

AN ABSTRACT OF THE THESIS OF


Donald E. Lyons for the degree of Master of Science in Wildlife Science.

Presented on May 13, 2004.

Title: Foraging Ecology of Caspian Terns and Double-crested Cormorants in the Columbia River Estuary

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Abstract approved: _____

Dr. Daniel D. Roby 

A detailed understanding of the foraging ecology of species preying upon threatened or endangered prey may contribute to identifying and evaluating management options to reduce predation, when such management is deemed appropriate. In the Columbia River estuary, Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) have been identified as significant predators on juvenile salmonids (*Oncorhynchus* spp.), many populations of which are listed under the U.S. Endangered Species Act. In 1998 and 1999, we studied the foraging ecology of Caspian terns and double-crested cormorants in the estuary using point count surveys. We also flew aerial strip

transect surveys throughout the estuary for terns, and in 1999 we used radiotelemetry to track terns during the chick-rearing period.

Terns and cormorants generally used habitat in relation to availability, with tidal flats and deep water channels both important foraging habitats, while tributaries, sloughs, and areas near ocean jetties were less important. Higher densities of cormorants were observed foraging in locations with pile dikes and/or pilings in 1999. More terns foraged in the freshwater portion of the estuary in 1998, than in 1999, when some terns nested on East Sand Island in the marine zone of the estuary. During the latter half of both seasons, use of upriver foraging sites became less prevalent for both terns and cormorants and use of sites in the marine and mixing zone more prevalent. Terns were observed foraging ≥ 50 km from the Rice Island colony (where all terns nested in 1998, and most did in 1999); however, $\leq 5\%$ of foraging occurred ≥ 27 km from this colony in both years.

In 1999, we compared the foraging ecology of radio-tagged Caspian terns raising young at the main estuary colony on Rice Island, in the freshwater zone of the estuary, to terns raising young at a newly restored colony site at East Sand Island in the marine zone. Early in the chick-rearing period, radio-tagged terns nesting at Rice Island (river km 34) foraged close to the colony in the freshwater zone of the estuary, while terns nesting on East Sand Island (river km 8) foraged in the marine or estuarine mixing zones close to that colony. Late in the chick-

rearing period, Rice Island terns shifted their foraging to the marine and mixing zones lower in the estuary; East Sand Island terns continued to forage in these areas. Tern diets at each colony corresponded to foraging location (freshwater zone vs. marine/mixing zone) of radio-tagged individuals: Rice Island terns relied heavily on juvenile salmonids (71% of identified prey) early in chick-rearing but this declined late in chick-rearing (46%). East Sand Island terns relied less upon salmonids (42% and 16%, respectively), instead utilizing marine fishes such as anchovy (*Engraulis mordax*) and herring (*Clupea pallasii*). Throughout chick-rearing, Rice Island terns foraged farther from the colony (median distance: 12.3 km during early chick-rearing and 16.9 km during late chick-rearing) than did East Sand Island terns (9.6 and 7.7 km, respectively). Colony attendance decreased for terns at both sites from similar high levels during early chick-rearing (60-70% of daylight hours) to lower levels (40-50%) during late chick-rearing, with attendance decreasing significantly more at Rice Island.

We conclude that Caspian terns and double-crested cormorants are generalist foragers and make use of the forage fish resources most available near the breeding colony. Predation rates on salmonids should decline if terns are attracted to colony sites, such as East Sand Island, where alternative prey are readily available. Precluding cormorant roosting at pile dikes and pilings, if feasible, might reduce consumption of salmonids, but additional studies would be required for verification.

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Foraging Ecology of Caspian Terns and Double-crested Cormorants
in the Columbia River Estuary

by
Donald E. Lyons

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented May 13, 2004
Commencement June 2005

Master of Science thesis of Donald E. Lyons presented on May 13, 2004.

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ACKNOWLEDGEMENTS

Funding for this work was provided by the Bonneville Power Administration (contracting officer's technical representative: Bill Maslen) and given priority by the Northwest Power Planning Council (Gustavo Bisbal). Numerous other agencies and folks supported this work, including the U.S. Army Corps of Engineers (Geoff Dorsey, Robert Willis), the U.S. Fish and Wildlife Service (Colleen Henson, Carol Shuler, Tami Tate-Hall, Tara Zimmerman), the National Marine Fisheries Service (Ben Meyer), Columbia River Inter-Tribal Fish Commission (Roy Beatty), the Oregon Department of Fisheries and Wildlife (Charlie Bruce, Holly Michael), and the Washington Department of Fisheries and Wildlife (Fred Dobler, Chris Thompson).

I sincerely thank my major advisor, Dr. Dan Roby, for providing opportunity, guidance, intellectual stimulation, and patience while I have pursued other endeavors prior to completion of this thesis. I am also indebted to the members of my committee, Drs. Robert Jarvis, Dan Schafer, and Carl Schreck, for their guidance and patience. I owe a large debt of gratitude to Ken Collis, of CRITFC and later Real Time Research, for his energy and optimism. Dr. David Craig has been an excellent mentor and inspiration during and since our days together in the field. Jessica Adkins and Bobby Begay were invaluable in the field; and terrific friends since then. The telemetry work could not have been

successful without the advice and support of Dr. Pat Jodice and Rob Suryan and the outstanding field assistance provided by Bruce Davis. Captain Ted Wirch made tracking radio-tagged terns possible with his amazing commitment to our success. Numerous others provided outstanding help in the field and I can't thank them enough: Stephanie Adamany, Darren Craig, Ryan Kerney, Anne Meckstroth, Bruce Robertson, Doug Robinson, Ian Rose, and Jeff Rosier. Various folks in the Department of Fisheries and Wildlife at OSU have helped me and I would like to thank them as well: Ellen Holsberry, LaVon Mauer, Charlotte Vickers, Jane Toliver, and Jan Cyrus.

Along the way I've benefited from friendship and interactions with a lot of folks in the Roby lab and on the Columbia River Avian Predation Project and at OSU and I would like to express my gratitude to Cindy Anderson, Scott Anderson, Cari Cardoni, Nate Chelgren, Chris Couch, Garrett Dorsey, Karen Fischer, Adrian Gall, Kristen Gorman, Andrew Hovey, Anne Mary Myers, Kim Nelson, Dan Rizzolo, Lisa Sheffield, Sadie Wright and many others.

I would like to thank my parents John and Edna Lyons and my brother John for their unending support throughout my life, despite them not really understanding why a 30-something gives up a perfectly good career and goes back to school to pursue something completely different. Finally, and most importantly, I thank my wife, Deanna Bergstrom, for her love and support, which has allowed me to pursue a dream.

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DEDICATION

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

CHAPTER 1

GENERAL INTRODUCTION

Donald E. Lyons

Many salmonid (*Oncorhynchus* spp.) populations in the Pacific Northwest have been in decline for over a century (Lichatowich 1999). In the Columbia River basin 12 of 20 evolutionarily significant units of salmonids are listed under the U.S. Endangered Species Act (ESA) as threatened or endangered (NMFS 2000b). Many recovery actions have recently focused on mitigating impacts of hydropower, hatcheries, harvest, and degraded freshwater habitat; however, resource managers have also considered predators as a possible factor inhibiting recovery (NMFS 1995, NMFS 2000a).

In the Columbia River basin, populations of colonial nesting piscivorous waterbirds have increased substantially in the last 20 years (Collis et al. 2002). Despite no documentation of Caspian terns (*Sterna caspia*) nesting in the Columbia River estuary prior to 1984 (Gill and Mewaldt 1983, Suryan et al. In press), by 1998 the largest known Caspian tern colony in the world, about 8,800 breeding pairs, existed at Rice Island, 34 km from the river mouth (Wires and Cuthbert 2000). Similarly, double-crested cormorant (*Phalacrocorax auritus*) populations in the estuary increased from 131 breeding pairs in 1980 (Carter et al. 1995), to a total estuary population of about 6,500 breeding pairs in 1998 (Collis et al. 2002), the largest concentration of this species on the Pacific Coast of North America (Carter et al. 1995).

Piscivorous birds have previously been cited as important predators on commercial fish stocks in other systems (Mace 1983, Wood 1987, Blackwell

1995). In 1997 and 1998, studies indicated that Caspian terns nesting at Rice Island in the Columbia River estuary relied upon juvenile salmonids for 73-77% of their diet (Collis et al. 2002). Using a bioenergetics approach, it was estimated that this single tern colony consumed 12.4 million juvenile salmonids (95% CI: 9.1-15.7 million) in 1998 (Roby et al. 2003). This consumption was estimated to represent up to 15% of some stocks of salmonids that reached the estuary (Collis et al. 2001, Roby et al. 2003). Double-crested cormorants nesting in the estuary relied upon juvenile salmonids less than terns, but salmonids were still an appreciable proportion of the diet (46% for cormorants nesting at Rice Island and 16% for cormorants nesting at East Sand Island, at river kilometer 8; Collis et al. 2002). Despite a smaller population size and lower prevalence of salmonids in the diet compared to terns, cormorants were estimated to consume several million smolts annually (D.E. Lyons, unpublished data).

Based on this evidence, regional resource managers concluded that avian predation could be a potential contributing factor limiting recovery of imperiled Columbia River salmon runs (NMFS 2000a). A pilot study was initiated in 1999 to investigate if relocating terns to East Sand Island, in the marine portion of the estuary, might cause terns to forage more on marine forage fish and reduce the reliance of terns on salmonids (USACE 1999). Resource managers also sought management options that might reduce consumption of smolts by double-crested cormorants in the estuary. Insufficient understanding of the foraging ecology of

each of these species, however, made identifying and predicting the likely outcome of potential management options difficult.

The foraging ecology of nest-based central place foragers, such as Caspian terns or double-crested cormorants, is constrained by the location of the nest site. Foraging close to the nest allows individuals to minimize travel time and energetic expense. Other factors may however, influence this fundamental constraint. More distant foraging sites may be utilized if they are particularly profitable either because of greater prey availability, greater nutritional value of prey, or because of some site-specific knowledge that confers an advantage to the forager.

A detailed understanding of the foraging ecology of terns and cormorants in the Columbia River estuary system would provide important information to managers seeking to reduce predation on ESA-listed juvenile salmonids. Knowledge of habitat preferences of either species might suggest strategies to reduce tern or cormorant foraging at sites where juvenile salmonids are particularly vulnerable. To assess the potential efficacy of Caspian tern colony relocation as a management tool, knowledge of the foraging range of Caspian terns is critical. The maximum foraging range of this species is ≥ 60 km (Soikkeli 1973, Gill 1976), much greater than the 21 km separating Rice and East Sand islands, suggesting terns attracted to nest on East Sand Island would be quite capable of returning to foraging sites near Rice Island, where salmonid smolts are

apparently readily available. The majority of foraging presumably occurs much closer to the colony site, however, and relocation of nesting activities may shift tern foraging closer to profitable alternative foraging sites, such as marine areas.

The studies included in this thesis investigate the foraging ecology of Caspian terns and double-crested cormorants in the Columbia River estuary. They specifically investigate potential habitat preferences of both terns and cormorants at several scales, various environmental factors that may affect foraging, and foraging range and spatial distribution of Caspian terns throughout the estuary. These studies were conducted in 1998, prior to any management of piscivorous waterbirds in the estuary, and in 1999, after the initiation of the pilot project to relocate nesting Caspian terns from the Rice Island colony. As such, they aid in understanding the foraging strategies of each species prior to management and, in the case of Caspian terns, allow an initial assessment of the efficacy of the colony relocation effort.

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CHAPTER 2

FORAGING PATTERNS OF CASPIAN TERNS
AND DOUBLE-CRESTED CORMORANTS
IN THE COLUMBIA RIVER ESTUARY

Donald E. Lyons, Daniel D. Roby, and Ken Collis

ABSTRACT

We examined the foraging ecology of Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary using point count surveys of foraging birds at 40 sites along the river's banks, and using aerial strip transect counts throughout the estuary for terns. Terns and cormorants generally used habitat in relation to availability, with tidal flats and deep channels both important foraging habitats, while tributaries, sloughs, and ocean jetty areas were less important. Higher densities of cormorants were observed foraging in locations with pile dikes and/or pilings in 1999. More terns foraged in the freshwater portion of the estuary in 1998, but not in 1999, when some terns nested in the marine zone of the estuary. During the latter half of both seasons, use of foraging sites in the marine/mixing zone became more prevalent by both species, while use of freshwater zone sites was generally less prevalent. Terns were observed foraging ≥ 50 km from the Rice Island colony; however, $\leq 5\%$ of foraging occurred ≥ 27 km from this colony in both years. Resource managers seeking to reduce impacts of tern predation on threatened Columbia River salmonids (*Oncorhynchus* spp.) can use this information to evaluate potential sites for tern colony relocation. Precluding cormorant roosting at pile dikes and pilings, if feasible, might reduce consumption of salmonids, but additional information would be required for verification.

INTRODUCTION

Large coastal estuaries provide dynamic foraging environments for colonial nesting piscivorous waterbirds. At these interfaces between freshwater and marine systems, diverse habitat types and high forage fish diversity and abundance can support large populations of nesting waterbirds, if suitable nesting habitat is also available. In estuaries fed by large freshwater systems, anadromous fish species may also be highly abundant seasonally, and an important resource for piscivorous waterbirds.

This study examined the foraging ecology of Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary during the 1998 and 1999 breeding seasons. The Columbia River estuary is a large estuary with high freshwater input that supports an abundance of a wide variety of forage fishes, such as anchovy (*Engraulis mordix*), herring (*Clupea pallasii*), smelt (Osmeridae), and surfperch (Embiotocidae), in addition to large seasonal runs of out-migrating juvenile salmonids (*Oncorhynchus* spp.; Bottom and Jones 1990). Populations of both Caspian terns and double-crested cormorants have grown dramatically in the Columbia River estuary over the past two decades as these birds have found suitable nesting habitat and have exploited apparently ample prey resources (Carter et al. 1995, Wires and Cuthbert 2000, Wires et al. 2001, Collis et al. 2002).

Caspian terns are plunge-diving piscivores that briefly submerge themselves during a shallow plunge from flight to capture prey. They have been documented to forage primarily in coastal or freshwater environments and rarely in open ocean areas (Cuthbert and Wires 1999). Previous studies of diet have found little evidence of prey selection, with diet usually considered a reflection of local prey availability (Cuthbert and Wires 1999). Double-crested cormorants are pursuit-diving piscivores and forage underwater sometimes at considerable depth (dives possible to at least 12m deep; Hatch and Weseloh 1999). They are more often observed foraging in freshwater or estuarine environments than in open seas. Previous diet studies in rivers with juvenile salmonids have indicated that cormorants may sometimes make substantial use of salmonids as prey, and have frequently been documented to respond rapidly to concentrations of prey, such as at dams on coastal rivers (Blackwell et al. 1997, Hatch and Weseloh 1999).

Caspian terns and double-crested cormorants nesting in the Columbia River estuary were found to significantly rely on juvenile salmonids as prey during the present study (Collis et al. 2002). In 1997-1998, Salmonids were 73-81% of the diet of terns and 46% of the diet of cormorants nesting at Rice Island (river kilometer 34; Collis et al. 2002). This reliance upon juvenile salmonids was cause for alarm for resource managers because 12 of the 20 evolutionarily significant units of salmonids in the Columbia River basin are federally listed as threatened or endangered under the U.S. Endangered Species Act (ESA; NMFS

2000b). In addition to conservation concerns for wild salmonids, vocal publics within the region advocate for commercial, sport, and tribal harvest opportunities, all of which have been reduced in the past two decades. While double-crested cormorants had been previously documented to be significant predators upon juvenile salmonids in some locations (Blackwell 1995, Hatch and Weseloh 1999), Caspian terns had not (Cuthbert and Wires 1999), and little was known of the foraging ecology of either species in this location or other large estuaries with high freshwater input.

Enhanced understanding of the foraging ecology of terns and cormorants in the Columbia River estuary would both add to our understanding of the ecology of piscivorous waterbirds in coastal environments and be of potential application for resource managers seeking to reduce impacts of these birds on declining and valuable salmonid resources. Our specific objectives in this study were to:

1. Examine potential foraging habitat preferences of terns and cormorants at multiple scales within the estuary.
2. Describe trends in tern and cormorant use of estuary foraging habitat across the breeding season and tidal cycles.
3. Quantify the foraging range of Caspian terns around their breeding colony in the estuary.

