THE OCCURRENCE, HABITAT USE, AND BEHAVIOR OF SHARKS AND RAYS ASSOCIATING WITH TOPOGRAPHIC HIGHS IN THE NORTHWESTERN GULF OF MEXICO

A Thesis

by

JEFFREY NATHANIEL CHILDS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2001

Major Subject: Wildlife and Fisheries Sciences

THE OCCURRENCE, HABITAT USE, AND BEHAVIOR OF SHARKS AND RAYS ASSOCIATING WITH TOPOGRAPHIC HIGHS IN THE NORTHWESTERN GULF OF MEXICO

A Thesis

by

JEFFREY NATHANIEL CHILDS

Submitted to Texas A&M University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Approved as to style and content by:

John McEachran
(Chair of Committee)

David Owens
(Member)

Stephen Gittings
(Member)

Robert Brown
(Head of Department)

May 2001

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

The Occurrence, Habitat Use and Behavior of Sharks and Rays Associating with Topographic Highs in the Northwestern Gulf of Mexico.

(May 2001)

Jeffrey Nathaniel Childs, B.S., Texas A&M University

Chair of Advisory Committee: Dr. John McEachran

Some wide-ranging elasmobranch species are frequently reported to occur at topographic highs, which are topographic prominences that rise from the sea floor and provide significant positive and structural relief in an otherwise level landscape. Examples of places where some sharks and rays appear to concentrate include Saint Paul's Rocks, the Bahamas, the Cocos Islands, Galapagos Islands, Hawaiian Islands, Aldabra Atoll, Johnston Atoll, and the Marshall Islands. In the northwestern Gulf of Mexico, an array of topographic highs comprising submerged hard-banks and reefs, and offshore petroleum platforms are notable. Among these features are the Flower Garden Banks, the northernmost coral reef communities on the North American continental shelf, where divers have reported several species of elasmobranchs aggregating. This paper reports on the biological and ecological diversity of elasmobranchs occurring at several topographic highs in the northwestern Gulf of Mexico, including the Flower Garden Banks; describes the seasonal habitat use, social organization and behavior of elasmobranchs at the sites surveyed; and evaluates topographic highs as habitat for some elasmobranch species. Species found utilizing the topographic highs surveyed include the nurse shark (*Ginglymostoma cirratum*), whale shark (*Rhincodon typus*), tiger shark

(*Galeocerdo cuvier*), silky shark (*Carcharhinus falciformis*), dusky shark (*C. obscurus*), Caribbean reef shark (*C. perezi*), sandbar shark (*C. plumbeus*), scalloped hammerhead shark (*Sphyrna lewini*), southern stingray (*Dasyatis americana*), roughtail stingray (*D. centroura*), spotted eagle ray (*Aetobatus narinari*), lesser devil ray (*Mobula hypostoma*), sicklefin devil ray (*M. tarapacana*), and manta ray (*Manta birostris*). Occurrence data indicate these species form three temporal assemblages: the winter pelagics, summer pelagics, and resident assemblages. Data also show that dissimilar topographic highs (mid-shelf, shelf-edge, and artificial shelf-edge) function as seasonal feeding, nursery, or mating habitat for different life stages and species. A model and postulate simplifying elasmobranch-topographic high habitat associations are presented from which future research and conservation plans may be organized.

DEDICATION

I dedicate this work to my wife Susan, whom I met while undertaking this study. We were friends upon meeting, but it was some years before we established a relationship and life-long commitment to one another. It is with her that I came to appreciate the wholeness that only a couple can achieve. It is through her that I gained perspective of what is important in living. It is with her that I learned to love deeply and accept another's love completely. It is with her that I am sharing life's adventures, both professionally and personally. It is to her that I dedicate this thesis and the rest of my life, for as long as she will have me.

ACKNOWLEDGMENTS

First, I thank my friend Brien Nicolau. Upon moving to Corpus Christi in 1998, our friendship grew, and it was Brien who proved to be a friend above others that I had known much longer. He made it possible for me to join the Center for Coastal Studies, TAMU-CC, and offered a stable and sane voice amidst the tempestuous seas that I experienced while completing this study, keeping me afloat and sailing toward my goal. My heartfelt thanks are extended to him for his friendship and support. May he enjoy many fair winds and following seas through life.

I am grateful to my committee: John McEachran, David Owens, and Steve Gittings. John accepted the challenge of taking me as a graduate student and planted the seed that lead to the elasmobranch-topographic high habitat association postulate. He was a loyal and patient advisor to a willful student, and I should have learned more from him. David listened and extended helpful advice, and I attribute my sea turtle rodeo expertise to him. And it was Steve Gittings that really augmented my graduate education and fueled my interest in marine science. Steve made it possible for me to conduct this study, and I am most grateful to him for his mentoring, friendship and support. Kirk Winemiller was also an important contributor and advisor, and I appreciate his input. It was his conservative criticism that lead to a more rigorous evaluation of the collected dataset.

Several administrators were also invaluable to my graduate experience, and I am truly indebted to them for all their assistance. My thanks are extended to J. Crenshaw and M. Rubio of the Department of Wildlife and Fisheries Sciences, TAMU, and to L.

Simmons and G. Krause at the Center for Coastal Studies, TAMU-CC. I am also indebted and grateful to J. Wes Tunnell Jr. for his support. He welcomed me as member of the Center for Coastal Studies, Texas A&M University-Corpus Christi.

Many entities were instrumental in carrying out this study. They include: Air Logistics, Inc., ANR Pipeline, British Petroleum, Center for Coastal Studies, Texas A&M University-Corpus Christi, the Department of Wildlife and Fisheries Sciences (TAMU), the Department of Oceanography (TAMU), the Flower Garden Banks National Marine Sanctuary, The Flower Gardens Fund, Gulf Reef Environmental Action Team, The Gulf of Mexico Foundation, The Houston Underwater Club, the Margaret Cullinan Wray Foundation, Minerals Management Service, Mobil Exploration and Production, the National Geographic Society, the National Oceanic and Atmospheric Administration, the National Underwater Research Center at UNC-Wilmington, the PADI Project AWARE Foundation, Rinn Boats, Inc., Reef Environmental Education Foundation, SeaSpace Inc., and the Texas Parks and Wildlife Department.

I am also indebted and appreciative to many individuals that contributed to this study in one manner or another. Emma and Joel Hickerson were invaluable contributors and great friends during this study and I wish them great happiness and prosperity together. Other contributors include: T. Sebastion, G. Bunch, P. Kott, S. Walker, D. Hagman, S. Dilworth, T. Clark, C. Beaver, G. Stanton, Q. Dokken, M. McCann, E. Albert, T. Bates, B. Bilir, G. Boland, L. Dauterive, A. Bull, D. Bull, K. Buch, J. Burek, F. Burek, G. Burgess, J. Carrier, S. Branstetter, P. Nillson, J. Carlson, R. Heuter, K. Mullin, C. Burks, J. Cancelmo, D. Zingula, S. Myers, J. Culbertson, D. Dowdy, J.

DuBose, S. DuPey, E. Heist, H. Konstantinou, J. Hewitt, L. Hyde, P. Klimley, R. Lehman, S. Mathew, C. Lingenfelder, E. Beckley, R. McElroy, B. Ponwith, C. Pattengill-Semmons, B. Semmons, T. Riggs, J. Reichman, P. Vize, F. Viola, K. Viola, J. Rooker, G. P. Schmahl, G. Notarbartolo-di-Sciara, M. Wicksten, G. Baumgardner, K. Vaughan, K. Withers, K. Deslarzes, K. Davis, A. Rutledge, J. Reeves, H. Gueterez, V. Buckbee, D. Bennett, and G. Sutton. These names are in no logical order of significance, and I have undoubtably left names out that deserved listing. To those who are not listed but contributed in some manner, please know I appreciated your assistance. Please accept my humble apology for overlooking you while writing this section.

Finally, I thank my family. To my mother, father and sisters who instilled in me a love for the natural history of all creatures great and small. To my brother Denis for his gentle encouragement. To the United States Navy and to my brother Gary, who introduced me to the underwater world. To my new family: Earl, Sandy, Kirk, Brenda, Greg, Jana, and Suzanne; thank you for all of the patience, support and love. And to my wife Susan, who has added much more meaning to this study and to my life, more than I could have imagined before we married.

TABLE OF CONTENTS

Page

LIST OF FIGURES

FIGURE Page

LIST OF TABLES

INTRODUCTION

The continental shelf of the northwestern Gulf of Mexico includes an array of submerged hard-banks and reefs (Cashman 1973, Rezak et al. 1985) (Figure 1) most of which support diverse reef communities (Rezak et al. 1985). The region also has a great concentration of offshore oil and gas platforms that, like many hard banks, provide substrate for reef communities (Sonnier et al. 1976, Gallaway & Lewbel 1982, Stanley & Wilson 1990, 1991,1997, 1998, Bright et al. 1991, Dokken et al. 1996, Rooker et al. 1997). Features such as hard banks, reefs, and offshore oil or gas platforms extending upward from the plane of the seafloor provide significant positive vertical and structural relief in an otherwise level landscape (Figure 2), and are referred to here as topographic highs.

Hard banks on the continental shelf of the northwestern Gulf of Mexico are classified according to their surrounding bathymetry and relief (Rezak et al. 1985). As such, mid-shelf banks rise from depths of 80 m or less and have a relief of at least 15 m (Rezak & Bright 1983), while shelf-edge banks occur between the 80-200 m isobaths with similar relief. Topographic highs are similarly classified for the purposes of this study.

This thesis follows the style and format of Environmental Biology of Fishes.

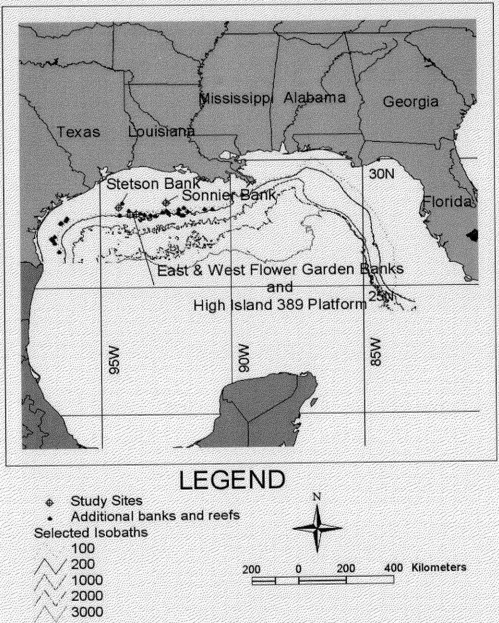

Figure 1. Hard banks and reefs punctuating the continental shelf of the northwestern Gulf of Mexico. These features, in addition to the numerous offshore petroleum platforms in the region, provide significant positive vertical and structural relief to the continental shelf and slope. Five study sites (Sonnier Bank, Stetson Bank, East & West Flower Garden Banks, and the High Island 389 platform) were visited from 1992 through 2000 to survey elasmobranch fauna occurring there.

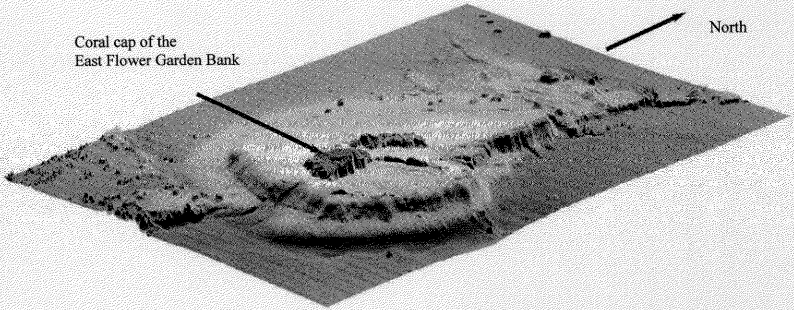

Figure 2. The East Flower Garden Bank. This three-dimensional characterization was based on surveys conducted by the United States Geological Survey Seafloor Mapping Project using a Kongsberg Simrad EM300 multibeam system.

Table 1. Historical records of elasmobranchs. Records of sharks and rays reported at Stetson and Sonnier Banks (MSB), the Flower Garden Banks (FGB), and various offshore oil and gas platforms in the scientific literature. In many cases, sharks were reported as "sharks" or unidentified sharks belonging to the families Carcharhinidae or Sphyrnidae. Number listed in the table cells indicate the references cited: 1. Bright & Cashman (1974), 2. Sonnier, Teerling, & Hoese (1976), 3. Boland, Gallaway, Baker & Lewbel (1983), 4. Dennis & Bright (1988), 5. Rezak, Bright & McGrail (1985).

Species	FGB	MSB	Platform
Ginglymostoma cirratum	2, 3, 4, 5	2, 4, 5	
Rhincodon typus	4	5	
Isurus oxyrinchus	3		
Mustelus canis	3		
Carcharhinus falciformis	1, 3, 4	4, 5	3
Carcharhinus leucas	3, 4	5	
Galeocerdo cuvier	3, 4	5	
Rhizoprionodon terraenovae	1, 5	4, 5	
Sphyrna lewini	3, 4, 5	4	
Squatina dumeril	4, 5		
Pristis sp.	4, 5		
Dipturus olseni	3		
Dasyatis americana	2, 3, 4, 5	2, 4, 5	2
Aetobatus narinari	3, 4, 5		
Rhinoptera bonasus	3		
Manta birostris	1, 3, 4, 5		

However, accounts of elasmobranchs at these sites are chiefly anecdotal, in many cases classified as "sharks" or "unidentified sharks" of the families Triakidae, Carcharhinidae or Sphyrnidae. Secondly, few specimens or photographs are available to confirm identifications, and often there is no information regarding the size, sex, social groups, abundance, or behavior of elasmobranch fishes.

As a result of coastal habitat loss, heavy fishing pressure, and bycatch, many sharks in the western Atlantic and Gulf of Mexico are considered to be overexploited (NMFS 1998). Of the sharks listed in Table 1, six species are listed as overfished in a report to Congress (NMFS 1998). Rays are rarely monitored by the National Marine Fisheries Service, so the status for most North American populations is unknown, yet they are exploited in the North Atlantic Ocean (Brander 1981, Walker & Heessen 1996, Walker & Hislop 1998, Walker et al. 1997, Casey & Myers 1998).

Recent declines in the abundance of some elasmobranchs have stimulated research on the life history strategies, habitat areas, and the social organization of some species. It is well established that some species segregate by size and sex into different bathymetric or geographic areas that function as nursery habitat, adult feeding habitat, and mating areas (Meek 1916, Springer 1940, 1967, Bass 1978, Branstetter 1990, Castro 1993, Simpfendorfer & Milward 1993). Additionally, many species inhabiting temperate regions that experience seasonal changes in water temperature demonstrate seasonal movements to habitat areas more environmentally tolerable to their physiological needs (e.g., summer vs. winter adult feeding areas) (e.g. Springer 1940, 1967, Bass 1978, Branstetter 1990, Castro 1993). Accordingly, a population may occupy an assortment of biotopes (e.g., bays, estuaries, coral reefs, open ocean) that serve as seasonal nursery habitat, adult feeding habitat, and a mating habitat to discernible social groups within the population.

To date, fisheries biologists have focused on some neritic shark species and their use of eulittoral waters (intertidal zone to approximately 50 m isobath) in temperate and subtropical regions of North America as summer nursery habitat (Gruber et al. 1988, Morrissey & Gruber 1993a, 1993b, Holland et al. 1993) while it is recognized these animals seldom occupy these waters during winter months (Springer 1967, Branstetter 1990, Castro 1993). Subsequently, there is little information regarding elasmobranch use of topographic highs as habitat in infralittoral (50-100 m isobaths) or circalittoral (100-200 m isobaths) landscapes.

The objectives of this paper are 1) to assess the biological and ecological diversity of elasmobranchs at several natural and artificial topographic highs, including the Flower Garden Banks, 2) to investigate the seasonal habitat use and social organization of elasmobranchs at the study sites, and 3) to evaluate topographic highs as habitats for some elasmobranch species.

METHODS

Study Sites

Five topographic highs (four natural banks and one offshore production platform) located in the northwestern Gulf were visited to study the behavioral ecology of elasmobranchs. Three sites (East and West Flower Garden Banks and the offshore production platform, High Island A-389A) are located in circalittoral waters along the shelf-edge, while two sites (Stetson and Sonnier Banks) are mid-shelf banks and situated in infralittoral waters (Figure 1).

Sonnier Bank

Sonnier Bank is located 220 km southeast of Sabine Pass on the Texas-Louisiana border at 28°20.0'N and 92°27.0'W. Three peaks rise up from the body of the bank to within 25 m of the sea surface in an arcuate pattern and are the remains of a collapsed salt diapir composed primarily of Tertiary sandstones, siltstones, and claystones (Rezak & Bright 1983). The bank is approximately 600 ha in area (Greg Boland, pers comm) though the peaks are much smaller in size. The base depth of the bank is about 52 m (Rezak & Bright 1983). Overall relief of Sonnier Bank is approximately 27 m. Hydrozoan fire corals (*Millepora alcicornis*) and various sponges including *Neofibularia nolitangere* and *Ircina* sp. are the dominant sessile fauna on the summit (Rezak & Bright 1983). Several anthozoan corals and encrusting coralline algae species occur in a transitional zone below the *Millepora*-Sponge zone. Mobile invertebrates and reef fishes are commonly found on the peaks of this bank (Rezak & Bright 1983).

Stetson Bank

Stetson Bank (Figure 3) is a mid-shelf bank (Rezak 1983) composed primarily of soft claystone (Neumann 1958). The bank is located 174 km south-southwest of Sabine Pass at 28°10.0'N and 94°'17'W. It consists of a relatively level claystone top penetrated in places by thin, nearly vertical beds of more highly indurated rock, often broken by abrupt upward outcropping claystone structures of approximately 0.3-3.0 m horizontal and vertical dimensions (Bright et al. 1974). The bank occupies approximately 4 ha, with a base depth of 48 m and crests at roughly 20 m (Bright & DuBois 1974). Bank margins are defined by areas of high relief with outcropping structures standing 4.5 m above the surrounding reef summit. These structures are sometimes separated by small "canyon-like" passages. The slope of the bank's margin varies from low angles to near vertical drops of 12 m or more (Bright & DuBois 1974). Total relief for Stetson Bank is approximately 28 m. Above 40 m, *Millepora alcicornis* and sponges dominate the sessile assemblage. The surrounding level soft-bottom at the base of the bank (below 48 m) supports a sparse assemblage of infauna and mobile invertebrates. Small aggregations of epifauna and benthic fishes occur among isolated rocks or sponges enveloped by the nepheloid layer, a turbid layer of water that varies in thickness, but persists around the base of the bank and over much of the continental shelf of the northwestern Gulf of Mexico (Bright & DuBois 1974).

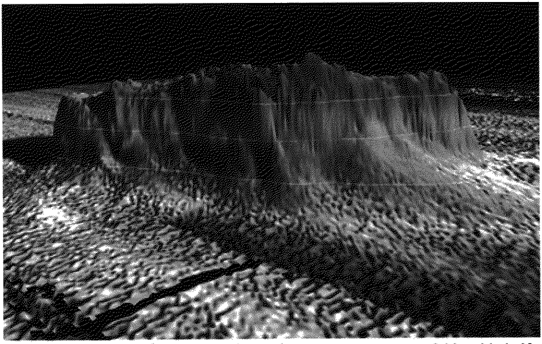

Figure 3. Stetson Bank. The three-dimensional characterization of this mid-shelf bank in the northwestern Gulf of Mexico was generated by the United States Geological Survey Seafloor Mapping Project using a Kongsberg Simrad EM300 multibeam system.

East and West Flower Garden Banks

The Flower Garden Banks are two separate banks with carbonate caps occurring near the continental shelf edge, approximately 198 km south of Sabine Pass on the Texas-Louisiana border. Each bank is the product of an upward migrating salt diapir, and supports the northernmost coral reef communities on the North American continental plate. These banks are similar in origin, general structure, and sediment distribution, but differ in details of orography, physiography, and sedimentology (Rezak 1983).

The East Flower Garden Bank (Figure 1) is located at 27°54′32″N and 93°36′00″W, covers an area of about 67 km^2, and is pear-shaped. Slopes are steep on the east and south sides, but gentle to the west and north. The bank rises to within approximately 20 m of the sea surface, whereas surrounding water depths are about 100 m to the west and north and about 120 m on the east and south sides. Total relief on the bank is roughly 116 m (Rezak 1983, Rezak et al. 1985). Figure 2 depicts the three-dimensional bathymetry of the East Flower Garden Bank.

The West Flower Garden Bank is 12 km west of the East Flower Garden Bank at 27°52′27″N and 93°48′47″W, and covers about 137 km^2 . The bank is oval-shaped and aligned northeast to southwest. The crest of the bank is approximately 20 m below the sea surface. Surrounding water depths vary from 100 m to the north, to 150 m to the south. Total relief on the bank is roughly 130 m (Rezak 1983, Rezak et al. 1985). The bathymetry of the West Flower Garden Bank is depicted in Figure 4.

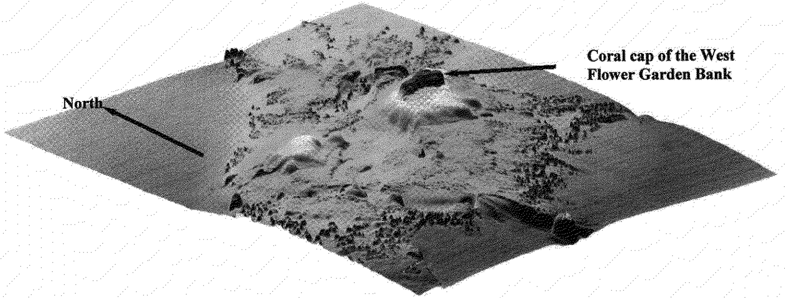

Figure 4. The West Flower Garden Bank. The three-dimensional characterization was produced by the United States Geological Survey Seafloor Mapping Project using a Kongsberg Simrad EM300 multibeam system.

The West Flower Garden Bank exhibits greater and more complex overall relief than the East Flower Garden Bank (Rezak 1983) and is probably older. Thus, the West Flower Garden Bank is classified as a mature salt dome, whereas the East Flower Garden Bank is considered an immature salt dome (Rezak 1983). Another detail differentiating the banks is the presence of a brine seep complex on the eastern side of the East Flower Garden Bank (Bright et al. 1980, Rezak 1983). Other seeps are evident at the bank, but do not contain the same magnitude of discharge.

The Flower Garden Banks are best known for their healthy coral reefs (Gittings et al. 1992a, 1992b, Gittings 1998). High diversity reefs are dominated by *Montastrea, Diploria, Colpophyllia,* and *Porites* coral species. Within or below the high diversity reef are *Madracis*, *Stephanocoenia-Millepora*, algal-sponge, antipatharian, and nepheloid zones (Rezak et al. 1985). Caribbean reef invertebrates and fishes inhabit the bank's reefs and other zones, and warm temperate or tropical pelagic species inhabit the surrounding waters.

High Island A-389A Offshore Production Platform

High Island A-389A (hereafter referred to as HI-389) is an offshore gas production platform installed in September 1981, and is the only study site to break the sea surface (Figure 5). The platform is located 1.5 km east of the coral reef at the East Flower Garden Bank in 125 m water depth at 27°54′26″N and 93°34′43″W. This eight pile structure's footprint is estimated at 0.38 ha at the mud-line and 0.05 ha at the sea surface. The underwater portion of the structure is a framework of horizontally, vertically, and diagonally laid pipes (Figure 6) that supports a diverse assemblage of

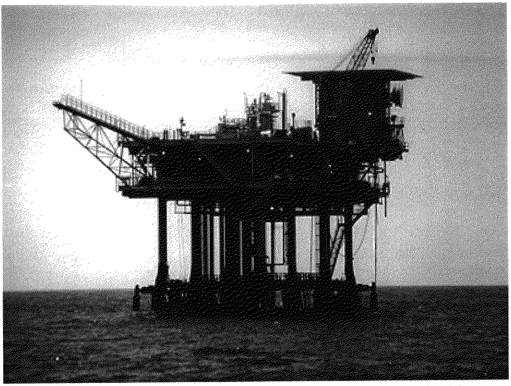

Figure 5. High Island 389 platform. The superstructure is located 1.5 km east of the coral cap of the East Flower Garden Bank in the northwestern Gulf of Mexico. The above-water structure functions as a steel island, providing roosting sites for migratory birds transiting the Gulf of Mexico.

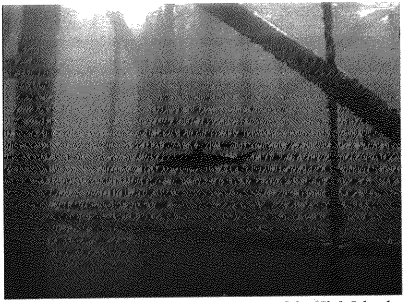

Figure 6. The underwater superstructure of the High Island 389 platform. It provides substrate for sessile marine organisms to attach. The structure functions as an artificial reef that supports a diverse assemblage of reef fauna and flora, including the silky shark (*Carcharhinus falciformis*).

sponges, hydroids, algae, molluscs, barnacles, tunicates, and corals (Dokken et al. 1996). Reef fishes inhabit the artificial reef, and pelagic fishes aggregate around the platform (Dokken et al. 1996, Rooker et al. 1997).

The Flower Garden Banks National Marine Sanctuary

Stetson and the Flower Garden Banks are protected as part of the Flower Garden Banks National Marine Sanctuary. The East and West Flower Garden Banks were designated in January 1992 as the tenth National Marine Sanctuary (NOAA 1991) following increased incidents of anchoring on the banks by large and small vessels in the early to mid 1980's, which often resulted in mechanical damage to the coral reefs. Among other threats, the Flower Garden Banks are protected from: oil and gas exploration within a "no-activity" zone, anchoring or mooring of vessels greater than 30 m in length, and the harvesting of corals and other sessile fauna and flora (NOAA 1991). Fishing is limited to conventional hook and line gear, and scientific collecting is greatly restricted. The HI-389 platform lies within Sanctuary boundaries, situated just outside a "no-activity" zone. Stetson Bank was added to the Sanctuary in October 1996 (P.L. 104-283). Sonnier Bank is not a marine sanctuary, however, the petroleum industry is prohibited from placing platforms or pipelines on the bank as part of any leasing contracts signed with the Minerals Management Service (MMS) under the Topographic Features Stipulation (MMS Regulation Notice to Lessees 98-12).

Data Collection

Results reported herein are based chiefly on in situ and photographic records gathered during elasmobranch surveys conducted from July 1992 through April 1998 using a variety of methods and personnel. Subsequent sightings made since April 1998 that contribute to the objectives of this study are also noted. The primary means of conducting surveys involved using SCUBA at the five study sites, where divers documented sightings of elasmobranchs. Additional aerial and surface sightings made from boats, helicopters, and offshore petroleum platforms were combined with underwater sightings into an 'in situ catalogue.' Video and still photography was frequently used to document elasmobranchs during surveys, and in some cases, videos and photographs taken prior to 1992 were used in the study. Photographic images were compiled into a 'photographic catalogue' to augment the in situ sightings data. Although the collection of specimens was not originally intended as part of this study, some specimens were obtained fortuitously from biologists or fishermen that unintentionally collected them as bycatch. Information related to these specimens was added to the in situ catalogue.

The majority of data were collected by myself, however, personnel contributing ancillary data to the study included trained observers, marine biologists, professional divers, underwater photographers, recreational divers, boat captains and crew, offshore petroleum industry workers, and helicopter pilots. Because personnel recording ancillary data exhibited disparate competence at identifying elasmobranchs, records were subjectively graded through personal interviews or as compared with photographic records supporting their records in order to gauge each observer's skill to properly identify each species.

Most underwater surveys at natural banks were conducted from 0-37 m, although some, with the aid of Nitrox or Trimix blends, were extended to the 58 m isobath. Underwater surveys were not standardized by area, depth, direction, or bottom time because of varying environmental conditions (e.g. current, visibility, sea state), physiographic differences of the sites, and variation in diving equipment and skill of the observers. Dives typically varied in duration from 15-90 minutes. Since HI-389 does not impose a 'hardbottom' to divers (at least within acceptable diving limits) like natural banks, HI-389 was typically surveyed from 0-63 m, and sometimes as deep as 100 m when visibility was optimal.

A series of microtopes were distinguished based on discernable features at the topographic highs for the purposes of this study. Microtopes recognized at the natural banks include the reef crest, sand patch, deep reef, escarpment, water column, and open water. Microtopes identified at HI-389 consist of the reef complex, water column, and open water. The reef crest includes the hermatypic coral substrate above approximately the 30 m isobath at each bank and the first 3 m of water over the sessile fauna, but excludes sand patches that fragment the reef crest on each Flower Garden Bank. Areas south and east of the pinnacles of Stetson Bank are also considered as sand patch microtope. Escarpments are areas where the reef slope changes markedly from the relatively level pitch of the reef crest. The comparatively level landscape below an escarpment was classified as deep reef. Elasmobranchs swimming between the sea surface and 3 m above the reef or sand substrates were regarded as occurring in the water column, as were all those occurring at HI-389 except elasmobranchs found resting on the structure or swimming more than 30 m from the structure. Areas greater than 30 m from the reef crest, escarpment, or HI-389 structure were considered open water.

Areas of the reef crest, sand flats, escarpment, and water column microtopes were typically surveyed during each dive conducted at natural banks. Small portions of the deep reef were only surveyed during summer months at mid-shelf and Flower Garden Banks. Open waters in the region were seldom surveyed, and only the sea surface was surveyed when helicopters were available.

Observers reported sightings on survey forms available on boats or HI-389. Information requested on forms included the observation date, study site, time of observation, observer's name(s), animal(s) identification to the lowest taxonomic group possible, estimated size(s) and sex(s), abundance, microtope where the animal(s) occurred, and notes concerning the animal(s) and their behavior. Each encounter with an elasmobranch species, whether as a solitary individual or group of conspecifics, was logged in the in situ catalogue as a separate observation and independent record. Shark size was reported as the estimated total length (TL), and ray size was reported as the estimated disc width (DW). Animal sizes were converted from "feet" to one meter categorical increments to diminish inaccuracies caused by estimating size in the water. Sex was determined by the presence or absence of claspers. Abundance was reported as the number of conspecifics observed within the observer's 360° spherical view during a sighting.

Observers were also requested to document the number of animals comprising a group of conspecifics in a sighting and the animals' orientation with respect to each other. Group size was delineated based on the number of conspecifics occurring within approximately five body sizes (TL for sharks, DW for rays) of one another. Animals more distant than five body sizes from the nearest conspecific during the entire observation period were treated as a different group or as solitary. For example, two conspecifics occurring within approximately five body sizes of one another were classified as paired animals, while an animal sighted in another quadrant of the observer's view and without conspecifics present within five body sizes of the sighted animal, was classified as solitary. An aggregation consisted of three or more animals occurring within five body sizes of each other, and aggregations were classified by the number of animals comprising the group, as small (3-10), medium (11-50), large (51-100), or massive (>100).

Animals occurring in groups of two or more animals were determined to be in polarized or nonpolarized alignment. Polarized groups involve animals moving together in a uniform manner, and non-polarized groups involve animals moving in independent directions, irrespective of the directed movements of a conspecific. Therefore, animals were recorded as occurring within one of the following social groups: solitary, polarized pair, non-polarized pair, polarized aggregation, or non-polarized aggregation, with aggregation sizes further differentiated as small, medium, large, or massive.

Data Management and Analysis

A fundamental premise made in this study is the belief that each species has the same detection potential in one season as another if present at the study sites. For example, it is assumed that if the whale shark (*Rhincodon typus*) was observed during summer months at the Flower Garden Banks, it also could be detected during winter months if present and surveys were conducted. And if sighted only during summer months, then a strong probability exists that the species does not occur at the Flower Garden Banks during winter months. Although species abundance or commonness can influence detection potential, the probability that rare, cryptic, or casual species occurring at the study sites were detected during this study was significantly increased because many people participated in opportunistic surveys during all seasons, as opposed to relying solely on the surveys of one or several individuals.

A graded scheme used to evaluate elasmobranch records gathered in this study was designed to address concerns regarding the quality of ancillary records and empower conservative critics to elevate sightings and photographic data to higher taxonomic levels if desired. Records graded as Quality Group 1 are considered accurately identified to species with my highest level of confidence; these records include my personal sightings identified to species, as well as collected specimens, photographic records in which animals were identified, and ancillary records that included photographic images confirming their identification. Taxa reported in Quality Group 2 are considered accurately identified to species, however, records lacked corroborating evidence (specimens or photographic images), but were documented by observers that correctly identified the same species in previous records with corroborating evidence. Quality Group 3 concerns animals I believe were correctly identified to species without corroborating evidence, however, animals could have been misidentified since similar species occur at the study sites. Observers reporting in this group were primarily scientific divers who are presumed to possess heightened skills for discriminating morphological characteristics, in contrast to people lacking scientific training. Quality Group 4 includes records of animals confidently identified to genus but that lacked corroborating evidence or are supported by photographic images of marginal quality, thus hindering the animals identification to species. Records included in this group were generally made by diving professionals. Quality Group 5 includes records confidently identified to the family level. The majority of records included in this group were largely obtained from recreational divers reporting animals without corroborating evidence to support their identification.

One notable exception to the graded scheme involves sharks of the genus *Carcharhinus*. While many skilled observers reported several carcharhinid species at the study sites, their abilities to discriminate the subtle yet important differences between similar *Carcharhinus* species are in doubt. Therefore, ancillary records of *Carcharhinus* species were assigned to Quality Groups 4 or 5, except when corroborating photographic images were available to include the record in Quality Group 1. The purpose of devaluing ancillary records of *Carcharhinus* species is to minimize effects of easily misidentified species on the data set.

The year was divided into six seasons based in part on changes in water temperature at the East Flower Garden Bank (Figure 7). Winter 1 included December and January, Winter 2 comprised February and March, Spring extended from April through May, Summer 1 included June and July, Summer 2 lasted from August through September, and Autumn spanned October and November.

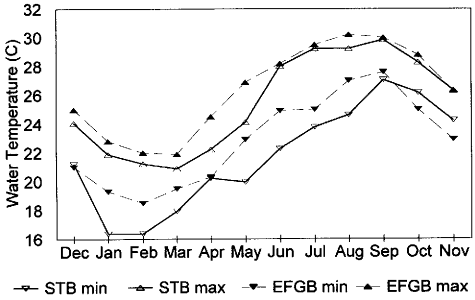

Figure 7. Maximum and minimum water temperatures for Stetson Bank (STB) and the East Flower Garden Bank (EFGB). Data were gathered using underwater thermistors placed on STB from October 1993 to May 1996, and on the EFGB from 1990-1995.

Sightings were pooled by topographic high type (mid-shelf banks, Flower Garden Banks, HI-389) and season to educe species-specific patterns of seasonal occurrence, habitat use by size and sex, abundance, commonness, and sociality.

RESULTS

Catalogue Statistics

The in situ catalogue comprises 615 records through April 1998, although additional sightings were collected during that period and discarded because they lacked vital data such as the month or location of the sighting. After devaluing 152 disputable records of potentially misidentified species from Quality Groups 2 or 3 to Quality Groups 4 or 5, the in situ data set used for the species accounts comprised 464 records. Additionally, 406 photographic records (photographs and video clips combined) were catalogued. Altogether, 870 records were used for the species accounts. Sightings known to duplicate data concerning the same animal(s) were not included in the in situ catalogue, unless the animal(s) were sighted later in a different quarter of the day. Some records in the in situ catalogue include duplicate records of the same animal(s) listed in the photographic catalogue. Regardless, some records in the in situ catalogue are likely duplicate sightings, particularly for abundant species forming aggregations such as *Sphyrna lewini* and *Aetobatus narinari*.

