are more vulnerable to tern predation. Also, the additive stress on juvenile salmonids from negotiating dams and/or being barged downriver may contribute to reduced physiological condition and/or enhanced disease, factors that will tend to further increase the vulnerability of smolts to bird predation in the estuary.

Should it be deemed necessary, there are a number of potential options for reducing avian predation on juvenile salmonids, including: (1) modification of hatchery rearing, smolt transport, and smolt release practices; (2) modification of habitat features to reduce the foraging efficiency of avian predators; (3) modification of nesting habitat at bird colonies to limit availability of nest sites and encourage potential recruits to nest elsewhere; (4) biological control of avian predators by encouraging natural predators and/or competitors; and (5) providing alternative nesting habitat for colonies of fish-eating birds at sites where smolts are less vulnerable to bird predation.

As part of option 1, efforts can be made to reduce the vulnerability of smolts to avian predators. Our first year of data suggests that hatchery-raised smolts are more vulnerable to Caspian tern predation than wild smolts. Hatchery rearing practices can potentially be modified to discourage smolts from foraging near the surface, where they are especially vulnerable to tern predation, and to encourage strong avoidance responses when exposed to stimuli associated with foraging birds. Also, hatchery smolts can be released in the estuary at nightfall and on an outgoing tide to minimize exposure to foraging birds immediately after release, a practice that some hatcheries on the estuary are currently using (J. Hill, CEDC, pers. comm.). Barging practices may also be modified to reduce stress prior to and during release, as well as to ensure that smolts do not arrive at the estuary before they are ready to enter saltwater.

Option 2 is to alter features of the environment so as to deter avian predators at the foraging site. This could consist of removing or modifying structures that foraging birds us for roosting (e.g., pile dikes, old channel markers). Bird wires can be installed in certain locales where smolts are especially vulnerable (e.g., tailraces of dams, natural eddies where smolts tend to collect). This method has proved effective at reducing avian predation at a number of mainstem dams, and its use could be expanded.

Option 3 seeks to limit the size of breeding colonies by limiting the amount of suitable nesting habitat at the colony. This may be accomplished in the case of Caspian tern colonies by vegetating the open sandy substrate that the terns use for nesting so as to render it unattractive for breeding terns. There is evidence that Caspian terns abandoned the East Sand Island colony in the mid 1980's because of encroaching vegetation (G. Dorsey, USACE, pers. comm.). In the case of double-crested cormorants, it may be necessary to establish shrubby vegetation around the colony in order to limit colony expansion.

Option 4 focuses on management of the birds themselves in an effort to limit the increase or reduce certain populations. Shooting has been used to a limited extent to discourage piscivorous waterbirds foraging in the tailrace of certain mainstem dams. While this has been an effective method for reducing avian predation at certain sites where smolts are especially vulnerable, it may not be a viable option for eliminating or reducing certain breeding colonies that may be causing extensive smolt mortality. An alternative is to encourage the natural predators of these colonial waterbirds. This can run the gamut from encouraging gulls and raptors by erecting perches around the colony to attracting gulls to the colony by providing supplemental food. These measures would not just increase adult mortality and reduce nesting success, but would also encourage breeding adults to nest elsewhere.

Option 5 consists of translocating breeding colonies to sites where they do not pose as serious a threat to the survival of juvenile salmonids. As an example, the Caspian tern colony on Rice Island might not be so dependent on juvenile salmonids as a food supply if it was located on East Sand Island, where more alternative prey species are available, as indicated by the more diverse diet of cormorants nesting at East Sand Island. Relocation of the Rice Island tern colony to former colony sites in Willapa Bay or Grays Harbor might further reduce the impact of the tern population on depleted Columbia River Basin salmonid stocks. Translocating the colony could be accomplished through a combination of attracting the birds to the new site with fresh dredge spoil as a nesting substrate, putting out tern decoys as a social attractant, and broadcasting playbacks of Caspian tern calls, as well as discouraging them from nesting at the old site using techniques described under options 3 and 4 above. In addition, some control of glaucous-winged/western gulls at the new colony site might be essential for establishing the colony and initially assuring some successful reproduction. These techniques have been developed by Steve Kress and co-workers with the Seabird Restoration Project of National Audubon Society as a means of reestablishing tern colonies at sites where they have not bred in decades, and could be adapted for translocating tern colonies away from ecologically sensitive areas.

Despite the ultimate factors responsible for the failure of Columbia and Snake river salmonid stocks to recover, avian predation may be a proximate factor that is currently limiting recovery. Management alternatives focusing on birds may be effective and efficient components of a comprehensive plan to restore salmonids, but it should be appreciated that if avian predation is a major source of mortality for juvenile salmonids in the Columbia River Basin, it is almost certainly a reflection of anthropogenic change. Furthermore, 1997 was by all accounts not a normal year for the out-migration of juvenile salmonids nor for their bird predators. Basing the need for management of avian predation on results from one year may lead to inappropriate management. Further investigation is necessary to identify which predator populations pose the greatest risk to salmon survival, what factors are most important in explaining variation in avian predation rates, and what management alternatives have the highest probability of success. This information is an important first step in developing a management plan to reduce avian predation that has the support of regional fish and wildlife managers, special interest groups, and the public.

New Directions in 1998

In 1998 we will implement three major new tasks: (1) testing the feasibility of several options for managing avian predators at their nesting colonies in order to reduce predation on smolts; (2) determination of factors influencing foraging success of avian predators on smolts; and (3) measurement of daily energy expenditure of piscivorous birds to better estimate smolt consumption rates. The first is crucial for designing and implementing an effective management plan for avian predators, if warranted. In 1997 the focus of colony-based research was the Caspian tern colony at Rice Island. In 1998 we plan on expanding our efforts to other colonies and to other species of fish-eating birds, especially cormorants nesting in the estuary.

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TABLES

Table 1. Population indices for piscivorous waterbird colonies as determined by aerial photography in 1997, and percent change from the 1996 census.

		Population Indices[a] (% change from 1996)		
Ref#[b]	Location	Terns[c]	Gulls[d]	Cormorants[e]
1	East Sand Is.	--	7,106 (+5%)	5,271 (+1%)
2	Rice Is.	9,415 (+16%)	1,583 (+51%)	1,221 (+92%)
3	Miller Sands[f]	--	1,268 (n/a)	--
4	Little Memaloose Is.	--	939 (+73%)	--
5	Miller Rocks	--	3,783 (+126%)	--
6	Three Mile Canyon Is.	571 (+106%)	13,305 (+51%)	--
7	Crescent Is.	990 (+200%)	5,769 (+73%)	--
8	Richland Is.	--	18,820 (+6%)	--
9	Island #18	--	14,495 (-15%)	--
	TOTALS	10,976 (+25%)	67,068 (+15%)	6,492[g] (+11%)

[a] Indices are direct counts of the number of adults on the ground from high resolution aerial photographs taken late in the incubation period. These numbers, once doubled, are a reasonable estimate of the colony population size.

[b] Numbers refer to locations on map of study area (Figure 1).

[c] Caspian tern

[d] California gull, ring-billed gull, glaucous-winged/western gull hybrids

[e] Double-crested cormorant

[f] 1996 census information not available

[g] An additional 200 pairs nest on pilings and channel markers in the Columbia River Estuary near Rice Island and Desdemona Sands

Table 2. Colony establishment, year first censused, census numbers, and average annual change in breeding population size from year of first census to 1997 for piscivorous waterbird colonies on the lower Columbia River (No census data available for Crescent Island prior to this study).

Species Location	Year Colony Established	Year First Censused	Number of Nesting Pairs at First Census	Average % Change in Breeding Population Size, per Year
Caspian tern				
Rice Island[a]	1987	1987	1,350	+ 21%
Three Mile Canyon[b]	Unknown	1977	184	+ 6%
California & ring-billed gull[b]				
Little Memaloose Is.	Unknown	1977	428	+ 4%
Miller Rocks	Unknown	1977	1,042	+ 7%
Three Mile Canyon	After 1968	1977	4,377	+ 6%
Richland Is.	1970	1977	4,155	+ 8%
Island 18	1971	1977	5,201	+ 5%
Double-crested cormorant[c]				
East Sand Is.	1987	1991	2,026	+ 17%
Rice Is.	1988	1991	1,211	0%

[a] A. Clark, USFWS, unpub. data
[b] Thompson and Tabor 1991
[c] Carter et al. 1995

Table 3. Caspian tern productivity based marked nests (N= 152) on Rice Island in 1997.

Variable (N)	Value ± SD	Range
Average clutch size (no. of eggs)	1.99 ± 0.70	1 - 4
Average no. of young hatched per initiated nest (approx. age: 1 - 5 days post-hatch)	0.52 ± 0.75	0 - 3
Average brood size (approx. age: 1 - 5 days post-hatch)	1.39 ± 0.53	0 - 3
Average percentage of clutch hatched per initiated nest	26 %	0 - 100%
Number of fledglings banded	264	
Estimated number of chicks fledged from colony	400	
Nesting success [a]	5%	

[a] proportion of initiated nests [ca. 8,017] fledging at least 1 young

Table 4. Double-crested cormorant productivity in the Columbia River estuary in 1997.