We predicted that Caspian terns would utilize shallow water environments (tidal mud flats, etc.) more frequently, given their ability to access only the top meter of the water column, and that double-crested cormorants would use deeper water channels within the estuary more frequently, given their ability to exploit prey throughout the water column. Additionally, we predicted that terns would forage more frequently in freshwater areas close to the Rice Island (river kilometer 34) colony site, and that cormorants would forage more frequently in marine habitats, closer to their primary nesting site at East Sand Island (river kilometer 8).

METHODS

Study Area

We studied the foraging habits of Caspian terns and double-crested cormorants in the Columbia River estuary in 1998 and 1999 (Figure 2.1). In 1998, all Caspian terns breeding in the estuary (8,650 pairs) nested on Rice Island, but in 1999 a small fraction of the estuary tern population was attracted to nest at a restored colony site on East Sand Island (Roby et al. 2002). In late May 1999, 550 pairs of terns were nesting at East Sand Island (6% of total), while 8,300 pairs nested at Rice Island (Roby et al. 2002). As the 1999 season progressed, some terns apparently moved their nesting activities from Rice Island to East Sand Island (Collis et al. 1999), with an estimated total of 1,400 nests (16% of all nests

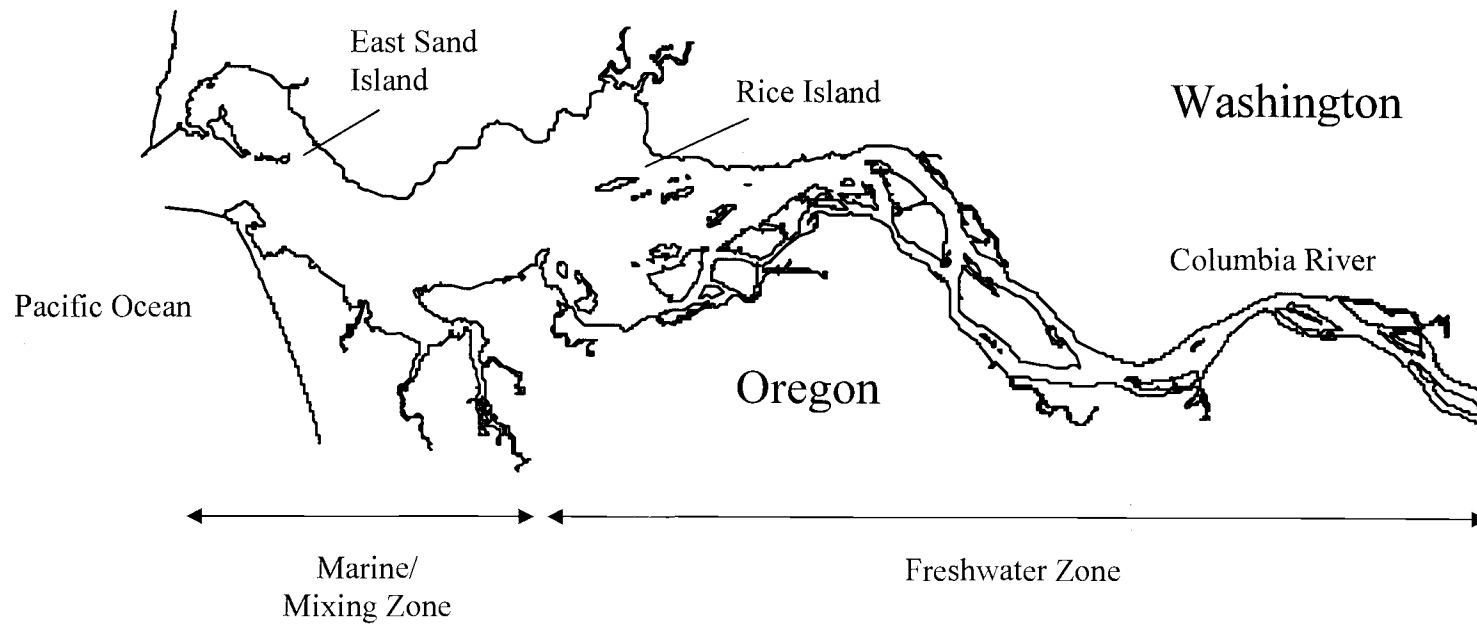


Figure 2.1. Columbia River estuary divided into the marine/mixing zone and the freshwater zone after Simenstad et al. (1990).

in the estuary) initiated there by early July (Roby et al. 2002). Rice Island, at river kilometer 34, is located slightly above the typical maximum saltwater intrusion into the estuary, while East Sand Island is situated in the middle of the marine zone of the estuary (Figure 2.1; Fox et al. 1984, Simenstad et al. 1990). Tidal amplitudes average 2.4 m at the river's mouth (Fox et al. 1984).

Double-crested cormorants nested at Rice Island (1,082 adults counted in an aerial photo taken there in late May) and at East Sand Island (7,501 adults counted) in 1998 (Collis et al. 2002). In 1999, 10,226 adult cormorants were counted at the East Sand Island colony in late May (authors' unpublished data); however, no cormorants nested at Rice Island. In both years, smaller numbers (50-150 pairs) of double-crested cormorants nested on channel markers and pilings throughout the estuary. Small numbers (< 300 pairs) of pelagic cormorants (*P. pelagicus*) and Brandt's cormorants (*P. penicillatus*) also nested in or nearby the estuary and were occasionally seen during surveys.

Data Collection

Point Count Surveys: Riverbank point count surveys were conducted at 40 sites weekly from early April through July in both years (Figure 2.2). Sites were selected based on (1) accessibility by automobile, (2) views of a large portion of the estuary, (3) views of various river habitat types, and (4) proximity to presumed piscivorous waterbird foraging locations (e.g., pile dikes). A total of

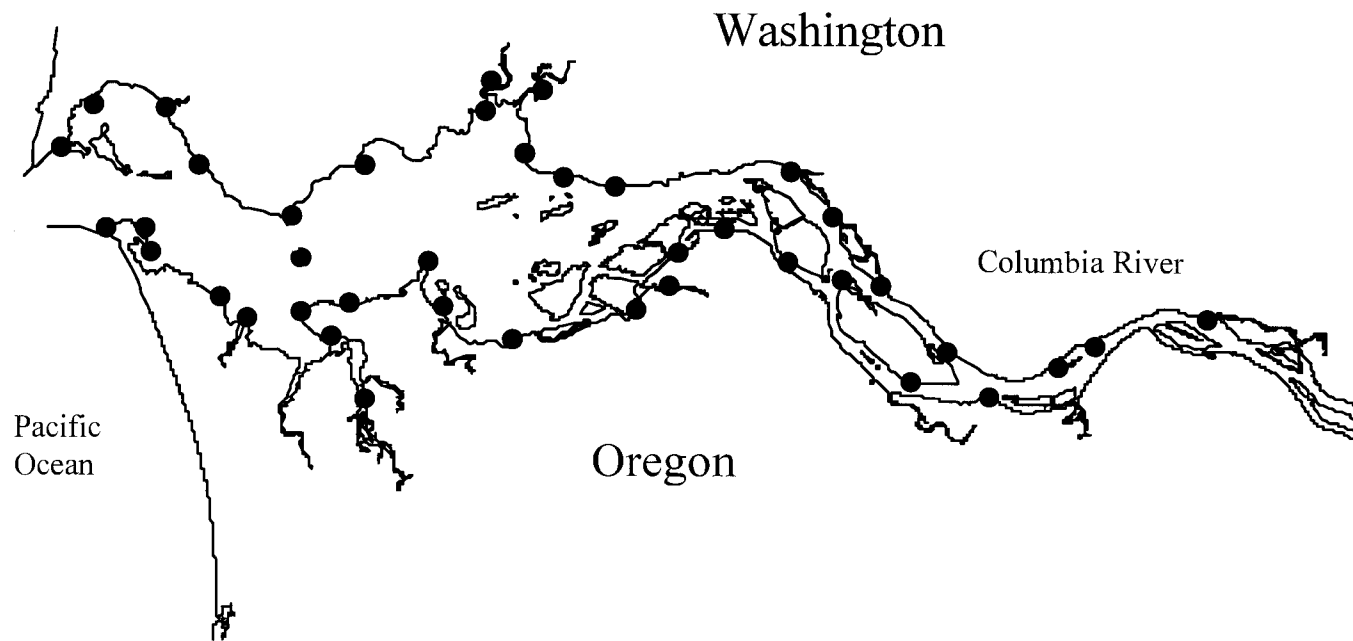


Figure 2.2. Point count survey sites in the Columbia River estuary.

21 sites were located on the Washington side of the river and 19 on the Oregon side. Rice Island was located at roughly the center of the survey area, with 22 and 18 sites located above and below the island, respectively. It was possible for a single observer to sample all sites on one side or the other of the river in a single day. For each day of surveying, the initial site visited was determined randomly; then the surveyor moved up-river until the most up-river site on that side had been visited. The surveyor then drove directly to the most down-river site and proceeded up-river again until all sites on that side of the river had been visited. This sampling pattern ensured that each site was visited at different times of day and at different stages of the tide cycle throughout the breeding season. During a 10-minute observation period at each site, all piscivorous waterbirds were counted and the maximum count of each species was recorded. Counts were broken down into foraging, roosting, and commuting birds by species; counts of foraging birds were used for subsequent analysis. Later, counts of foraging terns and cormorants were converted to densities using the estimated water area surveyed at each site.

Caspian Tern Aerial Strip Transect Surveys: Aerial strip transect surveys were conducted using a Cessna 206 fixed-wing aircraft. The plane was flown at an altitude of approximately 150 m above ground level and airspeed of 100 knots during surveys. Two observers counted Caspian terns seen within ca. 300 m of either side of the aircraft during 1-minute intervals. Location and count data were

recorded following each interval. Flying and roosting terns were counted separately; roosting terns were excluded from subsequent analyses. Flight transects covered all areas of the estuary, from the jetties at the river mouth to river kilometer 92 and from riverbank to riverbank, including the main channel, side channels, and all side bays and sloughs. In 1998, a total of 346 counts were conducted across seven different survey flights between 19 May and 6 July. In 1999, a total of 220 counts were conducted across five survey flights between 28 April and 21 June. Each 1-minute aerial count was converted into a measurement of Caspian tern density, assuming a constant airspeed of 100 knots, a transect width of 0.6 km, and an assumed blind spot below the plane of width 100 m. This density was considered an estimate of the density of foraging Caspian terns (birds/km²) at the midpoint of the strip covered by the airplane during the 1-minute counting period. Double-crested cormorants were not counted during aerial surveys because of the difficulties discerning cormorants in the water from the aircraft.

Data Analyses

Habitat Use: Because aerial strip transects better sampled the entire estuary than did the shoreline surveys, these data were used to evaluate habitat use by terns at large scales within the estuary. We divided the estuary into the freshwater zone (above river kilometer 29) and the marine/mixing zone (river

kilometer 29 and below) after Simenstad et al. (1990; Figure 2.1). For each flight, each strip transect density estimate was averaged together by salinity zone. These means were then pooled across all flights in each year for comparisons using Wilcoxon rank-sum tests. To estimate the actual numbers of terns using each salinity zone, mean densities for each flight were multiplied by the actual water area in each zone. Wilcoxon rank-sum tests were again used for comparisons. To assess habitat use by cormorants at this scale, point count densities were averaged for each site, grouped by salinity zone, and compared using Wilcoxon rank-sum tests. Estimates of the actual numbers of cormorants using each salinity zone were obtained by multiplying the density at each site by the actual water area in each zone, and comparisons of these estimates were also made using Wilcoxon rank-sum tests.

Point counts were used to examine use of intermediate scale habitat types by both terns and cormorants: main shipping channel areas (n = 15 sites), side channels (n = 8), tributaries and sloughs (n = 4), tidal flats (n = 11), and ocean jetty sites (n = 2). Main shipping channel areas referred to the channel defined and maintained by the U.S. Army Corps of Engineers for large cargo vessels. Other channels of greater than 3m depth at mean lower low water were classified as side channels. Shallower areas, frequently with exposed sand and mud flats at low tides, were classified as tidal flats. Tributaries and sloughs were waterways connected to the main river only at one end. Ocean jetty sites were at the very

mouth of the river, having the ocean jetties in view. Sites having a combination of habitats were classified according to the habitat type making up the largest proportion of the area viewed.

For each year, density measurements for both terns and cormorants were averaged at each site, then grouped by habitat type. Kruskal-Wallis one-way ANOVA on ranks was then used to compare densities of each species in different habitats. Actual numbers of terns and cormorants using each habitat type were estimated by multiplying the density at each site by the amount of that habitat present throughout the estuary. Comparisons of bird numbers in each habitat were performed again using Kruskal-Wallis one-way ANOVA tests on ranks.

Point counts were also used to make comparisons between fine scale habitat characteristics. For terns, sites having permanent roosting habitat (beaches or sand bars; $n = 8$) were compared to those without. For cormorants, sites with pile dikes ($n = 12$) or pile dikes and pilings ($n = 25$) were compared to those without. Comparisons were performed using Wilcoxon rank-sum tests.

Seasonal Trends: Seasonal changes in bird use of the estuary were examined using Wilcoxon rank-sum comparisons of the average density of foraging terns and cormorants at sites in April and May versus June and July. Sites were grouped into the freshwater zone (above river kilometer 29) and the marine/mixing zone (river kilometer 29 and below).

Tidal Influences: Effects of tides on densities of foraging terns and cormorants in each habitat type were investigated using point count data. Periods of high and low tide stages were determined by centering 3-hour time periods on peak high and low tides; flood and ebb tide stages were defined to be the intervening (approximately 3-hour) time periods. Data from the U.S. Coast Guard tide gauge at Tongue Point (river kilometer 29) were used to identify peak high and low tides. For each survey day, density observations for each tide stage (high, ebb, low, flood) in each habitat type were averaged together. Kruskal-Wallis one-way ANOVA tests on ranks were then used to compare these daily averages for each habitat type.

Tern Foraging Range: Strip transect surveys were used to relate the densities of foraging terns to the distance from Rice Island. For each survey flight, the average of estimated densities was calculated for concentric rings (of 5 km width) surrounding Rice Island. To estimate the relative distribution of terns from the Rice Island colony, these density estimates were multiplied by the amount of river habitat within each concentric ring.

RESULTS

No significant differences in densities of foraging Caspian terns were observed between the freshwater zone of the estuary and the marine/mixing zone; however, median densities were higher in freshwater in 1998, and similar in the

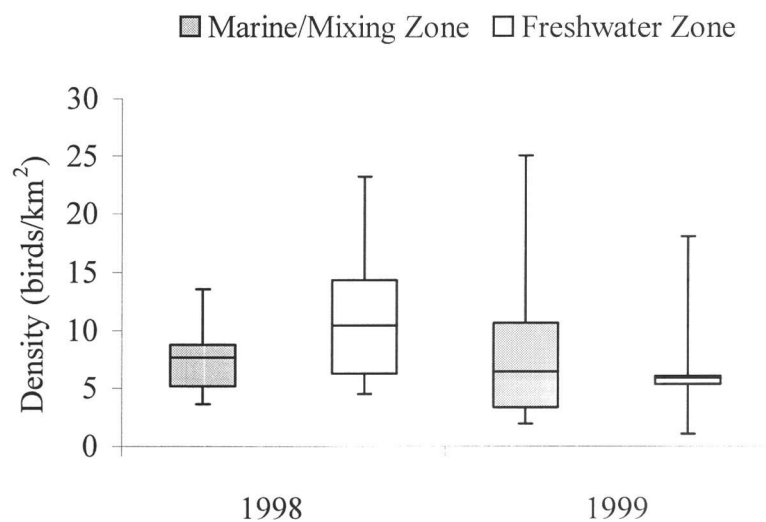
two zones in 1999 (Figure 2.3A). Estimated numbers of foraging terns were higher in freshwater in 1998 ($P = 0.04$), but were similar in each zone in 1999 (Figure 2.3B).

Densities of foraging terns were not different between habitat types in either year (Figure 2.4A). Estimated numbers of terns foraging in each habitat varied with habitat type in both years ($P < 0.001$ and $P = 0.01$ in 1998 and 1999, respectively), however, with more terns foraging in side channel and tidal flat habitats and fewer terns foraging in tributary streams or sloughs and near the ocean jetties in both years (Figure 2.4B). There were no differences between densities of foraging terns at sites with or without permanent roosting habitat in either year.

Across the entire breeding season, similar densities and numbers of foraging double-crested cormorants were observed in the marine/mixing and freshwater zones of the estuary in both years (Figure 2.5A and B). No differences in densities of cormorants in different habitat types were detected in either year (Figure 2.6A). Similarly, no significant differences in the estimated numbers of cormorants foraging in each habitat type were observed, although the results suggested that, consistent with terns, fewer cormorants foraged in tributary streams or sloughs and near ocean jetties (Figure 2.6B).

