Wilson Bull., 115(4), 2003, pp. 448–454

SEASONAL AND ANNUAL VARIATION IN THE DIET OF BREEDING, KNOWN-AGE ROYAL TERNS IN NORTH CAROLINA

ELLEN J. WAMBACH[1,2] AND STEVEN D. EMSLIE[1,3]

ABSTRACT.—We investigated banded, known-age Royal Terns (*Sterna maxima*) in North Carolina during 1999 and 2000 to determine seasonal variation in their diet and any age-related correlations in foraging. Systematic observations of adults returning with food indicated that at least 18 families of fish, squid, and crustaceans were exploited. The most common forage species in both years were anchovies (Engraulidae), herring (Clupeidae), and drum (Sciaenidae). In 1999 we also monitored a sample of 48 color-banded, known-age breeding birds ranging in age from 6–17 years to assess variations in diet with age. We detected no age-related differences in Royal Tern prey size or selection; however, our sample was relatively small and further research is warranted. *Received 12 May 2003, accepted 5 October 2003.*

Royal Terns (*Sterna maxima*) have been increasing along the Atlantic coast of the eastern United States since protected, dredge material islands with suitable nesting habitat were created in the 1960s (Parnell et al. 1997). The population size of nesting adults in North Carolina has fluctuated over the last few decades, ranging from as low as 9,755 nests during 1977 to as high as 17,029 nests during 1983 (Parnell et al. 1997). During the 1960s an extensive banding effort of Royal Tern fledglings was initiated along the Atlantic coast (Van Velzen and Benedict 1972) and has been continued by J. Weske annually to the present at colonies in Maryland, Virginia, and North Carolina. These efforts have resulted in the world's only known-age population of breeding Royal Terns. However, until now, studies of age-related variables in correlation with life history strategy, diet, and foraging ecology of Royal Terns have been limited to Buckley and Buckley's (1974) comparison of juveniles to adults.

Most seabirds are long lived and have adaptations to maximize reproductive success and survivorship in a variable marine environment (Furness and Monaghan 1987, Ricklefs 1990, Hamer et al. 2001). Royal Terns display reproductive traits that warrant investigation of age-related differences in foraging ecology, such as reduced clutch size, extended parental care, delayed sexual maturity, and long life span (Buckley and Buckley 1972). Most monogamous pairs lay one-egg clutches, although some occasionally lay two-egg clutches (Dunn 1972; Buckley and Buckley 1972, 2002). Moreover, adults have been observed feeding their young up to six months after hatching (Buckley and Buckley 1974, Erwin 1977), a behavior that likely evolved as a response to difficulty in locating and capturing prey and the time necessary for young birds to become proficient at foraging (Ashmole and Tovar 1968, Hamer et al. 2001).

Here, we investigated the diet of known-age Royal Terns in the Lower Cape Fear River, North Carolina, during two breeding seasons. Our primary objectives were to document for the first time in this species any seasonal variations in colony diet and prey size. In addition, we used systematic observations of marked, known-age adults to address the possible correlation of age with foraging behavior. We based this portion of our study on the premise that Royal Tern reproductive success improves with age, and that age correlates with previous breeding experience and increased foraging efficiency, as has been shown in other larids (Coulson and Horobin 1976, Ryder 1981, Pugesek and Diem 1983, Nisbet et al. 1984, Pyle et al. 1991, Sydeman et al. 1991, Galbraith et al. 1999). As such, older Royal Tern parents should return with higher quality prey for their chicks compared to younger birds.

METHODS

Study area.—We studied two colonies of Royal Terns on Ferry Slip (34° 02′ N, 77° 56′

[1] Univ. of North Carolina, Dept. of Biological Sciences, Wilmington, NC 28403, USA.

[2] Current address: 8783 Treasure Ave., Walkersville, MD 21793, USA.

[3] Corresponding author;
e-mail: emsliest@yahoo.com

W) and South Pelican (33° 56′ N, 77° 58′ W) islands in the Lower Cape Fear River from mid-May to early August, 1999 and 2000. Both islands were formed from dredge material and are managed by the National Audubon Society. In 1999, Ferry Slip was moderately vegetated with grasses, forbs, and shrubs. A mixed Royal and Sandwich tern (*Sterna sandvicensis* Latham) colony on Ferry Slip was comprised of approximately 1,600 nests (132 were Sandwich Tern) in three subunits. This colony was substantially reduced in 2000 (to <200 nests), possibly by plant succession in the nesting habitat (EJW and SDE pers. obs). Most Royal and Sandwich terns in the Lower Cape Fear region nested on South Pelican during 2000, where a colony of >4,300 nests (1,365 were Sandwich Tern) formed in a large contiguous area of bare sand. Five adults color banded on Ferry Slip in 1999 were found nesting on South Pelican in 2000 indicating that at least some individuals from the former colony moved to South Pelican.