Variable (N)	Value ± SD	Range
Channel Markers (64 nests)		
Total eggs produced	268	
Average clutch size	4.2 ± 1.3	2 - 8
Total eggs hatched	151	
Percentage of eggs hatched (268 eggs)	56%	
Average percentage of clutch hatched	60%	0 - 100%
Percentage of initiated nests hatching at least 1 egg	84.4%	
Average brood size at hatching (54 broods)	2.8	2-5
Number of nestlings banded	102	
Nestling survival to approx. 1500 g (151 chicks)	65.6%	
Mean brood size at fledging (47 broods) [a]	2.11 ± 0.70	0 - 3
Nesting success [b]	73.4%	
Productivity (no. young fledged/initiated nest)	1.55	
East Sand Island (50 nests)		
Mean brood size [c]	1.61 ± 0.75	0 - 3

[a] number of fledglings per nest that fledged at least 1 young
[b] proportion of initiated nests fledging at least 1 young
[c] number of chicks per nest; ages of chicks ranged from approx. 14-25 days post-hatching

Table 5. Growth rates in body mass (g) and wing length (mm) for double-crested cormorants and Caspian terns in the Columbia River estuary in 1997.

Variable	Double-crested cormorant [a]	Caspian tern [b]
Number of chicks measured at least once	119	264
Body mass growth rate during the linear phase	76.4 g/day	10.9 g/day
Wing length growth rate during the linear phase	7.3 mm/day	--
Growth performance index [c]	0.029	0.074

[a] linear growth phase for body mass and wing length was 10-24 days post-hatching and 14-35 days post-hatching, respectively

[b] linear growth phase for body mass was 8-18 days post-hatching

[c] slope of the regression of the square root of body mass vs. the natural log of the square root of wing length

Table 6. Percent mass (mass of prey type/total diet mass) and percent of prey items (number of prey items per prey type/total number of prey items) for piscivorous waterbirds nesting on the lower Columbia River in 1997.

	Estuary Colonies								**Upriver Colonies**			
	Double-crested cormorant		Caspian tern		Glaucous-winged/ western gull		Ring-billed gull		California gull		Ring-billed gull	
Prey Type	% Mass	% No.	% Mass	% No.	% Mass	% No.	% Mass	% No.	% Mass	% No.	% Mass	% No.
Crustacean	--	--	--	--	0.1	0.6	--	--	--	0.2	0.0	0.2
Mollusk	--	--	--	--	4.1	34.3	50.7	69.4	14.7	57.9	7.9	15.2
Insect	--	--	--	--	0.1	12.7	--	--	6.3	37.4	10.2	84.1
Vertebrate	--	--	--	--	0.2	0.6	--	--	18.6	2.5	8.6	0.5
Plant Material	--	--	--	--	0.5	--	5.2	na	17.4	na	36.4	na
Refuse	--	--	--	--	12.2	na	--	--	27.4	na	36.8	na
Fish	100.0	--	100.0	--	82.7	--	44.1	--	14.3	--	0.0	--
Pacific Lamprey[1]	0.1	0.4	--	--	--	--	--	--	--	--	--	--
White Sturgeon[2]	3.7	0.4	--	--	--	0.6	--	--	--	--	--	--
Pacific Herring[3]	0.5	0.2	--	--	--	--	--	0.1	--	--	--	--
Peamouth[4]	32.9	15.8	15.8	7.4	10.4	1.8	7.4	1.2	4.9	0.3	--	--
No. Pikeminnow[5]	1.6	1.1	--	--	--	--	--	--	0.2	0.2	--	--
Unident. Cyprinid[6]	--	0.4	--	--	--	--	--	--	--	--	--	--
Sucker[7]	8.1	2.3	--	--	7.1	0.6	--	--	--	--	--	--
Smelt[8]	0.1	0.9	--	--	--	--	--	--	--	--	--	--
Salmonid[9]	**23.7**	**30.3**	**74.5**	**84.5**	**10.8**	**10.8**	**0.5**	**0.1**	**6.0**	**1.1**	**0.0**	**0**
Stickleback[10]	1.6	21.2	--	0.1	0.5	9.6	2.9	3.5	--	--	--	--
Sculpin[11]	6.0	13.5	--	1.3	3.7	1.2	3.7	23.5	1.9	0.5	--	--
Shiner Perch[12]	3.5	8.6	1.7	1.3	--	--	--	--	--	--	--	--
Starry Flounder[13]	1.5	3.0	0.7	3.9	9.5	25.9	9.5	--	--	--	--	--
Other	1.2	1.9	--	0.1	7.2	1.2	7.2	--	--	0.2	--	--
Unknown fish	15.5	na	7.3	na	33.5	na	18.9	na	1.2	na	--	--
Samples Examined	154		92		80		23		156		53	
Total Mass and No.	10,637 g	532	3,893 g	155	1,470 g	166	195 g	170	2,586 g	653	874 g	592

[1] *Lampetra tridentata*, [2] *Acipenser transmontanus*, [3] *Clupea pallasi*, [4] *Mylocheilus caurinus*, [5] *Ptychocheilus oregonensis*, [6] Cyprinidae, [7] Catostomidae, [8] Osmeridae, [9] *Oncorhynchus sp*., [10] Gasterosteidae, [11] Cottidae, [12] *Cymatogaster aggregata*, [13] *Platichthys stellatus*

Table 7. Diet composition (% of total mass) of ring-billed and California gulls nesting at up-river colonies as determined by examination of adult stomach contents and chick regurgitations.

	Ring-billed gull colonies					
	Miller Rocks	Three Mile Canyon Is.	Crescent Is.	Island 18	Richland Is.	All Colonies
Crustacean	0	0	0	0	0	0
Mollusk	0	0	14	22	1	8
Insect	1	16	31	4	19	10
Vertebrate	64	0	0	0	0	9
Plant Matter	36	7	55	37	59	36
Fish	0	0	0	0	0	0
Refuse	0	77	0	37	21	36
Samples Examined	8	11	4	13	17	53

	California gull colonies						
	L. Memaloose Is.	Miller Rocks	Three Mile Canyon Is.	Crescent Is.	Island 18	Richland Is.	All Colonies
Crustacean	0	0	0	0	0	0	0
Mollusk	10	34	39	62	39	0	15
Insect	0	4	5	1	5	8	6
Vertebrate	0	10	0	0	0	24	19
Plant Matter	33	15	35	33	35	13	17
Fish	45	17	3	2	3	0	14
Salmonid	**16**	**0**	**0**	**0**	**0**	**0**	**6**
Refuse	12	21	18	0	18	51	27
Inorganic Material	0	0	0	0	0	3	0
Samples Examined	31	25	12	26	21	41	156

Table 8. Percent salmonids consumed by month by double-crested cormorants, Caspian terns, and glaucous-winged/western hybrid gulls nesting in the Columbia River estuary, as determined by examination of adult stomach contents and chick regurgitations for cormorants and gulls, and adult stomach contents only for terns.

Species	Month	Samples Examined	% Salmonid (by mass)
Double-crested cormorant[a]	April	19	14.4
	May	19	95.3
	June	62	6.6
	July	54	4.3
Caspian tern	April	23	99.4
	May	25	98.1
	June	22	62.9
	July	22	44.2
Glaucous-winged/ western hybrid gull[b]	April	6	2.5
	May	16	48.9
	June	24	4.9
	July	34	9.5

[a] Samples from Rice Island colonies and the East Sand colony are combined.
[b] Samples from Rice Island, Miller Sands and East Sand colonies are combined.

Table 9. Comparison between observed and expected numbers of PIT tags from steelhead vs. other salmonids from the 1996 migration year on the Rice Island Caspian tern colony. The expected number of PIT tags is based on the relative proportion of these species groups of the total number (a) sampled in-river in the estuary (Ledgerwood et al. 1997), and (b) PIT-tagged and released (PITAGIS 1997) in 1996.

(a)

	Observed # of tags				
	Caspian tern colony	In estuary	Relative proportion in estuary	**Expected # of tags**	**P**
Steelhead	**102**	140	22.1%	224 x .221 = **50**	<.0001
Other salmonids	**122**	493	77.9%	224 x .779 = **174**	
TOTAL	**224**	633	100%	**224**	

(b)

	Observed # of tags				
	Caspian tern colony	Released	Relative proportion released	**Expected # of tags**	**P**
Steelhead	**102**	80,412	18.5%	224 x .185 = **41**	<.0001
Other salmonids	**122**	354,882	81.5%	224 x .815 = **183**	
TOTAL	**224**	435,294	100%	**224**	

Table 10. Comparison between observed and expected numbers of PIT tags from (a) steelhead vs. other salmonids, and (b) chinook salmon vs. other salmonids from the 1997 migration year on the Rice Island Caspian tern colony. The expected number of PIT tags is based on the relative proportion of these species groups of the total number of juvenile salmonids PIT-tagged and released (PITAGIS 1997) in 1997.

(a)

	Observed # of tags				
	Caspian tern colony	Released	Relative proportion released	**Expected # of tags**	**P**
Steelhead	**182**	124,983	20.1%	321 x .201 = **65**	<.0001
Other salmonids	**139**	496,783	79.9%	321 x .799 = **256**	
TOTAL	**321**	621,766	100%	**321**	

(b)

	Observed # of tags				
	Caspian tern colony	Released	Relative proportion released	**Expected # of tags**	**P**
Chinook salmon	**97**	442,131	76.6%	321 x .766 = **246**	<.0001
Other salmonids	**224**	179,635	23.4%	321 x .234 = **75**	
TOTAL	**321**	621,766	100%	**321**	

Table 11. Comparison between observed and expected numbers of PIT tags from chinook salmon vs. other salmonids from the 1996 migration year on the Rice Island Caspian tern colony. The expected number of PIT tags is based on the relative proportion of these species groups of the total number (a) sampled in-river in the estuary (Ledgerwood et al. 1997), and (b) PIT-tagged and released (PITAGIS 1997) in 1996.

