

**ATOLL RESEARCH BULLETIN**

**NO. 482**

**SEABIRDS OF THE CAMPECHE BANK ISLANDS, SOUTHEASTERN GULF  
OF MÉXICO**

**BY**

**JOHN W. TUNNELL AND BRIAN R. CHAPMAN**

**ISSUED BY  
NATIONAL MUSEUM OF NATURAL HISTORY  
SMITHSONIAN INSTITUTION  
WASHINGTON, D.C., U.S.A.  
JUNE 2000**

---

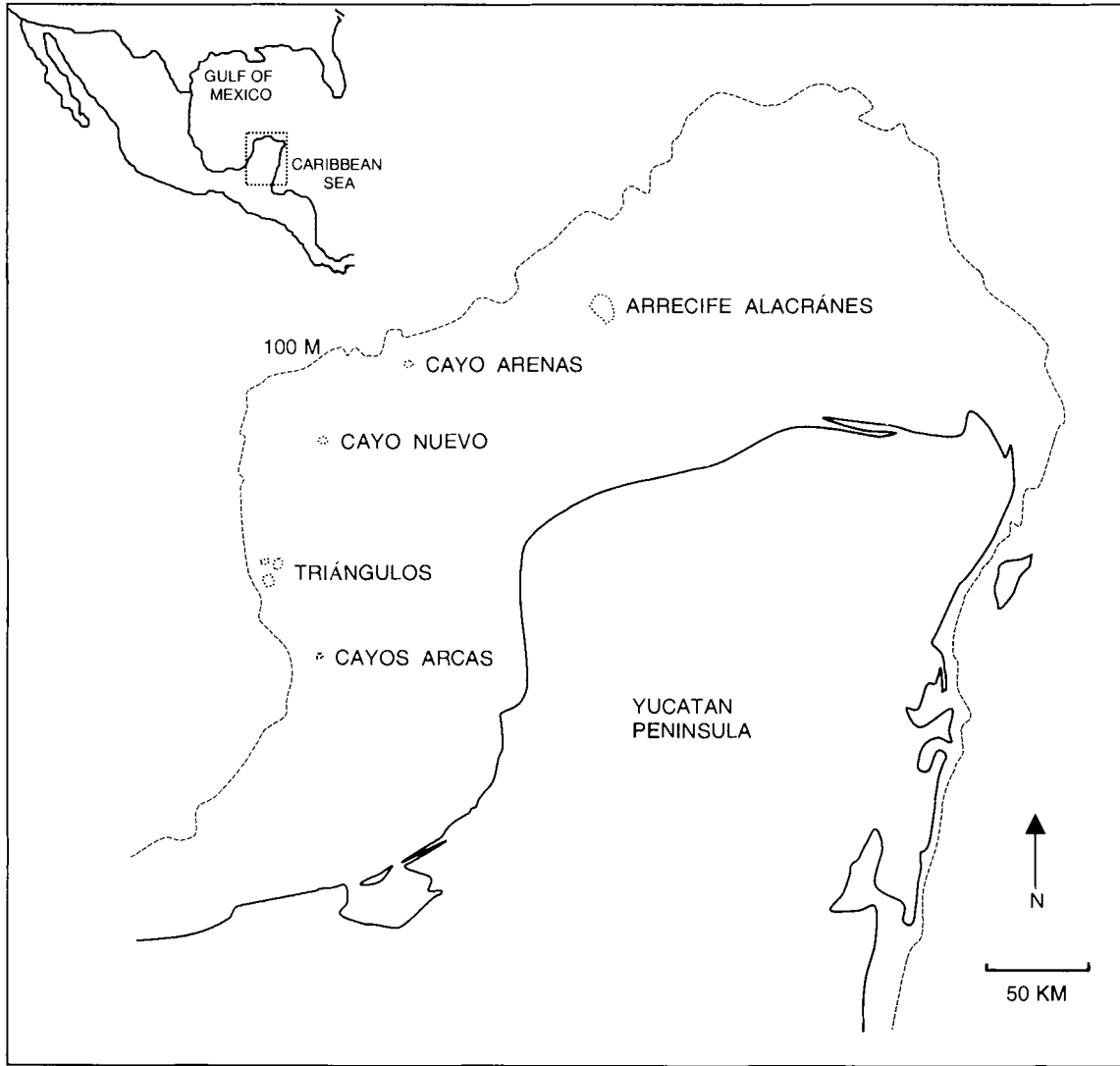


Figure 1. Location of reef island complexes on the Campeche Bank of the southeastern Gulf of México.

# SEABIRDS OF THE CAMPECHE BANK ISLANDS, SOUTHEASTERN GULF OF MÉXICO

BY

JOHN W. TUNNELL, JR.<sup>1</sup> and BRIAN R. CHAPMAN<sup>2</sup>

## ABSTRACT

Seabirds of the Campeche Bank islands in the Gulf of México were surveyed during 1986. Eight of 12 permanently emergent islands had active seabird nesting colonies during the study period from winter through summer. Nine species of colonial seabirds nested on the islands: Masked Booby, Brown Booby, Red-footed Booby, Magnificent Frigatebird, Laughing Gull, Royal Tern, Sandwich Tern, Sooty Tern, and Brown Noddy. Descriptions of colony locations in relation to vegetation or other island features along with bird censuses and historical records are presented. These large seabird populations in the southern Gulf of México appear to have remained fairly stable, and they should be surveyed on a regular basis and protected.

## INTRODUCTION

The Campeche Bank, an extensive submarine continuation of the limestone plateau that forms the Yucatán Peninsula (Macintyre et al. 1977), extends for about 650 km along the western and northern coasts of the Yucatán in the southeastern Gulf of México. The bank is characterized by relatively shallow waters with many shoals and coral reefs, but few emergent islands. Within the Campeche Bank there are only four groups of islands (Figure 1) that are large enough and sufficiently elevated to support terrestrial floras and faunas. These groups are known as Arrecife Alacrán (22° 23' N, 89° 40' W), Cayo Arenas (22° 07' N, 91° 24' W), Arrecifes Triángulos (20° 58' N, 92° 20' W), and Cayos Arcas (20° 13' N, 91° 58' W). A fifth, Cayo Nuevo (21° 50' N, 92° 04' W), consists of a low, barren sand cay that probably is inundated by storm tides and wave action and a submergent reef flat that may be exposed during extremely low tides. All of the islands in these groups are located more than 120 km from the mainland and rarely are visited by recreational boaters or fishermen, although considerable numbers of commercial fishermen regularly visit some of the islands, primarily the Alacrán and Arenas groups. All four of the main island groups have lighthouses that are staffed by keepers, and sometimes their families and pets. Some of the islands (Arcas group) also facilitate crude oil storage and transfer facilities by *Petroleos Mexicanos* (PEMEX), the national oil company of México, and are guarded by small (2-4 men) Naval detachments. Each island group has a Naval weather station.

---

<sup>1</sup> Center for Coastal Studies, Texas A&M University - Corpus Christi, 6300 Ocean Dr., Corpus Christi, TX, 78412, USA.

<sup>2</sup> College of Arts and Sciences, Sam Houston State University, Box 2209, Huntsville, TX 77341-2209, USA.

Geologic and topographic features (Kornicker et al. 1959, Fosberg 1961, Folk 1967, Macintyre et al. 1977, Wells 1988), submarine fauna (Kornicker et al. 1959, Kornicker and Boyd 1962, Farrell et al. 1983, Chávez et al. 1985) and terrestrial flora (Millspaugh 1916, Bonet and Rzedowski 1962) of certain Campeche Bank islands have been described, but terrestrial fauna of the islands has not been well documented. Much of the information about seabirds that visit or nest on the Campeche Bank islands must be gleaned from anecdotal accounts in cruise reports, geologic explorations, or floristic surveys. Although there have been several recent accounts of marine birds on the Campeche Bank reefs (Paynter 1955, Boswall 1978, Tunnell and Chapman 1988, Howell 1989, Lockwood 1989), thorough surveys of the seabird populations apparently have never been made during the probable period of peak nesting (Clapp et al. 1982).

The first account of the seabird colonies on the Campeche Bank islands was written by the English adventurer Dampier (1699), who first visited the area in 1675. Nearly two centuries passed before the avifauna of the islands north of the Yucatán Peninsula was again mentioned by Smith (1838), Marion (1884), Ward (1887) and Agassiz (1888). A British Navy officer visited two of the smaller islands in Alacrán Reef (islas Pájaros and Chica) in mid-May 1912, and provided the first indication that the Campeche Bank islands might be significant nesting areas for tropical terns (Kennedy 1917). However, these early accounts were based upon brief visits to one or two islands of a single reef and the avifauna of the islands remained poorly documented until the early 1950's.

During a survey of the birds of the Yucatán Peninsula, Paynter (1955) landed on four islands in 1952 and became the first scientist to describe the colonies of marine birds on more than one of the reef complexes. Although his visits to the islands were made during August and September, probably too late to observe the peak of nesting, Paynter found a few active nests of some species and speculated upon the extent of the colonies. Large flocks of many species remained in the area and the remnants of recently abandoned nests were evident. Interestingly, both Paynter (1953, 1955) and Siebenaler (1954) visited or anchored near several of the Campeche Bank islands in August and September, 1952, but Siebenaler did not mention the presence of nesting seabirds or the existence of seabird nests. Both of these researchers were recording the presence of avian species engaged in trans-Gulf migration.

Kornicker et al. (1959) were on Alacrán Reef in June 1959, but focused their attention on the marine features of the reef. They listed the birds that were seen nesting on the islands without providing information on avian numbers or colony locations. Alacrán Reef was examined again in August and September 1975 by Boswall (1978), who summarized most of the published information on the marine birds of the reef.

The IXTOC I oil spill in the Bay of Campeche focused renewed attention on the seabird colonies in the southern Gulf of México. The spill, which began on 3 June 1979, occurred when an offshore drilling rig blew out at a location just 75 km from a known seabird colony on Cayos Arcas (Clapp et al. 1982). Oil from IXTOC I flowed continuously until March 1980, and an estimated 3.3 billion barrels of oil were released into the Gulf of México (Woods and Hannah 1981). Although few oiled seabirds were recovered along the

Texas coast after the spill (Chapman 1981), the islands of the Campeche Bank were apparently never checked while oil was contaminating the waters of the Gulf (Clapp et al. 1982). The probability was high that many nesting birds were oiled because of the timing of the spill. Duncan and Havard (1980) determined that many species of pelagic birds regularly frequent the northern Gulf of México, an area that was heavily impacted by the spill. Consequently, Clapp et al. (1982) urged that seabird populations in the Gulf of México be surveyed.

Between January and July 1986, one of us (JWT) visited all four coral reef complexes, including 12 islands, on the Campeche Bank. Since some of the islands were visited during the probable peak of the seabird breeding season, we censused the nesting birds on each island and surveyed their colony locations relative to vegetative and topographic features. Although our visits to some islands likely did not coincide with the peak of the nesting season, we are providing the most comprehensive description of the avifauna on the Campeche Bank islands available to date. We suggest that colonies of nesting seabirds are much larger and more widely dispersed among the islands than previously believed. Furthermore, since Alacrán was recently designated as a protected area (Parque Marino Nacional Arrecife Alacrán) and the other Campeche Bank islands are under consideration for protection, we recommend monitoring and conservation programs be developed to sustain these populations as some of the most extensive seabird nesting colonies in the Gulf of México.

## STUDY AREA

The Campeche Bank extends seaward into the Gulf of México 190 to 290 km beyond the northern shoreline of the Yucatán Peninsula. The continental shelf slopes gently from the shoreline to the shelf-slope edge at an overall gradient of approximately 0.5 m per km. The submerged plateau is bordered on the west, north and east by steep slopes which drop from depths of 80-220 m at the shelf-slope edge to the abyssal zones of the Gulf of México. Three major submerged terraces are superimposed upon the bank and occur at depths of 90-110 m, 50-64 m, and 30-37 m (Logan 1962, 1969). A succession of rocky knolls are aligned along the shallowest portions of the 50-64 m terrace and form an almost continuous raised rim around the western and northern margins of the Campeche Bank. Although most of these knolls form topographic highs reaching elevations of 15-45 m below present sea levels, communities of hermatypic corals, encrusting and nodule-forming coralline algae and foraminifera colonize the flanks of some knolls, raising reefs and reef-banks to the surface. Four of these coral reef complexes have low islands (cays) of coral rubble or sand on their tops. These reef complexes consist of 15 permanently emergent islands, 12 of which are vegetated.

The island-reef complexes of the Campeche Bank consist of low islands encircled by shallow-water sand flats, seagrass meadows and reef flats. The reefs are surrounded by clear, tropical oceanic water that flows from the Caribbean Sea into the Gulf of México. Currents generally run from the east or northeast at all Campeche Bank reef complexes, but during the period from November to February, "*nortes*" (winter cold fronts) occasionally reach the area and generate strong winds, wave energy and surface currents from the north.

During most of the year, the prevailing winds are easterly, varying from northeast to southeast, and tidal ranges are minimal, fluctuating from 0.6m to 1.0 m (Wells 1988). Surface water temperatures in the area range from 29° to 30° C during the summer to a minimum of 24° C in the winter (Logan 1969). Brief descriptions of each reef-island complex and their habitats are given below.

### **Arrecife Alacrán**

Alacrán Reef is the largest (25 x 13 km) and most well known of the Campeche Bank reef formations (Kornicker et al. 1959, Fosberg 1962, Kornicker and Boyd 1962, Hoskin 1963, 1966, Bonet 1967, Folk 1967, Chávez et al. 1985, Wells 1988). The Alacrán atoll platform, located approximately 137 km north of Progreso, Yucatán, has five sand cays on its leeward margin (Figure 2). All of the islands are low-lying and their outlines vary seasonally with storms and changing wind directions (Kornicker et al. 1959). The cays support abundant vegetation (Millspaugh 1916, Bonet and Rzedowski 1962, Fosberg 1962) and seabird nesting colonies (Boswall 1978). The larger islands, islas Perez, Desertora, and Desterrada, are situated on the leeward shelf of the reef, whereas islas Chica and Pájaros are located on the southern tip of the inner reef flat. Isla Desterrada was once cut apart by a storm to form islets, East and West Desterrada (Fosberg 1962), that have since rejoined. A sand bar, called Desaparecida Bar, usually is emergent on the middle part of the leeward reef shelf during the summer months, but is eroded by wave action and disappears with the onset of northerly winds. Isla Perez, the largest of the cays (150 m x 870 m), is the only island on Alacrán Reef that has been altered by human activity. The island has a manned lighthouse and weather station and several abandoned buildings that are occasionally occupied by visiting fishermen. Isla Desterrada has an automated light. Some of the islands have local names (in parenthesis) that may cause confusion because they appear in some earlier reports: Desterrada (Utowane); Desertora (Allison; Muertos); and Pájaros (Blanca).

