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Nova Southeastern University Oceanographic Center

THE INFLUENCE OF SUPPLEMENTAL FEEDING ON THE MOVEMENT PATTERNS OF THE SOUTHERN STINGRAY,

DASYATIS AMERICANA, AT GRAND CAYMAN,

CAYMAN ISLANDS

BY

MARK JOHN CORCORAN

A THESIS SUBMITTED TO THE FACULTY OF NOVA SOUTHEASTERN UNIVERSITY OCEANOGRAPHIC CENTER IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE MASTER OF SCIENCE WITH A SPECIALTY IN:

MARINE BIOLOGY

NOVA SOUTHEASTERN UNIVERSITY 2006

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MASTER OF SCIENCE THESIS

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NOVA SOUTHEASTERN UNIVERSITY 2006

DEDICATION

This work is dedicated to my family, Barbara, Denis, Paula and Steven, whose love and support I always carry with me, especially when far from home.

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ABSTRACT

There are currently over 300 sites in nearly 40 countries where a variety of marine animals are provided supplemental food by humans. The influence of this supplemental feeding on the behavior, physiology, growth, reproduction and movements of the animals involved is seldom known. Intentional supplemental feeding of the southern stingray, Dasyatis americana, has occurred at Stingray City (SC) and Stingray City Sandbar (SCS) at Grand Cayman since 1986. There are no specific regulations governing the feeding of D. americana at Grand Cayman, and neither the species nor the feeding sites are afforded any official protective status. This study investigated how supplemental feeding influences the movement patterns of *D. americana* at Grand Cayman, including activity spaces, rates of movement, site fidelity and diel patterns. This research is the first detailed investigation into the influence of supplemental feeding on the movement patterns of a marine animal. The objectives of this study were to investigate and compare the movement patterns of *D. americana* at supplemental feeding sites and non-feeding 'wild' control sites. Passive Integrative Transponder (PIT) tags were implanted in 327 stingrays, 183 of which were recaptured; 100% of recaptured stingrays retained their tags over the duration of the study, based on tissue sample scarring. External tags were attached to 35 stingrays. Tagging data indicate that a spatially isolated community of approximately 160 D. americana utilize SCS. Seven wild and seven provisioned stingrays were tracked manually from five to 72 h, and five mature females at SCS were tracked automatically using an array of two bottom monitors. Provisioned female stingrays at SCS utilized significantly smaller 24 h activity spaces (0.132±0.079 km²) than wild female stingrays (0.876±0.171km²). Both groups utilized significantly larger activity spaces at night than during the day. However, there was a marked difference in the diel activity levels between provisioned and wild stingrays: provisioned stingrays were active over a small area during daytime supplemental feeding, whereas wild stingravs were more active and foraged during the night (nocturnal). Average rates of movement did not significantly differ between the two groups. Tidal phase had no effect on activity space size or rate of movement for either group. The core areas of provisioned stingrays showed significantly more overlap than those of wild stingrays, indicating that supplemental feeding has disrupted the spatial distribution of the community at SCS and increased the local density of D. americana to atypical levels. Provisioned female stingrays consistently frequented SCS during periods of supplemental feeding and exhibited long term (at least up to one year) site fidelity to this site. These findings suggest that provisioned stingrays are highly conditioned to the supplemental food resources provided at SCS. Provisioned stingrays exhibited optimal foraging and have reduced and centralized their core areas and activity spaces at SCS in order to maximize their accrual of food resources. The availability of food resources is a significant factor regulating the size and location of core areas and activity spaces, population density and the diel activities (i.e. the spatial and temporal distribution) of D. americana at Grand Cayman.

LIST OF TABLES	ix
LIST OF FIGURES	X
LIST OF APPENDICES	xiv
1. INTRODUCTION	1
1.1 Marine Animal Feeding	
1.2 The Southern Stingray, Dasyatis americana	
1.3 Stingray Feeding Sites, Grand Cayman	
1.4 Statement of Thesis Objectives	9
2. MATERIALS AND METHODS	
2.1 Study site	
2.1.1 Supplemental Feeding Sites	
2.1.1.1 Stingray City	
2.1.1.2 Stingray City Sandbar	
2.1.2 Control Sites	
2.1.2.1 South Sound	
2.1.2.2 Barkers	
2.1.2.3 Frank Sound	
2.1.2.4 Rum Point / Cayman Kai	
2.2 Manual Acoustic Telemetry (MAT)	
2.2.1 Telemetry Equipment	
2.2.2 Animal Capture and Handling	
2.2.3 Tracking protocol	
2.3 Automated Acoustic Telemetry (AAT)	
2.3.1 Telemetry Equipment	
2.3.2 Receiver Range testing	
2.3.3 Animal Capture and Handling	
2.3.4 Tracking protocol and data downloading	
2.4 Animal Tag and Recapture	
2.4.1 Internal tagging	
2.4.2 External tagging	
2.5 Diel Activity	
2.5.1 ACTIVITY Space	
2.5.2 Kate of Wovement.	
2.6 1 Tides and Animal Activity Space	
2.6.1 Hues and Animal Activity Space	
2.0.2 Trues and Annnai Kate of Wovement	
2.7 She Flaenty	

TABLE OF CONTENTS

3. RESULTS	
3.1 Manual Acoustic Telemetry	
3.1.1 Provisioned Stingrays	
3.1.2 Wild Stingrays	
3.2 Automated Acoustic Telemetry	
3.3 Tag and recapture	
3.3.1 Internal tagging	
3.3.2 External tagging	
3.4 Diel Activity	
3.4.1 Activity Space	
3.4.2 Rate of Movement	
3.5 Tides	
3.5.1 Tides and Animal Activity Space	
3.5.2 Tides and Animal Rate of Movement	
3.6 Site Fidelity	
3.7 Additional Observations	
4. DISCUSSION	
5. SUMMARY AND CONCLUSIONS	
6. LITERATURE CITED	

LIST OF TABLES

Table 1. Southern stingrays, *Dasyatis americana*, manually tracked at Grand Cayman. 55

 Table 4.
 Numbers and mean sizes of southern stingrays, *Dasyatis americana*, tagged with external spaghetti tags at Grand Cayman control sites.

 57

Table 5. Twenty-four hour core area (50%) and activity space (95%) sizes for manuallytracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays,Dasyatis americana, at Grand Cayman.58

Table 7. Rates of movement for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman..... 60

 Table 8. Pooled rates of movement for manually tracked provisioned (Stingray City

 Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand

 Cayman.
 60

Table 10. Tidal core area (50%) and activity space (95%) sizes for manually trackedprovisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatisamericana*, at Grand Cayman.62

Table 11. Pooled tidal core area (50%) and activity space (95%) sizes for manuallytracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays,Dasyatis americana, at Grand Cayman.63

 Table 12. Tidal rates of movement for manually tracked provisioned (Stingray City

 Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand

 Cayman.
 64

 Table 13. Pooled tidal rates of movement for manually tracked provisioned (Stingray

 City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand

 Cayman.
 64

LIST OF FIGURES

<i>Figure 1</i> . The location of the Cayman Islands in the Caribbean
<i>Figure 2.</i> Map of Grand Cayman showing the location of the supplemental feeding sites, Stingray City Sandbar and Stingray City, and the four control sites Barkers, Rum Point/Cayman Kai, South Sound and Frank Sound
<i>Figure 3.</i> Supplemental feeding site, Stingray City Sandbar, showing the location of the fringing reef and lagoonal zones
<i>Figure 4</i> . Two control sites, South Sound and Barkers, showing the location of channels and lagoonal zones
<i>Figure 5.</i> Two control sites, Frank Sound and Rum Point/Cayman Kai, showing the location of channels and lagoonal zones
<i>Figure 6.</i> Two binder clips placed over the spine and adjacent tail of a mature female southern stingray, <i>Dasyatis americana</i> , allowed safe and efficient handling
<i>Figure 7.</i> A wax covered V16 transmitter (Vemco, Nova Scotia) attached to the right pelvic fin of a mature female southern stingray, <i>Dasyatis americana</i> , using a Peterson disc tag (Floy Tag Company, Seattle, WA. 20 mm diameter)
<i>Figure 8.</i> Custom-built stationary receiver housing unit. (A) shows the unit sitting on a sandy substrate with the concrete base and anchors clearly visible. (B) shows the unit in situ at Stingray City Sandbar with the concrete base buried and anchors screwed in place, preventing any movement of the unit. The red hydrophone tip of the housed VR2 receiver (Vemco, Nova Scotia) is visible protruding from the top of the unit in (B)
<i>Figure 9.</i> The location of the Cayman Islands Government Mosquito Research and Control Unit (MRCU) tide station (red dot) in the North Sound of Grand Cayman
<i>Figure 10.</i> Disc width vs. weight scatter plot of provisioned southern stingrays, <i>Dasyatis americana</i> , at Stingray City Sandbar, Grand Cayman, showing the predominance of large

Figure 21. Photograph of a female southern stingray, *Dasyatis americana*, buried in a sandy groove within a 'spur and groove' coral community, approximately 350 m south of the South Sound, Grand Cayman. Water depth at this location is 20 m. This activity represents the typical mid-day behavior for all stingrays tracked in the South Sound. The yellow circle in the inset above represents the location where the photograph was taken.

Figure 32. Daytime core areas of manually tracked southern stingrays, *Dasyatis americana*, at Grand Cayman. The five stingrays tracked manually at Stingray City Sandbar exhibited almost total overlap of daytime core areas (*top*) whereas the five stingrays tracked manually at the South Sound exhibited very limited overlap (*bottom*).96

LIST OF APPENDICES

APPENDIX A:	Draft Guidelines f	or Feeding	and Interactio	n with the	Rays at
Stingray City	y and the Sandbar				104
APPENDIX B: I	Rules for Cayman Is	lands Marin	e Replenishmen	t Zone	105

1. INTRODUCTION

1.1 Marine Animal Feeding

Tourism involving wildlife observation is a large and rapidly growing industry (Duffus and Dearden 1990; Ryan 1998; Youth 2000), generating over US\$165 billion annually worldwide (TIES 2000). In many cases wildlife observation is unpredictable and inconsistent, and tour operators often provide supplemental food in order to reliably encounter wildlife (Orams 1995; 2002), thus ensuring a secure tourism product. The influence of this supplemental feeding on the behavior, physiology, growth, reproduction and movements of the animals involved is seldom known. This lack of knowledge is due largely to a poor understanding of these elements prior to supplemental feeding, resulting in a lack of control data for comparison. Therefore, valid scientific investigations into the influence of these feeding activities are often not possible.

There are currently over 300 sites in nearly 40 countries where a variety of marine animals are deliberately provided supplemental food by humans (Duffus and Dearden 1990; Ryan 1998; GIMEC 2001). In the tropical Northwest Atlantic Ocean, the supplemental feeding of marine animals has a long and controversial history (Bryant 1994; GIMEC 2001; FWC 2001). The feeding of wild Atlantic bottlenose dolphins by recreational boaters in the waters off the southeast coast of the United States received wide media attention in the early 1990s. Reports of dolphins exhibiting aberrant behaviors and numerous swimmers receiving bites from aggressive dolphins prompted the National Marine Fisheries Service (NMFS) to launch an investigation into the feeding of wild dolphins in these waters. NMFS solicited six marine mammal experts to conduct a scientific review of the effects of these feeding activities. All six experts concluded that "feeding wild populations of dolphins alters their natural behavior in ways that are harmful to individual marine mammals and marine mammal stocks...and may increase their risk of injury or death" (Bryant 1994). In its report to congress, NMFS stated that the most significant adverse effects of feeding wild dolphins are: the substantial alteration of natural behavior, including foraging and migration; the loss of wariness of humans; increased interaction with fishing boats; consumption of inappropriate or contaminated food and increased injuries to humans (Bryant 1994). The report concluded by stating that the activity of feeding wild dolphins is unanimously opposed by the scientific community and "the potential adverse impacts on the population stocks of Atlantic bottlenose dolphin and the marine ecosystem outweigh the potential benefit of the proposed activities". As a result of these findings, NMFS amended its definition of the term "take", under the Marine Mammal Protection Act (MMPA), to include "feeding" or "attempting to feed" (Bryant 1994). This amendment prohibited the feeding or attempted feeding of all wild marine mammals in U.S. waters. It is important to note that this decision was based on a review by six independent scientists and evidence presented in affidavits, and that no direct scientific investigation into the effects of the feeding was ever conducted.

