

The Foraging Ecology of Royal and Sandwich Terns in North Carolina, USA

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Abstract.—We studied the foraging ecology of Royal Terns (*Sterna maxima*) and Sandwich Terns (*S. sandvicensis*) in North Carolina during the breeding seasons in 1999 and 2000. Foraging habitats were surveyed using 95 fixed-point observations (30–45 min each) and over 100 h of inshore and offshore transects. Stable isotopes (¹³C, ¹²C, ¹⁵N, ¹⁴N, and ¹⁸O, ¹⁶O) in eggshells were analyzed for evidence of differences in foraging habitats. Water masses were delineated using satellite imagery of sea surface temperatures. We determined diet for each species with observations of chick provisioning and fecal analyses. Although Royal and Sandwich Terns nested together in the same colonies, their prey and foraging habitats differed. Sandwich Terns fed their chicks 48% anchovies (*Anchoa* sp.), 39% herring (Clupeidae)/jacks (Carangidae)/mackerels (Scombridae), and 9% drums (Sciaenidae)/porgies (Sparidae)/mulletts (*Mugil* sp.), and foraged primarily in the marine coastal environment. Conversely, Royal Terns provided their chicks with 9% anchovies, 30% herring/jacks/mackerels, and 41% drums/porgies/mulletts, and fed more frequently in the estuary. The species' foraging ranges overlapped at inlets and the river mouth. Stable isotope ratios also suggested that foraging differences occurred between colonies. The results of this investigation indicate that Royal and Sandwich Terns in North Carolina partition food resources by habitat and prey choice. *Received 2 December 2000, accepted 8 February 2001.*

Key Words.—Foraging ecology, Royal Tern, Sandwich Tern, North Carolina, stable isotopes, *Sterna maxima*, *Sterna sandvicensis*.

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The breeding range of the Sandwich Tern (*Sterna sandvicensis*) in the western Atlantic overlaps with that of the Royal Tern (*S. maxima*). The two species often nest in distinct groups or completely intermixed at the same colonies (Korschenewski 1969; Blus *et al.* 1979; Yorio *et al.* 1994; Quintana and Yorio 1997). Crèches (groups of flightless chicks) also are intermixed (Buckley and Buckley 1972; Quintana and Yorio 1997). Within these collective colonies, the cost of intra- and inter-specific aggression is outweighed by the benefits of communal living, as their association with one another may mutually reduce predation due to the fact that larger groups have proportionately lower numbers of eggs and chicks exposed at the perimeter (Cullen 1960; Lind 1963; Langham 1974; Quintana and Yorio 1997; but see Dunn 1973).

Outside North America, the Sandwich Tern sometimes benefits by nesting with other species that are more aggressive toward predators (Langham 1974; Shealer 1999). In Virginia and North Carolina, however, Buckley and Buckley (1972) did not find the Royal

Tern to be particularly aggressive toward predators, except when chicks were a few days old. Although Royal Tern presence seems to be essential for nesting by Sandwich Terns in North America, the Royal Tern, which is the first to arrive at the colony, sometimes nests without the Sandwich Tern (Bent 1921; Kale *et al.* 1965; Buckley and Buckley 1972; Blus *et al.* 1979; Parnell *et al.* 1995). Buckley and Buckley (1972) speculated that the Sandwich Tern might increase its own nesting success by settling where the Royal Tern is already productive, or by following the Royal Tern to food. Shealer (1999) noted that a comparative feeding and nesting study may be useful in determining what factors are important in maintaining the association between Royal and Sandwich Terns.

Royal Terns in the eastern U.S. feed up to 80 km from their colonies, both inshore (Buckley and Buckley 1972) and offshore (Lee 1995). According to Buckley and Buckley (1972), Royal Terns prefer foraging in large bays, often close to their colony, but regularly travel up to 65 km along the shore

and 20-30 km up tidal rivers. Bent (1921) noted that Sandwich Terns in North America primarily feed offshore, but more recent accounts by other authors characterize them as inshore feeders (Buckley and Buckley 1972; Lee 1986, 1995; Garth 1997; Shealer 1999). In North Carolina, Lee (1995) regularly observed Royal Terns offshore carrying fish toward colonies 50 km away, while Sandwich Terns were only occasionally observed feeding up to 20 km offshore. Both species in Patagonia fed out of sight of the shore and returned with the same prey species (Quintana and Yorio 1997). Seven tern species in the Gulf of Mexico, including Royal and Sandwich Terns, collectively showed a positive association with lower salinity and higher chlorophyll *a* concentrations in the Mississippi River plume (Ribic *et al.* 1997). No study has compared the foraging ecology of Royal and Sandwich Terns in North America.

The purpose of this study was to compare the feeding habitat and diet of Royal and Sandwich Terns and to determine if these species partition food resources. We tested the hypothesis that Royal and Sandwich Terns in North Carolina forage in different locations and/or select different prey during the nesting through chick-rearing season. Several techniques were used to address this hypothesis. Feeding areas were identified directly, from shore and by boat, primarily along the southern coast (Cape Fear), and indirectly by comparing isotopic ratios in eggshells for signatures of what and where terns foraged from a northern (Oregon Inlet),

middle (Cape Lookout) and southern (Cape Fear) colony. We used satellite imagery of sea surface temperatures to identify major water masses for offshore surveys and isotope analyses. Diet was assessed directly by observing chick feedings, and indirectly by analyzing fish regurgitations and fecal remains.