(a)

	Observed # of tags				
	Caspian tern colony	In estuary	Relative proportion in estuary	**Expected # of tags**	**P**
Chinook salmon	**120**	486	76.8%	224 x .768 = **172**	<.0001
Other salmonids	**104**	147	23.2%	224 x .232 = **52**	
TOTAL	**224**	633	100%	**224**	

(b)

	Observed # of tags				
	Caspian tern colony	Released	Relative proportion released	**Expected # of tags**	**P**
Chinook salmon	**120**	333,260	76.6%	224 x .766 = **172**	<.0001
Other salmonids	**104**	102,034	23.4%	224 x .234 = **52**	
TOTAL	**224**	435,294	100%	**224**	

Table 12. Comparison between observed and expected numbers of PIT tags from hatchery vs. wild salmonids from the 1996 migration year on the Rice Island Caspian tern colony. The expected number of PIT tags is based on the relative proportion of these rearing types of the total number (a) sampled in-river in the estuary (Ledgerwood et al. 1997), and (b) PIT-tagged and released (PITAGIS 1997) in 1996.

(a)

	Observed # of tags				
	Caspian tern colony	In estuary	Relative proportion in estuary	**Expected # of tags**	**P**
Hatchery	**213**	500	84.9%	223 x .849 = **189**	<.001
Wild	**10**	89	15.1%	223 x .151 = **34**	
TOTAL	**223**	589	100%	**223**	

(b)

	Observed # of tags				
	Caspian tern colony	Released	Relative proportion released	**Expected # of tags**	**P**
Hatchery	**213**	362,893	85.8%	223 x .858 = **191**	<.001
Wild	**10**	60,194	14.2%	223 x .142 = **32**	
TOTAL	**223**	423,087	100%	**223**	

Table 13. Comparison between observed and expected numbers of PIT tags from hatchery vs. wild spring/summer chinook salmon (i.e., from the NMFS's 1996 transportation study) on the Rice Island Caspian tern colony. The expected number of PIT tags is based on the relative proportion of these rearing types of the total number (a) sampled in-river in the estuary (Ledgerwood et al. 1997), and (b) PIT-tagged and released (PITAGIS 1997) in 1996.

(a)

	Observed # of tags				
	Caspian tern colony	In estuary	Relative proportion In estuary	**Expected # of tags**	**P**
Hatchery	**61**	167	78.8%	65 x .788 = **51**	<.05
Wild	**4**	45	21.2%	65 x .212 = **14**	
TOTAL	**65**	212	100%	**65**	

(b)

	Observed # of tags				
	Caspian tern colony	Released	Relative proportion released	**Expected # of tags**	**P**
Hatchery	**61**	91,004	80.0%	65 x .800 = **52**	<.05
Wild	**4**	22,777	20.0%	65 x .200 = **13**	
TOTAL	**65**	113,781	100%	**65**	

Table 14. Input parameters of a bioenergetics model for estimating the total population energy consumption of Caspian terns breeding on Rice Island in 1997

	Maximum	Best	Minimum
Daily energy expenditure (kJ bird^{-1} day^{-1}) [a]	1,138[b]	907[c]	736[d]
Assimilation efficiencies	0.70	0.75	0.80
Daily energy consumption (kJ day^{-1})	1,626	1,209	920
Average duration of predation (days)	100	90	80
Seasonal energy consumption (kJ)	162,570	108,810	73,600
Population size (individuals)	18,830	16,034	13,746
Total population energy consumption (kJ)	3.061×10^9	1.745×10^9	1.012×10^9

[a] Daily energy expenditure estimated on the basis of an average Caspian tern body mass of 654 g (unpubl. data, this study) and the allometric equations (Birt-Friesen et al. 1989) for:

[a] seabirds using flapping flight,

[b] all seabirds

[c] seabirds using non-flapping flight

Table 15. The percent of the total energy consumption by prey category based on input parameters of the bioenergetics model for Caspian terns breeding on Rice Island in 1997. See Diet Composition section for percent biomass of each prey category.

		Fish from Bill Loads		Adult Stomach Contents	
Species (N)	Mean Energy Density (kJ/g wet mass)	Mean Mass of Individual Prey Items (g)	% Total Energy Consumption	Mean Mass of Individual Prey Items (g)	% Total Energy Consumption
Steelhead (12)	4.61	58.02	39.89	59.38	31.45
Coho salmon (12)	5.04	23.83	34.19	28.80	7.85
Chinook salmon (12)	3.98	9.34	7.81	34.97	4.70
Sockeye salmon (1)	5.07	54.70	1.88		
Unknown salmonid [c]	4.00			12.86	32.35
All salmonids			**83.77**		**76.35**
Peamouth (12)	5.66	32.67	8.77	19.57	18.71
Herring (2)	6.36	23.38	3.02		
Sculpin (12)	3.96	16.90	0.91		
Shad (9)	5.67	11.34	0.87	14.32	4.94
Shiner perch (6)	4.31	12.15	0.35		
Smelt (1)	4.92	2.79	0.09		

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[a] Unknown salmonid is not classified to species due to missing diagnostic superficial tissue used in identification.

Table 16. Estimates of the number of prey consumed by Caspian terns nesting at Rice Island in 1997 using the bioenergetics modeling approach.

	Bill Loads			Stomach Contents		
Prey Type	Maximum	Best	Minimum	Maximum	Best	Minimum
Total Juvenile Salmonids	20,095,934	11,392,688	6,643,937	24,715,839	14,540,388	8,479,595
Coho	8,912,167	5,052,442	2,946,460	3,479,373	1,886,748	1,100,305
Chinook	6,636,981	3,762,605	2,194,259	1,932,499	1,046,988	610,577
Steelhead	4,231,029	2,398,634	1,398,825	3,679,203	1,994,009	1,162,857
Unknown Salmonids[a]				15,624,762	9,612,642	5,605,856
Other Fish	3,536,562	1,994,138	683,402	4,473,363	2,424,199	1,413,734
Total Fish	23,632,496	13,386,826	7,327,339	29,189,586	16,964,586	9,893,329

[a] Salmonids that could not be identified to species. Consumption estimates based on average mass and energy content for all juvenile salmonids in sample.

Table 17. Input parameters for the bioenergetics model used to estimate the number of juvenile salmonids consumed by double-crested cormorants nesting in the Columbia River estuary during the 1997 breeding season. Consumption estimates from the model are rough and subject to revision pending improved data on input variables.

Input variable	Value
Daily energy expenditure (kJ $bird^{-1}$ day^{-1}) [a]	1,927
Assimilation efficiency	0.80
Daily energy consumption (kJ $bird^{-1}$ day^{-1})	2,409
Seasonal energy consumption (kJ $bird^{-1}$ $season^{-1}$)	216,787
Population size (individuals)	12,984
Total population energy consumption (kJ)	2.81×10^9
Average duration of predation (days)	100
Percent salmonids in diet [b]	23.7

Average energy density of prey (kJ/g) [c]	Average mass of prey (g) [d]	Consumption of Juvenile Salmonids (in millions)
4.0	30	5.4
4.5	30	4.8
5.0	30	4.3
4.0	50	3.2
4.5	50	2.9
5.0	50	2.6

[a] values based on double-crested cormorants wintering in the Mississippi Delta (Glahn and Brugger 1995), therefore values for breeding cormorants in the lower Columbia River may be higher.

[b] percentage is based on % total wet biomass (see Table 8).

[c] energy density includes the range of values for salmonids (see Table 15).

[d] mean biomasses are educated estimates.