More recently, the feeding of wild sharks during 'shark dives' off the coast of Florida has become a contentious issue. In direct response to a petition filed by the Marine Safety Group, the Florida Fish and Wildlife Conservation Commission (FWC) held a public hearing, in September 1999, to discuss shark feeding in Florida waters. One year later the FWC ordered the dive industry to establish feeding guidelines. The Global Interactive Marine Experiences Council (GIMEC), a conglomeration of dive industry representatives, tour operators, scientists and divers, drafted the Florida Guidelines and Management Programs - Program for Interactive Marine Experiences (GIMEC 2001). These guidelines were later rejected by the FWC as inadequate, and they elected to draw up their own guidelines. These guidelines were in turn rejected by the dive industry, resulting in a decision by the FWC to draft a rule to prohibit the feeding of marine wildlife in state waters (CDNN 2004). This ruling prohibits the "introduction of food or other substance into the water by a diver for the purpose of feeding or attracting marine life" in Florida state waters (FWC 2001), and officially came into effect on January 1, 2002 despite widespread protest from the scuba diving industry. Shortly after this Florida ban, the Cayman Islands legislature prohibited the feeding of sharks (Billings 2002), and the state of Hawaii prohibited the feeding of all marine life (MSG 2002) in their respective waters. As with the dolphin-feeding ban, there was no direct scientific investigation into the effects of supplementally feeding sharks, with the ruling based on assumptions of effects provided by testimonies from scientists, conservationists, divers and concerned citizens. In fact, there are no comprehensive, published scientific data documenting the effects of supplementally feeding a marine animal in its natural habitat (GIMEC 2001; Orams 2002). Such data are essential to effectively manage marine animal feeding activities in a manner that minimizes adverse impacts to the animals and their ecosystems (Sitnik 2002).

While dolphin and shark feeding activities have been the focus of widespread controversy in the public and private sectors, the effects of the supplemental feeding of other groups of marine wildlife, such as stingrays, has received little consideration. The supplemental feeding of stingrays is now a common tourist attraction throughout the world, particularly in the Caribbean. The author knows of at least ten stingray feeding sites in six countries in the Caribbean, and this number continues to grow. Due to the abundance and opportunistic feeding pattern of the southern stingray, *Dasyatis americana*, in the Caribbean, they are the most abundant species at these feeding sites.

1.2 The Southern Stingray, Dasyatis americana

The southern stingray, *Dasyatis americana*, one of the most commonly encountered elasmobranchs in near shore waters throughout the Caribbean, ranges from New Jersey to Rio de Janeiro, Brazil (Bigelow and Schroeder 1953; McEachren and Fechhelm 1998). Despite its abundance and wide distribution, little is known about the behavior and movement patterns of this species in the wild.

A marked sexual dimorphism occurs in this species, with females attaining a maximum disc width of 1500 mm while males may only attain a disc width of 800 mm (McEachren and Fechhelm 1998). At similar sizes the male's claspers are the only external indicator of gender. The exact size at sexual maturity for *D. americana* is unknown. Bigelow and Schroeder (1953) reported the examination of a mature 510 mm (disc width) male and suggested that sexual maturity occurs for males at or below this size. Funicelli (1975) suggested that male *D. americana* in the Gulf of Mexico mature at a disc width of 750-800 mm or possibly smaller while Funicelli (1975) examined two gravid females of 698 and 710 mm disc width caught in the Gulf of Mexico, indicating a smaller maturation size, at least in that area.

Numerous studies have investigated the stomach contents and feeding habits of *D. americana*, the most extensive being that by Gilliam and Sullivan (1993). All investigations to date have suggested that small crustaceans, teleosts, molluscs and annelids make up a majority of their diet (Bigelow and Schroeder 1953; Randall 1967; Snelson and Williams 1981), with decapod crustaceans being the most important item (Funicelli 1975; Gilliam and Sullivan 1993). Based on the high percentage of stomachs containing a large number of prey items (>10) and the overall variety of prey categories found, Gilliam and Sullivan (1993) concluded that feeding is continual and opportunistic. Stokes and Holland (1992) examined a male *D. americana* captured in Old Tampa Bay, Florida whose stomach contained several hundred lancelets, *Branchiostoma floridae*. *B. floridae* comprised over 70% of the infaunal biomass at the capture site, so it appears that this individual was taking advantage of the most available prey species, further indicating that *D. americana* feed opportunistically.

Chapman et al. (2004) documented a mating sequence for *D. americana* based on the observation of two mating events at Grand Cayman, Cayman Islands and two at Bimini, Bahamas. Mating occurred 'ventral to ventral' with the male inverted underneath the female while maintaining an oral grasp on the posterior margin of her pectoral fin. Females were seen to mate with more than one male in quick succession. They noted that polyandrous mating may occur in this species through two modes: forced multiplemale restraint and female choice.

Notes on the reproduction of five captive adult female *D. americana* and their offspring by Henningsen (2000) revealed that litter size ranged from two to ten pups, with an average neonate size of 238 ± 1.6 mm DW. Average gestation was 175.4 ± 4.1

days with a range of 135–226 days. Henningsen (2000) also found a positive correlation between litter size and maternal size, and a negative correlation between litter size and neonate mean size and weight, although this should be considered cautiously due to a small sample size (n=5).

A symbiotic cleaning relationship between *D. americana* and the bluehead wrasse, *Thalassoma bifasciatum*, was described by Snelson et al. (1990) at Bimini, Bahamas. They described the cleaning of ectosparasites from *D. americana* by *T. bifasciatum* as occurring in either a mobile or stationary manner at well-defined cleaning stations.

Several dasyatid rays are taken in fisheries as target species (Mathews and Druck 1975; Francis 1998) or as by-catch (Stobutzki et al. 2002); however, the exploitation value of *D. americana* appears mainly non-consumptive.

While no previous studies have examined the movement patterns of *D. americana*, some aspects of the movement patterns of several other dasyatid rays have been investigated. Cartamil et al. (2003) used manual acoustic telemetry to track the movements of seven Hawaiian stingrays, *Dasyatis lata*, and found that this species has a distinct diel movement pattern. Pooled tracking data revealed that *D. lata* exhibited significantly larger activity spaces at night ($0.83\pm0.70 \text{ km}^2$) than during the day ($0.12\pm0.15 \text{ km}^2$); average total activity space size was ($1.32\pm0.75 \text{ km}^2$) (Cartamil et al. 2003). The movements of the Atlantic stingray, *Dasyatis sabina*, were investigated by several authors using conventional tag-and-recapture techniques. Schmid (1988) concluded that they had restricted movements and others suggested the occurrence of seasonal offshore migrations (Sage et al. 1972; Funicelli 1975; Schwartz and Dahlberg 1978; Lewis 1982). Teaf (1978) observed a strong relationship between direction of movement and the direction of tidal flow for *D. sabina* at Apalachee Bay, Florida. Snelson and Williams (1981) concluded that *D. sabina* was equally active during the day and night, based on frequency of capture data. An in-depth study of this species conducted by Snelson et al. (1988) at the Indian River Lagoon, Florida concluded that their movements were restricted by temperature, and that 15 - 17 °C is a critical thermal threshold, initiating the seasonal migrations. Struhsaker (1969) also noted that 15 °C was a lower temperature limit, restricting the movements of the rough-tail stingray, *Dasyatis centroura*. The bluntnose stingray, *Dasyatis sayi*, is thought to be more active at night than during the day, also based on frequency of captures (Snelson and Williams 1981; Snelson et al. 1988).

1.3 Stingray Feeding Sites, Grand Cayman

Intentional supplemental feeding of *D. americana* has occurred at two sites in the North Sound of Grand Cayman, Stingray City (SC) and Stingray City Sandbar (SCS), since 1986 (Nelson, 1995). Initially, stingrays scavenged the remains of fishers cleaning their catch at these sites (Nelson 1995), but they are now fed almost exclusively packaged California squid, *Loligo opalescens*, (previously frozen) as an attraction for tourists. This almost daily feeding has resulted in a large number of stingrays being conditioned to approach humans, providing an opportunity for humans to observe and interact closely with these animals in their natural habitat. This interactive marine experience generates significant income for tourist-related Grand Cayman businesses, whose patrons are predominantly cruise ship passengers. Since their inception, these feeding sites have

gained worldwide recognition and have been referred to as the most popular and successful dive sites in the world (Sterba 1993; Bradly 2001). Their success and popularity has grown to the extent where over 3000 people may visit SCS in a single day (pers. obs.).

The Cayman Islands Department of the Environment (DoE), the governmental body responsible for the management and sustainable use of the island's natural environment and resources, issued voluntary stingray feeding guidelines in 2000 (Appendix A), in an attempt to limit and regulate stingray feeding activities. The DoE preferred that stingrays not be fed, but recognized the popularity of the feeding sites and their significant contribution to the Cayman Islands tourism product (Ebanks-Petrie, 2000). Unfortunately, compliance with the voluntary guidelines has been minimal, resulting in unregulated and uncoordinated feeding of stingrays by many user groups at the two feeding sites.

In March 2003, the North Sound Sub-Committee of the Cayman Islands Tourism Association (CITA) Watersports Sector, a conglomeration of tour operators utilizing the stingray feeding sites, released its recommendations regarding the management of these sites. CITA members were concerned that the popularity of SCS had resulted in overcrowding at peak times. More than 30 large vessels may be present any one time at SCS (pers. obs.). CITA believed the overcrowding led to a poor tourism product and decreased safety levels for visitors (CITA 2003). They requested government regulation at the two sites and the demarcation of SCS with large buoys at the 1.5 m depth contour surrounding the sallow sandbar (CITA 2003). Demarcation would restrict anchorage to a water depth of 1.5 m or greater, resulting in less movement of sand by boat propellers and

permitting tour operators to take only patrons who were able to swim. CITA also expressed its desire for SCS to become an exclusive product again by standardizing prices amongst tour operators (CITA 2003).

In April 2003, the Cayman Islands Minister of the Environment and Tourism, Hon. McKeeva Bush, issued a letter to the Cayman Islands Port Authority (CIPA) ordering it to demarcate the Sandbar with buoys at the 1.2 m depth contour. It was hoped that these buoys would bring a sense of order to boat anchoring at SCS, thus reducing safety concerns and sand movement by propellers. In response to this letter, the CIPA, in conjunction with the DoE, placed over 25 buoys at SCS. The buoys were anchored, by rope, to a concrete cinder block. Over the following weeks the buoys were gradually destroyed by the propellers of boats that were anchored too close to them. Within six weeks, all that remained of the buoys were their cinder block anchors. Anchoring of boats at SCS became haphazard and unregulated once again.

Currently there are no specific regulations governing the feeding of *D. americana* at Grand Cayman, and neither the species nor the feeding sites are afforded any official protective status.

1.4 Statement of Thesis Objectives

Supplemental feeding of *D. americana* at Grand Cayman has far-reaching economic, social, psychological and environmental impacts (Orams 2002). However, the present study solely investigates how the supplemental feeding influences the movement patterns of *D. americana*, including activity spaces, rates of movement, site fidelity and diel patterns. This research is the first detailed investigation into the influence of

supplemental feeding on the movement patterns of a marine animal, and is part of a larger study investigating how growth rates, population size, size at maturity and reproductive success may be influenced by supplemental feeding.

The objectives of this study were to investigate and compare the movement patterns of *D. americana* at supplemental feeding sites and non-feeding 'wild' sites (also referred to as control sites) using a variety of methods. We simultaneously collected movement data from supplementally fed stingrays (herein referred to as 'provisioned' stingrays) at SCS and 'wild' stingrays at several control sites at Grand Cayman, using manual acoustic telemetry and mark/recapture techniques. Additionally, we utilized automated acoustic telemetry at SCS to investigate the diel patterns and site fidelity of stingrays visiting this site. Data collected from wild stingrays served as control data. Due to the similarities in body size and habitat of provisioned and wild stingrays observed in this study, differences between stingrays within these two communities are presumed to be a result of supplemental feeding.

Because there is strong selection for an animal to move within and among the environments that supply needed resources (Mitchell and Powell 2004; Jetz et. al; 2004) and the fact that supplemental feeding effectively constricts food resources to a specific location, we investigated the influence of supplemental feeding to determine if the activity space of *D. americana* is adaptive (Schoener and Schoener 1981) and thereby reduced by the consistent supplemental feeding in a small area, i.e. it is a function of food requirements and availability (McNab 1963; Harestad and Bunnell 1979; Koford 1992). We also investigated whether core area overlap increased between provisioned individuals, thus increasing the local population density.

The findings of this research will be presented to the Cayman Islands Department of the Environment (DoE), allowing them to better evaluate some of the biological implications of supplemental feeding on the biology of *D. americana*.