Diet observations.—We assessed Royal Tern diet during 15-min observation periods from a stationary point within 20 m of the crèche from 05:00–19:00 EST using 8 × 42 binoculars. All observations were conducted by EJW each year during chick rearing from late May or early June, when most chicks were hatching, until mid- to late July, when most chicks begin flying. Prey carried in the bill of adults flying directly above a portion of the colony were identified in most cases by visible characters; otherwise, they were categorized as unidentified finfish or unknown. Prey size was estimated relative to tern bill length (mean = 63.9 mm ± 2.4 SD, $n = 46$). Size was divided into five categories: <0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, and >2 × bill length (BL).

We conducted observations so that four tidal stages (ebb, low, flood, and high) were evenly represented in time spent observing prey. We also divided the season into 4–5 biweekly periods that corresponded to the full and new moon, so that spring tides were in the middle of each time period. We did not compare prey between years due to better prey identification ability during the second year.

Known-age adult observations.—In 1999, we captured 48 known-age birds, ranging from 6–17 years old, in a mist net placed at the edge of the colony and added a plastic color band combination corresponding to age (right leg) and individual (left leg) and marked their breast feathers with saturated (1.2%) picric acid to facilitate field observations; weight was recorded with a Pesola scale to the nearest 1.0 g. This procedure was not repeated in 2000 to limit disturbance to the colony.

We observed the colony for marked birds during both morning and afternoon at all tidal stages. When a marked bird carrying prey was seen, time of day, age class, and prey type and size were noted. Number and age of chicks could not be determined for this part of the study because we did not locate the nest of each marked bird. Because of small sample sizes for birds of different ages, the data were combined into three age classes: young (6–8 years old), middle-aged (9–11 years), and old (12–17 years) because most birds in this species do not begin breeding until age 5–6 (Buckley and Buckley 2002). Thus, the young age class would include birds with only 1–3 years of breeding experience.

Statistical analyses.—We analyzed all diet data, except for known-age diet results, with ANOVA when assumptions of normality of residuals and homogeneous variance were met. When assumptions of ANOVA were not achieved, we used Kruskal-Wallis (when df ≥ 2) or Wilcoxon (when df = 1) tests reported as χ^2 values. We used pairwise correlations to test for association between season and diet. We used Fisher's exact test to compare categories of prey composition and prey size among age classes in 1999 (Sokal and Rohlf 1969). All statistical analyses were completed with the JMP IN software program (Sall and Lehman 1996).

RESULTS

We observed a total of 2,310 and 4,148 prey items during 14.25 and 20.00 h of observations during 1999 and 2000, respectively (Table 1). In both years, the majority of identified prey remains were anchovy, herring, and drum. In 1999, fewer prey were observed than in 2000. The percentage of unidentified finfish to total prey observed was 46% in 1999 and 18% in 2000. Prey type fluctuated seasonally (Fig. 1; see statistical tests below for each major prey group), but the most common prey

TABLE 1. Taxa of Royal Tern prey observed at two colonies in the Lower Cape Fear River, North Carolina in 1999 and 2000 showing the diversity in prey consumed by this species. Numbers of observations are given for each prey item with percent of total prey in parentheses.