Personal sightings exceeded those made by other contributors (25 % of the 615 in situ records). Although 75 % of the in situ records were made by other observers, no other individual contributed more than 8 % individually to the catalogue. Similarly, the majority of video clips gathered in this study were made by me, although photographs used in this study came from other individuals.

Approximately 97 % of sightings (including photographic records) were gathered from underwater surveys, and nearly 3 % of sightings were made from the sea surface.

Less than 1 % of sightings were made from aircraft. Approximately 8 % of sightings were made at mid-shelf banks. Eighty five percent of sightings were made at the Flower Garden Banks, and 6 % of sightings were made at HI-389. One percent of sightings were made in open waters apart from the study sites.

Seven specimens were fortuitously collected during this study and included the species *Carcharhinus falciformis*, *C. obscurus*, and *C. perezi*. These specimens as well as an eighth specimen collected in 1980 and not documented in historic accounts were added to the in situ catalogue. The seven collected specimens are conserved in the Texas Cooperative Wildlife Collection at Texas A&M University. The jaws of the eighth specimen are conserved in the biological collections of the Department of Oceanography, Texas A&M University.

Sampling Effort

Many people contributed to the survey of elasmobranchs on assorted undocumented cruises, thus the overall sampling effort is unmeasurable. However, it is known that scientific divers visited the Flower Garden Banks and HI-389 during each pooled season, and in all but the Winter 1 season at mid-shelf banks. I personally attempted to visit each topographic high type at least once each season during 1994, 1995 and 1996, and opportunistically in other years. Despite my intentions, it was not feasible to visit each site during every season due to tempestuous weather or logistical problems. From July 1992 through April 1998, I logged 202 hours underwater at the five sites (42 h at mid-shelf banks, 95 h at the Flower Garden Banks, and 65 h at HI-389), and additional surveys were conducted post April 1998. Figure 8 depicts the number of days I surveyed each topographic high type by season from July 1992 through April 2000. Although more surveys were conducted during the summer seasons than in other seasons, at least one to three days were spent at the Flower Garden Banks and HI-389 in each of the pooled seasons. At least three survey days were achieved at mid-shelf banks during each pooled season, except during Winter 1, when no surveys were personally actualized. A typical survey day at these sites for me consisted of 3-4 dives of 50 minutes duration each.

Biological Diversity

Fourteen species of elasmobranchs were identified from published descriptions and figures (e.g. Bigelow & Schroeder 1948, 1953, Castro 1983, Compagno 1984a,b, Notarbartolo-di-Sciara 1987, Robins et al. 1986, Humann 1994, Hoese & Moore 1977, 1998) at the five study sites. These species represent three orders, seven families, and nine genera (Table 2) and are: *Ginglymostoma cirratum, Rhincodon typus, Galeocerdo cuvier, Carcharhinus falciformis, C. obscurus, C. perezi, C. plumbeus, Sphyrna lewini, Dasyatis americana, D. centroura, Aetobatus narinari, Mobula hypostoma, M. tarapacana*, and *Manta birostris*. Other species reported include *C. brevipinna, C. limbatus, Negaprion brevirostris, S. mokarran*, and *Sphyrna tiburo*, however, these identifications could not be authenticated, and are therefore not included in the species accounts. Table 3 enumerates the records compiled by species and the record quality groups used in the species accounts.

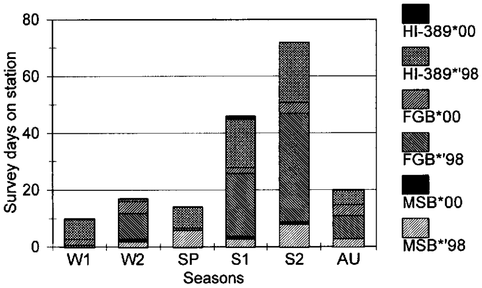

Figure 8. Personal survey effort. Surveys were conducted by J. Childs from July 1992 through April 1998 (*98), and from May 1998 through April 2000 (*00). Survey effort was based on the number of diving days spent on station and pooled by season (Winter 1:W1, Winter 2:W2, Spring: SP, Summer 1: S1, Summer 2: S2, Autumn: AU) and topographic high type (mid-shelf banks: MSB, Flower Garden Banks: FGB, and HI-389).

Table 2. Elasmobranch diversity. Sharks and rays occurring at topographic highs in the northwestern Gulf of Mexico, as documented in the literature and during this study. Species identification in this study was based from specimens (s), video (v), or photographs (p).

Order	Family	Species	Common name	Historic	Childs
Orectolobiformes	Ginglymostomatidae	*Ginglymostoma cirratum*	nurse shark	■	vp
	Rhincodontidae	*Rhincodon typus*	whale shark	■	vp
Lamniformes	Lamnidae	*Isurus oxyrinchus*	shortfin mako	■	
Carcharhiniformes	Triakidae	*Mustelus canis*	smooth dogfish	■	
	Carcharhinidae	*Galeocerdo cuvier*	tiger shark	■	vp
		Carcharhinus falciformis	silky shark	■	svp
		Carcharhinus leucas	bull shark	■	
		Carcharhinus obscurus	dusky shark		sv
		Carcharhinus perezi	Caribbean reef shark		svp
		Carcharhinus plumbeus	sandbar shark		vp
		Rhizoprionodon terraenovae	Atlantic sharpnose shark	■	
	Sphyrnidae	*Sphyrna lewini*	scalloped hammerhead shark	■	vp
Squatiniformes	Squatinidae	*Squatina dumerili*	Atlantic angel shark	■	
Pristiformes	Pristidae	*Pristis spp*	sawfish	■	
Rajiformes	Rajidae	*Dipturus olseni*	spreadfin skate	■	
Myliobatiformes	Dasyatidae	*Dasyatis americana*	southern stingray	■	vp
		Dasyatis centroura	roughtail stingray		v
	Myliobatididae	*Aetobatis narinari*	spotted eagle ray	■	vp
	Rhinopteridae	*Rhinoptera bonasus*	cownose ray	■	
	Mobulidae	*Mobula hypostoma*	lesser devil ray		v
		Mobula tarapacana	sicklefin devil ray		v
		Manta birostris	manta ray	■	vp

Unconfirmed Elasmobranch Species - c.f.

Species	Common name
Carcharhinus c.f. brevipinna	spinner shark
Carcharhinus c.f. limbatus	blacktip shark
Negaprion c.f. brevirostris	lemon shark
Sphyrna c.f. mokarran	great hammerhead shark
Sphyrna c.f. tiburo	bonnethead

Table 3. Catalogue statistics. In situ and photographic documentation of species occurrences at the study sites through April 1998. Species records gathered regardless of record quality group is provided (N), followed by the record quality groups (RQG) used to prepare the species accounts based on in situ (IS), photographic (P), and videographic (V) records. Records judged within the specified RQG for each species are tabulated by the topographic high types where they were documented.

Species	COMPREHENSIVE					Mid-Shelf Banks				Flower Garden Bank				HI-389			
	N	RQG	IS	P	V	IS	P	V	n	IS	P	V	n	IS	P	V	n
G. cirratum	71	1 to 5	53	0	18	15	0	1	16	38	0	17	55	0	0	0	0
R. typus	64	1 to 5	22	31	11	5	0	6	11	13	4	4	21	3	20	1	24
G. cuvier	22	1 to 4	16	3	3	0	0	0	0	16	3	3	22	0	0	0	0
C. falciformis	25	1	14	2	9	0	0	0	0	1	0	0	1	13	2	9	24
C. obscurus	7	1	3	0	4	0	0	0	0	3	0	4	7	0	0	0	0
C. perezi	11	1	8	1	2	0	0	0	0	8	1	2	11	0	0	0	0
C. plumbeus	11	1	7	0	4	4	0	2	6	3	0	2	5	0	0	0	0
S. lewini	107	1 to 3	74	2	31	0	0	0	0	74	2	31	107	0	0	0	0
D. americana	55	1 to 3	34	1	20	14	0	5	19	20	1	15	36	0	0	0	0
D. centroura	6	1 to 3	4	0	2	4	0	2	6	0	0	0	0	0	0	0	0
A. narinari	93	1 to 4	67	2	24	3	0	0	3	64	2	24	90	0	0	0	0
M. hypostoma	24	1 to 3	20	0	4	0	0	1	1	20	0	3	23	0	0	0	0
M. tarapacana	5	1 to 3	3	0	2	0	0	0	0	3	0	2	5	0	0	0	0
M. birostris	368	1 to 3	138	97	133	3	0	5	8	129	97	128	354	6	0	0	6
Sum of Record	869		463	139	267	48	0	22	70	392	110	235	737	22	22	10	54

Many species were observed at all three topographic high types, but some species were sighted at only one or two topographic high types. Species documented occurring at all three topographic high types include *R. typus*, *S. lewini*, and *M. birostris*. Species observed only at mid-shelf and Flower Garden Banks comprised *G. cirratum*, *C. plumbeus*, *D. americana*, *A. narinari*, and *M. hypostoma*. One species (*C. falciformis*) was observed at the Flower Garden Banks and HI-389, but not at mid-shelf banks. *Dasyatis centroura* was found only at mid-shelf banks, and *G. cuvier*, *C. obscurus*, and *M. tarapacana* were only sighted at the Flower Garden Banks.

SPECIES ACCOUNTS

Order Orectolobiformes (carpet sharks)

Family Ginglymostomatidae (nurse sharks)

Ginglymostoma cirratum (Bonnaterre 1788)

Nurse shark (Figure 9)

Ginglymostoma cirratum is a demersal shark that commonly occurs in shallow tropical and subtropical marine waters (Castro 1983, Compagno 1984a). It is the only member of the family Ginglymostomatidae known in the western North Atlantic (Castro 1983, Compagno 1984a) and the Gulf of Mexico (Gudger 1912, Bigelow & Schroeder 1948, Baughman & Springer 1950, Springer 1963, Clark & von Schmidt 1965, Hoese & Moore 1977, 1998, Klimley 1980, Snelson & Williams 1981, Carrier 1985a, 1985b, Carrier & Luer 1990, Carrier et al. 1994, Pratt & Carrier 1995, Castillo-Geniz et al. 1998, Carrier & Pratt 1998, Kohler et al. 1998, McEachran & Fechhelm 1998, Carlson & Brusher 1999). Because *G. cirratum* is the only ginglymostomatid in the region, records attributed to nurse sharks at the study sites are interpreted as accurately identified as *G. cirratum*, regardless of record quality group.

The in situ catalogue includes 53 sightings of *G. cirratum* of record quality groups 1-5. Additionally, 18 video clips were compiled of *G. cirratum*. The nurse shark was observed at mid-shelf and Flower Garden Banks, and was not detected at HI-389 to a depth of 100 m.

Figure 9. Nurse shark (*Ginglymostoma cirratum*). This shark was resting on the reef at a Flower Garden Bank and was initially detected with it's head beneath the adjacent brain coral colony. The picture was captured from video provided by the Flower Garden Banks National Marine Sanctuary office.

Mid-Shelf Banks: *Ginglymostoma cirratum* was documented at mid-shelf banks by 15 *in situ* records and one video clip during all seasons except Winter 1 (Table 4). Only solitary animals were recorded at mid-shelf banks, and their sizes ranged from 1-3 m TL (Figure 10). Animals with estimated sizes of 1-2 m TL comprised 66.7 % of in situ sightings at mid-shelf banks, making it the most common size group. Animals estimated between 2-3 m TL comprised 26.7 % of in situ sightings. Both sexes were documented, although the only male identified was observed during Summer 2. Eleven in situ sightings included unsexed animals.

Flower Garden Banks: The nurse shark was documented at the Flower Garden Banks during all seasons except Winter 1 in 38 in situ records and 17 video clips (Table 5). Fewer than four animals were sighted at a time. Solitary and paired animals made up 84 % and 11 % of in situ sightings respectively, and paired or aggregated animals formed both polarized or nonpolarized groups. Animals ranged in size from 1-4 m TL at the Flower Garden Banks (Figure 10), with 36.8 % of in situ sightings including animals 1-2 m TL, and 50.0 % of in situ sightings of animals 2-3 m TL. Animals estimated greater than 3 m TL were reported in 5.3 % of in situ sightings.

Ecology and Behavior: *Ginglymostoma cirratum* was observed day or night on reef crests, on sandy flats, and at escarpments. Sharks were often observed resting in sand flats or atop coral colonies that were domed in shape, and several sightings included animals with their heads under coral colonies.

Table 4. Nurse shark habitat use of mid-shelf banks. Based on sightings of *Ginglymostoma cirratum* at mid-shelf banks from data collected thru April 1998.

Ginglymostoma cirratum — **nurse shark**

Size at Birth:		~ 0.3 m
Size at Maturity:	Males	~ 2.2 m
	Females	~ 2.3 m
Maximum Size Attained:		~ 4.3 m

Mid-Shelf Banks (Sonnier & Stetson)

Record Quality	1	2	3		5	
Seasonal Occurrence	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m						
1 to 2 m		F	u		M U	U
2 to 3 m				F	F U	F
3 to 4 m						
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary			1.0.0		0.0.2		2.0.0		5.1.1		3.0.0	
Paired												
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

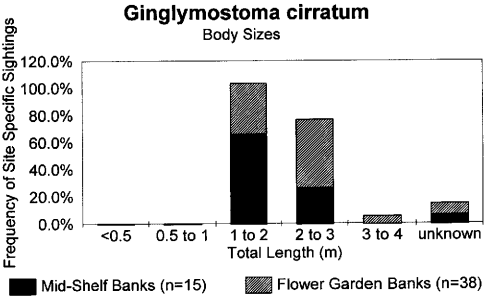

Figure 10. Body sizes reported for *G. cirratum*. Based on sharks observed at mid-shelf and Flower Garden Banks as recorded in in situ accounts through April 1998. All animals were reportedly greater than 1 m TL, with most sightings consisting of animals estimated to be 1-3 m TL.

Table 5. Nurse shark habitat use of the Flower Garden Banks. Based on sightings of *Ginglymostoma cirratum* at the Flower Garden Banks from data collected thru April 1998.

Ginglymostoma cirratum — **nurse shark**

Size at Birth:		~ 0.3 m
Size at Maturity:	Males	~ 2.2 m
	Females	~ 2.3 m
Maximum Size Attained:		~ 4.3 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality	1	2	3	[illegible]	5	
Seasonal Occurrence	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m						
1 to 2 m				F U	F U	
2 to 3 m		F U	U	B	F U	U
3 to 4 m				U	U	
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	Winter 1 NP	Winter 1 P	Winter 2 NP	Winter 2 P	Spring NP	Spring P	Summer 1 NP	Summer 1 P	Summer 2 NP	Summer 2 P	Autumn NP	Autumn P
Solitary			1.0.0		1.0.0		16.1.1		8.1.2		1.0.0	
Paired				1.0.0		0.0.1	[illegible]	1.0.0				
Small Aggr. (3 to 10)								1.0.0				
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

No more than one shark was sighted at a time at mid-shelf banks, however, as many as three sharks were observed in one sighting event at the Flower Garden Banks during Summer 1. While conducting surveys at the Flower Garden Banks, I encountered solitary nurse sharks as many as three times during a dive, however, I was unable to ascertain whether this was one animal sighted three times, three animals sighted once each, or some other combination. Based on the surveys conducted, I consider *G. cirratum* abundance to be low relative to gregarious species (i.e., *S. lewini* or *A. narinari*) observed in this study. I estimate each mid-shelf bank supports no more than three *G. cirratum*, and each Flower Garden Bank supports fewer than 10 nurse sharks in the coral reef zone.

Newborn *G. cirratum* are born at approximately 0.3 m TL (Compagno 1984a, Castro 2000). Compagno (1984a) states that male nurse sharks mature at approximately 2.2 m TL, and females mature at approximately 2.3 m TL. Growth studies conducted on free-ranging *G. cirratum* in the Dry Tortugas off Florida indicate that males and females mature at about 2.0 m and 2.4 m, respectively (Carrier 1991), although Beebe (1941) described six *G. cirratum* embryos collected from a female parent estimated at 1.5 m TL. More recently, Castro (2000) estimated that male and female nurse sharks mature at about 2.1 m TL. For the purpose of discussing the life history stages of nurse sharks inhabiting the study sites, I distinguish older (larger) juvenile nurse sharks to be animals approximately 1.0-1.5 m TL, subadults as animals whose sizes range comprise 1.5-2 m TL, and adults as greater than 2 m TL. Therefore, data shows *G. cirratum* (in size groups 1-4 m TL) observed at mid-shelf and Flower Garden Banks to be older (larger) juvenile, subadult, and adult animals.

While nurse sharks are reported in various ichthyological compilations of specific areas (eg. Bigelow & Schroeder 1948, Bohlke & Chaplin 1993, McEachran & Fechhelm 1998), little is documented in the scientific literature identifying specific areas utilized as habitat by different social groups or age classes of this species. Currently, the only publicized habitat areas comprise small areas of the Florida Keys and Dry Tortugas where *G. cirratum* utilize nearshore waters as mating habitat (Klimley 1980, Carrier & Luer 1990, Carrier et al. 1994). Neonate and juvenile nurse sharks have also been found in these areas, indicating use as primary and secondary nursery habitat (Carrier 1985a,b, 1990, Carrier & Luer 1990, Carrier et al. 1994). Clark and von Schmidt (1965) collected young juvenile *G. cirratum* in shallow waters along the central west coast of Florida, indicating the area functions as nursery habitat. Additionally, Bermuda serves as a nursery to *G. cirratum* since the pregnant female reported by Beebe (1941) was collected there.

Ginglymostoma cirratum is often described as sedentary, with limited migratory patterns. It is considered a resident to most of Florida and the Caribbean-West Indian region (Bigelow & Schroeder 1948). Farther north, adult *G. cirratum* demonstrate a limited degree of seasonal migration as evident by their summer occurrences and winter absences along the mid-Atlantic states (Bigelow & Schroeder 1948, Schwartz 1984) and tagging data shows that nurse sharks can travel distances of as much as 540 km (Kohler et al. 1998). However, wide ranging behavior may be limited to larger sharks, since neonates and younger (smaller) juveniles tagged in the Florida Keys show very little ranging activity based upon recaptured animals (Carrier 1985a,b, 1991, Carrier & Luer 1990).

Based on data gathered in this study and the literature, I conclude that mid-shelf and Flower Garden Banks function as year-round habitat to older (larger) juvenile, subadult and adult *G. cirratum*, although more data is necessary to determine if males persist throughout the year at these banks as do females. The abundant fauna associated with these banks include spiny lobsters, shrimps, crabs, gastropods, bivalves, octopi, squids, and reef fishes including stingrays (organisms that *G. cirratum* typically preys upon), in addition to the relatively warm waters that bathe these banks, making the sites suitable for *G. cirratum* to occupy throughout the year.

It is unknown if *G. cirratum* observed in this study are reproductively active. Mating behavior or evidence thereof, was not documented during this study [Courtship and mating behavior of *G. cirratum* are described in Klimley 1980, Carrier et al. 1994, and Pratt & Carrier 1995]. The presence of adult male and female sharks at these topographic highs makes mating feasible, though such behavior is typically described occurring in shallow (less than 12 m) eulittoral waters (Gudger 1912, Bigelow & Schroder 1948, Clark & von Schmidt 1965, Klimley 1980, Carrier et al. 1994, Pratt & Carrier 1995). Nonetheless, one photograph shows nurse sharks copulating in waters 34 m deep off eastern Florida (N. Rouse in Gruber 1991 and Carrier et al. 1994), thus revealing mating behavior is not limited to shallow water. Sections of the Florida Keys are utilized as mating habitat by *G. cirratum* (Carrier et al. 1994, Pratt & Carrier 1995); one section is now specifically closed to anthropogenic activity during the breeding season (Carrier & Pratt 1998).

Ginglymostoma cirratum is considered rare in coastal waters exceeding 12 m (Castro 1983, Compagno 1984a, McEachran & Fechhelm 1998), although Hoese & Moore (1998) noted the species occurs at offshore reefs in the northwestern Gulf of Mexico. Sharks observed in this study occurred from 17-37 m in depth on natural banks. Surveys conducted by the National Marine Fisheries Service along the Gulf and Atlantic coasts of the United States collected *G. cirratum* at depths to 73 m (Grace & Henwood 1997). Additionally, the Commercial Shark Fishery Observer Program of the Florida Museum of Natural History collected data showing that *G. cirratum* was taken in waters as deep as 87 m (George Burgess & Kevin Coyne, unpublished data). Considering that: 1) older (larger) juvenile, subadult and adult nurse sharks were observed at mid-shelf and Flower Garden Banks, 2) neonates or young (smaller) juvenile *G. cirratum* were not observed at the study sites, 3) waters exceeding 95 m encircle the Flower Garden Banks, 4) nurse shark nurseries and mating habitat occur in eulittoral waters of the Gulf coast, and 5) *G. cirratum* is considered a relatively sedentary species that can range as great as 540 km. It is reasonable to conclude that larger *G. cirratum* (1.0 m TL and larger) can and do disperse from nearshore eulittoral nursery habitats along the Gulf coast to mid-shelf and shelf edge banks where resources are available. Clearly, data show that *G. cirratum* traverse waters exceeding 95 m in depth, or they would not inhabit the Flower Garden Banks.

Although nurse sharks were not sighted at HI-389, it is reasonable to expect this species to occur at artificial topographic highs located in eulittoral and infralittoral waters. Artificial reefs serve as suitable habitat for many invertebrates and fish species (Rooker et al. 1997) that nurse sharks are known to prey on (Bigelow & Schroeder 1948, Castro 1983, Compagno 1984a). Moreover, it is likely that mid-shelf banks or offshore petroleum platforms facilitate dispersal from eulittoral habitats to shelf-edge banks by providing suitable habitat for "island hopping" dispersal.

Whether *G. cirratum* returns to eulittoral waters and contributes to the regional population gene pool has yet to be examined. Animals occurring at shelf-edge topographic highs such as the Flower Garden Banks may be what Springer (1963) described as 'bank loafers', or part of an accessory population in the region. If mating occurs at these sites, animals may migrate to eulittoral waters to deposit their offspring in suitable nursery areas, since neonates and young nurse sharks have yet to be reported at mid-shelf and Flower Garden Banks.

The majority of *G. cirratum* sightings were of solitary animals, though, five records were of paired animals, and one record was of three aggregated animals. Paired animals occurring at the study sites were observed in polarized and nonpolarized alignment, and the aggregation of three animals observed at the Flower Garden Banks were touching one another in polarized alignment. Two of these animals were estimated at 1-2 m TL, and the third animal was estimated at 2-3 m TL. These sharks were resting with their torsos exposed, and their heads inserted into a cavern located in the side of a *Diploria* coral colony. They were stationary and showed no movement until disturbed by the videographer, at which point the sharks departed in different directions. The function of these social groups is not clear, however, nurse sharks are reported to form aggregations of 3-36 animals in eulittoral waters that are attributed to mating or feeding activity (Bigelow & Schroeder 1948, Compagno 1984a, Carrier pers. comm.).

Carrier et al. (1994) found *G. cirratum* to be very social, based on their studies in mating habitat in the Florida Keys. Data collected in my study show that *G. cirratum* is sociable, however, considerably less so relative to the schooling elasmobranch species encountered at mid-shelf and Flower Garden Banks. Because solitary animals were frequently sighted, and few sightings were made of paired or aggregated animals, I believe *G. cirratum* to be primarily reserved in nature, except when coming together to mate or feed (as reported in Florida).

Ginglymostoma cirratum was not observed or reported interacting with other species. Underwater encounters with nurse sharks suggest that the animals are relatively dormant, often resting on coral heads or in sand patches during the day unless disturbed by divers. At night, nurse sharks were found actively swimming over the reef, but sometimes found resting in sand patches also. Experience suggests the animals may actively foraging at night and rest during the day.

Family Rhincodontidae (whale shark)

Rhincodon typus (Smith 1828)

Whale shark (Figure 11)

Rhincodon typus is an epipelagic shark occurring in neritic and oceanic provinces of tropical and warm temperate zones of the Atlantic, Pacific, and Indian Oceans (Bigelow & Schroeder 1948, Compagno 1984a). Although chiefly found in waters

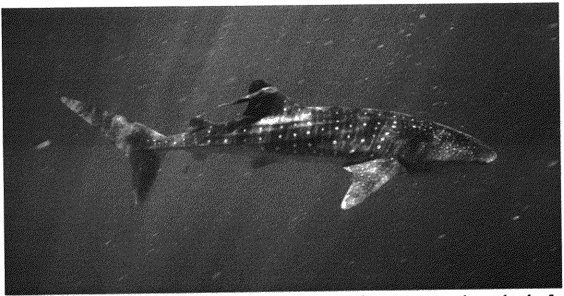

Figure 11. Whale shark (*Rhincodon typus*). This female shark was estimated to be 5-6 m TL, and was followed closely for approximately 2.5 hrs at the HI-389 platform in October 1992. Figure was captured from video taken by Greg Boland.

exceeding 15 m in depth, *R. typus* visits shallower waters that include coastal bays and lagoons (Compagno 1984a). The whale shark occurs in the Gulf of Mexico (Gudger 1923, 1939, Bigelow & Schroeder 1948, Baughman 1950, 1955, Baughman & Springer 1950, Gunter & Knapp, 1951, Breuer 1954, Reid 1957, Springer 1957, Hoese & Moore 1977, 1998, Hoffman et al. 1981; Rezak et al. 1985; Wolfson 1986, Dennis & Bright 1988, McEachran & Fechhelm 1998), and Childs et al. (in review) reports whale shark sightings documented in the northern Gulf of Mexico since 1933.

Rhincodon typus was documented in 22 in situ records (quality groups 1-5), 31 photographs, and 11 video clips. The whale shark is the sole species of the monotypic family Rhincodontidae and is unlikely to be misidentified due to its large size and unique shape and markings. Therefore, records identified as *R. typus* in this study are considered correctly identified. The whale shark was observed at each of the study sites and in open waters in the vicinity of the Flower Garden Banks.

Mid-Shelf Banks: Five *in situ* records and six video clips of the whale shark were collected at mid-shelf banks (Table 6). Records were documented during Summer 1 and 2 and Autumn. Animals ranged in size from 3-9 m TL (Figure 12). Only solitary animals were sighted, although animals estimated to be 3-4 and 6-7 m TL were separately observed by two dive teams during the same dive period. Both sexes were identified occurring at mid-shelf banks. The largest animal observed was an 8-9 m TL female during Summer 2.

Flower Garden Banks: *Rhincodon typus* was documented in 13 *in situ* records, four photographs, and four video clips at the Flower Garden Banks during both summer

Table 6. Whale shark habitat use of mid-shelf banks. Based on sightings of *Rhincodon typus* at the mid-shelf banks from data collected thru April 1998.

Rhincodon typus — **whale shark**

Size at Birth: smallest juvenile collected ~ 0.5 m

Size at Maturity: Males: ~ 9 m; Females: ~ 9 m

Maximum Size Attained: ~ 18 m (rarely known over 12 m)

Mid-Shelf Banks (Sonnier & Stetson)

Record Quality		1	2	3		5
Seasonal Occurrence	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
3 to 4 m				U		
4 to 5 m						
5 to 6 m						
6 to 7 m				M U	F	F
7 to 8 m						
8 to 9 m					F	
> 9 m						

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary							3.0.0		1.0.0		1.0.0	
Paired												
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
- M = males
- F = female
- B = both sexes
- U = unknown sex

Quality Groups 4 & 5
- m = male
- f = female
- b = both sexes
- u = unknown sex

Aggregations
- NP = nonpolarized
- P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

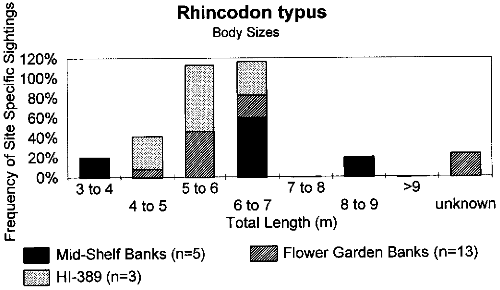

Figure 12. Estimated body sizes for *R. typus*. Based on animals documented in the in situ catalogue from July 1992 through April 1998. Reported animals were judged to be 3-9 m TL, and most animals were 5-7 m TL.

seasons and Autumn (Table 7). Animals ranged in size from 4-7 m TL (Figure 12), however, one pictured on video was estimated to be approximately 10 m TL. Males and females were identified, and all animals sighted were solitary.

Rhincodon typus was documented once in open waters 9 km south of the West Flower Garden Bank during an aerial survey conducted the day following a mass coral spawning event at the Flower Garden Banks in September. Three aggregated animals were sighted and estimated to be 4-5, 6-7, and 7-8 m TL. Sexes were not determined for these three animals.

HI-389: The whale shark was documented at HI-389 during Summer 1 and Autumn by three in situ records, 20 photographs, and one video clip (Table 8). Solitary and paired sharks were sighted that ranged in size from 4-7 m TL (Figure 12). Animals successfully sexed were females, although sex was not determined for all animals sighted. Two animals sighted together during Autumn showed nonpolarized movements with respective to one another.

Ecology and Behavior: *Rhincodon typus* was observed swimming in the water column from the sea surface to within approximately 3 m of the reef crest, as well as in open waters beyond the reef crest. Animals were observed at the study sites during daylight hours and not after dusk at the study sites, even during evenings that mass spawning events were observed at the Flower Garden Banks.

The maximum number of sharks sighted at mid-shelf banks and HI-389 was two, whereas abundance at the Flower Garden Banks was limited to one animal in a day. Aerial surveys conducted in the vicinity of the Flower Garden Banks as part of this

Table 7. Whale shark habitat use of the Flower Garden Banks. Based on sightings of *Rhincodon typus* at the Flower Garden Banks from data collected thru April 1998.

Rhincodon typus												whale shark
	Size at Birth:						smallest juvenile collected ~ 0.5 m					
	Size at Maturity			Males			~ 9 m					
				Females:			~ 9 m					
	Maximum Size Attained:						~ 18 m (rarely known over 12 m)					
Shelf-edge Banks (East & West Flower Garden Banks)												
Record Quality	1		2		3				5			
Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
3 to 4 m												
4 to 5 m							M					
5 to 6 m									B		M	
6 to 7 m									U			
7 to 8 m												
8 to 9 m												
> 9 m									U			
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary							1.2.1		5.0.2		2.0.0	
Paired												
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 & 5
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Table 8. Whale shark habitat use of HI-389. Based on sightings of *Rhincodon typus* at HI-389 from data collected thru April 1998.

Rhincodon typus												whale shark
	Size at Birth:					smallest juvenile collected ~ 0.5 m						
	Size at Maturity			Males:		~ 9 m						
				Females:		~ 9 m						
	Maximum Size Attained:					~ 18 m (rarely known over 12 m)						
Artificial Topographic High (HI-389 platform)												
Record Quality		1		2		3				5		
Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
3 to 4 m												
4 to 5 m							U					
5 to 6 m											U	
6 to 7 m											U	
7 to 8 m												
8 to 9 m												
> 9 m												
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary							1.0.0				1.0.0	
Paired											1.0.0	
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 & 5	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

study, located three animals aggregated 9 km south of the West Flower Garden Bank one day following a mass coral spawning event there. Additionally, aerial surveys of cetacean populations conducted in the region by NMFS biologists yielded sightings of varied whale shark aggregations (enumerating as many as 23 sharks in a group) at 28 Fathom and Bright Banks located 14 and 30 km east of the East Flower Garden Bank, respectively (Childs et al. in review).

Rhincodon typus is approximately 0.5 m TL at parturition (Joung et al. 1996, Kukuyev 1996, Chang et al. 1997), but the maximum size attained as adults is currently disputed. Although reported to attain lengths as great as 18 m, none greater than 13.7 m TL have been verified (Compagno 1984a). The largest whale shark reported, but unconfirmed, in the Gulf of Mexico is an 20.4 m TL animal, reported by a shrimp boat captain, who also collected the first living whale shark embryo known (Baughman 1955). Most documented sightings of *R. typus* are of individuals 4-12 m TL (Wolfson 1983). Information regarding the size at which *R. typus* matures is equally vague. Based on records of two 8-9 m female sharks examined from India that possessed immature ovaries (Pai et al. 1983, Satyanarayana Rao 1986), Coleman (1997) concluded that whale sharks of either sex probably do not mature until attaining a size of over 9 m. Taylor (1994) concluded that *R. typus* does not become reproductively active until at least 30 years old, and believes that whale sharks may live more than 100 years. Based on this information, the following sizes and life history stages are characterized for *R. typus* for the purposes of this study: neonates and young juvenile *R. typus* are approximately 0.5-3 m TL, older juveniles (3-6 m TL), subadults (6-9 m TL), and adults are animals 9 m TL or larger.

Whale sharks of both sexes sighted at mid-shelf banks were estimated to be 3-9 m TL; the largest being a 8-9 m TL female sighted during Summer 2. Similarly, sharks of both sexes were documented at the Flower Garden Banks, and animals were judged to be 4-7 m TL, although one shark documented on video is estimated to be nearly 10 m TL. Sharks observed nearby at HI-389 whose sexes were female or undetermined were estimated at 4-7 m TL. Animals sighted 9 km south of the West Flower Garden Bank were 4-8 m TL and of unknown sexes.

In summation, animals sighted at the different topographic high types were of similar sizes (3-9 m TL) and sexes, with one animal occurring at the Flower Garden Banks that was estimated to be 9-10 m TL. The data indicate that mid-shelf and shelf-edge topographic highs are visited primarily by older juvenile and subadult *R. typus* of both sexes, and occasionally by adult animals during the summer and Autumn seasons.

Ancillary narratives and personal observations made it readily apparent that animals persisted less than a day at the study sites. Sightings data from Childs et al. (in review) show *R. typus* to occur throughout neritic and oceanic waters of the northwestern Gulf of Mexico from June through November. Additionally, the presence of older juvenile, subadult, and adult *R. typus* at each of the study sites indicates that neritic waters of the northwestern Gulf of Mexico function as secondary nursery habitat and summer feeding habitat, until these waters cool in late November and early December. Consequently, whale sharks inhabit a much greater habitat area than any single topographic high or group of topographic highs.

Juveniles observed in this study exceeded 3 m TL, as is characteristic of reports elsewhere (Wolfson 1983, Compagno 1984a, Clark 1992, Clark & Nelson 1997). Observations of neonate and young juvenile sharks are sparse (Wolfson 1983, Kukuyev 1996, Clark & Nelson 1997), and probably due to the natural history of *R. typus* as well as sampling effort. All young juvenile *R. typus* reported to date are from oceanic waters exceeding 2000 m in depth (Wolfson 1983, Kukuyev 1996); the sole exception being the single whale shark embryo collected in 57 m of water off Port Isabel, Texas (Baughman 1955). Some scientists interpreted this unusual specimen, still encapsulated in its egg case, to be an aborted embryo and recent evidence supports this conclusion (Joung et al. 1996, Chang et al. 1997). Thus, due to the apparent absence of neonate and young juvenile whale sharks in neritic waters of the world, I believe *R. typus* releases its offspring in tropical and subtropical oceanic waters, possibly over the continental slope, where upwelling in some cases supports abundant planktonic prey for young sharks to consume. Kukuyev (1996) perchance inferred this, although he concluded that findings of two recently born whale sharks in oceanic waters of the tropical Atlantic support his conclusions concerning the ovoviviparity of the whale shark in the tropical waters of the open ocean. I attribute the overall lack of neonate and young juvenile sightings to date to inadequate biological surveys of tropical and warm temperate oceanic waters relative to those performed in eulittoral and infralittoral waters.