2. MATERIALS AND METHODS

2.1 Study site

Grand Cayman (19°18'N, 81°16'W) is the largest island in a three island chain known as the Cayman Islands (Figure 1). The Cayman Islands are exposed carbonate peaks of the Cayman Ridge, which originates in southeastern Cuba and extends westward toward Belize (Roberts 1994). This ridge lies to the north of the Cayman Trench, a deep trough with water depths exceeding 6000 m (Roberts 1994).

Grand Cayman is situated in the center of the Caribbean Basin, with the nearest large landmass over 250 km away, resulting in a climate that is strongly influenced by the sea (Burton 1994; Roberts 1994). The most apparent indicator of seasonal change on the island is variation in rainfall (Burton 1994). There is limited annual fluctuation in temperature; the annual range in high air and water temperatures is only 3.6 °C and 5.1 °C, respectively (Burton 1994). Tides have mixed diurnal and semidiurnal components with a relatively low average amplitude of 260 mm (Burton 1994; Roberts 1994).

The majority of the coastline of Grand Cayman is surrounded by a series of lagoons, the largest of which is the North Sound, with a surface area of 91 km² and a maximum depth of 5 m (Figure 2). These lagoons are commonly fringed on the landward side by mangroves and on the seaward side by a tidally-exposed, linear coral reef. The mangrove communities are a mixture of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* (Brunt and Burton 1994), while the fringing reefs are dominated by the coral *Acropora palmata*, with *Diplora strigosa*, *D. clivosa*, *Montastrea annularis*, *Millepora complanata*, *M. alcicornis*, *Agaricia agaricites*, *A. nobilis*, *Porites porites* and *P. asteroides* present, but less abundant (Rigby and Roberts 1976). Roberts (1994)

identified six major benthic zones within the lagoons: rubble flat, sand flat, moat, hardgrounds, grass plain and shore zone. The rubble flat is essentially the debris zone of lagoonward moving coral fragments derived from the reef crest by wave action and currents. Coral fragments deposited here are almost exclusively A. palmata which become heavily encrusted and bored by various organisms, including Milleporid corals, calcareous red algae, foraminiferans, serpulids and bryozoans. Clumps of brown algae are common in this zone. The sand flat, an extension of the rubble flat, is the deposition zone for finer grain reef-derived sediments. Conical mounds created by the burrowing shrimp Callianasa and worm Arenicola are prominent here, and both species are important nutrient recyclers in this zone. The green algae Halimeda and Penicillus are moderately abundant, while the sea grasses Thalassia testudinum and Syringodium filiforme are sparse. The queen conch, Strombus gigas, and cushion sea star, Oreaster reticulatus, are common. The moat, with a lower elevation than adjacent zones, is essentially a pathway for tidal exchange. This area of increased tidal flow is home to patch reef communities dominated by large boulders of *M. annularis* and colonies of *A. cervicornis* and alcyonarians. Hardgrounds occur in isolated areas within the sand flat and are characterized by a thinning or absence of sediment and a sudden increase in alcyonarian diversity and density. Brown algae are common here along with the longspined sea urchin Diadema antillarum. The grass plain is dominated by medium to dense belts of T. testudinum with S. filiforme and Halodule wrightii also present. The extensive subsurface network of rhizomes and roots of these vascular plants help stabilize sediments within the lagoon. The exposed shoots and leaves of the seagrasses serve as a substrate for encrusting sponges, serpulids, red algae, bryozoans and foraminiferans and

as an anchor for molluscan and ascidian egg cases. Various species of green algae are present along with numerous holothurians and gastropods. The West Indian sea egg, *Tripneustes ventricosa*, can be locally abundant. A healthy infauna of bivalves is dominated by *Chione*, *Codakia*, *Glycymeris*, *Laevicardium* and *Pinna*. The conical mounds of burrowing organisms, common on the sand flat, continue on to the grass plains but become less abundant. The shore zone is often covered by a thin layer of sediment with patches of rocky floor common. Brown and green algae are abundant. Small colonies of coral including *Porites divarcata*, *P. furcata* and *Siderastrea radians* are common. Alcyonarians and loggerhead sponges occur regularly, while the calcareous red alga, *Goniolithon strictum* can occur in dense patches locally among *T. testudinum*.

2.1.1. Supplemental Feeding Sites

2.1.1.1 Stingray City

Stingray City (SC) is located in the moat zone on the western edge of the North Sound, adjacent to the fringing reef (Figure 2). Water depth at this site is 3.5 - 4 m which limits visitors to scuba diving or snorkeling. This site has a surface area of 13,800 m² is located 850 m from the edge of a marine replenishment zone (Appendix B).

2.1.1.2 Stingray City Sandbar

Stingray City Sandbar (SCS) is a naturally occurring sandbar located in the North Sound, 3.5 km west of Rum Point (Figure 2). This site is bordered to the south by the vast, *T. testudinum* dominated, grass plain and to the north by the relatively deeper patch reefs of the moat zone (Figure 3). SCS has a surface area of approximately 7800 m² and

water depth as shallow as 0.5 m. A marine replenishment zone lies 370 m to the southeast of SCS. The shallow water at this site makes it accessible to the general nondiving public, and it is frequented by a considerably higher number of visitors and stingrays than SC; thus SCS was chosen over SC as the primary sampling site for investigating the movement patterns of provisioned stingrays.

2.1.2 Control Sites

Four control sites were identified and sampled based on the observation and accessibility of communities of wild *D. americana*.

2.1.2.1 South Sound

The South Sound is located off the southwest coast of Grand Cayman and has a surface area of 3 km² (Figure 2). The South Sound is a semi-enclosed lagoon system, open at the western edge near Pull-and-be-Damned Point, and through an artificial channel in the center of the fringing reef (Figure 4). Both openings serve as channels for tidal exchange. Water depth varies from 0.2 - 3 m within the lagoon. The entire South Sound is a marine replenishment zone (Appendix B). Moderately developed mangrove communities occur along the central and eastern shorelines and a sand flat covers a large portion of the southeastern lagoon. Dense grass plains of *T. testudinum* inhabit the northeast, north-west and central sections of the lagoon. A shallow moat occurs west of the artificial channel.

2.1.2.2 Barkers

Barkers is located at the northwest tip of the North Sound (Figure 2) and is enclosed in a marine replenishment zone (Appendix B). The study area covers approximately 0.55 km² and encompasses dense mangrove communities and both the shore zone and grass plain (Figure 4). A variety of habitats exist within these two zones, including rocky floor, sand bowls and dense *T. testudinum* beds interspersed with patches of the calcareous red alga *G. strictum*. Water depth varies from 0.2 - 1 m. This shallow, diverse site provides nursery habitat for juvenile *D. americana*, lemon sharks *Negaprion brevirostris* and several turtle species. The marine replenishment zone at Barkers and the adjacent land mass are awaiting designation as the Cayman Islands first national park (Bell, C. pers. comm. Cayman Islands Department of the Environment).

2.1.2.3 Frank Sound

The Frank Sound is located off the southeast coast of Grand Cayman (Figure 2) and is almost identical in size to the South Sound, with a surface area of 2.95 km². The Frank Sound is an enclosed lagoon system, open only through an artificial channel in the center of the fringing reef (Figure 5). Water depth varies from 0.2 - 3.7 m within the lagoon. The central and eastern portions of the lagoon are protected as a marine replenishment zone (Appendix B). Moderately developed moat zone patch reefs inhabit the central lagoon adjacent to the channel. Large sand flats occupy much of the center of the eastern and western portions of the lagoon. North of the sand flats are well developed, *T. testudinum* dominated grass plains. Well developed hardgrounds support lush communities of alcyonarians east of the channel. The urchins *D. antillarum* and *T*.

ventricosa are locally abundant in the rubble zone and grass plains, respectively, east of the channel. Poorly developed mangrove communities scatter the eastern shoreline, interspersed with rocky and sandy shores.

2.1.2.4 Rum Point / Cayman Kai

Rum Point is located at the northeast tip of the North Sound (Figure 2) and is enclosed in a marine replenishment zone (Appendix B). The study area contains sand flat and grass plain communities (Figure 5) and covers approximately 0.64 km². Water depth varies from 0.2 - 2 m within the study site. This shallow site also serves as a nursery for *D. americana*.

2.2 Manual Acoustic Telemetry (MAT)

2.2.1 Telemetry Equipment

Two models of ultrasonic transmitters were used for manual tracking. V16-4H-01 transmitters (Vemco, Nova Scotia. 16 mm diameter x 65 mm, 10 g [in water], frequencies 51 - 81 kHz, lifespan 218 days) were used to track stingrays with a disc width of 750 mm or greater, and V8SC-2H transmitters (Vemco, Nova Scotia. 9 mm diameter x 30 mm, 3.1 g [in water], frequencies 66 - 84 kHz, lifespan 25 days) were used to track individuals with a disc width of less than 750 mm. The transmitters were programmed to emit an ultrasonic pulse every two seconds. The selection of these transmitters was based on a compromise between maximizing signal strength and longevity while minimizing post-operative stress to the tracked animal.

Ultrasonic pulses were detected using an aluminum-housed, submersible directional hydrophone (Vemco model VH10) attached to the tracking vessel using a custom-made mount, built from polyvinylchloride (PVC) pipe. The hydrophone was connected to a portable receiver (Vemco model VR60-01-02-07-08) powered by an internal 12 volt sealed lead acid battery.

2.2.2 Animal Capture and Handling

Stingrays were located visually from a small boat and encircled in a hand-drawn seine net. A landing net was used to transfer stingrays into a seawater-filled canvas pool inside the boat. Once in the boat, two binder clips were placed over the animal's spine and adjacent tail, allowing safe and efficient handling (Figure 6). Prior to transmitter attachment all stingrays were sexed, measured (disc width), weighed and injected with an internal Passive Integrative Transponder (PIT) tag (Digital Angel Corporation, Minnesota).

Following Cartamil et al. (2003), transmitters were externally attached, using a swivel and split ring, to a Peterson disc tag (Floy Tag Company, Washington. 20 mm diameter) that passed dorso-ventrally through the right pelvic fin (Figure 7). The transmitters were coated with a thin layer of wax (50% beeswax, 50% paraffin wax) to reduce abrasion on the skin of the stingray. Stingrays were submerged in fresh seawater in the pool throughout the entire handling period to reduce stress. Handling time did not exceed seven minutes and stingrays were released at the capture site.

2.2.3 Tracking protocol

An outboard powered sport-fishing boat (Dusky, 25 ft) was used as the primary tracking vessel, with a smaller twin-hulled boat (Nautico, 14 ft) used occasionally as weather permitted. Both tracking vessels were equipped with a hull-mounted hydrophone adjacent to the center console, allowing for tracking, driving and navigation by a single person. The tracking vessel was crewed by a minimum of two people, a tracker/driver and an assistant responsible for anchoring and additional navigation. Stingrays were tracked for 24, 48 or 72 h depending on location, weather and availability of tracking assistants. The two-person tracking crew could track efficiently for 24 hr shifts, alternated by a 24 hr rest period. Following the rest period, stingrays were relocated by following a specific search pattern based on the previous shift, stopping frequently to search for ultrasonic signals.

During each track, the position of the tracking boat was automatically recorded every ten minutes by a handheld GPS unit (Garmin model 12). Latitude, longitude and time data recorded by the GPS unit were downloaded to a computer using a PC cable and Garmin Mapsource software. These data were divided into daytime and nighttime positions based on local sunrise and sunset information. These data were then reprojected to a Universal Transverse Mercator (UTM) coordinate system, allowing them to be viewed on a Grand Cayman aerial photo-mosaic in a GIS. ESRI Arcview GIS 3.3 software with Animal Movement Analyst Extension (AMAE) (Hooge and Eichenlaub 1997) was used for displaying all tracking data.

2.3 Automated Acoustic Telemetry (AAT)

2.3.1 Telemetry Equipment

V16-4H-01-R04K (Vemco, Nova Scotia. 16 mm diameter x 65 mm, 10 g, frequency 69 kHz, lifespan 570 days) coded ultrasonic transmitters with random pulse rates were used for automated tracking. An array of two single channel, stationary receivers (Vemco model VR2-69.0KHz-1.03-2-1431-C-211) were deployed at SCS, 180 m apart, and covering approximately 70% of the supplemental feeding area. Receiver number 2906 was placed 100 m NE of the center of SCS and receiver number 2907 was placed 100 m SW of the center of SCS. VR2 receivers automatically record the date and time that coded transmitters are within their detection ranges. The main body of the receivers were placed in custom-made housing units built from PVC pipe, threaded brass rods and concrete (Digirilamo, A. pers. comm. Bimini Biological Field Station) (Figure 8). The housing units did not enclose or interfere with the omnidirectional hydrophone, located at the tip of the receiver, but served to protect and stabilize the body of the receiver. Due to the shallow water, high level of boat traffic and the possibility of diver interference at SCS, the units were partially buried in the sediment and attached to two 1 m long 'garden shed' anchors with anchor chain and shackles (Figure 8).

