PAPER

Marine Reserve Design and Evaluation Using Automated Acoustic Telemetry: A Case-study Involving Coral Reef-associated Sharks in the Mesoamerican Caribbean

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ABSTRACT

A non-overlapping acoustic receiver array was used to track the movements of two common shark species, nurse *Ginglymostoma cirratum* (n=25) and Caribbean reef *Carcharhinus perezi* (n=5), in and around Glover's Reef Marine Reserve (GRMR), off the coast of Belize, between May and October, 2004. Although both species exhibited partial site fidelity in that they were most likely to be detected near the area of original capture, both species also moved widely throughout the 10 by 30 km atoll. One Caribbean reef shark was detected by a monitor at Lighthouse Reef, 30 km from Glover's Reef across deep (>400m) open water. The mean minimum linear dispersal (MLD) was 10.5 km for Caribbean reef sharks and 7.7 km for nurse sharks, with many individuals traveling more than the 10 km width of the no-take "conservation zone" of the marine reserve. Although most sharks were tagged within the conservation zone, individuals were detected outside this part of GRMR on average 48 days out of the 150 days of observations. However, of 7 nurse sharks tagged near the center of the conservation zone, 4 were never detected outside of this part of the reserve. In general, this study suggests that effective conservation of these large roving predators requires an ecosystem-based management approach including a zoned management plan, similar to that used at GRMR, in which a fairly large no-take reserve, incorporating diverse habitats and the connections between them, is surrounded by a larger area in which fishing is regulated.

INTRODUCTION

Sharks are increasingly threatened by overexploitation and habitat degradation around the world, and marine reserves are now being considered as a potential component of conservation strategies for these top-predators (Camhi, 1998; FAO, 2000; Watts, 2001; Baum et al., 2003; Simpfendorfer & Heupel, 2004). However, because sharks can range widely (Kohler et al., 1998; Holland et al., 1999; Boustany et al., 2002) and no-take marine reserves will always be restricted in size, there remains considerable uncertainty as to how effective reserves will be at enclosing shark activity spaces over medium and long-term time frames (months to years) and thus whether they will be effective for the conservation of these often heavily exploited species. For other migratory species, modeling studies have demonstrated that no-take reserves can effectively protect fish that migrate in and out of the reserve, but whether the reserve is beneficial or not depends on the life stages protected by the reserve, the migratory behavior of the fish, and the level of fishing effort and size-selectivity of the fishery outside the reserve (e.g. Apostolaki et al., 2002; Guénette et al., 2000). Without detailed information on the age-specific movements of sharks and other large predatory fish in relation to existing or proposed reserve boundaries, the evaluation and design of marine reserves aimed at protecting these animals remains very challenging (Simpfendorfer & Heupel, 2004; Sladek-Nowlis & Friedlander, 2004; Wetherbee et al., 2004).

Glover's Reef, one of Belize's three oceanic atolls, is encompassed by one of the largest marine reserves (Glover's Reef Marine Reserve [GRMR]) along the Mesoamerican Barrier Reef, the second largest barrier reef in the world (Gibson et al., 2004). Although there are ongoing studies of several components of this coral reef ecosystem (Acosta, 2001, 2002; Acosta & Robertson, 2003; McClanahan et al., 2003), its shark fauna has only recently been studied (Pikitch et al., in revision), despite the fact that these apex predators are increasingly exploited by fisheries in Belizean waters and the coral reefs in which they live are becoming degraded throughout the Caribbean region (Gardener et al., 2003; Gibson et al., 2004). The two numerically dominant shark species at Glover's Reef atoll are the nurse shark, *Ginglymostoma cirratum,* and the Caribbean reef shark, *Carcharhinus perezi*, both of which use this area as a breeding ground (Pikitch et al., in revision). Although both species are exploited in Caribbean fisheries for their fins and meat (Bonfil, 1997; Chan A Shing, 1999), their value as two of the most important species involved in the shark dive tourism industry in the region likely surpasses their value as food (Watts, 2001; Carwardine & Watterson, 2003). This is one reason that marine reserves have been established to help protect concentrations of these species in Belize, the U.S.A. (Florida) and the Commonwealth of the Bahamas (Carrier & Pratt, 1998; Watts, 2001; Cawardine & Watterson, 2003; Gibson et al., 2004). Unfortunately, as for most marine species (Sladek-Nowlis & Friedlander, 2004), very little is known about the movement patterns of these sharks and, as such, there is virtually no scientific framework for the design and evaluation of marine reserves as a conservation tool for these or related, ecologically-similar species throughout the world.

Short-term movement patterns of several species of coastal sharks, including a few coral reef-associated species of the Pacific (Johnson, 1978; McKibben & Nelson, 1986), have been described using acoustic telemetry, primarily through active tracking methods (i.e. affixing a transmitter to a shark and then following it with a hydrophone and vessel-based receiver to develop a continuous series of periodic positional fixes [Gruber et al., 1988; Holland et al., 1993; Morrissey & Gruber, 1993; Holland et al., 1999; Heithaus et al., 2002]). One emerging pattern from these studies is that juvenile sharks in tropical regions often exhibit some degree of repeatability of movements, that is, they often return to and reuse specific areas on a daily basis, often resulting in relatively restricted activity spaces over periods of a few days (Johnson, 1978; McKibben & Nelson, 1986; Gruber et al., 1988; Holland et al., 1993; Morrissey & Gruber, 1993). McKibben & Nelson (1986), tracking gray reef sharks (*Carcharhinus amblyrhyncos*) at a Pacific coral atoll, demonstrated that although sharks tracked inside the lagoon exhibited this type of daily site-fidelity, similar-sized sharks on the ocean reef moved tens of kilometers along the edge of the atoll over similar time-periods. Furthermore, active tracking studies of larger sharks have revealed that individuals often move considerable distances over short periods and may not reuse the same areas until weeks, months or even years later (Gruber et al., 1988; Strong et al., 1992; Holland et al., 1999; Heithaus et al., 2002). Information on how often sharks utilize specific areas, how far and how frequently they disperse and how these movement patterns relate to protected zones and potential threats is central to the process of designing and evaluating marine reserves for these predators, and requires some understanding of their movements over time-scales ranging from months to years. Although active tracking continues to provide useful information relevant to marine reserve design and the associated analytical procedures are well established, this method is often prohibitively expensive and labor intensive over the time-frame needed to fully evaluate whether or not a reserve will be successful for mobile, long-lived species like sharks (Sladek-Nowlis & Friedlander, 2004; Simpfendorfer & Heupel, 2004).

As an alternative to the active tracking method for assessing animal movement patterns, multiple specimens can be affixed with coded acoustic transmitters and then remotely tracked by an array of stationary omnidirectional hydrophone-receivers (hereafter referred to as "receivers"), which record the date, time and identification number of study animals as they pass through the detection range of the unit (Economakis & Lobel, 1998; Heupel & Hueter, 2002; Simpfendorfer et al., 2002; Simpfendorfer & Heupel, 2004). This method has proven especially effective when the study area is well enclosed, of uniform depth and of mostly low-relief topography (e.g. estuaries), where the detection ranges of multiple neighboring receivers can be overlapped and then used to estimate positional fixes for the study animals, often allowing these data to be analyzed in a manner analogous to active tracking data (Simpfendorfer et al., 2002; Simpfendorfer & Heupel, 2004). An overlapping receiver array can provide data on animal movements at a level of detail comparable to active tracking, and offers the substantial advantages of potentially greatly extending the duration and samples size of these types of studies while remaining economically efficient due to greatly reduced labor and running costs (Simpfendorfer et al., 2002; Simpfendorfer & Heupel, 2004). While a large, overlapping array is probably the ideal methodology for tracking studies focused within a specific area, the dimensions and physical characteristics of the majority of potential marine reserve sites (e.g. coral reefs) will be such that establishing this type of overlapping receiver array will not be economically feasible and a non-overlapping receiver array will have to be used to collect information on animal movements instead. This study design may prove to be very challenging for use on large, mobile species because study animals will probably spend considerable time outside of the detection range of the array, and generate a much patchier dataset that will not be amenable to the established analytical procedures used for active tracking data (Simpfendorfer & Heupel, 2004). Deriving useful, scientifically defensible information on animal movement patterns from non-overlapping receiver arrays for application to marine reserve design will therefore require further exploration and development (Simpfendorfer & Heupel, 2004).

