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RESEARCH ARTICLE

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Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground

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Abstract The movement patterns and long-term site-fidelity of primarily juvenile Caribbean reef sharks, *Carcharhinus perezi*, were investigated using tag-recapture and automated telemetry at an insular nursery area, the Fernando de Noronha Archipelago, Brazil. Of the 143 externally tagged juvenile sharks (< 110 cm), 22 (15.3%) were recaptured between 0 and 5 km from the site of tagging after 5–800 days at liberty, suggesting some site-fidelity in young individuals of this species. Site-fidelity and movement patterns of ten juvenile sharks ranging from 78 to 110 cm total length (TL) and one opportunistically captured adult female (224 cm TL) were also investigated for periods of up to 2 years with an array of automated telemetry receivers. Tagging and telemetry data from both inside and outside a marine protected area (MPA) show that shark abundance and activity is greatest along the part of the archipelago's coastline least disturbed by human activity. Telemetry tracking also showed that juvenile reef sharks demonstrated a high degree of site-fidelity and occupied specific locations along the coast throughout the year, with some evidence of an increase in activity space with ontogeny. Sharks appeared to range more widely at night and there were no seasonal variations in habitat use. Our results suggest that MPAs may be a useful conservation tool to protect young *C. perezi* and potentially other reef-dwelling carcharhinid sharks during their early life history.

Introduction

The Caribbean reef shark, *Carcharhinus perezi*, is one of the largest and most abundant apex-predators inhabiting reef systems throughout the tropical Western Atlantic (Compagno 1984). This species is exploited in commercial and artisanal fisheries for meat and fins in some parts of its range (Bonfil 1997; Compagno 1984, 2002) and is also valued economically as a living resource as the primary species associated with shark-diving eco-tourism in the region (Watts 2001; Compagno 2002). Along with other reef-associated sharks, it is believed to play a major role in shaping community structure on Caribbean coral reefs (Bascompte et al. 2005). Despite its ecological and economic importance, *C. perezi* remains one of the least studied large carcharhinid sharks. Given the growing concerns about shark populations in general and absence of information on the biology and stock status of this species, a few nations have established conservation measures for *C. perezi*: it is prohibited from landings in the US commercial shark fishery and several countries have initiated the development of marine protected areas (MPAs) around key shark-dive sites (Watts 2001). MPAs are now being widely advocated for the protection of coral reef ecosystems (Sobel and Dahlgren 2004), and since shark fisheries are largely unregulated in the developing nations where *C. perezi* are most common, MPAs may often be the only currently implemented local conservation measure that benefits this species (Chapman et al.

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2005). There is a growing awareness that MPAs and other forms of time-area closure have the potential to play a more important role in shark conservation, especially for the protection of site-attached species and vulnerable critical habitats, such as nursery and mating grounds (Bonfil 1999; Stevens 2002; Baum et al. 2003, Chapman et al. 2005; Heupel and Simpfendorfer 2005; Barker and Schluessel 2005).

Carcharhinus perezi is one of the most common sharks inhabiting the insular shelf surrounding Fernando de Noronha Archipelago, Brazil, with the zone from at least 0 to 30 m depth used by juveniles of this species (Garla 2004). As a result of a local fishery operating from 1992 to 1997 targeting sharks around the archipelago, the population of *C. perezi* is believed by local dive business operators to have become severely depleted. At least 498 *C. perezi* were landed in the last 18 months of this fishery, representing 60% of the total shark catch during this period (Noronha Oceanic Fisheries, Fernando de Noronha, unpublished data). Although cessation of this fishery has provided some respite from fishing mortality, recreational and commercial fishermen still occasionally land neonate and juvenile *C. perezi* when operating around the archipelago. The only local conservation measure that currently may benefit *C. perezi* is the umbrella protection of a ‘‘no-take’’ MPA, which encompasses approximately 70% of the insular shelf, extending from the shore to the 50 m isobath. However, a major factor influencing the effectiveness of this type of spatially fixed MPA is the extent of movement of highly mobile species out of protected and into unprotected areas, either as part of their daily movements or as part of long-term seasonal migrations (Holland et al. 1996; Chapman et al. 2005; Heupel and Simpfendorfer 2005).

Acoustic telemetry has become one of the primary tools used to investigate movements of marine species in relation to protected areas and potential anthropogenic threats (Lindholm 2005). Although there have been several acoustic tracking studies of sharks (McKibben and Nelson 1986; Gruber et al. 1988; Klimley et al. 1988; Holland et al. 1993; Morrissey and Gruber 1993), relatively few have directly addressed the movement patterns of sharks in relation to existing or potential MPA boundaries (Chapman et al. 2005; Heupel and Simpfendorfer 2005). One trend that has emerged from shark tracking studies is that individuals of many species reutilize the same areas on a regular basis (‘‘site-fidelity’’: McKibben and Nelson 1986; Gruber et al. 1988; Klimley et al. 1988; Holland et al. 1993; Morrissey and Gruber 1993), suggesting that MPAs could be an important component of conservation and fisheries management strategies for these species. This trend is particularly true for juveniles of tropical species which often have relatively restricted activity spaces and exhibit almost daily site-fidelity (Holland et al. 1993; Morrissey and Gruber 1993), whereas older individuals and larger shark species tend to range over much wider areas (McKibben and Nelson 1986; Gruber et al. 1988). Although little is known about the movements of small juvenile *C. perezi*, large juveniles (> 150 cm) and adult male *C. perezi* tracked at an oceanic atoll in Belize made excursions from 29 to 50 km during a 5 month period, although they did exhibit site-fidelity to the study area throughout the study period (Chapman et al. 2005). Given the high likelihood of differing movement patterns and ecology depending on developmental stage and geographical location, developing effective MPAs for younger *C. perezi* will benefit from detailed age-specific and area-specific information on their movements.