2.3.2 Receiver Range Testing

Prior to transmitter deployment, transects were run using an activated transmitter from each stationary receiver in four directions (North, South, East and West) to determine their reception range and overlap. The transmitter was placed low in the water column (where stingrays normally reside) at 100, 200, 300, 400 and 500 m from the stationary receivers. From this range testing polygons representing the receivers' detection ranges were calculated.

2.3.3 Animal Capture and Handling

Capture techniques for AAT were identical to those used for MAT (see 2.2.2). Stingrays were flipped dorso-ventrally and restrained for approximately thirty seconds to induce tonic immobility. This immobile state of relaxed muscle tone or torpor significantly reduced struggling by the stingray (Watsky and Gruber 1990; Henningsen 1994), eliminating the need for anesthetic, and also presented the ventral surface of the stingray for surgical transmitter implantation. The mouth and spiracles of stingrays were submerged in fresh seawater throughout the entire surgical procedure. Coded transmitters were coated in a thin layer of wax (50% beeswax, 50% paraffin wax) to reduce abrasion on the internal organs and reduce transmitter rejection (pers. comm., B. Wetherbee, University of Rhode Island.). They were then internally implanted in the peritoneal cavity through a 20 mm incision in the ventral surface of the stingray, which was closed with four non-absorbable silk sutures.

2.3.4 Tracking protocol and data downloading

The VR2 receivers were retrieved and presence/absence data were downloaded every three to four weeks using a VR1-PC interface cable (Vemco, Nova Scotia) and a personal notebook computer. The receivers were cleaned of biological fouling prior to redeployment.
2.4 Animal Tag and Recapture

2.4.1 Internal tagging

All captured stingrays were tagged internally with a Passive Integrative Transponder (PIT) tag (Digital Angel Corporation, St. Paul MN). Tags were injected into the left pelvic fin musculature with a syringe. The location of each capture was recorded using a handheld GPS unit (Garmin 12). We sampled SCS monthly, and control sites weekly, for previously tagged stingrays. When tagged stingrays were recaptured, their position and distance traveled since last capture were calculated. Scars from tissue samples, taken for a concurrent genetics investigation, served as a measure of tag retention.

2.4.2 External tagging

Stingrays captured at non-feeding sites were also tagged with an external spaghetti tag (Floy Tag Company, Seattle WA). This technique allowed for visual recognition of wild stingrays and was employed to further discern the presence of separate communities of *D. americana* at Grand Cayman.

2.5 Diel Activity

AAT presence/absence data were used to infer diel activity patterns of tracked stingrays at SCS. Data were examined using VR2PC software (Vemco, Version 1.12) and graphical analysis. Detections from individual transmitters were sorted into hourly bins and plotted against the percentage of 'pingered' days that stingrays were within the detection ranges of the receivers.

2.5.1 Activity Space

Activity space was calculated from MAT data using a fixed kernel home range utilization distribution within Arcview GIS 3.3 software with Animal Movement Analyst Extension (AMAE) (Hooge and Eichenlaub 1997). The kernel distribution is a density dependant model that describes an animal's space utilization within a selected output contour (Worton 1989; Seaman and Powell 1996). Following Hooge et al (1999) the 50% contour was chosen to represent the core areas of activity of tracked stingrays, and the 95% contour was chosen to represent their activity space. When calculating activity spaces, five percent of location points were removed to mitigate outlier effects (Hooge et al; 1999). Due to differences in track duration between stingrays, a standardized period of 24 h was chosen for all activity space comparisons. For stingrays tracked for more than one 24 h period, an average 24 h activity space size was calculated.

For each manually tracked stingray a day, night and total core area and activity space were calculated. These data were then pooled for the five manually tracked animals at each location (SCS and South Sound) according to time of day. Pooled day, night and total core area and activity space data were compared within and between provisioned and wild stingrays using a Mann-Whitney U Test. This non-parametric test was used because it is unknown whether the data approximate a normal distribution.

2.5.2 Rate of Movement

MAT data were converted from a point file to a poly-line file using AMAE. This conversion outputs a table of distances between successive position fixes. A day, night and total rate of movement were calculated for each stingray by dividing these distances

by the sampling interval. These rates of movement estimated the speed over ground of manually tracked stingrays. Pooled day, night and total rates of movement were compared within and between provisioned and wild stingrays using a Mann-Whitney U Test.

2.6 Tides

Tide data were obtained from the Cayman Islands Government Mosquito Research and Control Unit (MRCU), which monitors the tides from a measuring station located on the southern shoreline of the North Sound (Figure 9).

2.6.1 Tides and Animal Activity Space

To examine the influence of tides on the activity spaces of manually tracked stingrays, MAT data was divided into tidal phases of incoming, outgoing, high and low slack water. High and low tidal phases were delineated as periods from one hour before to one hour after high and low tide. Activity space size during the four tidal phases for each manually tracked stingray was calculated and these data were pooled for the five animals at each location (SCS and South Sound) according to tidal phase. Pooled tidal phase data were compared using a Kruskal-Wallis Test, which is used as a generalization of the Mann Whitney U Test when comparing three or more samples.

2.6.2 Tides and Animal Rate of Movement

Using the MAT data divided into four tidal phases (see 2.6.1), a rate of movement was calculated for each stingray over the four tidal phases to examine the influence of tides on the rate of movement of manually tracked stingrays. Rate of movement data were pooled for the five manually tracked animals at each location (SCS and South Sound) according to tidal phase and compared using a Kruskal-Wallis Test.

2.7 Site Fidelity

Site fidelity of stingrays visiting SCS was investigated using AAT data. Presence/absence data stored on the VR2 receivers was analyzed with VR2PC software to determine how often tagged stingrays were within the detection ranges of the receivers. The percentage of 'pingered' days that stingrays were detected by the receivers over the study period was calculated.

Data collected from PIT tagging stingrays were used as a qualitative measure of site fidelity for both provisioned and wild stingrays. The distance traveled between successive captures indicated the degree of side fidelity shown by individual stingrays.

3. RESULTS

3.1 Manual Acoustic Telemetry

Fourteen mature *D. americana* were tracked manually at Grand Cayman during two field seasons, from February to May 2002 and April to August 2003. Five of those stingrays were provisioned females ($\bar{x} = 108.8 \pm 9.0$ cm disc width [DW]), two were provisioned males (58 and 70.5 cm DW), five were wild females at the South Sound ($\bar{x} =$ 92.7 ± 10.1 cm DW) and two were wild stingrays at Rum Point (a male [49.5 cm DW] and female [81 cm]) (Table 1). Individual stingrays were continually tracked for five to 72 hours and a total of 2,542 geographic positions were recorded.

Mature females were chosen for the majority of manual tracks because they were the predominant demographic at SCS, representing 67% of all stingrays captured at this site (Figure 10). The South Sound was chosen as the primary control site for manually tracking wild stingrays because of its environmental similarity to the North Sound and the presence of an accessible population of wild mature female *D. americana*. All manually tracked stingrays were released in excellent condition. Stingrays at SCS were observed immediately returning to tourists and receiving food handouts.

3.1.1 Provisioned Stingrays

All stingrays tracked at SCS remained active (i.e. displayed almost continuous movements without stationary periods) at SCS during supplemental feeding periods, which occurred from approximately 0800 to 1700 h daily. Following the cessation of supplemental feeding, all manually tracked female stingrays moved to the adjacent moat and sand flat zones north of SCS, where they buried in the sand for several hours in large

congregations of con-specifics, all oriented toward the current (Figure 11). Between 1930 and 2130 h, the tracked female stingrays moved from this area to individual resting areas, where no movement was detected for several hours. All stingrays tracked at this location arrived back at SCS prior to the commencement of supplemental feeding activities the following day.

The following detailed descriptions provide a more in depth account of the movements of provisioned stingrays tracked manually at SCS. Stingray number 1 was tracked for 24 h (Figure 12). This female stingray moved away from the SCS area at 1945 h toward the southeast and stopped at three different locations during the night, where no movement was detected for a total of 8 hours 35 min. The farthest this stingray moved away from SCS was 545 m, and it returned to SCS at 0700 h the following morning.

Stingray number 2 was tracked for 24 h (Figure 13). This female stingray moved away from the SCS area at 1930 h toward the southwest and stopped at a location 427 m from SCS, where no movement was detected for 5 h 20 min. The farthest this stingray moved away from SCS was 535 m, and it returned to SCS at 0645 h the following morning.

Stingray number 3 was tracked for three 24 h periods (Figure 14). This female stingray moved away from the SCS area between 1900 and 2000 h each night. The stingray moved 1.1 km west across the sand flat and grass plain zones to an area of hardground, encircled by sand, approximately 70 m in diameter (Figure 15). The stingray arrived at this sandy circle between 2000 and 2130 h each night and stopped for an average of 6 h 20 min, with no detectable movement. The stingray then departed the

sandy circle, and returned to SCS, arriving between 0345 and 0500 h the following morning.

Stingray number 4 was tracked for 24 h (Figure 16). This female stingray moved away from the SCS area at 2015 h toward the southeast and stopped 490 m from SCS, where no movement was detected for 6 h 10 min. The furthest this stingray moved away from SCS was 550 m and it returned to SCS at 0530 h the following morning.

Stingray number 5 was tracked for three 24 h periods (Figure 17). This female stingray moved away from the SCS area between 2030 and 2130 h each night toward the southeast. The stingray stopped at a different location every night, where no movement was detected for more than 3 h (all locations were within 150 m of each other and approximately 500 m from SCS). The farthest this stingray moved away from SCS was 575 m, and it returned to SCS between 0230 and 0430 h the following morning.

Stingray number 6 was tracked for 24 h (Figure 18). This male stingray moved away from SCS at 1735 h toward the northeast, where it stopped in the shallow fringing reef crest, 200 m northeast of SCS; no movement was detected for 2 h 35 min. At 2010 h, the stingray began a long westward movement over the rubble flat zone, moving parallel to the fringing reef. The stingray stopped at 2130 h, 2.1 km west of SCS, at the mouth of the main channel entrance of the North Sound, and began swimming east, back toward SCS. At 0015 h, the stingray arrived back at the fringing reef adjacent to SCS, where it stopped with no movement detected over the following 5 h 30 min. The stingray began moving toward SCS at 0545 h, arriving at 0600 h.

Stingray number 7 was tracked for 24 h (Figure 19). This male stingray moved away from SCS at 1745 h toward the northeast. After circling over the fringing reef

adjacent to SCS, the stingray began a long westward movement over the rubble flat zone, moving parallel to the fringing reef. The stingray stopped at 2115 h, 2.1 km west of SCS, at the mouth of the main channel entrance of the North Sound, and began swimming east, back toward SCS. At 1135 h, the stingray arrived back at SCS, but immediately began another westward movement over the rubble flat zone back toward the main channel entrance. The stingray reached the main channel entrance at 0025 h, where it remained with little detectable movement for 5 h 20 min until it began moving eastward at 0545 h, arriving at SCS at 0745 h.

3.1.2 Wild Stingrays

All wild female stingrays tracked at the South Sound exited the lagoon, on at least one occasion, through one of the channels, during the middle of the day. All stopped and did not move for a minimum period of 4 h 15 min in water greater than 15 m deep, outside the lagoon during the day. All the stingrays showed more movement at night than during the day. Several wild stingrays were observed foraging during early morning and nighttime periods inside the lagoon over sand flat and grass plain zones. No foraging was observed during the middle of the day or outside the lagoon.

The following detailed descriptions provide a more in depth account of the movements of individual stingrays manually tracked at the South Sound. The track for stingray number 8 was initiated at 0810 h and continued for 24 h (Figure 20). The stingray exited the South Sound through the artificial channel at 1000 h and stopped on the deep fore-reef shelf, 375 m southeast of the channel entrance; no movement was detected for 6 h 30 min. Water depth at this location was approximately 20 m and the

bottom type was a 'spur and groove' coral community, 200 m north of the reef wall. This stingray was observed buried in a sandy 'groove' location (Figure 21) with additional mature female *D. americana* buried in the surrounding area. The stingray reentered the South Sound through the artificial channel at 1730 h. The stingray moved almost continually throughout the night, over the western grass plain and sand flat zones, stopping at four locations where no movement was detected for a total of 1 h 30 min.