STUDY AREA

Royal and Sandwich Terns in North Carolina nest in sparsely vegetated areas free of quadruped predators (Buckley and Buckley 1972; Parnell *et al.* 1995). Prior to anthropogenic habitat degradation of barrier islands, hurricanes and other severe storms maintained suitable nesting sites along the eastern U.S. coast for these species (D. Allen, pers. comm.). Dredge spoil islands, especially near inlets where water mixing leads to higher productivity, have replaced the natural nesting habitat of Royal and Sandwich Terns in North Carolina (Buckley and Buckley 1975). The United States Army Corps of Engineers began creating these islands in the sounds of North Carolina in the early 1800s, while deepening channels throughout the sandy North Carolina coast (Soots and Parnell 1975).

We gathered data at, or near, seven of the eight islands in North Carolina known to support mixed-species breeding colonies of Royal and Sandwich Terns (Table 1 and Fig. 1). Two colonies, at Oregon Inlet (Islands L and M) and Bigfoot Island, were at opposite ends of Pamlico Sound, the largest mesohaline estuary in the South Atlantic Bight (Laney 1976). Island L, occupied by terns only in 1999, is 5 km west of Oregon Inlet; the colony shifted to Island M (<1 km to the west) in 2000. Bigfoot Island is located in the southern end of Pamlico Sound, where salinity is 20‰, 6-11‰ higher than it is near Islands L and M (Pietrafesa *et al.* 1986). Three other colonies, at Wainwright Island, New Dump Island, and Cape Lookout (Sand Bag Island), are located in high salinity waters of the Core and Back Sounds (=30‰, Ortega and Sutherland 1992). Most of our research was conducted in the lower Cape Fear River area. Royal and Sandwich Terns nested at Ferry Slip and South Pelican Islands in the Cape Fear River in 1999 and 2000. Collectively, these two metapopulations are referred to as the Cape

Table 1. Royal and Sandwich Terns banded in North Carolina in 1999 and 2000. Royal Terns vastly outnumbered Sandwich Terns at all colonies except on New Dump Island. Virtually all chicks except on New Dump Island (*) were banded in these years (banding records from J. Weske, M. Browne and S. Emslie).

Island	Location	Royal Terns		Sandwich Terns	
		1999	2000	1999	2000
S. Pelican	33°56'N, 77°58'W	1505	3118	612	1365
Ferry Slip	34°02'N, 77°56'W	1446	163	132	9
Sand Bag	34°38'N, 76°31'W	1836	1881	491	458
New Dump*	34°53'N, 76°19'W	—	866	—	844
Wainwright	34°59'N, 76°12'W	5153	1365	483	37
Bigfoot	35°07'N, 76°06'W	754	1903	56	19
Clam Shoal	35°18'N, 75°40'W	5	1101	—	53
L and M	35°47'N, 75°34'W	884	1102	165	256

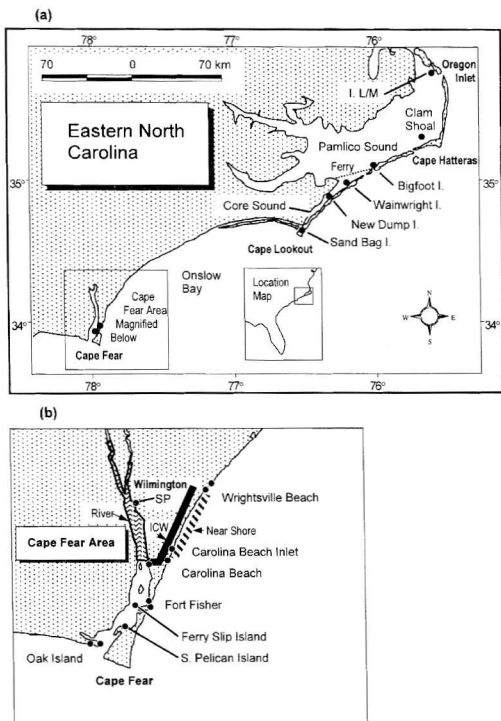


Figure 1. (a) Locations of all North Carolina Royal and Sandwich Tern colonies in 1999 and 2000. Box around Cape Fear area magnified in 1b for greater detail. (b) Areas surveyed by small boat include: upper estuary of the Cape Fear River (wave shading), Atlantic Intracoastal Waterway (ICW, black line), and nearshore (black and white striped line). Black dots indicate point survey locations and North Carolina State Port (SP).

Fear colony. The lower Cape Fear River is the second largest mesohaline estuary in North Carolina (Laney 1976). Surface salinity in the estuary is highly variable due to tidal flux and the amount of fresh water flow, but generally it is about 24‰ near South Pelican Island, decreasing to 2.5‰ at the State Port in Wilmington (Mallin *et al.* 1996).

