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Diet Composition of Royal Tern (*Thalasseus maximus*) and Sandwich Tern (*Thalasseus sandvicensis*) at Isles Dernieres Barrier Island Refuge, Louisiana, USA

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Abstract.—The Isles Dernieres Barrier Island Refuge in Louisiana, USA, constitutes a major colonial waterbird breeding site, and several restoration projects have been undertaken to sustain waterbird populations on the refuge. However, very little is known about food resources that colonial waterbirds depend on in the Gulf of Mexico. Royal (*Thalasseus maximus*) and Sandwich (*T. sandvicensis*) tern diet composition was investigated to determine important food resources during the breeding period. Regurgitated prey items in the 2013 and 2014 breeding seasons were used to compare diet composition, prey item frequency, and prey item mass among four groups: Royal Tern adults, Royal Tern chicks, Sandwich Tern adults, and Sandwich Tern chicks. The two most frequent prey items were Atlantic croaker (*Micropogonias undulatus*) and bay anchovy (*Anchoa mitchilli*). Royal Tern adults consumed significantly more Sciaenids than any other tern group, and Sandwich Tern adults consumed more Engraulids than any other tern group. Royal and Sandwich tern adults partitioned food resources by prey species and prey size, while chick diet showed more overlap in prey species composition. Royal and Sandwich tern diet closely reflected the species composition of trawls from nearby waters, suggesting opportunistic prey selection. The diets of both tern species contained a variety of demersal prey items indicating use of discards from local fisheries activities. Interactions between breeding waterbirds and fisheries in coastal Louisiana may be an important conservation consideration with profound implications on breeding abundance and breeding success of waterbirds. Received 26 August 2015, accepted 2 October 2015.

Key words.—barrier islands, colonial seabird, competition, diet, Gulf of Mexico, prey, resource partitioning, Royal Tern, Sandwich Tern, *Thalasseus maximus*, *Thalasseus sandvicensis*.

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The Mississippi Delta in coastal Louisiana is an extensive system of wetland habitats that is ecologically and economically important to the region (Batker *et al.* 2014). Louisiana's coastal estuaries are very productive, supporting commercial fisheries landings of over 500 million kg per year (Lowther and Liddel 2014). Within the estuarine system, barrier islands play a crucial role by protecting biologically productive inshore areas from the Gulf of Mexico and limiting wave action from eroding mainland saltmarshes (Salinas *et al.* 1986). In addition to protecting the natural and economic interests of southeastern Louisiana, barrier islands provide important habitat for wildlife (Penland *et al.* 2003). Barrier islands serve as critical nesting habitat for many species of colonial waterbirds including wading birds, pelicans, gulls, and terns (Spendelov and Patton 1988; Michot *et al.* 2003; Fontenot *et al.* 2012; Raynor *et al.* 2013). Louisiana's barrier islands support numerous species of conservation concern and historically hosted 16% of the

U.S. breeding population of Royal Terns (*Thalasseus maximus*) and 77% of the U.S. breeding population of Sandwich Terns (*T. sandvicensis*) (Spendelov and Patton 1988). Isles Dernieres Barrier Island Refuge (ID-BIR) sustains some of the largest waterbird breeding colonies in Louisiana (Michot *et al.* 2003), and recent surveys have found 21 species of colonial waterbirds totaling between 27,000 and 44,000 breeding pairs per annum (Raynor *et al.* 2013).

As barrier island restoration has become a major undertaking in Louisiana, a number of recent studies have sought to determine how waterbirds use these barrier island habitats (Raynor *et al.* 2012; Owen and Pierce 2013; Walter *et al.* 2013). While these studies provided much needed information, little is known about the foraging behavior and diet of colonial waterbirds breeding on Louisiana's barrier islands. Identification of important food resources to nesting birds is essential to understanding their breeding ecology and can inform conservation, management, and restoration decisions.

Royal and Sandwich terns nest on remote barrier islands where mammalian predator populations are low, human disturbance is limited, and surrounding waters offer plentiful food resources (Shealer 1999; Buckley and Buckley 2002). The two closely related species nest together in mixed-species colonies, and Sandwich Terns are considered obligate co-nesters with Royal Terns in North America (Shealer 1999; Buckley and Buckley 2002). Both species plunge-dive from the air to capture prey from the surface of coastal waters, but it is unknown how their diet may overlap. Comparison of diet composition between these species will help us to better understand their close breeding association (Shealer 1999).

Seabird diet typically reflects prey abundance and can be used as an index of fish abundance and ecosystem health (Montevocchi and Myers 1995, 1996; Piatt *et al.* 2007). Local food resources are an important aspect of breeding site quality, as highly mobile species become tied to a smaller foraging area during the breeding season. Many seabirds are single-prey loaders, which capture and transport a single prey item back to the nest. As single-prey loaders, Royal and Sandwich terns require prey items of appropriate size and quality to be readily available within a reasonable distance of the colony (McLeay *et al.* 2009). Additionally, with large aggregations of colonial seabirds breeding in close proximity, there is a high potential for competition in food resources (Ashmole 1963).

Identification of nesting waterbird diet composition will help identify important food resources, shed light on how species may be partitioning those resources, and offer a better understanding of the breeding habitat quality offered by Louisiana's barrier islands. Diet information could also indicate potential interactions with fisheries, possible exposure to contaminants, or impacts from oil spills such as the 2010 Deepwater Horizon spill. The objectives of this study were to determine the breeding season diet composition of Royal and Sandwich terns and to identify differences in diet among species and age groups (adults and chicks).

METHODS

Study Area

IDBIR is a chain of islands in Terrebonne Parish, Louisiana, USA (29° 03' N, 90° 57' W to 29° 05' N, 90° 36' W; Fig. 1). IDBIR is composed of (east to west) Wine, Trinity, Whiskey, East Raccoon, and West Raccoon Islands and has been cited as having the highest erosion rate of any coastline in the United States (McBride *et al.* 1989). Restoration projects such as sediment applications, installation of rock breakwaters, sand fencing, and plantings have been implemented in an attempt to stabilize the islands (Penland *et al.* 2003), but habitat degradation has continued to negatively impact nesting waterbirds (Raynor *et al.* 2013; Walter *et al.* 2013). During this study (2013-2014), Royal and Sandwich terns nested on East Raccoon Island and West Raccoon Island.