The track for stingray number 9 was initiated at 0515 h and continued for 24 h (Figure 22). The stingray was observed foraging in the southeastern sand flat zone from 0545 to 0615 h. From there the stingray moved west toward the artificial channel and exited the South Sound at 1045 h. The stingray stopped on the deep fore-reef shelf, 450 m southwest of the channel entrance; no movement was detected for 4 h 10 min. Water depth at this location was 18 m, and the bottom type was a 'spur and groove' coral community 225 m north of the reef wall. This stingray was observed resting in a sandy 'groove' location. The stingray reentered the South Sound through the artificial channel at 1545 h. The stingray continually moved from 1600 to 0020 h over the central grass plain zone. At 0030 h, the stingray began an eastbound commute across the rubble flat and moat zones west of the artificial channel. This stingray was observed foraging in shallow water numerous times. The stingray moved a total distance of 1.7 km, stopping in the rubbe flat east of the artificial channel at 0545 h.

Stingray number 10 was tracked manually tracked for two 24 h periods (Figure 23). This stingray exited the South Sound through the artificial channel at 1100 h on the first day and stopped on the deep fore-reef shelf, 330 m south of the channel entrance; no movement was detected for 5 h. Water depth at this location was approximately 20 m,

and the bottom type was a 'spur and groove' coral community 190 m north of the reef wall. The stingray reentered the South Sound through the artificial channel at 1630 h. The first night, the stingray moved continually over the central and eastern grass plain zones. This stingray was observed foraging between 0045 and 0115 h in a sandy bowl within the eastern grass plain zone. On the second day, the stingray remained inside the lagoon and stopped at a sandy location in the central lagoon, 145 m from shore; no movement was detected for 5 h 10 min. The stingray remained active throughout the second night, over the central grass plain zone.

Stingray number 11 was tracked manually tracked during two 24 h periods (Figure 24). This stingray exited the South Sound near Pull-and-be-Damned Point at 0645 h on the first day and stopped at a location 1 km southwest of the lagoon entrance; no movement was detected for 5 h 15 min. Water depth at this location was approximately 16 m, and the bottom type was flat and sandy, interspersed with large coral heads. The stingray reentered the South Sound through the artificial channel at 1455 h. Throughout the first night, the stingray remained active over the shallow western grass plain zones, remaining close to shore. On the second day the stingray exited the South Sound near Pull-and-be-Damned Point at 0815 hrs and stopped 80 m north of the first day's location. No movement was detected for 4 h 45 min, and the stingray reentered the lagoon at 1515 h. Throughout the second night, the stingray remained active over the western grass plain zone and also traveled further southeast than the first night, over the central grass plain and sand flat zones.

The track for stingray number 12 was initiated at 0930 h and lasted 24 h (Figure 25). This stingray exited the South Sound through the artificial channel at 1045 h and

stopped at the deep fore-reef shelf, 450 m southeast of the channel entrance; no movement was detected for 4 h 45 m. Water depth at this location was approximately 18 m, and the bottom type was a 'spur and groove' coral community 250 m north of the reef wall. This stingray was observed resting in a sandy 'groove' location. The stingray reentered the South Sound through the artificial channel at 1620 h. Throughout the night, the stingray remained active close to shore, traveling east over the central grass plain.

Track number 13 was of a wild male stingray at Rum Point for 5 h 15 m (Figure 26a). This track was initiated at 1010 h but aborted at 1525 h due to dangerous weather conditions. This stingray showed little movement, covering a total of 200 m during the entire track, and it was inactive for several hours. The stingray was last recorded approximately 130 m from shore in a water depth of less than 1 m.

Track number 14 was of a wild female stingray at Rum Point for 10 h 45 m (Figure 26b). This track was initiated at 1350 h but aborted at 0035 h due to dangerous weather conditions. This stingray remained stationary for the afternoon and began moving toward the northwest at 2000 h, following the northern coastline of Rum Point, remaining within 110 m of the shore. The stingray reached Rum Point at 2130 h and turned west then south, following the western coastline of Rum Point. This stingray was last recorded approximately 65 m from shore in a water depth of less than 1 m.

3.2 Automated Acoustic Telemetry

Coded transmitters were surgically implanted in five mature female *D. americana* at SCS during July and August 2003. Stingrays measured 95 to 114 cm DW ($\bar{x} = 102.2\pm8.0$ cm) (Table 2). All stingrays were released in excellent condition and were

observed immediately returning to tourists and receiving food handouts. Incisions made for transmitter implantation healed within 20 days. Transmitter retention and stingray survival were 100%.

Detection ranges for the two stationary receivers at SCS, based on range testing, were approximately 190 m radius, but this range was reduced in shallow regions (Figure 27). The SW receiver was deployed for 202 days, while the NE receiver was deployed for 389 days.

3.3 Tag and recapture

3.3.1 Internal tagging

A total of 327 *D. americana* were tagged with internal PIT tags at Grand Cayman during the two field seasons (Table 3). Based on the presence of scars from prior tissue sample removal, PIT tag retention was determined to be 100% over 19 months for the 183 recaptured stingrays. PIT tags did not appear to migrate within the stingrays' bodies.

3.3.2 External tagging

Thirty-five *D. americana* were tagged with external spaghetti tags at control sites at Grand Cayman during the first field season (Table 4). Based on recapture information, tag retention was determined to be approximately two months. Externally tagged individuals were only re-sighted or recaptured at their initial capture sites, i.e. there was no movement observed between study sites.

3.4 Diel Activity

AAT presence/absence data from both receivers showed that diel detection periodicity was positively correlated with supplemental feeding activities (Figures 28 and 29). This result is consistent with MAT data, indicating that provisioned stingrays utilize SCS during daytime feeding events and disperse from the feeding site at night.

3.4.1 Activity Space

Daytime, nighttime and total 24 h core areas and activity spaces for all manually tracked individual stingrays are listed in Table 5. Pooled data for the five females in each area (SCS and South Sound) are shown in Table 6 and Figure 30.

For provisioned female stingrays at SCS, pooled nighttime core areas $(0.031\pm0.033 \text{ km}^2)$ (mean±SD) and activity spaces $(0.207\pm0.193 \text{ km}^2)$ were significantly larger than pooled daytime core areas $(0.002\pm0.001 \text{ km}^2)$ and activity spaces $(0.014\pm0.003 \text{ km}^2)$ (Mann-Whitney U-test, *P* <0.05). For wild stingrays at the South Sound, pooled nighttime core areas $(0.106\pm0.049 \text{ km}^2)$ and activity spaces $(0.633\pm0.362 \text{ km}^2)$ were significantly larger than pooled daytime core areas $(0.032\pm0.011 \text{ km}^2)$ and activity spaces $(0.271\pm0.086 \text{ km}^2)$ (Mann-Whitney U-test, *P* <0.05).

Pooled daytime core areas $(0.002\pm0.001 \text{ km}^2)$ and activity spaces $(0.014\pm0.003 \text{ km}^2)$ of five female provisioned stingrays were significantly smaller than pooled daytime core areas $(0.032\pm0.011 \text{ km}^2)$ and activity spaces $(0.271\pm0.086 \text{ km}^2)$ of the five female wild stingrays (Mann-Whitney U-test, *P* <0.005). Pooled nighttime core areas $(0.031\pm0.033 \text{ km}^2)$ and activity spaces $(0.207\pm0.193 \text{ km}^2)$ of provisioned stingrays were significantly smaller than pooled nighttime core areas $(0.106\pm0.049 \text{ km}^2)$ and activity

spaces ($0.633\pm0.362 \text{ km}^2$) of wild stingrays (Mann-Whitney U-test, P < 0.05). Pooled total core areas ($0.024\pm0.014 \text{ km}^2$) and activity spaces ($0.132\pm0.079 \text{ km}^2$) of provisioned stingrays were significantly smaller than pooled total core areas ($0.091\pm0.031 \text{ km}^2$) and activity spaces ($0.876\pm0.171\text{ km}^2$) of wild stingrays (Mann-Whitney U-test, P < 0.01).

The two manually tracked provisioned male stingrays had a larger average nighttime $(1.230\pm0.490 \text{ km}^2)$ and total activity space $(0.824\pm0.776 \text{ km}^2)$ than the five females $(0.207\pm0.193 \text{ km}^2 \text{ and } 0.132\pm0.079 \text{ km}^2 \text{ respectively})$ (Figure 31). However the average daytime activity space of the tracked males $(0.033\pm0.006 \text{ km}^2)$ was similar to that of the tracked females $(0.014\pm0.003 \text{ km}^2)$.

The daytime core areas of the five manually tracked provisioned female stingrays overlapped each other by 72%, while the daytime core areas of five wild female stingrays from the South Sound overlapped by only 3% (Figure 32).

3.4.2 Rate of Movement

Rates of movement for manually tracked stingrays are shown in Table 7, with pooled data in Table 8 and Figure 33. Although rates of movement of wild stingrays were higher at night and rates of movement of provisioned stingrays were higher during the day, there were no significant differences between pooled daytime, nighttime or total rate of movement for wild and provisioned stingrays (Mann-Whitney U-test, P>0.05).

3.5 Tides

Times of peak high and low slack water for all manual tracking periods are listed in Table 9. Tide data confirmed findings by Burton (1994) that tidal amplitude at Grand Cayman is low, averaging 250-300 mm.

3.5.1 Tides and Animal Activity Space

Table 10 lists activity space sizes for individual stingrays over the four tidal phases; pooled data for provisioned and wild stingrays are shown in Table 11 and Figure 34. Statistical comparisons within each group over the four tidal phases revealed that tidal phase had no effect on the size of the core area or activity space of either provisioned or wild stingrays (Kruskal-Wallis test, P>0.05). Core area and activity space size of provisioned stingrays was significantly smaller than that of wild stingrays over all four tidal phases (Kruskal-Wallis test, P<0.05).

3.5.2 Tides and Animal Rate of Movement

Table 12 lists rates of movement for individual stingrays over the four tidal phases; pooled data for provisioned and wild stingrays are shown in Table 13 and Figure 35. Statistical comparisons of rates of movements over the four tidal phases revealed that tidal phase had no effect on the rates of movement of either provisioned or wild stingrays and that there were no differences in rates of movement between wild and provisioned stingrays (Kruskal-Wallis test, P>0.05).

3.6 Site Fidelity

AAT data showed that all tracked stingrays were recorded within the detection ranges of both of the receivers for at least part of every day of the study, indicating that provisioned stingrays exhibit strong site fidelity to SCS. MAT data from provisioned stingrays tracked for more than one 24 h period indicate that provisioned stingrays also show fidelity to predictable nighttime resting locations.

PIT tag and recapture data showed that 94% of PIT tagged, provisioned stingrays were recaptured at least once at SCS, some up to 11 times (Figure 36), totaling 986 individual recaptures at this site. All 986 recaptures of stingrays PIT tagged at SCS were of stingrays that were originally tagged at SCS, i.e. no stingrays originally tagged at other locations were ever recaptured or observed at SCS. Only one stingray initially tagged at SCS was subsequently recaptured at a different location. This individual (a 90 cm female) was tagged at SCS on February 12, 2002, recaptured at SC, 4.3 km away, on June 3, 2002, and subsequently recaptured at SCS on January 30 and April 16, 2003.

Based on PIT tag and recapture data, all 139 recaptures of wild stingrays were within close proximity of the original tagging site, and there was no observed movement of wild stingrays between control sites.

3.7 Additional Observations

A stingray cleaning station was discovered 75 m west of SCS. As Snelson et al. (1990) previously reported, the bluehead wrasse, *Thalassoma bifasciatum*, was observed cleaning numerous *D. americana* at a well-defined cleaning station. The cleaning station was an alcyonarian-dominated hardground within the sandflat zone.

Provisioned stingrays suffered a greater incidence of accidental boat strikes than wild stingrays; 12% of tagged provisioned stingrays had large wounds or scars caused by boat hulls or propellers, while no tagged wild stingrays had any such wounds. The large number of provisioned stingrays present at SCS during supplemental feeding periods occasionally attracted large, predatory great hammerhead sharks, *Sphyrna mokarran*, to the area.

Each day, for approximately two hours prior to the commencement of daily supplemental feeding at SCS, provisioned stingrays formed large synchronized schools, often comprising over 100 individuals (Figure 37). These schools contained male and female juvenile and mature stingrays. These schools moved back and forth across SCS in a coordinated manner, apparently awaiting the arrival of supplemental food. Wild stingrays were observed swimming only alone or in pairs.