Higher densities of foraging cormorants were observed at sites with pile dikes and/or pilings in 1999 ($P = 0.02$), but this trend was only suggestive in 1998

A. Densities



B. Proportion of foraging terns

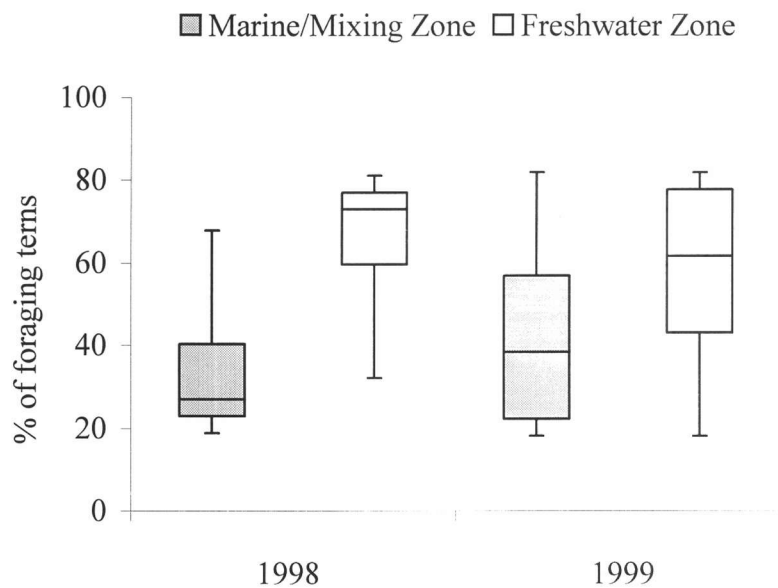
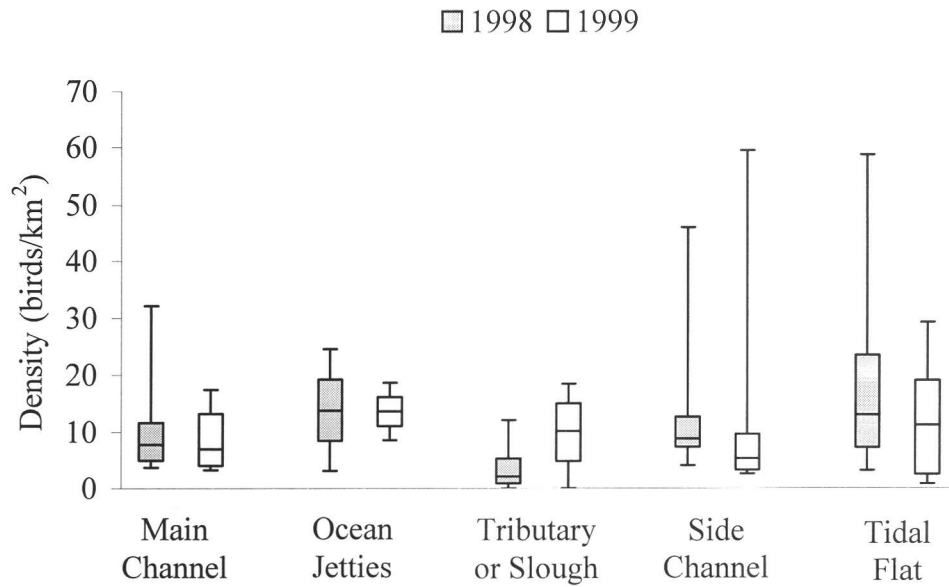


Figure 2.3. Densities (A) and estimated proportion (B) of foraging Caspian terns in the marine/mixing zone and the freshwater zone of the Columbia River estuary in 1998 and 1999. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

A. Densities



B. Proportion of foraging terns

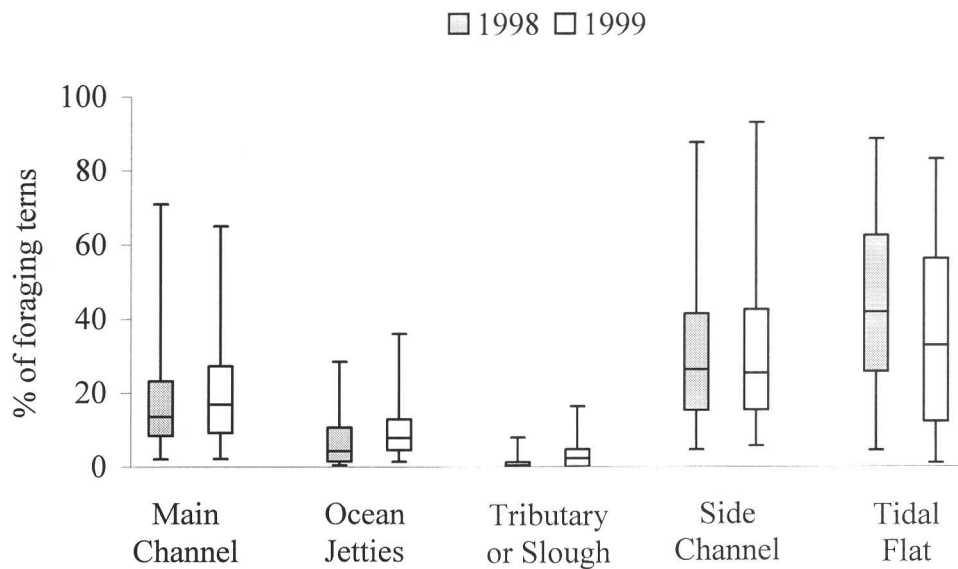
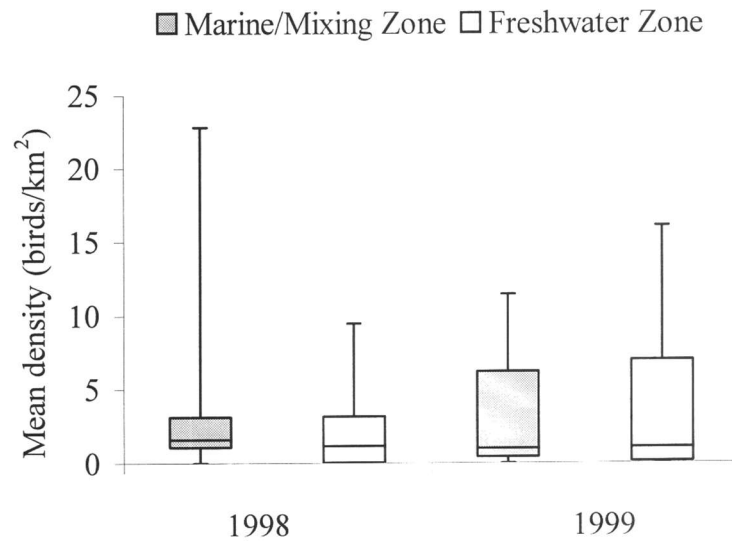


Figure 2.4. Densities (A) and estimated proportion (B) of foraging Caspian terns in several habitat types of the Columbia River estuary in 1998 and 1999.

Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

A. Densities



B. Proportion of foraging cormorants

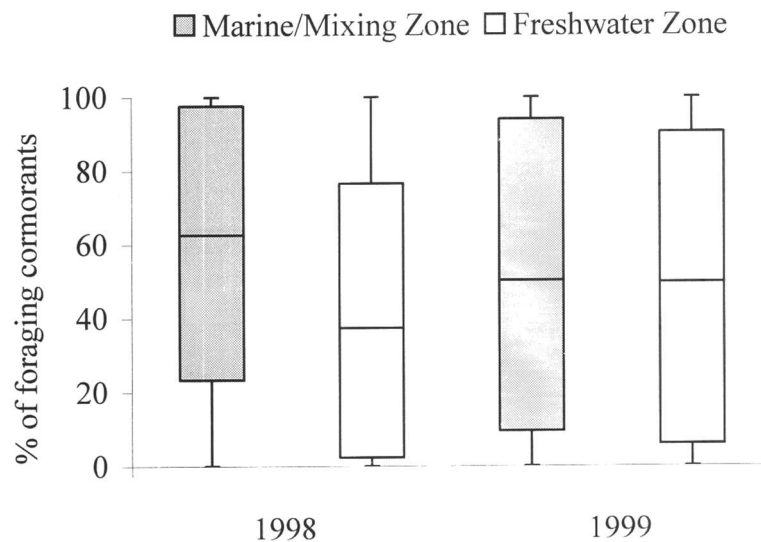
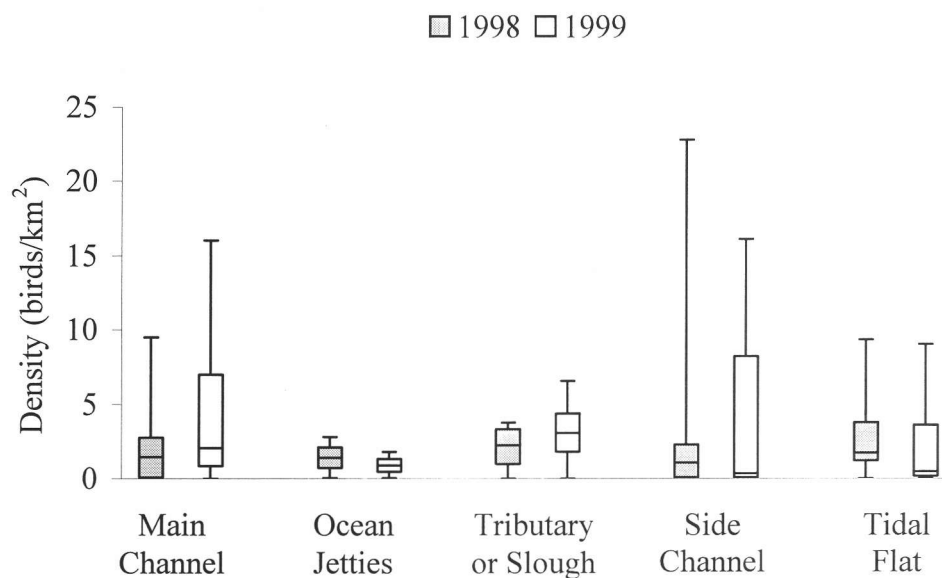


Figure 2.5. Densities (A) and estimated proportion (B) of foraging double-crested cormorants in the marine/mixing zone and the freshwater zone of the Columbia River estuary in 1998 and 1999. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

A. Densities



B. Proportion of foraging cormorants

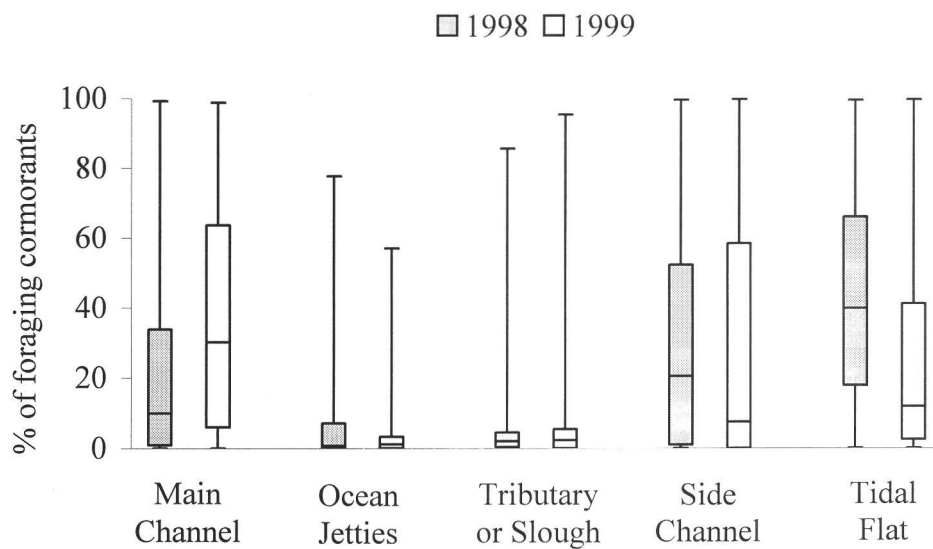


Figure 2.6. Densities (A) and estimated proportion (B) of foraging double-crested cormorants in several habitat types of the Columbia River estuary in 1998 and 1999. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

($P = 0.12$; Figure 2.7). A marginally significant trend for higher densities at sites with only pile dikes was seen in 1999 ($P = 0.08$) but not in 1998 ($P = 0.32$).

Densities of foraging terns and cormorants generally increased at sites in the marine/mixing zone during the latter half of the breeding season, while densities at sites in the freshwater zone either decreased or did not increase as substantially (Figures 2.8 and 2.9). The increase in densities at sites in the marine/mixing zone was significant for terns in 1998 ($P = 0.01$), but merely suggestive in 1999 ($P = 0.15$). For cormorants there was also a significant increase in densities in the marine/mixing zone in 1998 ($P = 0.01$), but not in 1999 ($P = 0.34$). At sites in the freshwater zone, tern densities increased in 1998 ($P < 0.005$), although not as markedly as sites in the marine and mixing zone, but in 1999 no difference in tern densities with stage of the breeding season was seen ($P = 0.22$). Densities of foraging cormorants at sites in the freshwater zone were significantly lower ($P = 0.01$) in the latter portion of the 1999 breeding season, but not significantly so in 1998 ($P = 0.90$).

Tide stage significantly affected densities of foraging terns and cormorants in some habitats during 1998. In tidal flats, tern densities were higher at low and flood tides than at high and ebb tides ($P < 0.01$; Figure 2.10). In side channel areas, mean cormorant densities were 15.8 cormorants/km² during high tides, compared to 1.9 cormorants/km² at other tide stages ($P = 0.02$). Near ocean jetties, mean cormorant densities were 2.1 and 1.8 cormorants/km² during high

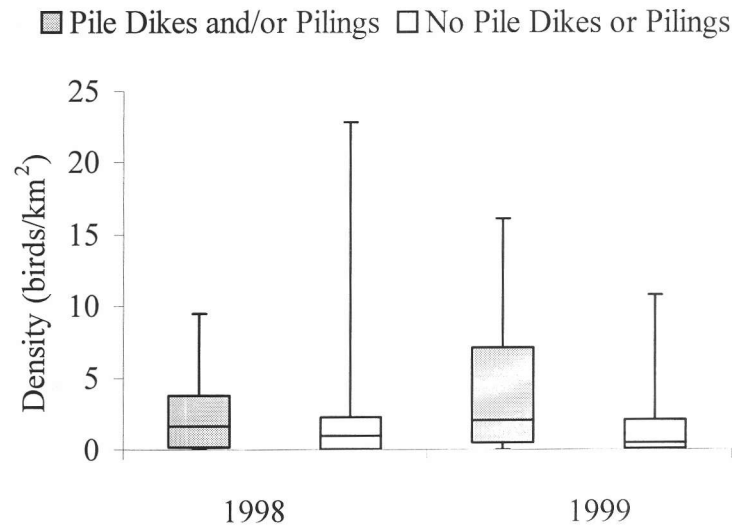
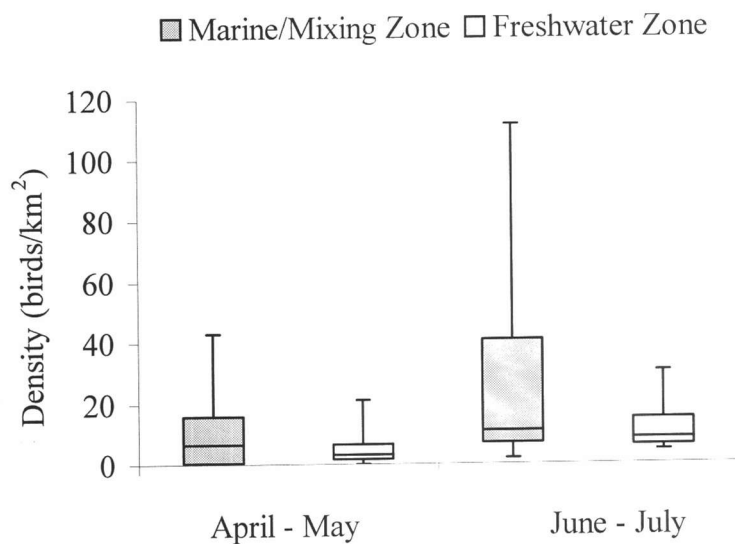


Figure 2.7. Densities of foraging double-crested cormorants at sites with and without pile dikes and/or pilings in the Columbia River estuary. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

and ebb tide stages and 0.9 and 0.5 cormorants/km² during low and flood tide stages ($P = 0.05$). No significant differences in foraging densities at different tide stages were seen for either terns or cormorants in any habitat in 1999.