Diet Samples

Royal and Sandwich tern diets were assessed through analysis of prey regurgitated as a defense mechanism during capture and banding for a related study during the 2013 and 2014 breeding seasons. Breeding adult and pre-fledgling Royal and Sandwich terns were captured from breeding colonies on East and West Raccoon Islands by hand or using dip nets. Adults were captured at the onset of chick-brooding (25 May to 2 July) when adult terns closely guard their young. During this period, researchers were able to approach the colony closely enough to enable capture of adult terns with a dip net. Chicks were captured from mixed-species crèches prior to fledging (approximately 4-28 days old; 21 June to 26 July). Regurgitations of prey items were assumed to be representative of prey items selected by Royal and Sandwich terns.

Prey items regurgitated from adult and chick proventriculi during capture and banding were placed in plastic bags and preserved on ice for later analysis. Prey items were identified to the lowest possible taxa using Hoese and Moore (1998), Jereb and Roper (2010), and Williams (1984) as references. Prey items were categorized as either whole or partially digested, and wet weight (nearest 0.01 g) and total length (nearest 1.0 mm) were measured for each prey item.

Prey Abundance

The Louisiana Department of Wildlife and Fisheries conducts monthly trawls to determine abundance and temporal trends in fish, crustaceans, and other marine life in coastal Louisiana. Sites were sampled for 10 min on a monthly basis with a 4.9-m flat otter trawl equipped with 1.9-cm bar mesh. All captured organisms were identified to species level and counted to estimate abundance. From the Louisiana Department of Wildlife and Fisheries' extensive trawl dataset, we selected all sites throughout the Terrebonne Basin within 35 km of IDBIR. Samples taken from the sites ($n = 29$) during May, June, and July of 2013 and 2014 (concurrent with

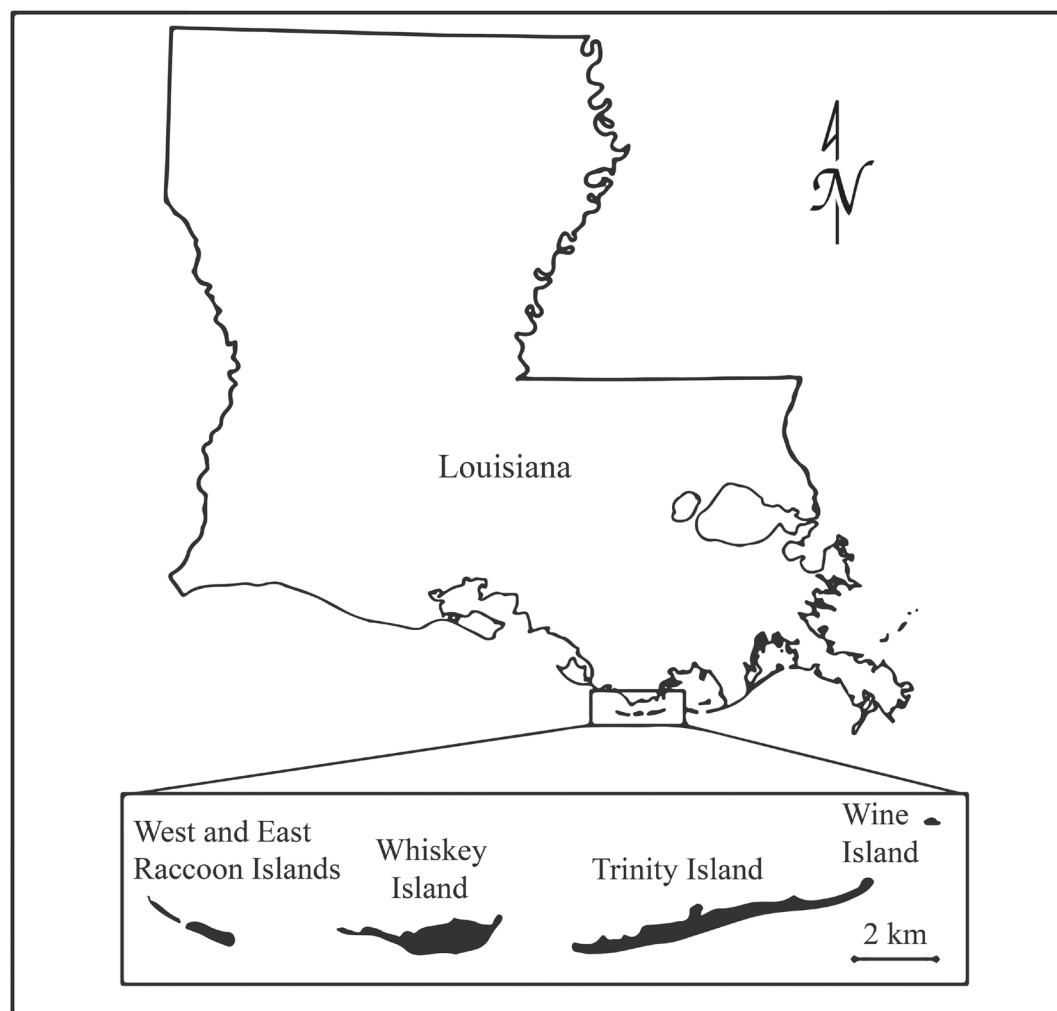


Figure 1. Location of Isles Dernieres Barrier Island Refuge, Louisiana.

tern diet sample collection) were combined and used as an indicator of relative prey abundance in the water surrounding IDBIR.