The purpose of this study was to investigate long-term movement patterns of small juvenile [defined in this study as those with < 110 cm total length (TL)] *C. perezi* to evaluate the potential of MPAs for protecting the very young individuals of this species. The northern coastline of Fernando de Noronha was selected as a study site because of the presence of numerous small juvenile *C. perezi*, coupled with the partial coverage of this area by an established, large MPA. The specific objectives of this study were to use automated acoustic telemetry and traditional tag-recapture to (1) examine behavioral patterns (i.e., site-fidelity, residency times, dispersal range, activity patterns) of small juvenile *C. perezi* and (2) describe movements of these sharks in relation to the current MPA boundaries. This information could provide useful insights for MPA design and modification around offshore reef systems in Brazil for enhanced conservation of Caribbean reef sharks.

Methods

Study site

Fernando de Noronha Archipelago is located 345 km off the northeastern coast of Brazil, at 03°51′S; 32°25′W (Fig. 1a) and consists of 1 large island and 19 small adjacent islets, totaling 26 km^2. About 70% of the main island and the coastline from the shore to the 50 m isobath constitute an MPA since 1988. Fishing is prohibited in this area, and boat traffic and diving are heavily regulated. A large section, including the remaining portion of the main island to the 50 m isobath, is an environmental protection area (EPA) designated for sustainable use (Fig. 1a). Boat traffic is high in this area because of its management status and its proximity to the archipelago’s main port (Fig. 1). The climate is tropical with an average air temperature of 25.4°C. Mean water temperature is 26–27°C and mean salinity is 36‰ (Maida and Ferreira 1997).

Animal collection, handling and external tagging

Fishing to obtain small juvenile *C. perezi* for external tagging and transmitter implantation was conducted from March 2001 to July 2002 at ten monitoring sites on

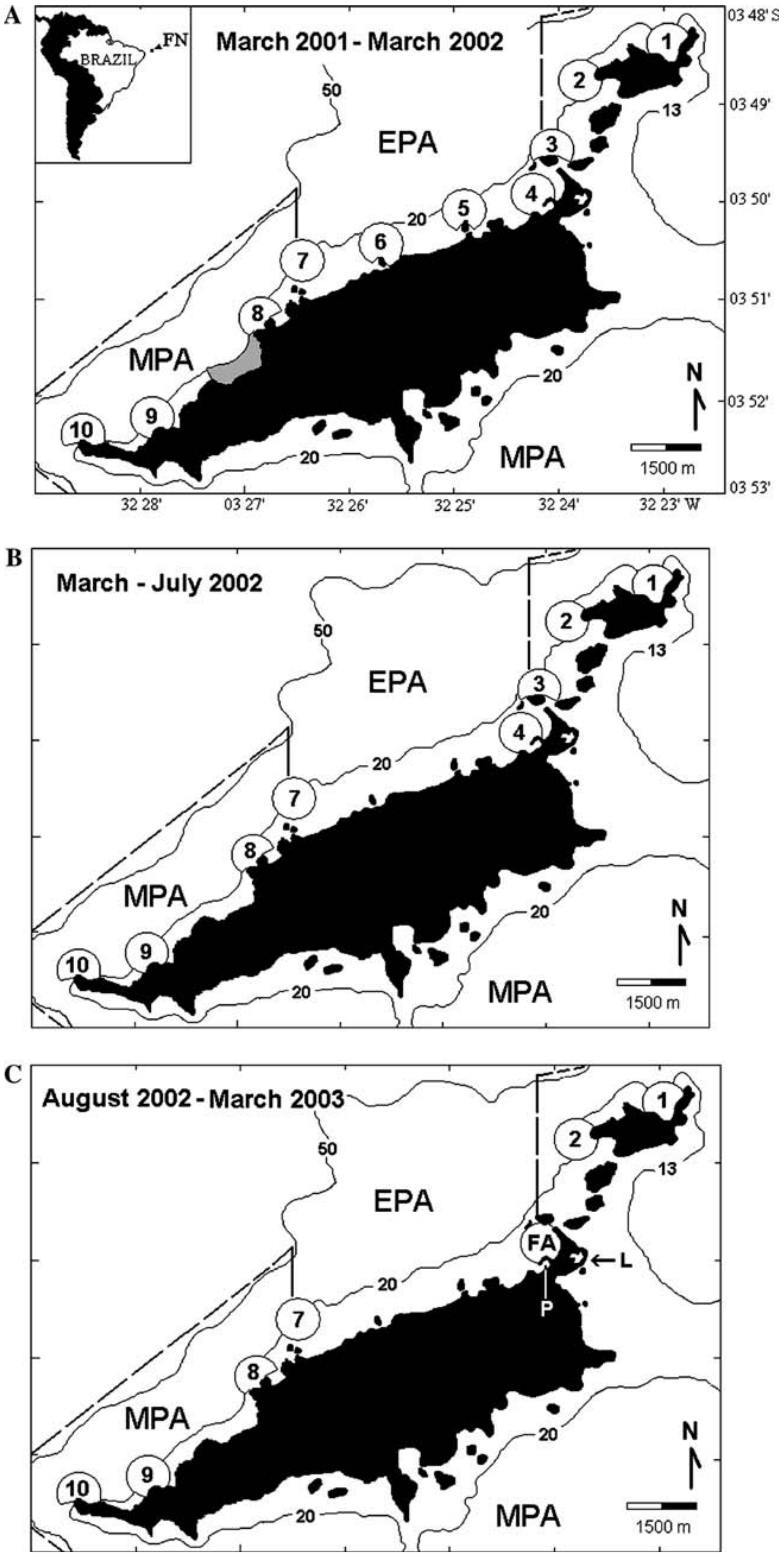


Fig. 1 Fernando de Noronha Archipelago. Location of the automated receivers on the leeward side of the archipelago during different periods of time of the study (**a**, **b** and **c**) and the approximate range of detection for each receiver. *MPA* marine protected area (National Marine Park), *EPA* sustainable use area, *FA* Fishers' Association, *L* lagoon opposite to the port at the windward side (P). The *gray shaded area* represents a section of the MPA where fishing surveys were prohibited

the approximately 14 km leeward side of Fernando de Noronha, using light handlines with 14 0/0 circle hooks baited with pieces of local teleost species (Fig. 1a). Fishing effort employed by researchers at this side of the archipelago was evenly distributed throughout the EPA and MPA management zones, though the catch (number of juvenile *C. perezi* captured/hour fishing) was dramatically higher in MPA sites (Garla 2004).