The goal of our ongoing research program is to better understand the movement patterns of roving reef predators in the GRMR, beginning with the two most common large shark species, the nurse and Caribbean reef. Since the atoll is very large (10 by 30 km) and structurally complex (there are more than 850 patch reefs in the lagoon) we employed a non-overlapping receiver array to track the movements of large juveniles and adults of these species, in order to evaluate the effectiveness of the no-take conservation zone at enclosing the medium-term activity spaces of these reef-associated sharks. This was achieved by (1) describing aspects of space utilization identified as being important for marine reserve design and evaluation in a recent review by Sladek-Nowlis & Friedlander (2004); e.g. types of habitats utilized, levels of site-fidelity, dispersal range, (2) determining whether sharks exhibited residency to Glover's Reef atoll throughout the five month study period and (3) quantifying levels of shark activity outside of the no-take part of the reserve. A second objective was to begin to use this information to gain insight into aspects of marine reserve design that will provide meaningful protection for these species throughout their range. It is further hoped that the framework developed will prove useful for related, ecologically similar reef-associated species around the world and provide a model of how relatively patchy datasets from non-overlapping receiver arrays can be incorporated into conservation planning for large, mobile reef species. Here, conservation-relevant results from the first five months (May to October 2004) of this ongoing study are presented.

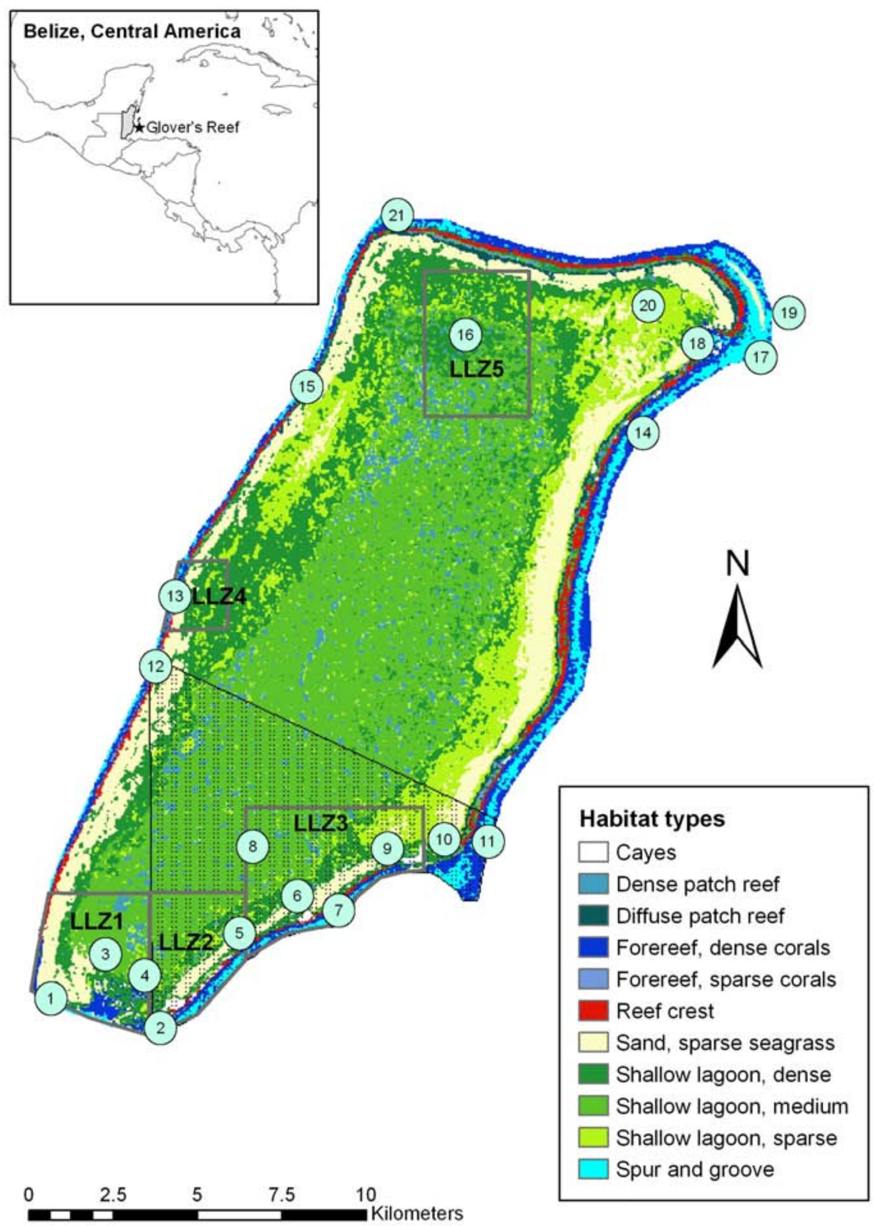
Materials and Methods

Study Site

Glover's Reef atoll (16° 44' N, 87° 48'W) lies approximately 25 km to the east of the Mesoamerican Barrier Reef and 45 km east of the Belizean mainland (Figure 1). To the north and west of the atoll, depths range from 300 to 400 m, while the east (windward) side rapidly drops off to over 1000 m. The edge of the insular slope at Glover's ranges from 15-45 m depth and the forereef is less than 500 m wide in most areas. The windward (eastern) ocean reefs, composed largely of low-relief spur and groove formations (mainly *Montastrea*, *Diploria*), are better developed and wider than the leeward (western) ocean reefs. The reef crest on the west side of the atoll is submerged (ca. 1.5-2 m depth), while the reef crest on the eastern side of the atoll is exposed and is broken by five cuts which connect the ocean reef and lagoon habitats. The largest of these cuts (approximately 4 km wide) is on the southern end of the atoll (hereafter referred to as the "southern entrance channel") and is an area of strong tidal currents. The lagoon is basin shaped and is up to 18 m deep in some areas, with approximately 850 patch reefs (10-300 m+ wide) scattered throughout the interior, which are composed largely of massive corals (*Montastrea*, *Diploria*,

FIGURE 1

Glover's Reef atoll, Belize, Central America (Inset). Map shows the location, identification number and approximate detection range of 21 omnidirectional hydrophone-receiver units (VR2, Vemco Ltd: numbered circles) used to monitor shark activity and movements in and around the atoll from May to October 2004. Boxes show the five general zones where sharks were collected with longlines and fitted with transmitters (LLZ1-5). The stippled triangle shows the conservation zone of the Glover's Reef Marine Reserve (GRMR), while the exterior edge of the atoll demarcates both the reef slope and the boundary of the general-use zone of GRMR (where fishing is permitted but bottom longlines and gillnets are prohibited). Habitat classification is courtesy of the Belizean Coastal Zone Management Authority and Institute (CZMAI), through an MOU with Wildlife Conservation Society (WCS).



Siderasteria). There are six cayes along the eastern edge of the lagoon, some of which are at least partially fringed with mangroves and surrounded on the lagoon-side by seagrass flats in shallow water (< 2 m depth). Average annual rainfall is 175 cm, with the main rainy season occurring from June to October, and normal marine salinities occur in the lagoon throughout the year. Water temperature usually ranges from 27-32° C (Summarized from: Gibson. 2003).

Established in 1993, the Glover's Reef Marine Reserve encompasses the entire atoll and is zoned for multiple uses, with an interior no-take "conservation zone" that covers approximately the southern third of the atoll (7226 hectares [Gibson et al., 2004]; Figure 1). This no-take zone is surrounded by the "general use zone," covering the entire atoll around the 180 m depth contour, which is effectively demarcated by the perimeter of the insular slope (32, 834 hectares [Gibson et al., 2004]; Figure 1). Fishing is allowed for all legal-to-harvest species by licensed fishers in the general use zone (Figure 1), although there are regulations that prohibit the use of fish-traps, longlines and gillnets (Gibson, 2003; Gibson et al., 2004).