Analysis

Royal and Sandwich tern prey items were grouped into five taxonomic categories; Clupeidae, Engraulidae, Penaeidae, Sciaenidae, and other (all other taxa of prey). Royal and Sandwich tern diet composition was similar between 2013 and 2014 and combined for all subsequent analyses. Frequency of prey groups regurgitated and mass of prey groups regurgitated were compared among Royal Tern adults, Sandwich Tern adults, Royal Tern chicks, and Sandwich Tern chicks using multivariate analysis of variance (MANOVA). Wilks' Lambda was used to identify significant differences ($\alpha = 0.05$). Kruskal-Wallis non-parametric test was used to compare prey group frequency and mass among tern groups where MANOVA identified differences. Tukey-Kramer multiple comparison test was used to identify differences between groups.

Principal Component Analysis (Primer-E, Ltd. 2015) of prey item frequency was used to identify important prey types and segregation of diet among Royal Tern adults, Sandwich Tern adults, Royal Tern chicks, and Sandwich Tern chicks. The two principal components (PC) with the highest eigenvalues were included. Coefficient loadings ≥ 0.30 were considered important variables in explaining principal components. Ninety-five percent confidence intervals were calculated for the mean scores of PC1 and PC2 of each tern group.

Analysis of variance (ANOVA) was used to compare mean whole prey item mass among tern species and age classes. All partially digested prey items were removed from the analysis of prey item size. Length and mass of whole prey items were highly correlated ($r = 0.86$), so only mass was used as a metric for prey size. Tukey Kramer multiple comparison was used to determine differences among groups. Analysis was performed with program SAS (SAS Institute, Inc. 2008) and results are reported as mean \pm 1 SE.

RESULTS

During the 2013 and 2014 breeding seasons, 745 Royal and Sandwich terns were captured and 921 prey items were collected (Table 1). From these samples, a total of 29 prey species, representing 21 unique families of fish and invertebrates, were identified (Table 2). Fish were the main prey of both Royal and Sandwich terns, constituting 94.5% of all prey items collected. Terns consumed both demersal fish (Sciaenids) and pelagic fish (Engraulids and Clupeids) as major parts of their diet (Fig. 2).

Prey Species

The most frequent prey item of Royal Tern adults, Royal Tern chicks, and Sandwich Tern chicks was Atlantic croaker (prey item scientific names are listed in Table 3), while Sandwich Tern adults most frequently regurgitated bay anchovy, followed by Atlantic croaker. In both tern species, chick prey composition largely reflected that of adults but with a reduced frequency of Engraulids. The mean frequency of Sciaenid and Engraulid prey items consumed by Royal and Sandwich tern adults and chicks were significantly different ($n = 229$, $df = 3$, $F = 4.43$, $P < 0.001$). Royal Tern adults consumed Sciaenids more frequently than any other tern group ($P < 0.001$), while Sandwich Tern adults consumed Engraulids more frequently than any other tern group ($P < 0.001$). Tern diet composition also differed by prey mass ($n = 229$, $df = 3$, $F = 10.70$, $P < 0.001$). Royal Tern adult samples had higher Sciaenid mass than Sandwich Tern adults

and Sandwich Tern chicks ($P < 0.001$), but not Royal Tern chicks. Sandwich Tern adult samples had higher Engraulid mass than all other terns ($P < 0.001$). Royal Tern adult samples contained higher Penaeid mass than Sandwich Tern adults ($P = 0.02$), but did not differ from Royal Tern chicks or Sandwich Tern chicks.

PCA demonstrated some separation among the diets of Royal Tern adults, Sandwich Tern adults, Royal Tern chicks, and Sandwich Tern chicks (Fig. 3). PC1 and PC2 accounted for 51.5% of the variation in prey item frequency. Royal Tern adults had the highest positive correlation with PC1, representing greater frequency of Sciaenid and lower frequency of Engraulid, Penaeid and Other prey groups. Sandwich Tern adults had the highest positive correlation with PC2, representing greater frequency of Engraulid and lower frequency of Penaeid and Clupeid prey groups. Royal Tern adult, Royal Tern chick, and Sandwich Tern chick diets had overlapping 95% confidence intervals, while Sandwich Tern adult diet did not overlap with any other group.

Prey Size

Mean whole prey item mass differed among Royal Tern adults, Sandwich Tern adults, Royal Tern chicks, and Sandwich Tern chicks ($n = 270$, $df = 3$, $F = 34.52$, $P < 0.001$; Table 1). Royal Tern adults selected larger prey items than Sandwich Tern adults, and both species provisioned their chicks with larger prey items than they consumed themselves. As Royal Tern adults and Sandwich Tern adults differed in both prey size

Table 1. Diet samples and mean whole prey item mass collected from Royal Tern adults, Sandwich Tern adults, Royal Tern chicks, and Sandwich Tern chicks at Isles Dernieres Barrier Island Refuge, Louisiana, during the 2013 and 2014 breeding seasons. Chick sample size precluded analysis of size within prey family. Means in the same row followed by a different letter are significantly different ($P = 0.05$).

Parameter	Royal Tern Adults	Sandwich Tern Adults	Royal Tern Chicks	Sandwich Tern Chicks
Individuals captured	187	181	190	187
Regurgitations	84	83	43	19
Total prey items	351	476	60	34
Mean prey mass (g)	6.29 ± 0.49 (B)	2.82 ± 0.22 (C)	11.83 ± 1.31 (A)	6.91 ± 0.97 (B)
Mean Sciaenid mass (g)	8.43 ± 0.54 (A)	6.15 ± 0.40 (B)		
Mean Engraulid mass (g)	1.94 ± 0.60 (A)	1.55 ± 0.08 (A)		

Table 2. Numerical frequency (%) of prey items identified from diet samples of Royal Tern adults, Sandwich Tern adults, Royal Tern chicks, and Sandwich Tern chicks at Isles Dernieres Barrier Island Refuge, Louisiana, during the 2013 and 2014 breeding seasons.