Hooked sharks were brought alongside the boat and examined for an umbilical scar, measured [fork length (FL) and TL], sexed and tagged while in the water. The condition of the umbilical scar was used to categorize small sharks into one of the following classes: neonate (umbilicus open or partially open), young-of-the-year (umbilicus closed but very obvious) and juvenile (umbilicus closed and not visible). Young-of-the-year and juvenile sharks captured in 2000 ($n = 47$) were tagged with a Billfish Foundation stainless steel dart-tag implanted near the base of the first dorsal fin. From 2001 to 2003, juvenile sharks of all classes ($n = 96$) were tagged with a nylon-barbed tag (Hallprint, South Australia) in the basal cartilage of the first dorsal fin.

Transmitter application

After conducting the procedures described in the above section, all the small sharks were landed and positioned with their ventral regions upward inside a PVC holding-trough with a hose providing seawater placed inside their mouths to aid ventilation of the gills. One adult female that was opportunistically captured with standard handline gear was inverted along the side of the boat. After periods ranging from a few seconds to a few minutes, the inversion resulted in the onset of tonic immobility (Henningsen 1994) allowing relatively quick surgery for transmitter implantation (usually less than 10 min per animal). Wax-coated, individually coded acoustic transmitters (Vemco Ltd, model V16, 16 mm diameter × 65 mm, frequency 69 kHz, life span 18 months) were implanted into the abdominal cavity of the animals through a 3–4 cm incision made in the abdominal wall anterior to the origin of one pelvic fin. The incision was closed with absorbable nylon sutures. The small sharks were returned to the water, revived until able to swim on their own (2–5 min) and released. Only sharks cleanly hooked in the mouth with no signs of significant injury received transmitters.

Shark movements were recorded from March 2001 to March 2003 by a linear array of up to ten VR1 (Vemco Ltd) omni-directional hydrophone/receiver units (Fig. 1). Receivers were anchored directly to the substrate with chains and buoyed with a rigid plastic float attached to the top of the unit. The ten receivers were initially moored approximately equidistantly along the same 14 km section of leeward coast where the sharks were fitted with transmitters. During the first year, the study area included both protected areas (MPA) and areas where fishing and other activities are permitted (EPA) (Fig. 1a).

Receivers recorded and stored data on the presence (transmitter number, date and time of signal reception) of sharks fitted with a transmitter when within the detection range, which field tests indicated as approximately 500 m. Receivers were retrieved using SCUBA at 2–3 months intervals, at which time the data were downloaded onto a laptop computer in the field, and the receivers refurbished and returned to their underwater mooring.

The telemetry study was conducted over a 2 year period (560 days) during which three temporal gaps occurred: the first gap encompassed 90 days (December 2001–March 2002) at sites 5 and 10 due to the loss of receivers from severe sea conditions; the second gap encompassed 40 days (March–April 2002) at site 7 due to a receiver malfunction; the third gap encompassed 160 days (April–August 2002) at all sites except site 7 due to laptop computer failure and loss of stored data. As a consequence of the loss of receivers at sites 5 and 10 and failure of the receiver at site 7, the receivers initially located at sites 4 and 6 were repositioned to sites 7 and 10 where a high frequency of detections had been recorded before receiver loss. Therefore, only receivers 1, 2, 3, 7, 8, 9 and 10 were in use during the first half of 2002 (Fig. 1b).

At the end of July 2002 commercial fishers reported the presence and capture of *C. perezi* in front of the Fishers Association facility (FA, Fig. 1c) at sunset, when fisheries by-products are discarded. Based on these reports the receiver at site 3 which had detected no sharks after 15 continuous months of monitoring at its original site was repositioned to 350 m in front of the FA. After being repaired, the receiver initially anchored at site 7 was positioned in a shallow (< 3 m depth) lagoon (L) opposite to the port, at the windward side of the archipelago (L, Fig. 1C), where these sharks are often observed. Therefore, from August 2002 to March 2003 receivers were at sites 1, 2, FA, L, 7, 8, 9 and 10 (Fig. 1c).

Data analysis

For each monitoring site, the total number of detection records (i.e., for all sharks combined), the detection density (i.e., number of detections recorded per day) and identities of sharks were determined and plotted on a map to ascertain general patterns of shark activity along the monitored section of the coast. The number of detection records from each shark visiting each monitoring site was collated and used to determine the degree of site-fidelity and measure the minimum "dispersal" range of each shark along the coast. For each shark a "primary site" (the site with the most detection records) was designated and, if needed, "adjacent sites" (sites with less frequent detection records). The minimum dispersal range of each shark along the coast was estimated by measuring the distance between the peripheries of the detection ranges of the two farthest receivers the shark was detected. The number of days each shark was recorded within the receiver array was used to calculate the minimum percentage of days it was present within primary and adjacent sites. The number of days each receiver was in the water and functioning was converted into time (given 1,440 min in 1 day) and was used to calculate the percentage of total monitoring hours individual sharks were detected within the array. The number of detections recorded for each shark during diurnal and nocturnal periods was collated separately for each receiver to examine diel patterns of activity at "primary" and "adjacent" sites. For each shark's "primary site", detection records were also plotted versus time of the day and month to further investigate diel and seasonal patterns of use of primary sites. For sharks tracked for more than one consecutive year, a comparison was made between their detection history during the first and second half of the study, to verify if a change in activity space (e.g., a shift in the location of the primary detection site, an increase in the overall number of sites where it was detected, a reduction in time spent within the array) occurred as the animal aged.

Results

Twenty-two tagged *C. perezi* (15.3% of 143 tagged animals) were recaptured after 5–800 days at liberty (mean = 161 days; Fig. 2). Twelve of these recaptures were made by local fishermen and ten recaptures were made during the fishing efforts of this study. Local fishermen only returned accurate tag numbers and recapture information for 4 out of the 12 recaptured animals. For all recaptures where tag information was available ($N = 14$), the distance between tag and recapture locations ranged from 0 to 5 km, and 12 of these sharks were recaptured at almost exactly the same location of tagging after 5–400 days at liberty. In mid-January 2003, a fisherman recaptured a shark that had previously been dart-tagged close to the coast at a depth of < 30 m in 2000 (based on tag type and color). Although the tag was lost after landing the shark and it was not possible to identify the individual, this recapture took place at a depth of 60 m, close to the insular slope (Fig. 2).