Shark Capture and Transmitter Implantation

Sharks were collected under a research permit from the Belize Department of Fisheries using long-lines fished in five general locations around the atoll (LLZ1-5; Figure 1). LLZ1 was located in the southern entrance channel at the interface between the ocean reef and the lagoon habitats, and just outside (< 2 km) of the conservation zone. LLZ2 was inside the lagoon and spanned the very edge to 2 km inside the conservation zone. LLZ3 was deeper inside the conservation zone (i.e.> 2 km from the edge). LLZ4 and 5 were northern sites more distant from the conservation zone (LLZ4 was ca. 1.5 km to the northeast of the boundary; LLZ5 was ca. 8 km to the northeast of the boundary). Additional details of the longline program, together with catch rates of each of these species in these zones and habitats can be found in Pikitch et al. (in revision). Hooked sharks were brought alongside the 7 m long fishing vessel and secured to the bow by the gangion and to the stern with a rope noose looped around the caudal peduncle. Each shark was then measured (total length [TL]), externally tagged (Hallprint Ltd, South Australia), and its sex determined while keeping the shark alongside the vessel and in the water. Female sharks were assigned into the categories "juvenile" or "mature" based on their TL, using lengths at maturity for nurse (223 cm +) and for Caribbean reef (200 cm +) provided by Castro (2000) and Compagno (1984) respectively. The size and degree of calcification of the claspers (intromittent organs) was used to assign males into one of these two categories (Castro, 2000). Sharks hooked cleanly in the mouth and without signs of significant injury or fatigue were considered for surgical implantation of a coded acoustic transmitter (V16, Vemco Ltd). Prior to surgery, the shark was rolled upside down to expose its ventral surface and to induce a state of tonic immobility (Davie et al., 1993; Henningsen, 1994). It was held in this position, slightly below the water's surface, throughout surgery. One person held the shark in place by gripping both pectoral fins while a second person used a disposable scalpel to make a ca. 5 cm incision into the shark's coelom, just anterior to the origin of one of the pelvic fins. The transmitter, previously coated with beeswax to reduce the possibility of physical irritation and immunological reaction, was inserted through this incision. Following this, the incision was closed with braided-nylon sutures. Upon completion of surgery the shark was rolled back over, the hook was entirely removed and the shark was released, with a diver in the water to assess its condition.

Receiver Array Set-up

In order to track the movements of these sharks, 21 VR-2 receivers (Vemco Ltd.) were anchored to the substrate in various locations around Glover's Reef atoll (Figure 1), with nine receivers positioned inside the conservation zone and twelve receivers placed in the general use zone. Eleven receivers were arranged in a circular transect along the edge of the reef slope surrounding the entire atoll, at depths of 20-30 m. These receivers were attached with shackles and heavy-duty plastic cable-ties to a length of rope that was anchored to the substrate by up to five cement blocks chained together and held upright in the water column by a subsurface plastic float. The remaining receivers were positioned inside the atoll using a similar anchoring system, with a smaller length of rope and fewer cement blocks, at depths of 1.5-18 m. The position of each receiver was obtained using a hand-held Garmin GPS and plotted using ArcMap 9.0 GIS software (ESRI, Redlands, California) on a habitat classification map of the atoll provided by the Belize Coastal Zone Management Authority and Institute (CZMAI). Field-testing indicated that the detection range for these receivers was approximately 500 m for units on the reef, and 350-400 m for those inside the lagoon. In some cases, the range of receivers in the lagoon was greatly reduced at certain angles due to physical obstruction by high-relief patch reefs. Because there are over 850 of these patch reefs scattered throughout the lagoon (Gibson, 2003), this problem was largely unavoidable when working in this area. All receivers generally sampled only one of the three broad macro-habitats classified in this study: shallow seagrass flats (< 2 m; receivers 5, 6, 9), lagoon (mixed substrate [sand, seagrass, patch reef], 3-18 m depth; receivers 3, 4, 8, 10, 16, 18, 20) and ocean reef (coral reef substrate, reef crest to > 20 m depth; receivers 1, 2, 7, 11, 12, 13, 14, 15, 17, 19, 21).

Data Analysis

Detection records were counted for each receiver from the date of deployment to the date of download, a period of 5 months (150 days) from May to October 2004. For each receiver, these detections were sorted by transmitter identity, date and time. Broad patterns of shark activity and habitat use around Glover's Reef were visualized by plotting the number of detections and the number of individual sharks of each species recorded at each receiver on the habitat classification map of the atoll. For each individual shark, the total number of detections and the total number of days the shark was detected were collated for every receiver and plotted on the same map, to illustrate whether the sharks exhibited site-fidelity (i.e. repeated utilization of particular areas of the atoll) over the five-month study period. For each shark, the proportion of detections recorded at each monitor was calculated to determine whether detection records for each shark were skewed towards particular receivers, which is another indicator of site-fidelity. The total number of days the shark was detected anywhere inside the array (i.e. by any receiver) was used to conservatively measure residency time over the five month period. In addition, the total number of days each shark was detected by a receiver anywhere outside the conservation zone was determined, in order to conservatively estimate how frequently sharks enter parts of the atoll where fishing is allowed. The minimum-linear dispersal (MLD) of each shark along Glover's Reef atoll over this 5 month period was defined as the straight-line distance between the two most distant receivers which detected the shark, assuming the shark was on the peripheral edge of each unit's detection range (500 m from the unit). Measurements were made using ArcMap.

Results

Between May 1 and 11, 2004, five Caribbean reef (117-215 cm TL) and 21 nurse sharks (136-240 cm TL) were implanted with coded V-16 transmitters. In addition, transmitters from 4 nurse sharks implanted for a pilot study in 2003 were still active over this period. Table 1 gives the size (TL), sex, life-stage (juvenile or mature), capture location, and date of transmitter implantation for all sharks. Seventeen of these sharks were captured and released within the conservation zone (15 nurse, 2 Caribbean reef), the remaining animals were captured and released in the general use zone (Table 1). Five sharks (nurse sharks 3332, 3347, 3382, 3392 and Caribbean reef 3342) were detected on fewer than 15 days (<10% of study period) and were considered data-deficient (i.e. we were unable to conclusively determine whether these sharks left Glover's Reef or occupied parts of the atoll away from any of the receivers). All of these animals except 3342 and 3347 were detected in September 2004, so the limited of data for these specimens cannot be explained by mortality (natural, fishing or induced by handling and transmitter application) or transmitter failure. All data-deficient animals were excluded from detailed individual analysis.

Sharks were detected throughout the array, with the exception of two receivers positioned in the northern part of the atoll, where relatively few sharks had been implanted with transmitters (receivers 14, 20; Figure 2 a, b), and one 3-year old receiver (12) that apparently flooded when placed underwater in May 2004. There were several high-use areas (i.e. areas with a high number of detections from a large number of sharks) concentrated in the southern entrance channel of the atoll (receivers 1, 2, 3, 4; Figure 2 a, b), with the four southernmost receivers each recording from 2529 to 10,654 detections, originating from 11 to 14 individual sharks (20 different individuals in total from all four receivers, including both nurse [16 sharks] and Caribbean reefs [4 sharks]) over the five month study period. Several receivers positioned elsewhere around the atoll also recorded a high number of detections (e.g. receivers 5, 6, 7, 8, 11, 16), but these originated from fewer individual sharks (Figure 2 a, b; e.g. receiver 6 recorded over 25, 000 detections, but from only 5 different animals [99% of these detection were from a single juvenile male nurse shark (3339) that was almost continuously recorded in this area]). Nurse sharks were detected on all but two of the 20 functioning receivers (they were not recorded on re-

TABLE 1

Study animals from May to October, 2004. R Date= Release date, R Loc= Release location, based on longline zone (LLZ: see Figure 1), TL= total length(cm), Class= maturity and sex: A=adult, J=Juvenile, M=Male, F=Female.