Prey	Royal Tern Adults	Sandwich Tern Adults	Royal Tern Chicks	Sandwich Tern Chicks
Fish				
Ariidae	< 1	—	—	—
Batrachoididae	< 1	—	—	3
Bothidae	1	< 1	—	—
Carangidae	—	—	3	—
Clupeidae	16	8	13	—
Cynoglossidae	—	—	2	3
Engraulidae	24	65	—	29
Gobiidae	< 1	< 1	—	—
Ophichthidae	1	—	2	—
Paralichthyidae	< 1	< 1	—	—
Rachycentridae	—	—	2	—
Sciaenidae	48	23	57	50
Sparidae	—	< 1	—	—
Stromateidae	< 1	< 1	2	—
Trichiuridae	1	< 1	—	—
Triglidae	< 1	< 1	—	—
Unidentified	—	< 1	—	—
Invertebrates				
Loliginidae	< 1	< 1	—	—
Lysiosquillidae	< 1	—	—	—
Palaemonidae	—	< 1	—	—
Penaeidae	6	1	17	15
Portunidae	< 1	—	3	—

selected and prey taxa selected, additional analysis was used to determine if difference in prey size was merely a function of selecting prey taxa in different proportions or if adult terns selected different prey sizes when consuming the same prey taxa. Whole prey item mass of the two most common prey types (Sciaenid and Engraulid) were compared between Royal Tern adults and Sandwich Tern adults (Table 1). Royal Tern chicks and Sandwich Tern chicks lacked sufficient sample size for inclusion in this analysis. Royal Terns adults had a greater mean Sciaenid mass than Sandwich Tern adults ($n = 85$, $df = 1$, $F = 8.14$, $P < 0.001$), but there was no difference in mean mass of Engraulids consumed by Royal and Sandwich tern adults ($n = 94$, $df = 1$, $F = 1.15$, $P = 0.29$).

Prey Abundance

Louisiana Department of Wildlife and Fisheries trawls conducted during May,

June, and July of 2013 and 2014 resulted in over 170,000 captures from which 86 different taxa of marine organisms were identified (Table 3). Bay anchovy was the most frequently captured species followed by Atlantic croaker, brown shrimp, spot, and Gulf menhaden. The five most frequently caught species represented 90.4% of all captures and were also the five most common tern prey items.

DISCUSSION

The majority of our understanding of Royal and Sandwich tern diet in North America comes from observations of food provisioning to pre-fledgling chicks (McGinnis and Emslie 2001; Wambach and Emslie 2003; Aygen and Emslie 2006); however, adult diet composition has yet to be studied in Royal and Sandwich terns in North America. Diet information for Royal and Sandwich terns in the northern Gulf of Mexico was previously

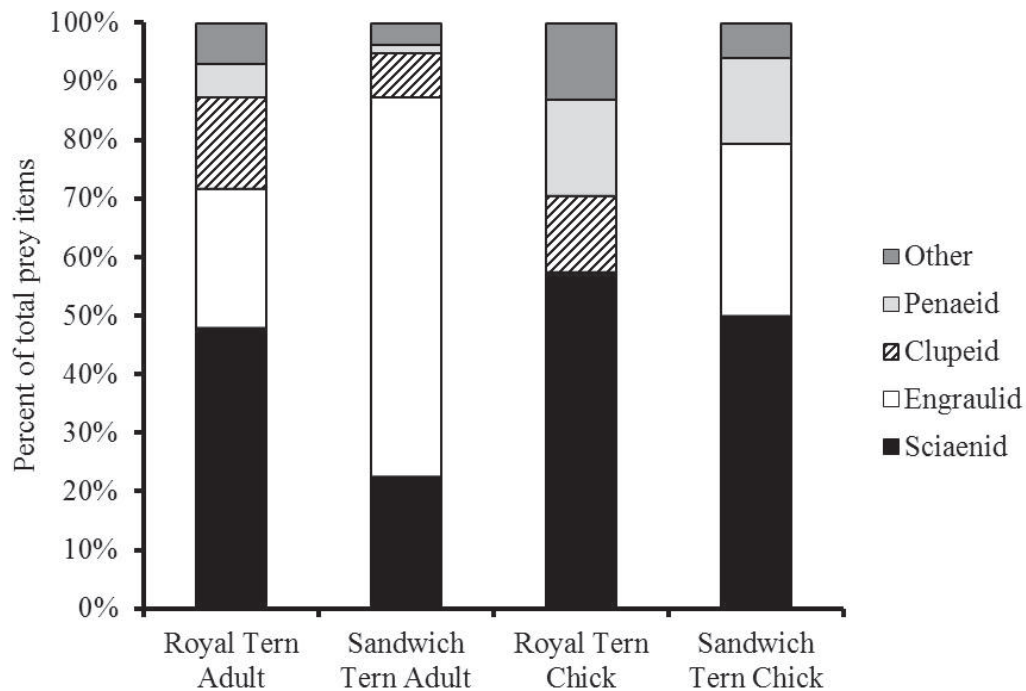


Figure 2. Diet composition of Royal Tern adults ($n = 84$), Sandwich Tern adults ($n = 83$), Royal Tern chicks ($n = 43$), and Sandwich Tern chicks ($n = 19$) by prey frequency at Isles Dernieres Barrier Island Refuge, Louisiana, during May, June, and July 2013 and 2014.

limited to eight prey items identified from the stomachs of Royal and Sandwich terns collected in Galveston Bay, Texas (Maedgen *et al.* 1982). The results of our study provide a more comprehensive understanding of Royal and Sandwich tern diet composition and indicates that their diets were diverse, opportunistic and frequently included Engraulids, Sciaenids, Clupeids, and Penaeid shrimp. Moreover, this study identified At-

lantic croaker and bay anchovy as the most common prey items.

Royal Terns are assumed to be highly opportunistic in prey selection (Buckley and Buckley 2002), and this study concurs with the existing literature on the diversity of prey in Royal Tern diet. Similar to the diet of Royal Tern adults in South America (Favero *et al.* 2000; Gatto and Yorio 2009), our results suggest that Engraulids and Sci-

Table 3. The 10 most abundant taxa of marine organisms captured by the Louisiana Department of Wildlife and Fisheries trawls conducted in May, June, and July of 2013 and 2014 taken from 29 sites within the Terrebonne Basin, Louisiana, and tern prey items collected at Isles Dernieres Barrier Island Refuge, Louisiana, during the 2013 and 2014 breeding seasons.