Densities of foraging terns were highest within 5 km of Rice Island in both 1998 and 1999 and generally decreased with increasing distance from Rice Island (Figure 2.11). In 1998, spikes in densities were observed 21-25 km from Rice Island and 36-40 km from Rice Island, corresponding to areas near the river mouth and at Eureka Bar (river kilometer 80-85). In 1999, densities of foraging terns trended higher for areas within 15 km of Rice Island compared to 1998.

A. 1998



B. 1999

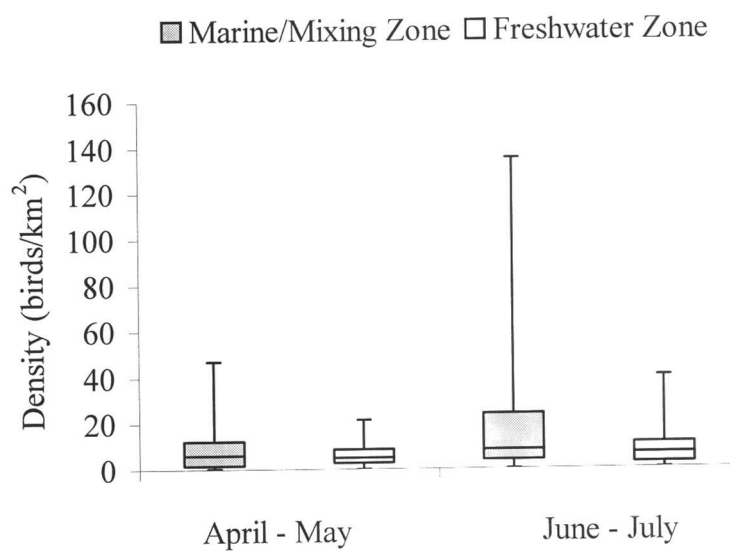
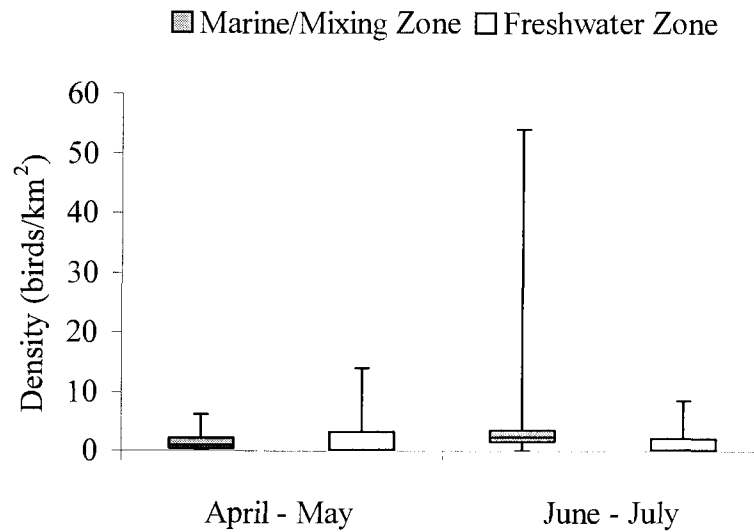


Figure 2.8. Seasonal use of the Columbia River estuary by foraging Caspian terns. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

A. 1998



B. 1999

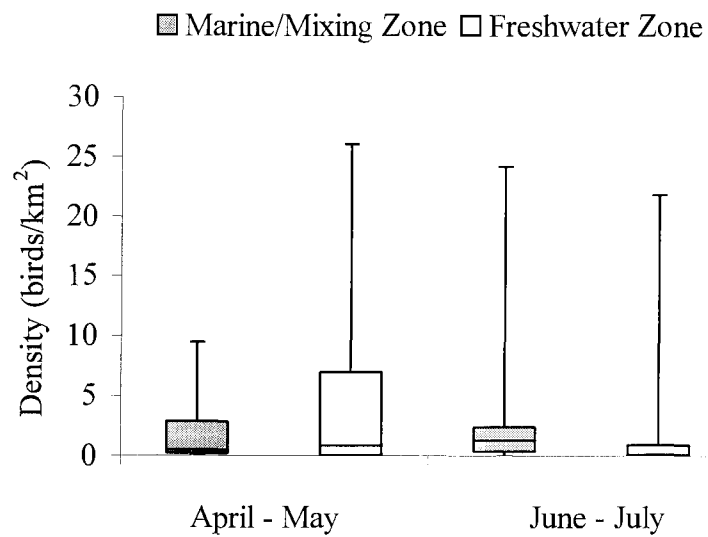


Figure 2.9. Seasonal use of the Columbia River estuary by foraging double-crested cormorants. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

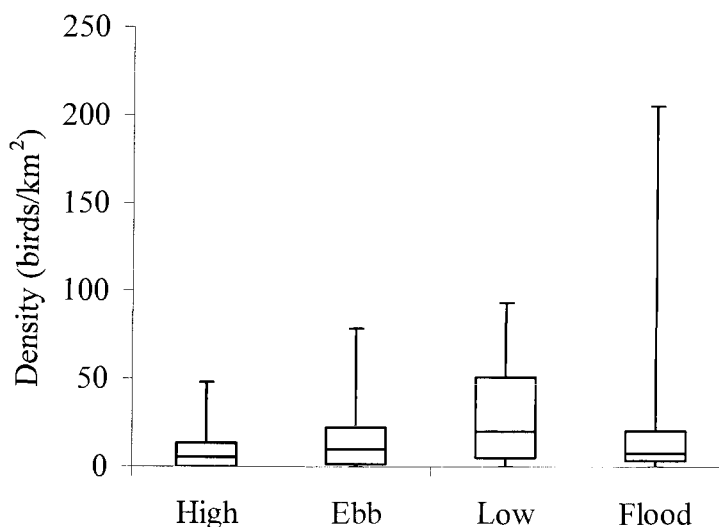


Figure 2.10. Densities of foraging Caspian terns in tidal flat habitat in the Columbia River estuary at each tide stage during 1998. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

Estimates of numbers of foraging terns sorted by distance from the Rice Island colony indicated that in 1998, 50% of foraging terns were within 8 km of Rice Island, 90% within 23 km, and 95% within 27 km (Figure 2.12). In 1999, 50% were within 8 km, 90% within 18 km, and 95% within 24 km.

DISCUSSION

In the Columbia River estuary during 1998 and 1999, Caspian terns and double-crested cormorants appeared to be generalist predators that utilized

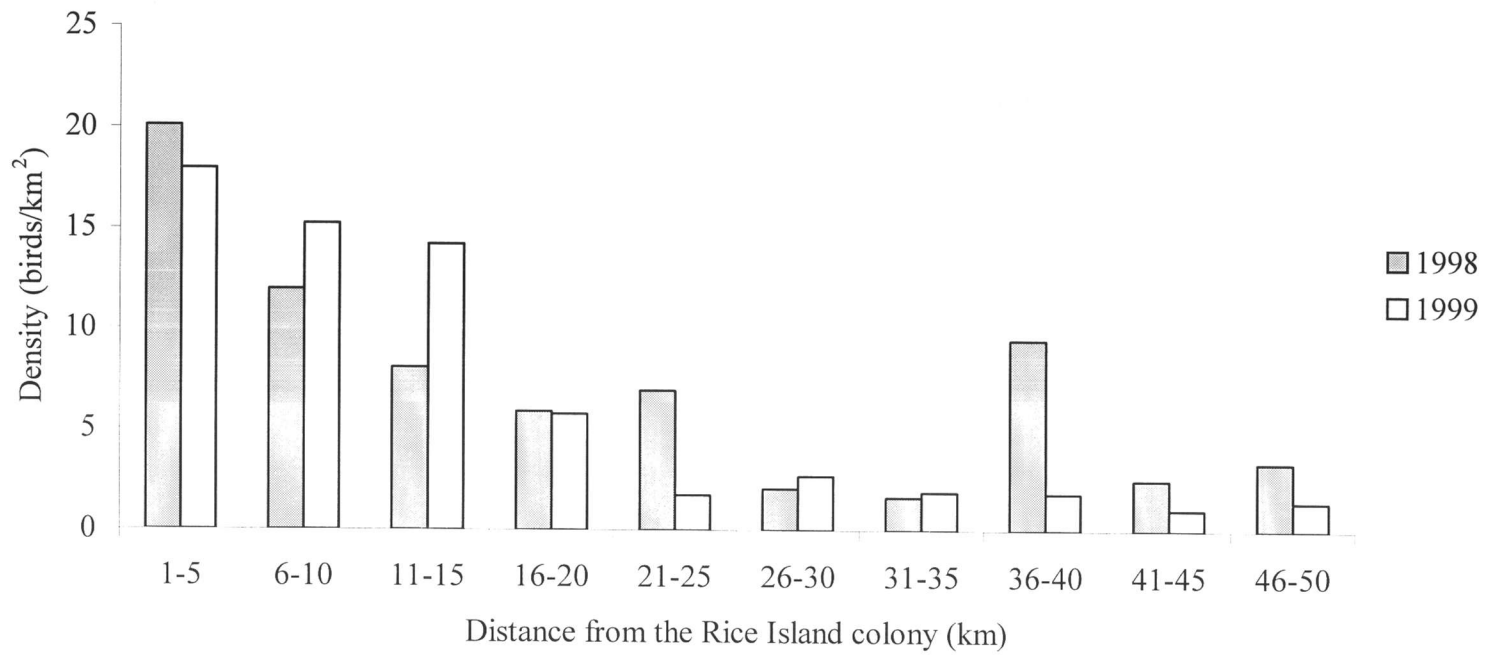


Figure 2.11. Densities of foraging Caspian terns by distance from the Rice Island colony site.

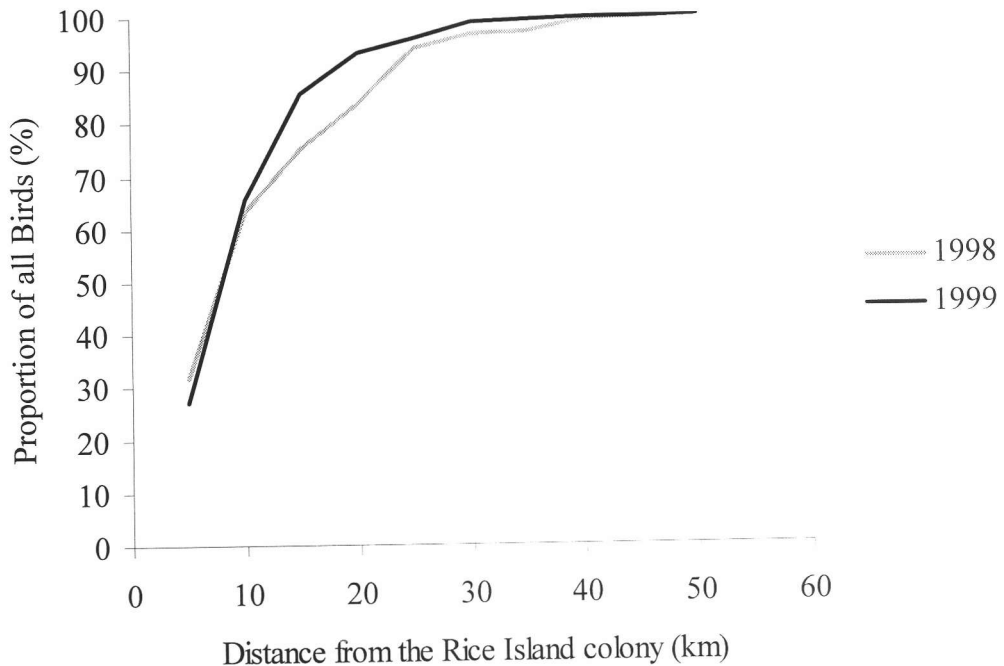


Figure 2.12. Cumulative proportions of foraging Caspian terns by distance from the Rice Island colony site in the Columbia River estuary.

habitats in proportion to their availability. Foraging densities of each species did not differ significantly among habitat types, in most cases. Numbers of birds estimated to be using each habitat did differ, however, tracking the relative amounts of each habitat available in the estuary, underlining the versatility of each species in habitat use. Widely abundant habitat types, such as tidal flats, side channels, and the main shipping channel, were used by greater numbers of terns and cormorants in both years. Conversely, relatively few birds used

tributaries, sloughs, and areas near ocean jetties, suggesting these relatively scarce habitat types were not important foraging areas for either species. One exception to this trend was the use of sites with pile dikes and/or pilings by cormorants. These sites occupy only a small proportion of the total area of the estuary, but offer roosting habitat and possibly enhanced foraging opportunities for cormorants near pile dikes. We frequently observed cormorant foraging aggregations (often associated with terns and gulls [*Larus* spp.]) in the downstream wake of pile dikes, perhaps taking advantage of disoriented or resting fish in the slower current of the wake.

At larger scales, more Caspian terns foraged in the freshwater portion of the estuary in 1998; however, there was no difference in 1999. This lack of greater foraging activity in the freshwater zone in 1999 reflects the attraction of a portion of the tern population to nest at East Sand Island, located in the marine zone of the estuary. The diet of terns attracted to nest at East Sand Island also suggests greater foraging in the marine/mixing zone of the estuary – marine fish species (e.g., anchovy, herring, surfperch) were 44.5% of the diet of East Sand Island terns but only 12.1% of the diet of Rice Island terns (Roby et al. 2002). These results suggest that, for terns, foraging habitat use was more a reflection of nest site location than habitat preference.

We did not see significantly greater numbers of double-crested cormorants in the marine/mixing zone of the estuary, close to their primary nesting site at

East Sand Island. This suggests the freshwater zone of the estuary is an important foraging area for cormorants, particularly early in the breeding season, and is consistent with Anderson's (2002) observations of male radio-tagged cormorants nesting at East Sand Island frequently traveling to the freshwater zone of the estuary. Most of the heavily attended sites having pile dikes and/or pilings were in the freshwater zone of the estuary. The numerous cormorants observed in the freshwater zone, often at pile dike and/or pilings sites quite distant from the primary nesting colony at East Sand Island, further suggests preference for these features.

Densities of foraging terns and cormorants generally increased in the marine/mixing zone of the estuary in the latter half of the breeding season. For terns, smaller increases in densities of foraging birds were also seen in the freshwater zone, suggesting terns spent more time foraging and less time attending their nests during this latter stage of the breeding season. The greater seasonal increase in foraging densities in the marine/mixing zone suggests, however, that this zone became more important for terns in the latter portion of the breeding season. This corresponds to the decline in abundance of out-migrating juvenile salmonids after early June (Fish Passage Center 2002) and also to the seasonal decline in salmonids in the diet of terns at both Rice and East Sand islands (Roby et al. 2002). Cormorant densities generally declined in the freshwater zone in the latter half of the season, also consistent with the decline in

availability of juvenile salmonids. These results indicate that seasonal foraging habitat preferences are more a reflection of shifting prey availability than a preference for particular foraging habitats, *per se*.

In 1998, higher densities of terns were observed foraging in tidal flat habitats at low tide and, occasionally, at flood tide. Two mechanisms might enhance foraging opportunities for terns at low tide, and may explain the higher densities of terns seen foraging at this tidal stage. Shallow water during low tide may make benthic fishes available to plunge-diving terns, which likely do not capture fish deeper than a meter below the water surface. Low tide may also concentrate fish in narrow channels surrounded by mud flats, which may make the fish more visible and vulnerable to tern predation. Because high tern densities were also seen occasionally at flood tides, following low tides, these data suggest that terns may continue to exploit these conditions even after tide stage has changed. Lack of a similar trend in 1999 suggests, however, that terns do not always find these conditions superior to other foraging opportunities.

Densities of foraging Caspian terns generally declined with distance from the Rice Island colony, the primary tern breeding site. Our data suggest that densities at distances 6 – 15 km from Rice Island were somewhat higher in 1999 than in 1998, consistent with a portion of the tern population breeding at East Sand Island in 1999 and some overlap in primary foraging areas of terns from each colony in the region between Rice and East Sand islands.

Despite documentation of foraging trips of breeding Caspian terns in excess of 60 km (Soikkeli 1973, Gill 1976), our results indicate that in the Columbia River estuary most foraging occurs much closer to the breeding colony. In both 1998 and 1999, less than 5% of foraging occurred further than 27 km from Rice Island. A slight contraction of foraging activity around Rice Island occurred in 1999, despite a portion of the population breeding 21 km downriver at East Sand Island, primarily due to reduced foraging ≥ 40 km upriver from Rice Island.