Prey	1999	2000
Engraulidae (anchovies)		
Anchoa hesetus, *A. mitchilli*	290 (12.6)	495 (11.9)
Clupeidae (herrings)		
Brevoortia tyrannus, *Alosa* spp.	265 (11.5)	843 (20.3)
Sciaenidae (drums)		
Micropogonias undulatus, *Leiostomus xanthurus*, *Stellifer lanceolatus*, *Bairdiella chrysoura*, *Cynoscion* spp., *Sciaenops ocellatus*	296 (12.8)	1,025 (24.7)
Mugilidae (mullets)		
Mugil cephalus	182 (7.9)	31 (0.8)
Pleuronectiformes (unidentified)	2 (0.1)	72 (1.7)
Cynoglossidae (tonguefishes)		
Symphurus spp.	38 (1.7)	171 (4.1)
Sparidae (porgies)		
Lagodon rhomboides, *Archosargus probatocephalus*	32 (1.4)	36 (0.9)
Carangidae (jacks)		
Caranx spp., *Seriola* spp.	9 (0.4)	94 (2.3)
Gadidae (hakes)		
Urophycis spp.	6 (0.3)	6 (0.1)
Trichiuridae (cutlassfish)		
Trichiurus lepturus	2 (0.1)	24 (0.6)
Triglidae (searobins)		
Prionotus spp.	2 (0.1)	7 (0.2)
Synodontidae (lizardfish)	1 (0.04)	8 (0.2)
Stromateidae (butterfish)		
Peprilus triacanthus	—	11 (0.3)
Haemulidae (grunts)	—	3 (0.1)
Pomatomidae (bluefish)		
Pomatomus saltatrix	—	17 (0.4)
Syngnathidae (pipefishes)	3 (0.1)	7 (0.2)
Ophichthidae (eels)	8 (0.4)	21 (0.5)
Loliginidae (squids)	32 (1.2)	109 (2.6)
Penaeidae (shrimps)		
Penaeus spp.	58 (2.5)	256 (6.2)
Brachyura (crabs)	14 (0.6)	85 (2.1)
Unidentified finfish	1,064 (46.1)	759 (18.3)
Unknown	6 (0.3)	68 (1.6)

proportions did not vary with tidal stage during both years (Kruskal-Wallis test, $\chi^2 = 0.64$, df = 3, $P = 0.28$).

Proportion of anchovies fed to chicks decreased across time periods during both years (1999: $\chi^2 = 27.6$, df = 3, $P < 0.0001$; 2000: $\chi^2 = 56.0$, df = 4, $P < 0.0001$) and was inversely correlated with date in both 1999 ($r_{57} = -0.59$, $P < 0.0001$) and 2000 ($r_{80} = -0.74$, $P < 0.0001$). Drum varied among time periods in both years (1999: $\chi^2 = 14.0$, df = 3, $P < 0.003$; 2000: $\chi^2 = 22.1$, df = 4, $P < 0.0002$) and were observed more per trial toward the end of the 1999 season ($r_{57} = 0.41$, $P < 0.002$). In 2000 there was no significant correlation between drum and date ($r_{80} = 0.18$, $P = 0.10$). Herring decreased by time period (1999: $\chi^2 = 9.8$, df = 3, $P = 0.021$; 2000: $F_{3,79} = 2.4$, $P = 0.059$) and date in 1999 only ($r_{57} = -0.37$, $P = 0.005$). Number of shrimp (Penaeidae) identified per trial was positively correlated with date in 1999 ($r_{57} = 0.30$, $P = 0.022$) and 2000 ($r_{80} = 0.22$, $P = 0.048$) and increased among time periods during both years (1999: $\chi^2 = 7.7$, df = 3, $P = 0.049$; 2000: $\chi^2 = 25.6$, df = 4, $P < 0.0001$). During 1999 mullet did not vary significantly among time periods ($\chi^2 = 6.3$, df = 3, $P = 0.10$). During 2000, Tonguefish (Cynoglossidae) abundance in the observed prey was not