FIGURES

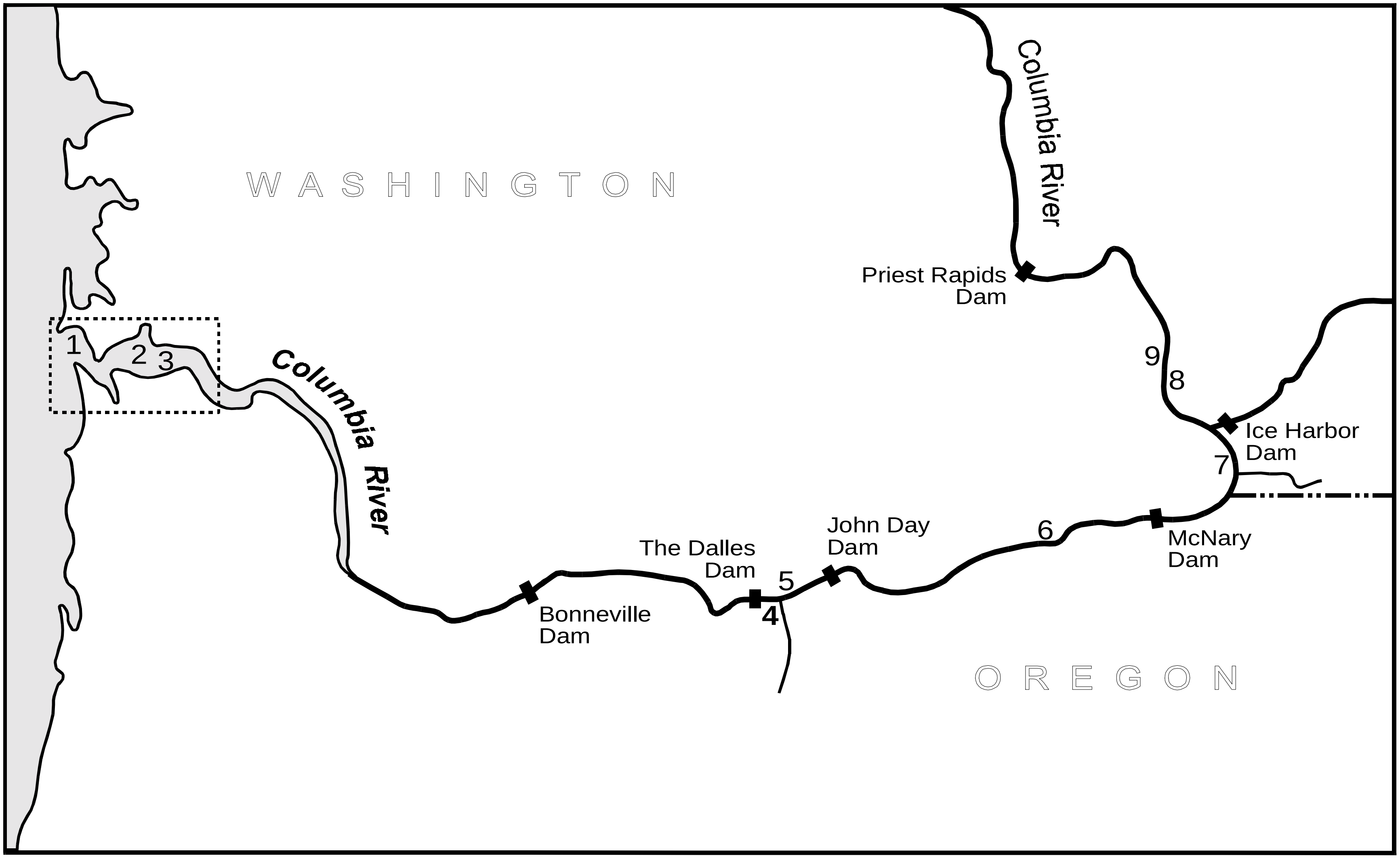


Figure 1. Lower Columbia River study area and locations of piscivorous waterbird colonies (estuary shown in dashed box). Colony locations are: 1 = East Sand Island; 2 = Rice Island; 3 = Miller Sands; 4 = Little Memaloose Island; 5 = Miller Rocks; 6 = Three Mile Canyon Island; 7 = Crescent Island; 8 = Richland Island (Island 20); and 9 = Island 18.

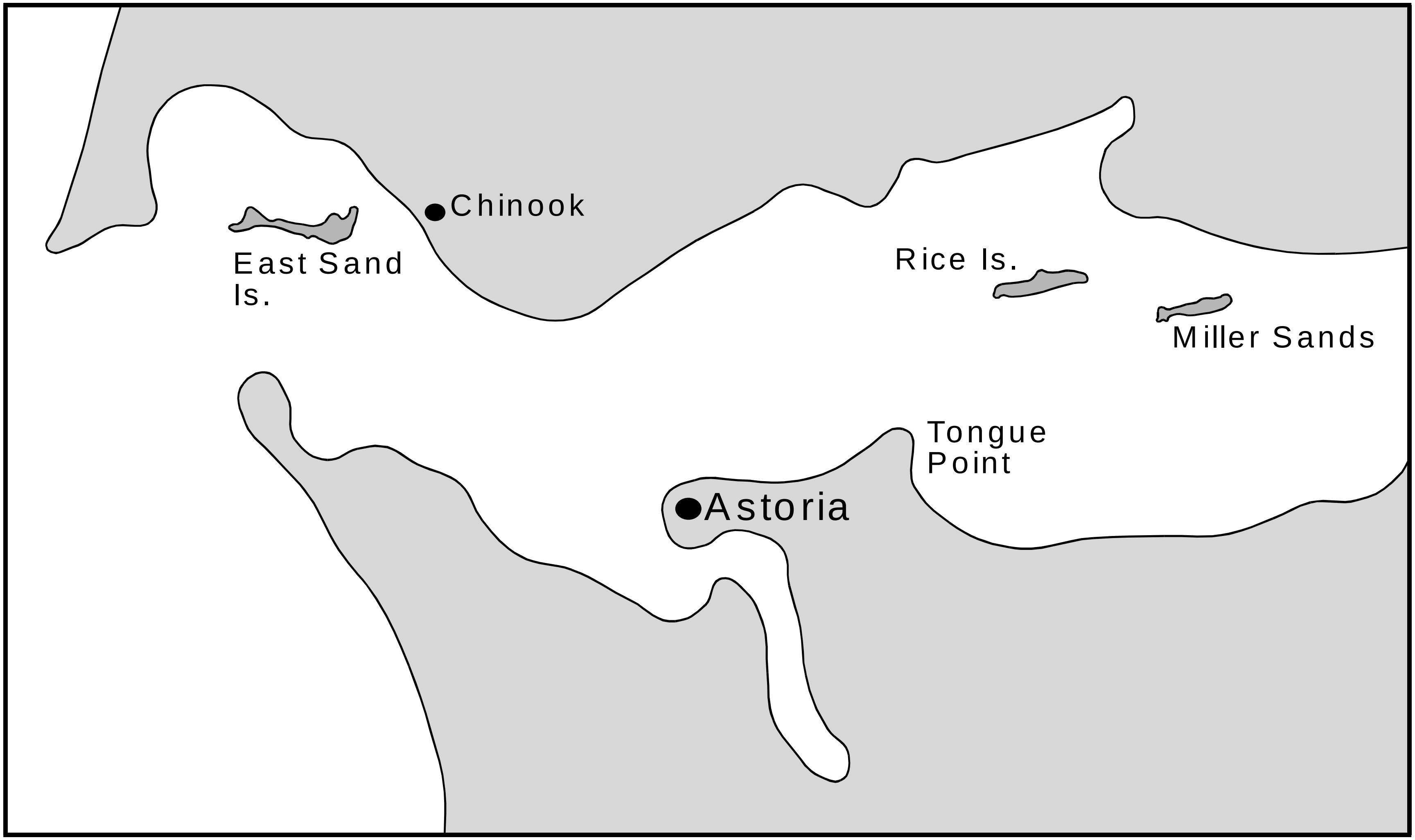


Figure 2. Columbia River Estuary study area and island locations of piscivorous waterbird colonies.