If whale sharks utilize oceanic waters in the northern Gulf as nursery habitat, it does not necessitate that whale sharks segregate by size as is known for some shark species. Sightings reported in Childs et al. (in review) show whale sharks exceeding 3 m

TL occupying oceanic waters of the northern Gulf throughout all seasons of the year. Data show that some larger whale sharks expand their habitat to include neritic waters during warmer months.

The majority of *R. typus* reported in this study were solitary, so that individuals were sighted without conspecifics within five body lengths of another. However, two animals occurring at a mid-shelf bank may have been traveling together. Other sightings such as the two *R. typus* observed together in nonpolarized formation at HI-389 show the animals occasionally travel in groups. Whale shark aggregations are often thought to be associated with feeding activity (Gudger 1941, Springer 1957, Clark 1992, Taylor 1994, 1996, Clark & Nelson 1997, Colman 1997, Zhardim et al. 1998), such as the aggregations of animals off Ningaloo Reef following annual mass coral spawning events (Clark 1992, Taylor 1994, 1996, Clark & Nelson 1997, Coleman 1997). Whale sharks also aggregate at Gladden Spit, Belize and feed on the freshly spawned gametes of large spawning aggregations of several lutjanid species during the full moon periods from April to June (Graham et al. 2000, Heyman et al. 2000). Aggregations of feeding whale sharks were sighted near shelf-edge banks by NMFS biologists (Childs et al., in review) and south of the Flower Garden Banks during this study.

Gudger (1939) reported several aggregations of *R. typus* in the Gulf of Mexico, however, each sighting was more than 370 km east by southeast of the Flower Garden Banks in oceanic waters. Such oceanic sightings of *R. typus*, including those along the outer continental shelf of the northern Gulf of Mexico, are probably more closely associated with loop current rings and companion eddies (anticyclones and cyclones).

The loop current boundary, current rings and companion eddies are known to support diverse aggregations of zooplankton (Lee et al. 1991, Biggs et al. 1997) on which *R. typus* may forage.

Whale sharks were observed feeding at or near the sea surface. The three *R. typus* sighted south of the West Flower Garden Bank the day following a mass coral spawning event in September were feeding together at the sea surface. Within the past decade, whale sharks have been found to associate with mass coral spawning events. For example, Clark (1992) reported 285 whale shark sightings that coincided with spawning of western Australian coral reefs. Similarly, Taylor (1994, 1996) reported that whale sharks appear on Ningaloo Reef following mass coral spawning events. Gunn et al. (1999) made 30 sightings of whale sharks at Ningaloo Reef in months that corals spawn *en masse* at Ningaloo Reef, although only one whale shark was observed feeding. From these observations, Gunn et al. (1999) suggested that whale sharks feed throughout the water column during brief dives to the sea floor. Furthermore, whale shark sightings increased within weeks following the mass coral spawning along the Ningaloo reef front where the current runs northward along the coast, instead of seaward. Taylor (1996) hypothesized that these feeding aggregations are the result of rapid growth in zooplankton abundance brought about with the available coral spawn, instead of whale sharks feeding directly on the coral gametes.

Whale sharks observed in the vicinity of the Flower Garden Banks on days following mass coral spawning may be feeding on the spawn slick or on small fishes possibly consuming the spawn. In the instance that I observed whale sharks feeding at the surface with other marine vertebrates one day after a mass spawning event at the Flower Garden Banks, I believe the sharks were feeding primarily on the smaller fishes, as well as the coral spawn. Floating gametes on the sea surface produced by reef fauna at the Flower Garden Banks are likely carried away from the bank due to the physiography and hydrography of the region. Although some submerged topographic highs may retain solid particles (e.g. coral gametes) within a trapped water parcel created by flow circulation around the bank or seamount (termed a Taylor column or Proudman pillar) (e.g. Sammarco & Andrews 1988), this phenomenon has not been reported at the Flower Garden Banks. Furthermore, the waters flowing over the Flower Garden Banks are not sufficiently stratified to retain particles such as coral gametes over the banks (a stratified Taylor column). Surface currents often extend to the coral reef (20-30 m below the sea surface), and scientists have followed gametes produced at the reef to the sea surface, thereupon forming a slick of gametes. Corals spawn at the Flower Garden Banks during evening hours (Hagman et al. 1998) and any resulting slick or gametes were not detected over the banks on subsequent mornings. Instead, gametes and larvae are likely transported eastward away from the Flower Garden Banks by the shelf edge current (that flows mostly eastward during spawning) (Lugo-Fernandez 1998). This is one probable reason that *R. typus* was not observed over the banks following the coral spawning events, but in waters nearby the banks where currents are likely to have carried the coral spawn.

Corals that broadcast spawn en masse are very predictable in the western Atlantic and at the Flower Garden Banks. Spawning events follow the summer seawater temperature maximum and occur between the seventh and tenth evenings after the full moon in August or September (Hagman et al. 1998). Other coral reef invertebrates have also been observed broadcast spawning en masse during the same period at the Flower Garden Banks. Other shelf-edge banks such as 28 Fathom and Bright Banks (14.9 and 28.9 km east of the East Flower Garden Bank respectively, and where whale sharks are reported to have aggregated during mass coral spawnings at the Flower Garden Banks, [Childs et al., in review]) support hermatypic corals and associated reef fauna (Rezak et al. 1985). It is reasonable for coral gametes originating at the Flower Garden Banks to be transported upshelf via the shelf-edge current to the vicinity of 28 Fathom and Bright Banks, thus attracting whale sharks. It is also likely that corals and other reef fauna at 28 Fathom and Bright Banks spawned strongly during the same period, thereby potentially attracting whale sharks. Still, however, there is no direct evidence linking whale sharks with mass spawning events in this region.

Observations made by divers at different locations at Ningaloo Reef indicate coral spawning is not necessarily uniform along the reef, with northern reefs in some years experiencing stronger spawning in March, and southern reefs experiencing stronger spawning in April (Taylor & Pearce, 1999). The Flower Garden Banks have received extensive attention by coral biologists in the last several decades (e.g., Bright & Pequegnat 1974, Gittings et al. 1992a,b, Gittings 1998, Hagman et al. 1998), while other shelf-edge banks have not. As such, the abundance and health of corals and associated reef fauna at these other banks have not been assessed within the past two decades. Corals and other invertebrates that broadcast spawn en masse may be healthy and productive at these banks and undergo spawning events as is seen at the Flower Garden Banks. Like Ningaloo Reef, coral reefs located at shelf-edge banks in the northern Gulf may exhibit some variation in the strength and timing of individual spawning events.

None of the photographed, video taped or personally observed whale sharks showed mating scars, nor was mating activity relayed to me. Some individual sharks bore scars on their dorso-lateral torso and fins (including caudal) (Fig. 13), however the nature of these scars is more indicative of collisions with sea-going vessels. Female sharks of other species bear mating scars following mating attempts, and another filter-feeding elasmobranch, *Manta birostris* (which only has teeth in the lower mandible), produces mating scars (Yano et al. 1999). Therefore, it is reasonable to expect reproductively active female whale sharks to bear mating scars after having recently copulated with a male shark.

Rhincodon typus was commonly and closely accompanied by a variety of fishes (Fig. 14), sometimes including *Rachycentron canadum*, *Remora remora*, *Echeneis naucrates*, *Elagatis bipinnulata*, *Seriola* spp., *Caranx ruber*, *C. bartholomaei*, *C. fusus*, *C. hippos*, *C. latus*, *Euthynnus alletteratus*, or unidentified fishes. Video of one whale shark shows two small fishes swimming at the shark's mouth that may be *Seriola zonata* or *Naucrates ductor* (Fig. 15), however, positive identification to species is not possible. The feeding aggregation of three whale sharks observed following a mass coral spawning event at the West Flower Garden Bank also included small unidentified fishes, jacks (*Carangidae* spp.), *Carcharhinus* spp., and unidentified larids (seagulls and terns).

Order Carcharhiniformes (ground sharks)

Family Carcharhinidae (requiem sharks)

Galeocerdo cuvier (Peron & LeSueur 1822)

Tiger shark (Figure 13)

Galeocerdo cuvier inhabits neritic and oceanic waters of tropical and warm temperate regions of the world (Castro 1983, Compagno 1984b). It is wide-ranging, pelagic, and reported by Compagno (1984b) as occurring on or adjacent to continental and insular shelves from the sea surface to possibly 140 m. Subsequent evidence gathered by Clark & Kristoff (1990) shows that *G. cuvier* occurs below 140 m in oceanic waters. They photographed *G. cuvier* off Grand Cayman from a submersible at a depth of 305 m. Holland et al. (1999) tracked tiger sharks moving from Oahu, Hawaii to offshore banks with dives to 335 m in depth. The tiger shark occurs in the Gulf of Mexico (Springer 1940, Bigelow & Schroeder 1948, Gudger 1949, Saunders & Clark 1962, Springer 1963, Clark & von Schmidt 1965, Hoese & Moore 1977, 1998, Parker & Bailey 1979, Branstetter 1981, Branstetter & McEachran 1986, Branstetter et al. 1987, Randall 1992, Russell 1993, Castillo-Geniz et al. 1998, Kohler et al. 1998, McEachran & Fechhelm 1998, Carlson & Brusher 1999, Heist & Gold 1999) in neritic and oceanic waters (Branstetter & McEachran 1986). However, McEachran and Fechhelm (1998) state that *G. cuvier* occurs in neritic waters adjacent to continents and islands, but omit oceanic waters. Tagging and release data collected since 1962 by the NMFS (Kohler et al. 1998) show *G. cuvier* occurs in waters exceeding 2000 m in the Gulf of Mexico.

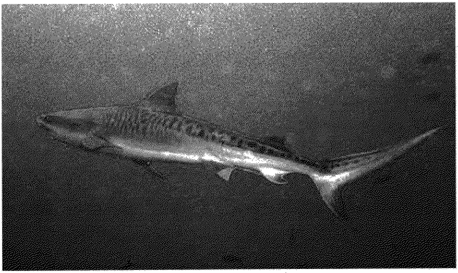

Figure 13. Tiger shark (*Galeocerdo curvier*). This sharks was photographed at the Flower Garden Banks during the Winter 2 season. Photograph by Joyce & Frank Burek.

Table 9. Tiger shark habitat use of the Flower Garden Banks. Based on sightings of *Galeocerdo cuvier* at the Flower Garden Banks from data collected thru April 1998.

Galeocerdo cuvier — **tiger shark**

Size at Birth:		~ 0.5 m
Size at Maturity:	Males	~ 3 m
	Females	~ 3 m
Maximum Size Attained		~ 9.1 m (unconfirmed, most < 5m)

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality			1		2				4		5	
Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
0 to 1 m												
1 to 2 m			U									
2 to 3 m			F U									
3 to 4 m	U		F U									
4 to 5 m												
5 to 6 m												
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitar	1.0.0		12.0.1									
Paired			1.0.									
Small Aggr. (3 to 10			2.0.									
Med. Aggr. (11 to 50												
Lg. Aggr. (51 to 100												
Massive Aggr. (100+												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

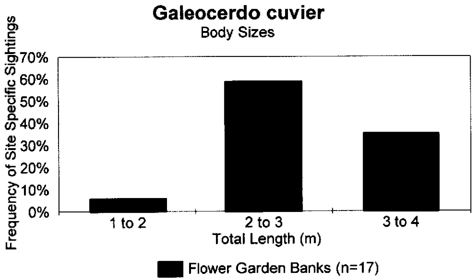

Figure 14. Estimated body lengths of *G. cuvier*. Based on sharks reported in the in situ accounts that ranged in size from 1-4 m TL. All sightings of *G. cuvier* were made at the Flower Garden Banks during winter months.

Ecology and Behavior: Sightings of *G. cuvier* were made during daylight in microtopes of less than 34 m at the Flower Garden Banks, although the animals did move into deeper regions of the reef. *Galeocerdo cuvier* was observed by divers throughout the day swimming over the reef crest, sand flats, reef escarpment, in the water column, and swimming up to the sea surface. Dives were not conducted after dusk during winter to minimize the risk of a shark attack by this aggressive species.

Tricas et al. (1981) found through tracking a 4 m TL female tiger shark in June, the animal spent 68 % of its daytime activity on the outer reef (of French Frigate Shoals, Hawaii) and close to the bottom, although it occasionally ascended into the water column. Near sunset, the shark moved into oceanic waters and made excursions to depths exceeding 140 m. Shortly before dawn, the animal returned to the reef where it persisted through the day. Sightings made in this study show that tiger sharks occur over the banks during the day, although it is not known where the animals occur at night. During a recent cruise made in late February to the Flower Garden Banks, two tiger sharks were observed at dusk swimming over the reef; this sighting indicates the animals can be active over the reef to at least dusk.

Divers simultaneously observed 2-5 sharks within view on multiple dives at each Flower Garden Bank during the winter seasons. Sharks were not reported during other seasons when diving activity was more intense. A more accurate assessment of abundance is not possible with the data available at this time.

Springer (1940, 1963) indicated that *G. cuvier* does not segregate by sex, however, recent findings suggest that it may (Clark & von Schmidt 1965, Branstetter 1981, Stevens & McLoughlin 1991, Simpfendorfer 1992, Schwartz 1998). Because 88 % of the individual sharks were not sexed, and 22 % of the individual sharks reported were identified as females, there are insufficient data available to indicate whether sharks occurring at the Flower Garden Banks are of predominantly one sex or not.

Galeocerdo cuvier pups are born at nearly 0.7 m TL in coastal waters of the Gulf of Mexico (Clark & von Schmidt 1965, Branstetter 1981, Branstetter & McEachran 1986, Branstetter et al. 1987) and are estimated to double their length within the first year of life (Branstetter et al. 1987). Sharks mature at approximately 3 m TL in the Gulf of Mexico (Branstetter & McEachran 1987, Branstetter et al. 1987), although conflicting literature states *G. cuvier* matures at about 2.2-2.9 m TL (males) or 2.5-3.5 m TL (females) (Compagno 1984b, Randall 1992, Simpfendorfer 1992, McEachran & Fechhelm 1998, Natanson et al. 1999). Based on the varied estimates regarding size at maturity, I consider animals less than 2.2 m TL to be juveniles, 2.2-2.9 m TL as subadults, and 3.0 m TL and larger as adults. Tiger sharks reported in this study were estimated at 1-4 m TL, however, ancillary narratives and personal experience indicate the smallest shark sighted was probably 1.3 m TL. Therefore, older (larger) juvenile, subadult, and adult tiger sharks occur at the Flower Garden Banks during the winter seasons.

Galeocerdo cuvier is abundant in 'shore waters' of the northern Gulf of Mexico in warm months, but absent in winter (Springer 1963), although it is not known what 'shore waters' encompass, (a frequent problem of many scientific accounts reporting elasmobranch occurrences; see Childs [1999]). Supporting data were collected by Branstetter (1981), who caught tiger sharks from April through December in continental shelf waters off Cape San Blas, Florida west to the Mississippi River. However, at the Flower Garden Banks, *G. cuvier* was observed during the winter seasons and abundance was sometimes measured at 3-5 sharks per sighting per bank. Tiger sharks were not observed by divers in other seasons, though a fisherman reported capturing a shark at the Flower Garden Banks in Summer 1. Without corroborating evidence, however, this sighting is of ambiguous value.

Based on the literature and data available, it is likely that *G. cuvier* occurs throughout the year in circalittoral waters of the northern Gulf and around the Flower Garden Banks, though not necessarily atop the banks. Furthermore, tiger sharks occurring during warmer months in eulittoral and infralittoral waters of the Gulf coast are likely to move south to circalittoral and oceanic waters of the northern Gulf as eulittoral and infralittoral waters cool due to arctic cold fronts advancing into the region as the winter season sets in. Such seasonal movements would increase the density of tiger sharks in circalittoral waters, and result in the frequent sightings made in winter months at the Flower Garden Banks. Regardless, the data show that the Flower Garden Banks function as a winter feeding habitat for older (larger) juvenile, subadult, and adult tiger sharks.

The absence of neonate and small (< 1.2 m TL) juvenile sharks at the Flower Garden Banks is noteworthy. This may be because pups are born during Spring (Clark &

von Schmidt 1965) in 'coastal waters' of the Gulf of Mexico (Branstetter et al. 1987), though it is not clear what they intended 'coastal waters' to include (e.g. eulittoral, infralittoral, and circalittoral waters, or some combination thereof). Branstetter et al. also stated that if juvenile tiger sharks remain within the Gulf of Mexico (instead of traveling into the North Atlantic via the Florida Straits), the pups apparently migrate short distances inshore-offshore seasonally. Natanson et al. (1999) reported that tiger sharks utilize continental shelf waters from the coast seaward to the 100 m isobath off the southeast Atlantic coast of the United States, and that juvenile tiger sharks remain in the nursery area until attaining a size of approximately 1.5 m fork length. The smallest tiger shark observed at the Flower Garden Banks was estimated to be 1.3-1.6 m TL, thereby indicating it could be young of the year. Most tigers sharks observed, however, were nearly 2 m TL or greater, and this may indicate that young (smaller) sharks 1) inhabit deeper waters around the banks than were surveyed, 2) avoid the banks until attaining a larger size, or 3) the nursery area for tiger sharks in the northwestern Gulf of Mexico may extend from the coast to approximately the 100 m isobath, and like the young sharks Natanson et al. reported, persist in the nursery area until attaining a larger size.

Galeocerdo cuvier is a wide-ranging species, as evident from tagging and recapture data reported by Kohler et al. (1998). For example, tiger sharks tagged in the western North Atlantic were recaptured in the eastern Gulf of Mexico, and sharks tagged off western Florida were recaptured off Texas. Sharks tagged near the center of the Gulf of Mexico (in waters exceeding 2000 m in depth) were recaptured off Louisiana and the Yucatan Peninsula, Mexico. Additionally, their data show that some tiger sharks move out of the Gulf of Mexico into the Caribbean Sea or up along the east coast of the United States. Therefore, it is unclear whether tiger sharks occurring at the Flower Garden Banks each winter are the same individuals (indicating philopatry), or different individuals utilizing the banks during winter as part of a much greater migratory circuit that encompasses the Gulf of Mexico, Caribbean Sea, and/or the western Atlantic that takes years to complete. The lack of sightings at the Flower Garden Banks during other seasons indicates that the sharks observed in winter are not 'bank loafers' or part of an accessory population.

The tiger shark is considered to be one of the most polyphagous fishes known, and there is considerable variation in the diets of sharks from different geographic areas (Springer 1940, 1963, Bigelow & Schroeder 1948, Gudger 1948, 1949, Saunders & Clark 1962, Clark & von Schmidt 1965, Dodrill & Gilmore 1978, Branstetter 1981, Castro 1983, Compagno 1984b, Lyle & Timms 1987, Stevens & McLoughlin 1991, Randall 1992, Simpfendorfer 1992, Lowe et al. 1996, Schwartz 1998). Furthermore, studies by Stevens & McLoughlin (1991), Simpfendorfer (1992), and Lowe et al. (1996) show *G. cuvier* to exhibit ontogenetic dietary shifts, with juveniles feeding predominantly on teleost fishes and other relatively small vertebrates, and adult tiger sharks consuming teleost fishes, and medium to large vertebrates including sea turtles. The Flower Garden Banks in winter support a diverse assemblage of fauna including many species that larger tiger sharks are known to prey upon, including smaller elasmobranchs and sea turtles.

Seventy-five percent of in situ records collected were of solitary tiger sharks, the remaining 25 % included animals in nonpolarized groups of 2-5 sharks. The tiger shark is considered semi-solitary, being frequently sighted alone or in nonpolarized groups of as many as six animals (Springer 1963). Data collected in this study supports the assessment that *G. cuvier* is semi-solitary.

No intraspecific interactions were distinguishable or noted by divers, nor was evidence of mating scars or activity described. Evidence of interspecific interactions was not documented.

Genus *Carcharhinus*

Four *Carcharhinus* shark species were identified at the study sites from photographs, video, specimens, and in situ observations. Sharks of the genus *Carcharhinus* were reported during all seasons and presented a considerable challenge because some species are difficult to identify without specimens to examine. Even with excellent photographic images, sharks of the genus *Carcharhinus* are troublesome to identify. For example, 130 records of probable *Carcharhinus* sharks were documented in the in situ and photographic catalogues and analyzed for this study. Only 57 % of these records were judged to be accurately identified to genus; the remaining 43 % could not be validated. Therefore, only records assigned to quality group 1 were used for the accounts of *Carcharhinus* species.

Carcharhinus falciformis (Müller and Henle 1839)

Silky shark (Figure 15)

Carcharhinus falciformis is a pelagic shark occurring from the sea surface to at least 500 m in depth in neritic and oceanic tropical and warm temperate waters of the world (Castro 1983, Compagno 1984b). It is found in the Gulf of Mexico (Springer 1967, Hoese & Moore 1977, 1998, Branstetter 1981, Garrick 1982, Castro 1983, Compagno 1984b, Branstetter & McEachran 1986, Branstetter 1987b, Bonfil et al. 1990, Applegate et al. 1993, Bonfil et al. 1993, Russell 1993, Kohler et al. 1998, McEachran & Fechhelm 1998) where it is abundant in continental shelf edge waters of the northwestern Gulf (Springer 1963, Branstetter 1987b).

The silky shark was documented in 14 in situ records (quality group 1), five photographs, and ten video clips. *Carcharhinus falciformis* was identified from several animals captured and released at the East Flower Garden Bank and HI-389.

Flower Garden Banks: Three female *C. falciformis* were caught at the East Flower Garden Bank one night in June (Summer 1) whose sizes were nearly 1 m TL. These sharks were the only *C. falciformis* confidently identified at the Flower Garden Banks, although divers reported silky sharks on other occasions. Social groups were not ascertained based on the captured animals.

HI-389: Silky sharks were documented at HI-389 in all seasons except Autumn (Table 10). Abundance of *C. falciformis* was estimated at 100-200 animals, however, these animals formed smaller social groups that moved around and through the underwater complex. Sizes varied from 0.5-2 m TL; 15 % of in situ sightings

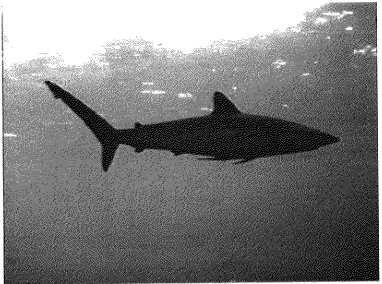

Figure 15. Silky shark (*Carcharhinus falciformis*). This species forms large aggregations at HI-389 platform and other offshore petroleum platforms, based on surveys conducted during this study. Figure was captured from video.

Table 10. Silky shark habitat use of HI-389. Based on sightings of *Carcharhinus falciformis* at HI-389 from data collected thru April 1998.

Carcharhinus falciformis												**silky shark**
	Size at Birth: ~ 0.8 m											
	Size at Maturity: Males: ~ 2.1 m; Females: ~ 2.2 m											
	Maximum Size Attained: ~ 3.3 m											
Artificial Topographic High (HI-389 platform)												
Record Quality		1		2		3		4		5		
Seasonal Occurrence	**Winter 1**		**Winter 2**		**Spring**		**Summer 1**		**Summer 2**		**Autumn**	
ESTIMATED SIZE												
0 to 1 m							M U					
1 to 2 m	U		U		U		U		U			
2 to 3 m												
3 to 4 m												
4 to 5 m												
5 to 6 m												
SOCIAL GROUPS	**NP**	**P**	**NP**	**P**	**NP**	**P**	**NP**	**P**	**NP**	**P**	**NP**	**P**
Solitary							1.0.0		0.1.0			
Paired						1.0.	1.0.0					
Small Aggr. (3 to 10)							2.0.0		2.0.0			
Med. Aggr. (11 to 50)	4.0.0	0.1.0							1.0.0			
Lg. Aggr. (51 to 100)			1.0.0									
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	**Quality Groups 4 & 5**
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

documented animals 0.5-1 m TL and 85 % were estimated at 1-2 m TL (Figure 16). Both sexes were present based on several captured animals. Sharks were observed alone, in pairs, and in aggregations of various sizes up to 100 animals. The largest aggregations (51-100 animals) were reported during Winter 2, although aggregations of 11-50 animals were observed during Summer 2. Paired and aggregated animals moved in polarized and nonpolarized formations. Individual sharks frequently transferred from one subgroup to another.

Animals inhabited the water column from the sea surface to at least 95 m and out to at least 63 m from the underwater structure. Sharks were typically observed swimming outside the perimeter of the structure, but it was also common to see solitary and paired *C. falciformis* swimming amidst the underwater structure (Figure 17).

Ecology and Behavior: Silky shark pups are born at 0.7-0.85 m TL (Strasburg 1958, Bane 1966, Springer 1960, Bass 1978, Garrick 1982, Branstetter & McEachran 1986, Branstetter 1987b, Bonfil et al. 1993). Male *C. falciformis* mature at 2.1-2.25 m TL and female sharks mature at 2.2-2.45 m TL in the Gulf of Mexico (Branstetter & McEachran 1986, Branstetter 1987b, Bonfil et al. 1993). Silky sharks observed in this study ranged in size groups 0.5-2 m TL, with most animals estimated at 0.9-1.6 m TL; none of the animals personally observed or examined showed signs of an umbilical scar, used to differentiate neonates from juveniles (Castro 1993). Therefore data indicate that these animals were juvenile sharks and of both sexes.

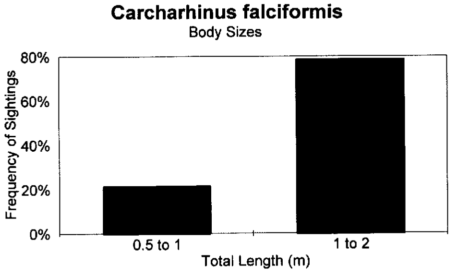

Figure 16. Body sizes reported for *C. falciformis*. Based on records in the in situ catalogue. The vast majority of animals personally sighted were approximately 1-1.5 m TL.

Figure 17. Silky sharks swimming through the HI-389 structure. Although *C. falciformis* was frequently observed moving outside the superstructure of HI-389, sharks were also observed swimming through the structure. These animals were all determined to be juveniles, and no large predatory sharks were reported entering the perimeter of the underwater superstructure. Figure was captured from video.

In the Gulf of Mexico, pups are released in nursery areas located along the sea floor along the outer rim of the continental shelf, often at depths of 80-100 m and frequently in reef areas that lutjanids (snappers) are found (Springer 1967, Branstetter 1981, 1987b). Elsewhere, pups have been found at Campeche Bank off the Yucatan, Mexico (Bonfil et al. 1993) and at oceanic banks in the Caribbean (Springer 1960, 1967). Although juvenile *C. falciformis* were caught at the East Flower Garden Bank, they were not abundant, based on the few animals captured and the lack of underwater sightings relative to other carcharhinids occurring at the bank. However, juvenile silky sharks were abundant at HI-389, with sightings of as many as 100-200 animals swimming around the platform. Additionally, dives conducted by myself at other offshore platforms on the continental shelf edge and slope have resulted in similar sightings of juvenile silky shark aggregations of similar abundance (Childs, unpublished data).

Consider the following: 1) juvenile silky sharks were found in large aggregations at HI-389 and other offshore platforms on the outer continental shelf and slope, 2) juvenile silky sharks chasing unidentified exocoetids (flying fishes) were observed from HI-389 late at night and it is believed the sharks were foraging on them, and 3) few silky sharks were documented at the Flower Garden Banks, and those that were, were caught on hook and line gear at the East Flower Garden Bank at dusk or later, suggesting the animals were foraging in the waters over and around the bank. Sightings data suggests then, that juvenile silky sharks employ a central refuging system about offshore platforms from which they disperse to forage at night. Central refuging systems involve the rhythmic dispersal of a conspecific social group that occupies a core area during the inactive phase of the diel cycle, and disperses into a larger area during the active phase of the diel cycle to forage either in smaller groups or as solitary individuals (Hamilton & Watt 1970). Klimley (1984) found *S. lewini* employs a central refuging system at seamounts in the Gulf of California. Other shark species Klimley (1984) identified as employing a refuging system include *Carcharhinus amblyrhincos* (gray reef shark), *Triaenodon obesus* (reef whitetip shark), and possibly *Heterodontus porthacksoni* (bullhead shark), based on the works of McLaughlin & O'Gower (1971), Randall (1977), Johnson (1978), and Nelson & Johnson (1980). Moreover, the aggregation of large numbers of individuals in a core area is advantageous only when core areas are a limited resource, and provide some advantage unavailable to one nomad or group of nomads. Offshore platforms are limited in number, particularly the farther one moves from the coast, although there is a growing trend to place petroleum platforms in Gulf waters exceeding 1000 m. Juvenile silky sharks are likely to benefit from offshore platforms because platforms are evidently not exploited by other shark species in the area (based on the lack of other shark species occurring at HI-389 and other platforms surveyed), as well as the refugia that platforms provide juvenile silky sharks from larger predatory sharks.

Branstetter (1987b, 1990) regarded the relatively small birth size for *C. falciformis* makes the pups vulnerable to predation by large pelagic sharks on the continental shelf edge, and that their rapid linear growth (a mean increase of 0.28 m between birth and first winter annulus) would increase their swimming efficiency and speed, thus enhancing their ability to avoid predation. He reasoned that neonates may spend the first months of life associated with banks and reefs on the outer shelf (based on Springer 1967), and later move to a pelagic existence by the first winter. Data collected in this study indicate the young juvenile silky sharks depart the primary nursery on the shelf edge bottom, and move to occupy offshore platforms on the outer shelf and slope where they refuge about the platforms until attaining sufficient size that either minimizes the risk of predation or that can no longer be supported by the potential prey occurring around the platforms. Thus, artificial topographic highs such as HI-389, can be viewed as secondary nursery habitat and refugia for juvenile silky sharks. Such nursery habitat and refugia are likely to enhance the survival of cohorts inhabiting artificial topographic highs relative to those pursuing a nomadic existence apart from offshore platforms in the region. The latter must locate nomadic prey and avoid predation by larger predatory sharks.

Carcharhinus falciformis forms aggregations (Strasburg 1958, Springer 1960, Bane 1966, Stevens 1984, Branstetter 1981, 1987b, 1990, Edwards & Lubbock 1982, Bonfil et al. 1993) and is reported to school (Branstetter 1987b, 1990), however, these accounts present no data showing that the species occurs in polarized groups (schools) as opposed to nonpolarized groups (aggregations). Silky sharks observed at HI-389 formed a massive aggregation as evident by the abundance reported (100-200 animals). However, smaller social groups, comprising solitary animals to large aggregations of 100 animals, moved within the massive social unit in polarized and nonpolarized formations, thus demonstrating that juvenile *C. falciformis* form aggregations and school.

Carcharhinus falciformis moved passively amidst reef and pelagic fishes occurring at HI-389 during the day, however, sharks were observed aggressively foraging on exocoetid and kyphosid fishes after dusk. On the occasion that a 5-6 m DW *Manta birostris* visited HI-389, a silky shark whose length slightly exceeded 1 m, rapidly charged and briskly rubbed the dorsal surface of the ray with its right lateral surface before quickly retreating within the perimeter of the underwater structure. It was also noted that numerous *C. falciformis* were observed hosting small *Echeneis naucrates*.

On several excursions to HI-389, commercial fishermen moored to the platform and commenced fishing operations, harvesting *C. falciformis*. It was routine to observe individual sharks with hooks and trailing leaders that sometimes exceeded a meter in length.

Carcharhinus obscurus (Lesueur 1818)

Dusky shark (Figure 18)

Carcharhinus obscurus is a large pelagic shark occurring in temperate and tropical marine waters of the world (Garrick 1982, Castro 1983, Compagno 1984b). It primarily inhabits neritic waters, but also occurs in oceanic waters (Branstetter 1981, Garrick 1982, Castro 1983, Compagno 1984b). The dusky shark occurs in the Gulf of Mexico (Springer 1940, Springer V. 1961, Clark & von Schmidt 1965, Hoese & Moore 1977, 1998, Branstetter 1981, Garrick 1982, Bonfil et al. 1990, Russell 1993, Castillo-Geniz et al. 1998, Kohler et al. 1998, McEachran & Fechhelm 1998).

Carcharhinus obscurus was documented by three in situ records (Quality Group 1) that includes two specimens and four video clips recorded prior to May 1998. The dusky shark was only observed at the Flower Garden Banks.

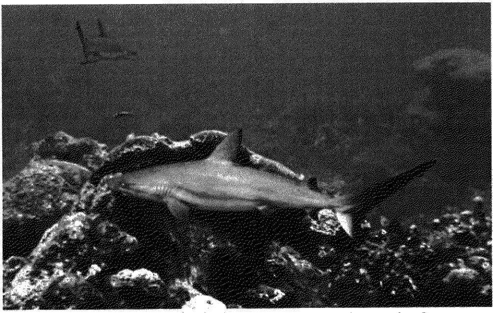

Figure 18. Dusky shark (*Carcharhinus obscurus*). These animals were photographed at the Flower Garden Banks by Joyce & Frank Burek.

Flower Garden Banks: Sharks were reported during both summer seasons and Autumn (Table 11). The dusky shark was observed swimming in the water column, over the reef crest, and escarpment. One female specimen (0.5-1 m TL) was collected at the East Flower Garden Bank in Summer 1 when a leader trailing from a hook imbedded in the sharks mouth became fouled on a coral head. A diver recovering the corpse noted that conspecifics were not observed in the area. On a different occasion, I observed and video taped an aggregation of ten sharks (estimated at 1-1.5 m TL) during Summer 2 at the East Flower Garden Bank whose sexes were not determined. Animals forming the aggregation moved together in both polarized and nonpolarized formations. Another specimen was collected at the East Flower Garden Bank in October of 1980 but was not reported in the literature. The animal was estimated at 2.6 m TL, but the collector could not recall the sex of the animal. The jaws of this animal were conserved in the Biological Collection of the Department of Oceanography, Texas A&M University. Two additional sharks of approximately the same size were observed when this specimen was captured, however, their species identification is unknown. Subsequent sightings and photographs of *C. obscurus* at the Flower Garden Banks have been made between April 1998 and August 2000. Their sizes were estimated at 0.5-1.5 m TL during each summer season. Dusky sharks were not observed interacting with other marine fauna.

Table 11. Dusky shark habitat use of the Flower Garden Banks. Based on sightings of *Carcharhinus obscurus* at the Flower Garden Banks from data collected thru April 1998.

Carcharhinus obscurus — **dusky shark**

Size at Birth:		~ 0.8 m
Size at Maturity:	Males:	~ 3.0 m
	Females:	~ 2.8 m
Maximum Size Attained:		> 4 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality: 1, 2, 3, 4, 5

Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
0 to 1 m			u				F		u		u	
1 to 2 m	u		u				u		m U		u	
2 to 3 m			f u				u		f		U	
3 to 4 m												
4 to 5 m												
5 to 6 m												
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary	0.1.0		0.9.0				1.6.0		0.19.0		0.4.0	
Paired			0.3.					0.1.0		0.2.0		
Small Aggr. (3 to 10)								0.1.0	1.1.0	0.2.0		
Med. Aggr. (11 to 50)			0.1.									
Lg. Aggr. (51 to 100												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Ecology and Behavior: Dusky sharks are born at approximately 0.8-1.0 m TL (Springer 1940, Clark & von Schmidt 1965, Bass et al. 1973, Bass 1978, Branstetter 1981, Castro 1983, Compagno 1984b, Smale 1991) in estuaries, bays or eulittoral waters (Bigelow & Schroeder 1948, Clark & von Schmidt 1965, Bass et al. 1973, Bass 1978, Compagno 1984b). In the Gulf of Mexico, *C. obscurus* deposits offspring along the southwest coast of Florida (Bigelow & Schroeder 1948, Clark & von Schmidt 1965) and off Bay Chaland, Louisiana (Bigelow & Schroeder 1948). Conversely, Springer (1960) noted that "the nursery grounds of *C. obscurus* are well offshore in deeper water", however, it is not clear what is meant by "deeper water".