Species	Trawl Total	%	Tern Total	%
Bay anchovy (Engraulidae; <i>Anchoa mitchilli</i>)	89,006	51.6	279	34.8
Atlantic croaker (Sciaenidae; <i>Micropogonias undulatus</i>)	27,763	16.1	243	30.3
Brown shrimp (Penaeidae; <i>Farfantepenaeus aztecus</i>)	23,505	13.6	48	6.0
Spot (Sciaenidae; <i>Leiostomus xanthurus</i>)	8,239	4.8	30	3.7
Gulf menhaden (Clupeidae; <i>Brevoortia patronus</i>)	7,434	4.3	94	11.7
Sand trout (Sciaenidae; <i>Cynoscion arenarius</i>)	3,273	1.9	17	2.1
Least puffer (Tetraodontidae; <i>Sphoeroides parvus</i>)	2,771	1.6	-	-
White shrimp (Penaeidae; <i>Litopenaeus setiferus</i>)	2,434	1.4	2	0.2
Blue crab (Portunidae; <i>Callinectes sapidus</i>)	1,094	0.6	3	0.4
Bay whiff (Paralichthyidae; <i>Citharichthys spilopterus</i>)	895	0.5	2	0.2

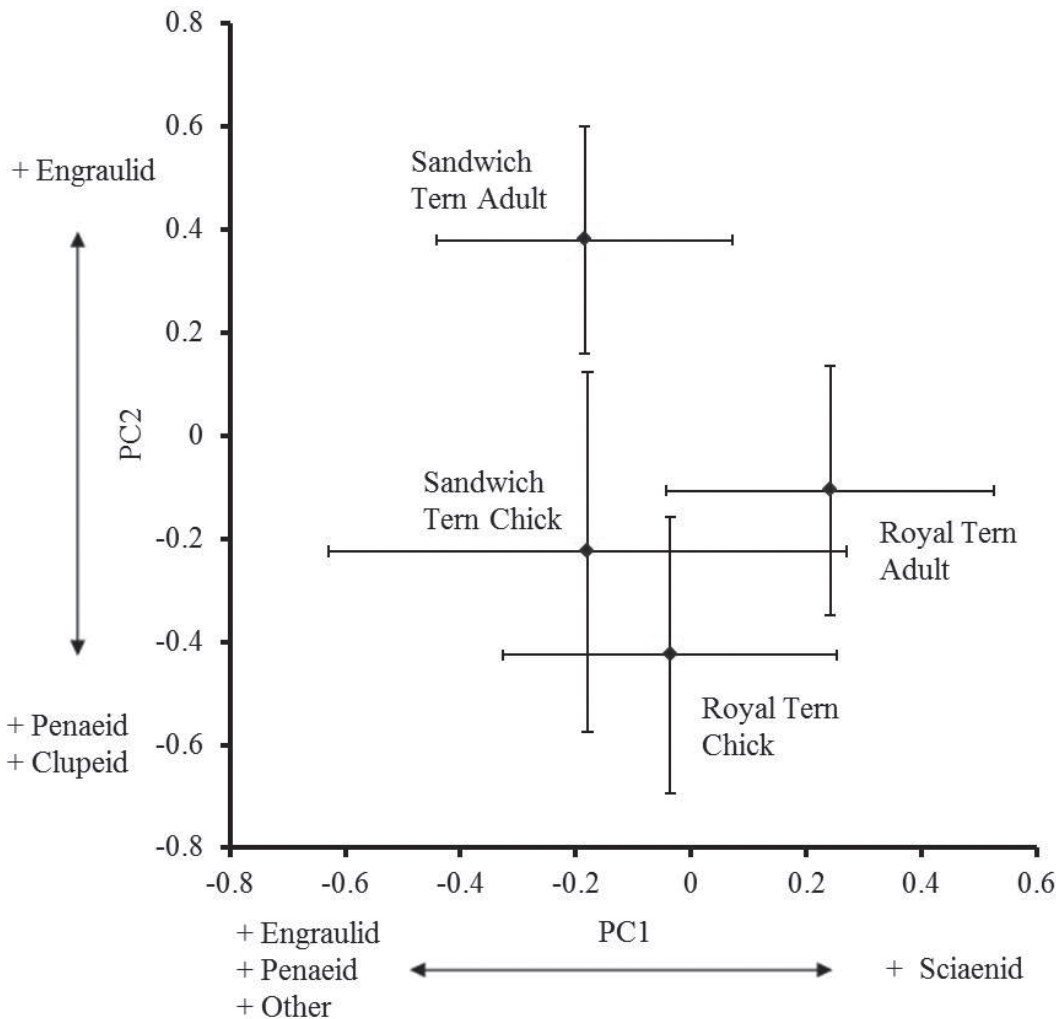


Figure 3. Principal component analysis (PCA) of breeding season diet composition for terns at Isles Dernieres Barrier Island Refuge, Louisiana, during May, June, and July 2013 and 2014. Error bars represent 95% confidence intervals.

aenids are important prey items. However, there seem to be regional differences in diet of Royal Tern chicks. This study, in the Gulf of Mexico, found a complete absence of Engraulids in Royal Tern chick diet, compared to 17-41% of overall chick diet in North Carolina and Virginia (Wambach and Emslie 2003; Aygen and Emslie 2006). Aygen and Emslie (2006) also found the proportion of Sciaenids fed to Royal Tern chicks to be < 2% of overall diet, a marked difference from the 57% found in this study.