Three major water masses exist along the North Carolina coast. Virginia Coastal Water generally extends south to Cape Hatteras and can intrude as far south as Cape Fear (Pietrafesa *et al.* 1994). South of Cape Hatteras is warmer, well mixed continental shelf water, called Carolina Coastal Water. East of these two water masses, the Gulf Stream, consisting of warm, clear tropical water, flows northeasterly at the edge of the continental shelf. Virginia Coastal Water (31-34‰) is 1-6‰ less saline than Carolina Coastal Water (35-37‰). The western Gulf Stream front (35-36‰) comes closest to the coast at Cape Hatteras, where it is only 50-60 km offshore (Pietrafesa *et al.* 1985). It is approximately 100 km east of the Cape Fear River mouth, but eddies randomly transport its water inshore.

METHODS

Point Surveys

Royal and Sandwich Terns were surveyed from land using 8 × 42 or 10 × 50 binoculars at ten sites in five

paired locations. A 20-45 × 60 spotting scope was used to identify resting terns. Pairs of fixed survey points were set in contrasting habitat types that were nearly equidistant from the breeding colonies (Fig. 1b). Observations lasted 30 minutes (45 minutes at Carolina Beach) during each of 95 observations to determine the species' relative use of different water masses. Surveys were conducted during a variety of tidal phases and weather conditions. Observations at Fort Fisher and Carolina Beach were conducted in June-July 1999 and May-July 2000. Oak Island and Wrightsville Beach were added in May 2000 and surveyed through July 2000, while Carolina Beach Inlet was surveyed in June and July 2000. We recorded weather and tidal phases, beginning and ending times, species, number of individuals and bird activities (flight direction, foraging, carrying fish, or resting). Terns that flew in random directions were recorded as "foraging", but birds that appeared to scan the water for fish, but did not change flight direction, were not recorded as foraging. No surveys were conducted while fishing boats were in the observation area.

In surveys from small boats, conducted to verify point surveys, we observed terns in sections of the lower Cape Fear River (May-July 2000, nine hours total in four trips), the Atlantic Intracoastal Waterway (May and June 2000, eight hours total in four trips), and near-shore ocean strips (July and August 2000, four hours total in three trips, Fig. 1b). We recorded weather conditions, beginning and ending times, numbers of Royal and Sandwich Terns within each water mass and activity (flight direction, foraging, carrying prey, resting). We visited one particularly large tern roost (National Gypsum conveyor-belt dock at the North Carolina State Port, Fig. 1b) twice by land to better characterize relative species abundance in the lower Cape Fear River, upstream of the Intracoastal Waterway. We recorded approximate locations, species, number of individuals and tern activities (May 1999, July 1999 and June 2000, four hours, Fig. 1a) from the Cedar Island-Ocracoke Ferry.

Offshore Surveys

In the Cape Fear area (May-July 2000), transects from the Intracoastal Waterway, crossing through Carolina Coastal Water and past the western Gulf Stream front were surveyed aboard the *RV Cape Fear* in a series of interdisciplinary cruises (Table 2). Continuous strip transects 300 m in width were generally conducted at two speeds: 24-27 km h⁻¹ (between sites and to or from shore) and <10 km h⁻¹ (while plankton nets were in the water). Stationary surveys were conducted when time allowed. In each survey, we recorded beginning and ending times, species observed, number of individuals, bird activities (flight direction, foraging, carrying fish, or resting) and times of sightings. Global positioning system (GPS) locations were automatically recorded every minute. Faster transects were conducted from the bow deck (1 m above water level) in a 90° arc from the bow to the side with the best viewing conditions, as used by Gould *et al.* (1978). At slower speeds and in stationary surveys, we scanned a 180° arc and identified tern species within 300 m. A range finder was used to estimate survey distance, as applied by Heinemann (1981).

We attempted to time birds as they flew through the quadrant to determine their absolute densities (Spear *et al.* 1992), but discontinued this method as birds were often out of view before they passed through the entire quadrant. Instead, apparent densities (numbers of birds

Table 2. Relative survey effort was not equal in offshore surveys of Onslow Bay, North Carolina, due to the course of the *RV Cape Fear* in a series of interdisciplinary cruises. Transects occurred between predetermined sampling stations. Concentric circles (radii listed in the first column) were drawn around the Cape Fear colony, passing through sampling stations. Ocean area (second column) equals the surface area of ocean between concentric circles. Strip area (third column) is the actual ocean surface area surveyed between sampling stations. Relative survey effort (fourth column) was determined relative to the most thoroughly surveyed ocean area (where 40 km² out of 552 km² were surveyed, and given an effort score of 1.000). Royal and Sandwich Tern densities (last two columns) are based on areas actually surveyed.