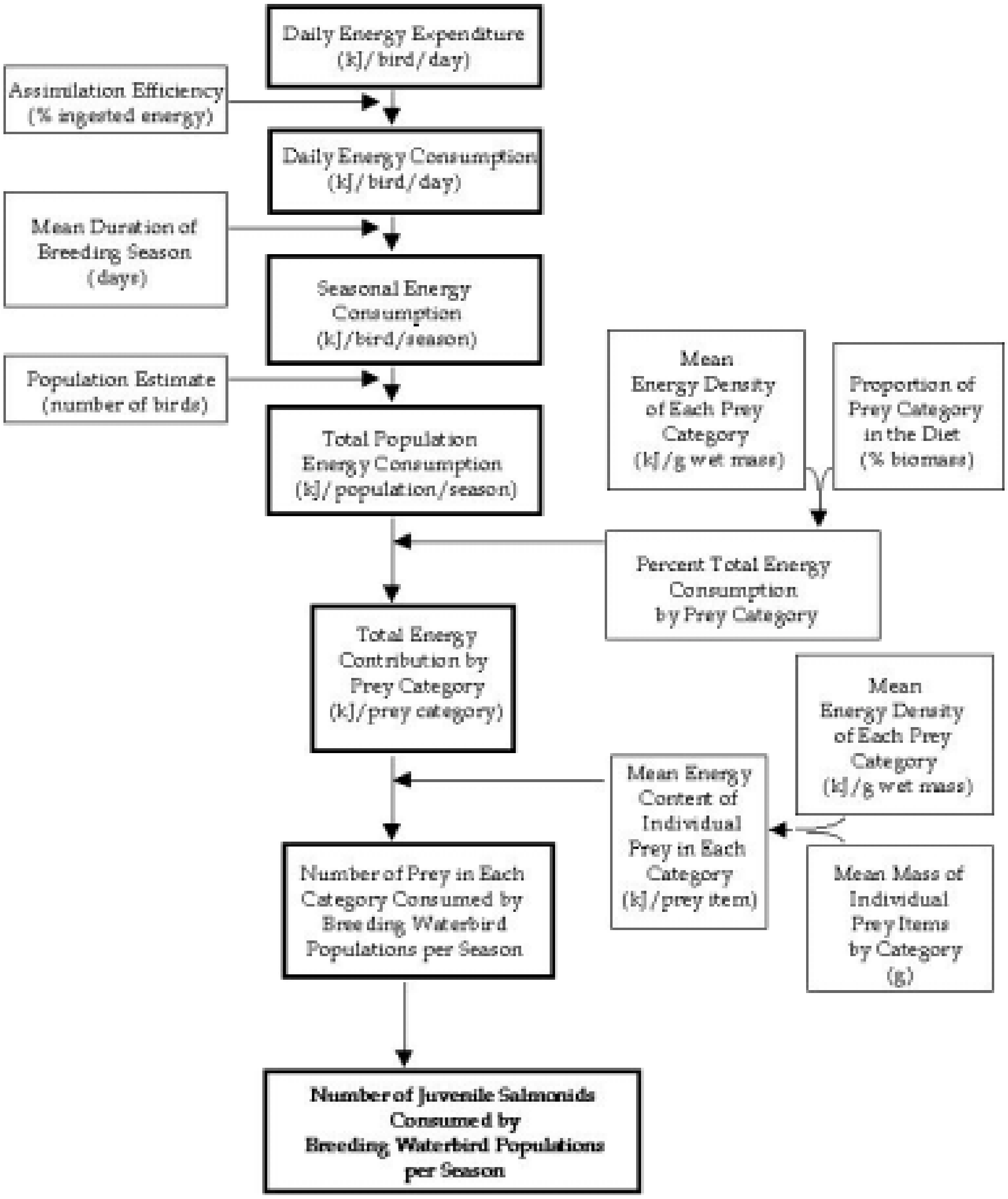
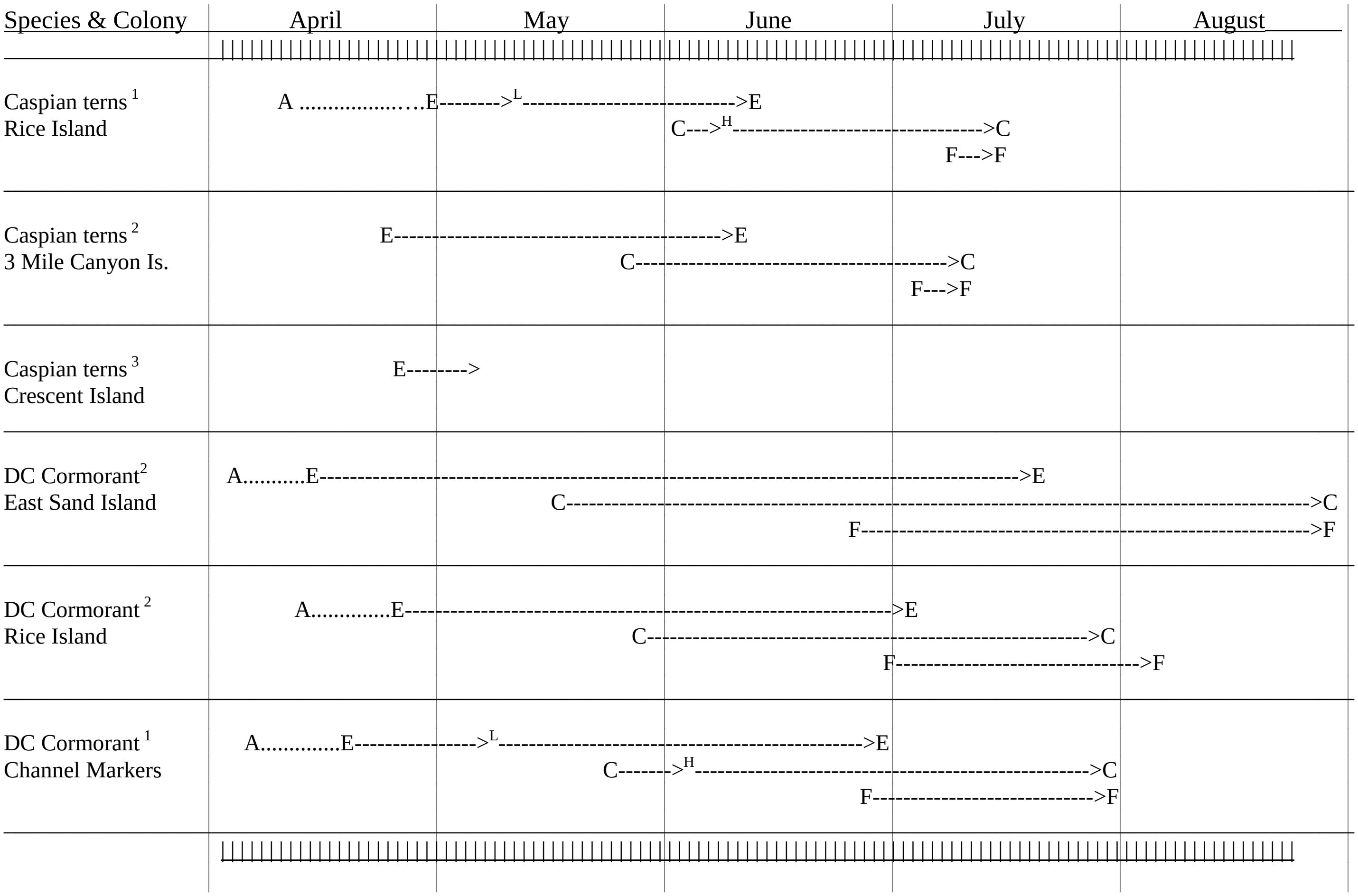


Figure 3. A bioenergetics model for estimating the number of juvenile salmonids consumed by colonial waterbirds in the lower Columbia River.

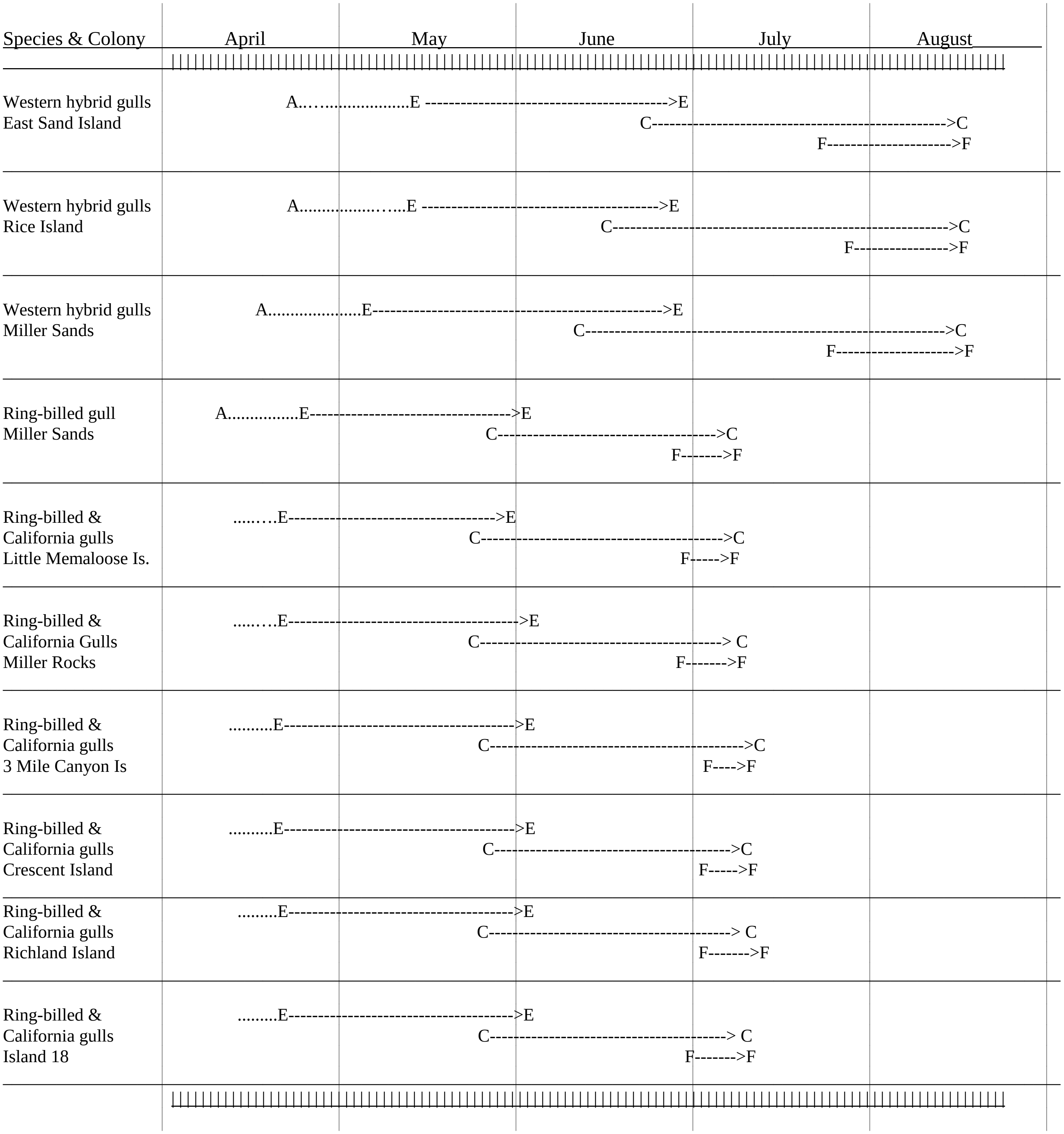
Figure 4a. Breeding chronology of Caspian terns and double-crested cormorant colonies of the Columbia River in 1997.



A = the period including the arrival of courting birds at the colony, before the first eggs were laid.
E = the period during which eggs were on the colony, including both the egg laying phase and incubation.
C = the period during which chicks were on the colony including the phases of hatchling, nestling, and crechlings
F = the period during which young of year were fledging
L = median laying date
H = median hatching date

[1] colony was monitored at least once a week
[2] colony was monitored once every two weeks
[3] colony were only sporadically visited

Figure 4b. Breeding chronology of gull colonies of the Columbia River in 1997 based on visits every 14 days.