Transmitters were implanted into nine female and five male sharks ($N = 14$) ranging from 78 to 224 cm TL (mean = 97.5 cm TL; Table 1, Fig. 2). Four sharks were neonates, six were young-of-the-year, three were juveniles and one 224 cm TL female was believed to be mature based on the estimated size at maturity for females (200 cm, Compagno 1984). Due to the very low CPUE within the EPA, sharks fitted with transmitters were only captured at sites within the MPA or very near the western EPA/MPA boundary (site 7; Table 1, Fig. 2). Eleven animals (80%) were detected following

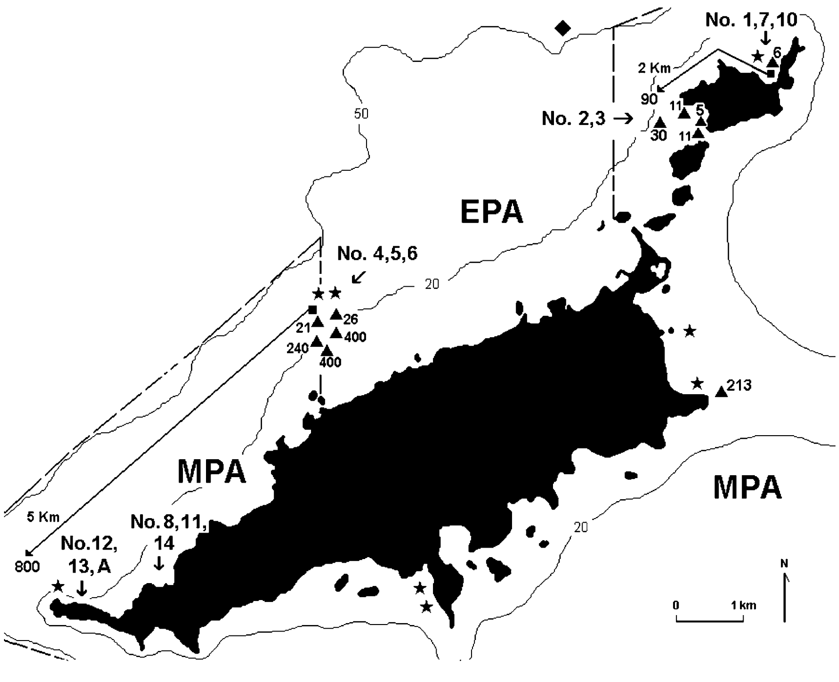


Fig. 2 Sites where *C. perezi* fitted with transmitters were captured ($N = 14$) and recapture locations at the leeward side of Fernando de Noronha Archipelago ($N = 21$). The *numbers with arrows* indicate the identification code for the individual sharks and the respective sites where transmitters were implanted (see Table 1). *Triangle* indicates recapture at same location of tagging and the *associated number* indicates the number of days at liberty since tagging. *Asterisk* indicates location of recapture reported by fishermen that released or killed tagged sharks and did not record the specific tag number. *Square* indicates capture location and *arrowhead* indicates recapture location; *numbers* indicate days at liberty and estimated distance traveled (km). *Diamond* indicates the location of a recapture of a tagged, older juvenile at the insular slope (tag number not reported by fisherman)

Table 1 *Carcharhinus perezi* with acoustic transmitters implanted into the abdominal cavity between March 2001 and March 2003

No.	Site	Date	TL (cm)	Sex	Weight (kg)	Life stage	No. monitoring days[a]	%Days detected	%Time	%Detections/period	> Activity	%Other sites
1	(1)	05/04/01	84	F	3	YOY	560	8.4	14	46.8%D; 53.8%N	1800 h	–
2	(2)	14/03/01	79	F	2.5	N	500	60.6	5	62.2%D; 31.7%N	1500 h	–
3	(2)	15/03/01	78	M	2.5	N	500	0	0	–	–	–
4	(7)	16/03/01	85	F	3	N	520	7	47	46.3%D; 53.7%N	0100 h	–
5	(7)	18/03/01	78	M	2.5	YOY	520	0.1	0	100%D	–	–
6	(7)	31/03/01	83	F	3	YOY	520	58.2	62	49.5%D; 50.5%N	1800 h	(8) = 0.57%
7	(1)	09/04/01	85	F	3.5	N	560	39.5	12.4	59.4%D; 40.6%N	1500 h	(7) = 1.25%
8	(9)	29/08/01	107	M	6.5	YOY	410	77.3	40.4	46.4%D; 53.7%N	0200 h	(10) = 13%
10	(1)	09/04/01	76	M	3	J	560	3.2	18.5	62.3%D; 37.7%N	1400 h	–
11	(9)	28/06/01	91	M	3	J	440	64.7	4.6	48.9%D; 51.1%N	0400 h	(7) = 1%; (8) = 6%
12	(10)	31/08/01	94	F	4.5	YOY	320	53	6	73.4%D; 26.6%N	1600 h	(9) = 17%
13	(10)	28/09/01	92	F	4	YOY	290	0	0	–	–	–
14	(9)	21/01/02	110	F	9	J	260	3.5	0.6	2.3%D; 97.7%N	0000 h	–
16	(10)	23/07/02	224	F	~80	AD	436	0	0.7	38.4%D; 61.6%N	0400 h	(L) = 39%

Site: original capture location; Life stage: defined on the condition of the umbilical scar—N (neonate), YOY (young-of-the-year), J (juvenile), AD (adult); %Days detected: percentage of the number of days with at least one record; %Detections/period: percentage of total number of detections during diurnal (D) (0600–1800 h) and nocturnal (N) (1800–0600 h) periods; %Time: percentage of the total amount of the monitoring hours within the receiver's array; > Activity: time of the 24 h cycle with the highest mean proportion of detections; %Other sites: percentage of the days in which the shark was detected in other locations than where it was captured

[a] Gaps during the monitoring period: 90 days at site 10 (01/12/2001–02/03/2002); 40 days at site 7 (02/03/2002–12/04/2002); 160 days at all sites

their release, and seven (50%) were recorded for more than 3 months. Two of the 14 sharks (Nos. 3 and 13, tagged at sites 2 and 10, respectively) were never detected on monitors, and one (No. 5, tagged at site 7) was detected only on the day of its release. These three sharks were not included in the analysis. Overall, four sharks (Nos. 1, 4, 10 and 14) were detected between 3 and 7% of the approximately 400–500 days that each monitor was in the water and functioning properly (Table 1). Two sharks (Nos. 7 and 16–the latter hereafter referred to in text and figures as "adult" [A]) were detected on 30–40% of the monitoring days, and five (Nos. 2, 6, 8, 11 and 12) were detected on 50–80% of the monitoring days (Table 1).