Throughout their range, Sandwich Tern diet appears to be composed mostly of forage fish with important prey including Am-

modytidae, Atherinopsids, Clupeids, and Engraulids (Shealer 1998; McGinnis and Emslie 2001; Stienen and Brenninkmeijer 2002; Gatto and Yorio 2009). Our results indicate that Sciaenids are also important to Sandwich Terns in the Gulf of Mexico, similar to findings of Sandwich Tern diet in Argentina (Favero *et al.* 2000). Shealer (1998) determined that prey species composition differed between Sandwich Tern adults and chicks in Puerto Rico. Similarly, we determined that Sandwich Tern adults consumed significantly more Engraulids than their chicks. In addition, Sandwich Tern adults consumed few Penaeids them-

selves (1.5% of overall diet), but provisioned their chicks with Penaeids 10 times more frequently (14.7%). This difference is even more notable when comparing mass, Penaeids represented 1.4% of Sandwich Tern adult prey mass and 23.7% of Sandwich Tern chick prey mass.

While Sandwich Tern adults feed heavily on Engraulids, they may not be the most important prey of Sandwich Terns in the Gulf of Mexico. Engraulids comprised the largest portion of Sandwich Tern adult diet by frequency (64.8%), but due to the small size of Engraulids selected (mean mass of 1.55 g, $n = 71$), they made up only 32.8% of the overall mass consumed by Sandwich Tern adults. Sciaenids represented 53.7% of Sandwich Tern adult diet by mass and may contribute more to the caloric intake of Sandwich Tern adults than Engraulids.

Adult Royal and Sandwich terns partitioned their two most frequent prey types (Sciaenid and Engraulid), with Royal Tern adults consuming more Sciaenids in both frequency and mass compared to all other groups. Royal and Sandwich terns also partitioned prey items by size, with Royal Terns consuming larger prey items than Sandwich Terns. For example, Sandwich Tern adults not only consumed less Sciaenids than Royal Tern adults, the Sciaenids that they did consume were 27% smaller in mass than those selected by Royal Terns. Other studies have found similar partitioning within sympatrically breeding tern communities (Surman and Wooller 2003; Catry *et al.* 2009; Robertson *et al.* 2014; Tayefeh *et al.* 2014), which may help species avoid competition for food resources.

Although there was considerable overlap in prey species composition of Royal Tern chicks and Sandwich Tern chicks, partitioning based on prey size was evident. Both tern species fed their young larger prey items than they consumed themselves, and similar to adults, Royal Tern chicks consumed larger prey items than Sandwich Tern chicks. Keeping chicks satiated during the energy-intensive growth and development phase likely requires provisioning of large, high-quality prey items, and the tendency for adult sea-

birds to provision chicks with different prey items than they consume themselves is well established in the literature (e.g., Barrett *et al.* 2007; Cherel *et al.* 2008; Fijn *et al.* 2012).

Louisiana Department of Wildlife and Fisheries trawl data taken concurrently with tern diet sampling offers an indication of prey availability in the waters surrounding IDBIR, with bay anchovy and Atlantic croaker being the two most abundant species captured. Royal and Sandwich tern diets showed a remarkable resemblance to available prey as the five most commonly caught species in trawls were also the five most common prey items recovered from terns. This supports the notion that Royal and Sandwich terns are opportunistic foragers and that their diets are a reflection of available prey resources (Montevecchi and Meyers 1995). Although Royal and Sandwich tern diets matched well with available prey, terns may be selecting for Atlantic croaker and Gulf menhaden as both prey items were more commonly encountered in tern diets compared with their relative abundance in trawl catches. Shrimp appeared less frequently in tern diets than their relative abundance in trawl catches, suggesting that Royal and Sandwich terns struggled to obtain these prey items or do not prefer them. One explanation for this is that Royal and Sandwich terns are feeding on shrimp trawling bycatch where shrimp have been retained and all other items discarded.

The quantity and diversity of demersal prey, such as scaly-tailed mantis shrimp (*Lysiosquilla scabricauda*) and various species of flatfish, found in the diets of both Royal and Sandwich terns may be the result of interactions with local fisheries. Demersal prey items may be made available to Royal and Sandwich terns as discarded bycatch or demersal prey may be scared toward the surface during the trawling process. Seabirds have long been associated with fisheries for food resources (Blaber *et al.* 1995; Montevecchi 2002), and Royal and Sandwich terns in particular have been identified as attending shrimp trawlers in South Carolina (Wickliffe and Jodice 2010; Jodice *et al.* 2011), Brazil (Yorio and Efe 2008), and Spain (Martinez-Abraín *et al.* 2002; Valieras 2003).

The impact that fisheries have on trophic interactions in the Gulf of Mexico warrants further investigation to better understand how fisheries may be affecting populations of prey, predators, and scavengers. The high discard rate of shrimp trawling, 4.6 kg of by-catch for every 1.0 kg landings, in the Gulf of Mexico (Harrington *et al.* 2005) could be promoting the large breeding populations of Royal and Sandwich terns along Louisiana's coast. Alternatively, abundant discards may be inflating gull populations, increasing kleptoparasitism and egg predation on breeding terns and thereby negatively impacting Royal and Sandwich tern reproductive success (Stienen and Brenninkmeijer 2002).

Fisheries discards vary temporally, and changes in fishing activity can influence seabird foraging behavior (Blaber *et al.* 1995; Bartumeus *et al.* 2010). Other *Thalasseus* sp. terns have demonstrated diet shifts between open trawling and closed trawling seasons (Blaber *et al.* 1995). Highly-mobile tern species, such as Royal and Sandwich terns, may even seek out areas throughout the year that offer more predictable prey availability via fishery discards (Bartumeus *et al.* 2010). Tern species may shift between foraging tactics (i.e., fishery-assisted vs. "natural") with changing environmental conditions, prey availability, and breeding phase (Blaber *et al.* 1995; Stienen *et al.* 2000; Shealer 2002; Gremillet *et al.* 2008).