Radius (km)	Ocean area (km ²)	Strip area (km ²)	Relative survey effort	Royal Terns km ⁻²	Sandwich Terns km ⁻²
26-31	552	40	1.000	0.597	2.139
31-39	1400	37	0.365	0.457	0.027
39-48	1869	41	0.300	0.147	—
48-56	2367	39	0.228	—	—
56-65	2745	35	0.177	—	0.028
65-68	1234	26	0.284	—	—
68-74	2254	31	0.190	—	—
74-81	2151	17	0.109	—	—
81-87	2466	15	0.084	—	—
87-93	3425	13	0.053	—	—
93-98	2877	9	0.044	—	—
98-104	2488	9	0.048	—	—
104-109	2788	9	0.046	—	—
109-128	14227	43	0.041	—	—

observed per strip area, without compensating for flight speed and/or direction) were determined (Spear *et al.* 1992). Carolina Coastal Water and the Gulf Stream were located using temperature imagery from Advanced Very High Resolution Radiometer (AVHRR) to assess which water masses were used by Royal and Sandwich Terns. Shelf and Gulf Stream water masses are oceanographic ecotones distinguished in infrared imagery by a sharp change in surface temperature (Haney 1989).

Transect observations were conducted between predetermined sampling stations and when time allowed during plankton tows. Although transect lengths were nearly equal, the distances traveled in relation to the nearest colony (in the Cape Fear River) were not equal, due to cruise direction. Using the ArcView Geographical Information System, we determined the total oceanic surface area available to terns within the radius parameters of each transect. Because these radii were not the same between stations, arcs of varying widths were created around the colony. Apparent species densities were estimated in each arc by multiplying the strip area by the number of observations in those strips. Relative survey effort (area surveyed versus ocean area within the arc, relative to that of the closest transect) was calculated for all transects (Table 2).

Eggshell Analyses

Eggshells were analyzed for stable isotope ratios to determine if foraging differed between Royal and Sandwich Terns. These analyses were possible, as stable isotopes from food and water are deposited in eggshells, resulting in potentially recognizable signatures of substances consumed within a 3-5 d period (Hobson 1997). During late May and early June 1999 and 2000, ten Royal and Sandwich Tern eggshells (half to whole shells) were collected from each of three colonies: Cape Fear, Cape Lookout, and Oregon Inlet. Eggshells of the two tern species were

easily distinguished based on size (Sandwich Tern eggs = 51.5 × 37.5 mm, Royal Tern eggs = 63 × 44.5 mm; Bent 1921). All but five of the analyzed Royal Tern eggshells were from fresh eggs (collected for another study at the perimeter of the colonies to minimize disturbance). All Sandwich Tern eggshells were from hatched eggs. We compared ¹⁵N:¹⁴N ratios in membranes of hatched and unhatched eggs of Royal Terns to determine if a change occurred through the incubation period.

Prior to analysis, all eggshells were rinsed in deionized water, then the calcareous outer shells were separated from the inner membranes, and broken into fine pieces. All isotope analyses (¹³C, ¹⁸O and ¹⁵N) were completed at Mountain Mass Spectrometry, Evergreen, Colorado, following published methodology for calculating isotopic ratios (Schaffner and Swart 1991; Hobson *et al.* 1994). We interpreted these results with respect to the water masses surrounding the colonies during the periods of eggshell synthesis.

Diet Observations

We assessed the diet of Royal and Sandwich Tern chicks with 1,080 (540 per species) prey observations in 18 observation periods. We observed adult Royal and Sandwich Terns (June-August 2000) bring prey items to chicks at South Pelican Island (N = 13) during a variety of tidal phases. Limited observations were conducted at Sandbag Island (N = 1), New Dump Island (N = 2) and Island M (N = 2). Prey items were identified to order, family, or species. Due to the difficulty of identifying some of the smaller fish, we did not attempt to distinguish between taxa with similar gross morphologies (Pearson 1968). One group included drum (Sciaenidae), porgies (Sparidae) and mullet (*Mugil* sp.), and the other included herring (Clupeidae), jacks (Carangidae) and mackerel (Scombridae). We categorized prey length relative to bill length (<1, 1-1.5 and >1.5 bill

lengths) for both tern species, as used by Dunn (1971, 1973) and Veen (1977). Although the approximate mass of the Royal Tern is twice that of the Sandwich Tern, its bill is just 8% longer (Olsen and Larsson 1995). We did not correct for this difference in scale in comparing prey lengths. In addition, regurgitated fish were opportunistically identified at four colonies in 1999 and 2000. We did not statistically analyze regurgitations because the sample size was insufficient.

Fecal samples from Royal and Sandwich Terns were collected by placing 1 m fabric squares (organza) within the colonies where a single species was grouped. Fabric was left for 30-60 minutes, in which time adults returned and defecated. We recovered otoliths (and one squid beak) from feces by rinsing the fabric in water and sorting through the hard prey remains under a dissecting microscope. We identified otoliths by comparing them to a reference collection at the University of North Carolina at Wilmington.

Statistical Analyses

Data from fixed-point surveys, including foraging data and overall activities (foraging, directional flying and resting), were compared using Student's *t*-tests or Welch ANOVA (modified *t* test for unequal variances, JMP Start Statistics 3.3.1, SAS Institute, Inc.). Levene tests were used to determine if variances were equal. Chi-square tests were used to determine if the apparent species densities from strip-transects followed a diffusion gradient. Expected values for the χ^2 tests were cal-

culated by multiplying the apparent densities of all transects containing terns, by the relative increase in ocean surface area in concentric rings around the Cape Fear colony (Table 2). Isotope results were analyzed using Student's *t*-tests for inter-specific comparisons at each colony. Intra-specific isotopic differences between colonies were tested using ANOVA and Tukey-Kramer tests. Chick feedings (prey type and size) were compared using Welch ANOVA.