Sharks documented at the Flower Garden Banks were estimated at approximately 1 m TL, with the exception of one 2-3 m TL animal collected in 1980. Based on the information available, sharks estimated at nearly 1 m TL are young juveniles. Since sharks approximately 1 m TL were observed during both summer and the Autumn seasons at the Flower Garden Banks, these sites are utilized as summer nursery habitat by *C. obscurus*. It is not clear from the available data whether the banks function as a primary nursery area, though data show they serve as secondary nursery habitat during warmer months of the year (June through October).

One possible reason that young juvenile *C. obscurus* have not been observed at the Flower Garden Banks during colder months (December through April) is the increased presence of *G. cuvier* in the area. *Galeocerdo cuvier* is known to prey on juvenile sharks, including *C. obscurus* (Springer 1940, 1960, 1967, Bass et al. 1973, Bass 1978, Branstetter 1990). It is reasonable to speculate that juvenile *C. obscurus* depart or are preyed upon at the Flower Garden Banks as the abundance of *G. cuvier* increases with the onset of colder weather. Additionally, colder weather could also be a factor in their habitat use of the Flower Garden Banks. Studies in the Indian Ocean show juvenile *C. obscurus* exhibit a complex migratory pattern with predominantly juvenile males migrating south from the primary nursery area, and juvenile females moving north from the primary nursery area; these movements were attributed to seasonal changes in water temperature at the nursery area (Bass et al. 1973, Bass 1978).

Carcharhinus obscurus matures at approximately 2.8-3.0 m TL, depending on sex (Bass et al. 1973, Bass 1978, Branstetter 1981, Garrick 1982, Castro 1983, Compagno 1984b). The 2-3 m TL specimen collected in 1980 at the Flower Garden Banks would therefore be an adult shark. Adult sharks chiefly inhabit infralittoral, circalittoral, and oceanic waters and tagging studies show *C. obscurus* occurring throughout these waters in the Gulf of Mexico, particularly in the northeastern Gulf (Kohler et al. 1998). Moreover, National Marine Fisheries Service data show the vast majority of *C. obscurus* recaptured in the Gulf of Mexico were tagged along the Atlantic seaboard from Massachusetts to Florida (Kohler et al. 1998), indicating a strong tendency for sharks to migrate into the Gulf of Mexico, though it is not clear how long they persist there during their life history.

Juvenile dusky sharks observed at the Flower Garden Banks were primarily grouped in polarized and nonpolarized formations of 10 or less animals. Based on personal experience, juvenile sharks quickly scattered when encountering divers. Such rapid scattering behavior may enhance the survival of juveniles if *C. obscurus* aggregations encounter larger predatory sharks (e.g. tiger shark). Similar behavior is known among other gregarious vertebrates including flocking passerine birds, herding ungulates and pinnipeds.

Carcharhinus perezi (Poey 1876)

Caribbean reef shark (Figure 19)

Carcharhinus perezi is the commonest shark associated with Caribbean-type coral reefs, yet little is known concerning its biology, ecology, and behavior relative to other carcharhinid species encountered in this study. The species occurs in tropical eulittoral waters near the sea floor to depths of at least 30 m (Castro 1983, Compagno 1984b). The Caribbean reef shark occurs throughout much of the Caribbean Sea and the Gulf of Mexico (Springer 1949, 1960, Limbaugh 1963, Garrick 1982, Castro 1983, Compagno 1984b, Bonfil et al. 1990, Castillo-Geniz et al. 1998, Kohler et al. 1998, McEachran & Fechhelm 1998) although records in the northern Gulf are rare and dubious.

Three specimens were collected and photographed at the East Flower Garden Bank during this study, confirming it's occurrence in the northwestern Gulf of Mexico. Additionally, *C. perezi* was documented in 8 in situ records (Quality Group 1) and two video clips. All records were collected at the Flower Garden Banks and these are summarized in Table 12.

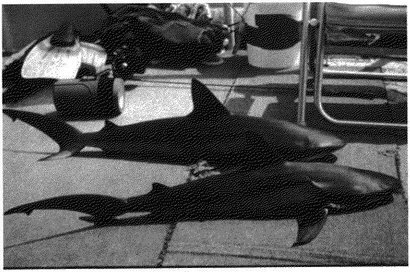

Figure 19. Caribbean reef shark (*Carcharhinus perezi*). Two of three juvenile specimens were inadvertently caught in fish traps set at approximately 63 m depth off the reef crest. Photograph by David Owens.

Table 12. Caribbean reef shark habitat use of the Flower Garden Banks. Based on sightings of *Carcharhinus perezi* at the Flower Garden Banks from data collected thru April 1998.

Carcharhinus perezi — **Caribbean reef shark**

Size at Birth:		< 0.7 m
Size at Maturity:	Males:	~ 1.7 m
	Females:	~ 2.0 m
Maximum Size Attained:		~ 2.9 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality		1	2	3	4	5
Seasonal Occurrenc	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m		u			u	u
1 to 2 m	u	u		U	B	u
2 to 3 m		f u		u	f	u
3 to 4 m						
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary	0.1.0		0.9.0				2.6.0		4.19.0		0.4.0	
Paired			0.3.					2.1.0		0.2.0		
Small Aggr. (3 to 10)								0.1.0	0.1.0	0.2.0		
Med. Aggr. (11 to 50)			0.1.									
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
M = males
F = female
B = both sexes
U = unknown sex

Quality Groups 4 & 5
m = male
f = female
b = both sexes
u = unknown sex

Aggregations
NP = nonpolarized
P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Carcharhinus perezi was recorded during both summer seasons at the Flower Garden Banks. It was observed swimming within 3 m of the reef crest, sand flats, or escarpment, and was not identified as one of the carcharhinid species swimming in the water column above or nearby the bank. The maximum number documented at one time was three animals caught in a fish trap resting on the bank at approximately 63 m. *Carcharhinus perezi* was chiefly reported as solitary, however, two animals moving in polarized formation were documented on two days.

Animals observed in this study were estimated at 0.5-2 m TL, with most individuals estimated at 1 m TL. The collected specimens (one female, two males) measured 0.99, 1.10, and 0.95 m TL and showed no evidence of an umbilical scar. Reef shark pups are likely born at 0.6-0.75 m TL (Castro 1983, Compagno 1984b), and it is thought that males mature at 1.5-1.68 m TL, and females at 2.0-2.95 m TL (Compagno 1984b). Based on the available information, animals occurring at the Flower Garden Banks were juveniles.

Coral reefs in eulittoral waters are generally regarded as nursery habitat for *C. perezi* (Springer 1960). Data gathered in this study indicate the Flower Garden Banks function as secondary nursery habitat to *C. perezi*, although it is not clear whether the banks also function as a primary nursery habitat. It seems likely, since tagging data of 546 *C. perezi* in the eastern portion of the Caribbean Sea and Gulf of Mexico show that Caribbean reef sharks are not wide ranging (the maximum distance traveled of 10 recaptured animals was 30 km) (Kohler et al. 1998). The presence of neonates possessing umbilical scars, as well as the occurrence of near-term pregnant females at the Flower Garden Banks would confirm that the sites are utilized as a primary nursery habitat.

Farther south, Gadig et al. (1996) collected four adult male *C. perezi* in addition to a pregnant female carrying four near-term embryos off northeastern Brazil, and the female shark had mating scars and wounds. They proposed the area functions as a pupping ground, and possibly as mating habitat. Adults were not observed at the Flower Garden Banks, indicating that adults may segregate from juveniles.

The maximum reported depth for *C. perezi* is approximately 30 m (Garrick 1982, Castro 1983, Compagno 1984b). The three specimens collected at the East Flower Garden Bank were caught in a fish trap situated on the sea floor at a depth of approximately 63 m. This is the deepest record known for *C. perezi*, though sharks emigrating to the Flower Garden Banks would have traversed waters nearly 100 m in depth.

Relatively few *C. perezi* were observed at the Flower Garden Banks, indicating animals occurring at these banks may be part of an ancillary population (Springer 1963, 1967). Animals were primarily solitary, however, paired sharks were observed swimming in polarized formation on two occasions. Insufficient data are available for assessing the sociality of the species. This species was not observed feeding or interacting with other marine fauna.

Carcharhinus plumbeus (Nardo 1827)

Sandbar shark (Figure 20)

Carcharhinus plumbeus is common to eulittoral waters of warm temperate and tropical seas worldwide, but also occurs in deeper waters of the outer continental shelf and slope (Bigelow & Schroeder 1948, Castro 1983, Compagno 1984b). Although pelagic, it associates closely with the sea floor. It occurs from nearshore waters out to at least 250 m (Springer 1960, Garrick 1982), and has been occasionally captured in waters exceeding 1000 m (Springer 1960, Kohler et al. 1998). The sandbar shark occurs along much of the eastern seaboard of the United States and in the Gulf of Mexico (Springer 1940, 1960, 1963, 1967, Bigelow & Schroeder 1948, Clark & von Schmidt 1965, Hoese & Moore 1977, 1998, Branstetter 1981, Garrick 1982, Castro 1983, Compagno 1984b, Bonfill et al. 1993, Russell 1993, Heist et al. 1995, Grace & Henwood 1997, Castillo-Geniz et al. 1998, Kohler et al. 1998, McEachran & Fechhelm 1998, Carlson 1999, Carlson & Brusher 1999, Heist & Gold 1999).

Carcharhinus plumbeus was documented in seven in situ records, one photograph, and six video clips . It was found at mid-shelf banks (six records) and at the Flower Garden Banks (five records).

Figure 20. Sandbar shark (*Carcharhinus plumbeus*). This female shark was video taped at the Flower Garden Banks during February. This animal was estimated to be 2-3 m TL. The picture was captured from video provided by the Flower Garden Banks National Marine Sanctuary office.

Mid-Shelf Banks: The sandbar shark was observed at mid-shelf banks during Summer 2 and Autumn (Table 13). *Carcharhinus plumbeus* was typically observed alone, though one animal was observed at Stetson Bank with two smaller unidentified sharks of the genus *Carcharhinus*. Sandbar sharks sighted at mid-shelf banks ranged from 1-3 m TL though most animals were estimated at 2 m TL. Three records are of female sharks estimated at 2-3 m TL.

Flower Garden Banks: *Carcharhinus plumbeus* was documented at the Flower Garden Banks during Winter 2 (Table 14). All *C. plumbeus* identified were solitary, and no more than one animal was sighted at a time. Sharks ranged from 1-3 m TL, though most animals were estimated at 2 m TL or somewhat greater. Females were reported, although three *in situ* records did not distinguish sex.

Ecology and Behavior: *Carcharhinus plumbeus* was observed swimming chiefly along reef escarpments at the study sites, but also over reef crests and sand flats. Rarely was an animal observed swimming more than 3 m above the sea floor, though animals were observed swimming in the water column just beyond the reef escarpment. In December 1999 while conducting surveys with a remotely operated vehicle, a female *C. plumbeus* (estimated size 2 m TL) was observed swimming over the deep reef at the West Flower Garden Banks. The species was extensively studied by Stewart Springer, who concluded that *C. plumbeus* is ordinarily not common around coral reefs or where the bottom is rough (Springer 1960). While this may be accurate in some areas, data reported herein show sandbar sharks occurring at mid-shelf banks that have rough bottoms, and at the Flower Garden Banks that support high-relief coral reefs in the Gulf

Table 13. Sandbar shark habitat use of mid-shelf banks. Based on sightings of *Carcharhinus plumbeus* at the mid-shelf banks from data collected thru April 1998.

Carcharhinus plumbeus												sandbar shark
Size at Birth: ~ 0.5 m												
Size at Maturity: Males: ~ 1.3 m												
Size at Maturity: Females: ~ 1.4 m												
Maximum Size Attained: ~ 3 m												
Mid-Shelf Banks (Sonnier & Stetson)												
Record Quality		1		2		3		4		5		
Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
0 to 1 m												
1 to 2 m							m u		U		U	
2 to 3 m			u		f u		u		F U		F	
3 to 4 m												
4 to 5 m												
5 to 6 m												
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary			3.1.0		0.4.0		0.5.0		1.3.0		3.4.0	
Paired								0.1.0				
Small Aggr. (3 to 10)											0.1.0	
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Table 14. Sandbar shark habitat use of the Flower Garden Banks. Based on sightings of *Carcharhinus plumbeus* at the Flower Garden Banks from data collected thru April 1998.

Carcharhinus plumbeus — **sandbar shark**

Size at Birth:		~ 0.5 m
Size at Maturity:	Males	~ 1.3 m
	Females	~ 1.4 m
Maximum Size Attained:		~ 3 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality		1	2	3	4	5
Seasonal Occurrenc	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m		u			u	u
1 to 2 m	u	U		u	m u	u
2 to 3 m		F U		u	f	u
3 to 4 m						
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	Winter 1 NP	Winter 1 P	Winter 2 NP	Winter 2 P	Spring NP	Spring P	Summer 1 NP	Summer 1 P	Summer 2 NP	Summer 2 P	Autumn NP	Autumn P
Solitary	0.1.0		3.9.0				0.6.0		0.19.0		0.4.0	
Paired			0.3.					0.1.0		0.2.0		
Small Aggr. (3 to 10								0.1.0	0.1.0	0.2.0		
Med. Aggr. (11 to 50)			0.1.									
Lg. Aggr. (51 to 100												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

of Mexico.

The sandbar shark is born at 0.56-0.75 m TL. Females reach maturity at 1.4-1.8 m TL, and males at 1.3-1.8 m TL (Springer 1960, Compagno 1984b). Sharks sighted at mid-shelf and Flower Garden Banks ranged in size from 1-3 m TL (Figure 21). Animals estimated at 1-2 m TL and 2-3 m TL comprised 43 % and 57 % of in situ sightings respectively, among banks. Although unidentified carcharhinid sharks less than 1.3 m TL were sighted at mid-shelf and Flower Garden Banks, my sightings of sandbar sharks were of animals exceeding 1.5 m TL. Based on data collected, subadult and adult sandbar shark occur at the natural banks surveyed.

Sightings documented in this study indicate seasonal habitat use and movement by *C. plumbeus*. Sandbar sharks were observed at mid-shelf banks during Summer 2 and Autumn only, and at Flower Garden Banks only during winter seasons. Additionally, 55 % of sightings were of female sharks, the other sightings were of unsexed animals. Sandbar sharks segregate by sex as adults (Springer 1960, 1967), thus data reported herein show mid-shelf banks function as summer feeding habitat to subadult and adult female *C. plumbeus*. Moreover, the Flower Garden Banks function as winter feeding habitat to subadult and adult female *C. plumbeus*.

Springer (1960, 1967) presented information regarding the seasonal distribution and migration of *C. plumbeus* in western Atlantic waters, reporting them to migrate southward along the North Atlantic seaboard to waters south of the Carolinas, including the Gulf of Mexico and Caribbean Sea. During warmer months, the animals moved northward to occupy the waters off the eastern United States to Cape Cod. It can be

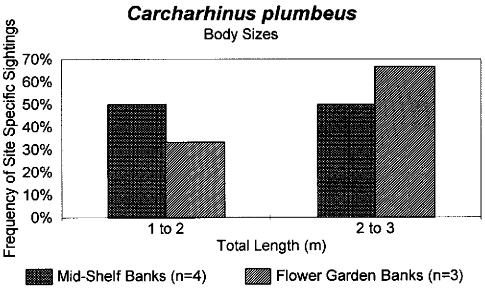

Figure 21. Estimated body lengths of *C. plumbeus*. Based on reports in the in situ accounts at mid-shelf and Flower Garden Banks through April 1998. Animals ranged in size from 1-3 m TL.

inferred from the data gathered in my study that adult *C. plumbeus* inhabiting mid-shelf banks and infralittoral waters in warmer months migrate seaward to circalittoral waters in winter, and reside at banks such as the Flower Garden Banks where prey is abundant, until water temperatures warm nearer to the coast in Spring.

'Nearshore waters' of the northern Gulf of Mexico are utilized by *C. plumbeus* as a primary nursery area, based on the capture of neonates, young juveniles, and gravid near-term females off Texas and Louisiana (Springer 1960, Branstetter 1987a, Carlson 1999). Another important primary nursery area for the species is eulittoral waters along the Atlantic coast from New York to Florida (Springer 1960). Tag and recapture data presented by Kohler et al. (1998) show *C. plumbeus* to be wide-ranging. Their data show one shark to have traveled 3776 km, and that sharks recaptured throughout the Gulf of Mexico were tagged along the Atlantic seaboard as far north as southern New England. Additionally, genetic analysis conducted on *C. plumbeus* specimens collected from coastal waters of Virginia and the Gulf of Mexico shows that animals from the East and Gulf coasts are likely of the same population (Heist et al. 1995). These studies suggest that the *C. plumbeus* observed in this study were likely born in nurseries located on the East or Gulf coasts.

The sandbar shark forms aggregations and schools (Springer 1960), however, such behavior may be associated with seasonal migrations, since all sandbar sharks reported in this study were solitary. Although sharks were solitary, two animals of different size categories were personally sighted on one dive at the Flower Garden Banks. Unfortunately, the data available are insufficient to estimate the abundance of sandbar sharks at either mid-shelf or Flower Garden Banks.

Sharks were not observed feeding, nor were mating scars or activity reported. On one occasion in December, I observed a carcharhinid shark that I believe was *C. plumbeus* (estimated to be 1.5 m TL) swimming within a meter of the reef crest at the East Flower Garden Bank. I followed behind the shark approximately 5 m, and as the shark passed beyond a large coral head, it quickly changed course back toward me. The shark evidently saw me, and changed direction by approximately 70° and it rapidly swam to the reef escarpment. At essentially the same moment that the shark rapidly retreated, eight *Sphyrna lewini* passed within approximately 4 m of the *Diploria* colony. Each of these male hammerhead sharks was approximately 3 m TL. The school of hammerhead sharks then altered course slightly, and swam a semi-circle around me before proceeding toward the center of the reef. Small *C. plumbeus* are often consumed by larger predatory sharks, such as *Galeocerdo cuvier* and *Carcharhinus leucas* (Springer 1960, 1967, Castro 1983, Compagno 1984b). A similar observation was made of a *Carcharhinus* sp. (2-3 m TL) during Winter 2 that quickly evaded a group of *S. lewini*. These sightings suggest that sandbar sharks and other *Carcharhinus* spp. avoid hammerhead sharks.

Family Sphyrnidae (hammerhead sharks)

Sphyrna lewini (Griffith and Smith 1834)

Scalloped hammerhead shark (Figure 22)

Sphyrna lewini is a cosmopolitan shark inhabiting tropical and warm temperate seas (Bigelow & Schroeder 1948, Castro 1983, Compagno 1984b, McEachran & Fechhelm 1998). It is pelagic, and occurs in neritic and oceanic waters, and is commonly found over continental and insular shelves. It is known to enter bays and estuaries where females give birth to pups. The species has been found as deep as 431.8 m (Jensen & Schwartz 1994). Little is known regarding the ecology and behavior of *S. lewini* inhabiting the Gulf of Mexico, although it has been documented in numerous accounts (Bigelow & Schroeder 1948, Baughman & Springer 1950, Clark & von Schmidt 1965, Parker & Bailey 1979, Branstetter 1981, 1987b, Bonfil et al. 1990, Russell 1993, Grace & Henwood 1997, Castillo-Geniz et al. 1998, Kohler et al. 1998, McEachran & Fechhelm 1998, Carlson & Brusher 1999). Additional reports by Boland et al. (1983), Dennis & Bright (1988), and Rezak et al. (1985) list *S. lewini* occurring at mid-shelf and Flower Garden Banks.

Sphyrna lewini was documented prior to May 1998 at the Flower Garden Banks in 74 in situ records (quality groups 1-3), although observers reported hammerheads at mid-shelf banks during this period that could not be confidently identified as *S. lewini.* Two photographs and 31 video clips were also collected. Subsequent surveys (post-April 1998) at the study sites have documented *S. lewini* occurring at mid-shelf and HI-389.

Figure 22. Scalloped hammerhead (*Sphyrna lewini*). This male hammerhead was swimming above the reef crest of a Flower Garden Bank. The animal was personally estimated to be approximately 2-2.5 m TL, and approached the videographer within 2.5 m. The picture was captured from video.

Flower Garden Banks: During the winter seasons, *S. lewini* was found in aggregations of 8-100 animals (Table 15). One sighting comprised eight robust, male *S. lewini* (3-4 m TL) swimming in polarized formation at the East Flower Garden Bank in early December. *Sphryna lewini* were reported ranging in size from 1-4 m TL, and 84 % of in situ records documented hammerheads estimated at 2-3 m TL (Figure 23). Approximately 44% of the Winter 2 sightings included males, 4% included females, and 66% included unsexed animals. All female sharks were solitary, but males were solitary, paired, or part of aggregations of as many as 100 hammerhead sharks. In situ records made during Winter 2 show 45%, 8% and 29% of sightings were of polarized groups, nonpolarized groups, and solitary animals respectively.

Sphyrna lewini was rarely reported in seasons other winter at the Flower Garden Banks. One sighting of a polarized pair of hammerheads (sexes undetermined, each estimated at 2-3 m TL) was reported in early April. Another record documented a solitary 2-3 m TL *S. lewini* (sex undetermined) in late August. Six in situ records documented solitary hammerheads during Summer 1 at the Flower Garden Banks, but these animals were not confidently identified to species. Ancillary photographs or video clips proving that *S. lewini* occurs at the Flower Garden Banks during warmer months were not obtained.

Table 15. Scalloped hammerhead habitat use of the Flower Garden Banks. Based on sightings of *Sphyrna lewini* at the Flower Garden Banks from data collected thru April 1998.

Sphyrna lewini — **scalloped hammerhead**

Size at Birth:		**~ 0.4 m**
Size at Maturity:	**Males:**	**~ 1.4 m**
	Females:	**~ 2.1 m**
Maximum Size Attained:		**~ 4.2 m**

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality			1		2		3		4		5	
Seasonal Occurrenc	**Winter 1**		**Winter 2**		**Spring**		**Summer 1**		**Summer 2**		**Autumn**	
ESTIMATED SIZE												
0 to 1 m												
1 to 2 m			M U				u					
2 to 3 m			B		U		u		U			
3 to 4 m	M		M U				u		u			
4 to 5 m												
5 to 6 m												
SOCIAL GROUPS	**NP**	**P**	**NP**	**P**	**NP**	**P**	**NP**	**P**	**NP**	**P**	**NP**	**P**
Solitary			31.1.0				0.3.0		1.1.0			
Paired			1.0.0	8.0.0		1.0.0						
Small Aggr. (3 to 10)			1.0.0	21.0.								
Med. Aggr. (11 to 50)				2.1.0								
Lg. Aggr. (51 to 100)			6.0.0									
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	**Quality Groups 4 & 5**
M = males	**m = male**
F = female	**f = female**
B = both sexes	**b = both sexes**
U = unknown sex	**u = unknown sex**

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

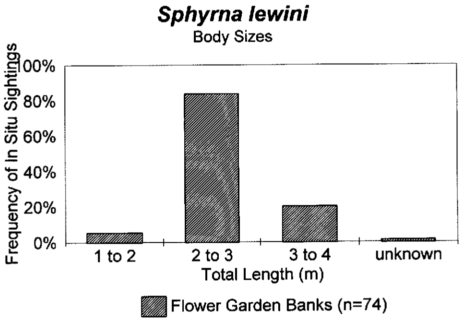

Figure 23. Estimated body lengths of *S. lewini*. Based on records in the in situ accounts through April 1998. The majority of animals reported were estimated to be 2-3 m TL.

HI-389: On several occasions since April 1998, solitary *S. lewini* were sighted during Summer 1 at HI-389. The sharks were sighted at the sea surface swimming toward the platform, where they approached to within 5 m of the structure each time before departing. The animals were easily observed from the main deck of the platform and estimated to be 2-3 m TL; sex was not determined.

Mid-Shelf Banks: Although *S. lewini* was not reported at mid-shelf banks prior to May 1998, personal and ancillary sightings validated by photo-documentation of the species have been made during surveys to Stetson Bank in February and March of 1999 and 2000. As similarly reported for animals at the Flower Garden Banks, hammerheads sighted at Stetson Bank were either identified as males or of unknown sex, and estimated at 2-3 m TL. However, sharks were observed in groups of no more than five animals. Paired and aggregated sharks were noted swimming in polarized formations.

Ecology and Behavior: *Sphyrna lewini* was observed swimming over reef crests, sand flats, along escarpments, and in the water column at the natural banks. Hammerheads were commonly sighted swimming along escarpments or basking at the sea surface during Winter 2 (Figure 24) when seas were calm (less than sea state 2).

The scalloped hammerhead is born at 0.38-0.55 m TL (Castro 1983, Compagno 1984b, Branstetter 1987b). The species exhibits some geographic variation regarding the size at which males and females mature, however. Branstetter (1987b) determined that males and females mature at 1.4-1.65 m TL and approximately 2.1 m TL, respectively, based on specimens collected from the northern Gulf of Mexico. Female hammerheads reported at the Flower Garden Banks were estimated to be 2-3 m TL, and male

Figure 24. Part of an aggregation of scalloped hammerheads. The animals were swimming at the sea surface over one of the Flower Garden Banks during Winter 2. An estimated 50-100 animals were sighted from the deck of the dive boats during this period with sea state 0. The picture was captured from video provided by the Flower Garden Banks National Marine Sanctuary office.

hammerheads were estimated at 1-4 m TL. Data taken in conjunction with Branstetter's conclusions regarding size at maturation indicate the observed hammerheads are subadult and adult animals.

Although it was not possible to ascertain the sex of many hammerheads sighted, I believe the vast majority of *S. lewini* inhabiting Stetson Bank and the Flower Garden Banks during winter months to be subadult and adult males. From my experiences, hammerheads that were approached to within approximately 12 m were readily sexed, and I noted such animals to be males. Animals not approachable to within approximately 12 m, sometimes proved difficult to sex.

These observations contrast with those of *S. lewini* occurring at seamounts in the Gulf of California. Hammerheads occurring there have been studied extensively (e.g. Klimley et al. 1988, Klimley 1993), and found to form polarized schools comprised predominantly of adult females (Klimley & Nelson 1981, 1984, Klimley 1982, 1985, 1987). It is known that *S. lewini* segregates by size and sex, however. One explanation for these difference regarding sexual composition of populations involves the location of the topographic highs within their respective ecosystems. The seamounts in the Gulf of California are located in oceanic waters greatly exceeding 200 m, whereas Stetson and the Flower Garden Banks are located within neritic waters. Some scientists have suggested that female hammerheads occur seaward of males, which are caught more frequently in neritic waters (Clarke 1971, Branstetter 1987b). Data collected in this study compares favorably with this notion, as only three solitary females were sighted, and 25 records included multiple males at the banks during the winter seasons.

Personal observations, photographic images, or narratives did not reveal mating scars or activity and intraspecific aggression was not reported. Female hammerheads were solitary, yet were actually part of a massive aggregation of hammerheads inhabiting the Flower Garden Banks during the winter seasons. Males were determined to move about the banks in subgroups that were often polarized, although some individuals were solitary or perceived so. I speculate that some solitary hammerheads were simply separated from one subgroup of the larger aggregation and moving about independently until locating another subgroup to join.

Sphyrna lewini is wide-ranging and individuals have traveled distances of 1670 km (Kohler et al. 1998). Tag and recapture data show that *S. lewini* tagged within the Gulf of Mexico were not recaptured outside it (Kohler et al. 1998). Likewise, hammerheads tagged outside the Gulf of Mexico were not recaptured in it. *Sphyrna lewini* is somewhat migratory (Compagno 1984b), as demonstrated by the population occurring along the East Coast of the United States that makes north-south migrations associated with seasonal/latitudinal changes in water temperature (Bigelow & Schroeder 1948, Compagno 1984b). Clarke (1971), however, suggested inshore-offshore migrations are responsible for the seasonal occurrence of *S. lewini* in the coastal waters of Hawaii. For example, in spring and early summer, gravid females move into bays, estuaries, and nearshore waters to deposit their offspring and possibly mate with males that have migrated also (Clarke 1971, Castro 1993). Data gathered in this study show that *S. lewini* seasonally populated the study sites, and that aggregations forming at the Flower Garden Banks were considerably larger than those observed at Stetson Bank.

Given that there are numerous estuarine and bay systems along the northern Gulf coast that might be utilized by *S. lewini* as primary nursery areas, it appears likely that *S. lewini* departing Stetson and the Flower Garden Banks in late March/early April migrate northward and inshore. I find no reason to expect *S. lewini* occurring at Stetson and the Flower Garden Banks in winter to migrate to nursery areas identified by Castro (1993) along the southeastern seaboard of the United States.

Interspecific aggression or predation by *S. lewini* was not observed or reported. On several occasions, I observed *S. lewini* and *Aetobatus narinari* swimming together in polarized groups without aggression between the species. During such observations, I estimated the distance between individuals of the two species to be nearly 3 m and in each case, the multi-species school maintained cohesiveness through the duration of the observation, which lasted approximately one minute each time. Conversely, I observed on two occasions a carcharhinid shark (1-2 m and 2-3 m TL) change direction to avoid small aggregations of *S. lewini* (2-3 m TL). *Sphyrna* spp. are reported to consume *A. narinari* and smaller elasmobranchs, including their own kind (Clarke 1971, Compagno 1984b).

My data compare favorably with those of P. Klimley and D. Nelson, who found *S. lewini* to form complex social groups that maintain a 'refuging central-position social system' at seamounts in the Gulf of California (Klimley & Nelson 1981, 1984, Klimley 1982, 1985); *S. lewini* occurring at the Flower Garden Banks in the northern Gulf of Mexico form seasonal large aggregations of smaller polarized schools that also centrally refuge about each topographic high. This appears to be the first account of hammerheads centrally refuging about topographic highs in the Atlantic Ocean.

Order Myliobatiformes (rays)

Family Dasyatidae (stingrays)

Dasyatis americana (Hildebrand and Schroeder 1928)

Southern stingray (Figure 25)

Dasyatis americana is a demersal stingray occurring in neritic waters of the tropical and warm temperate western Atlantic (Bigelow & Schroeder 1953, Bohlke & Chaplin 1993) including the Gulf of Mexico (McFarland 1963, Brockmann 1975, Hoese & Moore 1977, 1998, Parker & Bailey 1979, Stokes & Holland 1992, McEachran & Fechhelm 1998). To date, many published species compilations and accounts document it to be strictly a shallow-water species inhabiting 'nearshore waters' or semi-protected bays and estuaries (Bigelow & Schroeder 1953, Brockmann 1975, Hoese & Moore 1977, 1998, Parker & Bailey 1979, Snelson & Williams 1981, Schmid et al. 1988, Snelson et al. 1990, Stokes & Holland 1992, Bolke & Chaplin 1993, Gilliam & Sullivan 1993, McEachran & Fechhelm 1998). Contrary to this notion, however, published data shows that *D. americana* occurs in circalittoral waters at mid- and shelf-edge reefs and banks located in the northwestern Gulf of Mexico (Sonnier et al. 1976, Dennis & Bright 1988, Rezak et al. 1985). Data collected in this study adds further evidence that *D. americana* occurs well beyond nearshore waters of the Gulf coast.

Dasyatis americana was documented in 34 in situ records, one photograph, and 20 video clips. It was found at mid-shelf banks and the Flower Garden Banks.

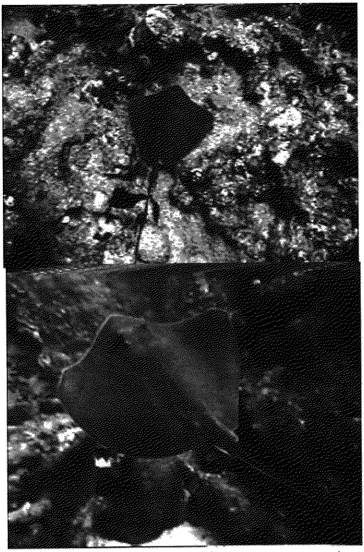

Figure 25. Southern stingray (*Dasyatis americana*). The species was often sighted on the live reef or in sand flats at mid-shelf and Flower Garden Banks. Pictures were captured from video.

Mid-Shelf Banks: The southern stingray was documented in 14 in situ records and five video clips at mid-shelf banks during Spring and each summer season (Table 16). The maximum number of animals observed in a sighting event was three animals, although all animals were solitary following the definitions used in this study. Animals ranged in disc width from 0.5-1 m (36%) and 1-2 m (64%), although most animals personally sighted were approximately 1 m DW. Both sexes were present, and records show both sexes to be approximately equally distributed in the 0.5-1 and 1-2 m DW size categories.

Flower Garden Banks: Twenty in situ records were made of *D. americana* at the Flower Garden Banks during all seasons except Winter 1 (Table 17). No more than two stingrays were sighted together, but solitary stingrays were sometimes sighted resting in different sand patches distributed across a bank during a dive, thereby making an assessment of abundance impractical. Both sexes were present during most seasons. Animals of size groups 0.5-1 m DW (60%) and 1-2 m DW (35%) were sighted during all seasons except Winter 1. Most animals sighted at the Flower Garden Banks were solitary (95% of in situ sightings). One sighting of two male *D. americana* (0.5-1 m DW each) resting in nonpolarized formation was made during Summer 1.

Ecology and Behavior: *Dasyatis americana* was observed at rest in sand flats or atop coral colonies, or swimming over these microtopes. Animals were also sighted retreating over escarpments if disturbed by divers on the reef crest or sand flats. Stingrays were not observed on deep reefs below escarpments.

Table 16. Southern stingray habitat use of mid-shelf banks. Based on sightings of *Dasyatis americana* at the mid-shelf banks from data collected thru April 1998.

Dasyatis americana		southern stingray
Size at Birth:	~ 0.17 m	
Size at Maturity: Males:	~ 0.5 m	
Size at Maturity: Females:	~ 0.7 m	
Maximum Size Attained:	~ 1.5 m	

Mid-Shelf Banks (Sonnier & Stetson)

Record Quality	1	2	3	4	5	
Seasonal Occurrenc	Winter 1	Winter 2	Spring	Summer 1	Summer 2	Autumn
ESTIMATED SIZE						
0 to 1 m			m	M F	F	U
1 to 2 m			B	F U	M U	
2 to 3 m					u	
3 to 4 m					u	
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	Winter 1 NP	Winter 1 P	Winter 2 NP	Winter 2 P	Spring NP	Spring P	Summer 1 NP	Summer 1 P	Summer 2 NP	Summer 2 P	Autumn NP	Autumn P
Solitary					5.2.1		6.0.0		2.1.1		1.0.0	
Paired									0.1.0			
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
M = males
F = female
B = both sexes
U = unknown sex

Quality Groups 4 &
m = male
f = female
b = both sexes
u = unknown sex

Aggregations
NP = nonpolarized
P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Table 17. Southern stingray habitat use of the Flower Garden Banks. Based on sightings of *Dasyatis americana* at the Flower Garden Banks from data collected thru April 1998.