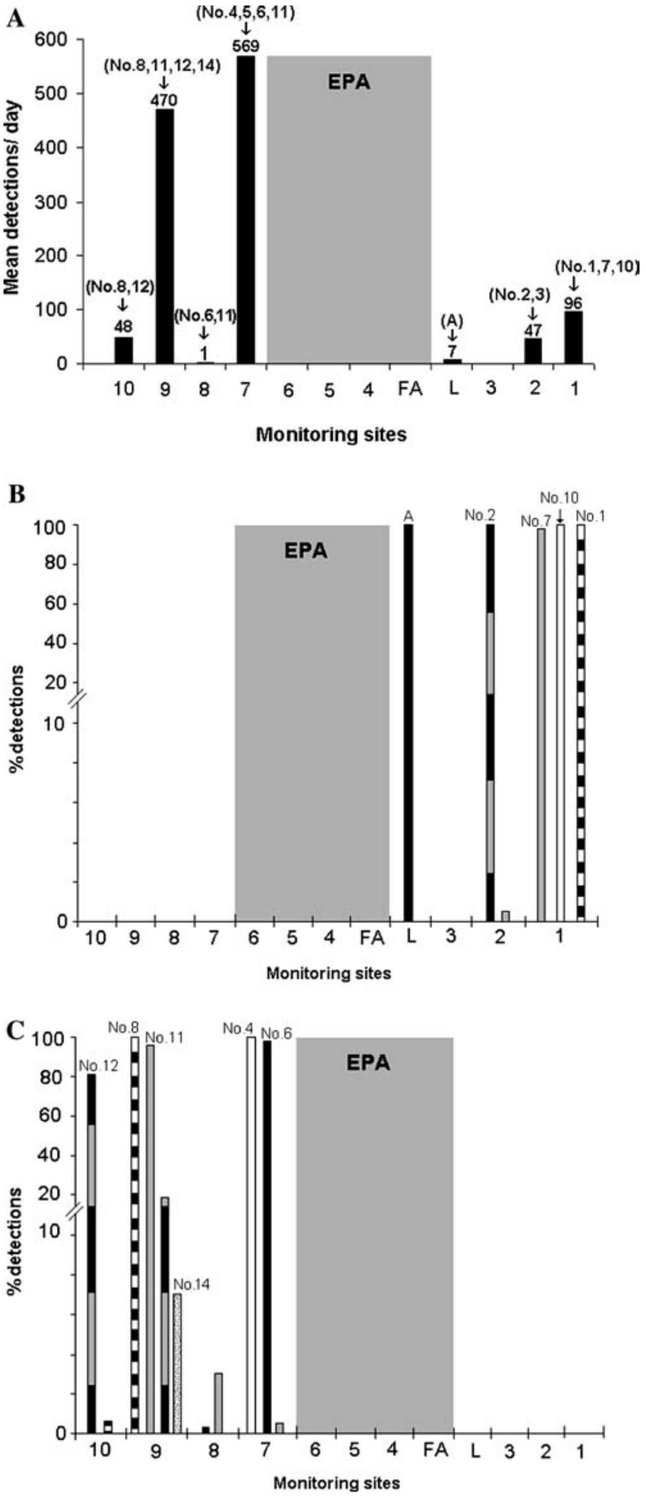
The numbers of records at each of the 12 sites monitored from March 2001 to March 2003 together with the identities of the sharks detected are shown in Fig. 3a. The detection density for each site (number of detection records per day) is shown in Fig. 3b. Both show that detection records were concentrated in several areas, with a very large number of detections of multiple individuals at Dois Irmaos reef (site 7—at the western limit of the EPA/MPA zones), and at the extremities of the archipelago (sites 1, 2, 9, 10), all of which are enclosed within the boundaries of the MPA. In contrast, there were no detections from any shark on the receivers placed in the EPA. Furthermore, no shark detected in the protected area on one side of the EPA was ever detected on the other side of this zone (Fig. 3a, b).

Movements of individual juvenile *C. perezi* were restricted to specific parts of the coastline (Figs. 3, 4). Five juveniles (Nos. 1, 2, 4, 6 and 10) were exclusively detected by the receiver located at the site of their capture, while the remaining five juveniles (Nos. 6, 7, 8, 11 and 12) were detected principally at their site of capture ("primary site"), but also occasionally at up to two neighboring areas ("adjacent sites") (Figs. 3, 4). Minimum linear distances traveled during these excursions to neighboring monitoring sites were conservatively estimated at 0.8–3.3 km. For all these juvenile sharks, detection records at adjacent monitoring sites predominantly occurred at night, while detections at the primary site usually occurred throughout the diel cycle (Fig. 5).

There was no evidence of a seasonal emigration of juvenile *C. perezi* away from the archipelago's northern coastline. Sharks were detected within the receiver array during all months of the year, with some individuals recorded almost daily for 6–18 months (Fig. 6). Six of the juvenile sharks, though detected almost daily, typically spent little time within the range of their primary receiver (0.6–18.5% of the total monitoring hours). However, three sharks (Nos. 4, 6, 8) spent from 40.4 to 64.0% of the monitoring hours within the range of their primary receiver (Table 1). For the juvenile sharks tracked for more than 1 year, there was no change in the location of the primary site, the number of adjacent sites visited or the number of days or time spent within the array during the early and later periods of the study.