RESULTS

Point Surveys

At Carolina Beach, the Royal Tern occurred at a higher frequency in the Cape Fear River than in the ocean ($t_{18} = 3.53$, $P < 0.05$). The reverse was true of the Sandwich Tern, which was frequently observed in the ocean and rarely in the river (Welch ANOVA, $F_{1,9} = 7.50$, $P < 0.05$). Frequencies of actively foraging terns were not significantly different in the river and ocean (Royal, $t_{18} = 1.96$, n.s.; Sandwich, $t_{18} = 1.37$, n.s.; Fig. 2).

At Fort Fisher, the Royal Tern did not show a habitat preference between the marine coastal habitat and the shallow (<2 m)

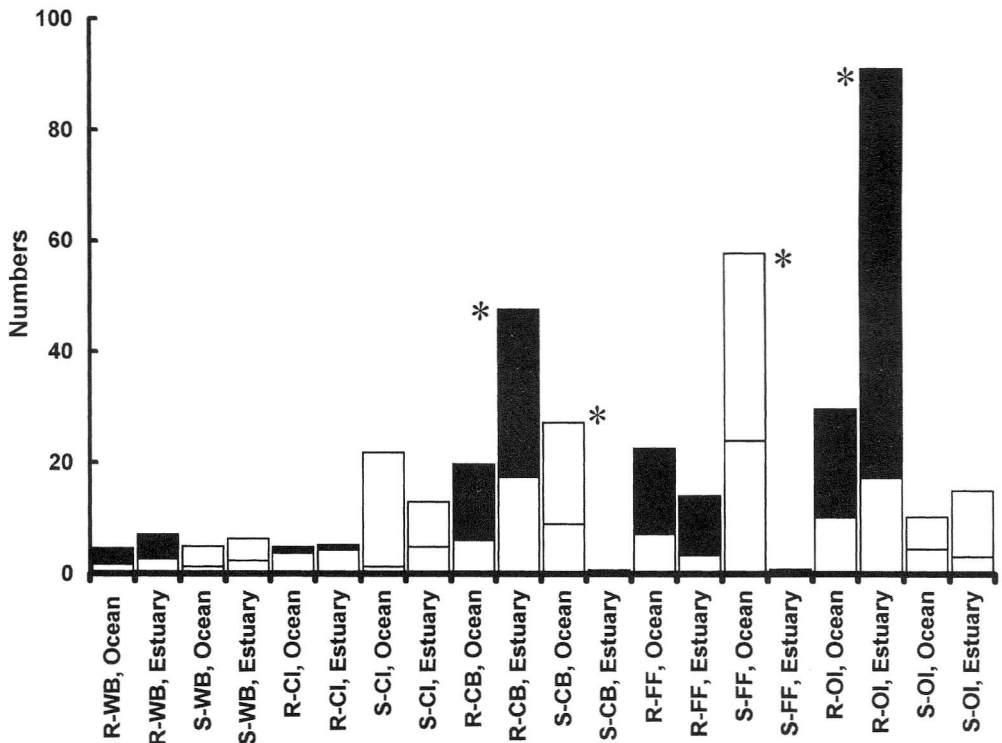


Figure 2. Mean numbers of Royal (R) and Sandwich (S) Terns observed at Wrightsville Beach (WB), Carolina Beach Inlet (CI), Carolina Beach (CB), Fort Fisher (FF) and Oak Island (OI) in the ocean and estuary in 1999 and 2000 (* $P < 0.05$, intraspecific comparison of oceanic and estuarine means). Lower portions of bars indicate mean numbers of actively foraging individuals at each site, upper portions (no fill for Royal Terns and black fill for Sandwich Terns) indicate mean numbers of terns in all activities (flying in a single direction, foraging and resting).

Cape Fear River estuary, east of the main channel (overall occurrence, Welch ANOVA, $F_{1,11} = 0.49$, n.s.; foraging, $t_{20} = 0.92$, n.s.). Again, the Sandwich Tern was observed in the ocean more than the estuary (Welch ANOVA, $F_{1,10} = 9.58$, $P < 0.05$). Sandwich Terns were never seen actively foraging at this river site. At Oak Island, more Royal Terns were observed in the Cape Fear River mouth than along the ocean beach (overall, Welch ANOVA, $F_{1,9} = 9.66$, $P < 0.05$; foraging, $t_{18} = 1.17$, n.s.), but Sandwich Terns showed no such distributional difference (overall, $t_{18} = 1.26$, n.s.; foraging, $t_{18} = 0.34$, n.s.; Fig. 2).

No differences were detected at Wrightsville Beach between inlet and ocean habitat use by Royal or Sandwich Terns (Royal overall, $t_{16} = 1.15$, n.s.; Royal foraging, $t_{16} = 0.75$, n.s.; Sandwich overall, $t_{16} = 0.15$, n.s.; Sandwich foraging, $t_{16} = 0.83$, n.s.). At Carolina Beach Inlet, neither species was seen more often in the ocean or the Intracoastal Waterway (Royal overall, Welch ANOVA, $F_{1,5} = 3.50$, n.s.; Royal foraging, $t_{10} = 0.25$, n.s.; Sandwich overall, $t_{10} = 0.33$, n.s.; Sandwich foraging, Welch ANOVA, $F_{1,6} = 2.59$, n.s.; Fig. 2).