### **Cayo Arenas**

Three reef masses on the northern margin of the continental shelf form the Arenas reef group which consists of four emergent islands (Logan 1969). Three of the emergent islands on this reef are unnamed (Figure 3A). These islands are small, unvegetated and composed primarily of coral rubble (Chávez et al. 1985). Only one island on this reef, Cayo Arenas, is large and elevated enough to support permanent vegetation. The island, which measures 240 m x 275 m across its widest points, is composed of sand in the central and leeward (westward) portions, but the substrate on windward side is mostly coral rubble and solidified beachrock (Busby 1966). A manned lighthouse and weather station are centrally located.

### **Cayo Nuevo**

Nuevo reef is a small reef knoll located on the northwestern margin of the Yucatán shelf (Logan 1969). Cayo Nuevo is a small, crescent-shaped sandy island that sits atop a limestone prominence. The cay remains barren because it is frequently inundated by storm

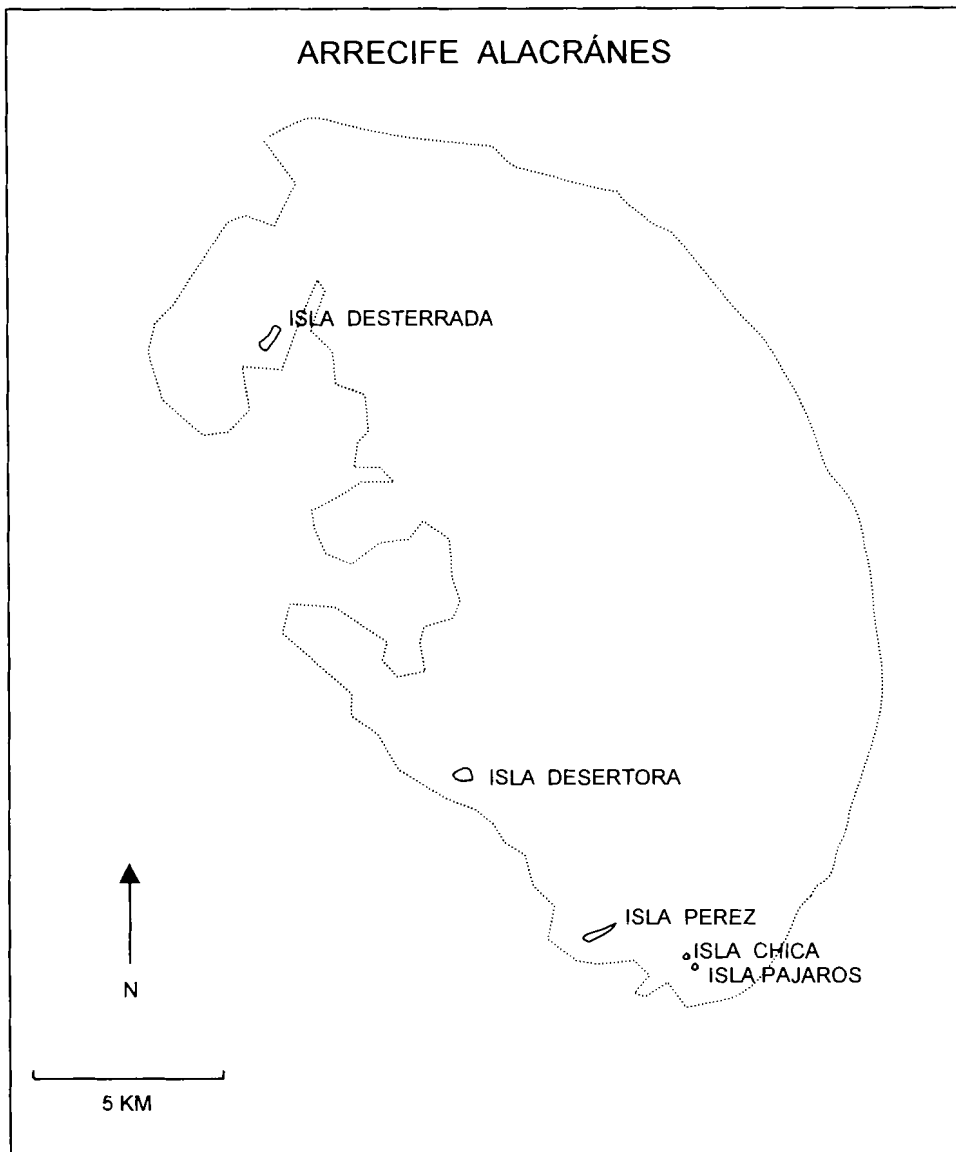


Figure 2. Map of Arrecife Alacrán (Alacrán atoll) showing reef islands on leeward margin.

waves and abnormally high tides. The low-lying island may serve as a roosting and loafing area for birds, but it may be too ephemeral to serve as a nesting area.

### **Arrecifes Triángulos**

The Triángulos reef group is the smallest and least known of the four major Campeche Bank reef-island formations (Chávez 1966, Logan 1969, Chávez et al. 1985). The reef group consists of two submerged ridges each with emergent islands that are located

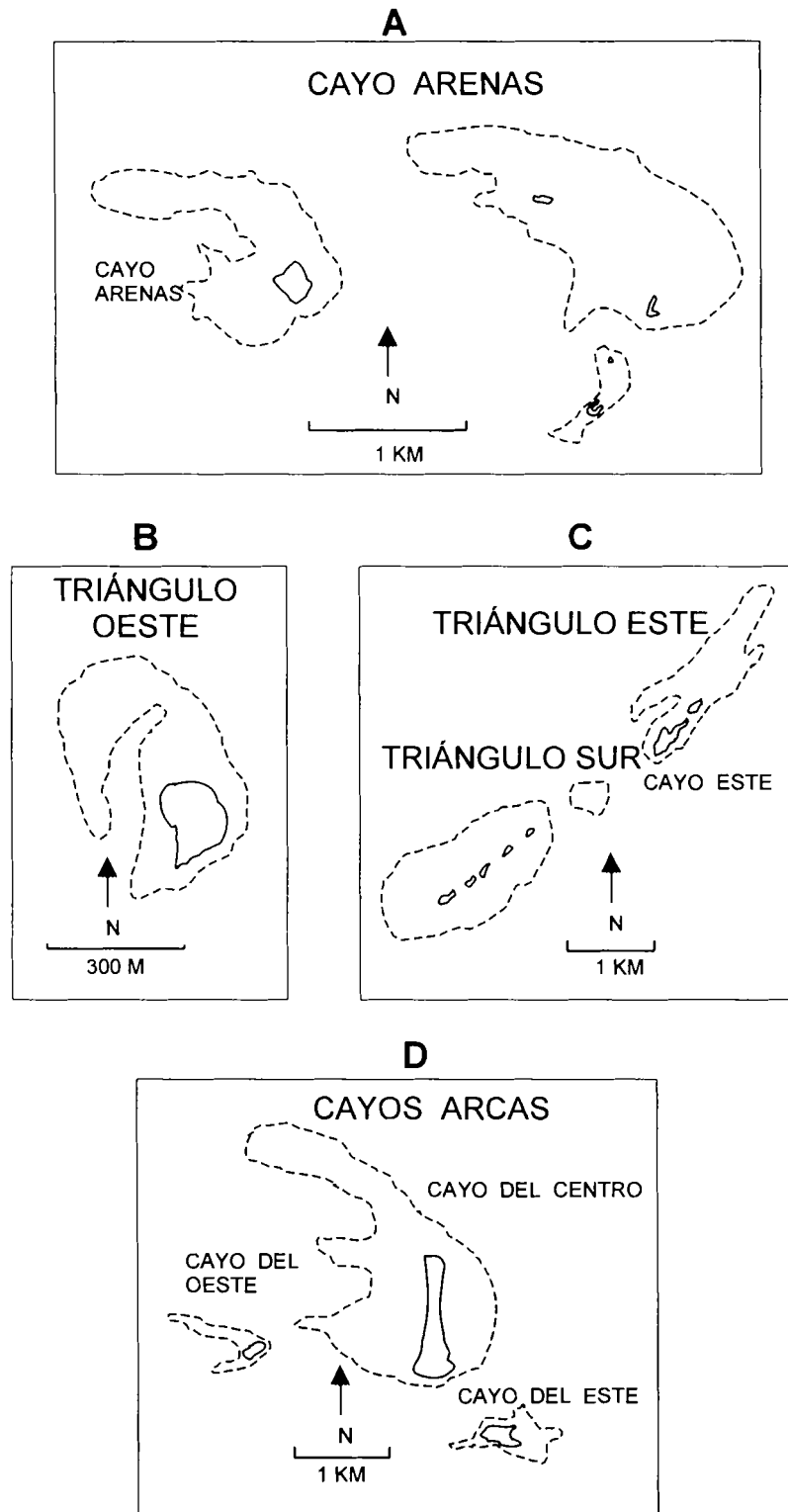


Figure 3. Maps of selected reef islands on Campeche Bank: A) Cayo Arenas; B) Triángulo Oeste; C) Triángulos Este and Sur; D) Cayos Arcas.



approximately 8 km apart (Figure 3B and C). The westernmost ridge has one emergent reef knoll, Triángulo Oeste, a small, sparsely vegetated island. Triángulo Oeste is composed primarily of coral rubble and has a lighthouse and several buildings that house a weather station and lighthouse keepers. The other ridge has several small, uninhabited islands located on two near-emergent reefs, Triángulo Este and Triángulo Sur, which are separated by approximately 800 m of water.

### Cayos Arcas

Cayos Arcas is the southernmost reef-island complex on the Campeche Bank (Figure 3D), and it is also the most impacted by human activity (Tunnell 1992, Chávez and Tunnell 1993). Three reef masses, each with a low sandy cay, are emergent at Cayos Arcas (Logan 1969). Cayo del Centro is the largest island and has a manned lighthouse and weather station in addition to PEMEX buildings, tugboat mooring facilities, two helicopter pads, a volleyball court and a soccer field. A brief description of the vegetation on this island was provided by Paynter (1953) and Howell (1989). Cayo del Este, located approximately 1,500 m southeast of Cayo del Centro, is a small (140 m x 340 m), teardrop-shaped island. A proprietary PEMEX report listed seven species of plants that are found in a low, vegetated ridge that transverses the island. Cayo del Oeste, a diminutive (95 m x 130 m) island, having only a small, centrally located patch of vegetation, is located approximately 600 m west of the southernmost tip of Cayo del Centro.

### METHODS

Initial access to the islands in the reef complexes of the Campeche Bank was aboard Mexican Navy vessels that disembarked from Progreso, Yucatán. A second trip to Arrecife Alacrán (July, 1986), was aboard a *Departamento de Pesca* vessel that departed from Yucalpeten, just east of Progreso. The islands of Arrecife Alacrán were visited during two periods from 20-31 January 1986 and 4-14 July 1986. The islands of Cayo Arenas were visited from 16-23 March, Arrecife Triángulos from 6-7 May, and Cayo Arcas from 20-26 April 1986. Surveys at the islands included camping on the islands, staying in lighthouse facilities at Alacrán, Arenas, and Arcas, and living aboard ship but making daily visits at Triángulo Oeste.

Complete counts of all nests on each island were made by dividing the island into sections, usually by vegetation type. However, the complexity of the vegetation and the close placement of nests made this technique impractical on Isla Perez and Isla Desertora, Arrecife Alacrán. Strip transects were used to estimate Brown Noddy (*Anous stolidus*) nests in 1.5-2.0 m-high *Suriana maritima* bushes on Isla Perez. A panoramic series of photographs were taken of the Masked Booby (*Sula dactylatra*) colonies on Isla Desertora and the photographic prints were overlapped in the laboratory to form total views of the colony areas. Counts of the birds on nests visible in each panorama were made to estimate the number of nests in each nesting area. Care was taken to identify situations where two adult birds might be present at a single nest and correct the nest count accordingly. We attempted to underestimate, rather than overestimate, the number of nests on each island.

In addition to counting or estimating nests, we also collected data on clutch size, the distance between nearest nests within colonies, and the ratio of occupied to empty nests on most islands. All avian censuses were conducted during the early morning or late evening hours to minimize disturbance to the birds and to avoid overheating of eggs or young.

## RESULTS

Eight of the 12 permanently emergent Campeche Bank islands had active seabird nesting colonies during the study period. Nine species of colonial seabirds nested on the islands: Masked Booby; Brown Booby (*Sula leucogaster*); Red-footed Booby (*Sula sula*); Magnificent Frigatebird (*Fregata magnificens*); Laughing Gull (*Larus atricilla*); Royal Tern (*Sterna maxima*); Sandwich Tern (*Sterna sandvicensis*); Sooty Tern (*Sterna fuscata*); and Brown Noddy. Descriptions of colony locations in relation to vegetation or other island features and the results of bird censuses on each island are presented in the island accounts. Information on total numbers, habitat use, and breeding status of each species is provided in the species accounts.

### Island Accounts

#### Arrecife Alacr nes

Arrecife Alacr nes was the only reef-island complex that was visited twice during the study. All five islands of this reef were sites of seabird nesting activity. The vegetation of the four most southerly islands was identified and mapped in 1899 by Millspaugh (1916), but Bonet and Rzedowski (1962) observed that the plant communities had changed considerably by the time of their survey in 1961. We found that additional changes in the species composition and distribution of vegetation had occurred in the intervening quarter of a century.

Isla Perez – The largest and most complex cay on the Alacr n platform, Isla Perez, was shaped like a shallow crescent with the long axis oriented towards the northeast (Figure 4). The island was flat with an average elevation of 1.3 m, but it had an elongate ridge that reached nearly 3.0 m in height just inland from the eastern shoreline. Bonet and Rzedowski (1962) listed 13 species of plants from Isla Perez. *Surina maritima* still covered most of the southern and northeastern ends of the island. The number of *Casuarina equisetifolia* (introduced Australian pine) increased since Bonet and Rzedowski's (1962) survey. The species was still common around the buildings and lighthouse in the central part of the island, but it had extended its distribution both northward and southward. The lee (west) side of the island was characterized by a broad, carbonate sand beach that fronted a low set of sand dunes dominated by *Tournefortia gnaphalodes*. A mixed grass-herbaceous community dominated by *Cenchrus* spp. occupied the strip between the dunes and the *S. maritima* stand. The *Opuntia dillenii* colonies had greatly expanded in size, but the small southwestern lagoon and mangroves had disappeared. A small pond encircled by *Avicennia germinans*, and not mentioned by Bonet and Rzedowski (1962), was found on the southeastern tip of the island. Two *Rhizophora mangle* plants also were found on the edge of the pond; this species was not reported previously on any Campeche Bank island.