Our results are potentially biased by the geographic extent of our survey sampling area. Opportunistic surveys at sites outside the Columbia River estuary, including the Oregon coast to the south, the Washington coast to the north, and Willapa Bay (a large coastal bay ≥ 8 km to the north of the Columbia River), indicated that terns and cormorants sometimes foraged in these areas. Observations of commuting flights indicated that at least a portion of these birds traveled between these sites and the Columbia River estuary, and presumably some portion were birds breeding in the Columbia River estuary. In general, densities of foraging terns and cormorants were lower in these areas than within the Columbia River estuary, and we did not find evidence of any preferred foraging sites outside the estuary. While some terns and cormorants breeding in the Columbia River estuary sometimes foraged outside the estuary, the estuary itself was by far a more important foraging area. While the potential bias in our survey area may have caused us to slightly underestimate Caspian tern foraging

range, the general conclusion that both species are generalist predators responding opportunistically to nearby prey resources is supported.

By 2001, all Caspian terns nesting in the Columbia River estuary were attracted to nest at East Sand Island, and Rice Island had been abandoned as a nesting site (Roby et al. 2002). Resource managers implemented this management activity to reduce terns' reliance upon Columbia River juvenile salmonids, some populations of which are ESA-listed (USACE 1999, USACE 2000). Juvenile salmonids made up a much smaller proportion of the diet of terns nesting at East Sand Island (32 – 46 % during 1999 – 2002) than at Rice Island (76 – 90% during 1997 – 2000). Our foraging range data help explain why this dietary difference occurred. Only a small fraction of foraging activity occurred farther than 20 km from the Rice Island colony when most or all of the terns nested there during the two years of this study. If foraging behavior was similar for terns nesting at East Sand Island, then the majority of foraging by those terns was confined to the surrounding marine/mixing zone of the estuary, where they were more often exposed to marine forage fish species, such as anchovy, herring, and surfperch – species rarely present in the freshwater zone of the estuary (Hinton et al. 1995).

Attraction of a portion of the Caspian terns currently nesting at the East Sand Island colony to new and/or restored colony sites elsewhere along the Pacific Coast has been suggested as a technique to further reduce impacts of terns

upon Columbia River salmonid populations (Roby et al. 2002). This technique may also reduce risks to this large fraction (ca. 2/3) of the Pacific Coast Caspian tern population from potential local catastrophes, such as disease, storms, predators, human disturbance, and oil spills (Roby et al. 2002). Many factors would influence site selection for any future relocation efforts, but proximity to local fisheries of conservation concern would be one important factor. The foraging range data presented here allow preliminary judgments on possible interactions between terns nesting at proposed colony sites and nearby forage fish resources, although investigation of local conditions may still be warranted.

Some resource managers have interpreted higher observed densities of foraging cormorants at sites with pile dikes and pilings to offer a possible method to reduce predation on salmonids, if these structures could be altered to eliminate roosting opportunities (NMFS 2000a, USACE 2000). Most pile dike and piling sites with high densities of foraging cormorants are in the freshwater zone of the estuary and our anecdotal observations do indicate that salmonids are the predominant prey type taken there. However, it is not clear that eliminating roosting opportunities is feasible at these sites (G. Dorsey, USACE, personal communication) and, if eliminated, whether that would reduce cormorant foraging at these sites (Collis et al. 2001). Additionally, even if foraging by cormorants was reduced at these sites, further studies would be necessary to demonstrate actual reductions in total salmonid consumption by the cormorant population,

given the numerous other foraging areas in the Columbia River estuary where cormorants may prey upon salmonids.

The majority of double-crested cormorants nesting in the Columbia River estuary have nested in the marine/mixing zone at the East Sand Island colony since 1999. A small reduction in cormorant predation upon juvenile salmonids might be achieved by shifting the cormorants still nesting in the freshwater zone (ca. 400 pairs in 2003, 3% of the estuary population) to East Sand Island. Shifting the nesting of a portion of the East Sand Island colony to sites outside the Columbia River basin, if achievable, might more substantially reduce cormorant predation on Columbia River juvenile salmonids, if such a management goal were deemed appropriate.

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CHAPTER 3

FORAGING ECOLOGY OF CASPIAN TERNS
IN THE COLUMBIA RIVER ESTUARY

Donald E. Lyons, Daniel D. Roby, and Ken Collis

ABSTRACT

We compared the foraging ecology of Caspian terns (*Sterna caspia*) raising young on two islands in the Columbia River estuary using radio telemetry and observations of prey fed to chicks and mates at each colony. Early in the chick-rearing period, radio-tagged terns nesting at Rice Island (river km 34) foraged mostly in the freshwater zone of the estuary close to the colony, while terns nesting on East Sand Island (river km 8) foraged in the marine or estuarine mixing zones close to that colony. Late in the chick-rearing period, Rice Island terns shifted more of their foraging to the two zones lower in the estuary; East Sand Island terns continued to forage in these areas. Tern diets at each colony corresponded to the primary foraging zone (freshwater vs. marine/mixing) of radio-tagged individuals: Rice Island terns relied heavily on juvenile salmonids (*Oncorhynchus* spp., 71% of identified prey) early in chick-rearing, but this declined late in chick-rearing (46%). East Sand Island terns relied less upon salmonids (42% and 16%, respectively), instead utilizing marine fishes such as anchovy (*Engraulis mordax*) and herring (*Clupea pallasii*). Throughout chick-rearing, Rice Island terns foraged farther from their colony (median distance: 12.3 km during early chick-rearing and 16.9 km during late chick-rearing) than did East Sand Island terns (9.6 and 7.7 km, respectively). We conclude that Caspian terns are generalist foragers and make use of the most proximate available forage fish resources when raising young. This trait may be of use to resource managers

who wish to reduce avian predation on populations of Columbia River basin salmonids listed under the U.S. Endangered Species Act. Predation rates on salmonids should decline if terns are attracted to colony sites where alternative prey are readily available.

INTRODUCTION

The foraging ecology of nest-based central place foragers, such as colonial waterbirds, is constrained by the location of the nest site. Foraging close to the nest allows individuals to minimize travel time and energetic expense, and thereby allocate a greater proportion of acquired energy to energy demands at the nest. Other factors may influence this fundamental constraint, however. More distant foraging sites may be utilized if they are particularly profitable, either because of greater prey availability, greater nutritional or energetic value of prey, or some site-specific knowledge that confers an advantage to the forager.

This study examined the foraging ecology of Caspian terns (*Sterna caspia*), a piscivorous central place forager, during the chick-rearing period at two breeding colonies in the Columbia River estuary. From 1986 to 1998, before this study was undertaken, terns had nested on Rice Island, a dredged material disposal island in the freshwater zone of the estuary (sensu Simenstad et al. 1990), and had been shown to rely primarily upon out-migrating juvenile salmonids (*Oncorhynchus* spp.) as prey (73-81% of diet; Collis et al. 2002). Of particular

management concern were potential impacts of tern predation upon the 12 of 20 evolutionarily significant units (ESUs) of Columbia River salmonids that are listed under the U.S. Endangered Species Act (ESA; NMFS 2000, Roby et al. 2003). In 1999, in addition to nesting on Rice Island, Caspian terns nested at a newly restored colony site on East Sand Island at river km 8 (Roby et al. 2002), in the marine zone of the estuary (*sensu* Simenstad et al. 1990). Resource managers hypothesized that terns nesting at East Sand Island would rely less on juvenile salmonids as prey and implemented a pilot study to attract terns there to test the hypothesis (USACE 1999).

Several factors suggested that terns attracted to nest on East Sand Island might continue to forage primarily in the freshwater zone of the estuary and continue to rely heavily on juvenile salmonids. Rice Island is 21 km (straight line distance) from East Sand Island, well within the 60 km documented maximum foraging range of nesting Caspian terns (Soikkeli 1973, Gill 1976). Salmonid abundance, buoyed by hatchery production, was high and predictable: annual hatchery production of juvenile salmonid smolts totaled 150-200 million fish per year throughout the Columbia River basin during 1987-1998 (Collis et al. 2001). Combined with wild production and subtracting estimated mortality during down-river migration, approximately 97 million smolts were predicted to enter the estuary in 1998, a typical year (USACE 2000). Additionally, the terns attracted to East Sand Island would likely be former Rice Island breeders and would

consequently have a history of foraging for salmonids in the Rice Island vicinity. Foraging site fidelity has been demonstrated in other piscivorous larids within a single breeding season (Becker et al. 1992, Irons 1998), though not previously with Caspian terns (Sirdevan and Quinn 1997).

Other factors, however, suggested that terns attracted to nest on East Sand Island might instead forage in close proximity to their colony and take alternative prey. Although relative abundance was unknown, previously published surveys indicated a greater diversity of forage fish species lower in the estuary (Bottom and Jones 1990), including marine fishes such as northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), smelt (Osmeridae), and surfperch (Embiotocidae). Comparisons of diets of double-crested cormorants (*Phalacrocorax auritus*) and glaucous-winged/western gulls (*Larus glaucescens* x *L. occidentalis*) nesting on both Rice and East Sand islands indicated less reliance upon salmonids by birds nesting on East Sand Island (Collis et al. 2002). Additionally, Caspian terns returning to Rice Island from foraging locations down-river relied less upon salmonids than did those returning from up-river locations (Collis et al. 2002). Finally, diet composition of common terns (*Sterna hirundo*) nesting on various islands within a large bay in the German Wadden Sea strongly reflected the location of the colony within the freshwater/marine spectrum (Frank 1992).

The primary objective of this study was to compare and contrast the spatial distribution of foraging and the resulting patterns of colony attendance and diet composition for Caspian terns nesting at the two colonies in the Columbia River estuary. Specific hypotheses to be tested were:

1. Caspian terns nesting at East Sand Island would forage in the marine/estuarine mixing zones near their colony site, as opposed to the freshwater zone closer to Rice Island.
2. Seasonal declines in availability of juvenile salmonids would be associated with less foraging in the freshwater zone for terns nesting on both Rice and East Sand islands.
3. Diet composition of terns would reflect the habitats in which they foraged; marine forage fishes would be more prevalent in the diet of terns that foraged in the marine or estuarine mixing zones of the estuary, while salmonids would be more prevalent in the diet of terns that foraged in the freshwater zone of the estuary.
4. Foraging conditions (quantified using the metrics of foraging distance from the colony and colony attendance) would be as favorable for terns nesting at East Sand Island as for those nesting at Rice Island.

Information on the effects of relocating the Caspian tern colony in the Columbia River estuary on tern diet and productivity are summarized elsewhere (Roby et al. 2002). This paper presents the spatial distribution and temporal patterns of

foraging by terns nesting in the estuary and how each relates to diet composition, specifically during the chick-rearing period.

METHODS

Study Area

We studied Caspian terns nesting in the Columbia River estuary (Figure 3.1) at two locations: Rice Island (river kilometer 34) and East Sand Island (river km 8) during the 1999 breeding season. In 1999 an estimated 8300 breeding pairs of terns initiated nests at the Rice Island colony and approximately 1400 pairs nested at the newly restored East Sand Island colony (Roby et al. 2002). Due to its position higher in the estuary, Rice Island is in the freshwater zone (above river kilometer 29), while East Sand Island is in the middle of the marine zone of the estuary (river kilometers 0 – 12; Fox et al. 1984, Simenstad et al. 1990). Tidal amplitudes average 2.4 m at the river's mouth (Fox et al. 1984).

Data Collection

Thirty terns were captured at Rice Island during May 11 – 22; one was caught using a net gun on a roosting beach and 29 were caught using noose mats around nest scrapes within the colony area. Twenty-two terns were captured at East Sand Island during May 24 – June 7; three using noose mats on a roosting

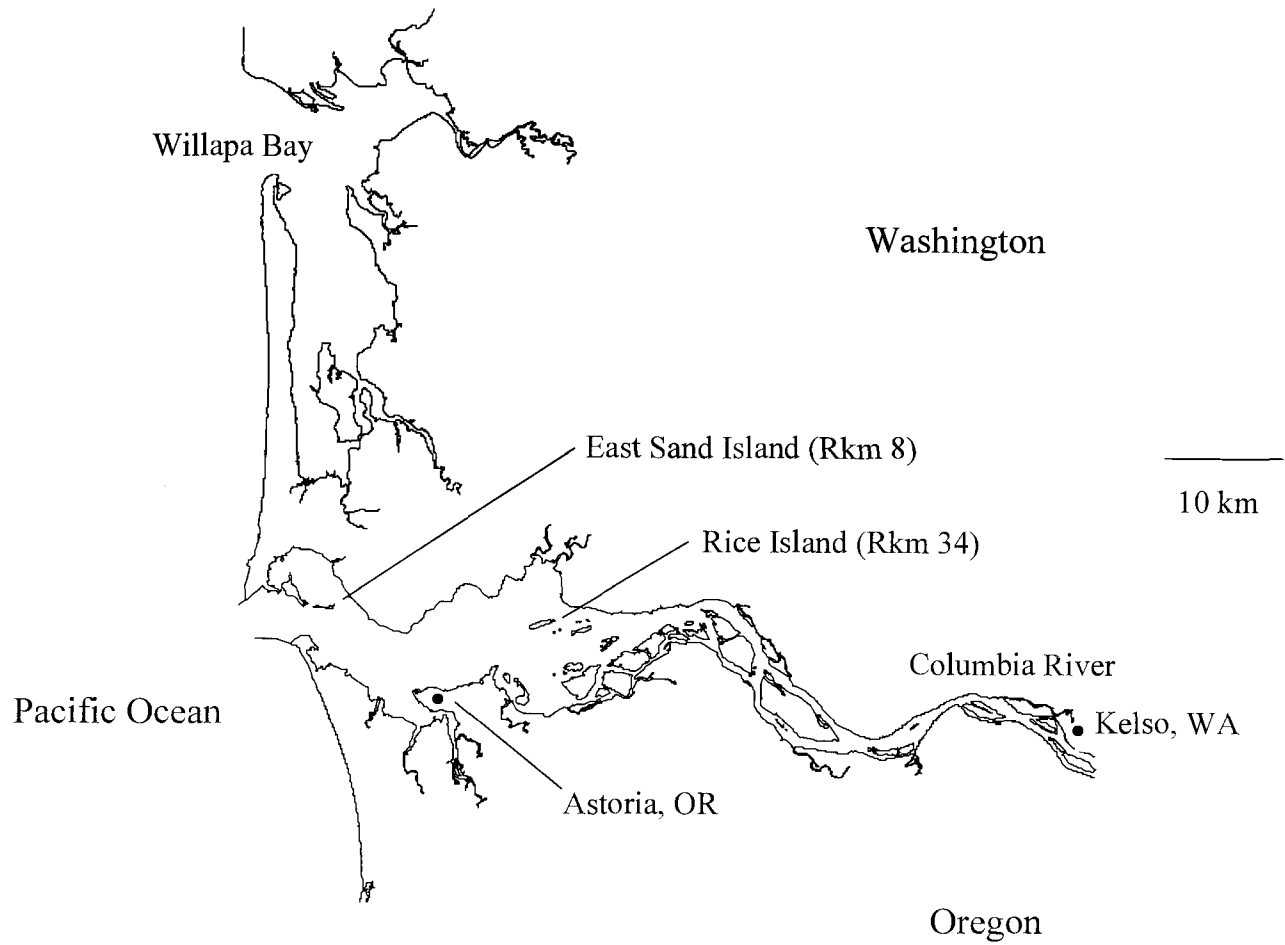


Figure 3.1. Columbia River estuary, with locations of Rice and East Sand islands, and Willapa Bay, the next large estuary to the north.

beach and 19 using noose mats around nest scrapes within the colony area. All terns were captured during the middle or late phase of incubation. Radio transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) weighing 9-10 g (~1.5% of body mass) were attached to the central 4-5 rectrices of each tern using plastic cable ties and Loctite 404 adhesive (Irons 1998). Subsequent observations of tagged terns indicated no behavioral abnormalities; normal breeding activities, such as courtship feeding and resumption of incubation shifts, were observed within a few hours of tagging and release.