4. DISCUSSION

PIT tags, injected in the pelvic fin musculature, were retained in 100% of the 183 recaptured provisioned and wild stingrays and were effective for long term (at least two years) identification of D. americana. External transmitter attachment to the pelvic fin and implantation of the transmitter into the animal body cavities by surgery appeared to have little visually observable effect on the behavior of tagged stingrays. Upon release, provisioned stingrays were observed immediately returning to tourists and receiving food handouts, whereas wild stingrays were observed slowly but robustly leaving the release site. Tagging (internal and external) and acoustic telemetry (manual and automated) results show evidence of spatially distinct provisioned and wild communities of stingrays at Grand Cayman. Only one of 190 tagged provisioned stingrays was captured or observed at a site other than its original capture site, and this site was another supplemental feeding location 4.3 km away. No movement between locations was observed for the 139 tagged wild stingrays. Tagging and tracking data indicate that approximately 160 D. americana utilize SCS. AAT data suggest that female provisioned stingrays consistently frequented SCS during periods of supplemental feeding and exhibited long term (at least up to one year) site fidelity to this site. These findings suggest that provisioned stingrays are highly conditioned to the supplemental food resources provided at SCS. Alevizon (2000) suggested that a dependency on long term supplemental food resources "alters natural food pathways and energy flow.... with unpredictable long-term consequences for the local marine ecosystem as a whole". An investigation into the food pathways in the North Sound, including the collection of quantitative biomass data, would be beneficial to determine the extent that supplemental

feeding affects the abundance and distribution of the conventional prey species of *D*. *americana*.

Provisioned stingrays had significantly smaller daytime, nighttime and total core areas and activity spaces than wild stingrays (Figure 30). This difference suggests that supplementally feeding *D. americana* at a restricted site has significantly reduced their core area and activity spaces. This finding is consistent with the ecological principle that activity space size is inversely related to food density and that an animal will live in the smallest area that provides its energetic requirements (Mitchell and Powell 2004). Numerous studies investigating the supplemental feeding of terrestrial vertebrates have revealed a similar decrease in the activity space size of provisioned animals (Koford 1992; Eifler 1996). In a review of food manipulation studies involving terrestrial vertebrates, activity space size decreased in 19 of 23 studies where supplemental food was introduced (Boutin 1990). It is hypothesized that provisioned stingrays exhibit optimal foraging and have reduced and centralized their core areas and activity spaces at SCS in order to maximize their accrual of food resources, suggesting that these spatial parameters are adaptive and a function of food resource requirements and availability (Schoener and Schoener 1982).

Comparisons within groups revealed that tidal phase had no apparent effect on the activity space size or rate of movement of either manually tracked provisioned or wild stingrays at Grand Cayman. This finding conflicts with Gilliam and Sullivan's (1993) suggestion that *D. americana* prefer to forage, and are thus more active, during phases of high tide. Marine animals that exhibit increased activity during phases of high tide often do so to capitalize on an increase in foraging area provided by the rise in sea level (Teaf

1978; Ackerman et al. 2000). The apparent lack of tidal phase influence on the movement patterns of *D. americana* at Grand Cayman may be due to the low tidal amplitude (26 cm), resulting in little change to available foraging habitat for *D. americana* at this location. Comparisons between groups revealed that the activity space of provisioned stingrays was significantly smaller than that of wild stingrays over all four tidal phases (Figure 34). The consistency of this difference, over all tidal phases, suggests that it occurs independently of tidal phase. This result further emphasizes that the activity space of provisioned stingrays is significantly smaller than that of wild stingrays that the activity space of provisioned stingrays is significantly smaller than that of wild stingrays that the activity space of provisioned stingrays is significantly smaller than that of wild stingrays over an entire 24 h period.

No significant difference in the rates of movements of provisioned vs. wild stingrays was detected (Figure 33). Although manually tracked provisioned stingrays were active at SCS during daytime feeding periods and subsequently moved to nighttime resting areas, this difference in diel activity was not detected in the rate of movement analysis. However, it should be noted that during periods of supplemental feeding at SCS, the tracking vessel was unable to follow the fine scale movements of tracked stingrays amongst the high density of boats and people in the water, resulting in underestimation of daytime rates of movement for provisioned stingrays. It was concluded that rate of movement calculations do not represent actual speed over ground, but demonstrate only relative activity, as movements between positional fixes are rarely in a straight line (Gruber et al. 1988).

While the small sample size of manually tracked provisioned male stingrays (n=2) prevented the use of statistical analyses, there was a marked difference between their average nighttime and total activity space sizes compared to that of the female

provisioned stingrays (Figure 31). This difference in activity space size may be a result of the sexual dimorphism in this species. The males may be getting out-competed for supplemental food provisions during the day by the larger and more numerous females (Figure 10). There is evidence for this competition in the numerous bite scars on the trailing edges of provisioned stingrays' pectoral fins (Figure 38). This type of size-based competition could result in male and small female stingrays receiving little to no supplemental food handouts during the day, forcing them to forage and be relatively more active at night, as was observed in the two manually tracked males from SCS. This hypothesis requires further support, with an increased number of manual tracks of males and small females, as well as observations of male and female interactions during periods of supplemental feeding.

Although tracked for less than 24 h, the two manually tracked wild stingrays at Rum Point appear to have similar movement patterns to those of the wild stingrays tracked at the South Sound. Both groups of wild stingrays exhibited little to no movement during the day and almost continuous movement at night, suggesting that this diel movement pattern is common for wild stingrays at Grand Cayman.

The amount of individual core area overlap, in a community of animals, is an indication of the density and spatial distribution of individuals within that community, and is dictated by numerous factors such as food availability, social systems and reproductive behavior (Samuel et al. 1985). The individual core areas of social vertebrate species commonly overlap each other (Holland et al. 1993; Bjoerge et al. 2002; Moreau and Vincent 2004), whereas individual core areas of solitary species, such as stingrays, rarely overlap (Ewer 1968; Ferreras et al. 1997; Samson and Huot 2001). Providing a

consistent food supply at the supplemental feeding sites has apparently resulted in a shift in the location of the daytime core areas of provisioned stingrays, from a situation of limited overlap, as occurs in wild animals, to significant overlap among multiple individuals (Figure 32). This shift in core area location has disrupted the spatial distribution of the community at SCS and increased the local density of *D. americana* to atypical levels, indicating that core area location is a function of food availability. Similar increases in density, due to the introduction of supplemental food, have been recorded in coyotes (Lyndaker 1987), hares (Monaghan and Metcalfe 1985), primates (Asquith 1989), squirrels (Sullivan 1990) and voles (Ostfeld 1986; Ims 1987). An increase in the density of stingrays at SCS leads to a higher frequency of interactions between con-specifics, which may result in increased disease transmission and aggression (Orams, 2002). Furthermore, increased density has apparently resulted in an increase in predator activity at SCS, with large great hammerhead sharks (*Sphyrna mokarran*) frequently observed in the vicinity of SCS (pers. obser.).

Average activity space size of wild *D. americana* tracked manually in this study $(0.876\pm0.171 \text{ km}^2)$ was smaller than that recorded for *D. lata* $(1.32\pm0.75 \text{ km}^2)$ (Cartamil et al. 2003), indicating that *D. americana* may have smaller habitat size requirements than *D. lata*.

The core area and activity space size of manually tracked provisioned and wild stingrays differed over the diel cycle; both groups exhibited significantly larger average core areas and activity spaces at night than during the day, similar to *D. sayi* and *D. lata* (Snelson et al. 1988; Cartamil et al. 2003). While both groups appear to be nocturnal, based on activity space size, it is important to note that activity space size alone reveals little information about how an animal uses the habitat within that activity space. Α comprehensive analysis of an animal's movements requires an understanding of spatial and temporal habitat utilization (White and Garrot 1990; Powell, 2000). Although provisioned stingrays had significantly larger activity spaces at night than during day, this diel pattern was not reflected in their actual level of activity, i.e. activity space size was inversely related to the amount of movement detected for provisioned stingrays. Because supplemental feeding occurred during the daytime at a spatially restricted site at SCS, provisioned stingrays exhibited a correspondingly restricted daytime activity space; however, they were continually moving and feeding within that restricted space throughout the day. In contrast, following the cessation of supplemental feeding, provisioned stingrays gathered in large aggregations north of SCS and buried in the sand, facing the prevailing current. After sunset, provisioned stingrays dispersed to nighttime resting locations, where no movement was detected for several hours. Following this long period of inactivity, provisioned stingrays began moving back to SCS, arriving prior to the commencement of supplemental feeding by tour operators. Although provisioned stingrays were inactive for a majority of the nighttime, the total nighttime activity space was relatively large because movements to and from SCS occurred at nighttime. In summary, provisioned stingrays were feeding and highly active over a small activity space during the daytime and relatively inactive over a significantly larger activity space during the nighttime. For wild stingrays, activity space size was positively related to the amount of movement detected. Wild stingrays remained relatively inactive in deep water during the daytime and actively foraged over large areas within the lagoon during the nighttime. Although wild stingrays moved between daytime resting areas and nighttime

foraging areas during daylight (i.e. mid–morning and late afternoon), nighttime activity spaces were larger than daytime activity spaces. These differences in diel activity levels between provisioned and wild stingrays indicate that a significant influence of the supplemental feeding is a reversal in the diel activity patterns of provisioned stingrays, from resting during the day and foraging at night, to feeding during the day and resting at night. This influence further illustrates the importance of food resources on the movement patterns of *D. americana*.

The findings of this study indicate the presence of a spatially isolated community of provisioned stingrays at SCS. However, it is unknown whether this spatial isolation has resulted in a corresponding reproductive isolation. The observation of pregnant females and the absence of neonates throughout the year at supplemental feeding sites, coupled with the high numbers of neonates and juveniles at the adjacent Rum Point and Barkers sites, suggest that provisioned stingrays may be pupping in these two areas. The high density of animals and the observations of several mating events at SCS (Chapman et al. 2003; pers. obser.) raises concerns that provisioned females may be mating with the small pool of provisioned males and flooding the island with large litters of pups from a very discrete gene pool. This potential inbreeding may lead to long term genetic health problems for *D. americana* at Grand Cayman. Therefore a long term genetics investigation on the extent of inbreeding is recommended for this species. Such a study could help determine the maternity and paternity of Rum Point and Barkers stingrays and investigate the long term effects of supplemental feeding on their gene pool.

The daily formation of large coordinated schools of provisioned stingrays at SCS prior to the commencement of supplemental feeding (Figure 37) demonstrates that

supplemental feeding is influencing the social behavior of provisioned stingrays. The presence of wounds and scars on provisioned stingrays, from accidental boat strikes, is likely a result of numerous stingrays and boats occurring simultaneously at the restricted feeding site at SCS, and provisioned stingrays losing their natural wariness of humans and boats. Several provisioned stingrays at SCS have developed skin conditions not observed in wild stingrays. These conditions include blotchy discolorations and open, bleeding welts (Figure 39). These conditions are likely due to one or more of the following: increased exposure to human pathogens, direct contact with human skin and sunscreen or receiving inappropriate food with low nutritional value. Similar health issues have been documented for many animals receiving food provisions from humans, including reef fish (GBRMPA 1993; Moribe 2000), dolphins (Bryant 1994; Wilson 1994) and kangaroos (Burger 1997).

5. SUMMARY AND CONCLUSIONS

Supplemental feeding at SCS has resulted in a community of approximately 160 provisioned D. americana which show strong site fidelity to the feeding site and night resting sites, and strong behavioral conditioning to the supplemental food resources received at SCS. The data presented here provide clear evidence that the movement patterns of *D. americana* have been influenced by supplemental feeding. Provisioned stingrays exhibited significantly smaller daytime, nighttime and total 24 h core areas and activity spaces than wild stingrays. The daytime core areas of all manually tracked provisioned stingrays significantly overlapped each other, whereas the daytime core areas of wild stingrays exhibited very limited overlap. This finding suggests that supplemental feeding at a defined location has resulted in a shift in the location of provisioned stingrays' core areas of activity, thus disrupting their typical spatial distribution and significantly increasing their local density. It is hypothesized that provisioned stingrays have shifted and centralized their core areas and activity spaces at SCS in order to maximize their accrual of food resources per unit area, suggesting that these spatial parameters are adaptive and a function of food requirements and availability. Supplemental feeding has apparently caused a reversal in the diel activity patterns of D. americana from resting during the day and foraging at night (nocturnal), to feeding during the day and resting at night. These findings suggest that food requirements and availability are significant factors determining the size and location of core areas and activity spaces as well as the diel movement patterns, spatial distribution, and density of D. americana at Grand Cayman. These findings are the first to demonstrate the effects of supplementally feeding on the movement patterns of a marine animal.