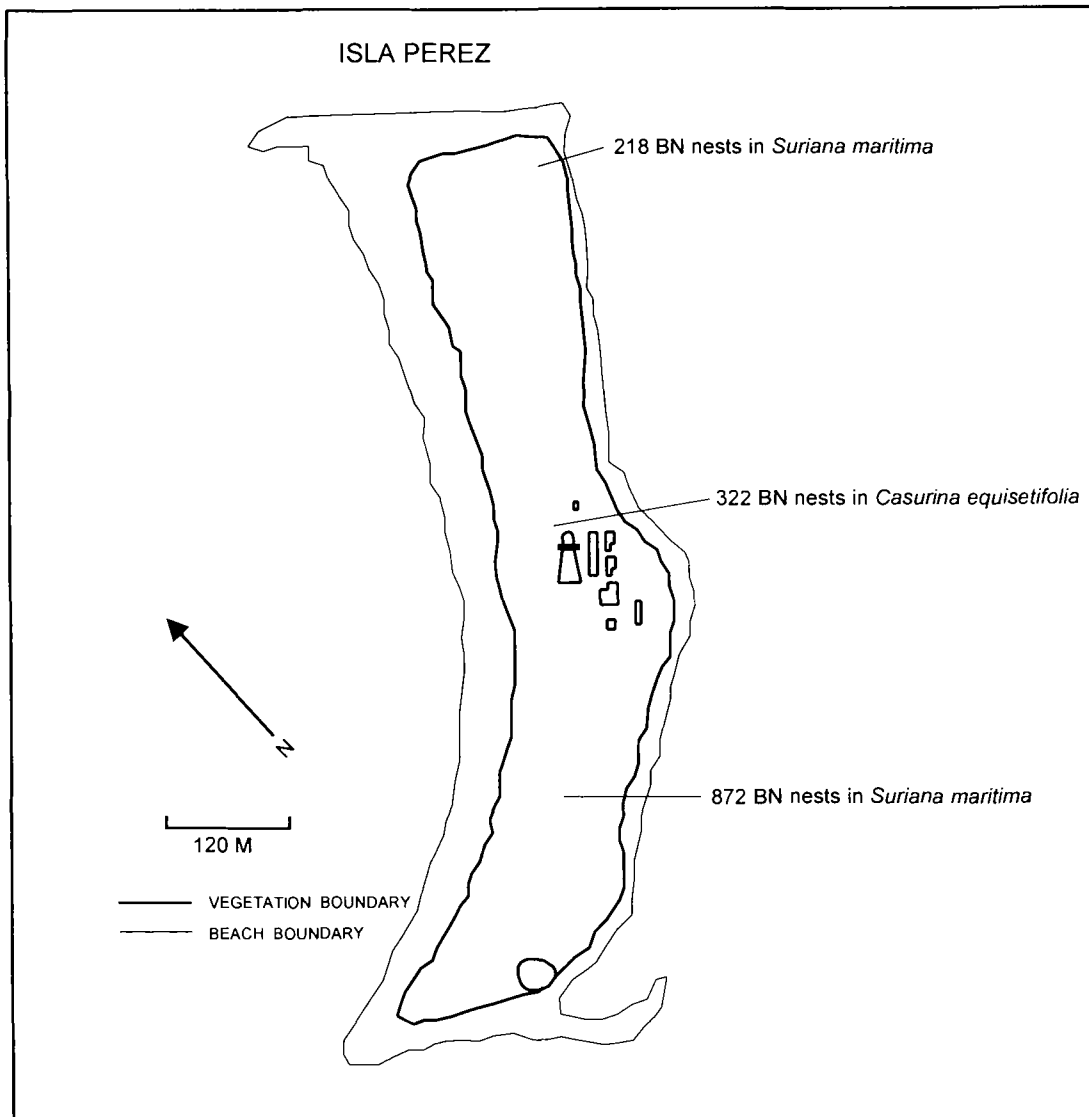


Figure 4. Schematic of Isla Perez, southwestern Alacrán Reef platform, showing Brown Noddy (BN) nesting locations.

No seabirds were nesting on Isla Perez when the island was visited in January. However, large colonies of Sooty Tern and Brown Noddy were active in July. The Sooty Tern colony occupied the northern portion of the island. Nests were scattered in barren areas within the *T. gnaphalodes* and *Cenchrus* spp. communities and beneath the *S. maritima* bushes. The Brown Noddy colony was located in the central and southern parts of the island. Nests were constructed in the branches of *S. maritima* and *C. equisetifolia*.

The Sooty Tern colony (Figure 5) was censused on 11 July 1986. It was impossible to obtain an accurate count of nests because the young birds had abandoned many nests to



Figure 5. View to south of Sooty Tern over *Cenchrus* spp. vegetation on northwestern corner of Isla Perez, Alácran Reef, 7 July 1986.

seek shade under the low bushes and trees. Consequently, we attempted to count the number of adult and juvenile birds in each vegetative community. Our counts were fairly accurate in the more open habitats, but we experienced difficulty in making counts of the immature birds in the *S. maritima* areas. Immature birds in this area continuously scrambled about below the bushes. We counted a total of 26,160 Sooty Terns on the island. Of these, 13,570 were adult birds and 12,590 were juveniles. No Sooty Tern eggs were found during this survey. Approximately 75% of the terns were concentrated in the northernmost 150 m of the island, the area farthest removed from the buildings.

The Brown Noddy colony on the southern part of Isla Perez was censused on 7 July 1986. Nine transects running perpendicular to the axis of the island were censused by four people walking abreast. We counted 872 nests, but 555 were empty, 283 contained chicks and 34 had one egg each. Approximately 90% of the empty nests appeared to have been used for nesting and recently abandoned; the remainder looked as if they had not been used recently. Most of the nests were constructed in *S. maritima* and were from 0.15-1.5 m above the ground (Figure 6). The remainder of the nests in *C. equisetifolia* were situated 0.6-6.1 m above ground. The nests were constructed of sticks and most contained broken pieces of mollusk shells, most commonly the shells of an abundant lagoonal bivalve, *Codakia orbicularis*.

Within the central portion of the island, Brown Noddy nested only in *C. equisetifolia* trees. As many as 20 nests were found in a single tree and up to eight nests were placed on a single tree branch. We counted 322 nests in this area and most nests contained incubating or brooding adults. Egg and chick counts were not possible because most nests were constructed several meters above the ground.

Approximately 218 Brown Noddy nests also were located in *S. maritima* bushes in the middle of the Sooty Tern colony on the northeastern end of the island. Consequently, a total of 1,412 Brown Noddy nests on Isla Perez were counted in the three areas (see Figure 4). We believe that at least 1,357 of these nests were active during the preceding six months.

Isla Pájaros – The dimensions of Isla Parajos were estimated to be 183 m x 655 m in 1960 (Folk 1967), but we found the elevated, vegetated portion to be only half of the indicated length. The southern part of the island and mangrove lagoon that was described by Folk existed in 1986 only as a barren coral rubble spit. The remaining island was triangular with the spit extending southward. The central part of the island was lower than the periphery and existed as a flat sand plateau that was 1.0-1.5 m above sea level and covered with low vegetation. Bonet and Rzedowski (1962) listed 11 species of plants on the island. *Sporobolus virginicus* occurred around the periphery of the plant community and *Sesuvium portulacastrum* occupied the center. A few *S. maritima* and *T. gnaphalodes* bushes were scattered on the north and west sides of the island.

Only three nesting pairs of Masked Booby were found on the island in January. Each nest contained a single egg. Three active Masked Booby nests were observed in July. One nest contained a large downy chick and the other two nests held juveniles that were almost



Figure 6. Brown Noddy on nest filled with broken bivalve shells in *Suriana maritima* bush on south end of Isla Perez, Alácran Reef, 6 July 1986.

mature enough to fly. During both survey periods, the nests were located in barren sites among the *S. portulacastrum* plants in the center of the island.

Isla Chica – Located north of Isla Pájaros and across a narrow, deep-water passage, Isla Chica, the smallest of the Alacrán islands, was estimated to be 122 m wide by 198 m long in 1960 (Folk 1967), but appeared to be 70 m x 150 m in 1986. The island was shaped like an acute triangle with the acute apex pointed toward the southwest. The island was flat except for a slightly raised rim. There was a central grassy flat that was dominated by *S. virginicus* but with some patches of *S. portulacastrum*. A few low shrubs of *S. maritima* and *T. gnaphalodes* were present on the northeastern side of the island.

Although 18 Magnificent Frigatebirds were seen loafing on Isla Chica in January, no nesting birds were observed during that visit. Three species, Laughing Gull, Royal Tern, and Sandwich Tern, were nesting when the July visit was made. All nests were situated along a sandy berm on the northeastern margin of the island (Figure 7). The Sandwich Terns nested in two subcolonies. One subcolony occupied an area that was about 5 m in diameter and contained 43 nests. Eight of these nests contained newly hatched chicks. The remainder of the nests contained single eggs. The other Sandwich Tern subcolony contained 108 nests, but many of these nests were occupied by chicks that were mobile.

Royal Tern numbers were estimated from the number of chicks present because the nests were placed close to the vegetation and were difficult to see. Twenty-eight chicks were counted. Three Laughing Gull nests also were found in the vegetation near the tern nests.

Isla Desertora – Like Isla Pájaros and Isla Chica, Isla Desertora also appeared to be smaller than Folk (1967) described. The island retained its triangular outline, but was shorter and broader, measuring approximately 300 m x 700 m. A wide sandy beach encircled the island in front of a 1.5-2.0 m-high berm. The central portion of the island behind the berm was sparsely vegetated with a variety of species including *Cenchrus* spp., which was probably the most common plant. There were widely scattered, but locally dense, patches of *S. portulacastrum*, *S. virginicus*, *Tribulus alacranensis*, *Cakile edentula*, *Portulaca oleracea*, *Chamaesyce buxifolia*, and *O. dillenii*. The sandy berm along the northern edge and in the southwestern corner of the island was occupied by stands of *T. gnaphalodes*. A few *S. maritima* also were scattered in the southwestern part of the island.

The largest nesting concentrations of Masked Booby and Magnificent Frigatebirds on all the Campeche Bank islands existed on Isla Desertora. There were twice as many active nests of Masked Booby and six times more active nests of Magnificent Frigatebirds in January than there were in July. Red-footed Booby also were nesting on the island during both survey visits (Tunnell and Chapman 1988).

The main concentrations of Masked Booby nests in January were in the barren to sparsely vegetated areas on the northwestern and north-central sides of the island (Figure 8). A few nests also were scattered in open areas throughout the island. Within the areas having dense aggregations of nests, the nests contained large downy young or pre-flight juveniles. The nests in peripheral locations, however, mostly contained single eggs. Only one nest with



Figure 7. View to north over nesting colony of Royal and Sandwich terns and Laughing Gull on eastern end of Isla Chica, Alácran Reef, 7 July 1986.





Figure 8. View to northwest over Masked Booby nesting colony in central Isla Desertora, Alácran Reef, 28 January 1986.

two eggs was observed. Based upon an analysis of panoramic photographs of the island taken on 28 and 29 January, we estimated that 2,533 Masked Booby nests were present on the island.

In July, the Masked Booby nests were concentrated in two areas. The north-central subcolony had approximately 750 nests. This estimate was made by attempting to count nests from a location about 20 m from the periphery of the subcolony; the subcolony area was not entered because the daytime temperatures were too high. The nests in this area all contained eggs. The second subcolony was located in a sparsely vegetated region on the southwestern end of the island. This subcolony contained approximately 225 nests. Some nests in this area contained eggs, but there were nests with young in all stages of development. About 75% of the nests with eggs contained two eggs. About 50 additional Masked Booby nests were scattered about the island. Some of these nests were occupied by pairs of birds that were engaged in courtship rituals.

The Magnificent Frigatebird nests were located exclusively in thickets of *T. gnaphalodes* bushes (Figure 9). In January, there were seven distinct subcolonies of frigatebird nests on bushes just inland from the northeastern berm and three subcolonies near the southwestern corner of the island. A total of 163 nests were found in the northeastern subcolonies and 43 were counted in the southwestern subcolonies. Most of the nests contained eggs, but a few held small downy chicks. Many of the bushes supporting the nests appeared to be dead. When the July visit was made, frigatebird nesting activity appeared to be near the end of a cycle. Only 33 active nests were found, 31 in the northeastern area and two in the southwestern corner. All of the nests but one were occupied by large chicks. One nest, however, held two freshly hatched, naked chicks.

The Red-footed Booby nests also were situated in *T. gnaphalodes* bushes (Figure 10). Two active nests were found in January and one nest was found in July (Tunnell and Chapman 1988). Each nest contained a single egg.

Although no other seabirds were nesting during the January visits to Isla Desertora, small flocks of Sooty Tern and Laughing Gull harassed us when we were near the southeastern portion of the island in July. We found 10 juvenile Laughing Gull and 10 juvenile Sooty Tern hiding under vegetation (*S. maritima*) so dense that we may have missed other chicks. Brown Pelican (*Pelecanus occidentalis*) and immature Brown Booby were resting on the northwestern shore of the island during the January visit.

Isla Desterrada – Formed from the union of two islands, East and West Desterrada (Folk 1967), Isla Desterrada was over 2,000 m long. Vegetated portions occupied what was once the centers of the two islands at either end. Low sand dunes existed on the northern shores of the two vegetated areas. *Tournefortia gnaphalodes* was found in patches on and just behind the dunes, but the central portions of each vegetated area were composed of low-growing plants. The plant association consisted of *C. edentula*, *C. buxifolia*, *P. oleracea*, *Cenchrus* spp., and *T. alacranensis*. An automated light was present on the western end of the island but the light was turned over onto its side and was not functional. A concrete



Figure 9. View to northeast over Magnificent Frigatebird nesting in *Tournefortia gnaphalodes* adjacent to low dunes and beach on north side of Isla Desertora, Alácran Reef, 9 July 1986.



Figure 10. Red-footed Booby nesting in *Tournefortia gnaphalodes* in north-central portion of Isla Desertora, Alácran Reef, 9 July 1986.

platform, apparently a base to an old light, stood about 150 m offshore of the eastern end of the island and was extensively used as a seabird loafing perch.

We observed no nesting activity on the western end of island in January. During July, we found 50 juvenile Laughing Gull either walking or flying about the western end of Isla Desterrada. Because the walking young appeared unable to fly, we concluded that the western part of the island served as a colony site for the gulls but we could find no nests. Approximately 400 adult Laughing Gull circled the island or rested on its beaches during the visit.

Brown Booby and Magnificent Frigatebird were nesting on the eastern end of Isla Desterrada in January. Ten active Brown Booby nests were found on sandy substrates within the sparsely vegetated area, but it appeared that many more Brown Booby had just completed their nesting activities. Five of the nests contained eggs (three with one egg; two with two eggs), and the other nests held chicks. Approximately 200 Brown Booby were seen on the eastern end of the island and about 35% of those were immature birds.