Dasyatis americana — **southern stingray**

Size at Birth:		~ 0.17 m
Size at Maturity:	**Males:**	~ 0.5 m
	Females:	~ 0.7 m
Maximum Size Attained:		~ 1.5 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality		1	2	3	4	5
Seasonal Occurrenc	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m				B		F
1 to 2 m		F U		B	U	
2 to 3 m						
3 to 4 m						
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary			1.1.0				16.4.0		1.0.1		1.0.0	
Paired							1.0.0					
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

The southern stingray was documented at each natural topographic high surveyed. Sightings were made during spring and summer seasons at mid-shelf banks, and during all seasons except Winter 1 at the Flower Garden Banks. Sightings of unidentified 0.5-2 m DW *Dasyatis sp.* (Quality Groups 4 and 5) followed this trend also. Moreover, subsequent surveys at Stetson and the Flower Garden Banks in February and March of 1999 and 2000 have contributed no additional sightings of *D. americana* during seasons where records are lacking (i.e. mid-shelf banks). Therefore, data suggest that *D. americana* inhabiting mid-shelf banks during warmer months may emigrate closer to the shelf-edge where waters are warmer during winter months. One observation bolstering this assessment is the accounting that the southern stingray is a summer visitor to coastal waters north of Cape Hatteras and is thought to migrate to warmer waters either southward or seaward for the winter (Bigelow & Schroeder 1953, Bohlke & Chaplin 1993). The lack of sightings at mid-shelf banks during winter months, and the relative few sightings of *D. americana* made at the Flower Garden Banks during the same period, compare favorably with this accounting.

Another factor may influence the seasonal occurrence of *D. americana* at mid-shelf and Flower Garden Banks during winter months though. As previously noted, large aggregations of *S. lewini* inhabit the waters over Stetson and the Flower Garden Banks during the winter seasons, as do other large predatory sharks. *Dasyatis* spp. are preyed upon by hammerhead sharks and sometimes seek refuge when *Sphyrna* spp. are in the area (Strong et al. 1990). The lack of *D. americana* sightings at mid-shelf and Flower Garden Banks may be attributed in part to the presence of *S. lewini* and other predatory sharks. Stingrays may either emigrate from the banks, seek refuge within the coral reef complex, or be consumed during winter seasons, thus remaining inconspicuous to divers conducting surveys. While a coral reef complex contains potential refuge in a network of hidden passages and caves, the sandstone structure of Stetson Bank does not. It is logical that stingrays emigrate from the Stetson Bank as waters cool in Autumn before the arrival of aggregations of *S. lewini*.

Dasyatis americana is thought to be born at 0.12-0.18 m DW (Bigelow & Schroeder 1953) and attain a maximum size of 1.5 m DW (Bigelow & Schroeder 1953, Hoese & Moore 1977, 1998, McEachran & Fechhelm 1998). Males are thought to mature at approximately 0.5 m DW, and females at 0.7-0.8 m DW (Bigelow & Schroeder 1953). Animals reported in this study ranged in estimated sizes of 0.5 m to nearly 2 m DW, and are probably mature animals. To date, neonate or juvenile animals have not been observed at the study sites.

Snelson and Williams (1981) collected eight *D. americana* (7 males and 1 female) in the northern Indian River lagoon system of eastern Florida, though Schmid et al. (1988) found no significant difference in the sex ratio of 35 *D. americana* that they collected near Sebastian Inlet, an artificially maintained inlet providing flow between the ocean and the Indian River lagoon system. In this study, both sexes were observed during the same seasons at the banks, also suggesting adult *D. americana* do not segregate by sex.

Southern stingrays were observed to be mainly solitary, although one sighting reported two adult male stingrays resting close to one another in nonpolarized formation.

Although *D. americana* is abundant at other locations relative to this study, there is little published regarding the sociality of the species. *Dasyatis americana* evidently forms aggregations, based on the groups that form at Stingray City in the Cayman Islands (Doubilet, 1989).

Interspecific interactions were not reported, although some animals showed evidence of surviving attempted predation. In such cases, animals bore injured pelvic fins, claspers, or tails, or sometimes lacked them. One male *D. americana* was identifiable based on injured and missing appendages and was observed at Sonnier Bank in three consecutive years by scientific divers. Neither mating nor feeding activity was observed or reported.

Dasyatis centroura (Mitchill 1815)

Roughtail stingray (Figure 26)

Dasyatis centroura is a large demersal stingray occurring chiefly in warm temperate waters. Although principally known from neritic waters, it has been collected beyond the continental shelf edge of the Grand Bahama Bank at the 275 m isobath (Bullis & Struhsaker 1961, Reed & Gilmore 1981). In the western Atlantic, it occurs from Georges Bank and Cape Cod south to the Florida Keys, and into the northeastern and north-central Gulf of Mexico (Bigelow & Schroeder 1953, Bullis & Struhsaker 1961, Hess 1961, Struhsaker 1969, Hoese & Moore 1977, 1998, Reed & Gilmore 1981, McEachran & Fechhelm 1998). To date, the eastern skirt of the Mississippi River delta is the most westerly area of the northern Gulf of Mexico that *D. centroura* is known to

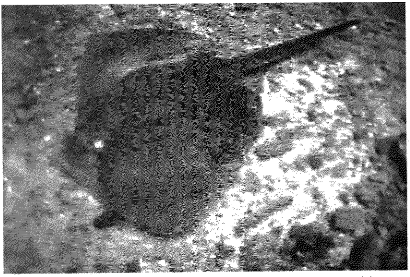

Figure 26. Roughtail stingray (*Dasyatis centroura*). This species was observed at mid-shelf banks during July in small aggregations. The picture was captured from video provided by Gary Rinn.

occur, based on two specimens reported by Springer & Bullis (1956).

Dasyatis centroura was documented in this study occurring at Stetson and Sonnier Banks, extending the species range west of the Mississippi River delta into the northwestern Gulf of Mexico. It was documented in four records in the in situ catalogue (Quality Groups 1-3), all occurring at Sonnier Bank. An additional two video clips taken in 1989, show the roughtail stingray at Stetson Bank. All records of *D. centroura* at mid-shelf banks were made in July (Table 18).

Mid-Shelf Banks: Roughtail stingrays were observed resting on sand flats and reef crests, or swimming over reef crests, sand flats, or escarpments. Three animals were observed at Sonnier Bank, two females (1-2 m DW) and one male (1-2 m DW). The same three *D. centroura* (two females and one male) were estimated at 2-3 m DW by one dive team. I personally estimated the size of these three animals to be between 1.8-2.2 m DW. Video clips show animals I similarly estimate to be 1.8-2.2 m DW, based on comparison to adjacent fishes and divers. Animals observed at Sonnier Bank formed a small aggregation whose movements were nonpolarized. For each sighting, males accompanied the female, except in one sighting that reported a single male and female moving in nonpolarized alignment. The three stingrays documented at Stetson Bank in July 1989 were determined to be females from the video clip. These animals were resting on sand flats in nonpolarized formation until disturbed by divers. Feeding was not reported.

Table 18. Roughtail stingray habitat use of mid-shelf banks. Based on sightings of *Dasyatis centroura* at the mid-shelf banks from data collected thru April 1998.

Dasyatis centroura												**roughtail stingray**
	Size at Birth:				~ 0.3 m							
	Size at Maturity:			Males:	~ 1.3 m							
				Females:	~ 1.4 m							
	Maximum Size Attained:				~ 2.1 m							
Mid-Shelf Banks (Sonnier & Stetson)												
Record Quality		1		2		3		4		5		
Seasonal Occurrence	**Winter 1**		**Winter 2**		**Spring**		**Summer 1**		**Summer 2**		**Autumn**	
ESTIMATED SIZE												
0 to 1 m												
1 to 2 m					u		B		u			
2 to 3 m					f		U					
3 to 4 m									u			
4 to 5 m									u			
5 to 6 m												
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary					0.2.0				0.1.0			
Paired							1.0.0		0.1.0			
Small Aggr. (3 to 10)							3.0.0					
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Ecology and Behavior: *Dasyatis centroura* is the largest dasyatid ray occurring in the northern Atlantic, and is reported to exceed 2 m DW and 4 m TL (Bigelow & Schroeder 1953). Struhsaker (1969) conducted the most extensive study to date on *D. centroura*, based on 147 specimens collected along the Atlantic seaboard of the U.S. He concluded that *D. centroura* is born at 0.34-0.37 m DW, that males mature at nearly 1.3-1.5 m DW, and that females mature at about 1.4-1.6 m DW. However, Capapé (1993) reported on the reproductive development of *D. centroura* collected off Tunisia, and found that Tunisian stingrays are born at and mature at smaller sizes than western Atlantic forms of *D. centroura*. Roughtail stingrays sighted at mid-shelf banks in this study were all broader than 1.5 m DW and several exceeded 2.0 m DW. Regardless of the ontogenetic differences between American and Mediterranean forms, roughtail stingrays observed in this study were all likely mature.

Both sexes were documented together at mid-shelf banks during the Summer 1 season (specifically in July), the only period *D. centroura* was found at the sites. Stingrays were observed in pairs or small aggregations of three animals organized in nonpolarized formations. For instance, I observed two adult male stingrays closely swimming with an adult female during multiple dives made over a two-day period at Sonnier Bank. Similar behavior was reported by recreational divers that described large *Dasyatis* spp. (estimated at nearly 3 m DW and exceeding 4 m TL), resting or swimming in pairs or small aggregations at Stetson Bank in multiple years during July. Moreover, video of a large female *Dasyatis* sp. (estimated at 2 m DW) at Stetson Bank during July shows mating scars along the edges of the dorsal surface (Figure 27), indicating mating

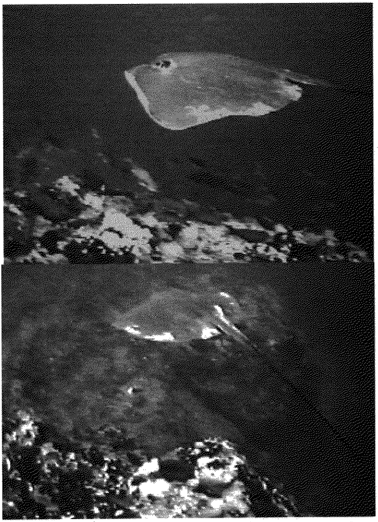

Figure 27. Probable mating scars. A female *Dasyatid* ray with an estimated disc width of 2-3 m at Stetson Bank during July. Note the mating scars along the distal edges of the pectoral and pelvic fins. Due to the estimated size and presence of other large stingrays, this animal is believed to be *Dasyatis centroura*. The picture was captured from video provided by Gary Rinn.

activity. Assuming the sizes were reasonably estimated by divers, the animals are best identified as roughtail stingrays.

Mating behavior has been described by Reed and Gilmore (1981), from sightings made of a pair of *D. centroura* observed from a submersible at the base of a deep reef off Ft. Pierce Florida. Their sighting, made at a depth of 80 m, showed white scratches on the mid-posterior edge of the female's pectoral fin, after the male dismounted from the female. Photographs taken before the mounting reveal no scratches on the female's dorsal surface. The sighting of mating activity on an 80 m deep reef off Florida, in conjunction with observations made in this study, indicate that *D. centroura* utilize mid-shelf topographic highs as mating areas.

Roughtail stingrays were not detected at mid-shelf banks during other times of the year, which suggests they utilize the sites briefly during summer. *Dasyatis centroura* is migratory along the east coast of the United States (Bigelow & Schroeder 1953, Bullis & Struhsaker 1961, Struhsaker 1969), making northerly migrations into New England waters during warmer months, but returning to neritic waters south of Virginia in Autumn (Struhsaker 1969). Struhsaker (1969) found their movements closely associated with seasonal changes in water temperature, and that the rays occur most commonly in waters ranging from 15° - 22° C. He also found that *D. centroura* was abundant in winter months along the Atlantic coast of the southeastern United States at live-bottom and shelf-edge biotopes, areas known to be productive and rich in reef fish and invertebrate fauna. However, during summer months he found *D. centroura* inhabiting shallow, inshore areas out to the 93 m isobath. Data collected in this study indicate *D.*

centroura occurring in the northwestern Gulf of Mexico are also migratory, although it is not clear whether they move seaward as infralittoral waters cool in autumn. If stingrays move seaward during colder months to the shelf-edge where waters are warmer, they apparently avoid the reef communities capping the Flower Garden Banks, based on the lack of sightings.

One noteworthy observation made in this study involves the association of the cobia (*Rachycentron canadum*) with *D. centroura*. One video taken at Stetson Bank shows a resting *D. centroura* accompanied by a *R. canadum* (Figure 28). Simliar sightings were made of *R. canadum* swimming nearby three *D. centroura* at Sonnier Bank. *Rachycentron canadum* was previously reported associating with *D. centroura* and the cownose ray (*Rhinoptera bonasus*) (Smith & Merriner 1982). Observations made during this study show *R. canadum* swim with or closely rest alongside *D. centroura* situated on the sea floor. The function of this association is not clear, though Smith and Merriner (1982) noted the two species feed on similar prey items and suggested that *R. canadum* benefits from the foraging behavior of rays rooting through bottom sediments. Sightings of *R. canadum* with *D. centroura* reported in this study add further evidence that the two species associate, though the association may benefit the cobia more than the stingray.

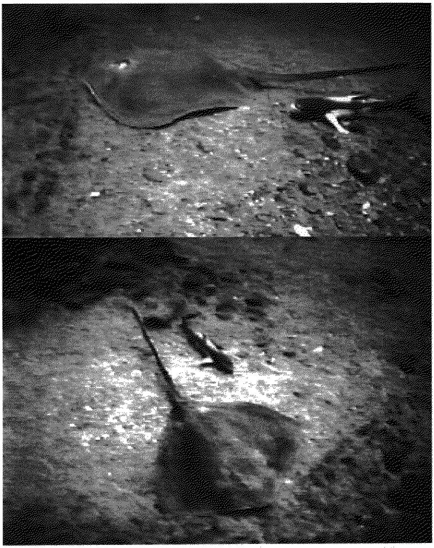

Figure 28. *Dasyatis-Rachycentron* association. A *Dasyatid* ray of an estimated disc width of 2-3 m resting on the substrate at Stetson Bank during July. Three rays of the same size were videoed resting within 10 m of one another, however, only one ray was accompanied by a cobia (*Rachycentron canadum*). Based on the information gathered, these rays are believed to be *Dasyatis centroura*.

Family Myliobatidae (eagle rays)

Aetobatus narinari (Euphrasen 1790)

Spotted eagle ray (Figure 29)

Aetobatus narinari is a pelagic ray occurring in tropical and temperate neritic waters of the three major oceans, including the Gulf of Mexico (Bigelow & Schroeder 1953, Clark 1963, Hoese & Moore 1977, 1998, Parker & Bailey 1979, Bohlke & Chapman 1993, McEachran & Fechhelm 1998). Most accounts state that *A. narinari* is principally found within several kilometers of land (Bigelow & Schroeder 1953,Bohlke & Chapman 1993, McEachran & Fechhelm 1998), however, some authors have recorded the presence of *A. narinari* at oceanic islands such as the Bahamas, Bermuda, and the Hawaiian Islands, which show the species traverses oceanic waters (Bigelow & Schroeder 1953, Bohlke & Chapman 1993).

Aetobatus narinari is documented by 67 in situ records (Quality Groups 1-4), two photographs, and 24 video clips. Animals were sighted at mid-shelf and Flower Garden Banks.

Mid-Shelf Banks: Spotted eagle rays were documented in three in situ records prior to May 1998 at mid-shelf banks during Spring, Summer 1, and Autumn (Table 19) and the maximum number observed at one time was one animal. Subsequent sightings of *A. narinari* were made at Stetson Bank in February and March (Winter 2) of 1999 and 2000, when as many as five animals were counted. Animals ranged in size from 1-2 m DW, including those sighted through March 2000. Eagle rays documented prior to May 1998 were determined to be males or of unknown sex, but subsequent sightings show

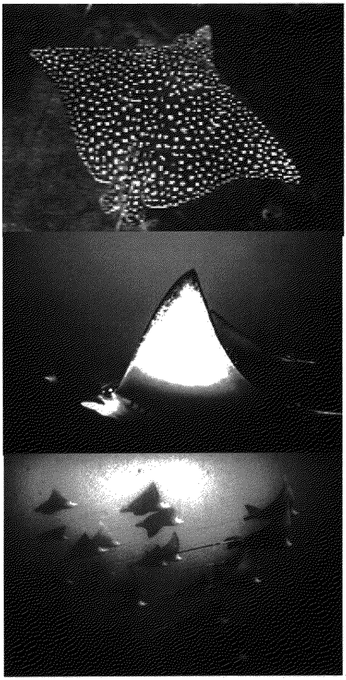

Figure 29. Spotted eagle ray (*Aetobatus narinari*). Spotted eagle rays occur in large aggregations at the Flower Garden Banks during colder months. All sightings indicate these animals to be adult rays, and aggregations include both sexes. The top picture was captured from video, the two subsequent photographs were taken by Jesse Cancelmo.

Table 19. Spotted eagle ray habitat use of mid-shelf banks. Based on sightings of *Aetobatus narinari* at the mid-shelf banks from data collected thru April 1998.

Aetobatus narinari — **spotted eagle ray**

Size at Birth:		~ 0.17 m
Size at Maturity:	Males:	uncertain, varies between populations
	Females:	uncertain, varies between populations
Maximum Size Attained:		~ 2.3 m

Mid-Shelf Banks (Sonnier & Stetson)

Record Quality: 1 | 2 | 3 | 4 | 5

Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
0 to 1 m												
1 to 2 m					M		U					
2 to 3 m												
3 to 4 m												
4 to 5 m												
5 to 6 m												
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary					1.0.0		1.0.0					
Paired												
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &	Aggregations
M = males	m = male	NP = nonpolarized
F = female	f = female	
B = both sexes	b = both sexes	P = polarized
U = unknown sex	u = unknown sex	

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

that females occur at Stetson Bank during Winter 2. Sightings made in Spring, Summer 1, and Autumn reported solitary animals, however, animals later sighted during Winter 2 were solitary, in polarized pairs, or in small polarized aggregations.

Flower Garden Banks: *Aetobatus narinari* was documented with 64 in situ sightings at the Flower Garden Banks and all photographs and video clips gathered (pre-May 1998) were taken at the Flower Garden Banks. Eagle rays were observed during both winter seasons, Summer 1, and Autumn (Table 20). During Winter 2, the maximum abundance reported exceeded 100 animals, as opposed to animals sighted in Summer 1, when one observer reported two animals together. Of 64 in situ sightings reported at the Flower Garden Banks, 80% included animals of 1-2 m DW, and 17% included animals of 2-3 m DW; the remaining sightings lacked data regarding animal size. Of 58 in situ sightings reported in Winter 2, 2% included males, 40% included females, and 60 % included unsexed animals. Also, social groups during Winter 2 varied from solitary individuals to massive aggregations. Three records were collected during Summer 1 of two solitary and one polarized pair of eagle rays. A small aggregation of 3-10 animals (1-2 m DW) was reported in Autumn whose sexes were not determined. All males were solitary, and females were in groups of two or more animals unless disturbed by divers. Additionally, eagle rays constituting pairs or aggregations moved in polarized formations. Animals separated from their counterparts (due to diver activity) swam rapidly to rejoin their social group. Individual rays forming polarized pairs or aggregations maintained compact groups whose inter-animal spacing rarely exceeded 3 body lengths from the nearest neighbor.

Table 20. Spotted eagle ray habitat use of the Flower Garden Banks. Based on sightings of *Aetobatus narinari* at the Flower Garden Banks from data collected thru April 1998.

Aetobatus narinari — **spotted eagle ray**

Size at Birth:		~ 0.17 m
Size at Maturity:	Males:	uncertain, varies between populations
	Females:	uncertain, varies between populations
Maximum Size Attained:		~ 2.3 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality	1	2	3	4	5	
Seasonal Occurrence	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m						
1 to 2 m	U	B		M U		U
2 to 3 m		B				
3 to 4 m						
4 to 5 m						
5 to 6 m						

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary	1.0.0		28.0.0				2.0.0					
Paired				14.0.				1.0.0				
Small Aggr. (3 to 10)				12.1.								1.0.0
Med. Aggr. (11 to 50)				3.0.0								
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)				1.0.0								

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 & 5
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Ecology and Behavior: Spotted eagle rays were observed swimming over reef crests, sand flats, escarpments, or in the water column at mid-shelf and Flower Garden Banks. During Winter 2, animals were frequently encountered swimming along the escarpments of each Flower Garden Bank. Some animals bore damaged pelvic fins or tails, or lacked tails partly or entirely, however, these injuries did not appear to be recently inflicted.

The size that *A. narinari* is born is unclear. Bigelow and Schroeder (1953) noted three free-living specimens measured between 0.18-0.28 m DW, but also collected three specimens that measured 0.35-0.36 m DW from a 2.2 m DW female ray. Adult female *A. narinari* probably mature at 1.4-2.1 m DW, and males apparently mature at 1.0-1.5 m DW (Schmid et al. 1988). The smallest eagle rays reported by observers at mid-shelf and Flower Garden Banks were estimated at approximately 1.5 m DW, though most were estimated at nearly 2.0 m DW or greater (Figure 30). Therefore, *A. narinari* occurring at mid-shelf and Flower Garden Banks were subadult and adult animals.

Aetobatus narinari was observed at mid-shelf banks during Winter 2, Spring, Summer 1 and 2. Eagle rays sighted during the spring and summer seasons were solitary, but animals sighted during Winter 2 were in small polarized aggregations. Eagle rays occurring at the Flower Garden Banks were rarely observed during Spring, summer and Autumn seasons, but were frequently observed and abundant during Winter 2, occurring in large aggregations of at least 100 rays. Along the East Coast of the United States, *A. narinari* migrates northward during warmer months, and southward as cooler seasons advance (Bigelow & Schroeder 1953). Since *A. narinari* is chiefly known

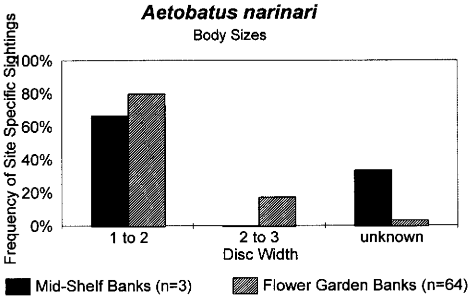

Figure 30. Estimated disc widths of *A. narinari*. Based on records in the in situ catalogue through April 1998. Most animals sighted at mid-shelf and Flower Garden Banks were estimated to be nearly 2 m TL, although some animals were judged to be somewhat larger.

to occupy eulittoral and infralittoral waters, data collected in this study indicate that eagle rays in the northern Gulf migrate to shelf-edge topographic highs such as the Flower Garden Banks (and to some lesser extent mid-shelf banks) during colder months, where they aggregate en masse. Data also indicate that subadult and adult *A. narinari* utilize the Flower Garden Banks as winter habitat. This is also true for mid-shelf banks, however, these banks do not attract and concentrate the same numbers of rays that the Flower Garden Banks do.

Both sexes of *A. narinari* were observed at the Flower Garden Banks, and most animals successfully sexed were females, though 60% of the eagle rays reported were not sexed. However, it is my belief that the majority of unsexed rays were females, since the claspers of adult males (1.0-1.5 m DW, Schmid et al. 1988) are quite apparent on eagle rays that I encountered during this study. Observers frequently expressed not viewing claspers on rays, and often lacked confidence recording the sex of animals sighted.

Schmid et al. (1988) also gathered data indicating that *A. narinari* may segregate by sex, based on their collection of 38 male and 18 female eagle rays from the Indian River lagoon system of Florida. Data collected in this study indicate that *A. narinari* segregates by size and sex, as do some species of sharks, since predominantly subadult and adult female rays were sighted at the Flower Garden Banks. This assessment is also supported to a lesser degree by observations of solitary males occurring at the natural banks in winter, and females that were in polarized groups of two or more animals.

Mating scars or activity was not evident. Eagle rays formed pairs or aggregations that were strongly polarized, indicating adult eagle rays are gregarious, at least among females. Although animals formed smaller social groups, it was apparent that animals occurring at Stetson or the Flower Garden Banks in colder months were part of a larger aggregation than what divers could enumerate effectively.

Aetobatus narinari was observed feeding with several carcharhinid sharks on discarded bycatch dispersed across Stetson Bank (assumed to originate from a shrimp trawler). Bycatch included teleost fishes and invertebrates that included crustaceans. Recently, divers documented the spotted eagle ray foraging in sand flats a Flower Garden Bank.

Eagle rays were sometimes observed swimming in multi-species schools with *S. lewini*. During such observations, eagle rays and hammerhead sharks appeared at ease; no aggressive behavior was noted. Eagle rays occurring in these multi-species schools were not reported to possess obvious injuries as noted previously, which is curious since *Sphyrna* spp. are known to prey on *A. narinari*. My observations and data indicate that *A. narinari* form complex social groups at the Flower Garden Banks, and maintain a refuging central-position social system (defined by Hamilton & Watt 1970), as has been similarly reported for *S. lewini* (Klimley & Nelson 1984) and *C. falciformis* herein.

Family Mobulidae (manta and devil rays)

Mobula hypostoma (Bancroft 1831)

Lesser devil ray (Figure 31)

Mobula hypostoma is a pelagic ray occurring in the western North Atlantic including the Gulf of Mexico (Coles 1913, 1916, Bigelow & Schroeder 1953, Schwartz 1984, Notarbartolo-di-Sciara 1987, Schmid et al. 1988, Hoese & Moore 1998, McEachran & Fechhelm 1998). It is poorly known in the region, although it seasonally visits the coast of North Carolina in July (Coles 1913, 1916, Bigelow & Schroeder 1953, Schwartz 1984), and has been found as far north as Rhode Island (Campbell & Monroe 1974). It is thought to inhabit neritic waters of tropical and warm temperate seas (Coles 1916, Bigelow & Schroeder 1953, Notarbartolo-di-Sciara 1987). In the Gulf of Mexico, *M. hypostoma* has been collected off the coast of Alabama and Louisiana (Notarbartolo-di-Sciara 1987).

Mobula hypostoma was documented at Stetson and the Flower Garden Banks, and is the first confirmed occurrence of the species in the northern Gulf of Mexico west of the Mississippi River delta. It was documented by 20 *in situ* records (quality groups 1-3) and four video clips at mid-shelf and Flower Garden Banks. [An additional six in situ records of quality groups 4 and 5 were gathered and identified as *Mobula* species.]

Mid-Shelf Banks: The sole animal documented at Stetson Bank was video taped in Summer 2 and is estimated at approximately 1 m DW. The animal was swimming in the water column above the bank, and was identified as a female.

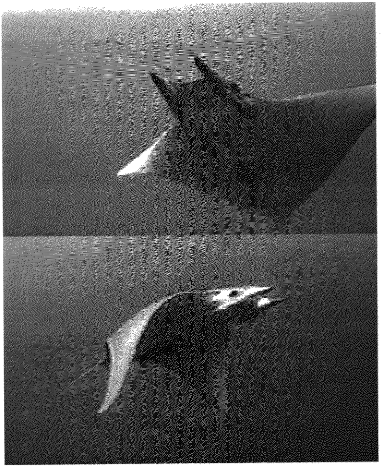

Figure 31. Lesser devil ray (*Mobula hypostoma*). This solitary ray was video taped by Gary Rinn at Stetson Bank during Summer 2. This was the only sighting made of *M. hypostoma* at mid-shelf banks during this study, however, aggregations of 11-50 animals were regularly encountered by divers at the Flower Garden Banks during Summer 1.

Flower Garden Banks: Twenty in situ records and three video clips documented *M. hypostoma* at the Flower Garden Banks during Summer 1 (Table 21). Animals between 1-2 m DW were reported in 95 % of in situ sightings, the remaining 5 % were estimated at 0.5-1 m DW. Both sexes were observed. The maximum number of rays observed at one time was estimated at as many as 50 animals. Sixty-five percent of in situ sightings at the Flower Garden Banks reported solitary rays. Groups comprising pairs or aggregations of 11-50 animals constituted 20 % and 10 % of in situ records, respectively. One sighting (5 %) was of a *M. hypostoma* swimming with a *M. birostris*. Paired and aggregated *M. hypostoma* (excluding the interspecies duo), formed polarized social groups, although video shows one pair swimming in nonpolarized formation. The sexual composition of paired and aggregated animals was not determined for all sightings, although one record includes a male and female pair swimming together, and another record includes two females together.

Six in situ records of record quality groups 4 and 5 were identified as *Mobula* species at the Flower Garden Banks during Spring and Summer 1 and animals were judged in size groups of 0.5-1m and 1-2 m DW. Sightings included solitary, paired, and aggregated *Mobula*, and groups of two or more animals were reported swimming in polarized formations.

Table 21. Lesser devil ray habitat use of the Flower Garden Banks. Based on sightings of *Mobula hypostoma* at the Flower Garden Banks from data collected thru April 1998.

Mobula hypostoma — **lesser devil ray**

Size at Birth: ~ 0.5 m
Size at Maturity: Males: ~ 1.1 m; Females: ~ 1.1 m
Maximum Size Attained: ~ 1.2 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality	1	2	3	4	5	
Seasonal Occurrenc	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m			u	U	u	
1 to 2 m		u	u	B	b	
2 to 3 m	f	u	u	b	b	m
3 to 4 m	u	u		f u	b	
4 to 5 m			u	u	u	u
5 to 6 m					u	

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary	0.0.2		0.0.8		1		13.0.34		0.0.37		0.0.3	
Paired			0.0.			1	0.0.1	4.0.1		0.0.1		
Small Aggr. (3 to 10)						1	0.0.2	0.1.0				
Med. Aggr. (11 to 50)								2.0.0				
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
M = males
F = female
B = both sexes
U = unknown sex

Quality Groups 4 &
m = male
f = female
b = both sexes
u = unknown sex

Aggregations
NP = nonpolarized
P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Ecology and Behavior: *Mobula hypostoma* was chiefly observed swimming in the water column above reef crests or beyond escarpments of the banks. Mating or feeding activity was not reported. Mobulid rays were observed leaping clear of the sea, sometimes performing somersaults or belly-flops when re-entering the sea. This behavior was typically observed within 4-5 hours post-dawn.

The lesser devil ray is believed to be roughly 0.5 m DW at parturition (Bigelow & Schroeder 1953). Adults are estimated to mature at approximately 1.1 m DW, and rarely exceed 1.25 m DW (Bigelow & Schroeder 1953). *Mobula hypostoma* observed during this study were estimated to be approximately 1 m DW or slightly larger, indicating the animals were subadults or adults. Previously, two juvenile male specimens (0.66-0.71 m DW) were collected along the north-central Gulf Coast (Notarbartolo-di-Sciara 1987).

During this study, *M. hypostoma* was observed in aggregations comprising 11-50 rays of both sexes at the Flower Garden Banks during the Summer 1. Additionally, a solitary female ray was video taped at Stetson Bank during Summer 2. This was the only record of the species at this bank. I consider the sighting at Stetson Bank an atypical occurrence, whereas the occurrence of *M. hypostoma* at the Flower Garden Banks during Summer 1 is a predictable annual event. Subsequent surveys since April 1998 have resulted in no further sightings that contradict this trend of seasonal occurrence and habitat use.

Lesser devil rays were frequently observed swimming in polarized pairs or aggregations, suggesting that the animals are quite gregarious during Summer 1. Paired animals were sometimes observed, during which a male ray was closely accompanying a female and within a meter of the sea surface. Such behavior is indicative of courtship and mating behavior among *M. hypostoma* (Coles 1910) and in accounts of other batoids (e.g. Brockmann 1975, Reed & Gilmore 1981, Uchida et al. 1990, Young 1993). Because both sexes of adult *M. hypostoma* predictably aggregate at the Flower Garden Banks in June and July, observations intimate the sites function as mating habitat and as summer feeding habitat during Summer 1.

Coles (1913, 1916) reported feeding aggregations of the lesser devil ray that included gravid females along the coast of North Carolina during July, and noted the species to be a seasonal summer migrant to mid-Atlantic bight waters. Additional accounts of *M. hypostoma* occurring along the east coast of Florida in July or August (Bigelow & Schroeder 1953, Schmid et al. 1988) indicate a northerly summer migration, followed by a southerly winter migration. Data collected in this study provide evidence that *M. hypostoma* is migratory in the region, although it is not known where the rays migrate to and from during other seasons or life stages (i.e. nursery areas).

No evidence of predation on *M. hypostoma* was evident. *Manta birostris* and *Echeneis naucrates* were the only species observed with *M. hypostoma* during this study.

Mobula tarapacana (Philippi 1893)

Sicklefin devil ray (Figure 32)

Mobula tarapacana is a large pelagic devil ray inhabiting circumtropical seas (Notarbartolo-di-Sciara 1987, 1988). The species was formerly known from the Indian and Pacific Oceans, however, Notarbartolo-di-Sciara and Hillyer (1989) reported aerial and shipboard sightings of large *Mobula* rays off eastern Venezuela that they identified as *M. tarapacana*. The only other large devil ray known in the North Atlantic Ocean is *Mobula mobular*, which is rarely reported along the East Coast of the United States and Jamaica (Bigelow & Schroeder 1953). It was most recently collected off the Carolinas by Schwartz (1984). Notarbartolo-di-Sciara (1987) conducted an extensive review of the genus *Mobula*, and found satisfactory morphological distinctions between *M. mobular* and *M. tarapacana* to confidently identify the Venezuelan animals as *M. tarapacana*. The Venezuelan rays are the first records of *M. tarapacana* in the western Atlantic, but specimens were not examined by Notarbartolo-di-Sciara and Hillyer to confirm their identification.

During August 1993, what appeared to be a pair of *Manta birostris* were video taped swimming at a depth of 24 m over the coral reef of the West Flower Garden Bank (Childs 1997). Upon inspection of the video, one animal was identified as *M. birostris*, and the other was determined to be *M. tarapacana*. The video footage shows a 2-3 m DW *Mobula* ray with a long neck, short caropteres, and a relatively short, whip-like tail. No white coloration was evident on the dorsal fin or tail. A cigar shaped, fleshy appendage was evident protruding from the base of the dorsal fin, however, the

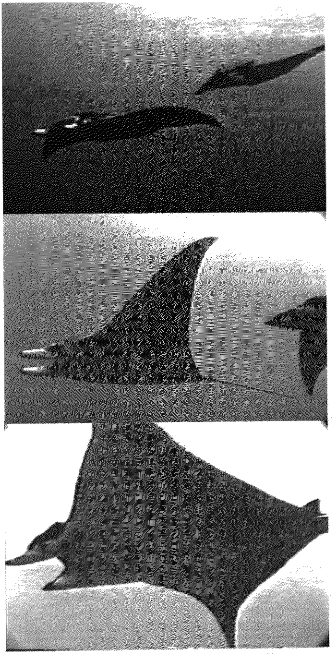

Figure 32. Manta ray and Sicklefin devil ray. A 2-3 m DW manta ray (*Manta birostris*) being closely followed by a large *Mobula* ray best identified as *Mobula tarapacana* was video taped at the West Flower Garden Bank during August by Steve Gittings. The animal was determined to be a female estimated to be approximately 2 m DW.

appendage appears to be an echeneid fish, although it could be a vestigial spine. Based on the observed morphological characteristics, the animal is best identified as *M. tarapacana* at present. Subsequent sightings of *M. tarapacana* at the Flower Garden Banks were made during the Summer 2 season during this study, and aerial photographs taken by National Marine Fisheries Service biologists in the northeastern Gulf (K. Mullen, pers comm) show the species also occurs throughout the northern Gulf during Summer 2. Accordingly, these sightings are the northernmost sightings in the western North Atlantic.

Mobula tarapacana was documented by three in situ records (Quality Groups 1-3) and two video clips. It was only observed at the Flower Garden Banks. Table 22 summarizes sightings data.

Flower Garden Banks: The sicklefin devil ray was sighted during Summer 2 within a fortnight of mass coral spawning events observed at the Flower Garden Banks. Animals were solitary and estimated to be 2-3 m TL, however, sex was not determined for all animals. The 2-3 m TL *M. tarapacana* that was video taped closely following an *M. birostris* of the same size group was determined to be a female (Figure 32). The video also shows *M. tarapacana* hosting an *R. remora* atop its head and what appears to be a small *E. naucrates* near the base of the tail. *Mobula tarapacana* was observed swimming throughout the water column to within 3 m of the reef crest.