The adult *C. perezi* was captured and fitted with a transmitter at site 10, but, unlike the juvenile sharks, this animal was never detected by the receiver anchored in this area. Although eight receivers covered the archipelago's leeward coast over this period of the study, the adult was only recorded by the receiver in the lagoon on the archipelago's windward side, approximately 10 km away from site 10. The shark was detected on 39% of 436 days this receiver was positioned at this site (Fig. 4) and was recorded during all months during this period

(Fig. 6). It spent 0.7% of the total 10,320 monitoring hours in the lagoon, and arrival and departure times suggest it entered and left this site several times a day. The longest visit to the lagoon lasted about 19 h, with several departures up to 15 min during this period. The highest mean proportion of detection records was at 0400 h (Table 1).



◀ **Fig. 3** **a** Mean detection density (number of detections recorded at the receiver/number of days the receiver was in the water and functioning properly) accumulated in 12 monitoring sites (listed from west to east) for 11 sharks monitored at Fernando de Noronha Archipelago. The *number in parentheses* indicates the identification number of the sharks detected at each site. The *gray shaded area* indicates the monitoring sites within the EPA. **b**, **c** Proportion of the total number of detections for individual sharks recorded at each site (see Table 1 for location of capture); **b** provides results for sharks captured to the east of the EPA while **c** shows results for sharks captured to the west of the EPA. Note that the sharks are only detected on from one to a few neighboring receivers throughout the study, none are ever detected within the EPA and none of the sharks captured on the east of the EPA move through this zone to the west and vice versa

Discussion

Tag and recapture data imply a fair amount of site-fidelity in *C. perezi*, particularly for small sharks. Not only were most sharks recaptured in almost the same location as the original tagging site, but this recapture rate also is high relative to those obtained in many other elasmobranch tagging studies (Kohler and Turner 2001). Longer distance recaptures of two larger *C. perezi* (110–150 cm TL), one at the archipelago's southwestern extremity and the other at the slope of the insular shelf, suggest that juveniles of this species may extend their movements as they grow, including more distant and deeper sites, as has been observed in other shark species (Merson and Pratt 2001).

Capture of *C. perezi* with single-hook handlines and surgical implantation of transmitters into the abdominal cavity proved to be an effective technique for the long-term monitoring of these animals, with at least 80% detected more than 24 h after surgery. The three sharks never detected or only detected on the day of their release may have died due to trauma associated with surgery. Juveniles released after surgery sometimes swam away relatively slowly and may also have been especially vulnerable to predators during their recovery. The detection of four other sharks only up to 2 months after surgery may be a result of transmitter failure, movement to unmonitored areas (e.g., the windward side of the archipelago) or mortality (natural or fishing). Given the relatively high estimates of juvenile mortality rates in other carcharhinids (Gruber et al. 2001; Heupel and Simpfendorfer 2002), it seems reasonable that natural mortality could account for the relatively brief contact with these individuals.

The extensive utilization of the archipelago's extremities (sites 1, 2, 9, 10) by juvenile *C. perezi* may result from the suitable habitat and productive foraging grounds provided by the well-developed reefs and strong currents, which support an abundant reef fish fauna. The apparently intensive use of the Dois Irmaos reef (site 7) bordering the MPA by juvenile *C. perezi* may be a result of its large size (~400 m^2), its structural

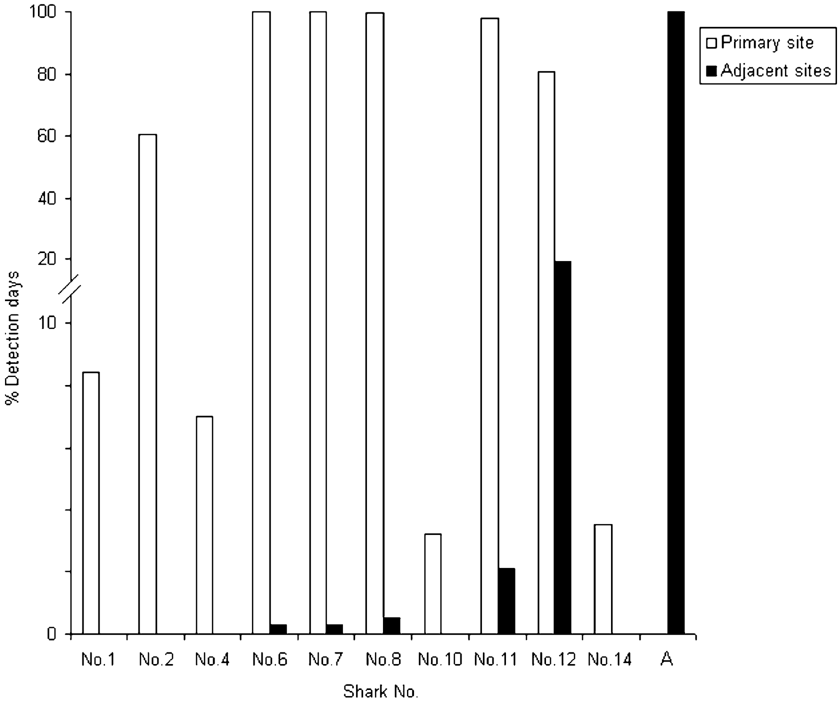


Fig. 4 Proportion of days with at least one detection record out of all of the days receivers were functioning (%Detection days) for 11 *C. perezi* monitored at Fernando de Noronha (see Table 1 for location of capture). *Open bars* indicate the %Detection days sharks were detected at their "primary site" (Table 1). *Solid bars* show the % Detection days sharks were recorded at up to two "adjacent sites" combined (see Table 1, Fig. 3)

complexity composed of massive coral heads that concentrate an abundant reef fish fauna and the use of the area by sharks as a cleaning station (Sazima and Moura 2000). It appears that a slight (1 km) eastward extension of the current EPA/MPA western border would fully encompass most of the habitat intensively utilized by juveniles of this species and would likely reduce fishing mortality. In contrast, results of the first year of automated telemetry monitoring coupled with abundance survey catch data suggest that juvenile *C. perezi* rarely frequent the contiguous coastal area within the EPA, despite the similarity of MPA and EPA sites in depth range, topography, substrate type. The relative scarcity of sharks inhabiting or even passing through the EPA may be the result of an intensification of anthropogenic use of this site over the past 5 years, especially fishing activities that may have eliminated residential *C. perezi* from this area. Another possibility is that direct human disturbance, in this case boat traffic along the entire EPA section, may have driven sharks away from this area and concentrated them in protected areas (Carrier and Pratt 1998). Although MPAs are generally thought of as benefiting exploited fish populations by reducing fishing mortality, the extreme spatial heterogeneity in the population density of this species observed at Fernando de Noronha may actually have been caused by the concentration of human activity in the EPA following the closure of the MPA. Since there is some evidence that growth and mortality in populations of young sharks may be density dependent (Gruber et al. 2001), this finding may indicate a possible negative effect of MPAs on shark early life stages that should be further investigated and possibly taken into account during the MPA design process.