Limited inshore and coastal surveys from small boats showed the same distribution patterns as point surveys; the frequency of Royal Tern observations was nine times greater in the estuary than in the marine coastal zone, and Sandwich Tern observations were twice as frequent in the marine coastal habitat than in the estuary. Only Royal Terns (664 total in five surveys, including the two dock counts from shore) were seen in the Cape Fear River north of the Intracoastal Waterway. Few Royal Terns were seen upriver from the State Port. Royal Terns were observed along the entire route of the Cedar Island-Ocracoke Ferry in the Pamlico Sound, while Sandwich Terns were only seen near the colonies.

Offshore Surveys

More Sandwich Terns than Royal Terns were observed on offshore transects during the May-July chick-rearing season. All observations of these species occurred within 55 km of the Cape Fear Colony, in Carolina Coastal Water. Both species were less numerous fur-

ther from shore, as would be expected as a result of scattering. In the first transect (26-31 km from the colony), the apparent density of the Sandwich Tern was 3.6 times higher than that of the Royal Tern. Two Sandwich and 23 Royal Terns were observed >31 km from the colony. In 135 pelagic observations of these species, two thirds were Sandwich Terns, yet this species was a third as numerous as Royal Terns at the Cape Fear River Colony (Table 1). Based on the scattering effect and compared to that of the first transect, survey effort was 3-6 times less in the second to seventh transects, 9-12 times less in the eighth and ninth transects, and 19-24 times less in the farthest five transects (Table 2).

Eggshell Analyses

Significantly higher $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ values occurred in the Sandwich compared to Royal Terns at the Cape Fear colony in 1999, indicating differences in foraging habitats ($\delta^{13}\text{C}$, $t_{18} = 2.76$, $P < 0.05$; $\delta^{15}\text{N}$, $t_{18} = 2.58$, $P < 0.05$; $\delta^{18}\text{O}$, $t_{18} = 3.73$, $P < 0.05$; Fig. 3). No other isotopic differences were detected between Royal and Sandwich Terns within the same colony in 1999. In 2000, the only significant inter-specific difference within a colony occurred with a higher mean $\delta^{13}\text{C}$ value in Sandwich Terns than in Royal Terns at Cape Lookout ($t_8 = 2.54$, $P < 0.05$). Four intra-spe-

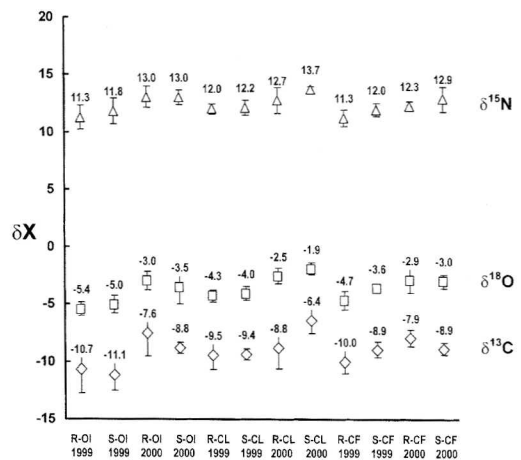


Figure 3. Mean isotope values ($\delta^{13}\text{C}$, diamonds; $\delta^{18}\text{O}$, squares; $\delta^{15}\text{N}$, triangles) from Royal (R) and Sandwich (S) Tern eggshells from Oregon Inlet (OI), Cape Lookout (CL) and Cape Fear (CF) in 1999 ($N = 10$) and 2000 ($N = 5$). Error bars indicate standard deviations.

cific, between-colony differences occurred in 1999, and one occurred in 2000 (Fig. 3).

In the Sandwich Tern, mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in 1999 were lower at Oregon Inlet than those of the other two colonies ($\delta^{13}\text{C}$, $F_{2,27} = 14.5$, $P < 0.05$; $\delta^{18}\text{O}$, $F_{2,27} = 14.6$, $P < 0.05$). In the same year, the mean $\delta^{18}\text{O}$ value in the Royal Tern at Oregon Inlet was lower than intra-specific values at the other colonies and the mean 1999 Royal Tern $\delta^{15}\text{N}$ values from Cape Fear and Oregon Inlet were lower than the mean intra-specific value for Cape Lookout ($\delta^{18}\text{O}$, $F_{2,27} = 8.38$, $P < 0.05$; $\delta^{15}\text{N}$, $F_{2,27} = 3.41$, $P < 0.05$). In 2000, the $\delta^{13}\text{C}$ value for the Cape Lookout Sandwich Tern was higher than those of Oregon Inlet and Cape Fear ($F_{2,12} = 16.5$, $P < 0.05$). Of the five hatched Royal Tern eggshells from Cape Fear in 1999, two analyzed that year had $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and $\delta^{15}\text{N}$ values that were the same as those from fresh eggs (standard deviations decreased slightly when these samples were included). Three 1999 $\delta^{15}\text{N}$ samples from hatched eggs tested in 2000, were 1‰ higher than the mean of fresh eggs tested in 1999. Most $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values increased by 2-3‰ between 1999 and 2000, while all mean $\delta^{15}\text{N}$ values were 1-2‰ higher in 2000.