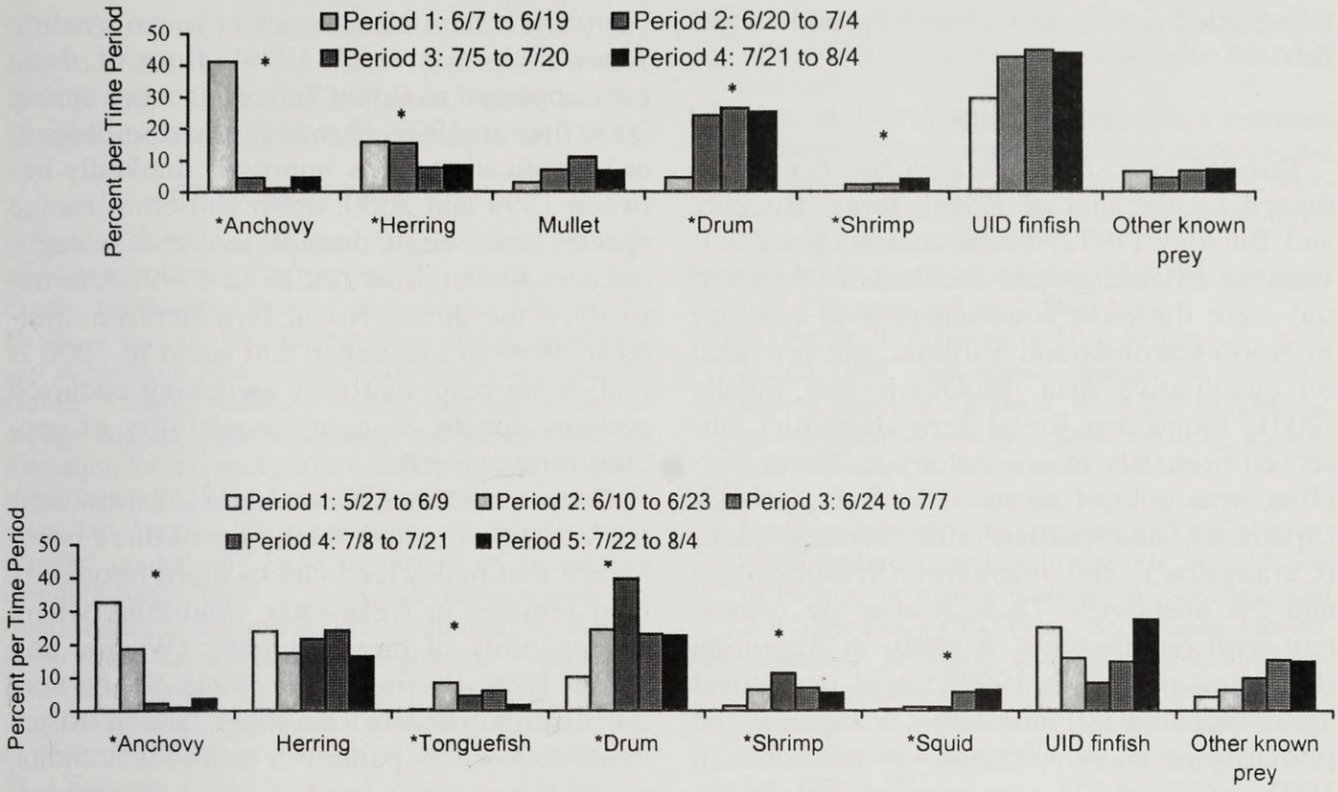

FIG. 1. Weekly variation in the proportion of major prey items of Royal Terns identified during 15-min periods. (Top) 1999: n = 2,310. (Bottom) 2000: n = 4,148. Asterisk indicates significant difference among periods.

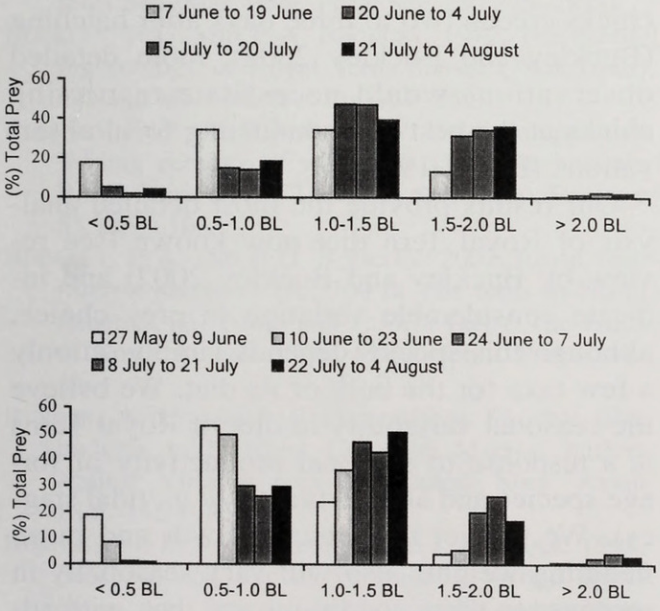

FIG. 2. Percentage of prey brought to Royal Tern chicks by size categories estimated relative to adult bill length (BL). Prey size increased significantly among time periods throughout the breeding season; (top) 1999: Pearson χ^2 = 169.81, df = 12, $P < 0.0001$ and (bottom) 2000: χ^2 = 896.81, df = 16, $P < 0.0001$.

significantly correlated to date (r_{80} = 0.04, P = 0.71), but among time periods proportion of tonguefish varied considerably (χ^2 = 23.2, df = 4, $P < 0.0001$). Squid (Loliginidae) were observed in 2000, but mostly at the end of the season (by periods: χ^2 = 42.6, df = 4, $P <$ 0.0001; by date: r_{80} = 0.60, $P < 0.0001$).