Species	Trans#	R Date	R Loc	TL	Class
C. perezi	3340	5/2/2004	LLZ1	197	AM
C. perezi	3342	5/5/2004	LLZ1	215	AF
C. perezi	3348	5/4/2004	LLZ3	188	AM
C. perezi	3349	5/5/2004	LLZ1	134	JF
C. perezi	3393	5/5/2004	LLZ1	117	JM
G. cirratum	3329	5/25/2003	LLZ2	240	AF
G. cirratum	3331	5/25/2003	LLZ2	223	AF
G. cirratum	3332	5/26/2003	LLZ2	212	JF
G. cirratum	3333	1/7/2004	LLZ2	176	JF
G. cirratum	3336	4/24/2003	LLZ4	233	AF
G. cirratum	3337	5/2/2004	LLZ3	238	AF
G. cirratum	3338	5/2/2004	LLZ2	208	JF
G. cirratum	3339	5/3/2004	LLZ3	169	JM
G. cirratum	3341	5/2/2004	LLZ3	182	AM
G. cirratum	3344	5/5/2004	LLZ1	197	AM
G. cirratum	3347	5/11/2004	LLZ5	164	JF
G. cirratum	3350	5/10/2004	LLZ2	185	JF
G. cirratum	3351	5/5/2004	LLZ1	200	AM
G. cirratum	3375	5/11/2004	LLZ5	183	AM
G. cirratum	3377	5/11/2004	LLZ5	231	AM
G. cirratum	3381	5/7/2004	LLZ1	155	JM
G. cirratum	3382	5/11/2004	LLZ5	224	AF
G. cirratum	3384	5/2/2004	LLZ2	165	JF
G. cirratum	3385	5/1/2004	LLZ3	136	JF
G. cirratum	3386	5/2/2004	LLZ3	155	JF
G. cirratum	3388	5/1/2004	LLZ3	145	JF
G. cirratum	3389	5/2/2004	LLZ3	164	JF
G. cirratum	3390	5/6/2004	LLZ3	152	JM
G. cirratum	3392	5/10/2004	LLZ3	145	JF
G. cirratum	3394	5/5/2004	LLZ1	157	JM

ceivers 14 and 20) and based on the positions of the receiver and using the detailed habitat map of the atoll in ArcMap, this species frequently utilizes a diverse variety of habitats ranging from very shallow (< 2 m depth) seagrass flats inside the lagoon (e.g. receivers 5, 6, 9) to the deeper (possibly >20 m depth) ocean reefs (e.g. receivers 1, 2, 7, 11, 13, 15, 21; Figure 2 a). The four Caribbean reef sharks were detected on 13 of the functioning receivers, with detections more frequently occurring on those placed on the deeper ocean reefs outside of the atoll (e.g. receivers 1, 2, 7, 11, 13; Figure 2 b). The two juvenile Caribbean reef sharks (3349, 3393) were also detected in the lagoon (3-18 m depth; receivers 3, 4, 8). Unlike the nurse sharks, only one Caribbean reef (3349) was ever detected on receivers (5, 6) placed on the shallow seagrass flats (<2 m depth) in the lagoon and then only for a period of a few minutes on a single day (Figure 2 b).

Medium-term (five month) MLD estimates for individual nurse (Fig. 3) and Caribbean reef sharks (Fig. 4) that were recorded on more than one receiver ranged from 1.1-29.3 km along Glover's Reef (mean 10.5 km, maximum 24.9 km for Caribbean reef; mean 7.7 km, maximum 29.3 km for nurse), with

FIGURE 2

a. Distribution of detection records from 25 nurse sharks on the 21 receivers from May to October 2004. The shade of each monitor is proportional to the log number of detection records (the key provided for this figure is applicable to all others), while the number associated with the receiver represents the number of individual sharks detected at that site. Monitors marked with "+" had no detection records. Note the wide distribution of the species around Glover's Reef, both inside and outside the conservation zone, and the diversity of habitats utilized (e.g. from shallow seagrass flats less than 2 m deep [receivers 6 and 9] to the deeper reef outside the lagoon [e.g. receivers 1, 2, 7, 13]). b. Distribution of detection records around Glovers' reef from 4 Caribbean reef sharks. Symbols, numbers and shading are as in (a) above. Note again the wide distribution of the species around Glover's, both inside and outside the conservation zone. Note also that although both the outer reef and lagoon were utilized, there was very limited activity of Caribbean reef sharks on the shallow seagrass flats less than 2 m deep (receivers 6 and 9). See Figure 1 for more detailed habitat classification of the atoll and the monitor identification numbers.

(a) (b)

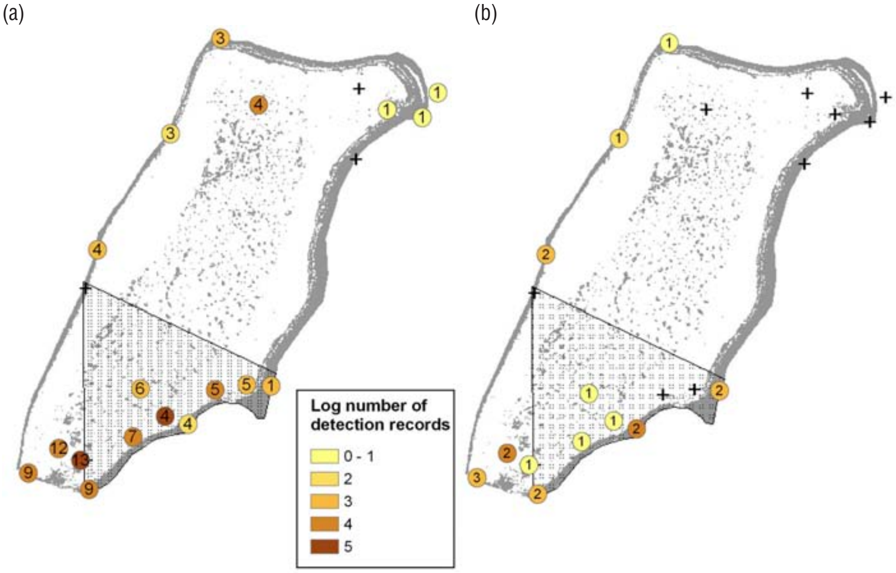
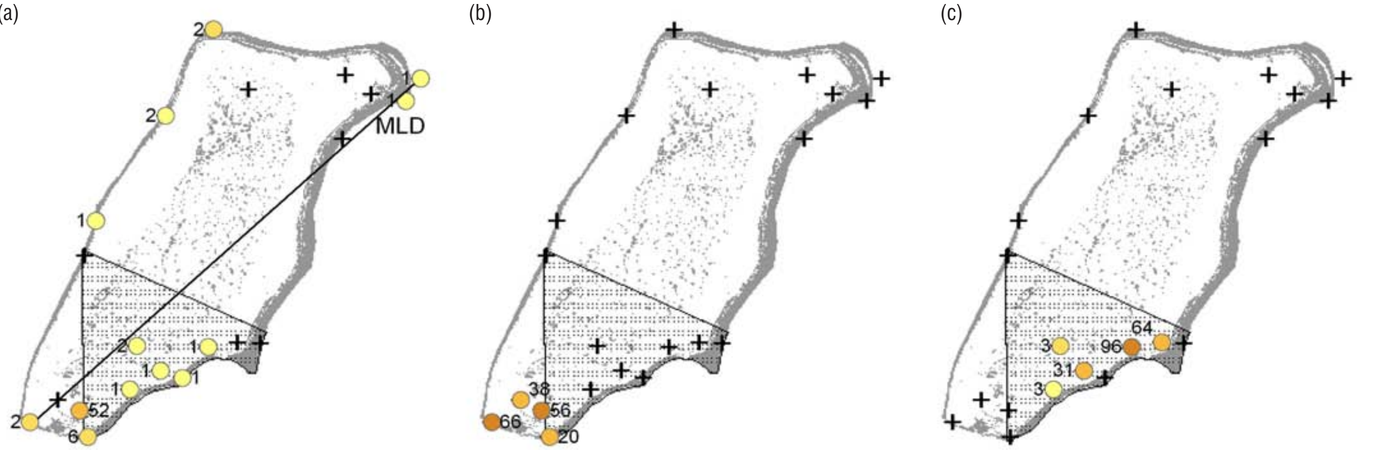


FIGURE 3

Distribution of detection records for individual nurse sharks. The shade of each receiver position is proportional to the log number of detections from the individual recorded at that site. The number associated with the receiver position is the total number of days (out of the 150 day study period) where that individual was detected at that site. "+" indicate the receivers where the individual was never detected. a. Shark 3333: this juvenile female was captured and released in LLZ2 (see Figure 1). Arrow shows how the minimum linear dispersal (MLD) was calculated for this and all other sharks, by measuring the straight-line distance between the peripheries of the ranges of the two most distantly spaced receivers the individual shark was detected on. Note that although this juvenile female was most frequently detected around the edge of the conservation zone (receiver 4), it nearly circumnavigated Glover's Reef over the five month study period. b. Shark 3351: this adult male released in LLZ1 (see Figure 1) was primarily active in the southern entrance of the atoll and frequently breached the boundary of the conservation zone. c. Shark 3337: Adult female released in LLZ3 was primarily active in the northeastern section of the conservation zone and was never detected outside of this zone.