Diet Observations

The diet of Royal Terns and Sandwich Terns differed significantly (Fig. 4). Of the top three prey types fed to chicks during the same time periods and with the same number of observations, the diet of the Royal Terns consisted of 9% anchovies, 30% herring, jacks and mackerel, and 41% drum, porgies and mullet. The Sandwich Tern fed its chicks 48% anchovies, 39% herring, jacks and mackerel, and 9% drum, porgies and mullet. In addition, 19% of the items brought to Royal Tern chicks consisted of less common prey items. Only 4% of the Sandwich Tern chick diet consisted of these less common prey items.

Chick provisioning by Royal Terns was more diverse than that of Sandwich Terns (Shannon-Wiener Index, Royal, $e^H = 4.9$; Sandwich, $e^H = 3.1$). More than half of the food provided to the chicks of both species measured 1-1.5 times the bill length; 58%

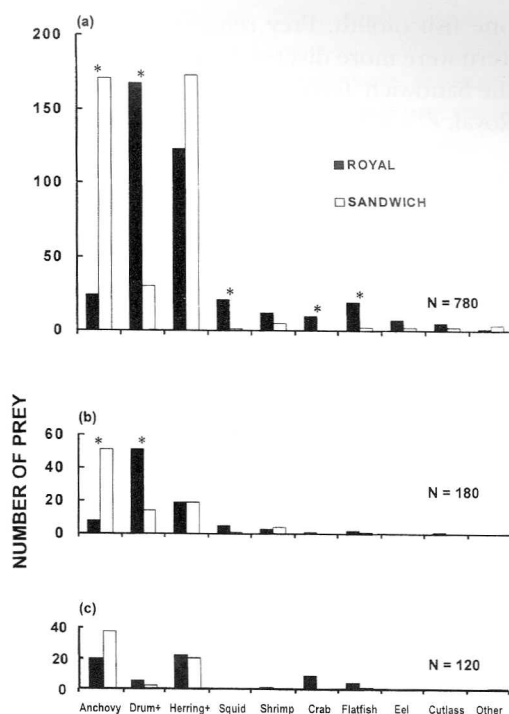


Figure 4. Number of prey items provided to Royal and Sandwich Tern chicks in 2000 at (a) South Pelican Island (13 observation periods), (b) Sand Bag and New Dump Islands (3 observation periods) and (c) Island M (2 observation periods). "Drum+" = drum/porgy/mullet, "herring+" = herring/jack/mackerel, flatfish = Pleuronectiformes and cutlass = Atlantic Cutlassfish (*Trichiurus lepturus*). Royal and Sandwich Tern observations were conducted simultaneously, until 30 prey items each were counted (* $P < 0.05$).

measured 5.2-9.5 cm in the Royal Tern and 73% were this length in the Sandwich Tern. The Royal Tern provided a significantly higher proportion of fish >9.5 cm (>1.5 bill length) than did the Sandwich Tern ($t_{32} = 3.86$, $P < 0.05$).

As with chick feedings, fecal analyses and regurgitations indicated that Sandwich Terns had a higher percentage of anchovies in their diet than did Royal Terns. In the Royal Tern, 22 of 47 otoliths were from Bay (*A. mitchilli*) or Striped (*A. hepsetus*) Anchovies, whereas 230 of 291 otoliths in Sandwich Tern feces were from these species. A disproportionately small number of otoliths from other species were recovered, compared to those observed during chick provisioning. One squid beak was recovered from a Royal Tern sample. All Sandwich Tern fecal samples and 69% of Royal Tern samples contained at least

one fish otolith. Prey remains of the Royal Tern were more diverse than prey remains of the Sandwich Tern (Shannon-Wiener Index, Royal, $e^H = 4.2$; Sandwich, $e^H = 2.3$).

DISCUSSION

Our data from point surveys demonstrated that niche partitioning existed between Royal and Sandwich Terns. In the Cape Fear area, Royal Terns primarily foraged in the river, while Sandwich Terns foraged in the marine coastal environment. The habitat of Royal Terns in the Cape Fear River extended past the river mouth, into the brackish plume at the north end of Long Bay. Ocean inlets, at the interface between riverine and oceanic habitats, were shared by both species. Although we did not detect significant differences in habitat use by terns actively diving for fish, proportions of diving to non-diving terns were similar in each habitat and species presence differed significantly between habitats. We assumed that the majority of the terns observed away from the colony, although not necessarily actively diving, were in or near their foraging habitat.