The size of prey increased seasonally during both 1999 and 2000 (Fig. 2). For 1999, during periods two through four, prey sizes from 1–2 BL were most prevalent (65–75% of all prey). In 2000, during periods one and two, prey items were mostly 0.5–1.0 BL (53% and 49%, respectively). Most prey observed during 2000 were between 0.5–1.5 BL (69–86%).

In 1999, the 48 marked, known-age birds included 11 in the young, 13 in the middle, and 24 in the old age classes. These birds were observed feeding chicks for a total of approximately 54 h. Prey size (Fisher's exact test, n = 127, P = 0.32) and type (Fisher's exact test, n = 126, P = 0.092) did not differ significantly among adult age classes with an analysis of eight prey categories (anchovy, herring, drum, crab, shrimp, mullet, other

thin-bodied finfish, and other deep-bodied finfish).

DISCUSSION

Prior to now, little research has been conducted on the diet of Royal Terns. Buckley and Buckley (1972) found that anchovy, silversides (Menidia) and menhaden (Brevoortia) were the most common prey at colonies in North Carolina and Virginia, but provided no quantitative data. McGinnis and Emslie (2001) found that Royal Tern chick diet, observed primarily at one colony in North Carolina, was comprised of 41% drum, porgies (Sparidae), and mullet; 30% herring, jacks (Carangidae), and mackerel (Scombridae); and 9% anchovies. These results are consistent with our findings. A study in Argentina (Quintana and Yorio 1997) found that Royal Terns breeding at Punta León, Patagonia, fed primarily on anchovy (*Engraulis anchoita*) in 1992 (>60% of 523 prey items observed), but switched to Fueguian sprat (*Sprattus fueguensis*, >30%) in 1993.

We found Royal Tern prey type to vary seasonally, as in other tern species during breeding (Safina and Burger 1989, Safina et al. 1990, Shealer 1998). The decline in anchovies after the first two weeks after hatching in both years suggests that parents either were choosing to feed their hatchlings a small, thin-bodied prey item, or anchovy availability near the lower estuary was greater early in the season and then declined by late June. Common anchovies of the Lower Cape Fear River estuary and coastal waters include striped (*Anchoa hepsetus*) and bay anchovy (*A. mitchilli*). These species occur year round in this estuary and spawn mostly at night offshore during late spring and summer (Zastrow et al. 1991, MacGregor and Houde 1996). Anchovy oceanic spawning coincides with tern nesting, and anchovy availability in the marine habitat may contribute to the onset of Royal Tern courtship along the Atlantic coast.

Later in the season, terns rely on a greater variety of larger-sized prey as their chicks increase in size. A trend repeated in both years was an increase in the proportion of drum and shrimp in mid- to late June. This trend coincides with the growth and movement of juvenile drum (e.g., *Leiostomus xanthurus* and *Micropogonius undulatus*) and brown shrimp (*Penaeus aztecus*) from upriver to more saline water (Schwartz et al. 1979). Both of these prey appeared in Royal Tern diets more during 2000 than in 1999. However, because observer identification skills improved markedly between 1999 and 2000, drum and other forage species may be underrepresented if categorized as unidentified finfish in 1999. Alternatively, if the shift in Royal Tern diet from mullet in 1999 to tonguefish and squid in 2000 is real, it suggests that prey switching occurred perhaps due to changing availability of specific forage species.

Common Terns (*Sterna hirundo*) show sexual variation in chick feeding, and there is evidence that males feed chicks more frequently than females in freshwater conditions where predictability of prey is greater (Wagner and Safina 1989, Burness et al. 1994). Sexes were not distinguished in our study, and if Royal Terns follow this pattern in estuarine habitats, then adult sex may explain some of the variation in our results.

Observations of marked, known-age birds failed to indicate any variation in prey size or type among three age classes. This result may be due to the relatively small sample size and number of observations we completed in 1999, as well as the large proportion of unidentified finfish that year; additional investigations are warranted. Because Royal Tern chicks crèche two to three days after hatching (Buckley and Buckley 2002), more detailed observations would necessitate restricting chicks at the nest and conducting focal observations (Erwin 1977).