A = the period including the arrival of courting birds at the colony, before the first eggs were laid.
E = the period during which eggs were on the colony, including both the egg laying phase and incubation.
C = the period during which chicks were on the colony, including the phases of hatchling, nestling, and crechlings
F = the period during which young of year were fledging

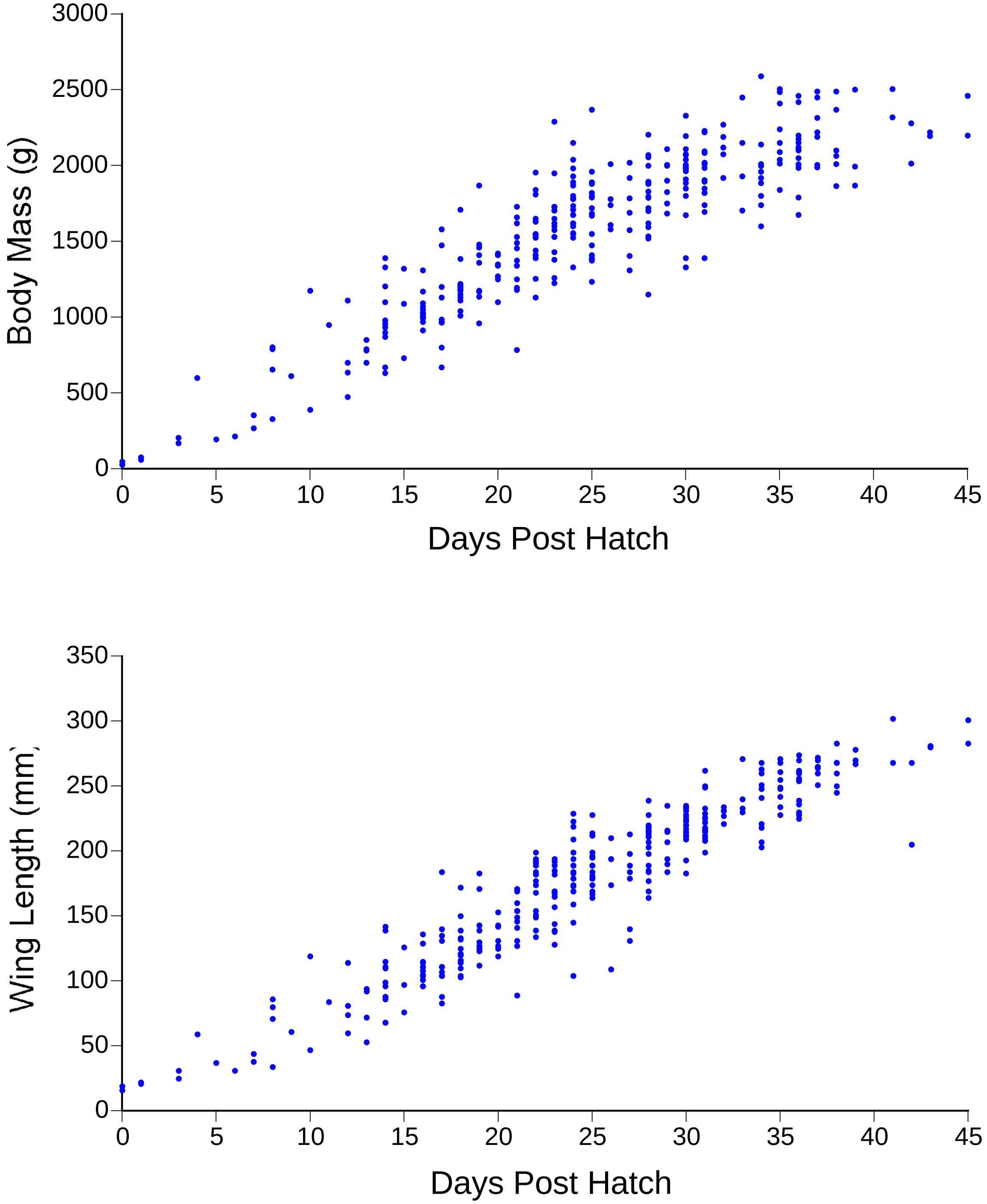
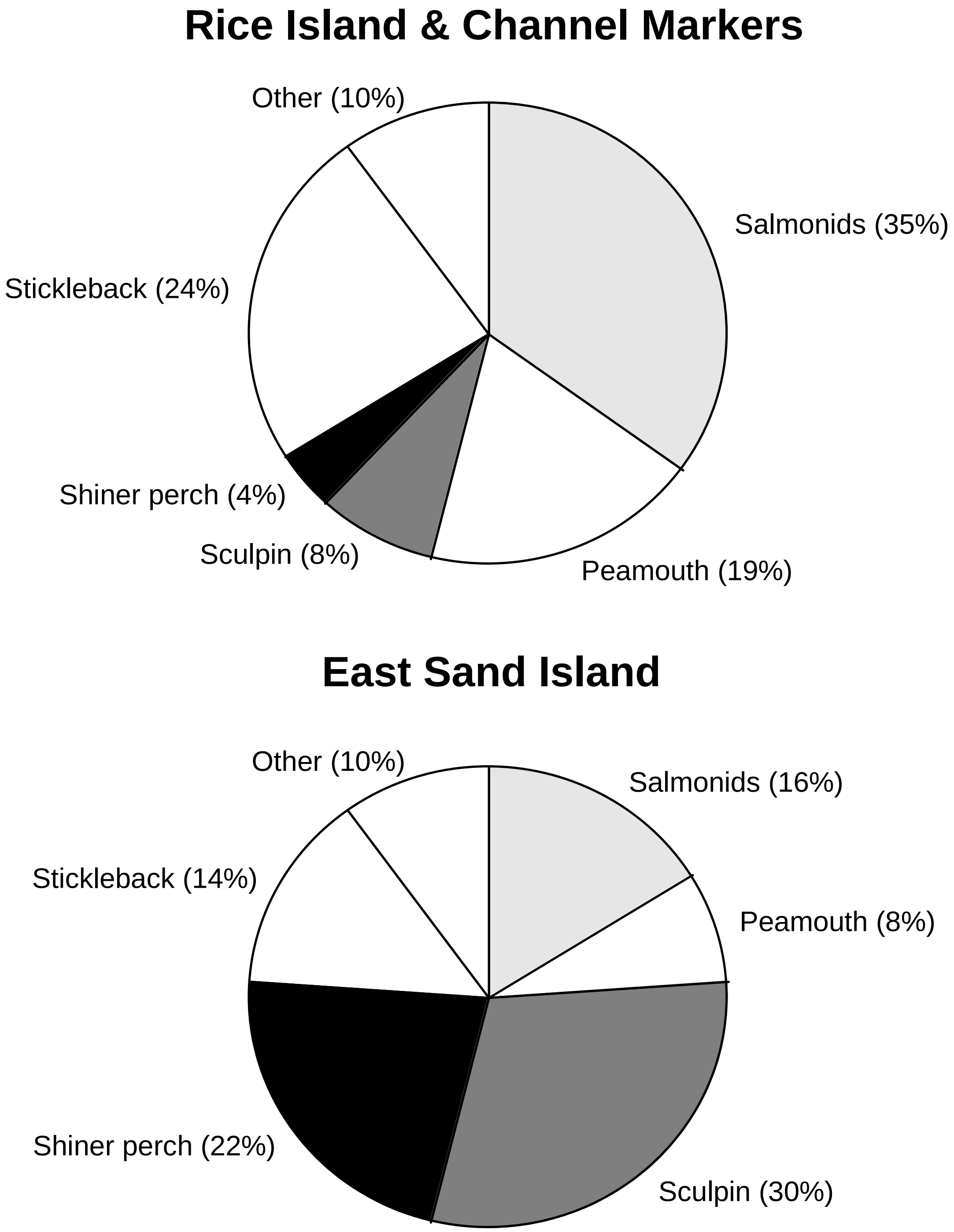


Figure 5. Growth rate of body mass and wing length of double-crested cormorants nesting on channel markers in the Columbia River estuary in 1997.



Rice Island & Channel Markers

East Sand Island

Figure 6. Comparison of the precent prey items in the diet of double-crested cormorants nesting at Rice Island and nearby channel markers vs. East Sand Island in 1997 based on adult stomach contents and chick regurgitations. A total of 120 samples and 392 prey items were analyzed for the Rice Island/channel marker group, compared to 31 samples and 132 prey items for the East Sand Island group.