(a) (b) (c)



the MLD estimates of several individuals very similar to or exceeding the 10 km length and breadth of the conservation zone. Four nurse sharks (3333: juvenile female, Fig. 3a, 3329: adult female, 3336: adult female, 3375: adult male) and two Caribbean reef (3349: juvenile female, 3348: adult male, Fig. 4 a, b) were documented to move from over halfway to nearly the entire length of the atoll, with 3333 nearly circumnavigating the atoll from May to October 2004 (Figure 3 a). In addition, one adult male Caribbean reef (3348) that was primarily detected on the windward ocean reef (receivers 2, 7, 11; Figure 4 a) was detected on a receiver belonging to another research group (N. Requena and K. Rhodes, pers comm.) on the morning and afternoon of July 27 on the western reef slope of Lighthouse Reef, an oceanic atoll approximately 30 km to the northeast of Glover's Reef across deep (>400 m) open water (Figure 4 b). The shark traveled back to Glover's Reef in approximately 30 hours, and was recorded within the array (receiver 13) on the evening of July 28 (50 km away from the receiver at Lighthouse Reef), suggestive of highly directional swimming behavior when traversing the pelagic zone between these two atolls.

Both nurse sharks and Caribbean reef sharks, although occasionally wide-ranging, exhibited site-fidelity to particular locations around the atoll (Figures 3, 4). All sharks were most frequently detected at the site nearest their capture ("primary receiver") and visited up to 13 additional, usually neighboring, receiver sites on a less frequent basis (Figure 5). Although less than 6 % of the total area of Glover's Reef was within the detection range of this non-overlapping receiver array, most sharks of both species were detected somewhere within the array on an almost daily basis from May to October 2004, with no evidence of seasonal emigration of these two species away from the atoll over this period (Figure 6, 7, 8; also see next paragraph). On average, nurse sharks were detected on 77 days out of the 150 day study period (i.e. at least once every two days; Figure 6), while Caribbean reef sharks were detected an average of 97 days (i.e. nearly two out of every three days; Figure 6). Typical examples of the high degree of residency of these sharks to the atoll throughout this five month period are shown in Figure 7 and 8 for individual nurse and Caribbean reef sharks respectively.

Individual nurse and Caribbean reef sharks were detected on at least one receiver positioned outside the conservation zone on from 0 (i.e. never detected outside of the conservation zone) to 133 days, with an overall average of 48 days out of the 150 day study period for both species combined. These numbers should be viewed as highly conservative estimates of the number of days individual sharks occurred outside of the conservation zone, because sharks are likely to have traveled outside the zone without being detected by the receiver array. Because all individuals showed fidelity to their site of capture (Figure 5), patterns of movement in relation to the boundaries of the conservation zone were examined for nurse sharks

FIGURE 4

Distribution of detection records for individual Caribbean reef sharks. The shading and numbering is as in Figure 3. a. Shark 3348: Adult male released in LLZ3 outside of the lagoon (see Figure 1). Note that this individual was most frequently detected along the windward ocean reef inside the conservation zone, but made occasional excursions to the southern and leeward ocean reefs. b. Longer distance movement of 3348 from July 24-28, 2004, when this individual left Glover's Reef for a period of 4 days and traveled 50 km across deep, open water to Lighthouse Reef Atoll (receiver marked with "X"). c. Shark 3340: Adult male, released in LLZ1 on the ocean reef. This individual was routinely detected at the southern apex of the conservation zone, with less frequent detections outside of this zone. d: Shark 3393: This juvenile male, released in LLZ1, was exclusively detected outside the conservation zone in the vicinity of the southern entrance channel.

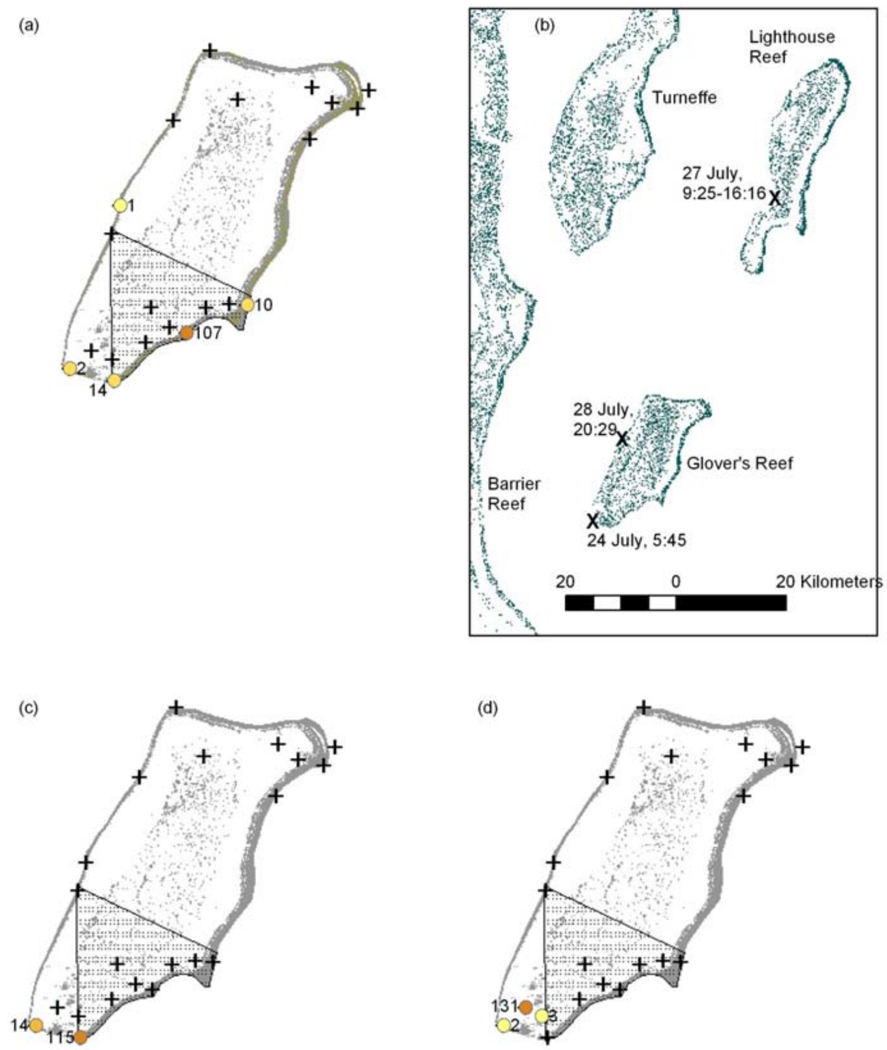


FIGURE 5

Histogram showing the relative proportion of detections recorded for individual sharks at their "primary" receiver (the one nearest their capture) to the proportion of detections at "other" receivers (other2=receiver with the second highest number of detections, other3=receiver with the third highest number of detections, other (comb)= all other receivers combined). The distribution of detection records for all ten sharks shown here is skewed towards their "primary" receiver, indicative of site-fidelity to these areas.