We counted 52 Magnificent Frigatebird nests in low *T. gnaphalodes* bushes. Only 17 of the nests contained eggs and the remainder were empty. However, approximately 750 frigatebirds were seen flying above the island in a large "kettle" as we approached in both January and July.

The eastern end of Isla Desterrada had no active nests during the July visit. However, 65 adult Brown Booby, two Brown Pelican, two Black Skimmer (*Rynchops niger*), and approximately 30 Royal Tern, 30 Sandwich Tern and 40 Laughing Gull were loafing on the beach.

### **Cayo Arenas**

Three small, unnamed, barren islands showed no sign that they were used as nest sites. Only the largest vegetated island, Cayo Arenas, contained an active colony of nesting Masked Booby. A strong "norte" causing rough seas confined investigators to the island for several days and consequently allowed the booby colony to be thoroughly surveyed.

Situated on the leeward reef platform, Cayo Arenas had a maximum elevation of 3 m and measured 240 m x 275 m at its widest points. A lighthouse was centrally located on the island (Figure 11). Calcareous sand formed most of the island substrate, but coral boulders were distributed along the eastern side. Large "thickets" of *T. gnaphalodes* occupied the dunes on the west side and the entire northern quarter of the island. Colonies of *O. dillenii* were distributed throughout the southern end of the island and the cactus appeared to be expanding and choking out the *T. gnaphalodes* in some locations. The cactus also occurred in a smaller area of the southwestern island corner. Low vegetation, including *Ipomoea pes-caprae*, *P. oleracea*, and *Cenchrus* spp., were found in zones surrounding the lighthouse area. The lighthouse was also surrounded by introduced vegetation such as *C. equisetifolia*, *Cocos nucifera* (coconut palm), *Crinum americanum* (spider lily), and *Cordia dodecandra* (siricote).

## CAYO ARENAS

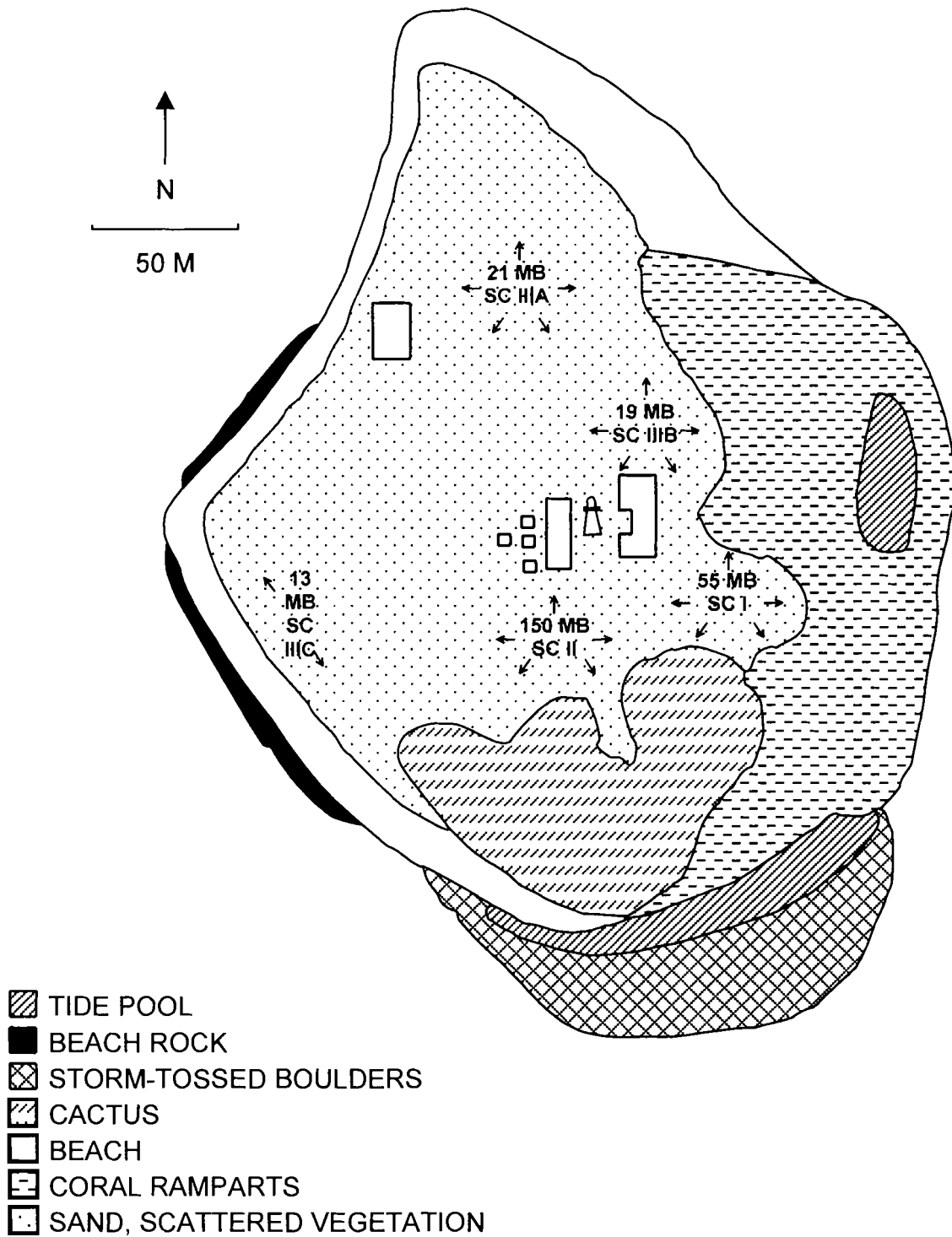


Figure 11. Cayo Arenas showing distribution of substrate types and location and number of nests in three Masked Booby subcolonies (I, II, III A, B, C).

Three Masked Booby subcolonies were evident. Subcolony I was located to the southeast of the lighthouse on the east-central part of the island and contained 55 nests. The nests were located in areas of bare sand interspersed among patches of *P. oleracea*, scattered coral rubble, and boulders. The colony area was bounded to the north by a coral boulder field and to the south by a stand of *O. dillenii*. The birds in this subcolony must have been the first to initiate nesting because most of the young were nearly ready for flight. A few nests, however, contained eggs or downy chicks.

Subcolony II, containing 150 nests, was located in a large, sandy, barren area south of the lighthouse (Figure 12). It was protected from prevailing winds by the lighthouse and the associated buildings to the north, dense colonies of *O. dillenii* to the east and southwest, and a hedge of *T. gnaphalodes* to the west. The nests contained eggs or chicks, but none of the chicks were over 20 days old. Average distances between nearest nests were determined for two sets of 20 adjacent nests in this subcolony. One set of nests was centrally located in a barren sandy area and the other set was in an area where *P. oleracea* grew between the "scrape" nests. Inter-nest distances were greater in the *P. oleracea* area. Mean inter-nest distance was 2.9 m ( $s = 1.08$ ) where vegetation was present but was only 1.6 m ( $s = 0.42$ ) when nests were in bare sand.

The third subcolony, located on the periphery of the island, was loosely defined. The nests in this subcolony were scattered through several low-growing vegetative associations or areas of bare sand. All 53 nests in this subcolony contained eggs.

A total of 258 active Masked Booby nests were counted on Cayo Arenas (Figure 13). We found an additional 17 abandoned nests that contained eggs in a bare sandy area between subcolonies I and II. A domestic cat and dog were kept as pets on the island and these animals may have been responsible for some egg and chick loss or nest abandonment. The dog, which on two occasions was observed returning to the lighthouse from the area of subcolony III, appeared to have severe puncture wounds all over his head, especially around his eyes and nose.

The coral boulder area on the northeastern margin of the island was used as both a daytime loafing area and a night roost by the boobies. Up to 300 birds congregated in the area at night. Other birds observed on or near Cayo Arenas included 15 Magnificent Frigatebird, an Osprey (*Pandion haliaetus*), 7 Great Blue Heron (*Ardea herodias*), 3 Great Egret (*Ardea alba*), 2 Tricolored Heron (*Egretta tricolor*), 7 Cattle Egret (*Bubulcus ibis*), a Black-crowned Night-Heron (*Nycticorax nycticorax*), 13 Ruddy Turnstone (*Arenaria interpres*), 3 Laughing Gull, 47 Royal Tern, 3 Sandwich Tern, 2 Yellow-rumped (Myrtle race) Warbler (*Dendroica coronata*), a Barn Swallow (*Hirundo rustica*), and many small shorebirds.

### **Arrecifes Triángulos**

An emergency sea-rescue operation diverted the ship before Triángulos Este or Sur could be visited. Triángulo Oeste was surveyed, however.



Figure 12. View to northwest of Masked Booby Subcolony II on Cayo Arenas, 17 March 1986.





Figure 13. Masked Booby nesting pair and chick on Cayo Arenas, 17 March 1986.

Triángulo Oeste – The only vegetation on Triángulo Oeste is a row of *T. gnaphalodes* that stretched eastward from the lighthouse, some scattered *C. buxifolia*, a single *S. maritima*, and one *C. nucifera*. No nesting activity was observed on this small coral rubble island.

Magnificent Frigatebird were the only seabirds seen in the area and they were riding the up-drafts next to, and over, the lighthouse and associated dwellings.

Triángulos Este and Sur – The lighthouse keeper on Triángulo Oeste reported that "gaviotas" nested on Triángulos Este and Sur. Unfortunately, "gaviota", which is Spanish for "gull" or "tern", is a generic term used by the local fishermen to include most species of seabirds. The presence of many gulls, terns and boobies roosting on or circling the islands was confirmed with binoculars from the ship's deck. However, we could not determine whether or not nesting was taking place.

### **Cayos Arcas**

Cayos Arcas has become an offshore staging area for a rapidly developing oilfield on the surrounding continental shelf. An offshore platform terminal, two floating oil loading terminals, and two oil tankers were visible from Cayo Centro during the bird census. Closer to shore, and within the natural protection of the leeward lagoon, 6-15 tugboats and oilfield service boats always were present. Oilfield debris was observed on the islands and surrounding reefs. Despite this level of human activity, two of the three islands in this reef-island complex had active colonies of Masked Booby and Magnificent Frigatebird.

Cayo del Centro – The largest of the islands in the Cayos Arcas complex, Cayo del Centro was approximately 850m long and oriented in a north-south direction (Figure 14). It was somewhat broader at the north end (300 m) than at the south end. A sandy beach encircled the island, but there were a few areas of coral rubble and tidal pools along the narrow eastern shore. The vegetation was predominately low ground cover. *Cenchrus* spp. and *S. portulacastrum* were the most common components of the ground cover, but the eastern beach ridge had scattered patches of *T. gnaphalodes* and *Scaevola plumieri* bushes. A small *A. germinans* swamp surrounded by *Batis maritima* was located on the southwestern edge of the island. Around the lighthouse and other buildings, there were several introduced species including *C. equisetifolia* and one *C. nucifera*.

Masked Booby nesting on Cayo del Centro were segregated into five subcolonies. Two subcolonies were situated on bare sand areas on the northwest and southwest margins of the island (Figure 15) and the other three were located within the low vegetation near the center of the island. We counted a total of 453 Masked Booby nests that contained eggs or young. An additional 203 immature booby chicks that had apparently left their nests also were counted. Based upon these counts, we estimated that the Masked Booby colony on Cayo del Centro contained in excess of 600 nests.

Magnificent Frigatebird also nested within distinct subcolonies on Cayo del Centro. All of the 15 subcolonies except one were located in clumps of elevated vegetation (Table 1). The highest densities of nests were located in *A. germinans* and atop *S. maritima* bushes.

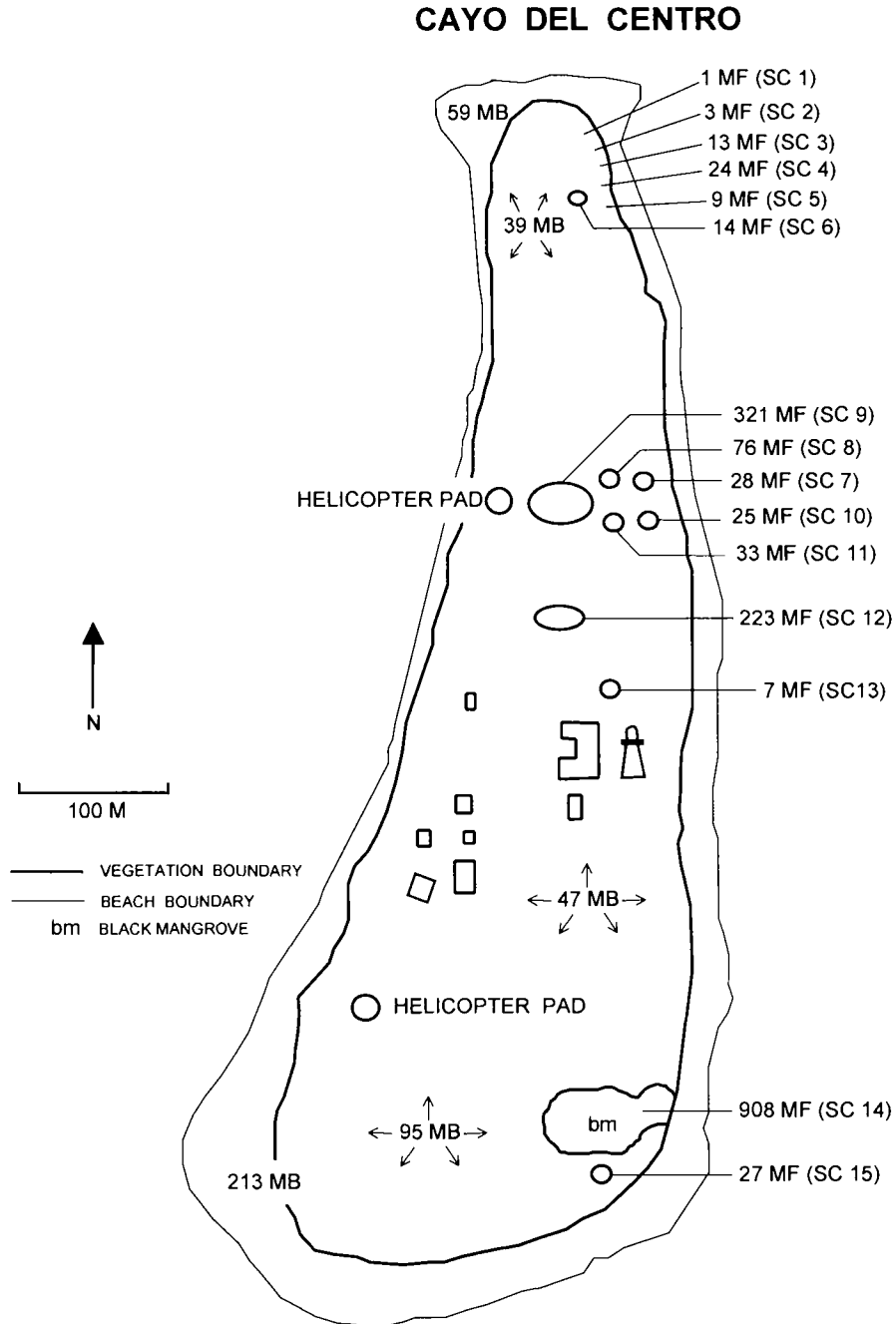


Figure 14. Cayo del Centro in Cayos Arcas reef group, showing Masked Booby (MB) and Magnificent Frigatebird (MF) subcolonies (SC), 21 April 1986.