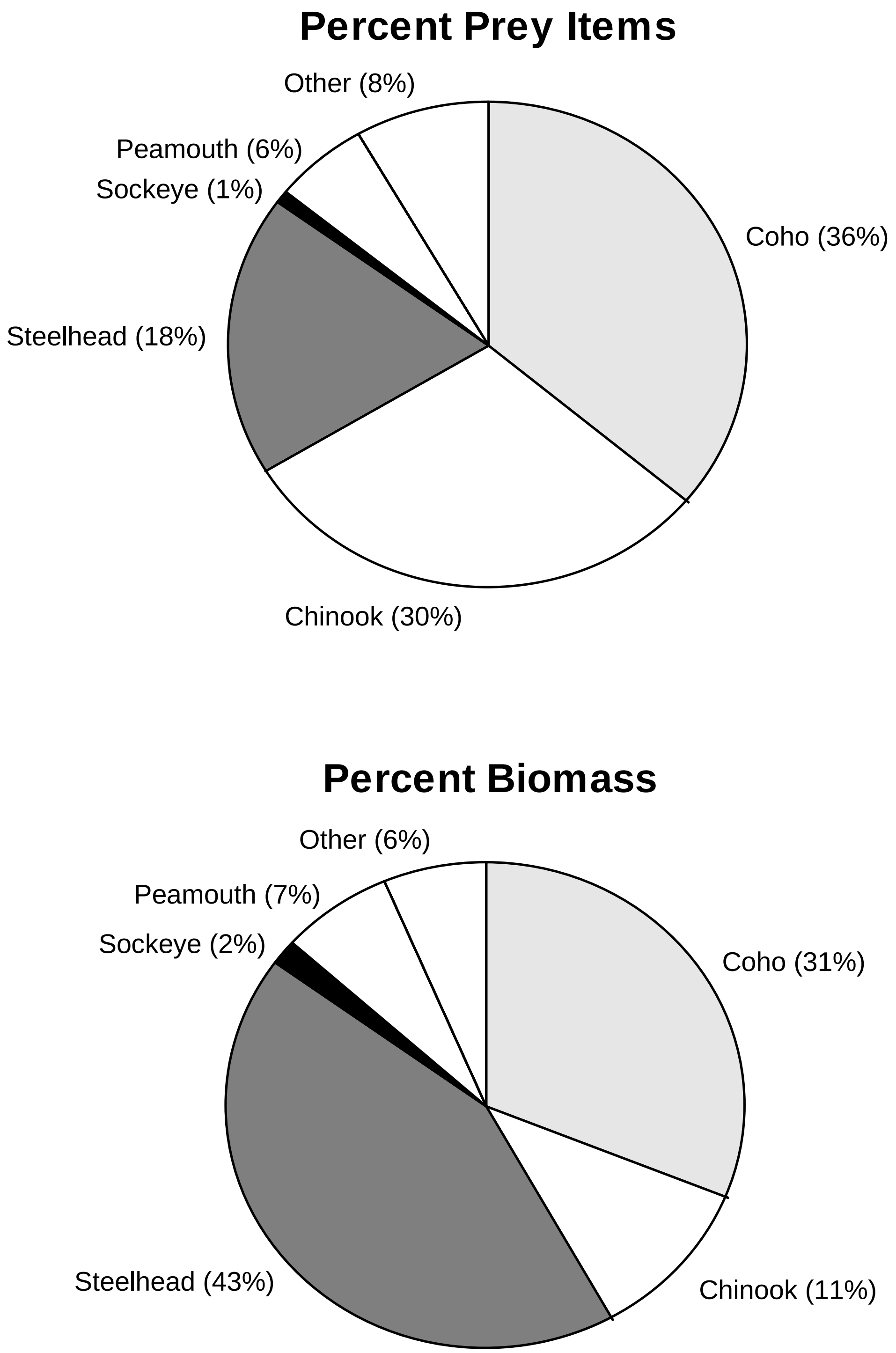


Figure 7. Percent prey items and biomass in the diet of Caspian terns nesting on Rice Island based on the collection of dropped fish in 1997. Analysis based on a total sample size of 119 dropped fish.

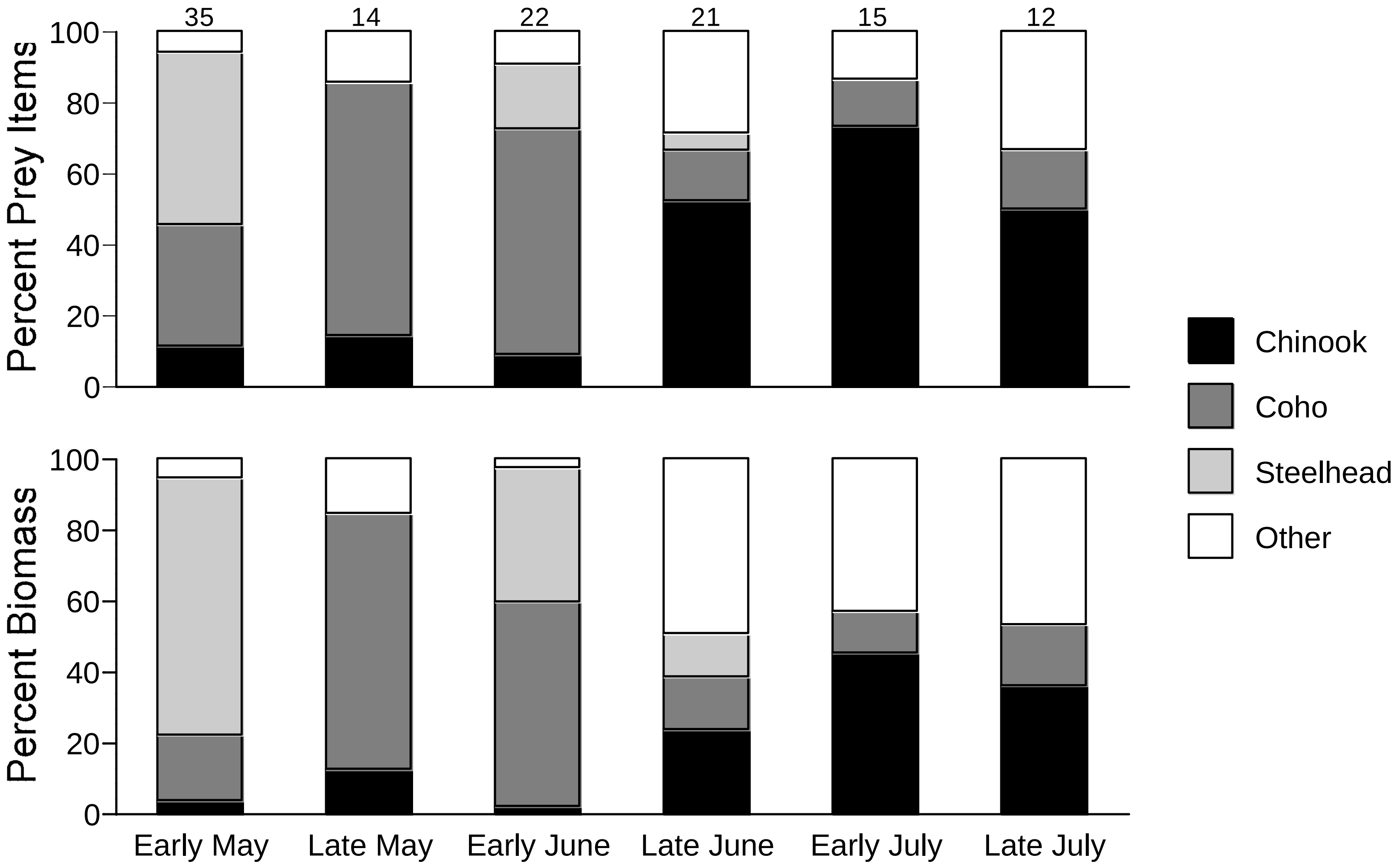


Figure 8. Percent prey items and biomass in the diet of Caspian terns by month based on the collection of dropped fish in 1997. Number of dropped fish in the sample are given over each bar.

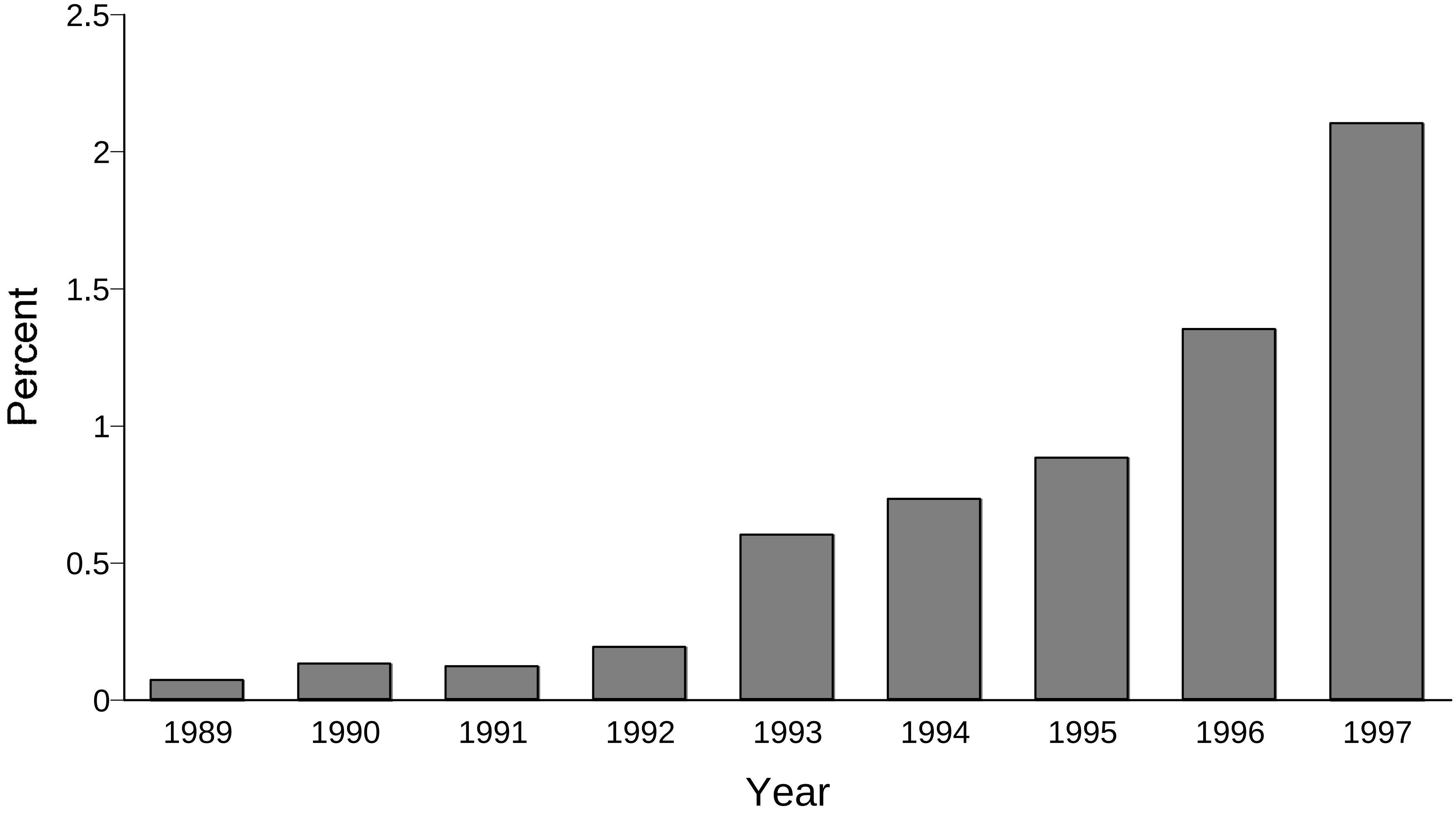


Figure 9. Percent of total smolt PIT tags released (by migration year) estimated to be on the Rice Island Caspian tern colony in 1997.