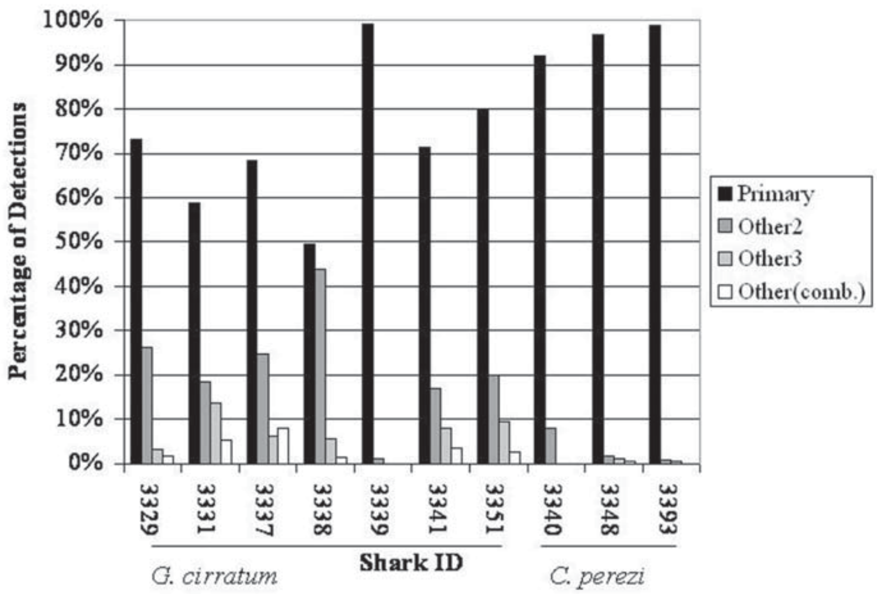
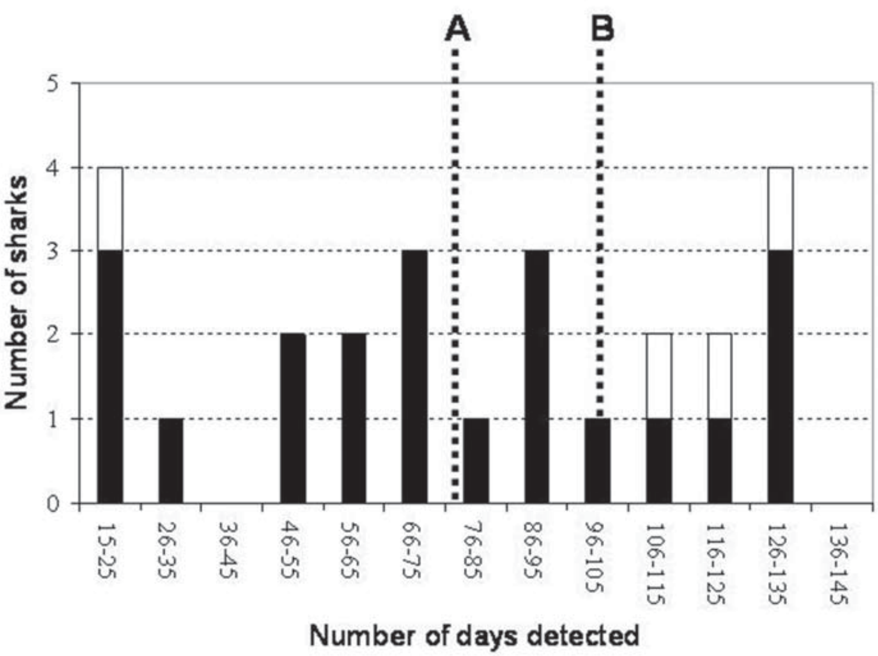


FIGURE 6

Histogram showing the number of days individual sharks were detected by at least one receiver within the array over the 5 month (150 day) study period. Solid bars are nurse sharks (n=21), open bars are Caribbean reef sharks (n=4). Dashed lines A (nurse) and B (C. reef) show the average number of days individuals of each species were detected anywhere within this array.



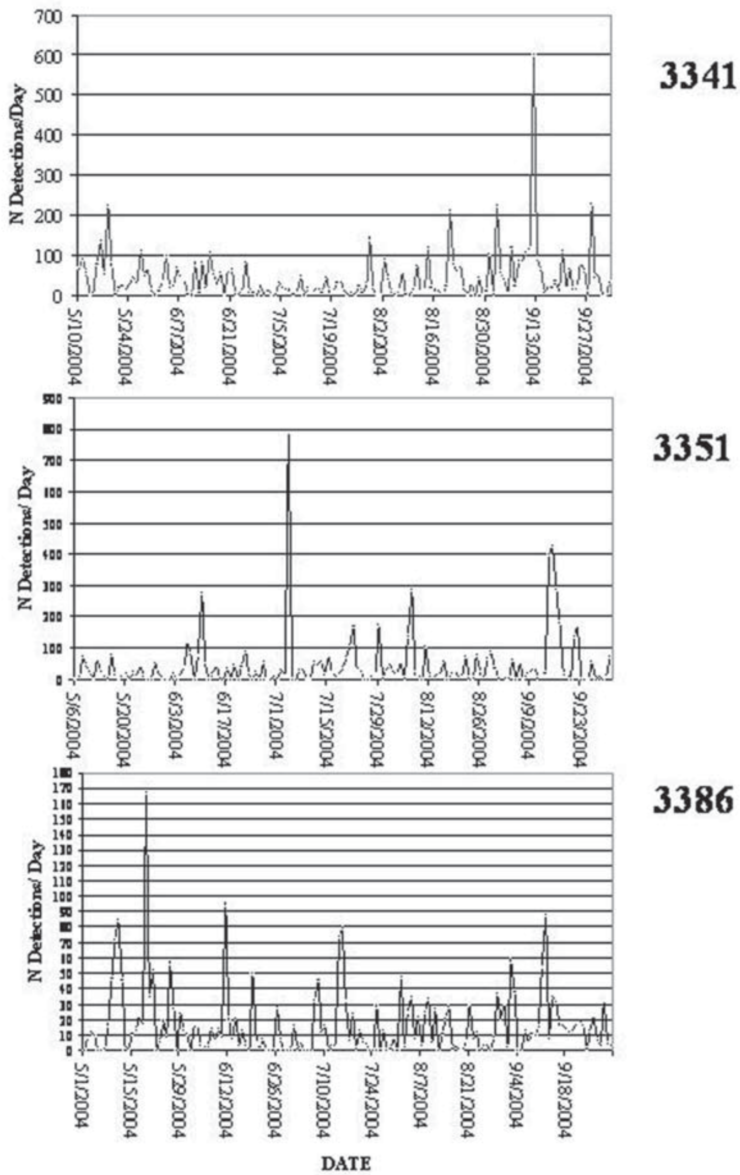
based on where they were caught and released. Eleven nurse sharks captured near the southern edge of the conservation zone (LLZ1 and 2) were detected within the array (i.e. by any receiver) on from 19-127 days (mean=77 days) of the 150 day study period, and were detected outside the conservation zone on from 19-127 of these days (mean= 72 days). All eleven of the nurse sharks captured in LLZ1 and 2 were documented to breach the conservation zone on many occasions (e.g. 3333, 3351 [Figure 3a, b]). In contrast, seven nurse sharks implanted with transmitters and released more centrally within the conservation zone (LLZ3) were detected within the array from 29-132 days (mean=90 days), but were only detected outside of this zone from 0-119 days (mean=18 days), with four of these sharks never being detected outside of this area (e.g. 3337 [Figure 3 c]). Three nurse sharks implanted with transmitters in locations further away from the conservation zone (LLZ 4 and 5) were detected from 15-88 days within the array (mean=42 days), and only one of these sharks (3375: adult male) was ever detected inside the conservation zone, and then for just a few minutes on one day. The preliminary tracking results for Caribbean reef sharks (from four individuals) showed that these sharks were detected within the array from 24-133 days out of the study period (mean=97 days). Individuals were detected outside the conservation zone from 7-133 days (mean=44.5 days), and all four animals were documented to leave the conservation zone at some point during the study period (Figure 4 a-d).

Discussion

Surgical implantation of acoustic transmitters and the establishment of a non-overlapping automated receiver array proved to be an efficient and effective technique for monitoring the movement patterns of both adult and large juvenile Caribbean reef and nurse sharks, with all but one of the study animals being detected within the array after surgery and over 80% of them providing data for periods of over 15 days. In general, both species were widely distributed

FIGURE 7

Line graph showing the daily number of detections recorded for individual nurse sharks throughout the receiver array (i.e. on any of the 20 functioning receivers) from early May to early October 2004. Results are shown for 3341 (adult male), 3351 (adult male) and 3386 (juvenile female), and demonstrate a high degree of residency to Glover's Reef by these sharks over this five month period, without any evidence of seasonal emigration away from the atoll. These results were typical of this species.