Our results provide the most detailed analysis of Royal Tern diet now known (see review by Buckley and Buckley 2002) and indicate considerable variation in prey choice, although this species depends largely on only a few taxa for the bulk of its diet. We believe the seasonal variability in diet of Royal Terns is a response to seasonal productivity of forage species and abiotic factors (e.g., tidal stages). We predict that chick growth and mean fledgling weights also will vary seasonally in response to these conditions and that, with additional data, Royal Terns could be used as an indicator for relative abundance of fish stocks of preferred prey, as has been demonstrated for the Arctic Tern (*Sterna paradisaea*; Monaghan et al. 1989a, 1989b), Northern Gannet

(*Sula bassanus*; Montevecchi et al. 1988), Atlantic Puffin (*Fratercula arctica*; Barrett 2002) and Common Guillemot (*Uria aalge*; Burger and Piatt 1990, Monaghan et al. 1994).

ACKNOWLEDGMENTS

This research was funded by grants to S. Emslie from NASA (NAG5-7629), NC Sea Grant, and the Center for Marine Science Research at UNCW. C. Hackney and D. Webster provided useful comments and suggestions on an earlier version of this paper. W. Golder, National Audubon Society, provided access to dredge islands, valuable advice, and background information for this study. The indefatigable chick-banding efforts of J. Weske and M. Browne in North Carolina and Virginia for more than two decades have resulted in the only large population of known-age breeding Royal Terns in the world. Without these efforts, studies of age-related effects on foraging behavior in Royal Terns would not be possible. Field assistance was provided by M. Tzeng, T. McGinnis, J. Minton, T. Maness, J. Eggleston, L. Harman, G. Siedinski, N. Norcross, A. Shipp-Penock, K. Nayda, S. Johnson, M. Chapman, J. McDaniel, D. Wade, C. Collura, T. Thompson, A. Bennet, and M. Polito. D. Frierson provided statistical advice.

LITERATURE CITED

Ashmole, N. P. and H. Tovar. 1968. Prolonged parental care in Royal Terns and other birds. Auk 85:90–100.

Barrett, R. T. 2002. Atlantic Puffin *Fratercula arctica* and Common Guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. Mar. Ecol. Prog. Ser. 230:275–287.

Buckley, F. G. and P. A. Buckley. 1972. The breeding ecology of Royal Terns *Sterna* (*Thalasseus*) *maxima maxima*. Ibis 114:344–359.

Buckley, F. G. and P. A. Buckley. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns (Aves: Lareidae, Sterninae). Ecology 55:1053–1063.

Buckley, P. A. and F. G. Buckley. 2002. Royal Tern (*Sterna maxima*). No. 700 *in* The birds of North America (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

Burger, A. E. and J. F. Piatt. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. Stud. Avian Biol. 14:71–83.

Burness, G. P., R. D. Morris, and J. P. Bruce. 1994. Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male Common Terns (*Sterna hirundo*). Can. J. Zool. 72:1243–1251.

Coulson, J. C. and J. Horobin. 1976. The influence of age on the breeding biology and survival of the Arctic Tern *Sterna paradisaea*. J. Zool. (Lond.) 178:247–260.

Dunn, E. K. 1972. Effect of age on the fishing ability of Sandwich Terns *Sterna sandvicensis*. Ibis 114: 360–366.

Erwin, R. M. 1977. Foraging and breeding adaptations to different food regimes in three seabirds: the Common Tern, *Sterna hirundo*, Royal Tern, *Sterna maxima*, and Black Skimmer, *Rynchops niger*. Ecology 58:389–397.

Furness, R. W. and P. Monaghan. 1987. Seabird ecology. Chapman and Hall, New York.

Galbraith, H., J. J. Hatch, I. C. T. Nisbet, and T. H. Kunz. 1999. Age-related changes in efficiency among breeding Common Terns *Sterna hirundo*: measurement of energy expenditure using doubly-labelled water. J. Avian Biol. 30:85–96.

Hamer, K. C., E. A. Schreiber, and J. Burger. 2001. Breeding biology, life histories, and life history-environment interactions in seabirds. Pp. 217–261 *in* Biology of marine birds (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.