Figure 15. View to northwest over Masked Booby nesting colony on upper beach berm, southwestern corner, Cayo del Centro, Cayos Arcas, 21 April 1986.

Table 1. Number of nests and chicks in the 15 different subcolonies of Magnificent Frigatebird on Cayo del Centro, Cayos Arcas, 21 April 1986.

Subcolony Number <sup>1</sup>	Number of Nests	Number of Chicks	Vegetation; Location
1	1	1	<i>T. gnaphalodes</i> ; northeast dunes
2	3	2	<i>T. gnaphalodes</i> ; northeast dunes
3	13	10	<i>T. gnaphalodes</i> ; northeast dunes
4	24	25	<i>T. gnaphalodes</i> ; northeast dunes
5	9	8	<i>T. gnaphalodes</i> ; northeast dunes
6	14	13	<i>S. maritima</i> ; inland from northeast dunes
7	28	24	<i>S. maritima</i> ; northeast central
8	76	71	<i>S. maritima</i> ; northeast central
9	321 <sup>2</sup>	255	<i>S. maritima</i> ; central, north
10	25	13	<i>S. maritima</i> ; northeast central
11	33	13	<i>S. maritima</i> ; northeast central
12	223	176	<i>S. maritima</i> ; central, north
13	7	4	<i>S. maritima</i> ; east, central
14	908 <sup>2</sup>	720	<i>A. germinans</i> ; southwest
15	27	23	<i>B. maritima</i> ; southwest
TOTAL	1,712	1,358	

<sup>1</sup> Arranged from north to south.

<sup>2</sup> Nests counts for subcolonies 9 and 14 were calculated by an average ratio of other subcolony nests to chicks, since densities were so high and nests were so close together, counting in the field proved impossible.

One subcolony was composed of nests placed on the ground within dense thickets of *B. maritima*. Almost all of the elevated nesting habitats preferred by the frigatebirds appeared to be utilized. In some subcolonies, the nests were less than 0.3 m apart and the guano deposits appeared to be killing the bushes. In others, the nests were built atop mounds of guano that were 0.5 m high (Figure 16). We counted 1,712 nests and all of the nests contained chicks.

Cayo del Este – The vegetation on this island was low and consisted predominantly of *Cenchrus* spp. and *S. portulacastrum*. Several clumps of dead *T. gnaphalodes* and *S. maritima* bushes also were scattered about the island (Figure 17). Only two species of birds, Masked Booby and Magnificent Frigatebird, were nesting on Cayo del Este, but Sooty Tern, Royal Tern, Sandwich Tern and Laughing Gull were common around the island.

Masked Booby nested within two subcolonies. One subcolony, located on the eastern end of the island, contained 58 nests. All of these nests held eggs except for two that contained chicks. The other subcolony, comprised of 40 nests with either eggs or chicks in various stages of development, was established on the western end of the island.



Figure 16. View to southeast of immature Magnificent Frigatebirds in nesting colony on dead or dying *Tournefortia gnaphalodes* bushes, north-central Cayo del Centro, Cayos Arcas, 21 April 1986.

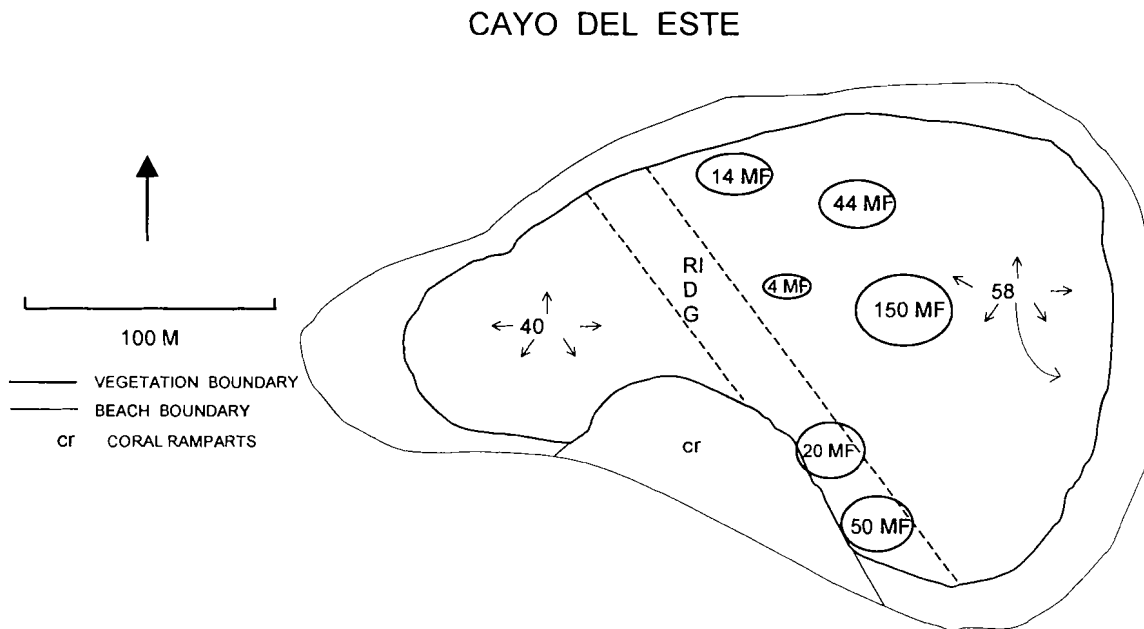


Figure 17. Cayo del Este in Cayos Arcas reef group showing Masked Booby (MB) and Magnificent Frigatebird (MF) subcolonies, 21 April 1986.

Magnificent Frigatebird nested in six subcolonies on Cayo del Este. The largest subcolony, located near the center of the island, was situated in a barren area where the nests were constructed on the ground or on small mounds of guano (Figure 18). Many of the nests appeared abandoned. The remainder of the subcolonies were positioned in clumps of *T. gnaphalodes* or *S. maritima* bushes. Most of the bushes in these clumps were dead. There was a total of 282 nests which contained 198 chicks in the six subcolonies. We found no eggs and all of the chicks were large but unable to fly.

Cayo del Oeste – There was no nesting activity on Cayo del Oeste when the island was visited late in the afternoon of 22 April. The small central patch of vegetation contained only two *S. maritima* bushes and these bushes were used as resting or roosting sites by frigatebirds.

### Species Accounts

The stage in the breeding cycle is one of the most important factors in determining the accuracy of population estimates in colonially nesting seabirds (Nelson 1979, Duffy and Nettleship 1992). In more equatorial regions some individuals of certain species breed during every month (Nelson 1978) and the adults and young leave the colonies when the young fledge. The constant turnover of breeding pairs at a site complicates the census of a seabird population.



Figure 18. View to northeast of immature Magnificent Frigatebirds in nesting colony of dead *Tournefortia gnaphalodes* surrounded by *Sesuvium portulacastrum*, Cayo del Este, Cayos Arcas, 21 April 1986.



Unfortunately, the annual breeding cycle of seabirds in the southern Gulf of México is poorly known and, consequently, we cannot be sure that our visits to the islands coincided with the peak of the breeding cycle. In the species accounts below we discuss the breeding status of the Campeche Bank seabirds and compare our notes to published information. English and scientific names in the species accounts, and the taxonomic sequence in which the species are listed, follow the American Ornithologists Union Checklist (A.O.U. 1998). The species accounts provide a complete historical summary of nesting records for each species on each island. We also comment on our survey results.

### **Masked Booby (*Sula dactylatra*)**

Masked Booby are among the most abundant and widely distributed members of the Sulidae and are found throughout the pan-tropical blue water belt (Nelson 1978). A highly pelagic species that feed primarily on flying fish and squid (Murphy 1936, Anderson 1993), Masked Booby rarely feed inshore (Kepler 1969). Throughout their range, these boobies nest on small barren or poorly vegetated islands (Gillham 1977) in colonies that are relatively small and of low density (Clapp et al. 1982). As few as a single pair may nest on some islands (Dorward 1962) but several colonies with up to 2,500 pairs are known (Nelson 1967), and at least one colony may have as many as 15,000 pairs (Hutchinson 1950). Most colonies contain from 50 to several hundred pairs (Nelson 1978, Clapp et al. 1982). Because the colonies on the Campeche Bank islands have been inadequately described, van Halewyn and Norton (1984) concluded that the Masked Booby was the scarcest booby in the Caribbean.

Probably because of their size and conspicuousness, there are more historical records of Masked Booby nesting on the Campeche Bank islands than any other species (Table 2). At various times Masked Booby have been recorded nesting on all but four of the 12 islands in the four largest reef complexes. We found a combined total of 4,519 active nests on five of the islands and we provided the first record of a Masked Booby colony on Cayo del Este.

The period of peak nesting for Masked Booby on the Campeche Bank islands is not known. The inhabitants of Cayos Arcas told Paynter (1955) that the peak nesting season was in June and July and Clapp et al. (1982) concurred. Nelson (1978) suggested that Masked Booby in the Caribbean and Atlantic nested annually with the period of heaviest laying occurring between February and mid-August. A second season of an intermediate amount of laying may also occur from November to January (Nelson 1978). The historical record (Table 2) indicates that Masked Booby nesting activities have been observed in all months except December and February. Since we found many more active nests in January than we did in July on Isla Desertora and Boswall (1978) reported that 2,000 adults and young were present on Isla Desertora in September, the nesting cycle on the Campeche Bank islands may differ from those found elsewhere in the region. We suspect that some Masked Booby may be engaged in various stages of breeding activities throughout the year in the southern Gulf of México. Peaks in the breeding cycle and usage of some islands may be somewhat irregular as is common elsewhere among Masked Booby populations (Nelson 1978, Anderson 1993).

Table 2. Historical record and summary of seabird colonies on Campeche Bank reef islands (NC = no comment on colony status or size; “?” = date not mentioned).

Reef Group or Island	Species/Colony Size	Date	Source
<b>Arrecife Alacrán</b>	Boobies/“vast abundance”	1675	Dampier 1699
	Magnificent Frigatebird/NC	1675	Dampier 1699
	Egg-birds/(? = Sooty Terns)/NC	1675	Dampier 1699
	Boobies /“swarms”	?	Smith 1838
	Magnificent Frigatebird/NC	?	Smith 1838
	Sooty Tern/“nesting”	?	Lowery & Newman 1954
	Masked Booby/“nesting”	June 1959	Kornicker et al. 1959
	Brown Booby/“nesting”	June 1959	Kornicker et al. 1959
	Magnificent Frigatebird/“nesting”	June 1959	Kornicker et al. 1959
	Laughing Gull/“nesting”	June 1959	Kornicker et al. 1959
	Royal Tern/“nesting”	June 1959	Kornicker et al. 1959
	Sooty Tern/“nesting”	June 1959	Kornicker et al. 1959
	Brown Noddy/“nesting”	June 1959	Kornicker et al. 1959
Isla Perez	Sooty Tern/“carpeted with eggs in nesting season”	?	Paynter 1955
	Brown Noddy/“over 1,000 birds must breed on the island”	?	Paynter 1955
	Laughing Gull/“numerous” eggs	1955-61	Bonet & Rzedowski 1962
	Brown Noddy/“numerous” eggs	1955-61	Bonet & Rzedowski 1962
	Magnificent Frigatebird/NC	1955-61	Bonet & Rzedowski 1962
	Sooty Tern/10s of 1,000’s of birds	July 1961	Fosberg 1962
	Brown Noddy/many nests	July 1961	Fosberg 1962
	Magnificent Frigatebird/48 empty nests	Sept. 1975	Boswall 1978
	Brown Noddy/2,000 birds	Sept. 1975	Boswall 1978
	Royal Tern/800 birds	Oct. 1984	Howell 1989
	Sandwich Tern/250 birds	Oct. 1984	Howell 1989
	Laughing Gull/500 birds	Oct. 1984	Howell 1989
	Sooty Tern/26,160 birds	July 1986	This paper
	Brown Noddy/1,357 nests	July 1986	This paper
Sooty Terns/~20,000 birds	Apr. 1988	Lockwood 1989	
Brown Noddy/~2,000 nesting	Apr. 1988	Lockwood 1989	
Isla Chica	Masked Booby/50 nests	May 1912	Kennedy 1917
	Masked & Brown Booby/6-8 pairs nesting	1955-61	Bonet & Rzedowski 1962
	Magnificent Frigatebird/“nesting”	1955-61	Bonet & Rzedowski 1962
	Masked Bobby/8-10 nests	July 1961	Fosberg 1962
	Laughing Gull/3 nests	July 1986	This paper
	Royal Tern/28 nests	July 1986	This paper
	Sandwich Tern/151 nests	July 1986	This paper

Table 2. Continued.