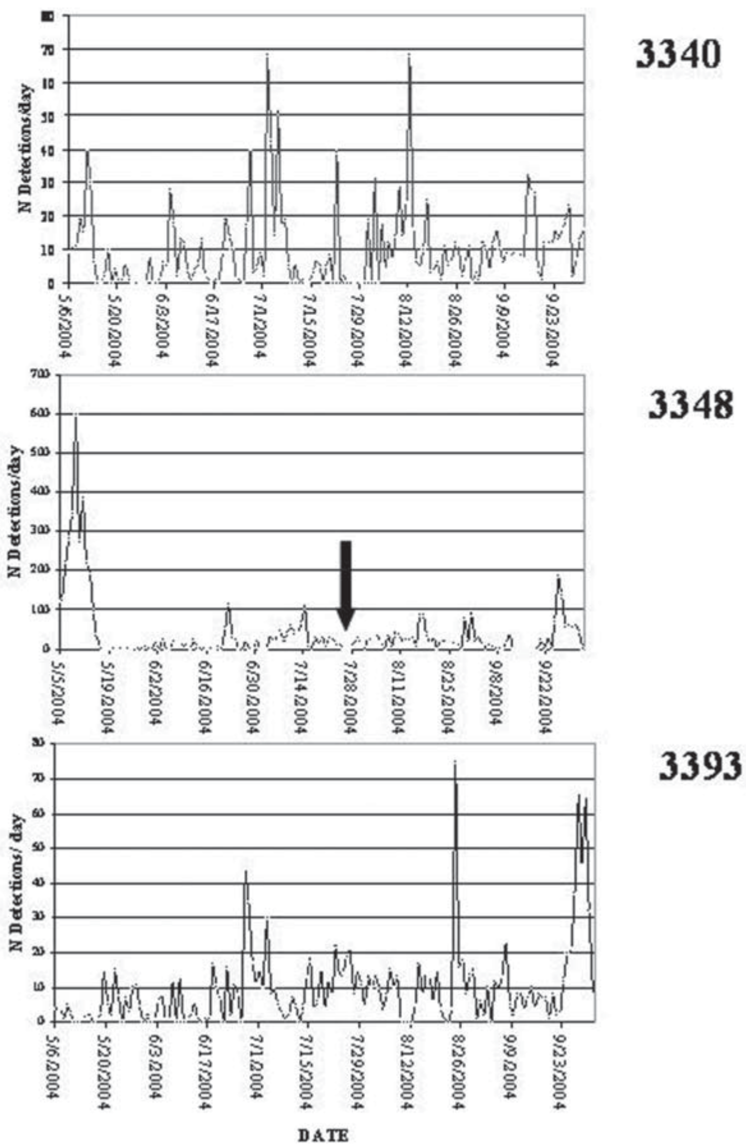


around Glover's Reef atoll and utilized a wide range of habitats, although these preliminary data for Caribbean reef sharks suggest that this species may generally avoid shallow seagrass flats (< 2 m deep), which is consistent with the very low longline CPUE of this species in this habitat (Pikitch et al., in revision). Individuals of both species exhibited evidence of site-fidelity over this five-month period, repeatedly utilizing the part of the atoll where they were originally captured and fitted with a transmitter. This result is similar to and extends short-term tracking results for several other tropical shark species (Johnson, 1978; McKibben & Nelson, 1986; Gruber et al., 1988; Holland et al., 1993). Unlike sharks of temperate latitudes (Castro, 1993), there was no evidence of a synchronous seasonal emigration of either of these two species away from the area between May and October (late spring, summer and early fall), with the majority of individuals clearly exhibiting a high-degree of residency to the atoll over this period.

The results demonstrate that although most of the sharks were captured and released within the conservation zone, individuals were detected outside of this zone on an average (both species combined) of 48 out of the 150 day study period (i.e. the average shark was detected outside the conservation zone on at least 32% of the days of the study, or on an average of one out of every three days). Once again, this should be viewed as a highly conservative estimate of the number of days individuals utilized areas outside of the conservation zone, because they are likely to have sometimes done so without being detected by the receiver array. Activity outside of the conservation zone was apparent in sharks originally captured and released near the boundaries of this zone (LLZ1 and 2) and especially so in those captured and released in more distant parts of the atoll (LLZ4 and 5). Notably, however, four of the seven nurse sharks captured and released near the center of the conservation zone (LLZ3) were never detected outside of this zone, which suggests that a significant portion of the medium-term activity space of some large juvenile and adult nurse sharks may be enclosed by this strictly protected part of the reserve at this time of the year. On the other hand, the three other nurse sharks captured in this area occasionally breached this boundary and entered parts of the atoll where fishing was allowed, and it is conceivable the other four did so and were not detected. We suggest that the number of days individuals enter areas where fishing is allowed is a critical parameter to attempt to measure when trying to evaluate the effectiveness of a marine reserve for shark conservation. Our data show that nurse and Caribbean reef shark populations remain exposed to fishing within Glover's Reef Marine Reserve because individuals of both shark species were frequently detected outside of the conservation zone. If longline or gillnet fishing activities were ever reinstated in the general use zone of Glover's Reef Marine Reserve, the threat

FIGURE 8

Line graph showing the daily number of detections recorded for individual Caribbean reef sharks throughout the receiver array (i.e. on any of the 20 functioning receivers) from early May to early October 2004. Results are shown for 3340 (adult male), 3348 (adult male) and 3393 (juvenile male), and demonstrate a high degree of seasonal residency of these sharks to the atoll. The black arrow shows the period where 3348 traveled to Lighthouse Reef Atoll (50 km away from its last point of detection at Glover's Reef, receiver 1). Note that both 3348 and 3340 exhibit short periods of multi-day absence from the array (e.g. in mid-May, mid-June, late July for both, mid September for 3348), which could represent similar movements to neighboring reef systems.



to these species would most likely increase, because these gear types are usually set for long periods (i.e. from several hours to overnight) to maximize the catch. Therefore, even if sharks spend only a small amount of time each day outside the no-take zone, but do so on a regular basis (i.e. over many days), it becomes highly probable they will eventually encounter the fishing gear and potentially be captured.

A large number of individuals of both species (20) were shown to utilize the large southern entrance channel, in many cases leaving the conservation zone as they apparently moved between the lagoon and windward ocean reef habitats. This is reminiscent of active tracking results for some Pacific reef sharks (grey reef and blacktip reef [*Carcharhinus melanopterus*]), which showed that these species also frequent channels between lagoons and ocean reefs (Johnson, 1978; McKibben & Nelson, 1986). The frequent use of this channel coupled with the heterogeneous habitat use by these two shark species emphasizes not only the importance of maximizing habitat diversity within protected areas of marine reserves (Sobel & Dahlgren, 2004), but also the importance of ensuring the connectivity of these habitats within the protected zone, to ensure that animals moving between these areas are not forced to traverse parts of the reef where they are exposed to fishers. The latter principle reveals a key design deficiency in the Glover's Reef Marine Reserve: the exposed reef crest that runs nearly continuously along the eastern edge of the atoll effectively bisects the sections of ocean reef and lagoon habitats contained within the conservation zone, which means that nurse sharks, Caribbean reef sharks and likely a wide variety of other mobile species that utilize both habitats must routinely traverse one of the five cuts. Our results demonstrate that the large southern entrance channel, which is almost entirely outside of the conservation zone, is frequently utilized by many individuals of these two shark species, and we therefore suggest that any future expansion or repositioning of the Glover's Reef conservation zone should aim to encompass most or all of this channel to ensure it does not act as a sink for these species. Furthermore, these findings suggest that resource managers should consider these types of large channels as potential high-priority areas to include within coral reef marine reserves in the future.