Table 22. Sicklefin devil ray habitat use of the Flower Garden Banks. Based on sightings of *Mobula tarapacana* at the Flower Garden Banks from data collected thru April 1998. The polarized pair record (*) was of a *M. tarapacana* closely following a *Manta birostris*.

Mobula tarapacana — **sicklefin devil ra**

Size at Birth:		unknown
Size at Maturity:	Males	~ 2.4 m
	Females	~ 2.7 m
Maximum Size Attained		~ 3.0 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality		1	2	3	4	5
Seasonal Occurrenc	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m			u	u	u	
1 to 2 m		u	u	u	b	
2 to 3 m	f	u	u	b	F U b	m
3 to 4 m	u	u		f u	b	
4 to 5 m			u	u	u	u
5 to 6 m					u	

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
Solitary	0.0.2		0.0.8		0.0.3		0.0.34		3.0.37		0.0.3	
Paired			0.0.			0.0.	0.0.1	0.0.1		*1.0.1		
Small Aggr. (3 to 10						0.0.	0.0.2	0.1.0				
Med. Aggr. (11 to 50												
Lg. Aggr. (51 to 100												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3	Quality Groups 4 &
M = males	m = male
F = female	f = female
B = both sexes	b = both sexes
U = unknown sex	u = unknown sex

Aggregations

NP = nonpolarized

P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Ecology and Behavior: Little is known regarding *M. tarapacana*, however, Notarbartolo-di-Sciara (1988) estimated that males begin maturing at 2.4-2.5 m DW, and females begin maturing at 2.7-2.8 m DW, based on six specimens examined from the Gulf of California. *M. tarapacana* sighted at the Flower Garden Banks were estimated at 2-3 m DW, and are therefore believed to be subadult or adult animals.

Sightings of *M. tarapacana* were rare relative to sightings made of *M. hypostoma* and *Manta birostris*. Additionally, only solitary animals were sighted and occurred within a fortnight of mass coral spawning events at the Flower Garden Banks. Although mass coral spawning is a predictable annual event at the Flower Garden Banks, the occurrence of *M. tarapacana* is not; rays were not seen each year.

Mobula tarapacana is not common in the Gulf of California, and is strictly a summer and autumn visitor where it was found farther from the coast than other mobulid rays inhabiting the region (Notarbartolo-di-Sciara 1987). Likewise off Venezuela, *M. tarapacana* is less common than *M. birostris*, and typically found at the sea surface in oceanic waters between April and November (Notarbartolo-di-Sciara & Hillyer 1989). Data gathered in this study indicate that subadult or adult sicklefin devil rays are casual visitors to the Flower Garden Banks near the date that corals spawn en masse there. The species is apparently migratory, and may inhabit oceanic waters of the Gulf of Mexico during other seasons.

Manta birostris (Walbaum 1792)

Manta ray (Figure 33)

Manta birostris is a large pelagic ray occurring worldwide in tropical and warm temperate seas (Bigelow & Schroeder 1953, Bohlke & Chapman 1993, McEachran & Fechhelm 1998). It is documented in eulittoral waters of the Gulf of Mexico along the west coast of Florida, off the Mississippi River delta, and southward to Corpus Christi, Texas (Bigelow & Schroeder 1953, Clark 1963, Hoese & Moore 1977, 1998, Parker & Bailey 1979). Additionally, *M. birostris* was documented at mid-shelf and Flower Garden Banks (Bright & Cashman 1974, Rezak et al. 1985, Dennis & Bright 1988).

Manta birostris is documented in 138 in situ records (Quality Groups 1-3), 97 photographs, and 133 video clips. An additional 20 *in situ* records (record quality group 4) are attributed to the genus *Manta*, but were not used in the following account because some observers confused *Mobula* and *Manta* species. The manta ray was documented at each study site.

Mid-Shelf Banks: Three in situ records and five video clips of *M. birostris* were documented at mid-shelf banks during Summer 2 and Autumn (Table 23). Mantas of both sexes were identified whose sizes ranged from 2-4 m DW. Animals were solitary at mid-shelf banks.

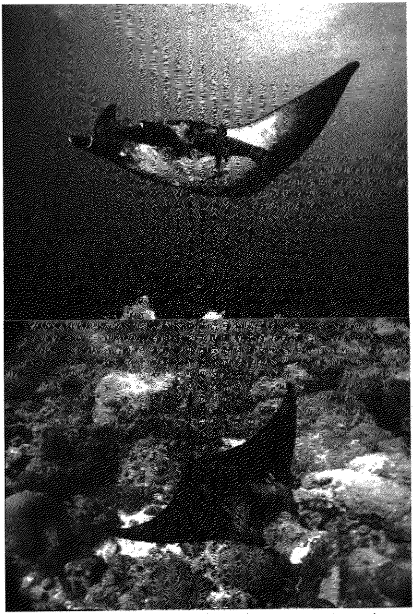

Figure 33. Manta ray (*Manta birostris*). The manta ray is commonly encountered at the Flower Garden Banks and to a lesser extent at Stetson and Sonnier Banks. Manta rays were often accompanied by a variety of fishes, including the diskfishes *R. remora* and *E. naucrates*.

Table 23. Manta ray habitat use of mid-shelf banks. Based on sightings of *Manta birostris* at the mid-shelf banks from data collected thru April 1998.

Manta birostris — manta ray

Size at Birth: ~ 1.2 m
Size at Maturity: Males: ~ 4.0 m (3.6 m specimen immature)
Females: ~ 4.0 m (4.2 m specimen gravid)
Maximum Size Attained: ~ 6.7 m

Mid-Shelf Banks (Sonnier & Stetson)

Record Quality		1	2	3	4	5
Seasonal Occurrenc	Winter 1	Winter 2	Spring	Summer 1	Summer 2	Autumn
ESTIMATED SIZE						
0 to 1 m						
1 to 2 m					u	
2 to 3 m					F U	F U
3 to 4 m					M U	
4 to 5 m					u	
5 to 6 m						

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary									0.0.2		3.2.1	
Paired												
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
M = males
F = female
B = both sexes
U = unknown sex

Quality Groups 4 &
m = male
f = female
b = both sexes
u = unknown sex

Aggregations
NP = nonpolarized
P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Flower Garden Banks: *Manta birostris* was documented in 129 in situ records, 97 photographs, and 128 video clips in all seasons but Spring at the Flower Garden Banks (Table 24). Underwater sightings sometimes included 3-5 animals occurring within sight of divers. Sizes varied from 1-5 m DW (Figure 34) and both sexes were present. Ninety percent of animals reported at the Flower Garden Banks were solitary. Nine percent of sightings included paired animals, and 1% of sightings noted small aggregations of 3-5 animals. Paired animals of one or both sexes were reported in both summer seasons, and small aggregations were noted during Summer 1. Pairs were polarized or nonpolarized in orientation, though most sightings were of nonpolarized duos. Small aggregations formed nonpolarized groups as a whole, but individuals sometimes followed other animals within these groups.

HI-389: Nearby at HI-389, *M. birostris* was documented in six *in situ* records occurring in Spring and each summer season (Table 25). One animal was sighted at a time, and animals ranged in size from 1-6 m DW (Figure 34). Two records documented male animals, and four records were of animals that were not sexed.

Ecology and Behavior: *Manta birostris* inhabits neritic and oceanic waters, although most sightings occur at the sea surface within several kilometers of the coast (Bigelow & Schroeder 1953, McEachran & Fechhelm 1998). However, the perception that *M. birostris* is common and abundant in eulittoral waters may be in error, and likely the result of increased human activity in eulittoral waters relative to circalittoral or oceanic waters. The abundant sightings collected during this study (relative to other species documented) indicate *M. birostris* is common offshore, particularly at the Flower

Table 24. Manta ray habitat use of the Flower Garden Banks. Based on sightings of *Manta birostris* at the Flower Garden Banks from data collected thru April 1998. Polarized pair record (*) was of a *M. birostris* followed closely by a *Mobula tarapacana*.

Manta birostris — manta ray

Size at Birth: ~ 1.2 m
Size at Maturity: Males ~ 4.0 m (3.6 m specimen immature)
Females ~ 4.0 m (4.2 m specimen gravid)
Maximum Size Attained: ~ 6.7 m

Shelf-edge Banks (East & West Flower Garden Banks)

Record Quality			1		2		3		4		5	
Seasonal Occurrenc	Winter 1		Winter 2		Spring		Summer 1		Summer 2		Autumn	
ESTIMATED SIZE												
0 to 1 m					u		u		u			
1 to 2 m			U		u		U		B		U	
2 to 3 m	f		B		u		B		B		B	
3 to 4 m	u		F U				B		B		F	
4 to 5 m					u		U		F u		U	
5 to 6 m									u			
SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary	0.0.2		16.4.8		0.0.3		44.5.34		48.7.37		7.1.3	
Paired			2.0.	1.1.		0.0.	3.0.1	1.0.1	3.0.0	*1.0.1		
Small Aggr. (3 to 10						0.0.	2.0.2					
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
M = males
F = female
B = both sexes
U = unknown sex

Quality Groups 4 &
m = male
f = female
b = both sexes
u = unknown sex

Aggregations
NP = nonpolarized
P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

Table 25. Manta ray habitat use of HI-389. Based on sightings of *Manta birostris* at HI-389 from data collected thru April 1998.

Manta birostris — **manta ray**

Size at Birth: ~ 1.2 m
Size at Maturity: Males: ~ 4.0 m (3.6 m specimen immature)
Females: ~ 4.0 m (4.2 m specimen gravid)
Maximum Size Attained: ~ 6.7 m

Artificial Topographic High (HI-389 platform)

Record Quality	1	2	3	4	5	
Seasonal Occurrenc	**Winter 1**	**Winter 2**	**Spring**	**Summer 1**	**Summer 2**	**Autumn**
ESTIMATED SIZE						
0 to 1 m						
1 to 2 m					U	
2 to 3 m					M U	
3 to 4 m				U	U	
4 to 5 m						
5 to 6 m			M			

SOCIAL GROUPS	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P
Solitary					1.0.0		1.0.0		4.0.0			
Paired												
Small Aggr. (3 to 10)												
Med. Aggr. (11 to 50)												
Lg. Aggr. (51 to 100)												
Massive Aggr. (100+)												

Key to Abbreviations

Sexes (by Quality Groups)

Quality Groups 1, 2 & 3
M = males
F = female
B = both sexes
U = unknown sex

Quality Groups 4 & 5
m = male
f = female
b = both sexes
u = unknown sex

Aggregations
NP = nonpolarized
P = polarized

Key to Social Group Data

Three numbers in a social group block (e.g. 1.2.1) indicates the taxa level (species/genus/family) that in situ records were reported for the animals.

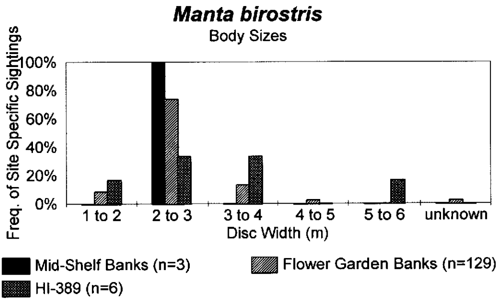

Figure 34. Estimated disc widths of *M. birostris*. Based on records from the in situ catalogue through April 1998. Manta rays ranged in sizes 1-6 m DW, however, the majority of animals were estimated to be 2-4 m DW.

Garden Banks, and account for significantly more sightings than those documented in eulittoral waters along the northern Gulf coast.

Manta birostris was observed swimming just above the reef crest and sand flats, along escarpments, and in the water column at mid-shelf and Flower Garden Banks. Mantas were also observed swimming near HI-389 and the open waters approximately 0.5 km north of the platform. Sightings were made day and night, and mantas were observed jumping from the sea, as similarly described for *M. hypostoma* previously. Feeding was observed with animals loop-feeding along escarpments or within the water column over the reef crest. Additionally, *M. birostris* was observed swimming and loop feeding along the escarpment/deep reef interface (approximately 50 m isobath) at the Flower Garden Banks in February and March of 2000 using a remotely operated vehicle.

Manta birostris is approximately 1.2-1.3 m DW at parturition (Bigelow & Schroeder 1953). Animals are thought to mature at approximately 3.8 m DW, based on the few specimens examined by Bigelow & Schroeder (1953). Manta rays sighted during this study ranged in size from 1-6 m DW, although 72 % of animals sighted among sites were estimated at 2-4 m DW (Figure 34, based on in situ records). Fourteen percent of mantas were estimated at 3-4 m DW. Mantas reported in the 1-2 m DW size group were actually estimated by divers at 1.3-2 m DW, indicating that some mantas are likely young of the year and may have been born in the vicinity of the banks. Based on the available life history information from the literature, the following life history stages are discerned by disc width: neonates and young (smaller) juveniles are 1.2-2 m DW, older (larger) juveniles are 2-3 m DW, subadults and adults are 3 m DW or larger.

Therefore, *M. birostris* occurring at mid-shelf banks are older (larger) juvenile, subadult, and adult rays. Animals occurring along the shelf-edge at the Flower Garden Banks and HI-389 are of all life history stages, though predominantly juveniles.

The manta ray is believed to be a resident in tropical waters, but migratory in warm temperate waters north of southern Florida, as shown by historical records collected along the East Coast of the United States (Bigelow & Schroeder 1953). These accounts indicate that *M. birostris* occurs there only during warmer months of the year. In the Caribbean Sea off eastern Venezuela, Notarbartolo-di-Sciara and Hillyer (1989) found the distribution of mantas within their study area to be constant throughout the year. Furthermore, mantas showed a preference for neritic waters that were less than 50 m from shore. In my study, older (larger) juvenile, subadult, and adult mantas were documented at mid-shelf banks during Summer 2 and Autumn seasons and not during other seasons, indicating mid-shelf banks function as summer feeding habitat for these life history stages. Manta rays of all life history stages were observed at the Flower Garden Banks during all seasons except Spring, however, mantas were sighted during Spring at HI-389 (located 1.6 km east of the East Flower Garden Bank), thus demonstrating *M. birostris* utilizes the Flower Garden Banks and circalittoral waters year-round. The presence of juveniles also show that the Flower Garden Banks function as nursery habitat for *M. birostris*. Since sightings of mantas at mid-shelf banks were limited to Summer 2 and Autumn, I believe older (larger) *M. birostris* expand their summer feeding activity from circalittoral waters to include infralittoral and eulittoral waters of the northwestern Gulf of Mexico during warmer months. And, as eulittoral and infralittoral waters cool with the advancement of arctic cold fronts into the northern Gulf region, older (larger) mantas in these waters move to circalittoral waters along the shelf-edge where water temperatures are warmer than those closer to the northern coast.

Although most sightings documented solitary mantas, it was common to encounter different individuals over a series of dives conducted in a day. Many individuals were identifiable based on ventral blotching patterns unique to each individual manta ray, and a catalogue was developed using methodology similarly used for identifying individual cetaceans. Based on photographs and video clips taken since 1980, 36 individual manta rays have been identified, with an additional five animals that pose some difficulties in repeated identification (Childs, unpublished data). Many individual manta rays have been repeatedly sighted and photographed at the study sites since first being documented and identified. Some animals have been re-sighted in consecutive years, however, others have been re-sighted after several years of hiatus. One animal documented in 1989 at the Flower Garden Banks was re-sighted there after a nine-year hiatus.

Popular diving articles concerning manta rays frequently report the species to aggregate and school in the waters around Yap, Micronesia and Hawaii, USA. However, 75 % of mantas sighted from aircraft and vessels off eastern Venezuela were apparently solitary, and schooling was not observed (Notarbartolo-di-Sciara & Hillyer 1989). The latter study compares favorably with underwater sightings made in this study, since *Manta birostris* was rarely observed in pairs or aggregations (8.0 % and 1.5 % of in situ sightings, respectively). Instead, mantas were chiefly determined to be solitary (90.5 %

of in situ sightings), although multiple individuals were observed over the banks. In the few instances that mantas were observed in groups at the Flower Garden Banks, the animals formed primarily nonpolarized groups (only 2.2% of in situ sightings were of polarized pairs). Venezuelan mantas within 10 disc widths of conspecifics formed uncoordinated groups, comprising as many as 50 individuals. It is not clear why manta rays occurring in the Gulf of Mexico and Caribbean Sea are predominantly solitary in nature, but mantas sighted at Yap and Hawaii are prone to regularly form schools or aggregations, although it may result from tidal changes that flush plankton and small nekton through channels from lagoon and mangrove areas. Since four of the five topographic highs surveyed in this study are submerged and exist well out in the Gulf of Mexico, they do not experience the same effects of tidal changes as coastal areas.

There was no evidence of mating activity or scars documented [mating behavior among manta rays was recently described by Yano et al. 1999], however, animals did manifest scars and injuries not attributed to mating. One manta was observed swimming at the sea surface towing approximately 15 m of commercial fishing net behind it, and the net had sawed approximately 0.1 m into the leading edge of the animals' pectoral fin. Several animals showed scarring originating at the mouth and across the dorsal surface to the insertion point of the dorsal fin. Mantas were observed bumping vertical lines used by divers, sometimes catching the lines between their caropteres (two cephalic lobes located on the right and left margins of the mouth), and then struggling to free themselves. During such observations, mantas freed themselves by swimming down and received rope burns across the mouth and dorsal surface that persisted for days. Another type of scar or injury noticed during in situ interactions with *M. birostris* included crescent-shaped cuts on the pectoral fins or tail base. Some individuals had crescent-shaped sections of their pectoral fins or pelvic fins completely removed, or lacked all or part of the tail. I attribute the crescent-shaped injuries to predatory attacks made by sharks.

A variety of fishes were observed interacting with manta rays, and typically were of a passive nature. Manta rays were often sighted with a variety of accompanying teleost fishes, that included the rainbow runner (*Elagatis bipinnulata*), bar jack (*Caranx ruber*), blue runner (*C. crysos*), horse-eye jack (*C. latus*), crevalle jack (*C. hippos*), black jack (*C. lugubris*), almaco jack (*Seriola rivoliana*), greater amberjack (*S. dumerili*), great barracuda (*Sphyraena barracuda*), cobia (*Rachycentron canadum*), remora (*Remora remora*), and sharksucker (*Echeneis naucrates*). On several occasions, I observed jacks of the genus *Caranx* and *Seriola*, closely shadowing a manta swimming within 3 m of the reef. In addition to the teleost fishes noted, *M. birostris* was also observed being closely followed by *M. hypostoma* and *M. tarapacana* on several occasions. One dynamic interaction was observed however, between *M. birostris* and *C. falciformis* at the HI-389 platform where a juvenile shark briskly rubbed its side against the dorsal surface of a large manta ray. There was no apparent response by the manta during this encounter, and I expect some fishes might resort to such activity to dislodge ectoparasites from their bodies.

Manta rays have been reported by divers to regularly utilize stationary cleaning stations established on reefs in Yap and Hawaii. Cleaning behavior was not observed during this study. Some manta rays were infested with parasitic copepods on the head, caropteres, and both dorsal and ventral surfaces. I noted however, such infestations only on manta rays that lacked concomitant *R. remora* or *E. naucrates*. Following this discovery, I examined video clips collected of *M. birostris* during this study. Although many video clips did not show the entire body of the animals documented, the head, caropteres, and dorsal and ventral surfaces were typically filmed. My examination of the video clips revealed that approximately 99 % of the animals accompanied by concomitant diskfishes rarely showed parasitic copepods on their bodies or heads. Animals without *R. remora* or *E. naucrates* were sometimes infested by parasitic copepods.

Mantas and other elasmobranchs often host *R. remora* and *E. naucrates*, diskfishes that have been shown to feed on parasitic copepods (Cressey & Lachner 1970). I believe data collected in this study, in conjunction with the literature, suggest that mantas occurring at the study sites rely on concomitant diskfishes for cleaning ectoparasites from their bodies. Such a mutual relationship would certainly be advantageous to both the host and concomitant.

Mantas hosting "traveling" cleaners would not need to locate or return to a stationary cleaning station. The benefits derived by *Remora remora* and *E. naucrates* are obvious, and it is not expected that individual diskfishes would be sustained entirely on parasitic copepods. Diskfishes evidently derive nutrition from other sources while accompanying mantas, as suggested by Figure 35. On several occasions, *R. remora* was observed refuging inside the cloaca of a manta, and *R. remora* and *E. naucrates* were

Figure 35. Rectal refuging of *Remora remora* in *Manta birostris*. Diskfishes were also observed in the oral cavity of *M. birostris*.

each observed inside the mouth cavity of mantas. It is possible that diskfishes retreat to either oral or rectal orifices of *M. birostris* for shelter, though I suspect the true nature of rectal refuging is associated with coprophagy or the consumption of parasites occurring in the rectal orifice.

DISCUSSION

Many elasmobranch species are shy, wide-ranging animals whose activities are extremely challenging to study (Gruber & Myrberg 1977, Nelson 1977). This is due mainly to the challenges posed by conducting studies in the offshore environment, a medium that effectively conceals these highly mobile animals (Gruber & Myrberg 1977, Nelson 1977). Additionally, observations of these animals tend to be brief, providing one is located, and some sharks pose a threat to those studying them in situ (Myrberg et al. 1972, Johnson & Nelson 1973).

Topographic highs on the mid and outer shelf provide scientists an opportunity to study elasmobranchs associating with these features. Data gathered in this study show that these features attract and concentrate some wide-ranging elasmobranchs, making it possible to study what are otherwise difficult-to-locate animals. Since little is known concerning the habitat use and social behavior of many wide-ranging elasmobranchs, in situ observations of elasmobranchs at topographic highs are a useful means of gathering data to study such behaviors.

Critique of Methods and Data

Traditionally, information regarding elasmobranch ecology and behavior was gained from fisheries data or opportunistic sightings made from the sea surface. Each method biases the data collected, the results, and conclusions drawn. For example, fisheries data gathered using hook and line gear may sample carnivorous sharks and rays in an area, but will fail to sample filter-feeding elasmobranchs. Likewise, nets used to gather fisheries data fail to sample fishes smaller than the mesh size used. Fisheries data also tend to be gathered during periods when conditions are most favorable (i.e. warmer months in temperate waters) for harvesting fishes or in areas known to concentrate fishes. On the other hand, scientific cruises sampling for ichthyological collections are similarly selective in the scheduling of cruises, the areas sampled, and ultimately the specimens retained for collections. Most ichthyological collections are not capable of storing fish specimens exceeding approximately 2 m TL, and if able to do so, they are not capable of conserving multiple specimens of the same species exceeding 2 m TL. It is for this reason that complete specimens of *R. typus*, *M. tarapacana*, and *M. birostris* are exceptionally rare in ichthyological collections around the world, and are not likely to be adult animals.

Sightings made from the sea surface may also be misinterpreted. For example, Gill (1908), reported that mantas rest on the sea floor based on sightings made from the sea surface. Scientific or recreational divers have yet to corroborate such behavior. Many eyewitnesses using scuba during this study, including myself, closely observed manta rays slowly gliding or nearly motionless within a meter of the benthos, moving no more than a meter per 10 seconds. Similar sightings were made from the surface, approximately 20-25 m above the bank substrate, giving the viewer the impression that the manta might be settled on the substrate. Upon descending 10-15 m below the sea surface, it was evident the manta ray was slowly gliding over the substrate.

Various challenges were encountered while conducting this study. Four of five study sites are within a national marine sanctuary and the harvest of specimens is strongly discouraged or illegal, depending on the species and means by which they are sought. Furthermore, the principal user group of the Sanctuary is the recreational diving community, which expressed considerable displeasure at the possibility that megafauna might be harmed, regardless of the purpose. During the course of this study, a significant effort was made to educate people visiting the Sanctuary concerning the minimal impact exercised while collecting data. As a result, a constituency was established with the recreational diving community and offshore workers who became valuable contributors to the study, without unnecessarily sacrificing sharks and rays they sought to observe while visiting the Sanctuary.

A 'shotgun' approach to data collection was adopted to locate and observe elasmobranchs during this study. Surveys of the sea surface were conducted from boats and the HI-389 platform and yielded sightings of pelagic species such as whale sharks, requiem sharks, hammerheads, eagle and manta rays. Aerial surveys conducted in the vicinity of the Flower Garden Banks following mass coral spawning events produced sightings of whale sharks in waters beyond the banks. Underwater surveys generated the most detailed records of species occurrence, relative abundance, sex, size, intra- and interspecies behavior, information that was often not included in sightings records made during aerial or sea surface surveys.

The quality of data generated from underwater surveys was influenced multiple factors. Sea state affected diving conditions and the ability to detect and observe animals. Water clarity influenced the range that elasmobranchs could be detected, and visibility often varied substantially between dives. As a result, group size and relative abundance of some pelagics were certainly underestimated. Strong currents sometimes limited divers to surveying small areas that included fewer microtopes.

The quantity of underwater data collected per sighting was strongly influenced by the proximity to the subject animal(s) and the interaction time. Subjects that were closely approached were more likely sexed accurately and sizes were estimated more accurately. For example, it was often not feasible to discern the sex of individuals detected on the distal side of an aggregation. Longer interaction times also increased the opportunity to gather accurate data. Subject proximity and interaction time were dependent on the species under observation, since some species were more approachable than others. Species that interacted well with divers included the nurse shark, whale shark, scalloped hammerhead, southern stingray, roughtail stingray, spotted eagle ray, and manta ray. Subject proximity and interaction time was best with whale sharks and manta rays.

Another valuable component of this study was the use of photographic records for identifying and documenting species occurrence. Frequently, subjects documented in photographic images were identifiable to species. Factors influencing the quality of the images included focus, photographic angle, lighting, glare, and turbidity, as well as the proximity to the subjects. Photographic images made before the initiation of this study were also instrumental, such as the single video clip of *Mobula hypostoma* at Stetson Bank. Nonetheless, photographic records could not be used to determine group size, since it was impossible to discover what animals might exist beyond the scope of the subjects photographed or video taped, unless accompanied by some narrative.

Other factors affecting the data sets include the terms and definitions used in data categories (e.g. size, abundance, group size). For example, the use of five body sizes between conspecifics to determine group size was arbitrarily chosen, and had another number (such as two or ten) been used, the patterns regarding social groups would result in significantly different patterns. Other problems experienced included narratives lacking photographic records, or the photographic images lacked accompanying written narratives or survey forms. In such cases, records were either devalued by quality group, or limited to the data available; many were not added to the data sets.

Quantification of survey effort poses the most critical methodological challenge to this study. Survey effort was greatest during the summer and least during winter and spring. Since survey effort was weakest during the winter and Spring seasons, these seasons serve as the baseline from which to gauge the occurrence data. For example, solitary *Galeocerdo cuvier* and large aggregations of *Sphyrna lewini* and *Aetobatus narinari* were observed during winter months, and not documented during summer months when survey effort was greatest. Furthermore, the patterns of species occurrence, abundance, and composition observed during winter months were consistent between sampling years and different from those observed during summer months of the same years. While additional surveys during the winter and Spring seasons are desirable, the surveys conducted during the summer seasons were more than adequate to document the occurrence of most species inhabiting the sites during summer.

Another criticism concerns the volume of areas surveyed, which varied between the study sites. This influenced the volume of area surveyed by divers, the species documented, abundance estimates, as well as the patterns of social group dynamics. For example, the benthos was not surveyed at HI-389 due to the great depth (125 m), consequently, benthic elasmobranchs were not documented there. Also, large aggregations of some species such as *S. lewini* were spread out in subgroups over the Flower Garden Banks during winter months, based on sea surface and underwater sightings. Yet, divers whose detection range was at most 30 m horizontally were afforded a different perspective of abundance, occasionally encountering subgroups, but rarely documenting aggregations of more than 50 sharks at a time. In contrast, divers surveying the HI-389 platform could survey the entire study area from the center of the platform under similar environmental conditions existing at the Flower Garden Banks. The smaller area surveyed at HI-389 enabled the diver to detect and discern the general aggregation of silky sharks, while also gaining perspective of the subgroup dynamics, which was not necessarily evident when surveying elasmobranchs at mid-shelf or Flower Garden Banks.

In summary, the 'shotgun' approach of data collection generated sightings whose qualities varied, but that were instrumental to achieving the goals set forth in this study. Each survey method used (i.e. aerial, sea surface, and underwater surveys, in combination with the photographic documentation and specimens collected) produced unique and valuable data that yielded conclusive results regarding the seasonal habitat use and social behavior of elasmobranchs occurring at the study sites.

Species Previously Identified in the Literature,

But Not Documented During This Study

Eight species (shortfin mako [*Isurus oxyrhincus*], smooth dogfish [*Mustelus canis*], bull shark [*Carcharhinus leucas*], Atlantic sharpnose shark [*Rhizoprionodon terraenovae*], Atlantic angel shark [*Squatina dumerili*], sawfish [*Pristis* spp.], spreadfin skate [*Dipturus olseni*], and cownose ray [*Rhinoptera bonasus*]) reported in previous accounts of surveys conducted at the study sites were not documented during this study. *Isurus oxyrhincus* was identified from video shot from an unmanned sled towed behind a research vessel over the West Flower Garden Bank (Boland et al. 1983). The video clip of the shark was personally examined using computer imaging software (Adobe's Premiere and PhotoShop) (Figure 36), and found to show a shark with the following useful characteristics: a moderately fusiform body on which the first dorsal fin is of moderately large size with its origin at or behind the trailing edge of the pectoral fins, a rostrum of moderate length, and a caudal fin with a somewhat long lower lobe, estimated at nearly three quarters the length of the upper lobe. However, the size of the lower lobe is apparently misleading, because the camera angle creates an illusion of a greater caudal fin size. Careful examination of the video revealed the relative length of the caudal fin lower lobe to change as the angle and distance increased between shark and camera. Based on the video inspected, the shark is best identified as a *Carcharhinus* spp., possibly *C. obscurus* or *C. perezi*. Both species were observed at the Flower Garden Banks during this study.

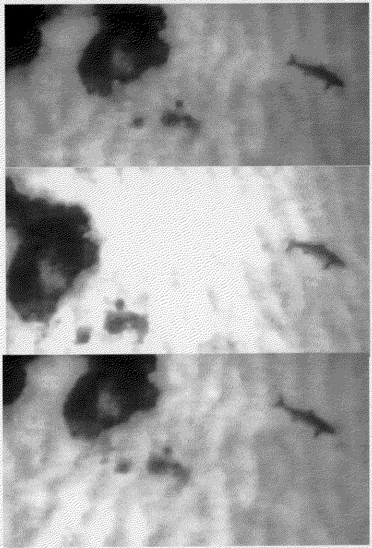

Figure 36. A shark misidentified? Pictures captured from video of a shark previously identified as *Isurus oxyrhincus*. Examination of the video indicates that the animal was misidentified and is likely to be either *Carcharhinus obscurus* or *Carcharhinus perezi*.

Specimens of *Mustelus canus* and *Rhizoprionodon terraenovae* were caught using hook and line equipment in open waters off the East or West Flower Garden Banks during previous surveys (Bright & Cashman 1974, Boland et al. 1983). *Rhizoprionodon terraenovae* was not documented in surveys conducted during this study, probably due to sampling methodology, since underwater surveys were not conducted in open waters and fishing was not undertaken to collect specimens. Nonetheless, underwater photographers recently photographed a shark that is best identified as *Mustelus sinusmexicanus* at Stetson Bank during June of 2000 (Figure 37). Heretofore, some *Mustelus* specimens were collected in the northwestern Gulf of Mexico and identified as *M. canus*, but later determined to be *M. sinusmexicanus* (Heemstra 1997). It is not known if the *Mustelus* sharks previously reported at mid-shelf and Flower Garden Banks (Bright & Cashman 1974, Rezak et al. 1985, Dennis & Bright 1988) were correctly identified, since corroborating evidence is lacking.

The bull shark (*Carcharhinus leucas*) was previously reported at both mid-shelf and shelf edge banks of the region, including the Flower Garden Banks (Boland et al. 1983, Dennis & Bright 1988, Rezak et al. 1985). Some divers reported this species at the sites surveyed during this study. However, I was often present when these sightings were made and observed sharks that I identified as *Carcharhinus plumbeus*. In some cases, these animals were video taped and later confirmed to be *C. plumbeus*. Similarly, interviews with divers reporting *C. leucas* at the study sites communicated characteristics that were best associated to *C. plumbeus* or *C. obscurus*. Many species of *Carcharhinus*, particularly juveniles, are difficult to identify in the field. Because scientists who

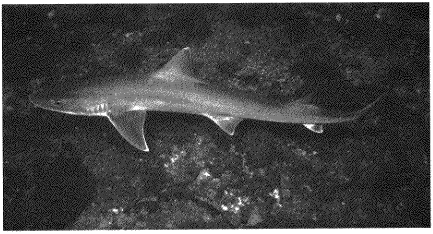

Figure 37. *Mustelus* species. A *Mustelus* sp. shark that was photographed at Stetson Bank in June 2000 by Joyce Burek. Characteristics evident in the picture suggest it may be *Mustelus sinusmexicanus*.

previously reported *C. leucas* at the study sites were not elasmobranch specialists or did not furnish supporting evidence confirming their identifications of *C. leucas* (in the form of photographs or voucher specimens), their records are dubious, as at least four other *Carcharhinus* sp. occur at the study sites. Furthermore, *C. leucas* is common in coastal waters of the northern Gulf of Mexico (Springer 1960, Castro 1983, Hoese & Moore 1977, 1998, Branstetter 1981, McEachran & Fechhelm 1998) landward of the 30 m isobath, but is also known to range into deeper water close to shore down to 152 m (Compagno 1984b). Therefore, I believe that earlier accounts of *C. leucas* were erroneously identified, and the sharks were likely to be one of the *Carcharhinus* spp. identified in this study.

Benthic species such as *Squatina dumerili*, *Pristis* spp., and *Dipturus olseni* were not observed during this study because few surveys were conducted below 40 m in waters where they typically might dwell. Previous surveys using fishing trawls collected specimens of *S. dumerili* and *D. olseni* around the Flower Garden Banks in depths of 100 to 130 m (Boland et al. 1983). Diving surveys at the Flower Garden Banks never exceeded 58 m during this study.

One record of *Rhinoptera bonasus* was documented in a table of fishes identified from video transects conducted over the Flower Garden Banks (Boland et al. 1983). The sighting was made at the West Flower Garden Bank in April 1981, but was not discussed in the narrative concerning sharks and rays. *Rhinoptera bonasus* was not documented during this study, nevertheless, it is conceivable that it might occur at the study sites. It is also possible that the ray identified as *R. bonasus* in the earlier account was misidentified. The video was not available for examination and the record remains undisputed.