MacGregor, J. M. and E. D. Houde. 1996. Onshore-offshore pattern and variability in distribution and abundance of bay anchovy *Anchoa mitchilli* eggs and larvae in Chesapeake bay. Mar. Ecol. Prog. Ser. 138:15–25.

McGinnis, T. W. and S. D. Emslie. 2001. The foraging ecology of Royal and Sandwich terns in North Carolina, USA. Waterbirds 24:361–370.

Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine, and J. Blackwood. 1989a. The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. J. Anim. Ecol. 58:261–274.

Monaghan, P., J. D. Uttley, and J. D. Okill. 1989b. Terns and sandeels: seabirds as indicators of changes in marine fish populations. J. Fisheries Biol. 35SA:339–340.

Monaghan, P., P. Walton, S. Wanless, J. D. Uttley, and M. D. Burns. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. Ibis 136:214–222.

Montevecchi, W. A., V. L. Birt, and D. K. Cairns. 1988. Dietary changes in seabirds associated with local fisheries failures. Biol. Oceanog. 5:153–161.

Nisbet, I. C. T., J. M. Winchell, and A. E. Heise. 1984. Influence of age on the breeding biology of Common Terns. Col. Waterbirds 7:117–126.

Parnell, J. F., W. W. Golder, M. A. Shields, T. L. Quay, and T. M. Henson. 1997. Changes in nesting populations of colonial waterbirds in coastal North Carolina 1900–1995. Col. Waterbirds 20: 458–469.

Pugesek, B. H. and K. L. Diem. 1983. A multivariate study of the relationship of parental age to reproductive success in California Gulls. Ecology 64: 829–839.

Pyle, P., L. B. Spear, W. J. Sydeman, and D. G. Ainley. 1991. The effects of experience and age on the breeding performance of Western Gulls. Auk 108:25–33.

QUINTANA, F. AND P. YORIO. 1997. Breeding biology of Royal and Cayenne terns at a mixed-species colony in Patagonia. Wilson Bull. 109:650–662.

RICKLEFS, R. E. 1990. Seabird life histories and the marine environment: some speculations. Col. Waterbirds 13:1–6.

RYDER, J. P. 1981. The influence of age on the breeding biology of colonial nesting seabirds. Pp. 153–164 *in* Behavior of marine animals, vol. 4, marine birds (J. Burger, B. L. Olla, and H. E. Winn, Eds.). Plenum, New York.

SAFINA, C. AND J. BURGER. 1989. Inter-annual variation in prey availability for Common Terns at different stages in their reproductive cycle. Col. Waterbirds 12:37–42.

SAFINA, C., R. H. WAGNER, D. A. WITTING, AND K. J. SMITH. 1990. Prey delivered to Roseate and Common tern chicks: composition and temporal variability. J. Field Ornithol. 61:331–338.

SALL, J. AND A. LEHMAN. 1996. JMP Start Statistics. SAS Institute, Inc., Belmont, California.

SCHWARTZ, F. J., P. PERSCHBACHER, M. MCADAMS, L. DAVISON, C. SIMPSON, K. SANDOY, J. DUNCAN, J. TATE, AND D. MASON. 1979. An ecological study of fishes and invertebrate macrofauna utilizing the Cape Fear River estuary, Carolina Beach inlet, and adjacent Atlantic Ocean. Inst. Mar. Sci. Spec. Publ. No. 14, Morehead City, North Carolina.

SHEALER, D. A. 1998. Differences in diet and chick provisioning between adult Roseate and Sandwich terns in Puerto Rico. Condor 100:131–140.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry, 1st ed. W. H. Freeman, San Francisco, California.

SYDEMAN, W. J., J. F. PENNIMAN, T. M. PENNIMAN, P. PYLE, AND D. G. AINLEY. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. J. Anim. Ecol. 60:135–149.

VAN VELZEN, W. T. AND R. D. BENEDICT. 1972. Recoveries of Royal Terns banded in Virginia, part I: the Caribbean. Raven 43:39–41.

WAGNER, R. H. AND C. SAFINA. 1989. Relative contribution of the sexes to chick feeding in Roseate and Common terns. Wilson Bull. 101:497–500.

ZASTROW, C. E., E. D. HOUDE, AND L. G. MORIN. 1991. Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy *Anchoa mitchilli* in mid-Chesapeake Bay. Mar. Ecol. Prog. Ser. 73:161–171.