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Track No.	Sex	Disc Width (cm)	Location Start Date		Duration (h)
1	F	106.0	Stingray City Sandbar	26-Feb-02	24
2	F	102.0	Stingray City Sandbar	12-Mar-02	24
3	F	104.0	Stingray City Sandbar	19-Apr-03	72
4	F	124.5	Stingray City Sandbar	3-May-03	24
5	F	107.5	Stingray City Sandbar	28-May-03	72
6	М	58.0	Stingray City Sandbar	3-Mar-02	24
7	М	70.5	Stingray City Sandbar	14-Mar-02	24
8	F	99.0	South Sound	20-Mar-02	24
9	F	79.5	South Sound	2-May-02	24
10	F	89.0	South Sound	19-Jul-03	48
11	F	106.0	South Sound	30-Jul-03	48
12	F	90.0	South Sound	27-Aug-03	24
13	Μ	49.5	Rum Point	30-Apr-02	5
14	F	81.0	Rum Point	27-May-02	11

Table 1. Southern stingrays, *Dasyatis americana*, manually tracked at Grand Cayman.

Table 2. Southern stingrays, *Dasyatis americana*, tagged with coded telemetry transmitters and detected on two VR2 automated receivers at Grand Cayman.

Transmitter	PIT No.	Sex	Disc Width (cm)	Location	Start Date	Detection Duration (days)
1	5021920	F	107	Stingray City Sandbar	08-Jul-03	389
2	5022312	F	98	Stingray City Sandbar	08-Jul-03	389
3	5018230	F	97	Stingray City Sandbar	11-Jul-03	386
4	5022560	F	114	Stingray City Sandbar	11-Jul-03	386
5	5918204	F	95	Stingray City Sandbar	14-Aug-03	353

	Stingrays PIT tagged					
Location	Male		Female		Total	
Location	No.	Mean Size DW (cm)	No.	Mean Size DW (cm)	No.	
Stingray City Sandbar	28	52.3	136	93.79	164	
Stingray City	5	51.7	19	94.29	24	
South Sound	3	46.83	19	86.14	22	
Barkers	31	38.38	31	48.35	62	
Frank Sound	3	42.08	19	75.16	22	
Rum Point / Cayman Kai	13	38.15	20	55.4	33	
	83		244		327	

Table 3. Numbers and mean sizes of southern stingrays, *Dasyatis americana*, tagged with Passive Integrative Transponder (PIT) tags at Grand Cayman.

Table 4. Numbers and mean sizes of southern stingrays, *Dasyatis americana*, tagged with external spaghetti tags at Grand Cayman control sites.

	Stingrays spaghetti tagged								
Location	Male		Female		Total				
Location	No.	Mean Size DW (cm)	No.	Mean Size DW (cm)	No.				
South Sound	0	0	4	88.5	4				
Barkers	6	42.2	8	66.6	14				
Frank Sound	0	0	5	69.7	5				
Rum Point / Cayman Kai	5	47.6	7	81.1	12				
	11		24		35				
			Kernel Contours (km ²)						
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Track No.	Sex	Location	Da	ıy	Ni	ght	Total		
			50%	95%	50%	95%	50%	95%	
1	F	Stingray City Sandbar	0.002	0.012	0.012	0.135	0.017	0.100	
2	F	Stingray City Sandbar	0.002	0.013	0.009	0.067	0.019	0.114	
3*	F	Stingray City Sandbar	0.003	0.019	0.086	0.524	0.048	0.272	
4	F	Stingray City Sandbar	0.003	0.015	0.010	0.058	0.022	0.092	
5*	F	Stingray City Sandbar	0.002	0.013	0.036	0.253	0.013	0.083	
6	Μ	Stingray City Sandbar	0.006	0.028	0.136	0.776	0.080	0.275	
7	Μ	Stingray City Sandbar	0.008	0.037	0.161	1.469	0.184	1.373	
8	F	South Sound	0.024	0.146	0.029	0.163	0.050	0.270	
9	F	South Sound	0.018	0.226	0.110	0.580	0.125	0.832	
10**	F	South Sound	0.031	0.287	0.146	1.178	0.072	1.259	
11**	F	South Sound	0.046	0.350	0.092	0.578	0.091	0.880	
12	F	South Sound	0.039	0.346	0.151	0.666	0.117	1.140	

Table 5. Twenty-four hour core area (50%) and activity space (95%) sizes for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

* Indicates average core area and activity space sizes for animals tracked for three 24 hour periods.

** Indicates average core area and activity space sizes for animals tracked for two 24 hour periods.

Table 6. Pooled 24 h core area (50%) and activity space (95%) sizes for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) female southern stingrays, *Dasyatis americana*, at Grand Cayman.

Sex (n)	Mean		Mean ± SD Kernel Contours (km ²)							
	Location	Disc	D	Day		Night		Total		
		(cm)	50%	95%	50%	95%	50%	95%		
Female (5)	Stingray City Sandbar	108.8	0.002 ± 0.001	0.014 ± 0.003	0.031 ± 0.033	0.207 ± 0.193	0.024 ± 0.014	0.132 ± 0.079		
Female (5)	South Sound	92.7	0.032 ± 0.011	0.271 ± 0.086	0.106 ± 0.049	0.633 ± 0.362	0.091 ± 0.031	0.876 ± 0.383		

Track	Corr	Lagation	Disc	Rates of	Rates of Movement (km h ⁻¹)				
No.	Sex	Location	(cm)	Day	Night	Total			
1	F	Stingray City Sandbar	102.0	0.280	0.110	0.200			
2	F	Stingray City Sandbar	106.0	0.255	0.245	0.248			
3	F	Stingray City Sandbar	104.0	0.261	0.290	0.276			
4	F	Stingray City Sandbar	124.5	0.266	0.141	0.205			
5	F	Stingray City Sandbar	107.5	0.252	0.419	0.328			
8	F	South Sound	99.0	0.190	0.103	0.149			
9	F	South Sound	79.5	0.366	0.357	0.358			
10	F	South Sound	89.0	0.323	0.339	0.333			
11	F	South Sound	106.0	0.483	0.357	0.371			
12	F	South Sound	90.0	0.250	0.239	0.248			

Table 7. Rates of movement for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

Table 8. Pooled rates of movement for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

Corr (m)	Loodian	Mean Disc	Mean ± SD R	D Rates of Movement (km h ⁻¹)			
Sex (n)	Location	Width (cm)	Day	Night	Total		
Female (5)	Stingray City Sandbar	108.8	0.263 ± 0.011	0.241 ± 0.124	0.251 ± 0.053		
Female (5)	South Sound	92.7	0.322 ± 0.112	0.279 ± 0.110	0.292 ± 0.093		

Track No.	Start Date	Start Time	Tides During Track				Stop Time	Stop Date
1	26-Feb-02	1648	H 2015	L 0245	H 0830	L 1515	1650	27-Feb-02
2	12-Mar-02	1819	H 2045	L 0315	H 0830	L 1515	1835	13-Mar-02
3	19-Apr-03	1545	L 2030	H 0300	L 0945	H 1515	1600	20-Apr-03
	21-Apr-03	1849	L 2245	H 0530	L 1145	H 1630	1850	22-Apr-03
	23-Apr-03	1740	H 1900	L 0130	H 0715	L 1345	1745	24-Apr-03
4	3-May-03	1632	L 1745	H 0000	L 0615	H 1100	1633	4-May-03
5	28-May-03	1605	H 1800	L 0015	H 0600	L 1415	1610	29-May-03
	30-May-03	1645	H 2015	L 0200	H 0730	L 1500	1630	31-May-03
	1-Jun-03	1745	H 2200	L 0400	H 0815	L 1545	1745	2-Jun-03
8	20-Mar-02	0810	L 0815	H 1315	L 2030	H 0245	0800	21-Mar-02
9	2-May-02	0515	L 1030	H 1445	L 2130	H 0430	0520	3-May-02
10	19-Jul-03	0930	H 1045	L 1730	H 0000	L 0430	0931	20-Jul-03
	21-Jul-03	1700	H 1200	L 1900	H 0115	L 0630	1650	22-Jul-03
11	30-Jul-03	1802	H 2300	L 0445	H 1045	L 1745	1800	31-Jul-03
	1-Aug-03	1545	H 2000	L 0200	H 0830	L 1315	1540	2-Aug-03
12	27-Aug-03	0931	H 1015	L 1545	H 2130	L 0400	0935	28-Aug-03

Table 9. Times of high and low tide during periods of manual tracking of southern stingrays, *Dasyatis americana*, at Grand Cayman. Data provided by the Cayman Islands Government Mosquito Research and Control Unit (MRCU).

Table 10. Tidal core area (50%) and activity space (95%) sizes for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

T	Tidal Kernel Contours (km ²)									
I rack No	Hi	High		Out)W	I	In		
110.	50 %	95 %	50 %	95 %	50 %	95 %	50 %	95 %		
1	0.026	0.191	0.015	0.129	0.001	0.010	0.004	0.052		
2	0.019	0.065	0.026	0.110	0.041	0.137	0.026	0.156		
3	0.002	0.022	0.020	0.090	0.227	0.633	0.162	0.633		
4	0.055	0.156	0.033	0.145	0.002	0.016	0.018	0.103		
5	0.032	0.226	0.012	0.104	0.002	0.022	0.004	0.041		
8	0.212	0.538	0.102	0.546	0.011	0.081	0.087	0.459		
9	0.059	0.724	0.081	0.376	0.016	0.167	0.114	0.520		
10	0.643	2.694	0.147	1.078	0.081	0.453	0.201	1.080		
11	0.513	2.065	0.527	2.066	0.462	1.863	0.909	3.309		
12	0.102	0.736	0.102	0.562	0.125	0.610	0.218	0.924		

			Mean \pm SD Tidal Kernel Contours (km ²)							
Sex (n) L	Location	Mean Disc Width (cm)	High		Out		Low		In	
			50%	95%	50%	95%	50%	95%	50%	95%
Female (5)	Stingray City Sandbar	108.8	0.027 ± 0.020	0.132 ± 0.086	0.021 ± 0.009	0.115 ± 0.022	0.055 ± 0.098	0.164 ± 0.268	0.043 ± 0.068	0.197 ± 0.248
Female (5)	South Sound	92.7	$\begin{array}{c} 0.306 \pm \\ 0.259 \end{array}$	$\begin{array}{c} 1.351 \pm \\ 0.968 \end{array}$	$\begin{array}{c} 0.192 \pm \\ 0.189 \end{array}$	$\begin{array}{c} 0.926 \pm \\ 0.690 \end{array}$	$\begin{array}{c} 0.139 \pm \\ 0.187 \end{array}$	0.635 ± 0.719	$\begin{array}{c} 0.306 \pm \\ 0.342 \end{array}$	1.258 ± 1.176

Table 11. Pooled tidal core area (50%) and activity space (95%) sizes for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

Track No.	Ti	Tidal Rates of Movements (km h ⁻¹)							
I FACK NO.	High	Out	Low	In					
1	0.259	0.257	0.081	0.354					
2	0.053	0.196	0.216	0.336					
3	0.368	0.350	0.136	0.395					
4	0.124	0.210	0.192	0.241					
5	0.241	0.352	0.330	0.382					
6	0.076	0.214	0.173	0.146					
7	0.468	0.350	0.344	0.098					
8	0.564	0.282	0.490	0.360					
9	0.121	0.235	0.394	0.239					
10	0.420	0.141	0.255	0.295					

Table 12. Tidal rates of movement for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

Table 13. Pooled tidal rates of movement for manually tracked provisioned (Stingray City Sandbar) and wild (South Sound) southern stingrays, *Dasyatis americana*, at Grand Cayman.

Sex (n)	Location	Mean Disc	Mean ± Sl	Mean ± SD Tidal Rates of Movement (km h ⁻¹)					
	Location	Width (cm)	High	Out	Low	In			
Female (5)	Sandbar	108.8	0.209 ± 0.123	0.273 ± 0.075	0.191 ± 0.094	0.342 ± 0.061			
Female (5)	South Sound	92.7	$\begin{array}{c} 0.330 \pm \\ 0.218 \end{array}$	0.244 ± 0.078	0.331 ± 0.123	0.228 ± 0.107			



Figure 1. The location of the Cayman Islands in the Caribbean.



Figure 2. Map of Grand Cayman showing the location of the supplemental feeding sites (Stingray City Sandbar and Stingray City), and the four control sites (Barkers, Rum Point/Cayman Kai, South Sound and Frank Sound).