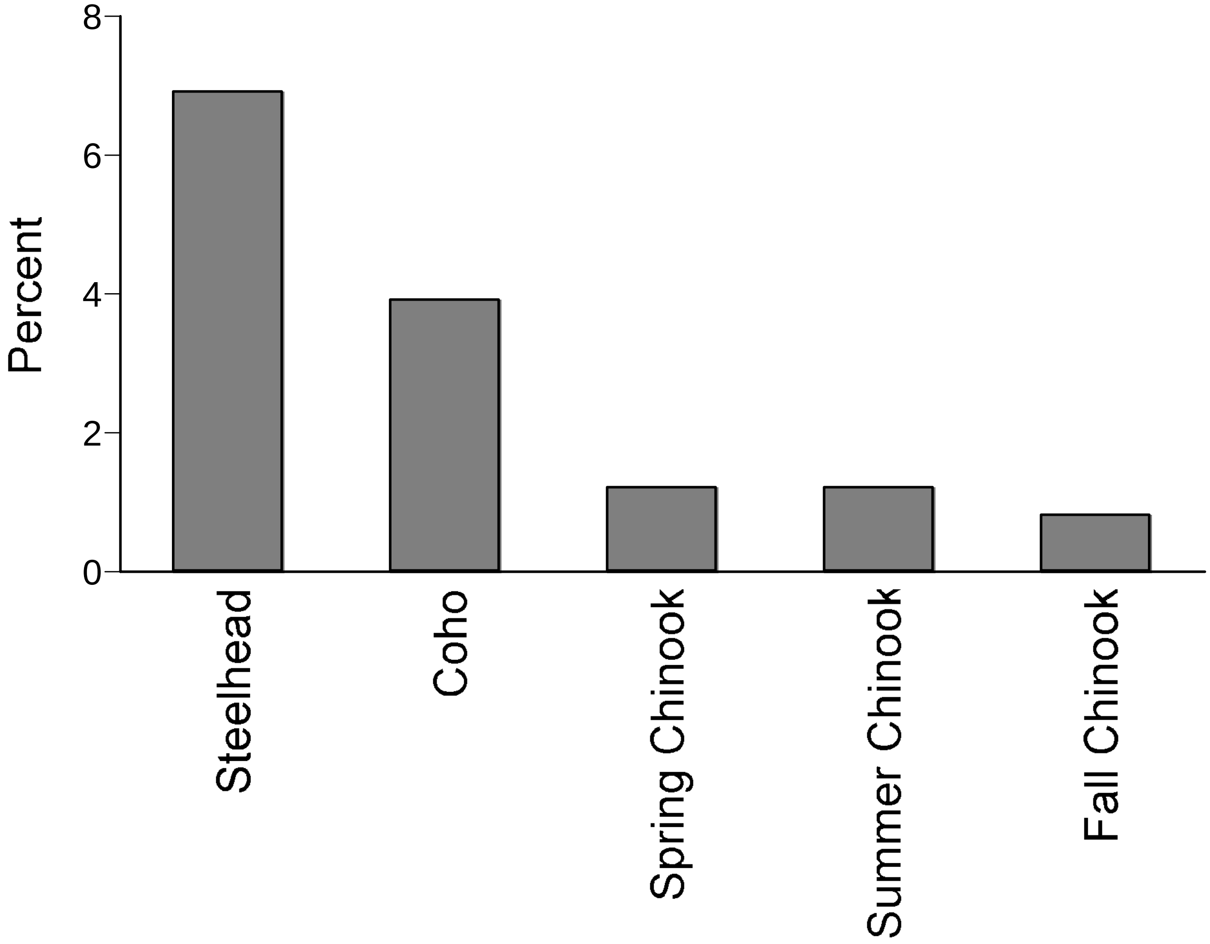


Figure 10. Percentage of the total PIT-tagged steelhead, coho salmon, and chinook salmon released in 1997 that were estimated to be on the Rice Island Caspian tern colony.

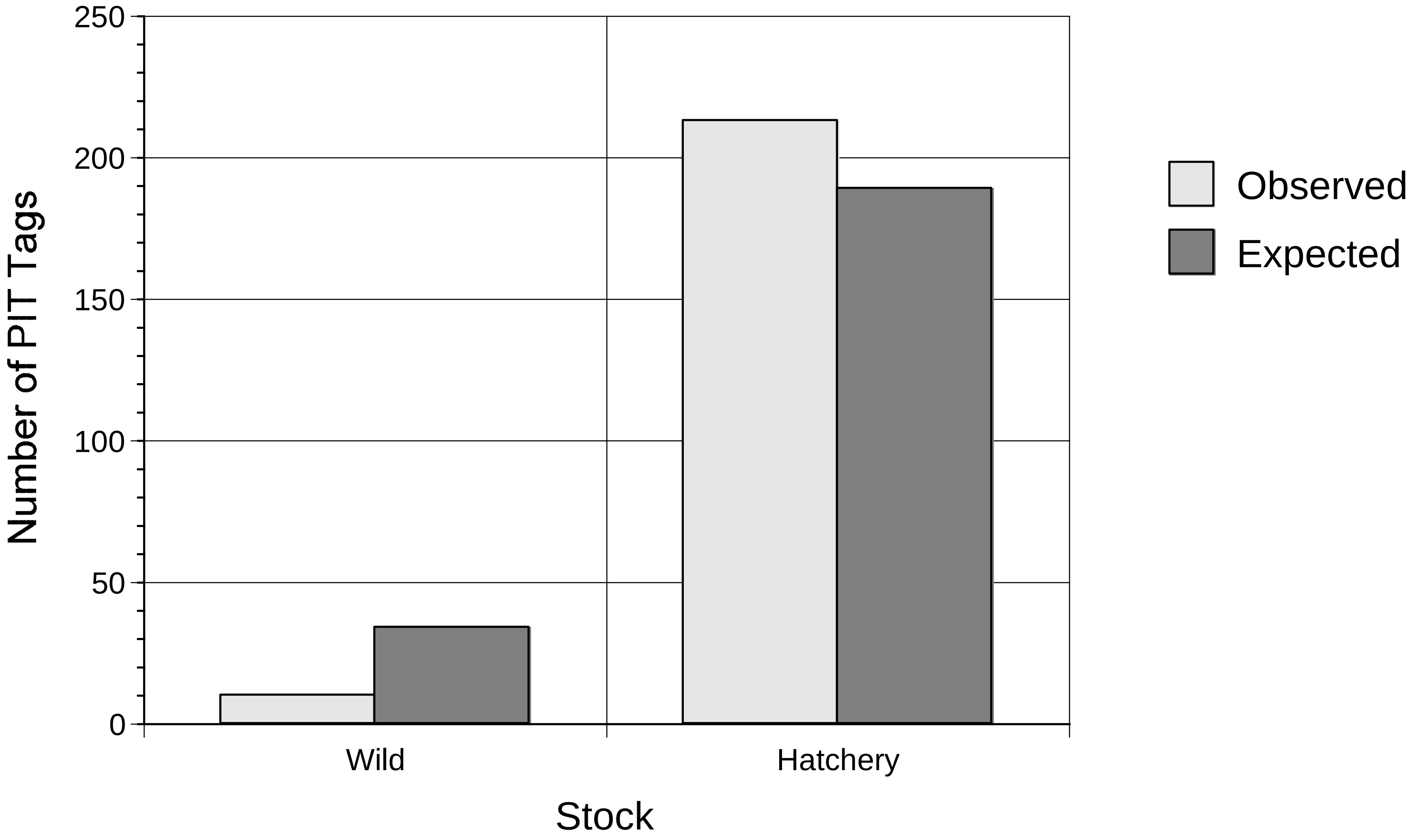


Figure 11. Relative vulnerability of PIT-tagged wild versus hatchery salmonid stocks to predation by Caspian terns nesting on Rice Island in 1996. Observed values were the number of PIT tags from fish of each rearing type recovered on the colony from the 1996 migration year. The expected values were derived from the relative proportion of PIT-tagged hatchery verses wild salmonid stocks interrogated in-river at Jones Beach in the Columbia River estuary (Ledgerwood et al. 1997).