Reef Group or Island	Species/Colony Size	Date	Source
Isla Pájaros	Sooty Tern/"thousands"	May 1912	Kennedy 1917
	Sandwich Tern/50 nests	May 1912	Kennedy 1917
	Masked Booby/1 nest	May 1912	Kennedy 1917
	Laughing Gull/4 nests	May 1912	Kennedy 1917
	Masked Booby/200 birds	Sept. 1952	Paynter 1955
	Brown Booby/500 birds (nesting reported)	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/numerous	Oct. 1952	Siebenaler 1954
	Brown Booby/NC	Oct. 1952	Siebenaler 1954
	Brown & Masked Booby/"nesting"	1955-61	Bonet & Rzedowski 1962
	Magnificent Frigatebird/"nesting"	1955-61	Bonet & Rzedowski 1962
	Masked Booby/100+ nests	July 1962	Fosberg 1962
	Masked Booby/3 nests	Jan. & July 1986	This paper
	Masked Booby/"a few nesting"	Apr. 1988	Lockwood 1989
Isla Desertora	Magnificent Frigatebird/NC	1899	Millsbaugh 1916
	Masked Booby/NC	1899	Millsbaugh 1916
	Masked & Brown Booby/"nesting"	1955-61	Bonet & Rzedowski 1962
	Masked Booby/100s "nesting"	July 1961	Fosberg 1962
	Magnificent Frigatebird/"many" nesting	July 1961	Fosberg 1962
	Masked Booby/2,000 nests	Sept. 1975	Boswall 1978
	Magnificent Frigatebird/2,000-3,000 birds	Oct. 1984	Howell 1989
	Red-footed Booby/2 nests	Jan. 1986	Tunnell & Chapman 1988
	Masked Booby/2,533 nests	Jan. 1986	This paper
	Magnificent Frigatebird/206 nests	Jan. 1986	This paper
	Red-footed Booby/1 nest	July 1986	Tunnell & Chapman 1988
	Masked Booby 1,025 nests	July 1986	This paper
	Magnificent Frigatebird/33 nests	July 1986	This paper
	Laughing Gull/10 nests	July 1986	This paper
	Sooty Tern/10 nests	July 1986	This paper
	Magnificent Frigatebird/"nesting"	Apr. 1988	Lockwood 1989
	Masked Booby/"nesting"	Apr. 1988	Lockwood 1989
Red-footed Booby/1 nest	Apr. 1988	Lockwood 1989	
Isla Desterrada	Brown Booby/300 birds (nesting reported)	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/"many nests"	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/2,500 nests	Oct. 1952	Paynter 1955
	Boobies/"nesting"	1955-61	Bonet & Rzedowski 1962

Table 2. Continued.

Reef Group or Island	Species/Colony Size	Date	Source
	Royal Tern/nesting (?)	July 1961	Fosberg 1962
	Brown Booby/10 nests	Jan. 1986	This paper
	Magnificent Frigatebird/52 nests	Jan. 1986	This paper
	Laughing Gull/50 nests	July 1986	This paper
	Brown Booby/"nesting" (small colony)	Apr. 1988	Lockwood 1989
<b>Cayo Arenas</b>	Masked Booby/400 birds	Sept. 1952	Paynter 1955
	Masked Booby/500 pairs	Oct. 1984	Howell 1989
	Masked Booby/258 nests	Mar. 1986	This paper
3 Unnamed Islands	No vegetation or nesting reported		
<b>Triangulos</b>	Boobies/"plenty"	1675	Dampier 1699
	Magnificent Frigatebird/NC	1675	Dampier 1699
Triangulo Oeste	No official nesting records		
Triangulo Sur	No nesting records; fisherman & lighthouse keeper at Triangulo Oeste report nesting		
Triangulo Este	Masked Booby/"nesting"	1886(?)	Ward 1887
	Magnificent Frigatebird/"nesting"	1886(?)	Ward 1887
	Royal Tern/"observed"	1886(?)	Ward 1887
<b>Cayos Arcas</b>	Sooty Tern/"nesting"?	?	Lowery & Newman 1954
	Masked Booby/500 birds	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/500 birds nesting	Aug. 1952	Paynter 1955
	Masked Booby/250 pairs (+2,000 birds)	Oct. 1984	Howell 1989
	Magnificent Frigatebird/~2,500 pairs	Oct. 1984	Howell 1989
Cayo del Centro	Masked Booby/600+ nests	Apr. 1986	This paper
	Magnificent Frigatebird/1,712 nests	Apr. 1986	This paper
Cayo del Este	Masked Booby/98 nests	Apr. 1986	This paper
	Magnificent Frigatebird/282 nests	Apr. 1986	This paper
Cayo del Oeste	No nesting recorded		

We found that the Masked Booby is much more abundant in the eastern Caribbean than formerly believed. If the IXTOC-I oil spill severely affected the population of Masked Booby in the southern Gulf of México (Duncan and Havard 1980), the species appears to have recovered. Based upon the summaries of known colonies listed in Nelson (1978), the colony on Isla Desertora is the largest nesting concentration of the species in the eastern Caribbean region. If the colonies on the Campeche Bank islands are considered as either a temporal or a geographical unit, the nesting concentration may rank among the largest in the world.

### **Brown Booby (*Sula leucogaster*)**

The Brown Booby, which often nests in association with Masked and Red-footed boobies, may be the most common booby in the world (Nelson 1978). It breeds pantropically and occupies habitats that are similar to those of the Masked Booby (Dorward 1962), but the Brown Booby feeds closer to shore and can tolerate muddier water (Murphy 1936). The breeding ecology of the species was described by Chapman (1908), Thayer (1911), Dorward (1962), Simmons (1967) and Nelson (1978).

Despite Lowery and Newman's (1954) claim that the species did not breed on islands in the Gulf of México, Brown Booby colonies were reported from three islands on Arrecife Alacrán. Kornicker et al. (1959) listed the species as one of seven seabirds that they observed nesting on the Alacrán islands in June, 1959, but they did not indicate where they saw the birds or the stage of the nesting cycle. Paynter (1955) saw 300 birds on Isla Pájaros in early September 1952, but the birds were not nesting at the time. Bonet and Rzedowski (1962) however, photographed a pair of Brown Booby on the nest sometime during their visits to Isla Pájaros in 1960 or 1961. They also photographically documented the nesting of Brown Booby on Isla Desertora. Neither Paynter (1955) nor Boswall (1978) saw Brown Booby nests on Isla Desterrada, but according to the lighthouse keeper on the island, the boobies nested there in the spring. Our visit to Isla Desterrada predated Lockwood's (1989) by almost a year, and we also found a small colony of Brown Booby. Lockwood's account does not mention the stage of nesting that he observed in April, but we found that most of the young had fledged in January and we saw no signs of nesting activity in July. Boswall (1978) found no signs of nesting activity when he visited Isla Desertora in mid-September.

Although Nelson (1978) indicates that the period of heaviest laying in the Caribbean and Atlantic occurs from October to May and a limited amount of egg laying may occur during the remainder of the year, we feel that the breeding season for Brown Booby is much more restricted in the southern Gulf. The heaviest period of laying probably occurs from October to March. Some laying activity may also occur from April through June but there appears to be no nesting activity during the rest of the year. We found no evidence in historical accounts to justify the assumption by Friedmann et al. (1950) that Brown Booby nested on Cayos Arcas. Although the habitats on Cayo del Centro appear suitable, we did not find any indication that Brown Booby nested there recently. Since the Brown Booby is the least pelagic booby, van Halewyn and Norton (1984) suggested the species might be more vulnerable to oil spills. If the species nested on Cayos Arcas in the past, contamination

from the IXTOC-I oil spill may have affected the population. Cayos Arcas is the reef complex that is located closest to the site of the IXTOC-I well blowout.

### **Red-footed Booby (*Sula sula*)**

Although the Red-footed Booby is distributed pantropically (Nelson 1978, Schreiber et al. 1996) and is among the world's most abundant boobies, it has rarely been observed in the Gulf of México (Lowery and Newman 1954, Clapp et al. 1982). It had not been recorded nesting in the Gulf until Tunnell and Chapman (1988) reported active nests in January and July on Isla Desertora, Alacrán reef. The following year, Lockwood (1989) again found an active nest on the same island during an April visit. Since the nearest known colony of Red-footed Booby was at Half Moon Cay, Belize (Verner 1961), approximately 600 km away, this represented a significant extension of the breeding range of the species.

Since the Red-footed Booby is one of only two sulid species that regularly nest in shrubs or low trees (Nelson 1969, Schreiber et al. 1996), its presence as a breeding bird is generally limited to islands with vegetation tall enough to support an elevated nest (Murphy 1936). The occurrence of low *T. gnaphalodes* bushes on Isla Desertora has been relatively recent. Millspaugh (1916) found no shrubby vegetation during his survey in 1899 and Bonet and Rzedowski (1962) and Fosberg (1962) found only a few scattered bushes some 60 years later. By the time of our visit, the *T. gnaphalodes* had developed substantially, forming hedge-like clumps.

According to Nelson (1978), the period of heaviest egg laying for the Red-footed Booby in the Atlantic and Caribbean is from August to March. Based on only three observation periods of a total of four nests, we cannot speculate about the breeding season for the species in the southern Gulf. However, the nesting season on Isla Desertora is probably from November to April as occurs on Half Moon Cay (Verner 1961) and Little Cayman Island (Diamond 1980).

### **Magnificent Frigatebird (*Fregata magnificens*)**

The Magnificent Frigatebird, one of five species of the pantropically distributed Fregatidae (Nelson 1975), breeds on both coasts of México and Central America and the northern coasts of South America (A.O.U. 1998). Colonies in the Gulf of México have been reported from Laguna de Tamiahua, Veracruz (Lowery and Newman 1954), and the Marquesas Keys, Florida (Harrington et al. 1972). A single frigatebird nest containing eggs also was reported on the Texas coast (J. J. Carroll *in* Oberholser and Kincaid 1974).

Throughout their range, frigatebirds construct nests in shrubs or low trees on islands where there is a minimum of human disturbance (Chapman 1908, Eisenmann 1962). Because frigatebirds are adept at perching, they can nest in a wide range of habitats (Nelson 1975). Nests appear to be oriented to permit easy landing (Diamond 1973, 1975), but the spatial distribution of nests is not random or uniform. Frigatebirds nest in distinct clumps (Nelson 1975) and reported nest densities range from 1.3 nests/m<sup>2</sup> (Eisenmann 1962) to 0.28 nests/m<sup>2</sup> (Diamond 1973).

According to Diamond (1973), Magnificent Frigatebird on Barbuda have an egg-laying season that extends from September through January. An examination of the historical record of the Campeche Bank colonies indicates that the laying season in the southern Gulf is similar to that on Barbuda. Nest construction was initiated in August (Paynter 1955), but eggs were not seen in nests until September (Paynter 1955) or October (Howell 1989).

Colonies of Magnificent Frigatebird were primarily limited to those islands with sufficient shrubby vegetation to support nests. On Arrecife Alacr anes only Isla Chica and Isla P jaros were not used as nesting sites. These islands possessed a few low shrubs, but the woody plants were scattered and had not formed clumps of significant size for nesting. If more woody vegetation develops on these islands, Magnificent Frigatebird may nest there. The colony that we recorded on Cayo del Este, Cayos Arcas, represented the first record of Magnificent Frigatebird nesting on that island. There, many of them nest directly on the ground and not in the usual woody shrubs. Some nesting may eventually be seen on Cayo del Oeste as well because frigatebirds frequent the small clumps of *S. maritima* and *T. gnaphalodes* for roost sites.

### **Laughing Gull (*Larus atricilla*)**

Colonies of nesting Laughing Gull are found primarily along the Atlantic and Gulf coasts of the United States, but they also breed in the Caribbean, on the northern coast of South America, and along the Pacific coast of southern M xico (A.O.U. 1998, Clapp et al. 1983, Burger 1996). The habitats chosen as nesting sites vary considerably throughout the range of the species and colony descriptions from nesting areas along the Atlantic and Gulf of M xico are summarized by Clapp et al. (1983). Nesting habits in the Caribbean and southern Gulf of M xico are less well known. Brief descriptions of Laughing Gull colonies from Caribbean locations are provided by Dewey and Nellis (1980) and Burger and Gochfield (1985).

The report of four nests of Laughing Gull on Arrecife Alacr anes by van Halewyn and Norton (1984) was possibly based upon the account by Kennedy (1917) who reported four Laughing Gull nests on Isla P jaros. Bonet and Rzedowski (1962: Fig. 11) included a photograph of a Laughing Gull colony on Isla Perez in their report on the vegetation of Alacr an and, based on a count of the visible nests, the colony contained a minimum of 100 pairs. Fosberg (1962) found 20-30 Laughing Gull on Isla Chica during his visit in July 1962, but was able to locate only a single nest with eggs.

We found no nesting Laughing Gull during our January visits to the islands of Arrecife Alacr anes, but we found nests on Isla Chica, Isla Desertora and Isla Desterrada in July. Dinsmore and Schreiber (1974) and Schreiber et al. (1979) reported that courtship behavior in Florida begins in March and the peak of the nesting season is reached in May and June. Most young fledge in July. Our observations of pre-flight young on the islands in July indicate that the breeding cycle of Laughing Gull in the southern Gulf of M xico is similar to that in Florida but may begin one to two weeks earlier in the year.

We did not find direct evidence that Laughing Gull nest on other islands of the Campeche Bank reefs. However, the presence of adults and young on the islands of Arrecife Alacr nes may indicate that the breeding population of Laughing Gull is increasing in the southern Gulf of M xico. It is too early to speculate about the effects that such an increase might have on the reproductive success of other species. However, Ansingh et al. (1960) reported that 10% of the eggs and chicks in a Sandwich Tern colony on Curacao were lost to Laughing Gull predation. Further expansion of the Laughing Gull population on the Campeche Bank should be closely monitored.

### **Royal Tern (*Sterna maxima*)**

Although Royal Tern breed primarily along the Atlantic and Gulf coasts, they also breed throughout the Caribbean, along the Pacific coast of M xico, and on the Atlantic coast of South America (A.O.U. 1998). A small breeding population also occurs in the Old World (Clapp et al. 1983). Royal Tern nest colonially on isolated and sparsely vegetated islands (Buckley and Buckley 1972).

Lowery and Newman (1954) indicated that Royal Tern did not nest on the Campeche Bank islands and Paynter (1955) found no nests during his survey in August and September 1952. However, Paynter mentioned that the lighthouse keepers informed him that Royal Tern bred on islands of Arrecife Alacr nes and Cayos Arcas. Bonet and Rzedowski (1962) also mentioned that Royal Tern nested on Isla Chica and Isla Desterrada but provided no description of the colonies or the number of pairs. Fosberg (1962) found 11 nests on Isla Desterrada after causing an enormous flock, estimated to be about 1,000 birds, to take flight. Consequently, our account of the Royal Tern on Isla Chica is the second documentation that the species nests on the Campeche Bank.

When we visited the island in early July, the Royal Tern chicks were about two weeks old and were part of a cr che that contained Sandwich Tern chicks. The best time to survey the islands to determine the extent of Royal Tern nesting would be from late April through late May when the terns are most likely to be on eggs.

### **Sandwich Tern (*Sterna sandvicensis*)**

Sandwich Tern are a cosmopolitan species, but the main concentration of breeding colonies is along the Atlantic and Gulf coasts of North America, the Atlantic coast of South America and in western Eurasia (A.O.U. 1998, Clapp et al. 1983). Throughout its range, its colonies are located on barren or sparsely vegetated sandy or shelly spits or beaches (Shealer 1999). In the southeastern United States, Sandwich Tern commonly nest in association with other terns or gulls (Shealer 1999), commonly with Royal Tern (Buckley and Buckley 1980).