Together with geographic positioning, agreeing on the size of a protected area is usually the most contentious aspect of the marine reserve design process, because the maximum dimensions of a marine reserve are often strongly constrained by socio-economic pressures and are typically determined politically rather than scientifically (Sobel & Dahlgren, 2004). The findings of this study suggest that information derived from automated acoustic arrays may be useful for helping to establish minimum size limits for marine reserves, to counterbalance the political pressures that tend to constrain the size of these areas. Specifically, we suggest that the average and maximum recorded MLD for multiple-key species can be a very useful and easily understood dimension to convey to stakeholders in order to illustrate the dispersal range of these species and to help set scientifically defensible guidelines for establishing marine reserve size. This study has provided the average and maximum-recorded MLD around the atoll for nurse (7.7 and 29.3 km, respectively) and Caribbean reef sharks (10.5 km and 24.9 km, respectively) over a five-month period in the late spring, summer and early fall. Although the sample size for Caribbean reef is small and our estimate of MLD is conservative, these measurements indicate that both species make substantial and frequent movements around Glover's Reef over these five months of the year. For each species the maximum recorded MLD greatly exceeded the maximum length and breadth of the current conservation zone (10 km), while the average MLD for each species was very similar to this distance, indicating many individuals would be likely to occasionally breach the conservation zone boundaries, with the possible exception of individuals that primarily live near the center of this protected area. This result, after only five months, suggests the current size of the conservation zone is not large enough to enclose the activity space of many of these sharks over medium and long-term time frames, which bolsters the case for expanding this zone in the future.

Some of the long-distance movements observed during this study were quite surprising for nurse sharks, based on expectations derived from our own conventional tagging studies (of over 30 nurse sharks tagged and recaptured at Glover's Reef from 2001-2004, all but one were recaptured within 1 km of the site of original tagging after 1-3 years at liberty) and tagging and short-term active tracking studies conducted in the southern U.S.A. (Carrier, 1991; Kohler et al., 1998), all of which emphasize the predominantly non-dispersive nature of this demersal species. Despite this, our results show that at least four nurse sharks (1 adult male, 2 adult females, 1 juvenile female; 23 % of the study animals) moved from over halfway to almost the entire length of Glover's Reef (30 km), with the juvenile female almost circumnavigating the atoll, over the 5 month study period. The preliminary tracking results of four Caribbean reef sharks also suggest that this species is more dispersive than recent, but limited, conventional tagging studies in the Bahamas and Bermuda have suggested (Kohler et al., 1998). Although Caribbean reef sharks exhibited site fidelity, this was punctuated in some cases by long distance movements around Glover's Reef (up to 24.9 km), similar to results of short-term active tracking and tagging studies of several species of Pacific carcharhinid reef sharks (Randall, 1977; Johnson, 1978; McKibben & Nelson, 1986). Overall, these tracking results indicate that if no-take reserves are to be effective conservation tools for these two reef-associated shark species, and possibly ecologically similar relatives, they will have to be very large (boundaries of at least tens of kilometers) to significantly encompass the movements of these sharks over medium and long-term time frames.

One finding of particular interest with regard to understanding the dispersal range of these sharks was that one adult male Caribbean reef shark was documented to move at least 50 km between Glover's Reef and Lighthouse Reef atolls, including at least 30 km of travel over deep (> 400 m), open water, the first documented instance of this species crossing pelagic waters between reef systems anywhere in its range. The shark made this excursion over a four-day period in late July and returned to Glover's Reef from its last known detection at Lighthouse Reef within 30 hours, suggestive of directional swimming behavior (which would indicate a swimming speed of approximately 1.6 km/hr). Some species of larger sharks (e.g. tiger sharks, *Galeocerdo cuvier*, white sharks, *Carcharodon carcharias*) are also known to make highly directional movements between islands or reefs separated by deep, open water (Strong et al., 1992; Holland et al., 1999; Boustany et al., 2002), raising intriguing questions as to how frequently Caribbean reef sharks move across the pelagic zone between reefs and how they navigate while doing so. This finding underscores the need to establish marine reserve networks along the Mesoamerican Barrier Reef and its offshore atolls, perhaps connected by legislatively protected pelagic corridors, to allow for dispersal of this and other mobile species between reef-systems. It also suggests that Caribbean reef sharks may be vulnerable to incidental capture in pelagic longline fisheries if Belize were ever to open up their oceanic waters around coral reefs to pelagic longlining.

Our results indicate that the conservation zone of GRMR offers a fair amount of medium-term protection (i.e. over a five month period from May to October) for some nurse sharks that live near the center of this part of the reserve, however three major findings of this study (frequent utilization of the general use zone by many individuals of both species, relatively high estimates of MLD for both species, oceanic movements by a Caribbean reef shark) indicate that this no-take zone by itself has limitations as a long-term conservation measure for these populations. Fortunately, our data shows that many individual sharks of both species were residents of the GRMR as a whole (i.e. conservation and general use zones combined) over this period and so regulations associated with the larger general use zone (i.e. gear restrictions) likely augment the no-take zone and provide substantial protection for these two species from at least May to October. This is because in Belize (Gibson, 2003), as in many other parts of the world (Bonfil, 1997; Camhi, 1998; Chan A Shing, 1999; FAO, 2000), longlines and gillnets are the primary methods used by fishers to catch sharks in sufficient quantities to make targeting them economically profitable. Since fishers cannot legally use these gears anywhere within the GRMR, the development of a targeted shark fishery is unlikely to occur at Glover's Reef (assuming the continuation of enforcement efforts) and the fishing pressure on these sharks will probably remain limited to occasional incidental catches by fishers targeting large fish (e.g. snappers) with single-hook handlines in the general use zone. Future research priorities will be to assess the longer-term residency

(2-3 years) and winter-spring movement patterns of these species, in order to fully evaluate the conservation benefits of GRMR to populations of these sharks.

Overall, the results of this study suggest that a zoned marine reserve model, similar to the Glover's Reef Marine Reserve, could be an especially important component of a comprehensive ecosystem-based fishery management approach (EBFM; Pikitch et al., 2004), because this design provides a very broad zone of protection (based on gear-restrictions and perhaps other fisheries management methods) for mobile species (e.g. reef-associated sharks) while keeping the strictly no-take portion of the reserve at a size that is likely to be politically acceptable, enforceable and functionally useful for the conservation of relatively stationary commercially harvested species (e.g. smaller fishes and macro-invertebrates). Under this model of ecosystem-based fisheries management, a central no-take area could be surrounded by a much larger zone allowing limited fishing but with gear-restrictions imposed to reduce exploitation of larger, wider-ranging predators. In addition, given that at least one Caribbean reef shark traveled from Glover's Reef to Lighthouse Reef during the study period, restricting the use of gillnets and longlines in areas that form pathways between reef habitats may be a useful component of an EBFM plan for the Greater Belize Barrier Reef ecosystem.

Conclusions and Future Directions

Although this non-overlapping acoustic receiver array has only been in place for a short period of time, it has already provided important information about the movement patterns of two economically important shark species, with direct implications for designing and evaluating marine reserves to protect these, and perhaps other, reef-associated shark species around the world. The findings suggest that effective no-take marine reserves need to be large (boundaries of at least tens of kilometers) and need to encompass not only diverse habitats (ocean reefs, seagrass flats, lagoons) but also the areas that connect them (i.e. major channels). In addition, this study has documented for the first time that Caribbean reef sharks cross the pelagic zone between reefs, which underscores the need for reserve networks and regulation of pelagic fisheries in the conservation of this species. Overall, these findings suggest that an effective design for marine reserves to ensure some level of meaningful protection for these reef-associated sharks, may be to build upon the zoned-reserve model used for the Glover's Reef Marine Reserve, combining no-take zones with traditional fisheries management approaches and pelagic corridors.

Future work at this site will aim to determine longer-term residency patterns for these sharks (over 2-3 years), expand the sample size for Caribbean reef sharks, refine longer-term MLD estimates, quantify habitat use patterns for both species and expand the scope of the study to include other roving reef predators (e.g. snappers [Lutjanidae], jacks [Carangidae], stingrays [Dasyatidae], eagle rays [Myliobatidae]). In conclusion, the initial results of this ongoing study illustrate that non-overlapping, automated acoustic telemetry arrays can be an extremely useful and relatively efficient method to provide much needed, easily communicated, scientifically-defensible information on the movement patterns of large, roving reef predators that is critical for addressing key aspects of marine reserve design and evaluation.

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