This is the first quantitative information on the diets of Royal and Sandwich tern adults in North America and the first comparison of adult and chick diets of Royal and Sandwich terns in the region. This study also provides the first substantive information on tern diets in the Gulf of Mexico, an important area for U.S. breeding populations. Both species appear highly adaptable and opportunistic in exploiting available prey. Royal and Sandwich terns partitioned their diets by both prey size and prey species as found in South America (Gatto and Yorio 2009), thereby limiting competition for food resources during the breeding season. In contrast to other studies (Shealer 1998; Stienen *et al.* 2000; Gatto and Yorio 2009), Sandwich Tern diet in Louisiana was not restricted to schooling forage fish but

included a substantial number of Sciaenidae as well as other demersal species. Fisheries activities appear to broaden Royal and Sandwich tern diet composition by providing food types that would not naturally be available to terns. Breeding success can often be correlated to food abundance (Cairns 1992), and commercial fisheries may be increasing prey availability and indirectly impacting reproductive success (Oro *et al.* 1996), site fidelity, and population dynamics (Oro *et al.* 2004), and ultimately promoting a large breeding population of scavenging seabirds (Furness 2003).

Although the breeding season is a critical period, Royal and Sandwich tern diet composition likely changes throughout the remainder of the year, especially given the mobility of these species. Throughout the year, tern species are likely exposed to a variety of coastal environments and exposed to different fishing activities and hazards. Fishery resources may even influence their movements throughout the year. Both quality of diet and exposure to potentially dangerous fishing activities during non-breeding periods could have important consequences for survival and body condition of Royal and Sandwich terns leading into the breeding season.

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LITERATURE CITED

- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458-473.
- Aygen, D. and S. D. Emslie. 2006. Royal Tern (*Sterna maxima*) chick diet at Fisherman Island National Wildlife Refuge, Virginia. *Waterbirds* 29: 395-400.

- Barrett, R. T., K. Camphuysen, T. Anker-Nilssen, J. W. Chardine, R. W. Furness, S. Garthe, O. Huppopp, M. F. Leopold, W. A. Montevecchi and R. R. Veit. 2007. Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science* 64: 1675-1691.
- Bartumeus, F., L. Giuggioli, M. Louzao, V. Bretagnolle, D. Oro and S. A. Levin. 2010. Fishery discards impact on seabird movement patterns at regional scales. *Current Biology* 20: 215-222.
- Batker, D., S. K. Mack, F. H. Sklar, W. K. Nuttle, M. E. Kelly and A. M. Freeman. 2014. The importance of Mississippi delta restoration on the local and national economies. Pages 141-153 *in* Perspectives on the Restoration of the Mississippi Delta (J. W. Day, G. P. Kemp, A. M. Freeman and D. P. Muth, Eds.). Springer Science Business Media, Dordrecht, The Netherlands.
- Blaber, S. J. M., D. A. Milton, G. C. Smith and M. J. Farmer. 1995. Trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. *Marine Ecology Progress Series* 127: 1-13.
- 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.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Cairns, D. K. 1992. Population regulation of seabird colonies. *Current Ornithology* 9: 37-61.
- Catry, T., J. A. Ramos, S. Jaquemet, L. Faulquier, M. Berlincourt, A. Hauselmann, P. Pinet and M. Le Corre. 2009. Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. *Marine Ecology Progress Series* 374: 259-272.
- Cherel, Y., M. Le Corre, S. Jaquemet, F. Menard, P. Richard and H. Weimerskirch. 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology Progress Series* 366: 281-291.
- Favero, M., M. P. Silva R. and L. Mauco. 2000. Diet of Royal (*Thalasseus maximus*) and Sandwich (*T. sandvicensis*) Terns during the austral winter in the Buenos Aires Province, Argentina. *Ornitologia Neotropical* 11: 259-262.
- Fijn, R. C., J. A. Van Franeker and P. N. Trathan. 2012. Dietary variation in chick-feeding and self-provisioning Cape Petrel *Daption capense* and Snow Petrel *Pagodroma nivea* at Signy Island, South Orkney Islands, Antarctica. *Marine Ornithology* 40: 81-87.
- Fontenot, W. R., S. W. Cardiff, R. A. DeMay, D. L. Dittmann, S. Hartley, C. W. Jeske, N. Lorenz, T. C. Michot, R. D. Purrington, M. Seymour and W. G. Vermillion. 2012. A catalog of Louisiana's nesting seabird colonies. Report Number 34, Barataria-Terrebonne National Estuary Program, Thibodaux, Louisiana.
- Furness, R. W. 2003. Impacts of fisheries on seabird communities. *Scientia Marina* 67: 33-45.
- Gatto, A. J. and P. Yorio. 2009. Provisioning of mates and chicks by Cayenne and Royal Terns: resource partitioning in northern Patagonia, Argentina. *Emu* 109: 49-55.
- Gremillet, D., L. Pichegru, G. Kuntz, A. G. Woakes, S. Wilkinson, R. J. M. Crawford and P. G. Ryan. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society B: Biological Sciences* 275: 1149-1156.
- Harrington, J. M., R. A. Myers and A. A. Rosenberg. 2005. Wasted fishery resources: discarded by-catch in the USA. *Fish and Fisheries* 6: 350-361.
- Hoese, H. D. and R. H. Moore. 1998. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters. Texas A & M University Press, Austin, Texas.
- Jereb, P. and C. F. E. Roper. 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date, v. 2. Myopsid and Oegopsid squids. Food and Agriculture Organization Species Catalogue for Fishery Purposes No. 4, Vol. 2, Food and Agriculture Organization of the United Nations, Rome, Italy.
- Jodice, P. G. R., L. C. Wickliffe and E. B. Sachs. 2011. Seabird use of discards from a nearshore fishery in the South Atlantic Bight, USA. *Marine Biology* 158: 2289-2298.
- Lowther, A. and M. Liddel. 2014. Fisheries of the United States 2013. Current Fishery Statistics No. 2013, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, Maryland.
- Maedgen, J. L., C. S. Hacker, G. D. Schroder and F. W. Weir. 1982. Bioaccumulation of lead and cadmium in the Royal Tern and Sandwich Tern. *Archives of Environmental Contamination and Toxicology* 11: 99-102.
- Martinez-Abraín, A., R. Maestre and D. Oro. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. *ICES Journal of Marine Science* 59: 529-539.
- McBride, R. A., S. Penland, B. E. Jaffe, S. J. Williams, A. H. Sallenger and K. A. Westphal. 1989. Erosion and deterioration of the Isles Dernieres barrier island arc-Louisiana, U. S. A: 1853-1988. *Transactions of the Gulf Coast Association of Geological Societies* 39: 431-444.
- McGinnis, T. W. and S. D. Emslie. 2001. The foraging ecology of Royal and Sandwich terns in North Carolina, USA. *Waterbirds* 24: 361-370.
- McLeay, L. J., B. Page, S. D. Goldsworthy, T. Ward and D. C. Paton. 2009. Size matters: variation in the diet of chick and adult Crested Terns. *Marine Biology* 156: 1765-1780.
- Michot, T. C., C. W. Jeske, J. C. Mazourek, W. G. Vermillion and R. S. Kemmerer. 2003. Atlas and census of wading bird and seabird nesting colonies in south Louisiana, 2001. Report No. 32, Barataria-Terrebonne National Estuary Program, Thibodaux, Louisiana.
- Montevecchi, W. A. 2002. Interactions between fisheries and seabirds. Pages 137-178 *in* Biology of Marine Birds (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.