The pattern of a short-range foraging in Sandwich Terns and long-range foraging in Royal Terns was consistent with Lee's (1995) offshore observations in North Carolina. The Sandwich Tern we observed 55 km from the Cape Fear colony (50 km offshore) may have been an anomaly. Whereas Lee (1995) observed Royal Terns carrying fish to colonies from *Sargassum* patches near the Gulf Stream, 50 km from Oregon Inlet, large patches of this seaweed usually occurred 80-100 km offshore of the Cape Fear colony, where we did not see either tern species. For terns in the Cape Fear area, we speculate that *Sargassum* patches were too far offshore for profitable foraging. Due to the diffusion of terns at an increasing radius from the Cape Fear colony, our offshore survey efforts were insufficient to conclude that these species did not forage in *Sargassum*, however, it was evident that both species primarily fed close to shore.

The preliminary results from isotopic analyses suggest that foraging differences early in the breeding season can produce

recognizable isotopic signals in the eggshells of Royal and Sandwich Terns. Schaffner and Swart (1991) demonstrated that eggshells of ocean foraging birds have higher $\delta^{18}\text{O}$ values than those of estuarine foragers, as the lighter ^{16}O isotope selectively evaporates in the hydrologic cycle. In addition, proportionately less ^{18}O vaporizes at lower temperatures (Kakiuchi and Matsuo 1979), therefore rain from higher latitudes contains relatively less ^{18}O (Yurtserver and Gat 1981). Oxygen does not fractionate in the food chain, but $\delta^{18}\text{O}$ values in eggshells are 2.3‰ (converted from SMOW to PDB notation), relative to ingested water (Schaffner and Swart 1991).

Since estuarine vs. oceanic salinity was most divergent in the Cape Fear area and salinity within the Cape Fear River itself was highly variable, this colony would be predicted to have the greatest divergence in $\delta^{18}\text{O}$ values between tern species. The 1999 results followed these predictions—ocean foraging Sandwich Terns had significantly higher $\delta^{18}\text{O}$ values in the Cape Fear Colony than did Royal Terns, and Royal Terns at this colony had a wide range of $\delta^{18}\text{O}$ values. Although the interspecific means were slightly higher in Sandwich Terns at the Cape Lookout and Oregon Inlet colonies, the differences were not significant. Similar values at these colonies may be explained by one or two of the following possibilities: a) no niche segregation occurred at these sites early in the breeding season, b) niche segregation occurred, but was masked by similar salinities in the ocean and estuary, and/or c), the sample size was insufficient to detect real differences. It would be interesting to determine when segregation occurs, by increasing the sample size and separately analyzing early and late-season eggs.

Intra-specific isotopic comparisons between colonies in 1999 indicated that distinct estuary (Royal Tern) and ocean (Sandwich Tern) signatures could become apparent with additional samples, as $\delta^{18}\text{O}$ values followed the salinity gradient in 1999 for both habitat types (Fig. 3). The higher $\delta^{18}\text{O}$ values in 2000 cannot be explained without background isotopes, and ambiguous results may be due, in part, to the small sample size (half that of 1999).

The $\delta^{15}\text{N}$ values reflect trophic positions in the same food chain (Hobson *et al.* 1994) and are highly affected by organic and inorganic factors in source water (Paerl and Fogel 1994). The $\delta^{13}\text{C}$ values are affected by organic compounds in water, trophic position and pelagic vs. benthic food chains (Hobson *et al.* 1994). Without background values from different water masses and prey species, interpretations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in eggshells would be speculative, other than to say that significant differences probably reflect foraging differences. As with $\delta^{18}\text{O}$, the causes of higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and few significant inter- and intra-specific differences in 2000 are not known.

Observations of chick provisioning measured diet differences between Royal and Sandwich Terns in the Cape Fear and Cape Lookout regions, and seemed to cause minimal disturbance to the colonies, as adults actively fed chicks in our presence. The same diet trends were observed at Oregon inlet, where non-significant differences probably resulted from the small sample size there. Although chick provisioning observations yielded the most data on diet, only anchovies seemed to be well represented in fecal samples. Larger otoliths may be regurgitated in pellets. Jobling and Breiby (1986) noted that otoliths from certain species quickly dissolve. This may account for the low number of herring and jack otoliths, which are approximately the same size as those of Striped Anchovies, but more fragile.

Royal and Sandwich Terns may be suitable indicators of biological or environmental factors, such as fish stocks and water pollution, for those water masses they most inhabit. Annual diet observations, for instance, could be used to detect changes in fish abundance that occur near the surface in the estuary and in the marine coastal environment. Because of their high trophic positions, these species also are subject to bioaccumulants. For example, the Sandwich Tern was nearly extirpated from The Netherlands in the 1960s when organochlorine residues from pesticides caused eggshell thinning (Koeman *et al.* 1967). Less apparent effects of pollution, such as weakening of the immune system, may be difficult to quantify when these effects act synergistically with other

diseases (McLandress 1983). One disadvantage of using Royal and Sandwich Terns as bio-indicators is that their numbers fluctuate widely due to unknown causes, and unnatural declines may not be immediately apparent.

Our results support the hypothesis that Royal and Sandwich Terns partition food resources by foraging locations or choice of prey. Knowledge of foraging habitats is critical to management of these species. Although not presently at risk, Royal and Sandwich Tern numbers in North Carolina have fluctuated greatly in the past decade. It is not known if these fluctuations are related to inter-specific competition, either at or away from the colony. Resource partitioning, however, may be a mechanism that reduces competition in these species, where prey is limiting.

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