Radio-tagged terns were tracked on 18 occasions during May 28 – July 13 using a Cessna 206 fixed-wing aircraft with an antenna mounted to each wing strut on either side of the fuselage. Locations of all radio-tagged terns heard during a flight (usually >95% of all tagged birds) were pinpointed to within approximately 1 square kilometer by circling the location of the transmitter signal. Precision of locations was verified through blind tests of tracking personnel, using reference transmitters placed at unannounced locations within the study area. Aboard the aircraft, locations of radio-tracked terns were plotted on maps from which GPS coordinates were later derived. During any particular flight, radio-tagged terns were detected either at one of the two colony sites or away from both colonies (hereafter designated as “off-colony” locations). Flights departed from Kelso, Washington (river km 110) and followed a consistent flight path: down-river to the mouth of the river, overland north to Willapa Bay, north to the mouth

of the bay, south along the Washington coast, across the mouth of the Columbia River, south to approximately Seaside, Oregon, overland to Astoria, Oregon, and finally back up-river to Kelso. Four flights included side trips to Grays Harbor, Washington, > 65 km to the north of the Columbia River estuary, to investigate tern use of this large, distant estuary.

At each colony site, radio-tagged terns were continuously monitored between May 28 and July 11 using a telemetry receiver and automated data collection computer (Advanced Telemetry Systems, Inc., Isanti, MN). These systems scanned continuously (day and night) for all radio-tagged terns, with an approximate cycle time of 30 minutes, depending on how many terns were detected in each cycle. Correct system operation was verified using a reference transmitter located at each colony and by scanning “dummy” frequencies (where no transmitters were in operation) during every cycle, in addition to periodic manual confirmation of system results. At both sites, the reference transmitters were correctly detected in > 95% of all cycles and “dummy” transmitters were detected (false positive detections) during < 1% of all cycles. On occasions when system functionality was poor or lost (due to loss of battery power, etc.), data for the entire day were omitted from the analysis. During periods of normal system operation, lack of detection by the colony data loggers was interpreted as an absence from the colony area and immediate surroundings, presumably due to the bird engaging in a foraging trip. Terns were classified as breeding at Rice Island

or East Sand Island based on continuous nighttime attendance at the respective colony. This classification was opportunistically confirmed through visual observation of breeding activity by the radio-tagged terns throughout the season. Terns that did not attend either colony at night were assumed to be failed breeders, and were excluded from data analysis.

Diet composition of Caspian terns nesting at each colony site was assessed using visual identification of fish brought back to the colony in the bills of terns as courtship or chick meals (Collis et al. 2002). Approximately 25 fish were identified to family using binoculars and spotting scopes from blinds adjacent to the colony at daytime high and low tides on each day of the study period (Roby et al. 2002).

Statistical Analyses

Distributions of off-colony detections were categorized into five spatial areas, three within the Columbia River (after Simenstad et al. 1990) and two outside: (1) the estuary freshwater zone (river km 30 and above), (2) the estuarine-mixing zone (river km 13-29), (3) the estuary marine zone (river km 0-12), (4) Willapa Bay to the north, and (5) coastal Oregon and Washington. Distributions of off-colony detections in these areas were compared for terns nesting on Rice and East Sand islands using Fisher's Exact Test (White and Garrott 1990). Because repeated off-colony detections for an individual bird are

not independent, a single detection for each bird was randomly selected for inclusion in these analyses.

Distance from colony for all off-colony detections throughout the time periods of interest (early chick-rearing period [May 28 – June 18], late chick-rearing period [June 19 – July 13], entire chick-rearing period) were first averaged for each tern, then pooled to make within season and between colony comparisons of foraging range. Wilcoxon rank-sum tests were used to make comparisons.

To analyze patterns of colony attendance of breeding Caspian terns, presence/absence data at each colony (as measured by the automated data loggers) were examined at two temporal scales. To investigate diurnal patterns of attendance, data for each bird was divided into one-hour time blocks across daytime hours (dawn to dusk) and pooled for all days in the sampling period. The proportion of all data logger cycles when the bird was detected during each daylight hour block was used as the measure of colony attendance. As the distribution of this proportion was approximately normal for all birds, multiple linear regression was used to investigate daily attendance patterns for each bird separately (PROC REG; SAS Institute, Inc., Cary, NC). Models investigating linear, quadratic, and cubic relationships between time of day and colony attendance were tested and the most appropriate model for each bird was selected using extra-sum-of-squares F-tests. Possible serial correlation was tested for using the Durbin-Watson test statistic; if serial correlation was detected or could

not be ruled out, regressions were recalculated using first-order autoregressive corrections.

Trends in colony attendance across the season were investigated by pooling data (proportion of all daytime data logger cycles when the bird was detected) for each bird into five 1-week blocks that covered the duration of the chick-rearing period. All birds were considered in a single logistic regression analysis, along with co-variates for week, tide series, and colony. Tide conditions were described by the average proportion of daylight hours that were in a low or ebb tide stage for all days in each week. Because consecutive weekly measures of colony attendance for each bird may lack independence, quasi-likelihood generalized estimating equations (GEE; Liang and Zeger 1986, Hardin and Hilbe 2003) were used for the regression (PROC GENMOD; SAS Institute, Inc., Cary, NC), assuming an autoregressive (AR(1)) correlation structure, to more appropriately estimate regression coefficient variances. Interaction terms between week, tide series, and colony were tested for inclusion in the model individually using drop-in deviance χ^2 tests. To avoid possible problems associated with missing or incomplete data, temporal analyses were performed using data collected between June 7 (after all birds had been captured and radio-tagged) and July 11 (after which most tagged birds soon concluded their breeding effort) and using only birds that were actively breeding during this entire period (Rice Island $n = 12$, East Sand Island $n = 17$).

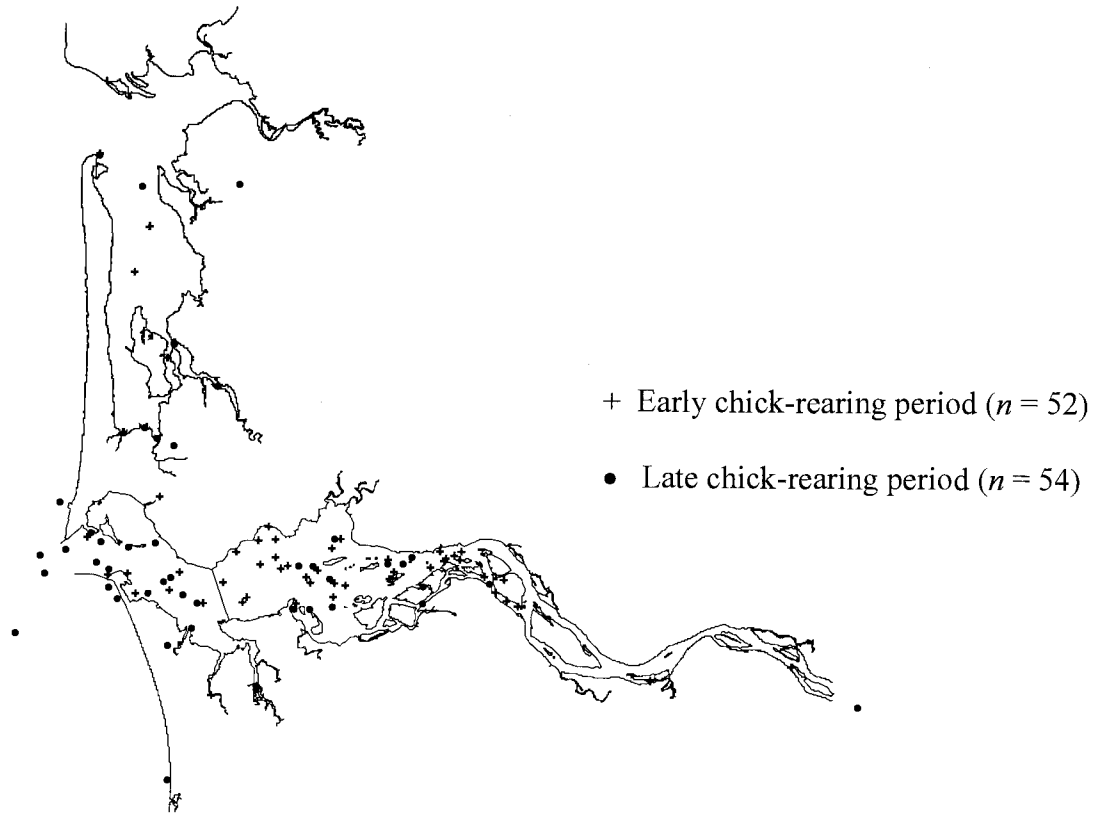
The salmonid proportion of the diet was compared between sites using a ratio test. Other comparisons of diet data were made using χ^2 tests. Significance was accepted at the 0.05 level for all tests.

RESULTS

Of the 52 terns trapped and radio-tagged at Rice and East Sand islands, 47 were determined to be breeders for at least a portion of the study period; 25 birds nested exclusively at Rice Island, 20 birds nested exclusively at East Sand Island, and 2 birds first attempted to nest at Rice Island, apparently suffered nest failure there, then attempted to re-nest at East Sand Island.

Off-colony detections of breeding, radio-tagged terns ranged from the mouth of the Columbia River to river kilometer 106, and included many detections along the Oregon or Washington coast (although generally < 1 km from the coastline) and in Willapa Bay to the north (Figure 3.2). A few radio-tagged terns were detected in Grays Harbor to the north of Willapa Bay, but these detections were only for failed breeders or those that had already fledged young. Terns nesting on Rice Island were more frequently detected in the freshwater portion of the estuary and less frequently in areas outside the estuary than terns nesting on East Sand Island ($P < 0.001$; Figure 3.3). In addition, a seasonal shift was observed in the off-colony distribution of Rice Island terns; during the late chick-rearing period, Rice Island terns were more frequently detected in the lower

A. Rice Island Breeders



B. East Sand Island Breeders

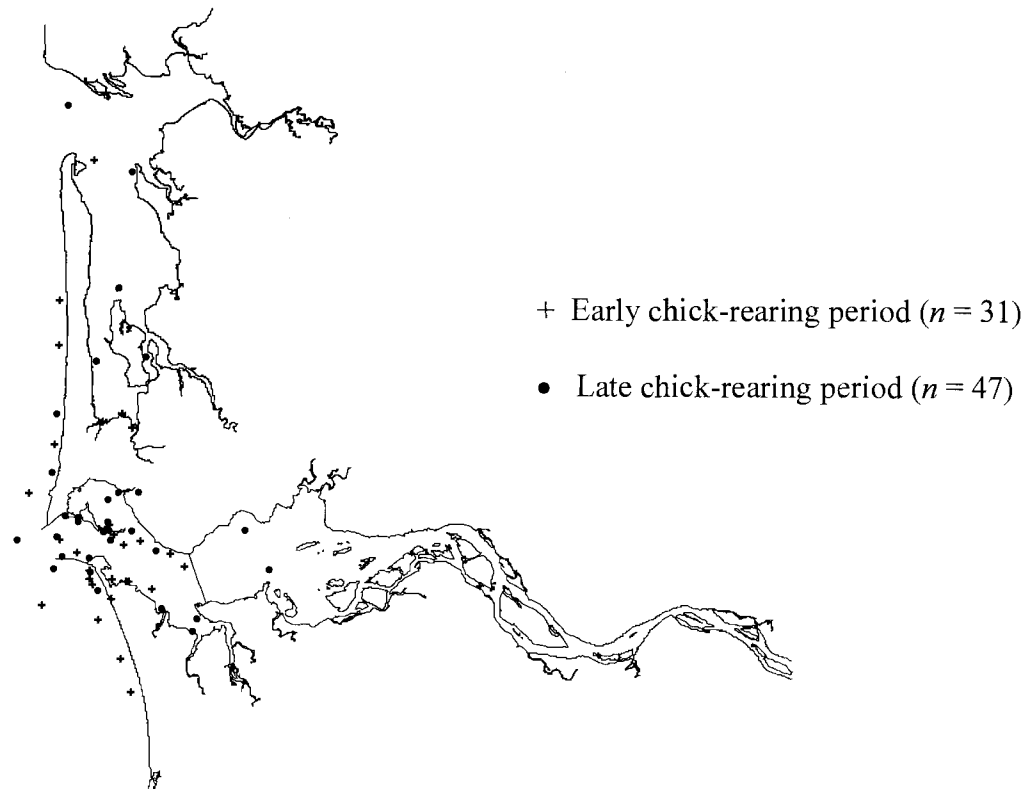


Figure 3.2. Location of all off-colony detections of radio-tagged Caspian terns nesting on (A) Rice Island and (B) East Sand Island in 1999, each divided into detections made during the early chick-rearing period (May 28 – June 18) and the late chick-rearing period (June 19 – July 13).

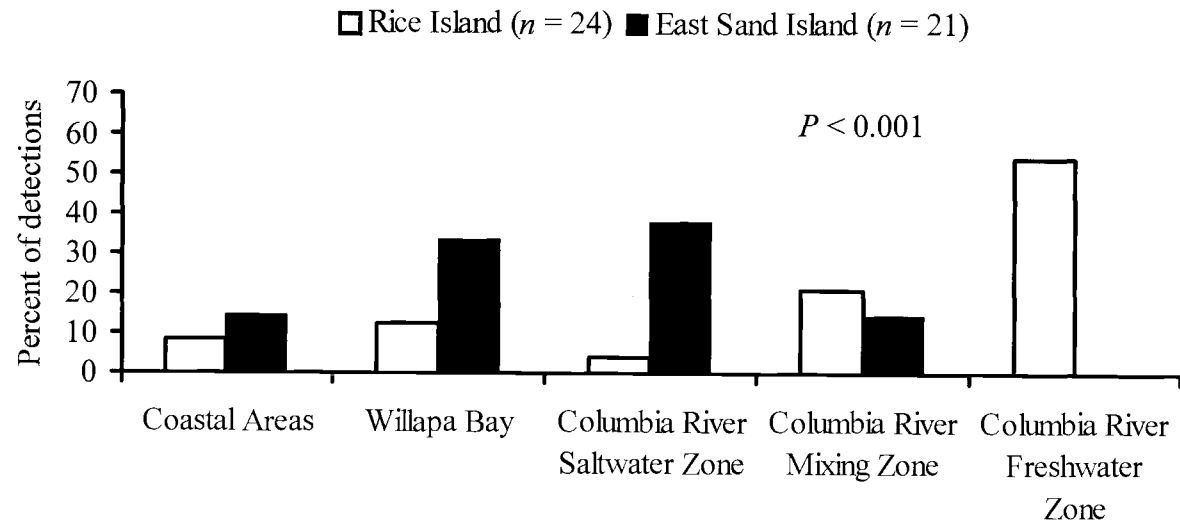


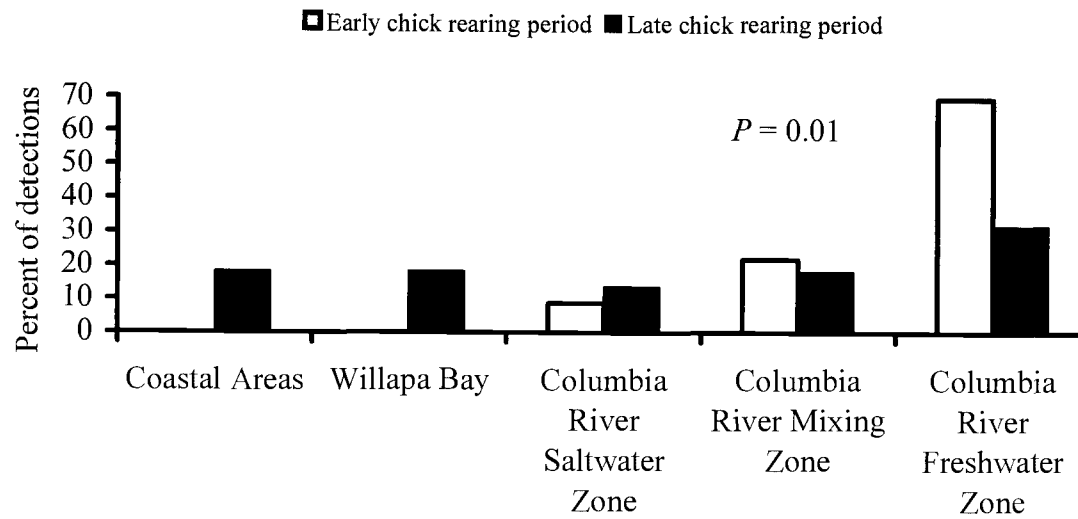
Figure 3.3. Distribution of off-colony detections of nesting, radio-tagged Caspian terns between May 28 and July 13, 1999. A single detection for each radio-tagged bird was randomly selected from all detections during the season.

estuary or outside the estuary ($P = 0.01$; Figure 3.4 (A)). No significant seasonal shift in the spatial distribution of off-colony detections was seen for terns nesting at East Sand Island ($P = 0.80$; Figure 3.4(B)).