Automated telemetry and tag-recapture results suggest that most juvenile *C. perezi* show long-term site-fidelity to the leeward coastline. Five of the ten juvenile *C. perezi* tracked for extended periods were detected only by the receiver positioned at the site of their capture, and the remaining juvenile sharks were recorded most often at the receiver positioned at their capture site, with less-frequent excursions usually up to two adjacent monitoring sites. No shark was detected by more than three consecutive monitors along the whole length of the coast during the entire course of the study, despite the relatively close proximity of receivers. This type of site-fidelity appears typical of many juvenile sharks inhabiting tropical and subtropical areas (McKibben and Nelson 1986; Holland et al. 1993; Morrissey and Gruber 1993) and suggests the potential of MPAs of even limited size for protecting early life stages of *C. perezi* and perhaps its ecologically similar relatives. Additional species- and area-specific studies of shark movement and distribution should be carried out to better evaluate this premise and assess proposed MPA locations.

Although further research is required to more precisely quantify the dimensions of daily activity patterns of young *C. perezi*, our results suggest their activity space may be quite small. This is inferred from the high percentage of hours of contact for several sharks with receivers in their primary site (areas of less than 0.785 km^2), the high percentage of days that sharks were recorded in their primary or adjacent sites and by the observation that sharks did not appear to move over an area greater than that covered by three consecutive monitors (a maximum distance of 3.3 km). However, since most of the juvenile sharks were not recorded continuously each day, active tracking or automated

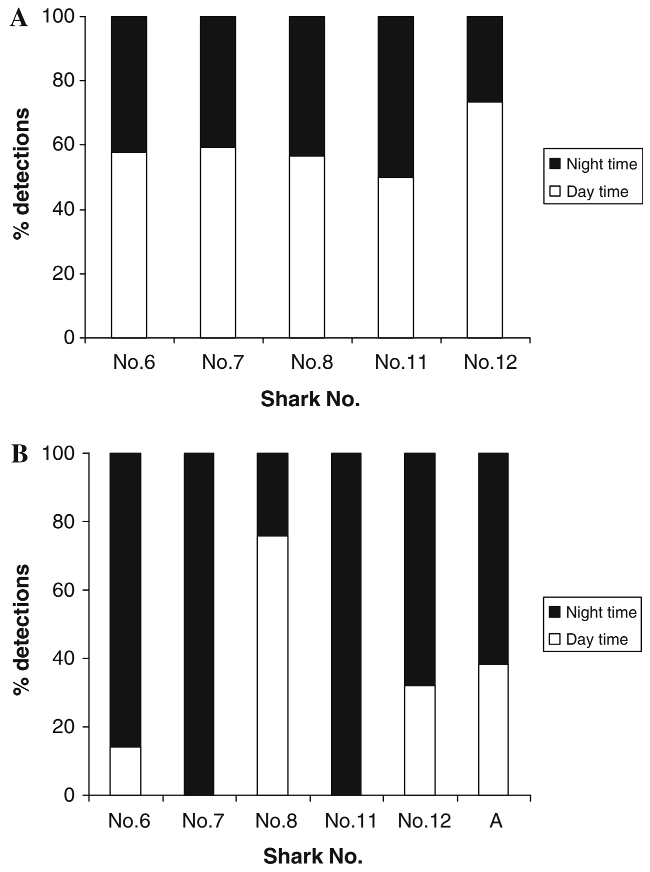


Fig. 5 a Relative proportions of daytime/nighttime detections recorded at the primary site for five juvenile *C. perezi* that were recorded at more than one monitoring site during the study. *Solid bars* indicate proportion of nighttime detections and *open bars* indicate the proportion of daytime detections. Note that all sharks are recorded both day and night at their primary site, with a slightly higher proportion of daytime detections. **b** Relative proportions of daytime/nighttime detections recorded at the adjacent site(s) for the same five juvenile sharks. Note, with the exception of shark 8, that most sharks were detected predominantly at night by the receivers adjacent to the primary site. Relative proportions of daytime/nighttime detections are also shown for the adult female A. This animal was most frequently detected at night in the lagoon

telemetry with a greater number of overlapping receivers would be needed to adequately measure the size of daily activity spaces in juvenile *C. perezi*.

Although they exhibited site-fidelity, the occasional detection of many juvenile *C. perezi* at adjacent sites up to 3.3 km away mostly at night suggests wider nocturnal movement, a behavioral trait also observed in other shark species and often thought to be related to feeding (McKibben and Nelson 1986; Gruber et al. 1988; Klimley et al. 1988; Holland et al. 1993; Heupel and Simpfendorfer 2005). Although the diet of *C. perezi* is not well characterized, small to medium-sized reef fishes (families Scaridae, Carangidae, Serranidae) have been found in stomachs of four sharks captured by fishermen at Fernando de Noronha (R. Garla, unpublished data). It is possible that juvenile *C. perezi* may be active nocturnal predators, especially when preying on scarids that are inactive at night. Regardless of the reasons behind increased nocturnal activity in juvenile *C. perezi*, this characteristic would make sharks more likely to breach MPA boundaries at night and illustrates the importance of understanding diel patterns of fishing pressure exerted near protected areas for conservation planning and for evaluation of the effectiveness of MPAs (Heupel and Simpfendorfer 2005).