Although northern Caribbean colonies are known from the United States Virgin Islands (Dewey and Nellis 1980) and Cuba (Bond 1971), little is known about the occurrence of breeding colonies in the southern Gulf of M xico (Clapp et al. 1983, van Halewyn and Norton 1984). Kennedy (1917) found a group of 50 Sandwich Tern nests in the midst of a large Sooty Tern colony in mid-May on Isla P jaros. Paynter (1955) did not see any nests



during his August and September visits to Campeche Bank, but he observed many roosting on the beaches of several islands. According to Alacrán inhabitants, the main nesting colony was located on Isla Desterrada (Paynter 1955). Our observation of the Sandwich Tern nests on Isla Chica provides the first documentation in nearly 70 years that the species still breeds on Campeche Bank. We did not locate Sandwich Tern nests on Isla Desterrada and we found no historical or physical evidence to support the A.O.U. (1998) claim that Sandwich Tern nest on Cayos Arcas.

### **Sooty Tern (*Sterna fuscata*)**

The Sooty Tern is a widely distributed species with breeding colonies on islands in tropical and subtropical waters associated with both the Atlantic and Pacific oceans (A.O.U. 1998, Clapp et al. 1983). The most comprehensive summary of known Sooty Tern breeding colonies and nesting seasons was provided by Ashmole (1963) who also detailed the nesting biology of the species. According to van Halewyn and Norton (1984), Sooty Tern are the most numerous breeding seabirds in the Caribbean region with a breeding population that exceeds 100,000 pairs. A large colony exists on the Dry Tortugas (Howell 1932, Sprunt 1954, Dinsmore 1972) where the breeding ecology was described by Watson (1966).

Several small nesting aggregations have been reported from the Gulf of México in Florida (Stevenson 1972), Mississippi (Paynter 1955), Louisiana (Purrington 1970, Portnoy 1977), and Texas (Chaney et al. 1978) and all of the islands of Arrecife Alacrán. We could not verify, however, that Sooty Tern have ever been recorded nesting on islands of Cayos Arcas as stated by Friedmann et al. (1950) and A.O.U. (1998). During our visit in April, we observed many adult Sooty Tern roosting on, and flying near, Cayo del Este but we did not find any sign of nesting activity.

Dampier (1699) was the first to record the presence of nesting Sooty Tern on Arrecife Alacrán with a description "Egg birds." Kennedy (1917) followed over two centuries later with his account of the ground "carpeted" with hundreds of nests on Isla Pájaros. Since there are so many accounts, we will summarize them by island.

Isla Perez – Although Paynter (1955) did not observe nesting during his visit, he was assured by the inhabitants of Alacrán that Sooty Tern nested by the thousands on the reef complex and Isla Perez had the largest concentration of nests. Folk (1967) was on the island in June and July 1960, and reported "myriads" of Sooty Tern nests. When Fosberg visited in July two years later, however, Sooty Tern were not nesting. Lockwood (1989) found over 20,000 Sooty Tern engaged in excavating nest scrapes on Isla Perez in April 1988. Only 1,000 nests contained eggs. Boswall found only two young left on the island in September, 1975, and Howell reported a single immature tern during his October 1984 visit. Lighthouse keepers described accounts of egg harvesting, a practice that probably continues today (Paynter 1955, Boswall 1978). Lockwood (1989) reported that 15,000 eggs were taken from Isla Perez during one year, but Boswall (1978) indicated that egg harvesting ceased after Easter each year.

Isla Chica – Bonet and Rzedowski (1962) found Sooty Tern nesting with Sandwich Tern on Isla Chica. However, they provided no details other than a brief account of the sparse vegetation at the colony site.

Isla Pájaros – The only account of nesting Sooty Tern on Isla Pájaros is that of Kennedy (1917). When he visited in May, he found eggs in late stages of incubation, but no hatchlings.

Isla Desertora – We provide the first record of Sooty Tern nesting on Isla Desertora. Although we only found 10 juvenile birds, the area appeared to have been used by a large colony.

Isla Desterrada – Both Bonet and Rzedowski (1962) and Wells (1988) report Sooty Tern colonies on Isla Desterrada.

According to Fosberg (1962), the inhabitants of Isla Perez said Sooty Tern leave in September and return each February. This is consistent with the nesting schedule described for the Dry Tortugas colony (Sprunt 1954, Watson 1966). Most nesting probably occurs from April to June and the adults and young birds may remain in the area for several months after fledging. For the remainder of the year, Sooty Tern are highly pelagic (Dinsmore 1972).

### **Brown Noddy (*Anous stolidus*)**

Like many seabirds, Brown Noddy occur pantropically (A.O.U. 1998). Unlike many seabirds, these birds use many different habitats for colony locations (Chardine and Morris 1996) and, consequently, they occupy a large number of colony sites around the world (Clapp et al. 1983). Colonies may contain up to 50,000 pairs of birds (Clapp et al. 1983), but the majority of birds in a colony never venture far from the colony location (Watson 1908, King 1970). Some Brown Noddy populations abandon the colony site at the completion of the nesting cycle, but most remain in the vicinity of the colony throughout the year (King 1970).

A large proportion of the Atlantic Brown Noddy population nests in the Caribbean region (van Halewyn and Norton 1984). The species is widespread in the Caribbean and is the second most abundant seabird. The largest colony in the Gulf of México is located in the Dry Tortugas (Sprunt 1948, Robertson 1964, Voous 1966, Clapp and Buckley 1984, Morris and Chardine 1992). Robertson (1978) estimated that the colony contained approximately 1,500 nests but indicated that the maximum number of birds present could approach 10,000. At one time the colony may have had 35,000 birds but the number declined to about 300 by 1950 (Robertson 1964).

The colonies on Arrecife Alacránés now may exceed the Dry Tortugas colony in total numbers of breeding pairs. Paynter (1955) was the first to note that Brown Noddy nested on the Campeche Bank when he reported that over 1,000 birds were nesting on Isla Perez in September 1952. Bonet and Rzedowski (1962) and Fosberg (1962) both reported many

Brown Noddy during their visits to Isla Perez in the early 1960s. Boswall (1978) reported 2,000 adults and young associated with nests when he visited in September, but the lighthouse keeper on Isla Perez told him that these were only a fraction of the population that nested there earlier in the year. Lockwood (1989) found 2,000 Brown Noddy nests in the shrubs and low dense vegetation during his visit in April 1988.

The period of egg-laying in the Caribbean is assumed to occur from April to June (van Halewyn and Norton 1984, Morris and Chardine 1992), but we suggest that it may occur later on Isla Perez in some years. Of 1,412 nests that we examined in early July, one-third still contained eggs or chicks and several authors mentioned that eggs were still present in the colony as late as September.

## DISCUSSION AND CONCLUSIONS

Ornithologically, the Gulf of México is a tropical sea (Lowery and Newman 1954). The majority of its breeding pelagic avifauna consists of species that approach the northern limits of their normal breeding range. The southern Gulf of México remains one of the areas of the world least understood ornithologically. Although colonies of breeding seabirds have long been known from the islands on the Campeche Bank reefs, most investigators have reported relatively small breeding populations. The Campeche Bank islands are significant nesting areas for marine birds, and the seabird populations in the Gulf of México are much larger than previously believed.

There are many problems associated with the estimation of tropical seabird populations (Schreiber and Schreiber 1986). Our estimates of colony size were made conservatively, but our numbers may be further limited because all of our observations of nesting birds were diurnal. Several researchers (Kepler 1969, Schreiber and Schreiber 1986, Clapp 1990) noted that populations of birds roosting at night on Pacific islands were much larger than those seen during the day. For example, Schreiber and Schreiber (1986) demonstrated that estimates of tern nests on one Pacific atoll might underestimate total numbers of terns by two orders of magnitude and the maximum number of birds seen at any one time could represent only about 5% of the total number of terns using the atoll throughout the year. If a similar relationship between bird counts and total annual use exists on the islands in the southern Gulf of México, the estimate of 13,570 adult Sooty Tern seen during the day on Isla Perez in July 1986 might signify a much higher number using the island annually.

The islands of the Campeche Bank may serve as habitat bases for interactive metapopulations of seabirds. The term "metapopulation" was originally coined by Levins (1969, 1970) to describe the interactions of insect subpopulations in patchy environments. Since the original description of the term, the concept of metapopulations has been expanded to include any situation in which subdivided populations are distributed as discrete, interbreeding units that regularly occupy, then abandon, habitat patches (Gilpin and Hanski 1991, McCullough 1996). Insular-nesting seabirds in restricted geographic regions meet all of the criteria for metapopulations (Buckley and Downer 1992).

Although the historical record of the seabird colonies on the Campeche Bank is fragmented and sparse, patterns of colony use and abandonment are evident. Frequent alternations of site use and abandonment may be common in organisms that are obligatorily colonial (Buckley and Buckley 1972, Buckley and Downer 1992). Seabirds may change nesting locations in concert with shifting food resources or in response to local disturbances. Unless the species practices group adherence (Buckley and Buckley 1980), the individuals or pairs that constitute a colony also will change each time a colony is abandoned and relocated.

If the seabirds of the Campeche Bank do comprise metapopulations, the dynamics of the situation likely produce beneficial effects. Disturbances that have occurred on some islands have been offset by population shifts to other locations within the Campeche Bank complex. As a result, populations of seabirds in the southern Gulf have remained relatively stable. It is unfortunate that such large populations of seabirds have been so overlooked by the scientific and conservation communities. The islands of the Campeche Bank should be surveyed on a regular basis and human use of the islands should be curtailed to the maximum extent possible.

#### ACKNOWLEDGMENTS

Support for this research was provided by a Fulbright Scholar Award to Tunnell and by financial assistance from Texas A&M University - Corpus Christi. Trips to the Campeche Bank reefs on ships of the *Armada de México* were arranged by Dr. and Mrs. E. A. Chávez of *Centro de Investigaciones y de Estudios Avanzados del Instituto Polytecnico Nacional-Unidad Mérida*, where Tunnell was working. Each is gratefully acknowledged. We also thank M. A. Garduno, A. González, K. Tunnell, Jace Tunnell, and James Tunnell for field assistance; F. Trevino and G. Krause for help in preparing the manuscript; and Kathryn Harvey for drafting figures.

#### LITERATURE CITED

- Agassiz, A. 1888. Three cruises of the United States Coast and Geodetic steamer "Blake". *Harvard Museum of Comparative Zoology* 1:70-73.
- A.O.U. (American Ornithologists' Union). 1998. Check-list of North American birds, 7th edition. American Ornithologists' Union. Washington D.C. 829 pp.
- Anderson, D.J. 1993. Masked Booby (*Sula dactylatra*), No. 73. In A. Poole and F. Gill (eds.), *The Birds of North America*. Philadelphia Academy of Natural Sciences and American Ornithologists' Union. Washington, D.C.
- Ansingh, F. H., H. J. Koelers, P. A. van der Werf, and K. H. Voous. 1960. The breeding of the Cayenne or Yellow-billed Sandwich Tern in Curacao in 1958. *Ardea* 48:51-65.
- Ashmole, N. P. 1963. The biology of the Wideawake or Sooty Tern *Sterna fuscata* on Ascención Island. *Ibis* 103:297-364.

- Bond, J. 1971. Birds of the West Indies, 2nd edition. Collins. London, United Kingdom. 256 pp.
- Bonet, F. 1967. Biogeología subsuperficial del Arrecife Alacrán, Yucatán. Universidad Nacional Autónoma de México, Instituto Geología Boletín 80. Mexico, D.F. 192 pp.
- Bonet, F., and J. Rzedowski. 1962. La vegetación de las islas del Arrecife Alacrán, Yucatán (México). *Anales Escuela Nacional de Ciencias Biológicas* 11:15-59.
- Boswall, J. 1978. The birds of Alacrán Reef, Gulf of México. *Bulletin of the British Ornithological Club* 98:99-109.
- Buckley, P. A., and F. G. Buckley. 1972. The breeding ecology of Royal Terns (*Sterna (Thalasseus) maxima maxima*). *Ibis* 114:344-359.
- Buckley, P. A., and F. G. Buckley. 1980. Habitat selection and marine birds, pp. 69-112. In J. Burger, B. L. Olla and H. E. Winn (eds.), Behavior of Marine Animals, Volume 4: Marine Birds. Plenum Press. New York, New York.
- Buckley, P. A., and R. Downer. 1992. Modelling metapopulation dynamics for single species of seabirds, pp. 563-585. In D. R. McCullough and R. H. Barrett (eds.), Wildlife 2001: Populations. Elsevier Applied Science. New York, New York.
- Burger, J. 1996. Laughing gull (*Larus atricilla*), No. 225. In A. Poole and F. Gill (eds.), The Birds of North America. Philadelphia Academy of Natural Sciences and American Ornithologists' Union. Washington, D.C.
- Burger, J., and M. Gochfield. 1985. Nest site selection by Laughing Gulls: comparisons of tropical colonies (Culebra, Puerto Rico) with temperate colonies (New Jersey). *Condor* 87:364-373.
- Busby, R. F. 1966. Sediments and reef corals of Cayo Arenas, Campeche Bank, Yucatán, México. U. S. Naval Oceanographic Office Technical Report TR-187. Washington, D.C. 58 pp.
- Chaney, A. H., B. R. Chapman, J. P. Karges, D. A. Nelson, R. R. Schmidt and L. J. Thebeau. 1978. Use of dredged material islands by colonial seabirds and wading birds in Texas. U.S. Army Corps of Engineer Waterways Experiment Station Technical Report D-78-8. Vicksburg, Mississippi. 170 pp.
- Chapman, B. R. 1981. Effects of the IXTOC I Oil Spill on Texas shorebird populations, pp. 461-465. In Proceedings of the 1981 Oil Spill Conference. American Petroleum Institute Publication 4334. Washington, D.C.
-

- Chapman, F. M. 1908. A contribution to the life histories of the booby (*Sula leucogaster*) and Man-O'-War Bird (*Fregata aquila*). *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington* 103:139-151.
- Chávez, H. 1966. Peces colectados en el Arrecife Triángulos Oeste y en Cayo Arenas, Sonda de Campeche, México. *Acta Zoologica Mexicana* 8:1-12.
- Chávez, E. A. and J. W. Tunnell, Jr. 1993. Needs for management and conservation of the southern Gulf of México, pp. 2040-2053. In O.T. Magoon, W. S. Wilson, H. Converse, and L. T. Tobin (eds.), *Coastal Zone '93: Proceedings of the Eighth Symposium on Coastal and Ocean Management*. American Society of Civil Engineers. New York, New York.
- Chardine, J.W., and R.D. Morris. 1996. Brown Noddy (*Anous stolidus*), No. 220. In A. Poole and F. Gill (eds.), *The Birds of North America*. Philadelphia Academy of Natural Sciences and American Ornithologists' Union. Washington, D.C.
- Chávez, E. A., E. Hildigao, and M. A. Izaguirre. 1985. A comparative analysis of Yucatán coral reefs, pp. 355-361. In C. Gabrie and M. Marmelin Vivien (eds.), *Proceedings of the Fifth International Coral Reef Congress Volume 6: Miscellaneous Papers (B)*. Antenne Museum-Ephe. Moorea, French Polynesia.
- Clapp, R. B. 1990. Notes on the birds of Kwajalein Atoll, Marshall Islands. *Atoll Research Bulletin* 342:1-94
- Clapp, R.B., and P.A. Buckley. 1984. The status and conservation of seabirds in the southeastern United States, pp. 135-155. In J.P. Croxall, P.G.H. Evans, and R.W. Schreiber (eds.), *Status and Conservation of the World's Seabirds*. ICBP Technical Publication 2. Cambridge, United Kingdom.
- Clapp, R. B., R. C. Banks, D. Morgan-Jacobs, and W. A. Hoffman. 1982. Marine birds of the southeastern United States and Gulf of México, Part I. Gaviiformes through Pelecaniformes. U.S. Fish and Wildlife Service, Office of Biological Services, FWS/OBS-82/01. Washington, D.C. 637 pp.
- Clapp, R. B., D. Morgan-Jacobs, and R. C. Banks. 1983. Marine birds of the southeastern United States and Gulf of México, Part III: Charadriiformes. U. S. Fish and Wildlife Service, Office of Biological Services, FWS/OBS-83/30. Washington, D.C. 853 pp.
- Dampier, W. 1699. *Voyages and Descriptions, Volume 2, Part 2: Two Voyages to Campeachy*, 2nd edition (Microfiche). James Knapton. London, United Kingdom.
- Dewey, R. A., and D. W. Nellis. 1980. Seabird research in the U. S. Virgin Islands. *Transactions of the North American Wildlife and Natural Resources Conference* 45:445-452.