Caspian terns nesting at Rice Island were detected at greater distances (median distance = 15.6 km) from their colony than those nesting at East Sand Island (9.3 km) throughout the chick-rearing period ($P < 0.01$; Figure 3.5). For terns nesting at Rice Island, detection distance from the colony increased between the early (12.3 km) and late (16.9 km) chick-rearing periods ($P = 0.03$). At East Sand Island there was no significant difference in detection distance between early and late chick-rearing (9.6 and 7.7 km, respectively, $P = 0.91$).

Radio-tagged terns were detected at their breeding colonies an average of 51.1% of daytime data logger cycles (range of individual means: 37 – 64%) between June 7th and July 11th. Individual birds displayed a variety of attendance patterns across daytime hours: no detectable trend ($n = 9$), a linearly increasing trend ($n = 5$), a single period of low attendance in the middle of the morning (9:00 – 10:00, $n = 2$), or lowest attendance early in the morning (before 9:00) followed by generally increasing attendance throughout the day, except for a slight dip in late afternoon (15:00 – 18:00, $n = 13$). Data for all birds averaged together attendance as the breeding season progressed ($P < 0.001$; Table 3.1, Figure 3.7). The decline in colony attendance by Rice Island terns, however, was greater

A. Rice Island



B. East Sand Island

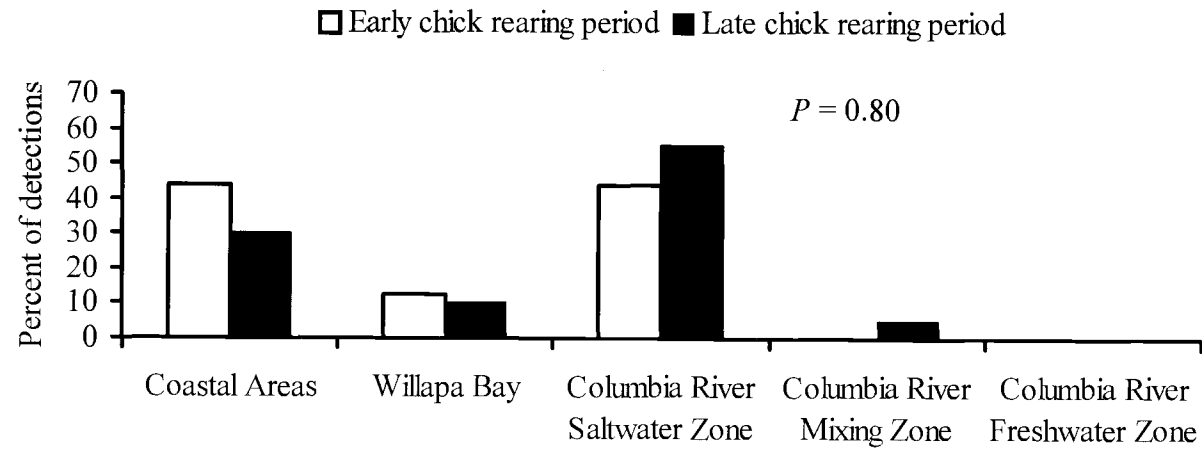


Figure 3.4. Distribution of off-colony detections during the early chick-rearing period (May 28 – June 18) and the late-chick rearing period (June 19 – July 13) for radio-tagged Caspian terns nesting at (A) Rice Island (n = 22) and (B) East Sand Island (n = 16) in 1999. One detection from each bird from each time period was randomly selected for analysis, including only birds detected during both time periods.

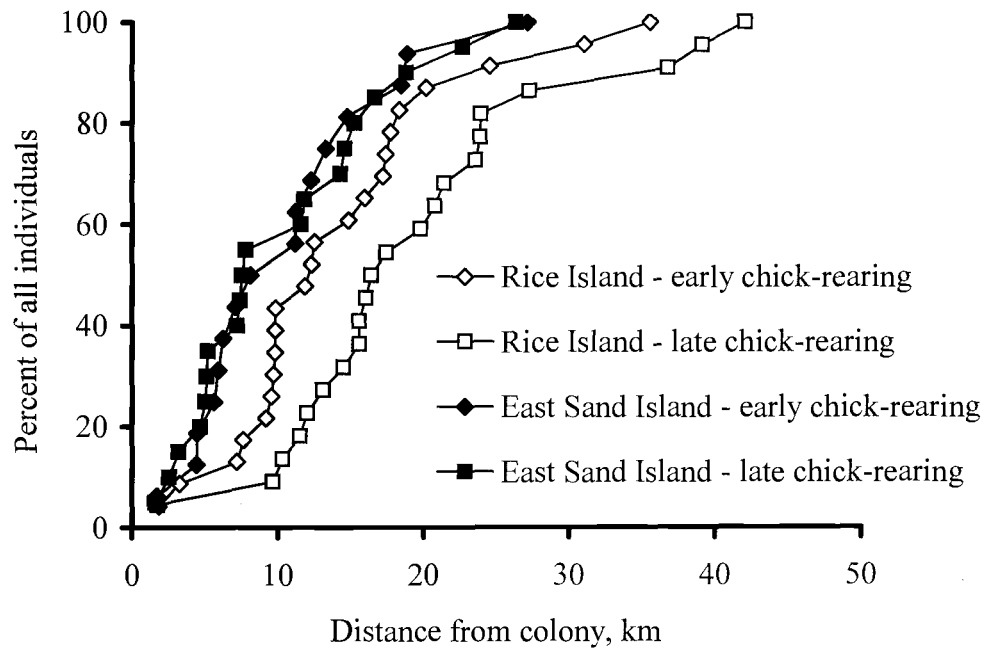


Figure 3.5. Cumulative distribution of distance from colony for off-colony detections of Caspian terns breeding at Rice Island ($n = 22$) and East Sand Island ($n = 16$). Averages for each bird in each time period were used to assemble the cumulative distribution, including only birds detected in both time periods.

(for a given week, 16% less likely to be present than during the previous week; 95% CI: 11 – 21%; $P < 0.001$; Table 3.1) than for East Sand Island terns (7% less likely each week; 95% CI: -3 – 16%). By early July, colony attendance for East Sand Island terns was 1.6 times higher than for Rice Island terns. Tidal cycles also had a significant effect on colony attendance (Table 3.1, $P < 0.001$). during weeks when a large proportion of daylight hours were in a low or ebb tide stage,

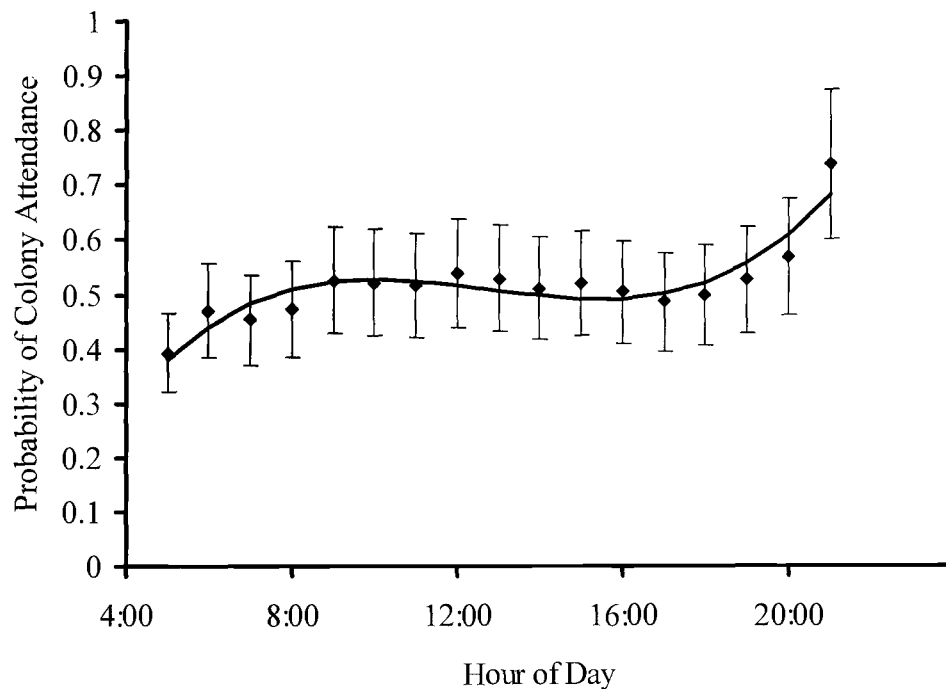


Figure 3.6. Colony attendance of nesting, radio-tagged Caspian terns across daylight hours. Data are averages (± 1 SE) of birds nesting at Rice Island and East Sand Island during the 1999 chick-rearing period.

terns were significantly more likely to be in attendance at the colony, presumably spending less time foraging (Figure 3.8).

Across the study period, 58% of the identified prey of Caspian terns nesting at Rice Island consisted of salmonids, substantially more than the 29% salmonids in the diet of East Sand Island terns ($z = 21.3$, $P < 0.001$; Figure 3.9). High proportions of anchovies, clupeids (primarily herring), surfperches, and other alternative prey replaced salmonids in the diet of East Sand Island

Table 3.1. Model coefficients of the generalized estimating equations (GEE) logistic regression model used to assess factors affecting colony attendance by radio-tagged Caspian terns during the chick-rearing period. Standard errors (SE) are given for all parameters assuming independence (IND) of all observations and assuming an autoregressive (AR(1)) correlation structure; *P*-values are for the AR(1) standard errors.

Variable	Parameter Range	Model Coefficient Estimate			<i>P</i>
		Mean	IND SE	AR(1) SE	
Colony site	East Sand Island (1) or Rice Island (0)	-.08	.06	.11	0.49
Week of season	June 7-13 (1) – July 5-11 (5)	-.18	.01	.03	< 0.001
Tide Series	0.41 – 0.57	1.03	.17	.22	< 0.001
Colony x Week	0 – 5	.11	.02	.04	< 0.01

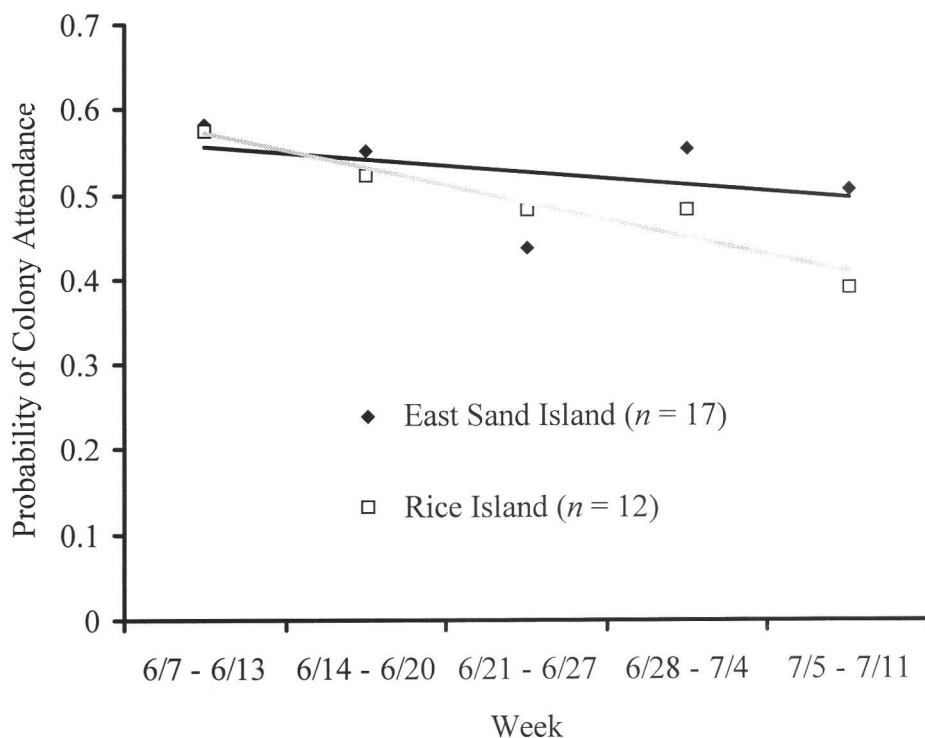


Figure 3.7. Colony attendance of radio-tagged Caspian terns nesting in the Columbia River estuary across the 1999 chick-rearing period, separated by colony.

terns ($\chi^2_4 = 743.2$, $P < 0.001$). Significant differences in diet composition were observed between the early chick-rearing period and the late chick-rearing period at both Rice Island ($\chi^2_6 = 238.6$, $P < 0.001$) and at East Sand Island ($\chi^2_6 = 273.8$, $P < 0.001$), with the prevalence of salmonids declining and the prevalence of anchovies and surfperches increasing at both colonies (Table 3.2). Diet composition also differed significantly between high and low tides at both islands (Rice Island: $\chi^2_6 = 32.9$, $P < 0.001$, East Sand Island: $\chi^2_6 = 72.5$, $P < 0.001$), with

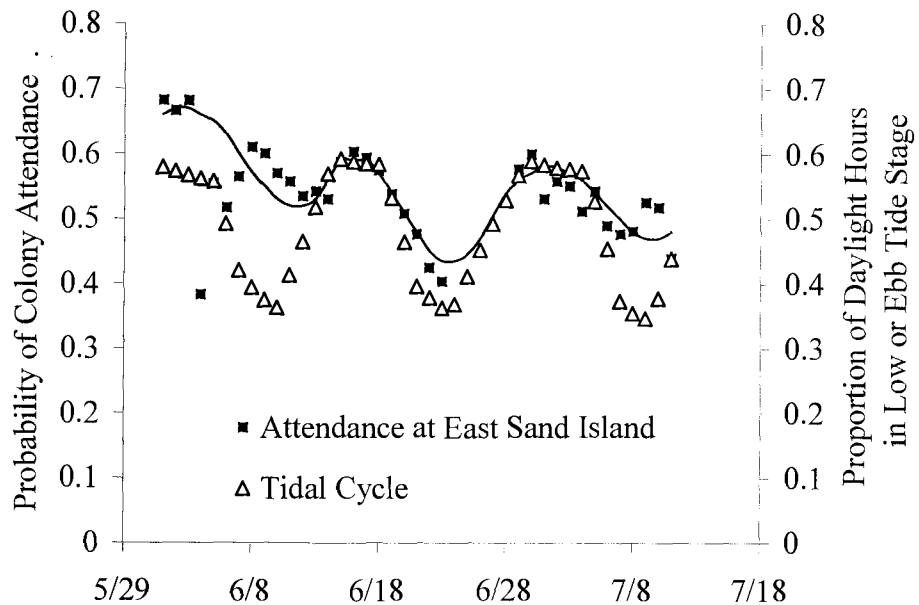


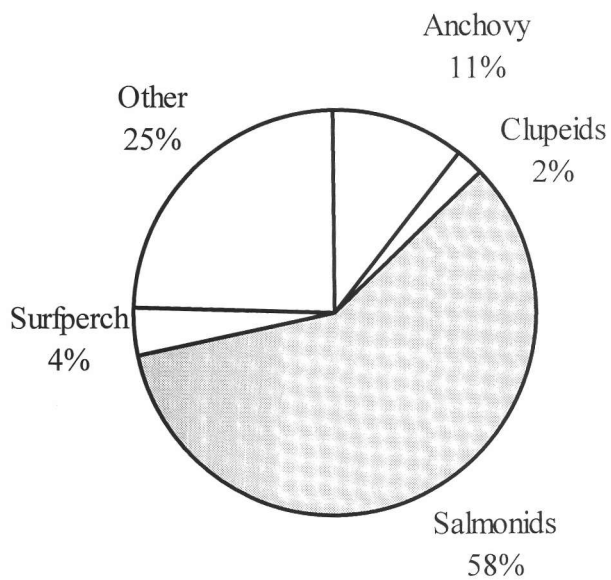
Figure 3.8. Relationship between tide cycle and colony attendance for terns breeding at East Sand Island. An arbitrary polynomial function has been added to the figure to emphasize the trend in daily average colony attendance.

the proportion of salmonids and sculpins in the diet being higher at low tides, and the proportion of anchovies being higher at high tides (Table 3.3).