- Montevecchi, W. A. and R. A. Myers. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. *Marine Ecology Progress Series* 117: 1-9.
- Montevecchi, W. A. and R. A. Myers. 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. *Sarsia* 80: 312-322.
- Oro, D., L. Jover and X. Ruiz. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. *Marine Ecology Progress Series* 139: 19-29.
- Oro, D., E. Cam, R. Pradel and A. Martínez-Abraín. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society of London B: Biological Sciences* 271: 387-396.
- Owen, T. M. and A. R. Pierce. 2013. Hatching success and nest site characteristics of Black Skimmer (*Rynchops nigra*) on the Isles Dernieres Barrier Island Refuge, Louisiana. *Waterbirds* 36: 342-347.
- Penland, S., P. Connor, F. Cretini and K. Westpahl. 2003. Coastal Wetlands Planning, Protection and Restoration Act adaptive management: assessment of five barrier island restoration projects in Louisiana. Unpublished Proceedings of Coastal Sediments 2003, Clearwater, Florida.
- Piatt, J. F., W. J. Sydeman and F. Wiese. 2007. Introduction: a modern role for seabirds as indicators. *Marine Ecology Progress Series* 352: 199-204.
- Primer-E, Ltd. 2015. Primer 7 v. 7.0.5. Primer-E, Ltd., Plymouth, U.K.
- Raynor, E. J., A. R. Pierce, C. M. Leumas and F. C. Rohwer. 2012. Breeding habitat requirements and colony formation by Royal Terns (*Thalasseus maximus*) and Sandwich Terns (*Thalasseus sandvicensis*) on barrier islands in the Gulf of Mexico. *Auk* 129: 763-772.
- Raynor, E. J., A. R. Pierce, T. M. Owen, C. M. Leumas and F. C. Rohwer. 2013. Short-term demographic responses of a coastal waterbird community after two major hurricanes. *Waterbirds* 36: 88-93.
- Robertson, G. S., M. Bolton, W. J. Grecian, L. J. Wilson, W. Davies and P. Monaghan. 2014. Resource partitioning in three congeneric sympatrically breeding seabirds: foraging areas and prey utilization. *Auk* 131: 434-446.
- Salinas, L. M., R. D. DeLaune and W. H. Patrick, Jr. 1986. Changes occurring along a rapidly submerging coastal area: Louisiana, USA. *Journal of Coastal Research* 2: 269-284.
- SAS Institute, Inc. 2008. SAS statistical software v. 9. 2. SAS Institute, Inc., Cary, North Carolina.
- Shealer, D. 1998. Differences in diet and chick provisioning between adult Roseate and Sandwich Terns in Puerto Rico. *Condor* 100: 131-140.
- Shealer, D. 1999. Sandwich Tern (*Sterna sandvicensis*). No. 405 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Shealer, D. 2002. Foraging behavior and food of seabirds. Pages 137-178 in *Biology of Marine Birds* (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.
- Spendelov, J. A. and S. R. Patton. 1988. National atlas of coastal waterbird colonies in the contiguous United States, 1976-82. Biological Report 88/5, U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- Stienen, E. W. M. and A. Brenninkmeijer. 2002. Foraging decisions of Sandwich Terns in the presence of kleptoparasitising gulls. *Auk* 119: 473-486.
- Stienen, E. W. M., P. W. M. van Beers, A. Brenninkmeijer, J. M. P. M. Habraken, M. H. J. E. Raaijmakers and P. G. M. van Tienen. 2000. Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*. *Ardea* 88: 33-49.
- Surman, C. A. and R. D. Wooller. 2003. Comparative foraging ecology of five sympatric terns at a sub-tropical island in the eastern Indian Ocean. *Journal of Zoology* 259: 219-230.
- Tayefeh, F. H., M. Zakaria, H. Amini, J. Mohammadnejad, K. Darvishi and S. Karimi. 2014. Dietary segregation between breeding tern species on the Persian Gulf Islands, Iran. *Waterbirds* 37: 307-318.
- Valeiras, J. 2003. Attendance of scavenging seabirds at trawler discards off Galicia, Spain. *Scientia Marina* 67: 77-82.
- Walter, S. T., M. R. Carlross, T. J. Hess and P. L. Leberg. 2013. Hurricane, habitat degradation, and land loss effects on Brown Pelican nesting colonies. *Journal of Coastal Research* 29: 187-195.
- Wambach, E. J. and S. D. Emslie. 2003. Seasonal and annual variation in the diet of breeding, known-age Royal Terns in North Carolina. *Wilson Bulletin* 115: 448-454.
- Wickliffe, L. C. and P. G. R. Jodice. 2010. Seabird attendance at shrimp trawlers in nearshore waters of South Carolina. *Marine Ornithology* 38: 31-39.
- Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.
- Yorio, P. and M. A. Efe. 2008. Population status of Royal and Cayenne terns breeding in Argentina and Brazil. *Waterbirds* 31: 561-570.