Ecological Assemblages

Biogeographic Assemblages

Fishes are sometimes grouped as assemblages based on ecological patterns of biogeographic distribution, seasonal occurrences, trophic dynamics, or social interactions. Such groupings may then be useful for discerning underlying ecological processes affecting distribution. For example, of the fourteen elasmobranch species documented at the study sites in this study, 11 are chiefly neritic, and three are chiefly oceanic. Additionally, 11 % of species reported at mid-shelf banks, 23 % at the Flower Garden Banks, and 50 % occurring at HI-389 are oceanic (Figure 38). Conversely, 89 %, 77 %, and 50 % of species occurring at mid-shelf banks, Flower Garden Banks, or HI-389 respectively, are neritic in nature. The resulting pattern indicates that neritic species constitute a smaller percentage of the elasmobranch assemblages occurring at sites adjacent to the shelf-edge than assemblages occurring at mid-shelf banks. Conversely, oceanic species comprise a greater percentage of the species occurring at sites along the shelf-edge. Such trends are to be expected, but it is worthwhile noting that a greater percentage of species occurring at HI-389 are oceanic in nature relative to those occurring at the nearby Flower Garden Banks. This anomaly may result from the fact that the Flower Garden Banks support elasmobranch species that associate with hard banks and reefs, such as *G. cirratum*, *G. cuvier*, *C. perezi*, *C. plumbeus*, and *D. americana*. Although HI-389 supports reef fauna and is frequented by juvenile

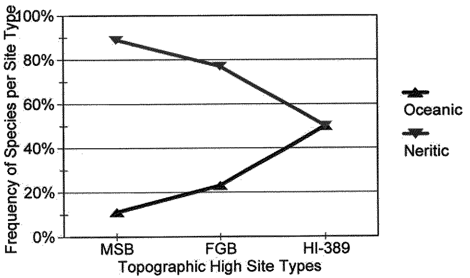

Figure 38. Neritic vs. oceanic elasmobranch occurrences by topographic high types. The frequency of chiefly neritic or oceanic elasmobranch species reported in this study by the topographic high types surveyed. Note the trend that fewer neritic species (relative to oceanic species) make up the elasmobranch assemblages at shelf-edge topographic highs than at mid-shelf topographic highs and vice versa.

C. falciformis (a pelagic-oceanic species), the artificial structure is evidently not suitable habitat for some sharks and rays that associate with natural bottoms.

Temporal Assemblages

Data indicate that there are at least three temporal assemblages of elasmobranchs utilizing the Flower Garden Banks, and that many species exhibit seasonal movements relative to the topographic highs surveyed. From the data gathered, I deduce the following temporal elasmobranch assemblages at the Flower Garden Banks: winter pelagics assemblage, resident assemblage, and summer pelagics assemblage. Mid-shelf banks host slight variations of these assemblages and HI-389 sustains only one species year-round.

The Winter Pelagics Assemblage

Large aggregations of *Sphyrna lewini, Aetobatus narinari*, and several *Carcharhinus* species form at or immigrate to the Flower Garden Banks during Winter 1. Other species such as *Galeocerdo cuvier* and *C. plumbeus* apparently immigrate to these banks during Winter 1, but are not as plentiful as species forming concentrated aggregations. These species persist at the Flower Garden Banks through Winter 2, and depart the banks in March and April. Therefore, *G. cuvier*, *C. plumbeus*, *Carcharhinus* spp., *S. lewini*, and *A. narinari* are the principal species comprising the winter pelagics assemblage at the Flower Garden Banks. While these species are quite evident during the winter seasons, other species such as *Rhincodon typus*, *Mobula hypostoma*, and *M. tarapacana* are notably absent.

The Resident Assemblage

Several species persist throughout the year at the Flower Garden Banks. *Ginglymostoma cirratum*, *Dasyatis americana*, and *Manta birostris* persist at these banks, as may also *C. obscurus* and *C. perezi*, although reliable records are lacking. The coral reefs are likely to offer *G. cirratum* and *D. americana* the necessary abiotic and biotic variables, such as refuge and prey, necessary for their survival.

The majority of *M. birostris* sightings made throughout the year at the Flower Garden Banks were of juvenile and subadult animals, indicating these features function as nurseries. The primary role of a nursery area entails affording juvenile animals increased access to prey organisms, without their expending excessive effort to locate or acquire prey. *Manta birostris*, a filter feeding elasmobranch, may find the Flower Garden Banks and other shelf-edge banks suitable habitat throughout the year because of the banks' physiography, which may stimulate upwelling or benefit from upwelling along the shelf-edge. Such upwelling stimulates plankton productivity that in turn supports small nekton, and in turn may support *M. birostris*. Thus smaller and younger manta rays inhabiting the Flower Garden Banks conceivably may have consistent access to prey that are regarded as ephemeral elsewhere in the marine environment. As such, these juvenile mantas may not expend energy unnecessarily to locate ephemeral prey. Larger and more mature manta rays were observed less often at the Flower Garden Banks, and are presumably more capable and efficient than smaller and younger mantas are at ranging farther between features where plankton and small nektonic prey occur.

The Summer Pelagics Assemblage

During March and April, the winter pelagics assemblage disperses from the Flower Garden Banks, while resident elasmobranch species persist. In May and June, resident species at the Flower Garden Banks are joined by species comprising the summer pelagics assemblage. The abundance of *G. cirratum* and *D. americana* increases, and *C. obscurus* and *C. perezi* are encountered over the coral reefs. Medium-sized aggregations of *M. hypostoma* are common in June, numbering as many as 24 animals per polarized aggregation. June is also the month that *R. typus* may be initially sighted at the Flower Garden Banks. Ergo, three filter-feeding species (*R. typus*, *M. hypostoma*, and *M. birostris*) inhabit the banks during Summer 1. In late-June and July, *M. hypostoma* departs the banks and *M. tarapacana*, another filter-feeder, may appear within a fortnight of mass spawning events that occur in August and/or September. Species comprising the winter pelagics assemblage are not entirely absent from circalittoral waters during summer months, and *S. lewini* and *A. narinari* may occur at the Flower Garden Banks during warmer months, albeit rarely. As such, I do not consider *S. lewini* and *A. narinari* as members of the summer pelagics assemblage. The composition of elasmobranch species inhabiting the banks shifts again in October and November, which yield the last sightings for the year of *R. typus*. November is the earliest month that small aggregations of *A. narinari* appeared at the Flower Garden Banks. By December, the winter pelagics assemblage has resumed residency.

Variations in the Temporal Assemblages at Other Sites Surveyed

Ginglymostoma cirratum, *Carcharhinus* spp., *S. lewini*, and *A. narinari* inhabit mid-shelf banks during the winter seasons, although their densities are not as great as those found at the Flower Garden Banks. In Spring, the small aggregations of *S. lewini* and *A. narinari* depart mid-shelf banks, although solitary individuals are sometimes sighted during warmer months. *Dasyatis americana* becomes evident in Spring, and its occurrence may coincide with the departure of *S. lewini*. During the summer seasons, *R. typus* and *M. birostris* visit the banks to feed, although they do not appear to remain for more than a day at a time. In July, small aggregations of *D. centroura* appear at mid-shelf banks, and observations indicate courtship and mating activity. *Mobula hypostoma* may visit mid-shelf banks during the summer seasons, though data indicate that its occurrence is casual (i.e. species that arrive irregularly in small numbers in areas outside their normal range). In Autumn, *R. typus* and *M. birostris* occurrences at mid-shelf banks decrease. Moreover, *R. typus* and *M. birostris* have yet to be sighted at mid-shelf banks during the winter seasons, and I believe these species inhabit circalittoral or oceanic waters of the northwestern Gulf during colder months.

A true assemblage of elasmobranch species does not likely occur at HI-389, as documented at the mid-shelf and Flower Garden Banks. *Carcharhinus falciformis* inhabit HI-389 during the year. Waters close to the platform are visited by other species during the year, though individuals do not persist there for more than several hours at a time. Deeper surveys at the base of the platform may reveal demersal species that were not detected in this study.

Elasmobranch Movements Relative to Seasonal Changes in Water Temperature

Seasonal changes of water temperature in neritic waters are believed responsible for the shifts of seasonal elasmobranch assemblages at mid-shelf and Flower Garden Banks. During the winter seasons, water temperatures recorded at the Flower Garden Banks are 2-3 °C warmer than those recorded at Stetson Bank (Figure 7). As water temperatures warm in Spring, the winter pelagics depart the Flower Garden Banks and probably migrate toward the coast where mating and nursery areas are located. As waters over the continental shelf continue to warm, the warmest water temperatures recorded at Stetson Bank during Summer 1 closely approach the warmest temperatures recorded at the Flower Garden Banks during the same period. During this period, oceanic-pelagics such as *R. typus*, *M. hypostoma* and *M. birostris* expand their foraging activities to include circalittoral, infralittoral, and eulittoral waters of the region. Species comprising the winter pelagics assemblage remain active in neritic waters, although they are not concentrated in aggregations at mid-shelf or shelf-edge topographic highs. Temperatures reach their annual maxima at mid-shelf and Flower Garden Banks during Summer 2, and it is during this period that *M. tarapacana* may visit the Flower Garden Banks. Additionally, multiple aggregations of *R. typus* form in the vicinity of shelf-edge banks possibly to feed on gametes released during mass spawning events or small nekton. As water temperatures cool over the continental shelf in Autumn, oceanic-pelagics inhabiting neritic waters move seaward to circalittoral and oceanic waters that are warmer than infralittoral and eulittoral waters of the region. Similarly, species such as *G. cuvier*, *C. plumbeus*, *S. lewini*, and *A. narinari* that inhabit eulittoral and infralittoral waters of the northwestern Gulf during summer months ostensibly immigrate to the Flower Garden Banks and possibly other shelf-edge banks, arriving during Winter 1. Their initial occurrence at the Flower Garden Banks is well synchronized with decreasing water temperatures in eulittoral and infralittoral waters along the the Texas-Louisiana coasts as cold fronts cool the region.

Although data show that *S. lewini* and *A. narinari* occur in large aggregations at the Flower Garden Banks during the winter seasons, it is not known whether *S. lewini* and *A. narinari* form aggregations prior to or upon arriving at the banks. I suspect that both species assemble to migrate as waters cool near to the coast, migrate seaward, and consequently form larger aggregations as multiple groups congregate at the banks. For instance, I observed an aggregation of approximately 50 *S. lewini* swimming about an offshore petroleum platform cut off 25 m below the sea surface in July 1999. These sharks were estimated to be approximately 2 m TL. Additionally, anecdotal accounts by recreational fishermen and boaters have reported schools of *A. narinari* along the Texas coast during summer months. Since sightings indicate that *S. lewini* and *A. narinari* aggregate during summer months in eulittoral and infralittoral waters of the region, I expect them to migrate in aggregations, and upon arriving at the Flower Garden Banks in Winter 1, form larger aggregations with other conspecifics that immigrated to the banks. What is not clear is when and from where these animals depart, or if multi-species aggregations form and migrate together, since multi-species schooling was observed at the banks.

Data also suggest that demersal species at the banks such as *G. cirratum* and *D.*

americana adjust their behavior with seasonal changes in water temperature. Observers commonly sighted *G. cirratum* and *D. americana* on the reef crests of mid-shelf and Flower Garden Banks during warmer months, but rarely sighted them during colder months. Sightings indicate that *G. cirratum* and *D. americana* either immigrate from the reefs or seek refuge amidst the coral colonies where they are difficult for divers to locate. I suspect the latter to be the case. Emigration from the reefs requires that *G. cirratum* and *D. americana* traverse relatively deep waters, which is uncharacteristic of both species. Furthermore, those *G. cirratum* and *D. americana* departing the reefs would be exposed to predators such as *G. cuvier* and *S. lewini*, since the surrounding landscape of the continental shelf offers little relief for refuging. Finally, where would *G. cirratum* and *D. americana* immigrate to for colder months? Both species are not regarded as wide-ranging, but instead are languid. As both species were detected at mid-shelf and Flower Garden Banks during Winter 2, it is reasonable to deduce, therefore, that *G. cirratum* and *D. americana* do not depart the banks during winter months, but instead seek sanctuary in the coral reef from predators such as *G. cuvier* and *S. lewini*. In Spring, as water temperatures warm and predatory sharks depart the banks, *G. cirratum* and *D. americana* become more visible again, particularly so during the summer seasons when they are often found exposed on corals or in sand patches.

Topographic Highs as Habitat for Elasmobranchs

Certain topographic highs reported in the literature are frequented by some wide-ranging elasmobranchs. For example, Saint Paul's Rocks located on the mid-Atlantic ridge near the equator supports dense populations of *C. falciformis* and *Carcharhinus galapagensis* (Galapagos shark), and *R. typus*, *I. oxyrhincus* (shortfin mako), and *Sphyrna* spp. (hammerhead sharks) sometimes occur (Edwards & Lubbock 1982). Stevens (1984) reported on the ecology of ten shark species inhabiting the waters of Aldabra Atoll, in the Indian Ocean. Moreover, the behavior of *S. lewini* schooling at seamounts in the Gulf of California is well studied (Klimley & Nelson 1981, 1984, Klimley 1982, 1985, 1987, 1993, Klimley et al. 1988). Other studies show that the lemon shark (*Negaprion brevirostris*) utilizes the shallow water in North Sound, Bimini, Bahamas as nursery habitat (Morrissey & Gruber 1993a,b), and that adult gray reef sharks (*Carcharhinus amblyrhynchos*) aggregate at the Marshall Islands and Johnston Atoll in the Pacific Ocean. Secondly, a cursory examination of recreational diving literature will yield numerous sites such as the Turks and Caicos Islands, Bay Islands, Cocos Islands, Galapagos Islands, Hawaiian Islands, Yap, Japan, Seychelles, and Maldives, where elasmobranchs predictably occur and aggregate, sometimes in appreciable numbers. Less known are underwater topographic highs such as the Flower Garden Banks, or the Protea Banks and Aliwal Shoal off South Africa, where elasmobranchs aggregate. Nevertheless, a comprehensive hypothesis relating elasmobranchs with topographic highs has not been advanced to date.

Data presented in this study show that some elasmobranch species utilize topographic highs as habitat. Some species persist as residents, other species are seasonal occupants. Data also show that the species utilizing the sites 1) are socially segregated by sex or life stage (neonate, juvenile, subadult, adult) or both, 2) utilize other biotopes during life stages not observed at the study sites, and 3) are therefore wide-ranging.

How are topographic highs utilized as habitat by elasmobranchs? Based on the elasmobranch habitat model concept advanced by Springer (1940, 1967) and others (Bass et al.1973, Bass 1975, Branstetter 1990, Castro 1993, and Simpfendorfer & Milward 1993), topographic highs surveyed in this study function as seasonal feeding habitat, nursery habitat, and as mating habitat, and the purpose varies among elasmobranch species.

Data also indicate habitat selection by some elasmobranchs among the three topographic high types. For example, *C. falciformis* aggregate at HI-389, but was rarely detected at the nearby East Flower Garden Bank. Likewise, the Flower Garden Banks are utilized by juvenile *C. obscurus*, *C. perezi*, and *M. birostris*, species that were either not detected or observed to persist at other topographic high types. Data also indicate that *M. hypostoma* utilizes the Flower Garden Banks and not mid-shelf banks or HI-389. Similarly, data indicate that mid-shelf banks function as a mating area to *D. centroura*, a species not detected at the Flower Garden Banks. Most elasmobranch species documented in this study are wide-ranging and are capable of traversing the Gulf of Mexico, based on species patterns of distribution and tagging studies discussed in the species accounts. As the distances between the topographic high types surveyed in this study range from 1.5 to 154 km apart, they are well within the ranging ability of the elasmobranchs documented. Because some elasmobranchs were found utilizing one topographic high type and not another, there is strong evidence for habitat selection between mid-shelf banks, Flower Garden Banks, and HI-389 by some species.

Elasmobranch habitat use of topographic highs appears to be influenced by the orographic characteristics of the different topographic high types. For instance, data show that the large aggregations of juvenile silky sharks utilize HI-389 as a core area, but not the nearby East Flower Garden Bank. Orographic characteristics differ greatly between HI-389 (an artificial shelf-edge topographic high) and the East Flower Garden Bank (a natural shelf-edge topographic high). The platform represents a skeletal framework that juvenile silky sharks congregate about or may seek refuge within the structure from larger predatory shark species. Such artificial topographic highs located on the continental shelf-edge or slope are likely to benefit some epipelagic-oceanic species during juvenile stages that are more susceptible to predation than adult stages. Conversely, natural topographic highs such as the Flower Garden Banks function as nursery habitat to *C. obscurus* and *C. perezi*, and orographic characteristics are truly different than those of HI-389. *Carcharhinus obscurus* and *C. perezi* are pelagic species that associate with some seafloor features, and juveniles are subject to predation by larger predatory sharks. My observations of juvenile *C. obscurus* and *C. perezi* at the Flower Garden Banks revealed juvenile sharks furtively moving along the reef crest, escarpment, and sand patches. Such behavior may make juvenile sharks difficult to detect by larger predatory sharks and afford them an opportunity to escape predators by seeking refuge amidst the coral reef. Consequently, topographic highs such as HI-389 are not likely to have suitable characteristics to meet the habitat requirements of juvenile *C. obscurus* or *C. perezi.*

Area and relief also appear to be orographic factors influencing the abundance of elasmobranchs inhabiting a topographic high. Species employing a refuging central-position social system, such as *S. lewini* and *A. narinari*, were observed in significantly fewer numbers at mid-shelf banks than at the Flower Garden Banks during the winter seasons. A fundamental premise of the refuging concept is that as a population of individuals occupying a core area increases, so does the area required to provide resources (Hamilton & Watt 1970). The larger area and relief of the Flower Garden Banks relative to that of the mid-shelf banks surveyed in this study support larger aggregations of *S. lewini* and *A. narinari.*

Physiography also influences elasmobranch habitat use of topographic highs. For example, data show that topographic highs located in eulittoral or infralittoral waters such as Stetson and Sonnier Banks, function as habitat to *D. centroura*, a species that was not detected at shelf-edge topographic highs. Additionally, shelf-edge banks such as the Flower Garden Banks, appear to concentrate larger aggregations of elasmobranchs in winter than do mid-shelf banks. It is not clear if this phenomenon is related to the size of the topographic highs (each Flower Garden Bank is larger than Stetson or Sonnier Banks) or due to the close proximity of the Flower Garden Banks to the shelf-edge, where water temperatures are 2-3 °C warmer than at mid-shelf banks in winter months. Both size and proximity are likely to be important factors. Besides, the proximity of the

Flower Garden Banks to the shelf-edge is also likely to positively influence the diversity and richness of species encountered there relative to the mid-shelf banks, since the shelf-edge represents an ecotone between oceanic and neritic assemblages.

The Elasmobranch-Topographic High Habitat Association Postulate

Why are topographic highs utilized as habitat by wide-ranging elasmobranchs? Several factors appear to contribute to this phenomenon. First, topographic highs such as banks, reefs, offshore artificial structures, seamounts, and small islands provide significant structural and positive relief in an otherwise homogeneous three-dimensional landscape typical of the continental shelf or oceanic province. Upper portions of these features may occur within the photic zone and provide suitable substrate on which benthic communities form, such as the coral reefs of the Flower Garden Banks. Substrate with access to sunlight in the underwater environment can therefore lead to increased productivity, diversity, and food web complexity. Sessile communities forming on the substrate subsequently support assemblages of demersal invertebrates and fishes that may establish stable populations at the topographic highs. Topographic highs and their resident members thereby congregate and organize resources in the region otherwise not supported or organized on the adjacent seafloor. Many elasmobranchs can benefit from the aggregated prey and refugia (particularly for juvenile animals) these resources impart relative to the surrounding landscape, consequently increasing the fitness of individual sharks and rays inhabiting topographic highs. An association is established when animals select a topographic high in place of other biotopes in the region, as demonstrated through habitat use (occurrence, foraging, parturition, mating, etc.).

Another factor possibly contributing to the phenomenon of elasmobranchs associating with topographic highs involves their social systems. Data presented in this study and by others (i.e. Klimley & Nelson 1984, McKibben & Nelson 1986, Economakis & Lobel 1998) show that some elasmobranch species maintain a refuging central-position social system (Hamilton & Watt 1970). A refuging central-position social system involves the use of a core area from which rhythmic radial dispersal takes place, but which is occupied by individuals during a portion of the rhythmic cycle (e.g. the diel cycle). As the population of individuals occupying the core area increases, so does the area required to provide resources. An advantage is gained by animals aggregating in a central area if the 'advantage' (often in the form of resources) is not available to nomadic animals (Hamilton & Watt 1970). Given that there are few fixed features in infralittoral, circalittoral, or oceanic waters for wide-ranging animals to orient to, assemble at, or consistently locate prey at, topographic highs pose an advantage to some elasmobranchs that would otherwise roam the landscape in search of randomly distributed mates, prey, navigation aids, and refugia.

An important component of the habitat association postulate is the degree of association between elasmobranchs and topographic highs. Elasmobranch species need be evaluated for 1) an association with topographic highs, and 2) the degree to which they associate with topographic highs. Both qualitative and quantitative measures could be developed to assess further associations and degrees of association. For example, a qualitative assessment of elasmobranch-topographic high associations is modeled in

Table 26. The model is based on the distribution of elasmobranchs across a marine landscape that includes a topographic high. Possible distributions include elasmobranchs chiefly concentrated at the topographic high, elasmobranchs distributed evenly or randomly across the landscape, including at the topographic high, and elasmobranchs that are dispersed across the landscape, but avoid the topographic high. A temporal component needs to be factored into the model, as evident from the data presented. Thus, species should be distinguished as occurring seasonally across the landscape or persisting within the landscape throughout the year. Therefore, the model comprises the following groups: Type I species chiefly concentrating and persisting throughout the year at topographic highs, Type II species chiefly concentrating seasonally at topographic highs, Type III species randomly distributed across the landscape throughout the year, including at topographic highs, Type IV species seasonally occurring within the landscape, and at topographic highs, Type V species distributed across the landscape throughout the year, and avoiding topographic highs, and Type VI species seasonally occurring across the landscape and avoiding topographic highs. Elasmobranch species characterized as Types I or II exhibit strong associations with topographic highs. Examples of Type I and II species encountered at the Flower Garden Banks during this study include *G. cirratum*, *C. perezi*, *D. americana*, *M. birostris*, *S. lewini*, *A. narinari*, *C. plumbeus*, and *M. hypostoma*. Types III and IV represent elasmobranchs with moderate to weak associations for topographic highs. These animals do not necessarily orient to topographic highs, but instead to larger scale features such as regions of the neritic or oceanic provinces (e.g. infralittoral or circalittoral zones). Elasmobranchs

Table 26. Qualitative model for assessing the degree of association between elasmobranchs and topographic highs. The topographic high and landscape should each be delimited. Sharks and rays whose distributions and occurrences are best described as Types I and II exhibit a strong association with the topographic high. Types III and IV animals exhibit moderate to weak associations, while species not found at the topographic high, but are distributed within the landscape show no association with the topographic high. Species listed in the categories of this model are examples based on surveys conducted at the Flower Garden Banks.

Degree of Association:	strong association	moderate to weak association	no association
	Spatial Distribution and Occurrence		
Topographic High Type: Flower Garden Banks	species concentrated *chiefly* about a topographic high in the landscape	species distributed across the landscape, and occurring at the topographic high	species distributed across the landscape, but not occurring at the topographic high
Temporal Distribution and Occurrence: species persisting throughout the year in the landscape	Type I *G. cirratum* *C. perezi* *D. americana* *M. birostris*	Type III *C. obscurus* *M. birostris*	Type V not surveyed for in study
Temporal Distribution and Occurrence: species seasonally occurring in the landscape	Type II *S. lewini* *C. plumbeus* *A. narinari* *M. hypostoma*	Type IV *R. typus* *G. cuvier* *M. tarapacana*	Type VI not surveyed for in study

reported at the Flower Garden Banks and characterized by Types III and IV include *C. obscurus*, *D. americana*, *M. birostris*, *R. typus*, *G. cuvier*, *C. plumbeus* and *M. tarapacana*. Lastly, Types V and VI represent elasmobranch species that avoid topographic highs in the landscape. Animals demonstrating such habitat avoidance show no association with topographic highs; since open waters beyond the study sites were not surveyed during this study, none of the elasmobranchs reported at the Flower Garden Banks are considered as Type V or VI species.

It is important to note that the characterization of species into the various Types is not mutually exclusive. This is possible because data gathered in this study show that one life stage of a species may associate strongly with a topographic high type, but later during another life stage, the same species may associate weakly with the same topographic high type. This is conveniently illustrated by the occurrence of *M. birostris* at the Flower Garden Banks. Juvenile *M. birostris* inhabit the banks throughout the year, however, adult *M. birostris* are rarely encountered at the banks. Additionally, the spatial scales at which the landscape is delimited will influence the characterization of species within the model.

It is reasonable to expect species occurring at the study sites to be distributed across the landscape and not concentrated around topographic highs. Such interpretation of the data is justified, demonstrating the need for additional surveys both at topographic highs and in open waters of the landscape. Yet, many of the species predictably occurred at the topographic highs surveyed (e.g. *G. cirratum*, *M. tarapacana*, and *M. birostris*), often in considerable numbers (e.g. *S. lewini*, *A. narinari*, and *M. hypostoma*). Whereas many elasmobranchs are known to socially segregate into discrete habitat areas often associated with specific biotypic communities, it is reasonable to conclude that elasmobranchs consistently occurring at topographic highs (Type I and II species) in appreciable numbers actually do concentrate chiefly about topographic highs rather than distributing evenly about the landscape. It is also credible that certain species may associate with topographic highs, but do not occupy the crest of the topographic high. For example, the *R. terraenovae* and *C. falciformis* specimens collected in the past and present studies were all taken in waters adjacent to the coral reef caps of the Flower Garden Banks. There may be various zones of occurrence, not unlike a target pattern of concentric rings, that elasmobranch species inhabit about topographic highs.

Conservation Issues and Future Research Initiatives

As people become more knowledgeable that human activities alter the web of life in the worlds' seas, biologists and resource managers are challenged to find solutions to problems arising from these activities. One of the first steps necessary for mitigating the negative impacts of human activities in the seas involves the identification of essential habitats for each impacted species. The 1996 amendments to the Magnuson-Stevens Fishery Conservation and Management Act (P. L. 104-297) set forth a new mandate to federal agencies, to identify and protect important marine and anadromous fish habitat. To that end, Essential Fish Habitat is defined in the Magnuson-Stevens Fishery Conservation and Management Act as '...those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity.' Identifying such habitats is a chore of mammoth proportions, given the minute information presently available concerning most marine and anadromous fishes. The Final Fishery Management Plan for Atlantic Tuna, Swordfish, and Sharks (NMFS 1999) states:

> Defining the habitat of sharks found in the temperate zone is difficult because most species are highly mobile or migratory, utilizing diverse habitats in apparently non-specific or poorly understood ways. Most migratory sharks traverse a variety of habitats in their movements. Generally, the migrations of sharks are poorly understood, and can be defined only in very broad terms. In addition, the different life stages of a given shark species are often found in different habitats. In most cases the neonates and juveniles occupy different habitats than the adults....There is little published information correlating life stages and migratory movements, and there are few descriptions correlating shark habitat use to physical habitat characteristics....Within the constraints of current knowledge, any generalizations on the habitat of a given coastal shark species can be made only in very broad terms. Given the lack of precise data to define the habitat characteristics of sharks in a specific and consistent manner, a more practical approach may be to define the habitat by geographic location instead of by the physical parameters within the location.

These statements also hold true for oceanic sharks, as well as all ray species. The document lists Essential Fish Habitat for certain shark species for which there is available data. The document also notes that many of the species listed display complex habitat use that varies with ontogenetic development. Because vital information concerning the habitat use of different life stages for many shark species are not known, the document recurrently describes the species-specific habitats as thus: 'At this time, available information is insufficient for the identification of Essential Fish Habitat for this life stage.' Consequently, the only shark species that the document identified Habitat Areas of Particular Concern for is the sandbar shark (*Carcharhinus plumbeus*). (Habitat Areas of Particular Concern are sub-areas of Essential Fish Habitat which are rare, particularly susceptible to human-induced degradation, especially ecologically important, or located in an environmentally stressed area.)

Data presented in this study show that different topographic high types function as habitat to some elasmobranch species of different life stages and for different purposes. Marine areas in the Gulf of Mexico such as the water column, live bottoms, coral and artificial reefs, geologic and continental shelf features, have been listed as Essential Fish Habitat in the region's Fishery Management Plan. Therefore, features such as the Stetson, Sonnier, and the Flower Garden Banks are regarded as Essential Fish Habitat, and the Flower Garden Banks National Marine Sanctuary has also been classified as a Habitat Area of Particular Concern. However, these sites attained indemnity as a result of their classification as essential habitat for coral reef fishes, not for elasmobranchs. If the conservation/management plans undertaken to safeguard some elasmobranch species are to succeed, it is essential that humankind recognize that topographic highs function as essential habitat areas to some life stages of diverse elasmobranch species. This is particularly true since topographic highs are rare, particularly susceptible to human-induced degradation, ecologically important, and sometimes located in an environmentally stressed area. It is for these reasons that fishery managers should distinguish topographic highs as Essential Fish Habitat for some elasmobranch species. Moreover, because topographic highs represent habitats with specific geographic locations, they can be protected as Habitat Areas of Particular Concern for some elasmobranch species. Such designation should permit topographic highs to be gingerly exploited and avoid abuse by humankind, and concurrently safeguarding essential habitat to some elasmobranch species.

Human activities that could negatively impact elasmobranch habitat use of the study sites include fishing, offshore oil and gas exploration and production operations, maritime traffic and anchoring, eco-tourism, pollution, coastal land use, and fresh water inflow into the Gulf of Mexico. These activities pose direct or indirect hazards to elasmobranchs associating with the study sites. Because elasmobranch species that predictably utilize the study sites are wide-ranging and migratory, they may directly depart or disassociate from a site if disturbed. For this reason, elasmobranch species associating with topographic highs in the northwestern Gulf of Mexico may be valuable indicator species of ecosystem health and disturbance vectors for the Gulf of Mexico and adjacent large marine ecosystems which are utilized by these species.

As this study demonstrates, topographic highs are auspicious sites for locating and studying some wide-ranging and highly migratory elasmobranch species. Ichthyologists aspiring to conduct studies of some wide-ranging and migratory species should consider initiating studies at topographic highs that concentrate sharks and rays, thus making it possible to study what are otherwise difficult-to-study fishes. The next phase of recommended elasmobranch studies at the sites surveyed in this study include: biotelemetry studies to ascertain the short and long term movements of elasmobranchs to other habitat areas, surveys of the deep microhabitats and adjacent waters, genetic studies, photo-identification studies of individual animals, and behavioral studies regarding intra- and interspecific sociality and social systems.

Future research concerning the elasmobranch-topographic high habitat association postulate is needed. A universal classification scheme for topographic high types need be developed based on a variety of characteristics that include physiography, orography, and hydrographic processes. Additional studies need be conducted to ascertain what topographic high types are utilized by different elasmobranch species and life history stages. Attention should be given to distinguishing the function that different topographic high types serve to wide-ranging sharks and rays (e.g. nursery habitat), and the degree to which different species associate with different topographic high types. Also, certain topographic highs may not be utilized by elasmobranch species in the same manner that other topographic highs are. For instance, seamounts, hard banks, and reefs (underwater topographic highs) differ from small islands (e.g. Johnston Atoll, Pacific Ocean) which differ from large islands (New Zealand). At what size do the characteristics, patterns and processes specific to a larger topographic high type mimic that of a continental land mass and thus alter elasmobranch habitat use relative to that exhibited at smaller topographic highs? Do topographic highs need be limited to prominences that do not break the sea surface? Further investigation is deserved to examine elasmobranch habitat use of artificial topographic highs such as platforms placed on the continental shelf, slope, and rise (Hueter & Childs 2001).

Additional studies elsewhere may lend scientific support to the postulate and future studies of topographic high associations should not be limited to elasmobranch species. Supporting studies of various clades (i.e. sea turtles, marine birds, some wide-ranging teleost fishes such as scombrids or carangids) may demonstrate that a variety of wide-ranging or migratory species associate with topographic highs. Such studies may lead to a comprehensive wide-ranging marine species-topographic high habitat association axiom.

SUMMARY

1. Topographic highs are prominences that rise from the seafloor and provide significant structural and positive relief in a surrounding homogeneous landscape. Such natural and artificial features concentrate or facilitate the organization of resources otherwise not organized in the landscape and provide habitats to a wide spectrum of marine life. They are analogous to oceanic islands or continental landscape patches that break up homogeneous landscapes.
2. Data presented in this study show that some elasmobranch species inhabit or aggregate at topographic highs in the northwestern Gulf of Mexico, making it possible to study what are otherwise difficult-to-locate animals.
3. Data show that elasmobranch species may be residents of a topographic high community throughout the year, or inhabit it during certain seasons. Elasmobranch species that form seasonal assemblages then interact as temporary members of a topographic high community.
4. Topographic highs are utilized as nursery, feeding, and mating habitats, but that function is species-specific.
5. The behavior and sociality of elasmobranch species inhabiting topographic highs varies between habitats or localities (e.g. nurse sharks of the Flower Garden Banks vs. Florida Keys, manta rays of the Flower Garden Banks vs. Yap, Micronesia).
6. Orographic, physiographic, and hydrographic characteristics specific to each topographic high, juxtaposed with the historic geology and biogeography of the

region, influence the composition, habitat use, and movements of elasmobranchs associating with each topographic high.

7. A prime ingredient in the conservation of exploited fauna is the identification and protection of habitats essential for the completion of a species' life cycle. Data reported in this study demonstrate that topographic highs in the northwestern Gulf of Mexico are utilized by different life stages of different species, demonstrating these features are essential fish habitats to some elasmobranch species. Such features should be designated as Habitat Areas of Particular Concern for species known to utilize topographic highs.

8. Topographic highs are auspicious sites at which to initiate studies of wide-ranging and highly migratory elasmobranch species, given the subjects of interest associate with certain topographic high types. Scientists seeking to study wide-ranging elasmobranchs ought consider initiating studies at topographic highs to gain further insight and data regarding their intended subjects.

9. The elasmobranch-topographic high habitat association postulate is offered as a comprehensive explanation addressing the phenomenon that mixed species of wide-ranging or migratory sharks and rays inhabit and/or concentrate at various topographic highs around the world. These species utilize topographic highs as habitat during certain life stages for different purposes.

REFERENCES CITED

Applegate, S. P., F. Soltelo-Macias & L. Espinosa-Arrubarrena. 1993. An overview of Mexican shark fisheries, with suggestions for shark conservation in Mexico. pp. 31-37. *In*: S. Branstetter (ed.) Conservation Biology of Elasmobranchs. NOAA Tech. Rep. NMFS 115.

Bane, G. W. Jr. 1966. Observations of the silky shark, *Carcharhinus falciformis*, in the Gulf of Guinea. Copeia 1966:354-356.

Bass, A. J. 1978. Problems in studies of sharks in the southwest Indian Ocean. pp. 545-594. *In*: E. S. Hodgson & R. F. Mathewson (eds.) Sensory Biology of Sharks, Skates and Rays. Office of Naval Research. Dept. of the Navy, Arlington, VA.

Bass, A. J., J. D. D'Aubrey & N. Kistnasamy. 1973. Sharks of the east coast of southern Africa I. The genus *Carcharhinus* (Carcharhinidae). Invest. Rep. Oceanogr. Res. Inst. 33:1-168.

Baughman, J. L. 1950. Random notes on Texas fishes. Tex. J. Sci. 2:117-138.

Baughman, J. L. 1955. The oviparity of the whale shark, *Rhineodon typus*, with records of this and other fishes in Texas waters. Copeia 1955:54-55.

Baughman, J. L. & S. Springer. 1950. Biological and economic notes on the sharks of the Gulf of Mexico, with especial reference to those of Texas and with a key for their identification. Amer. Midland. Nat. 44:96-152.

Beebe, W. 1941. External characters of six embryo nurse sharks, *Ginglymostoma cirratum* (Gmelin). Zoologica 26(4):9-12.

Bigelow, H. B. & W. C. Schroeder. 1948. Fishes of the Western North Atlantic. Pt. 1. Lancelets, Cyclostomes and Sharks. Mem. Sears Fdn. Mar. Res., New Haven, CT. 576 pp.

Bigelow, H. B. & W. C. Schroeder. 1953. Fishes of the Western North Atlantic. Pt. 2. Sawfishes, Guitarfishes, Skates and Rays. Mem. Sears Fdn. Mar. Res., New Haven, CT. 588 pp.