DISCUSSION

Despite the close proximity (21 km straight line separation) of the two colonies of Caspian terns in our study, we observed substantial differences in the foraging ecology of terns nesting at each site. In particular, the foraging distribution and colony attendance were significantly different between the two colonies and food habits reflected these differences. Even in highly vagile

A. Rice Island



B. East Sand Island

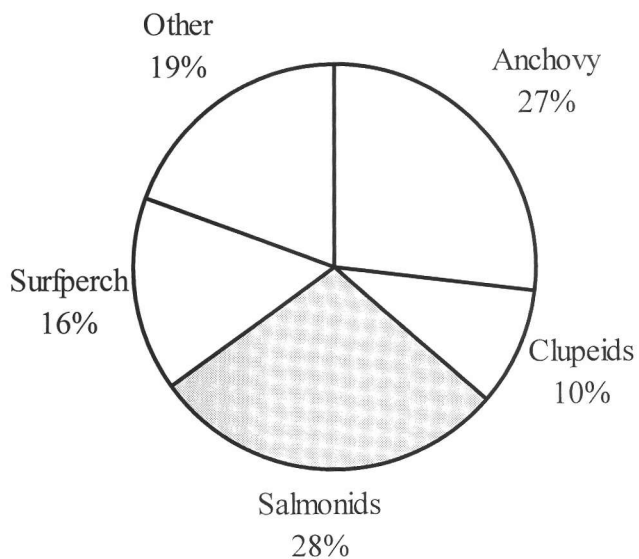


Figure 3.9. Diet composition (% identifiable prey items) of Caspian terns nesting on (A) Rice Island ($n = 2605$) and (B) East Sand Island ($n = 2498$) from May 28 – July 13, 1999. For more information on diet composition see Roby et al. (2002).

Table 3.2. Comparison of diet composition (% identifiable prey items) between the early (May 28 – June 18) and late (June 19 – July 13) chick-rearing periods for Caspian terns breeding at two sites in the Columbia River estuary.

Prey Type	Rice Island		East Sand Island	
	Early	Late	Early	Late
Anchovy ^a	3.6	16.6	15.1	37.5
Clupeid ^b	0.4	4.1	9.9	9.2
Peamouth, pike minnow ^c	0.8	3.4	0.3	1.4
Salmonid ^d	70.7	46.2	42.3	16.3
Sculpin ^e	0.6	2.3	3.1	4.5
Smelt ^f	3.2	1.0	7.7	2.2
Surfperch ^g	1.3	5.6	11.1	19.5
Other ^h	19.4	20.8	10.5	9.3
<i>n</i>	1198	1407	1188	1310

^a Engraulidae, ^b Clupeidae, ^c Cyprinidae, ^d *Oncorhynchus* spp., ^e Cottidae, ^f Osmeridae, ^g Embiotocidae, ^h lamprey (*Lampetra* spp.), stickleback (*Gasterosteidae*), sucker (*Catostomus* spp.), or unidentified non-salmonids

species, such as Caspian terns, individuals appear to adjust their behavior in relation to their local environment.

Our detections of radio-tagged terns at off-colony locations suggested that terns from both sites foraged primarily in the vicinity of their colony during late incubation (immediately following capture) and early in the chick-rearing period. Terns nesting at Rice Island frequently were found in the freshwater zone of the

Table 3.3. Comparison of diet composition (% identifiable prey items) between high and low tide stages for Caspian terns breeding at two sites in the Columbia River estuary from May 28 – July 13, 1999.

Prey Type	Rice Island		East Sand Island	
	High	Low	High	Low
Anchovy ^a	13.7	8.6	31.2	22.3
Clupeid ^b	1.9	1.5	9.5	9.6
Peamouth, pike minnow ^c	2.0	2.0	0.8	0.8
Salmonid ^d	52.0	64.2	26.9	31.5
Sculpin ^c	0.7	1.9	0.8	7.0
Smelt ^f	2.6	1.8	5.0	5.1
Surfperch ^g	4.4	2.4	14.8	14.3
Other ^h	22.6	17.5	11.0	9.4
<i>n</i>	992	1180	1062	1043

^a Engraulidae, ^b Clupeidae, ^c Cyprinidae, ^d *Oncorhynchus* spp., ^e Cottidae, ^f Osmeridae, ^g Embiotocidae, ^h lamprey (*Lampetra* spp.), stickleback (Gasterosteidae), sucker (*Catostomus* spp.), or unidentified non-salmonids

upper estuary, where juvenile salmonids were presumably the most available prey. In contrast, terns nesting at East Sand Island only occasionally traveled to the freshwater zone, instead utilizing the estuarine mixing and marine zones for foraging, where marine forage fish species (e.g., anchovy, herring, surfperch) were presumably more available. The diet of each colony was consistent with the observations of foraging in these zones. Rice Island terns relied heavily on

juvenile salmonids early in the season, whereas East Sand Island terns much less so.

Late in the chick-rearing period, radio-tagged terns nesting at Rice Island were more frequently detected in the lower estuary and areas outside the estuary (north or south along the coast or north in Willapa Bay) than they had been during the early chick-rearing period. Concurrently, the proportion of salmonids in the diet of Rice Island terns declined significantly from 71% to 46%. Both of these trends are consistent with an observed decline in the number of juvenile salmonids entering the estuary as the season progresses. The peak out-migration of juvenile salmonids from the Columbia River basin, particularly the larger species (steelhead and coho salmon) and age classes (yearling chinook salmon), occurs during the month of May (Fish Passage Center 2002). Relatively high numbers of smolts move through the estuary early in June but the numbers decline throughout the month (Fish Passage Center 2002).

East Sand Island terns foraged in the same areas during the late chick-rearing period as they did during early chick-rearing. Their diet during late chick-rearing, however, included significantly fewer salmonids and more anchovy and surfperch. This also tracks the declining abundance of juvenile salmonids as the chick-rearing period progresses, but may also indicate that substantially more marine forage fish entered the lower estuary and/or Willapa Bay as the season progressed and were more readily available to terns there. Median detection

distance from the colony for terns nesting on East Sand Island was less during the late chick-rearing period, though not significantly, so the apparent decline in availability of juvenile salmonids did not cause them to shift to foraging areas farther from the colony, as was the case with Rice Island terns.

In addition to differences in foraging distribution and diet composition, regression analysis indicated that as the season progressed, colony location became a significant factor in colony attendance. Lower colony attendance, coupled with greater average detection distances from the colony, suggests that terns nesting at Rice Island took longer foraging trips.

Lower attendance at the nest can have negative consequences for chick survival. During the first few days post-hatch, tern chicks are dependent on their parents for thermoregulation and require nearly continuous brooding. Small chicks are also vulnerable to predation by glaucous-winged/western gulls (*Larus glaucescens* X *L. occidentalis*) that nest in close proximity to the tern colonies on each island. As chicks age, they gain thermoregulatory ability and predation risk declines; however, aggressive encounters with conspecific adults (that are not their parents) can result in displacement from the nest territory, injury, or even death. In this case, unsupervised or unprotected chicks that wander from their nest scrape are still at some disadvantage. Given these scenarios, the higher food availability that allows terns nesting at East Sand Island to attend the colony more

during chick-rearing would seem to be an advantage, contributing to greater per capita nesting success (Roby et al. 2002).

Lower colony attendance and foraging farther from the colony for Rice Island terns may also translate into lower meal delivery rates to the brood. This might result in smaller broods and/or slower growth and development of chicks, which could prolong the rearing period and increase exposure to the above mentioned mortality factors. Nutritional status during growth and development has also been observed to impact post-fledging survival in other terns and gulls (Coulson and Porter 1985, Keedwell 2003).

While colony site and day of season played critical roles in foraging behavior, our study suggested tidal conditions also affected behavior. During weeks with a higher proportion of daytime low and ebb tide conditions, colony attendance at both colonies was higher. This indicates higher foraging efficiency during low or ebb tide conditions. Tide stage has often been shown to influence when other larids visit foraging sites (e.g., Burger 1982, Burger 1983, Irons 1998) and ultimately colony attendance (Galusha and Amlaner 1978). Tidal cycles also influenced diet: anchovy were a larger portion of the diet at high tides, consistent with greater salt water intrusion into the estuary allowing entry further up-river, perhaps in greater numbers and closer to tern colonies.

Central place foraging around colony sites appeared to be the leading cause of differences in foraging ecology between terns nesting on Rice Island and

East Sand Island; however, two other possible factors should be considered. First, density-dependent effects might have been much more important at Rice Island, where the tern colony was estimated at 8300 breeding pairs, compared to 550 pairs on East Sand Island (Roby et al. 2002). Localized depletion of available prey in areas near the Rice Island colony (“Ashmole’s Halo”) might have caused individual terns to forage farther from the colony than terns nesting at East Sand Island (Ashmole 1963). Second, East Sand Island is downstream of Rice Island, and Rice Island terns could potentially deplete a significant proportion of the available salmonids migrating down the river, leaving less for East Sand Island terns to utilize. We estimated that in 1998 the Rice Island tern colony (8700 pairs) consumed 9-17% of all salmonids that entered the estuary (Roby et al. 2003). In 1999, slightly fewer terns bred at Rice Island than in 1998 (Roby et al. 2002), presumably consuming a similar or slightly smaller fraction of all salmonids. If this potential up-stream prey depletion effect was an important influence on foraging behavior, terns nesting at both islands should benefit from foraging in areas up-river of their respective colonies. Our results do not suggest any preferential foraging up-river of the colony site by terns from either island, however.

By the foraging metrics examined in this study, the location of East Sand Island in the marine zone appeared to be more favorable as a Caspian tern colony site than the location of Rice Island in the freshwater zone. The position of East

Sand Island lower in the estuary allowed terns to travel shorter distances during foraging trips, especially important later in the chick-rearing period when chick energy requirements are high. Colony attendance was also higher for terns nesting at East Sand Island during the chick-rearing period. In addition, East Sand Island terns were less reliant on one prey type, juvenile salmonids, to meet their food requirements, which may have conferred an advantage as the size and abundance of smolts traveling through the estuary declined rapidly during the chick-rearing period (Fish Passage Center 2002).

The apparently enhanced foraging conditions at East Sand Island presumably contributed to higher production of fledglings. Per capita productivity at the East Sand Island colony in 1999 was much higher: 1.20 fledglings/breeding pair compared to 0.55 fledglings/pair at Rice Island (Roby et al. 2002). This result is confounded by targeted removal of problem gulls to limit nest predation at East Sand Island and facilitate the restoration of the tern colony there (Roby et al. 2002); however, it seems likely that favorable foraging conditions contributed to the ability of some breeding pairs to provision and raise multiple-chick broods. Similarly, our only observations of radio-tagged terns attempting to reneest at a new site after presumably failing at one site were moves from Rice Island to East Sand Island – East Sand Island radio-tagged terns that failed did not attempt to breed at Rice Island. This apparent migration of breeding birds from Rice Island to East Sand Island (and the lack of migration in

the opposite direction) again suggests East Sand Island was a more favorable breeding location in 1999.

We observed that colony location within the Columbia River estuary had a significant effect on the foraging ecology of Caspian terns, and likely fledgling production, in 1999. Even on spatial scales that were small relative to the maximum foraging range of the species, significant differences were observed in several measures of foraging behavior. Colony sites in marine zones of coastal estuaries may generally provide benefits for Caspian terns over sites in freshwater zones, at least in terms of proximity to a more diverse and perhaps more abundant prey base, at least during periods of coastal upwelling. These traits might be of use to resource managers who wish to reduce tern predation on ESA-listed salmonids from the Columbia River basin, if terns can be attracted to colony sites where alternative prey are available. East Sand Island appears to be such a site, and substantial reductions in tern predation upon Columbia River salmonids might be achieved if more or the entire Rice Island Caspian tern colony was shifted to East Sand Island (Roby et al. 2002). Reductions in tern predation on anadromous salmonid species and stocks throughout the region might be achieved if terns were redistributed to colony sites in the marine zone of other estuaries. Further analysis would still be required to assess to what extent reductions in tern predation might potentially increase salmonid population levels (Roby et al. 2003).

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CHAPTER 4

SYNOPSIS AND CONCLUSIONS

A detailed understanding of the foraging ecology of species preying upon threatened or endangered prey may contribute to identifying and evaluating management options to reduce such predation, when management is deemed appropriate. In 1998 and 1999, we studied the foraging ecology of Caspian terns and double-crested cormorants in an effort to assist managers in achieving their goal of reducing predation upon juvenile salmonids in the Columbia River estuary. In addition to acquiring information for immediate management application, we characterized how each of these piscivorous waterbird species utilized a large estuary having high freshwater input and significant anthropogenic alterations.

Our work suggests that Caspian terns are opportunistic, generalist predators, utilizing habitats in relation to availability and, when possible, concentrating the majority of their foraging in areas much closer to their breeding site than their maximum foraging range. We observed no significant differences in densities of foraging terns in different habitat types, but found large numbers of terns utilized abundant habitat types – both deep water channels and tidal flats. Less common habitat types, such as tributaries, sloughs, and ocean jetties, were

not found to be important foraging areas; nor were nearshore ocean areas. In 1998, more terns foraged in the freshwater zone of the estuary; however, in 1999, when some terns nested near the river's mouth at East Sand Island, some terns shifted their foraging activity to the marine/mixing zone and terns were distributed evenly between that zone and the freshwater zone. In 1999, radio-telemetry results indicated that terns nesting on East Sand Island foraged in the marine/mixing zone of the estuary, seldom venturing into the freshwater zone, while radio-tagged terns nesting on Rice Island were detected more frequently in the freshwater zone.

We observed differences in the foraging behavior of terns seasonally and across tide stages, no doubt reflecting changes in prey availability. More foraging occurred in the freshwater zone early in the season, corresponding to the large seasonal out-migration of juvenile salmonids. Later in the season, foraging shifted more to the marine/mixing zone, and the tern diet included a greater proportion of marine forage fish. Low tides may have corresponded to opportunities for more efficient foraging, particularly in tidal mud flat habitat. Diet composition likely reflected differences in prey availability at different tide stages.

Colony site was the most important factor in determining Caspian tern foraging behavior. Foraging activities of terns were strongly tied to colony location and the resulting diet composition reflected these constraints. The nearby

foraging environment for East Sand Island terns appeared to be as good or better than for Rice Island terns in 1999, as East Sand Island terns were detected closer to their colony site and were able to attend their colony during a greater proportion of the day, particularly later in the chick-rearing period. This likely contributed to higher overall productivity of terns nesting at East Sand Island, compared to those at Rice Island. The management hypothesis that Caspian tern predation upon juvenile salmonids might be reduced by attracting terns to nest at East Sand Island was confirmed by our data. Relocating terns 21 km closer to the river's mouth was sufficient to shift the majority of their foraging activities and induce a large reduction in the proportion of salmonids in the diet.

We observed few habitat preferences for foraging double-crested cormorants. Cormorants did forage at higher densities at sites with pile dikes and/or pilings in 1999, suggesting that these sites may offer enhanced foraging opportunities on at least some occasions. Further study would be required, however, to demonstrate that precluding roosting on these structures would in fact reduce cormorant predation upon juvenile salmonids.

FUTURE DIRECTIONS

Additional understanding of how these piscivorous waterbirds select foraging areas might assist managers in further reducing predation upon Columbia River salmonids.

Assessing habitat preferences of foraging Caspian terns is difficult. Rather than commuting directly to a foraging site, foraging at that site, then commuting back to the colony, we observed terns opportunistically foraging during much of the time spent away from the colony. Terns may leave the colony intending to utilize a particular foraging site; however, it seems most terns begin opportunistically foraging soon after leaving the colony and long before reaching the maximum extent of the particular foraging trip. Preferred or advantageous foraging habitats or behavioral strategies would likely be more easily identified if individual birds were observed for the entirety of a foraging trip.

Attracting terns to nest at sites outside the Columbia River basin is a strategy that would reduce predation on Columbia River salmonids. Conflicts with other fisheries may, however, be an issue for any newly enhanced or restored colony site. The information in this study informs managers on likely foraging behavior in other locations; however, site specific conditions may also be important. Presumably, the Columbia River estuary harbors abundant forage fish populations; numerous marine forage fish enter the estuary and salmonid populations are buoyed by large scale hatchery production within the basin. Other sites where tern colony restoration might occur may not match these prey resources and consequently terns may extend their foraging range or utilize particularly profitable habitats very preferentially. Investigations into tern foraging ecology at such sites may provide useful insights to managers.

Quantifying actual losses of juvenile salmonids to double-crested cormorants at sites having pile dikes and/or pilings would be helpful to assess the potential efficacy of any site-specific management proposals to reduce this predation. Prey capture rates and data on prey composition at these sites might be used to estimate total take of salmonids at such sites, which might be compared to bioenergetic estimates of total salmonid consumption by all cormorants in the estuary. In this manner, it might be possible to determine if predation at these sites constitutes a significant portion of all cormorant predation on salmonids, and thus enable an assessment of the efficacy of any management action to reduce that predation.

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