The persistence of site-fidelity in juvenile *C. perezi* throughout the year contrasts with the seasonal migrations out of primary nursery areas during the first year of life displayed by subtropical and temperate *Carcharhinus* species (Merson and Pratt 2001; Heupel and Hueter 2002; Heupel and Simpfendorfer 2005). The lack of seasonal emigration in sharks such as juvenile *C. perezi* may be typical of tropical carcharhinid species and would enhance the effectiveness of MPAs since these sharks may remain within protected areas for prolonged periods of time during the first few years of their lives.

The adult shark monitored in this study was the only *C. perezi* documented to move the entire length of the archipelago (based on its tagging at the opposite extremity of the island). This observation, coupled with recaptures of two large juvenile sharks (110–150 cm TL) at locations at least 5 km away from their tagging location, suggests that the activity space of *C. perezi* increases with shark size, as has been shown for other sharks (Nelson 1990; Heupel and Hueter 2002). Indeed, large juveniles and adult male *C. perezi* tracked in Belize ranged much farther than the young sharks in this study, with one animal moving more than 50 km between reefs across deep open water (Chapman et al. 2005). However, ontogenetic changes in movements were not detected in the neonate and young-of-the-year sharks monitored by telemetry for two consecutive years, which suggests these may occur during a later phase of their development or are too subtle at this stage to detect using stationary acoustic receiver. Further research is required to characterize the details of ontogenetic changes in movements of *C. perezi*.

Conclusions

Tagging and telemetry monitoring of the movements of juvenile *C. perezi* at Fernando de Noronha Archipelago showed that: (1) sharks exhibit high site-fidelity to specific parts of the coast and live year-round at this site; (2) there are no apparent seasonal variations in movement patterns; (3) sharks range more widely at night; (4) activity space likely increases with ontogeny; (5) the areas most heavily used by sharks are those areas of the archipelago that are least disturbed (i.e., the MPA). These data suggest that the movements of small juvenile *C. perezi* are conducive to use MPAs for the conservation of the early life stages of this species, and perhaps also those of ecologically similar congeners. However, results also suggests that increased human pressure in

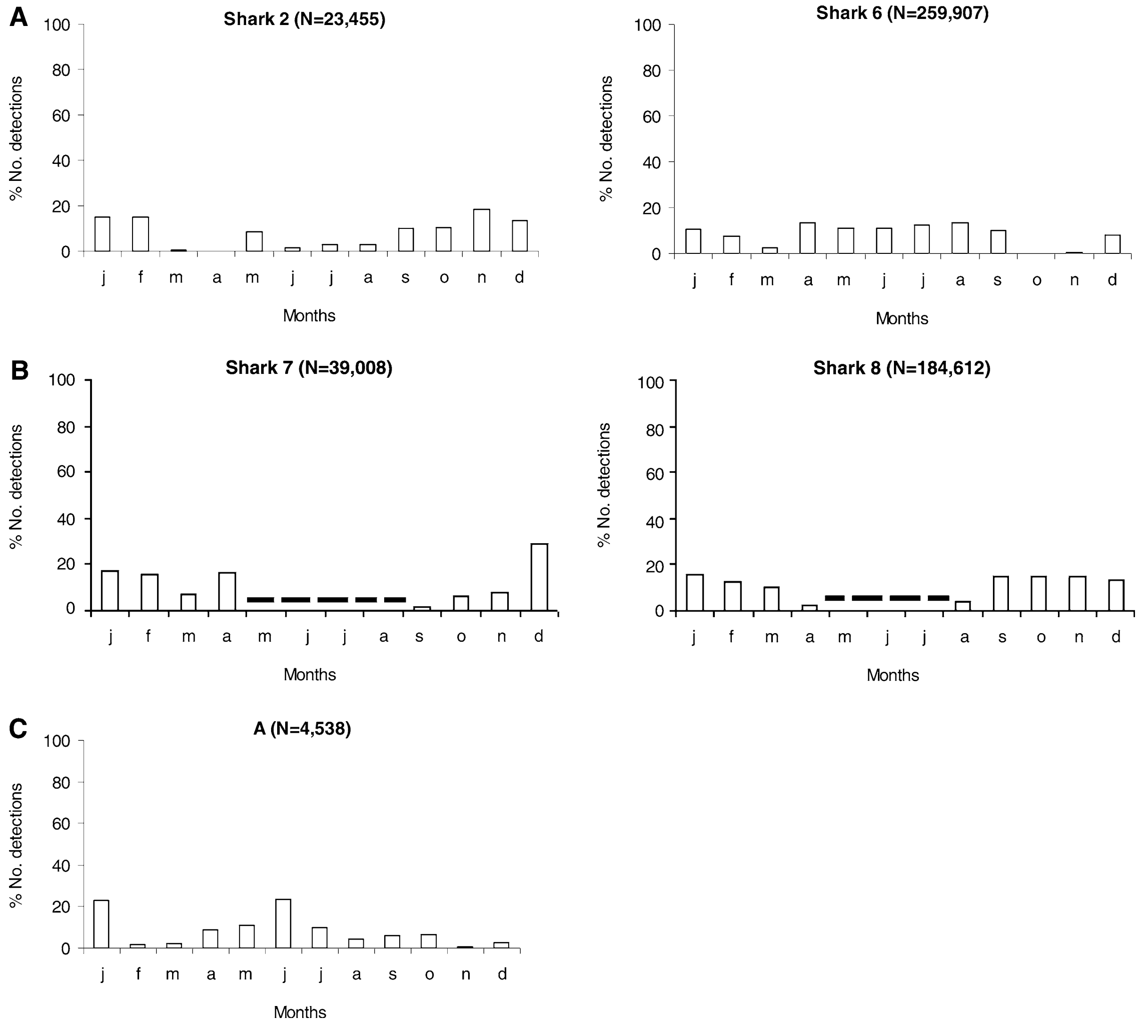


Fig. 6 **a** Percentage of all detection records plotted by month for two juvenile sharks tracked in 2001–early 2002 (all receivers combined). Total number of detections in parentheses. **b** Percentage of all detection records plotted by month for two juvenile sharks tracked in mid 2001–late 2002 (all receivers combined). *Dashed lines* represent the period from April to August 2002 where data are missing. **c** Percentage of all detection records for the adult female shark plotted by month

areas contiguous to MPAs may result in spatial heterogeneity of protected populations, which must be taken in account together with potential benefits of these reserves.

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