Biggs, D. C., R. A. Zimmerman, R. Gasca, E. Suárez-Morales, I. Castellanos & R. R. Leben. 1997. Note on plankton and cold-core rings in the Gulf of Mexico. Fish. Bull. 95:369-375.

Böhlke, J. E. & C. C. G. Chaplin. 1993. Fishes of the Bahamas and Adjacent Tropical Waters. Univ. of Texas Press, Austin. 771 pp.

Boland, G. S., B. J. Gallaway, J. S. Baker & G. S. Lewbel. 1983. Ecological Effects of Energy Development on Reef Fish of the Flower Garden Banks. National Marine Fisheries Service, Contract No. NA80-GA-C-00057, Galveston, TX. 466 pp.

Bonfil, R., D. de Anda, & R. A. Mena. 1990. Shark fisheries in Mexico: the case of Yucatan as an example. pp. 427-441. *In*: H. L. Pratt Jr., S. H. Gruber & T. Taniuchi (eds.) Elasmobranchs as Living Resources. NOAA Tech. Rep. NMFS 90.

Bonfil, R., R. Mena & D. de Anda. 1993. Biological parameters of commercially exploited silky sharks, *Carcharhinus falciformis*, from Campeche Bank, Mexico. U.S. Natl. Mar. Fish. Serv., NOAA Tech. Rep. 115:73-86.

Brander, K. 1981. Disappearance of common skate *Raia batis* from Irish Sea. Nature 290:48-49.

Branstetter, S. 1981. Biological notes on the sharks of the north central Gulf of Mexico. Contributions Mar. Sci. 24:13-34.

Branstetter, S. 1987a. Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 1987:291-300.

Branstetter, S. 1987b. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Env. Biol. Fish. 19:161-173.

Branstetter, S. 1990. Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. pp.17-28. *In*: H. L. Pratt Jr., S. H. Gruber & T. Taniuchi (eds.) Elasmobranchs as Living Resources. NOAA Tech. Rep. NMFS 90.

Branstetter, S. & J. D. McEachran. 1986. Age and growth of four Carcharhinid sharks common to the Gulf of Mexico: a summary paper. pp. 361-371. *In*: T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura (eds.) Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyol. Soc. Jpn., Tokyo.

Branstetter, S., J. A. Musick, & J. A. Colvocoresses. 1987. A comparison of the age and growth of the tiger shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern Gulf of Mexico. Fish. Bull. 85:269-279.

Breuer, J. P. 1954. The littlest biggest fish. Texas Game Fish. 12(2):4-5, 29.

Bright, T. J. & C. W. Cashman. 1974. Fishes. pp. 340-374. *In*: T. J. Bright & L. H. Pequegnat (eds.) Biota of the West Flower Garden Bank. Gulf Publ., Houston.

Bright, T. J. & L. H. Pequegnat. 1974. Biota of the West Flower Garden Bank. Gulf Publ., Houston. 435 pp.

Bright, T. J., W. Pequegnat, R. DuBois & D. Gettleson. 1974. Baseline survey of Stetson Bank, Gulf of Mexico, Biology. Dept. of Oceanography, Texas A&M Univ. 38 pp.

Bright, T. J., P. A. LaRock, R. D. Lauer & J. M. Brooks. 1980. A brine seep at the East Flower Garden Bank, northwestern Gulf of Mexico. Int. Rev. Ges. Hydrobiol. 65:535-549.

Bright, T. J., G. P. Kraemer, G. A. Minnery & S. T. Viada. 1984. Hermatypes of the Flower Garden Banks, northwestern Gulf of Mexico: a comparison to other western Atlantic reefs. Bull. Mar. Sci. 34:461-476.

Bright, T. J., S. R. Gittings & R. Zingula. 1991. Occurrence of Atlantic reef corals on offshore platforms in the northwestern Gulf of Mexico. Northeast Gulf Sci. 12:55-60.

Brockman, F. W. 1975. An observation on mating behavior of the southern stingray, *Dasyatis americana*. Copeia 1975:784-785.

Bullis, H. R. Jr., & P. Struhsaker. 1961. Life history notes on the roughtail stingray, *Dasyatis centroura* (Mitchell). Copeia 1961:232-234.

Campbell, R. A. & T. A. Monroe. 1974. Discovery of the lesser devil ray, *Mobula hypostoma*, in southern New England waters. Chesapeake Sci. 15(2):114-115.

Capapé, C. 1993. New data on the reproductive biology of the thorny stingray, *Dasyatis centroura* (Pisces: Dasyatidae) from off the Tunisian coasts. Env. Biol. Fish. 38:73-80.

Carlson, J. K., 1999. Occurrence of neonate and juvenile sandbar sharks, *Carcharhinus plumbeus*, in the northeastern Gulf of Mexico. Fish. Bull. 97:387-391.

Carlson, J. K., & J. H. Brusher. 1999. An index of abundance for coastal species of juvenile sharks from the northeast Gulf of Mexico. Marine Fisheries Rev. 61:37-45.

Carrier, J. C. 1985a. Nurse shark of Big Pine Key: comparative success of three types of external tags. Florida Sci. 48:146-154.

Carrier, J. C. 1985b. Nurse sharks (*Ginglymostoma cirratum*) of Big Pine Key, Florida (U.S.A.): an investigation of growth and movement, and a comparison of the success of several types of external tags. pp. 655-661. *In*: C. Gabrie & V. Harmelin (eds.). Proc. 5th Int. Coral Reef Congress, Vol. 6. 27 May-1 June, 1985. Tahiti, French Polynesia. Antenne Museum-EPHE, Moorea, French Polynesia.

Carrier, J. C. 1991. Growth and aging: life history of the nurse shark. pp. 68-69. In: S. H. Gruber (ed.) Discovering Sharks. American Littoral Society. Highlands, NJ.

Carrier, J. C. & C. A. Luer. 1990. Growth rates in the nurse shark, *Ginglymostoma cirratum*. Copeia 1990:686-692.

Carrier, J. C., H. L. Pratt Jr. & L. K. Martin. 1994. Group reproductive behaviors in free-living nurse sharks. Copeia 1994:646-656.

Carrier, J. C. & H. L. Pratt. 1998. Habitat management and closure of a nurse shark breeding and nursery ground. Fish. Res. 39:209-213.

Casey, J. & R. Myers. 1998. Near extinction of a large, widely distributed fish. Science 281:690-692.

Cashman, C. W. 1973. Contributions to the ichthyofaunas of the West Flower Garden Reef and other reef sites in the Gulf of Mexico and western Caribbean. PhD. Dissertation. Texas A&M Univ., Dept. of Oceanography, College Station, TX.

Castillo-Géniz, J. L., J. F. Márquez-Farias, M. C. Rodriguez de la Cruz, E. Cortéz, & A. Cid del Prado. 1998. The Mexican artisanal shark fishery in the Gulf of Mexico: towards a regulated fishery. Mar. Freshwater Res. 49:611-620.

Castro, J. I. 1983. The Sharks of North American Waters. Texas A&M Univ. Press, College Station, TX. 180 pp.

Castro, J. I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Env. Biol. Fish. 38:37-48.

Castro, J. I. 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. Env. Biol. Fish. 58:1-22.

Chang, W-B., M-Y. Leu & L-S. Fang. 1997. Embryos of the whale shark, *Rhincodon typus*, early growth and size distribution. Copeia 1997:444-446.

Childs, J. 1997. Range extension of *Mobula tarapacana* into the northwestern Gulf of Mexico. Gulf Mexico Sci. 15:39-40.

Childs, J. 1998. Avian diversity and habitat use within the Flower Garden Banks National Marine Sanctuary. Gulf Mexico Sci. 16:208-225.

Childs, J. 1999. Are we communicating elasmobranch distributions effectively? American Elasmobranch Society Quarterly Newsletter, Winter 2000.

Childs, J. 2000. Sharks and rays of Stetson and the Flower Garden Banks. pp. 183-193. *In*: McKay, M. & J. Nides. 2000. Proceedings: Eighteenth Annual Gulf of Mexico Information Transfer Meeting, December 1998. U. S. Dept. of Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS 2000-030.

Childs, J. N., E. L. Hickerson & K. J. P. Deslarzes. 1996. Spatial and temporal resource use of the Flower Garden Banks by charismatic megafauna. pp. 74-79. *In*: Proceedings: Fifteenth Information Transfer Meeting, December 1995. OCS Study MMS 96-0056. U.S. Dept. of Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA.

Childs, J., C. Burks, K. Mullin, & J. Hewitt III. Whale shark, *Rhincodon typus*, occurrences in the northern Gulf of Mexico. Fish. Bull. In Review.

Clark, E. 1963. Massive aggregations of large rays and sharks in and near Sarasota, Florida. Zoologica 48:61-64.

Clark, E. 1992. Whale sharks: gentle monsters of the deep. Natl. Geogr. December 123-138.

Clark, E. & K. von Schmidt. 1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

Clark, E. & E. Kristoff. 1990. Deep-sea observed from submersibles off Bermuda, Grand Cayman, and Freeport, Bahamas. pp. 269-284. *In*: H. L. Pratt Jr., S. H. Gruber & T. Taniuchi (eds.) Elasmobranchs as Living Resources. NOAA Tech. Rep. NMFS 90.

Clark, E. & D. R. Nelson. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. Env. Biol. Fish. 50:63-73.

Clarke, T. A. 1971. The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pac. Sci. 25:133-144.

Coles, R. J. 1913. Notes on the embryos of several species of rays, with remarks on the northward summer migration of certain tropical forms observed on the coast of North Carolina. Bull. Amer. Mus. Nat. Hist. 32:29-36.

Coles, R. J. 1916. Natural history notes on the devil-fish, *Manta birostris* (Walbaum) and *Mobula olfersi* (Müller). Bull. Amer. Mus. Nat. Hist. 35:649-657.

Colman, J. G. 1997. A review of the biology and ecology of the whale shark. J. Fish Biol. 51:1219-1234.

Compagno, L. J. V. 1984a. FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes. FAO Fish. Synop., (125)Vol.4,Pt.1:249p.

Compagno, L. J. V. 1984b. FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 2. Carcharhiniformes. FAO Fish. Synop., (125)Vol.4,Pt.2:251-655.

Cressey, R. F. & E. A. Lachner. 1970. The parasitic copepod diet and life history of diskfishes (Echeneidae). Copeia 1970:310-318.

Dennis G. D. & T. J. Bright. 1988. Reef fish assemblages on hard banks in the northwestern Gulf of Mexico. Bull. Mar. Sci. 43:280-307.

Dodrill, J. W. & R. G. Gilmore. 1978. Land birds in the stomachs of tiger sharks *Galeocerdo cuvieri* (Peron and Lesueur). Auk 95:585-586.

Dokken, Q. R., C. Beaver, S. Cox, C. Adams, J. Rooker, & J. Childs. 1996. Characterization of biofouling communities on oil and gas production platforms: impact on finfish assemblage. p. 142-153. *In*: Proceedings, Fifteenth Annual Gulf of Mexico Information Transfer Meeting, December 1995, OCS report MMS 96-0056. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, New Orleans.

Economakis, A. E. & P. S. Lobel. 1998. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, central Pacific Ocean. Env. Biol. Fish. 51:129-139.

Edwards, A. J. & H. R. Lubbock. 1982. The shark population of Saint Paul's Rocks. Copeia 1982:223-225.

Gadig, O. B. F., M. A. Bezerra, & M. A. A. Furtado-Neto. 1996. Nota sobre a biologia do tubarão *Carcharhinus perezi* (Poey, 1861) (Chondrichthyes, Carcharhinidae) do norte-nordeste do Brasil. Revista Nordestina de Biologia. 11(1):31-36.

Gallaway, B. J. & G. S. Lewbel. 1982. The ecology of petroleum platforms in the northwestern Gulf of Mexico: a community profile. U.S. Fish Wildl. Serv., Gulf of Mexico OCS Reg. Off., Open-file Rep. 82-03. 93 pp.

Garrick, J. A. F. 1982. Sharks of the genus *Carcharhinus*. NOAA Tech. Rep. NMFS Circular 445:1-194.

Gill, T. 1908. The story of the devil-fish. Smithsonian Misc. Coll. No. 1816. Vol 52:155-180.

Gilliam, D. & K. M. Sullivan. 1993. Diet and feeding habits of the southern stingray *Dasyatis americana* in the central Bahamas. Bull. Mar. Sci. 52:1007-1013.

Gittings, S. R. 1998. Reef community stability on the Flower Garden Banks, northwest Gulf of Mexico. Gulf Mex. Sci. 16:161-169.

Gittings, S. R., G. S. Boland, K. J. P. Deslarzes, C. L. Combs, B. S. Holland & T. J. Bright. 1992a. Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, northwest Gulf of Mexico. Bull. Mar. Sci. 51:420-428.

Gittings, S. R., K. J. P. Deslarzes, D. K. Hagman & G. S. Boland. 1992b. Reef coral populations and growth on the Flower Garden Banks, northwest Gulf of Mexico. Proc. 7th Int. Coral Reef Symp. 1:90-96.

Grace, M. & T. Henwood. 1997. Assessment of the distribution and abundance of coastal sharks in the U.S. Gulf of Mexico and Eastern Seaboard, 1995 and 1996. Mar. Fish. Rev. 59(4):23-32.

Graham, R. T., W. D. Heyman, & B. Kjerfve. 2000. Population size estimates of whale sharks, *Rhincodon typus*, off the Belize Barrier Reef. Abstracts from the 80th Annual Joint Meeting of the American Society of Ichthyologists and Herpetologists and the American Elasmobranch Society, June 14-20, 2000. La Paz, B.C.S., Mexico. 400 pp.

Gruber, S. H. (ed.) 1991. Discovering Sharks. American Littoral Soc. Highlands, NJ. 121 pp.

Gruber, S. H. & A. A. Myrberg Jr. 1977. Approaches to the study of the behavior of sharks. Amer. Zool. 17:471-486.

Gruber, S. H., D. R. Nelson & J. F. Morrissey. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahama lagoon. Bull. Mar. Sci. 43:61-76.

Gudger, E. W. 1912. Summary of work done on the fishes of Tortugas. Carnegie Inst. Wash. Yearbook, vol 11:148-150.

Gudger, E. W. 1923. A fourth capture in Florida waters of the whale shark. Science 58: 180-181.

Gudger, E. W. 1939. The whale shark in the Caribbean Sea and the Gulf of Mexico. Sci. Mo. 48:261-264.

Gudger, E. W. 1941. The food and feeding habits of the whale shark, *Rhineodon typus*. J. Elisha Mitchell Sci. Soc. 57(1):57-72.

Gudger, E. W. 1948. The tiger shark, *Galeocerdo tigrinum*, on the North Carolina coast and its food and feeding habits there. J. Elisha Mitchell Sci. Soc. 64:221-233.

Gudger, E. W. 1949. Natural history notes on tiger sharks, *Galeocerdo tigrinus*, caught at Key West, Florida, with emphasis on food and feeding habits. Copeia 1949:39-47.

Gunn, J. S., J. D. Stevens, T. L. O. Davis & B. M. Norman. 1999. Observations on the short-term movements and behavior of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. Mar. Biol. 135:553-559.

Gunter, G. & F. T. Knapp. 1951. Fishes, new, rare or seldom recorded from the Texas coast. Tex. J. Sci. 3(1):134-138.

Hagman, D. K. & S. R. Gittings. 1992. Coral bleaching on high latitude reefs at the Flower Garden Banks, NW Gulf of Mexico. Proc. 7th Int. Coral Reef Symp. 1:38-43.

Hagman, D. K., S. R. Gittings, & K. J. P. Deslarzes. 1998. Timing, species participation, and environmental factors influencing annual mass spawning at the Flower Garden Banks (northwestern Gulf of Mexico). Gulf Mexico Sci. 16:170-179.

Hamilton, W. J. III & K. E. F. Watt. 1970. Refuging. Annual Rev. Ecol. & Syst. 1970. 1:263-287.

Heemstra, P. C. 1997. A review of the smooth-hound sharks (genus *Mustelus*, family Triakidae) of the western Atlantic Ocean, with descriptions of two new species and a new subspecies. Bull. Mar. Sci. 60:894-928.

Heist, E. J., J. E. Graves & J. A. Musick. 1995. Population genetics of the sandbar shark (*Carcharhinus plumbeus*) in the Gulf of Mexico and Mid-Atlantic Bight. Copeia 1995:555-562.

Heist, E. J. & J. R. Gold. 1999. Genetic identification of sharks in the U. S. Atlantic large coastal shark fishery. Fish. Bull. 97:53-61.

Hess, P. W. 1961. Food habits of two dasyatid rays in Delaware Bay. Copeia 1961:239-241.

Heuter, R. & J. Childs. 2001. Gulf of Mexico petroleum and gas rigs as FADs for sharks and rays. Abstracts from the Deep Rigs as FADs Technical Session, American Fisheries Society Southern Division Midyear Meeting. February 22-25, 2001. Jacksonville, FL. 72 pp.

Heyman, W. D., R. T. Graham, & B. Kjerfve. 2000. Whale sharks feed on gametes released from snapper spawning aggregations in Belize. Abstracts from the 80th Annual Joint Meeting of the American Society of Ichthyologists and Herpetologists and the American Elasmobranch Society, June 14-20, 2000. La Paz, B.C.S., Mexico. 400 pp.

Hoese, H. D. & R. H. Moore. 1977. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press, College Station, TX. 327 pp.

Hoese, H. D. & R. H. Moore. 1998. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press, College Station, TX. 422 pp.

Hoffman, W., T. H. Fritts & R. R. Reynolds. 1981. Whale sharks associated with fish schools off south Texas. Northeast Gulf Sci. 5(1):55-57.

Holland, K. N., B. M. Wetherbee, J. D. Peterson & C. G. Lowe. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. Copeia 1993:495-502.

Holland, K. N., B. M. Wetherbee, C. G. Lowe & C. G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Marine Biology 134:665-673.

Humann, P. 1994. Reef Fish Identification: Florida, Caribbean, Bahamas. New World Publ., Inc. Paramount Miller Graphics, Inc., Jacksonville, FL. 396 pp.

Jensen, C. F. & F. J. Schwartz. 1994. Extreme habitat occurrences for the two species of hammerhead sharks (Family Sphyrnidae) in North Carolina and western Atlantic Ocean waters. J. Elisha Mitchell Sci. Soc. 110(1):46-48.

Johnson, R. H. 1978. Sharks of Polynesia. Les Editions de Pacifique, Papeete.

Johnson, R. H. & D. R. Nelson. 1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. Copeia 1973:76-84.

Joung, S-J., C-T. Chen, E. Clark, S. Uchida & W. Y. P. Huang. 1996. The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma' supreme. Env. Biol. Fish. 46:219-223.

Klimley, A. P. 1980. Observations of courtship and copulation in the nurse shark, *Ginglymostoma cirratum*. Copeia 1980:878-882.

Klimley, A. P. 1982. Grouping behavior in the scalloped hammerhead. Oceanus 24:65-71.

Klimley, A. P. 1985. Schooling in *Sphyrna lewini*, a species with low risk of predation: a non-egalitarian state. Z. Tierpsychol. 70:297-319.

Klimley, A. P. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Env. Biol. Fish. 18:27-40.

Klimley, A. P. 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Marine Biology 117:1-22.

Klimley, A. P. & D. R. Nelson. 1981. Schooling of the scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California. Fish. Bull. 79(2):356-360.

Klimley, A. P. & D. R. Nelson. 1984. Diel movement patterns of the scalloped hammerhead shark, (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-postion social system. Behav. Ecol. Sociobiol. 15:45-54.

Klimley, A. P., S. B. Butler, D. R. Nelson & A. T. Stull. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. J. Fish Biol. 33:751-761.

Kohler, N. E., J. G. Casey & P. A. Turner. 1998. NMFS Cooperative Shark Tagging Program, 1962-93: an atlas of shark tag and recapture data. Mar. Fish. Rev. 60(2):1-87.

Kukuyev, E. I. 1996. The new finds in recently born individuals of the whale shark *Rhiniodon typus* (Rhiniodontidae) in the Atlantic Ocean. J. Ichthyology 36:203-205.

Lee,T. N., J. A. Yoder & L. P. Atkinson. 1991. Gulf Stream frontal eddy influence on productivity of the southeast U.S. continental shelf. J. Geophys. Res. 96:22191-22205.

Limbaugh, C. 1963. Field notes on sharks. pp. 63-94. *In*: P. W. Gilbert (ed.) Sharks and

Survival. A.I.B.S., D. C. Heath & Co., Boston.

Lowe, C. G., B. M. Wetherbee, G. L. Crow & A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Env. Biol. Fish. 47:203-211.

Lugo-Fernández, A. 1998. Ecological implications of hydrography and circulation to the Flower Garden Banks, northwest Gulf of Mexico. Gulf Mexico Sci. 16:144-160.

Lyle, J. M. & G. J. Timms. 1987. Predation on aquatic snakes by sharks from northern Australia. Copeia 1987:802-803.

McEachran, J. D. & J. D. Fechhelm. 1998. Fishes of the Gulf of Mexico. Vol. 1. Univ. of Texas Press, Austin. 1112 pp.

McFarland, W. N. 1963. Seasonal change in the number and biomass of fishes from the surf at Mustang Island, Texas. Institute of Marine Science, Univ. of Texas, Port Aransas. 9:91-105.

McKibben, J. N. & D. R. Nelson. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. Bull. Mar. Sci. 38:89-110.

McLaughlin, R. H. & A. K. O'Gower. 1971. Life history and underwater studies of a heterodont shark. Ecol. Monogr. 41(4):271-289.

Meek, A. 1916. The Migrations of Fish. Edward Arnold, London. 427 pp.

Morrissey, J. F. & S. H. Gruber. 1993a. Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 1993:425-434.

Morrissey, J. F. & S. H. Gruber. 1993b. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Env. Biol. Fish. 38:311-319.

Myrberg, A. A. Jr., S. J. Ha, S. Walewski & J. C. Banbury. 1972. Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull. Mar. Sci. 22:926-949.

Natanson, L. J., J. G. Casey, N. E. Kohler & T. Colket IV. 1999. Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging. Fish. Bull. 97:944-953.

Nelson, D. R. 1977. On the field study of shark behavior. Amer. Zool. 17:501-507.

Nelson, D. R. & R. H. Johnson. 1980. Behavior of the reef sharks of Rangiroa, French Polynesia. Natl. Geogr. Res. Rep. 12:479-499.

Neumann, A. C. 1958. The configuration and sediments of Stetson Bank, northwestern Gulf of Mexico. Project 24, Section VII, Res. Rep. Texas A&M Univ. 125 pp.

NMFS. 1998. Annual Report to Congress on the Status of Fisheries of the United States. National Marine Fisheries Service. Silver Spring, MD. 94 pp.

NMFS. 1999. Final Fishery Management Plan for Atlantic Tuna, Swordfish, and Sharks; Including the Revised Final Environmental Impact Statement, the Final Regulatory Impact Review, the Final Regulatory Flexibility Analysis, and the Final Social Impact Assessment. U.S. Dept. of Commerce, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division. Silver Spring, MD. 302 pp.

NOAA. 1991. Final Environmental Impact Statement and Management Plan for the Proposed Flower Garden Banks National Marine Sanctuary. U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Sanctuaries and Reserves Division. 141 pp.

Notarbartolo-di-Sciara, G. 1987. A revisionary study of the genus *Mobula* Rafinesque, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. Zool. J. Linn. Soc.91:1-91.

Notarbartolo-di-Sciara, G. 1988. Natural history of the rays of the genus *Mobula* in the Gulf of California. Fish. Bull. 86:45-66.

Notarbartolo-di-Sciara, G. & E. V. Hillyer. 1989. Mobulid rays off eastern Venezuela. Copeia 1989:607-614.

Pai, M. V., G. Nandakumar& K. Y. Telang. 1983. On the whale shark, *Rhineodon typus* Smith landed at Karwar, Karnataka. Indian J. Fisheries 30:157-160.

Parker Jr., F. R. & C. M. Bailey. 1979. Massive aggregations of elasmobranchs near Mustang and Padre Islands, Texas. Tex. J. Sci. 31:255-266.

Pattengill-Semmens, C. V. & B. X. Semmens. 1998. An analysis of fish survey data generated by nonexpert volunteers in the Flower Garden Banks National Marine Sanctuary. Gulf Mexico Sci. 16:196-207.

Pratt, H. L. Jr. & J. C. Carrier. 1995. Wild mating of the nurse sharks. Natl. Geogr. May 44-53.

Randall, J. E. 1977. Contributions to the biology of the whitetip reef shark (*Triaenodon obesus*). Pac. Sci. 31:143-164.

Randall, J. E. 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). Aust. J. Mar. Freshwater Res. 43:21-31.

Reed, J. K. & R. G. Gilmore. 1981. Inshore occurrence and nuptial behavior of the roughtail stingray, *Dasyatis centroura* (Dasyatidae), on the continental shelf, east central Florida. Northeast Gulf Sci. 5:59-62.

Reid, G. K. 1957. External morphology of an embryo whale shark, *Rhincodon typus* Smith. Copeia 1957:157-158.

Rezak, R. 1983. Geology of the Flower Garden Banks. pp. 111-140. *In*: R. Rezak, T. J. Bright & D. W. McGrail (eds.) Reefs and Banks of the Northwestern Gulf of Mexico: Their Geological, Biological, and Physical Dynamics. Final Report. Tech. Rep. No. 83-1 T. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA.

Rezak, R. & T. J. Bright. 1983. Classification and characterization of banks. pp. 311-399. *In*: R. Rezak, T. J. Bright & D. W. McGrail (eds.) Reefs and Banks of the Northwestern Gulf of Mexico: Their Geological, Biological, and Physical Dynamics. Final Report. Tech. Rep. No. 83-1 T. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA.

Rezak, R., T. J. Bright, & D. W. McGrail. 1985. Reefs and Banks of the Northwestern Gulf of Mexico: Their Geological, Biological, and Physical Dynamics. JohnWiley & Sons, New York. 259 pp.

Robins, C. R., G. C. Ray & J. Douglass. 1986. A Field Guide to Atlantic Coast Fishes. Houghton Mifflin Co., Boston. 354 pp.

Rooker, J. R., Q. R. Dokken, C. V. Pattengill & G. J. Holt. 1997. Fish assemblages in artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. Coral Reefs 16:83-92.

Russell, S. R. 1993. Shark bycatch in the northern Gulf of Mexico tuna longline fishery, 1988-91, with observations on the nearshore directed shark fishery. pp. 19-29. *In*: S. Branstetter (ed.) Conservation Biology of Elasmobranchs. NOAA Tech. Rep. NMFS 115.

Sammarco, P. W. & J. C. Andrews. 1988. Localized dispersal and recruitment in Great Barrier Reef corals: the Helix experiment. Science 239:1422-1424.

Saunders G. B. & E. Clark. 1962. Yellow-billed cuckoo in stomach of tiger shark. Auk 79:118.

Satyanarayano Rao, K. 1986. On the capture of whale sharks off Dakshina Kannada coast. Marine Fisheries Information Service, Technical & Extension Series 66:22-29.

Schmid, T. H., L. M. Ehrhart & F. F. Snelson Jr. 1988. Notes on the occurrence of rays (Elasmobranchii, Batoidea) in the Indian River Lagoon System, Florida. Fla. Sci. 51(2):121-128.

Schwartz, F. J. 1984. Sharks, sawfish, skates, and rays of the Carolinas. Special Pub. Institute of Marine Sciences, Morehead City, NC. 101 pp.

Schwartz, F. J. 1998. History of the Poor Boy Shark Tournament in North Carolina, 1982-1996. J. Elisha Mitchell Sci. Soc. 114:149-158.

Simpfendorfer, C. 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland Shark Meshing Program off Townsville, Australia. Aust. J. Mar. Freshwater Res. 43:33-43.

Simpfendorfer, C. A. & N. E. Milward. 1993. Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Env. Biol. Fish. 37:337-345.

Smale, M. J. 1991. Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus*, and *Sphyrna zygaena*, on the eastern cape coast of South Africa. S. Afr. J. mar. Sci. 11:31-42.

Smith, J. W. & J. V. Merriner. 1982. Association of cobia, *Rachycentron canadum*, with cownose ray, *Rhinoptera bonasus*. Estuaries 5:240-242.

Snelson Jr., F. F. & S. E. Williams. 1981. Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River lagoon system, Florida. Estuaries 4:110-120.

Snelson, F. F. Jr., S. H. Gruber, F. L. Murru, & T. H. Schmid. 1990. Southern stingray, *Dasyatis americana*: host for a symbiotic cleaner wrasse. Copeia 1990:961-965.

Sonnier, F., J. Teerling & H. D. Hoese. 1976. Observations on the offshore reef and platform fish fauna of Louisiana. Copeia 1976(1):105-111.

Springer, S. 1940. The sex ratio and seasonal distribution of some Florida sharks. Copeia 1940 (3):188-194.

Springer, S. 1949. An outline for a Trinidad shark fishery. pp. 17-26. *In*: Proceedings of the Gulf and Caribbean Fisheries Institute. Vol. 2. Gulf and Caribbean Fisheries Institute. Coral Gables, Florida, Institute of Marine Science, Univ. of Miami.

Springer, S. 1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. Ecology 38(1):166-171.

Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. U. S. Fish. Wildl. Fish. Bull. 61. 38 pp.

Springer, S. 1963. Field observations in large sharks of the Florida-Caribbean region. pp. 95-113. *In*: P. W. Gilbert (ed.) Sharks and Survival. A.I.B.S., D. C. Heath & Co., Boston.

Springer, S. 1967. Social organization of shark populations. pp. 149-174. *In*: P. W. Gilbert, R. F. Mathewson & D. P. Rall (eds.) Sharks, Skates, and Rays, Johns Hopkins Univ. Press, Baltimore, MD.

Springer, S. & H. T. Bullis. 1956. Collections made by the *Oregon* in the Gulf of Mexico. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 196:1-134.

Springer, V. 1961. Notes on and additions to the fish fauna of the Tampa Bay area in Florida. Copeia 1961(4):480-482.

Stanley, D. R. & C. A. Wilson. 1990. A fishery dependent based study of fish species composition and associated catch rates around petroleum platforms off Louisiana. Fish. Bull. 88:719-730.

Stanley, D. R. & C. A. Wilson. 1991. Factors affecting the abundance of selected fishes near petroleum platforms in the northern Gulf of Mexico. Fish. Bull. 89:149-159.

Stanley, D. R. & C. A. Wilson. 1997. Seasonal and spatial variation in abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico. Can. J. Fish. Aquat. Sci. 54:1166-1176.

Stanley, D. R. & C. A. Wilson. 1998. Spatial variation in fish density at three petroleum platforms as measured with dual-beam hydroacoustics. Gulf Mexico Sci. 16:73-82.

Stevens, J. D. 1984. Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proc. R. Soc. Lond. 222:79-106.

Stevens, J. D. & K. J. McLoughlin. 1991. Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. Aust. J. Mar.

Freshwater Res. 42:151-199.

Stokes, M. D. & N. D. Holland. 1992. Southern stingray (*Dasyatis americana*) feeding on lancelets (*Branchiostoma floridae*). J. Fish Biol. 41:1043-1044.

Strasburg, D. W. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. Fish. Bull. 138 Vol. 58:1-361.

Strong, W. R. Jr., F. F. Snelson, & S. H. Gruber. 1990. Hammerhead shark predation on stingrays:an observation of prey handling by *Sphryna mokkarran*. Copeia 1990:836-840.

Struhsaker, P. 1969. Observations on the biology and distribution of the thorny stingray, *Dasyatis centroura* (Pisces: Dasyatidae). Bull. Mar. Sci. 19:456-481.

Taylor, G. 1994. Gentle giants of the deep. Austr. Geogr. Apr-Jun 92-103.

Taylor, J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. Mar. Freshwater Res. 47:637-642.

Taylor, J. G. & A. F. Pearce. 1999. Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. J. Royal Soc. Western Aust. 82:57-65.

Tricas, T. C., L. R. Taylor & G. Naftel. 1981. Diel behavior of the tiger shark, *Galeocerdo cuvier*, at French Frigate Shoals, Hawaiian Islands. Copeia 1981:904-908.

Uchida, S., M. Toda & Y. Kamei. 1990. Reproduction of elasmobranchs in captivity. pp. 211-237. *In*: H. L. Pratt Jr., S. H. Gruber & T. Taniuchi (eds.) Elasmobranchs as Living Resources. NOAA Tech. Rep. NMFS 90.

Walker, P. A. & H. J. L. Heessen. 1996. Long-term changes in ray populations in the North Sea. ICES J. Marine Science 53:1085-1093.

Walker, P. A., G. Howlett & R. Millner. 1997. Distribution, movement and stock structure of three species in the North Sea and eastern English Channel. ICES J. Marine Science 54: 797-808

Walker, P. A. & J. Hislop. 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray and skate composition in the central and north-western North Sea between 1930 and the present day. ICES J. Marine Science 55:392-402.

Wolfson, F. H. 1983. Records of seven juveniles of the whale shark, *Rhiniodon typus*. J. Fish Biol. 22:647-655.

Wolfson, F. H. 1986. Occurrences of the whale shark, *Rhincodon typus* Smith. pp. 208-226. *In*: T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura (eds.) Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Soc. Japan, Tokyo.

Yano, K., F. Sato & T. Takahashi. 1999. Observations of mating behavior of the manta ray, *Manta birostris*, at the Ogasawara Islands, Japan. Ichthyological Research 46:289-296.

Young, R. F. 1993. Observation of the mating behavior of the yellow stingray, *Urolophus jamaicensis*. Copeia 1993:879-880.

Zhardim, M. F., A. A. Nesterov & L. A. Pereira. 1998. A whale shark *Rhiniodon typus* on the beach of Musul Island (Angola). J. Ichthyology 38(3):272-274.

VITA

Jeffrey Nathaniel Childs
4421 Bonner Dr.
Corpus Christi, TX 78411
Oceanauts@aol.com

EDUCATION

- M.S., Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX. 2001.
- B.S., Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX. 1993.

SELECTED PUBLICATIONS

- Childs, J. 2000. Sharks and rays of Stetson and the Flower Garden Banks. pp. 183-193. *In*: McKay, M. & J. Nides. (eds.) 2000. Proceedings: Eighteenth Annual Gulf of Mexico Information Transfer Meeting, December 1998. U.S. Dept. of Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS 2000-030.
- Childs, J. 1999. Avian Diversity and Habitat Use within the Flower Garden Banks National Marine Sanctuary. Gulf of Mexico Sci. 16(2):208-225.
- Childs, J. 1999. Nocturnal parking behavior of three monacanthids at an offshore production platform in the northwestern Gulf of Mexico. Gulf of Mexico Sci. 16(2):228-232.
- Childs, J. 1997. Range extension of *Mobula tarapacana* in the northwestern Gulf of Mexico. Gulf of Mexico Sci. 15:39-40.
- Childs, J. N., E. L. Hickerson & K. J. P. Deslarzes. 1996. Spatial and temporal resource use of the Flower Garden Banks by charismatic megafauna. *In*: Proceedings: Fifteenth Information Transfer Meeting, December 1995. OCS Study MMS 96-0056. U.S. Dept. of Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA.

SELECTED AWARDS and ACHIEVEMENTS

- member of the National Honor Society of Phi Kappa Phi. 2001.
- NOAA/Dept. of Commerce National Environmental Hero Award. 2000.
- Oryx Student Fellowship. 1996.
- SeaSpace Scholarship. 1995.
- Graduate of Distinction, The Ocean Corp. 1984.
- Submarine Squadron Eight Letter of Commendation, U.S. Navy. 1983.
- Navy Achievement Medal, U.S. Navy. 1982.