Figure 3. Supplemental feeding site, Stingray City Sandbar, showing the location of the fringing reef and lagoonal zones.



Figure 4. Two control sites, South Sound and Barkers, showing the location of channels and lagoonal zones.



Figure 5. Two control sites, Frank Sound and Rum Point/Cayman Kai, showing the location of channels and lagoonal zones.



Figure 6. Two binder clips placed over the spine and adjacent tail of a mature female southern stingray, *Dasyatis americana*, allowed safe and efficient handling.



Figure 7. A wax covered V16 transmitter (Vemco, Nova Scotia) attached to the right pelvic fin of a mature female southern stingray, *Dasyatis americana*, using a Peterson disc tag (Floy Tag Company, Seattle, WA. 20 mm diameter).



Figure 8. Custom-built stationary receiver housing unit. (A) shows the unit sitting on a sandy substrate with the concrete base and anchors clearly visible. (B) shows the unit in situ at Stingray City Sandbar with the concrete base buried and anchors screwed in place, preventing any movement of the unit. The red hydrophone tip of the housed VR2 receiver (Vemco, Nova Scotia) is visible protruding from the top of the unit in (B).



Figure 9. The location of the Cayman Islands Government Mosquito Research and Control Unit (MRCU) tide station (red dot) in the North Sound of Grand Cayman.



Figure 10. Disc width vs. weight scatter plot of provisioned southern stingrays, *Dasyatis americana*, at Stingray City Sandbar, Grand Cayman, showing the predominance of large females (n=136) over males (n=28) in size and number.



Figure 11. An aggregation of provisioned southern stingrays, *Dasyatis americana*, buried in the sand flat zone, oriented toward the current, north of Stingray City Sandbar, Grand Cayman.



Figure 12. Track number 1. Twenty-four hour activity space of a provisioned 106 cm DW, mature female southern stingray, *Dasyatis americana*, on 26 February 2002 at Stingray City Sandbar, Grand Cayman.



Figure 13. Track number 2. Twenty-four hour activity space of a provisioned 102 cm DW, mature female southern stingray, *Dasyatis americana*, on 12 March 2002 at Stingray City Sandbar, Grand Cayman.



Figure 14. Track number 3. Representative 24 hour activity space of a provisioned 104 cm DW, mature female southern stingray, *Dasyatis americana*, on 21 April 2003 at Stingray City Sandbar, Grand Cayman.



Figure 15. Photograph of an alcyonarian dominated hardground area, encircled by sand, 1.1 km west of Stingray City Sandbar in the North Sound of Grand Cayman. Track number 3, of a provisioned 104 cm DW female, stopped at this area to rest for an average of 6 hr 20 m every night during three continuous 24 hr manual tracks. Inset shows an aerial view of the sand encircled hardground.



Figure 16. Track number 4. Twenty-four hour activity space of a provisioned 124.5 cm DW, mature female southern stingray, *Dasyatis americana*, on 3 May 2003 at Stingray City Sandbar, Grand Cayman.



Figure 17. Track number 5. Representative 24 hour activity space of a provisioned 107.5 cm DW, mature female southern stingray, *Dasyatis americana*, on 31 May 2003 at Stingray City Sandbar, Grand Cayman.



Figure 18. Track number 6. Twenty-four hour activity space of a provisioned 58 cm DW, mature male southern stingray, *Dasyatis americana*, on 3 March 2002 at Stingray City Sandbar, Grand Cayman.



Figure 19. Track number 7. Twenty-four hour activity space of a provisioned 70.5 cm DW, mature male southern stingray, *Dasyatis americana*, on 14 March 2003 at Stingray City Sandbar, Grand Cayman.



Figure 20. Track number 8. Twenty-four hour activity space of a wild 99 cm DW, mature female southern stingray, *Dasyatis americana*, on 20 Mar 2002 at South Sound, Grand Cayman.



Figure 21. Photograph of a wild female southern stingray, *Dasyatis americana*, buried in a sandy groove within a 'spur and groove' coral community, approximately 350 m south of the South Sound, Grand Cayman. Water depth at this location is 20 m. This activity represents the typical mid-day behavior for all stingrays tracked in the South Sound. The yellow circle in the inset above represents the location where the photograph was taken.



Figure 22. Track number 9. Twenty-four hour activity space of a wild 79.5 cm DW, mature female southern stingray, *Dasyatis americana*, on 2 May 2002 at South Sound, Grand Cayman.



Figure 23. Track number 10. Representative 24 hour activity space of a wild 89 cm DW, mature female southern stingray, *Dasyatis americana*, on 19 July 2003 at South Sound, Grand Cayman.



Figure 24. Track number 11. Representative 24 hour activity space of a wild 106 cm DW, mature female southern stingray, *Dasyatis americana*, on 30 July 2003 at South Sound, Grand Cayman.



Figure 25. Track number 12. Twenty-four hour activity space of a wild 90 cm DW, mature female southern stingray, *Dasyatis americana*, on 27 August 2003 at South Sound, Grand Cayman.



Figure 26. Total movements of two wild southern stingrays, *Dasyatis americana*, at Rum Point, Grand Cayman. (A) represents five hours of movements for male stingray number 13; (B) represents 11 hours of movement for female stingray number 14.



Figure 27. Approximate detection ranges of two VR2 receivers used for automated tracking of southern stingrays, *Dasyatis americana*, at Grand Cayman.



Figure 28. Time of day that five southern stingrays, *Dasyatis americana*, outfitted with coded V16 transmitters, were within the detection range of receiver 2906, located 100 m northeast of Stingray City Sandbar, Grand Cayman. Yellow bars indicate usual times of supplemental feeding.



Figure 29. Time of day that five southern stingrays, *Dasyatis americana*, outfitted with coded V16 transmitters, were within the detection range of receiver 2907, located 100 m southwest of Stingray City Sandbar, Grand Cayman. Yellow bars indicate usual times of supplemental feeding.


Figure 30. Average 24 h core area (A) and activity space (B) sizes of five provisioned and five wild female southern stingrays, *D. americana*, at Grand Cayman.



Figure 31. Average day, night and total 24 h activity space sizes of manually tracked provisioned female and male southern stingrays, *Dasyatis americana* at Grand Cayman.



Figure 32. Daytime core areas of manually tracked southern stingrays, *Dasyatis americana*, at Grand Cayman. The five stingrays tracked manually at Stingray City Sandbar exhibited almost total overlap of daytime core areas (*top*) whereas the five stingrays tracked manually at the South Sound exhibited very limited overlap (*bottom*).



Figure 33. Average day, night and total 24 h rates of movement of five provisioned and five wild female southern stingrays, *D. americana*, at Grand Cayman.



Figure 34. Average core area (A) and activity space (B) sizes over four tidal phases of five provisioned and five wild female southern stingrays, *D. americana*, at Grand Cayman.



Figure 35. Average rates of movement over four tidal phases of five provisioned and five wild female southern stingrays, *D. americana*, at Grand Cayman.



Figure 36. Number of times 164 PIT tagged, provisioned southern stingrays, *Dasyatis americana*, were captured at Stingray City Sandbar, Grand Cayman.



Figure 37. A school of southern stingrays, *Dasyatis americana*, photographed at 0730 h at Stingray City Sandbar, prior to the commencement of supplemental feeding.



Figure 38. A provisioned male southern stingray, *Dasyatis americana* at Stingray City Sandbar, Grand Cayman, showing numerous large bite scars on the leading and trailing edges of both pectoral fins, presumably from large female *D. americana*.



Figure 39. Ventral surface of a provisioned female southern stingray, *Dasyatis americana*, showing open bleeding lesions. These lesions and other skin conditions were only observed on provisioned stingrays at Grand Cayman.

APPENDIX A

Department of Environment.

Draft Guidelines for Feeding and Interaction with the Rays at Stingray City and the Sand Bar.

- 1. Restrict the feeding to an appointed tour operator staff member on each boat, who would be responsible for feeding the rays while the tourist watched and took part if they wanted. Australian guidelines recommend that fish should not be fed directly by hand. No food should be available for sale to tourists and plastic containers, bags and other litter should be kept out of the water.
- 2. Although not the rays' natural food, squid or fish are more preferable than manufactured meats, processed cheese, breads or pasta.
- 3. Limits on the amount of food fed to the rays should also be considered. Australian guidelines recommend 1 kg (approx. 2.2 lbs.) of food per fish feeding station with a maximum of two feeding stations in any one area. However with many boats arriving at different times limits would probably have to apply to individual boats rather than the area. Each boat should be restricted to an agreed maximum amount of food. Assuming a maximum of ¹/₂ kg of food per boat and 12 boats visit the sand bar in any one day, each taking their maximum allowance, 6 kilos of food would be available to the rays. Assuming there are approximately 50 rays on the sand bar at any one time and each ray gets an equal share then each should receive around 120 grams. A limit of 1 kilo per boat would allow 240 grams per ray and two kilos would allow each ray nearly half a kilo of food! This figure is still probably lower than what they receive at the moment.
- 4. Individual tour operators should be responsible for ensuring uneaten food is retrieved and not left on the Sand Bar. All litter and other objects taken into the water must be removed.
- 5. Handling the rays should be prohibited. Rays should not be lifted out of the water or prevented from moving in any way.
- 6. Laminated sheets explaining the agreed guidelines and basic ray biology should be displayed in prominent locations aboard tour boats.
- 7. Participants in the feeding program must be given practical and adequate warning of the potential dangers of feeding and interactions with the rays.

APPENDIX B

Rules for Cayman Islands Marine Replenishment Zone

Courtesy of the Cayman Islands' Department of Environment

REPLENISHMENT ZONE:

- No taking of conch or lobster by any means
- Line fishing (See Fishing Licenses section in Summary of Cayman Islands Marine Conservation Laws) and anchoring permitted
- Anchor, chain or line must not touch coral
- Spear guns, pole spears, fish traps and nets prohibited, except that fry and sprat may be taken with a fry or cast net

NOTE: These zones include the outside edge of the reef to a depth of 20 feet.

Protection of Certain Species:

Whelks

- Closed Season May 1 October 31
- Open Season catch limit 2 1/2 gallons in the shell or 2 1/2 lbs of processed whelks per person per day.
- No one may purchase or receive more than 2 1/2 gallons in the shell or 2 1/1 lbs of processed whelks from Cayman waters in any one day.
- Chitons, Periwinkles and Bleeding Teeth may not be taken from Cayman waters at any time.

Echinoderms

• Echinoderms (includes Starfish, Sea Eggs/Urchins, Sea Cucumber, Sand Dollars etc) may not be taken from Cayman waters at any time.

Turtles

- No one may disturb, molest or take turtle in Cayman waters without a license from the Cayman Marine Conservation Board
- Possession of turtle eggs is prohibited
- For licensed fishermen, closed season is 1 May through 31 October

Sharks

• No one may feed, attempt to feed, or provide or use food to attract any shark in Cayman waters

Nassau Groupers

- Closed season January 1 through December 31 2003 and every alternate year thereafter (i.e. 2005, 2007, 2009, etc)
- Designated grouper spawning areas are protected. Open Season Catch limit (2004, 2006, 2008 etc) 12 grouper per person or per boat per day, applies in these areas
- During Open Season only line fishing is permitted in these areas by Caymanians.
- Size limit 12 inch minimum size limit applies throughout Cayman waters year round.

Other Fish

- Protected Jew Fish, Tilefish (whities), Filefish (pipers) and Angelfish, including Gray, French and Queen Angels (old monks) may not be taken from Cayman waters at any time.
- Size limits: Eight inch minimum size on all other fish except Goggle Eyes, Herrings (including Sprats), Anchovies and Silversides (including Loggerhead and Fine Fry).

FISHING LICENSES

- Unless licensed by the Marine Conservation Board, residents who do not possess Caymanian status may not take or attempt to take by any means any marine life while he is on shore or in any part of Cayman waters in which he can stand.
- No license is required for catch and release fishing.

GENERAL RULES

- Damaging coral by anchor, chains or any other means ANYWHERE in Cayman waters is prohibited
- No taking of ANY marine life while on scuba
- No taking of any coral, sponges, etc. from Cayman waters
- Wearing gloves while diving or snorkeling in Cayman waters is prohibited
- Export of live fish or other marine life is prohibited
- Fishing with gill nets, poison or other noxious substances is prohibited
- Dumping ANYTHING in Cayman waters is prohibited
- The export of conch shells and/or black coral requires a CITES permit issued through the DOE.

PENALTIES

Violation of any of these laws is an offence carrying a maximum penalty of CI\$500,000 fine and one year in jail. Upon conviction forfeiture of the vessel or other equipment may also be ordered.