- Diamond, A. W. 1973. Notes on the breeding biology and behavior of the Magnificent Frigatebird. *Condor* 75:200-209.
- Diamond, A. W. 1975. Biology and behavior of frigatebirds *Fregata* spp. on Aldabra Atoll. *Ibis* 117:302-323.
- Diamond, A. W. 1980. The Red-footed Booby on Little Cayman: size, structure and significance. *Atoll Research Bulletin* 241:165-170.
- Dinsmore, J. J. 1972. Sooty Tern behavior. *Bulletin of the Florida State Museum, Biological Sciences* 16:129-179.
- Dinsmore, J. J., and R. W. Schreiber. 1974. Breeding and annual cycle of Laughing Gulls in Tampa Bay, Florida. *Wilson Bulletin* 86:419-427.
- Dorward, D. F. 1962. Comparative biology of the White Booby and the Brown Booby *Sula* spp. at Ascension. *Ibis* 103(b):174-220.
- Duffy, D. C., and D. N. Nettleship. 1992. Seabirds: Management problems and research opportunities, pp. 525-546. In D. R. McCullough and R. H. Barrett (eds.), *Wildlife 2001: Populations*. Elsevier Applied Science. London, United Kingdom.
- Duncan, C. D., and R. W. Havard. 1980. Pelagic birds of the northern Gulf of México. *American Birds* 34:122-132.
- Eisenmann, E. 1962. Magnificent Frigatebird, pp. 367-380. In R. S. Palmer (ed.). *Handbook of North American Birds, Volume I*. Yale University Press. New Haven, Connecticut.
- Farrell, T. M., C. F. D'Elia, L. Lubbers III, and L. J. Pastor, Jr. 1983. Hermatypic coral diversity and reef zonation at Cayos Arcas, Campeche, Gulf of México. *Atoll Research Bulletin* 270:1-7.
- Folk, R. L. 1967. Sand cays of Alacrán Reef, Yucatán, México: morphology. *Journal of Geology* 75:412-437.
- Fosberg, F. R. 1961. Atoll news and comments. *Atoll Research Bulletin* 84:6-9.
- Fosberg, F. R. 1962. A brief survey of the cays of Arrecife Alacrán, a Mexican atoll. *Atoll Research Bulletin* 93:1-25.
- Friedman, H., L. Griscom, and R.T. Moore. 1950. Distributional checklist of the birds of México, Part 1. Cooper Ornithological Club, Pacific Coast Avifauna No. 29. Santa Clara, California. 202 pp.

- Gillham, M. E. 1977. Observations on the vegetation of Blue-faced Booby colonies on Cosmededo Atoll, western Indian Ocean. *Atoll Research Bulletin* 199:1-11.
- Gilpin, M., and I. Hanski (eds.). 1991. Metapopulation dynamics: Empirical and theoretical investigations. Academic Press. London, United Kingdom.
- Harrington, B. A., R. W. Schreiber and G. W. Woolfenden. 1972. The distribution of male and female Magnificent Frigatebirds, *Fregata magnificens*, along the Gulf coast of Florida. *American Birds* 26:927-931.
- Hoskin, C. M. 1963. Recent carbonate sedimentation on Alacrán Reef, Yucatán, México. National Academy of Science, National Research Council Publication 1089. Washington, D. C. 160 pp.
- Hoskin, C. M. 1966. Coral pinnacle sedimentation, Alacrán Reef Lagoon, México. *Journal of Sedimentary Petrology* 36:1058-1074.
- Howell, A. H. 1932. Florida bird life. Coward-McCann, Inc. New York, New York. 597 pp.
- Howell, S. N. G. 1989. Additional information on the birds of the Campeche Bank, México. *Journal of Field Ornithology* 60:504-509.
- Howell, S. N. G., S. Webb, and B. M. de Montes. 1990. Notes on tropical terns in México. *American Birds* 44:381-383.
- Hutchinson, G. E. 1950. The biogeochemistry of vertebrate excretion. Bulletin of the American Museum of Natural History 96. New York, New York. 554 pp.
- Kennedy, J. N. 1917. A little-known bird colony in the Gulf of México. *Ibis* 10:41-43.
- Kepler, C. B. 1969. Breeding biology of the Blue-faced Booby *Sula dactylatra personata* on Green Island, Kure Atoll. *Publications of the Nuttall Ornithological Club* 8: 1-97.
- King, W. B. 1970. The trade wind zone oceanography pilot study, part 7: observations of sea birds March 1964 to June 1965. U. S. Fish and Wildlife Service Special Scientific Report - Fisheries No. 586. Washington, D.C. 136 pp.
- Kornicker, L. S., and D. W. Boyd. 1962. Shallow-water geology and environments of Alacrán Reef complex, Campeche Bank, México. *Bulletin of the American Association of Petroleum Geologists* 46:640-673.
- Kornicker, L. S., F. Bonet, R. Cann, and C. M. Hoskin. 1959. Alacrán Reef, Campeche Bank, México. *Publications of the Institute of Marine Science, University of Texas* 6:1-22.



- Levins, R. 1969. Some demographic and environmental consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237-240.
- Levins, R. 1970. Extinction, pp. 77-107. In M. Gerstenhaber (ed.), *Some Mathematical Problems in Biology*. American Mathematical Society. Providence, Rhode Island.
- Lockwood, C. C. 1989. *The Yucatán Peninsula*. Louisiana State University Press. Baton Rouge, Louisiana. 145 pp.
- Logan, B. W. 1962. Submarine topography of the Yucatán platform, pp. 101-104. In G. E. Murray and A. E. Weidie (eds.), *Guide Book: Field Trip to the Peninsula of Yucatán, February 1-5, 1962*. New Orleans Geological Society. New Orleans, Louisiana.
- Logan, B. W. 1969. Carbonate sediments and reefs, Yucatán Shelf, México, part 2: coral reefs and banks, Yucatán Shelf, México (Yucatán Reef Unit). *American Association of Petroleum Geologists Memoir* 11:129-198.
- Lowe, P.R. 1909. Notes on some birds collected during a cruise in the Caribbean Sea. *Ibis* 51:304-347.
- Lowery, G. H., Jr., and R. J. Newman. 1954. The birds of the Gulf of México. *Fishery Bulletin of the Fish and Wildlife Service* 55:519-540.
- Macintyre, I. G., R. B. Burke, and R. Stuckenrath. 1977. Thickest recorded Holocene reef section, Isla Perez core hole, Alacrán Reef, México. *Geology* 5:749-754.
- Marion, A.F. 1884. Excursion aux isles Alacrás. *Bulletin Societe Academique de Brest, (France, Serie 2)* 9:5-21.
- McCullough, D. R. (ed.). 1996. *Metapopulations and Wildlife Conservation*. Island Press. Washington, D.C. 429 pp.
- Millspaugh, G. C. 1916. Vegetation of the Alacrán Reef. *Field Museum of Natural History, Botanical Series* 187(2):421-431.
- Morris, R.D., and J.W. Chardine. 1992. The breeding biology and aspects of the feeding ecology of Brown Noddies nesting near Culebra, Puerto Rico, 1985-1989. *Canadian Journal of Zoology* 226:65-79.
- Murphy, R. C. 1936. *The Oceanic Birds of South America*. American Museum of Natural History. New York, New York. 1,245 pp. (2 volumes).
- Nelson, J. B. 1967. The breeding behaviour of the White Booby *Sula dactylatra*. *Ibis* 109:194-231.

- Nelson, J. B. 1969. The breeding behaviour of the Red-footed Booby *Sula sula*. *Ibis* 111:357-385.
- Nelson, J. B. 1975. The breeding biology of frigatebirds: a comparative review. *Living Bird* 14:113-155.
- Nelson, J. B. 1978. The Sulidae: Gannets and Boobies. Oxford University Press. London, United Kingdom. 1012 pp.
- Nelson, J. B. 1979. Seabirds: Their Biology and Ecology. A & W Publishers. New York, New York. 224 pp.
- Oberholser, H. C. and E. B. Kincaid, Jr. 1974. The Bird Life of Texas, Volume I. University of Texas Press. Austin, Texas. 530 pp.
- Paynter, R. A., Jr. 1953. Autumnal migrants on the Campeche Bank. *Auk* 70:338-349.
- Paynter, R. A., Jr. 1955. The ornithogeography of the Yucatan Peninsula. *Bulletin of the Peabody Museum of Natural History* 9:1-329.
- Portnoy, J. W. 1977. Nesting colonies of seabirds and wading birds: coastal Louisiana, Mississippi, and Alabama. U.S. Fish and Wildlife Service, Office of Biological Services, FWS/OBS-77/07. Washington, D. C. 126 pp.
- Purrington, R. D. 1970. Nesting of the Sooty Tern in Louisiana. *Auk* 87:159-160.
- Robertson, W. B., Jr. 1964. The terns of the Dry Tortugas. *Bulletin of the Florida State Museum* 8:1-94.
- Robertson, W. B., Jr. 1978. Species of special concern: Noddy Tern, pp. 95-96. In H. W. Kale, III (ed.), Rare and Endangered Biota of Florida, Volume 2: Birds. University Presses of Florida. Gainesville, Florida. 121 pp.
- Schreiber, E. A., and R. W. Schreiber. 1986. Seabird census and study techniques, pp. 207-218. In MEDMARAVIS and X. Monbailliu (eds.), Mediterranean Marine Avifauna. NATO ASI Series G, Ecological Sciences, Volume 12. Springer-Verlag. New York, New York.
- Schreiber, E.A., R.W. Schreiber, and G.A. Schenk. 1996. Red-footed Booby (*Sula sula*), No. 241. In A. Poole and F. Gill (eds.), The Birds of North America. Philadelphia Academy of Natural Sciences and American Ornithologists' Union. Washington, D.C.
- Schreiber, E. A., R. W. Schreiber, and J. J. Dinsmore. 1979. Breeding biology of Laughing Gulls in Florida, part I: nesting, egg, and incubation parameters. *Bird-Banding* 50:304-321.

- Shealer, D. 1999. Sandwich Tern (*Sterna sandvicensis*), No. 405. In A. Poole and F. Gill (eds.), *The Birds of North America*. Philadelphia Academy of Natural Sciences and American Ornithologists' Union. Washington, D.C.
- Siebenaler, J. B. 1954. Notes on autumnal trans-Gulf migration of birds. *Condor* 56:43-48.
- Simmons, K. E. L. 1967. Ecological adaptations in the life history of the Brown Booby at Ascension Island. *Living Bird* 6:187-212.
- Smith, T. 1838. Description of Alacrán and Cay Arenas in the Gulf of México. *Nautical Magazine* 7:804-805.
- Sprunt, A., Jr. 1948. The tern colonies of the Dry Tortugas Keys. *Auk* 65:1-19.
- Sprunt, A., Jr. 1954. Florida bird life. Coward-McCann, Inc. and National Audubon Society. New York, New York. 527 pp.
- Stevenson, H. M. 1972. Recent breeding of the Sandwich Tern (*Thalasseus sandvicensis*) in Florida. *Florida Naturalist* 45:94-95.
- Thayer, J. E. 1911. A nesting colony of Heerman Gulls and Brewster Boobies. *Condor* 13:104-106.
- Tunnell, J. W., Jr. 1992. Natural versus human impacts to southern Gulf of México coral reef resources, pp. 300-305. In R. H. Richmond (ed.), *Proceedings of the Seventh International Coral Reef Symposium, Volume 1*. University of Guam Press. Mangilao, Guam.
- Tunnell, J. W., Jr., and B. R. Chapman. 1988. First record of Red-footed Boobies nesting in the Gulf of México. *American Birds* 42:380-381.
- van Halewyn, R., and R. L. Norton. 1984. The status and conservation of seabirds in the Caribbean, pp. 169-222. In J. P. Croxall, P. G. H. Evans and R. W. Schreiber (eds.), *Status and Conservation of the World's Seabirds*. ICBP Technical Publication 2. Cambridge, United Kingdom.
- Verner, J. 1961. Nesting activities of the Red-footed Booby in British Honduras. *Auk* 78:573-594.
- Voous, K. H. 1966. The terns of the Dry Tortugas. *Auk* 83:145-146.
- Ward, H.L. 1887. Notes on the life history of *Monachus tropicalis*, the West Indian Seal. *American Naturalist* 21:257-264.
- Watson, J. B. 1908. The behavior of Noddy and Sooty Terns. *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington* 103:189-255.

- Wells, S. M. (ed.). 1988. Coral Reefs of the World, Volume 1: Atlantic and Eastern Pacific. United Nations Environment Programme and International Union for Conservation of Nature and Natural Resources. Gland, Switzerland and Cambridge, United Kingdom. 373 pp.
- Woods, E. G., and R. P. Hannah. 1981. IXTOC I Oil Spill - the damage assessment program and ecological impact, pp. 439-443. *In* Proceedings of the 1981 Oil Spill Conference. American Petroleum Institute Publication 4334. Washington, D.C.