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Reef shark movements relative to a coastal marine protected area

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HIGHLIGHTS

- We monitored the use of a protected area by three species of reef sharks.
- Adult reef sharks had larger activity spaces than juvenile reef sharks.
- Juveniles are likely better protected than adults due to limited movements.
- Residency ranged between 12 and 96%; many individuals were resident year round.
- We observed a migration of 275 km made by a female blacktip reef shark.

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ABSTRACT

Marine protected areas (MPA) are one management tool that can potentially reduce declining shark populations. Protected-area design should be based on detailed movements of target animals; however, such data are lacking for most species. To address this, 25 sharks from three species were tagged with acoustic transmitters and monitored with a network of 103 receivers to determine the use of a protected area at Mangrove Bay, Western Australia. Movements of a subset of 12 individuals (*Carcharhinus melanopterus* [$n = 7$]), *C. amblyrhynchos* [$n = 2$], and *Negaprion acutidens* [$n = 3$]) were analysed over two years. Residency for all species ranged between 12 and 96%. *Carcharhinus amblyrhynchos* had <1% of position estimates within the MPA, compared to *C. melanopterus* adults that ranged between 0 and 99%. Juvenile sharks had high percentages of position estimates in the MPA (84–99%). Kernel density activity centres for *C. melanopterus* and *C. amblyrhynchos* were largely outside the MPA and mean activity space estimates for adults were 12.8 km^2 (±3.12 SE) and 19.6 km^2 (±2.26), respectively. Juveniles had smaller activity spaces: *C. melanopterus*, 7.2 ±1.33 km^2; *N. acutidens*, 0.6 km^2 (±0.04). Both *C. melanopterus* and *C. amblyrhynchos* had peaks in detections during daylight hours (1200 and 0900 h, respectively), whereas *N. acutidens* had a peak in detections at 0200 h. Long-distance movements were observed for adult *C. melanopterus* and *C. amblyrhynchos*, the longest being approximately 275 km. These migrations of *C. melanopterus* might be related to reproductive behaviours, because they were all observed in adult females during the summer months and provide links between known in-shore aggregation and possible nursery areas. The MPA at Mangrove Bay provided some protection for juvenile and adult reef sharks, although protection is likely greater for juveniles due to their more restricted movements.

1. Introduction

Marine protected areas (MPA) are one of the many approaches currently employed to manage and conserve fish populations. Some consider protected areas to be superior to other

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management techniques such as bag limits because a well-defined protected area is easier to monitor and enforce (Holland et al., 1996). However in reality, the effectiveness of designated protected areas also depends *inter alia* on placement, size and use of relevant biological knowledge of the organisms targeted for protection (Roberts, 2000). Although protected areas often have positive effects on biomass (Roberts, 2000), the magnitude and extent of most benefits depend on the rate and scale of animal movement in relation to reserve size (Kramer and Chapman, 1999). If the rate of movement from protected into non-protected areas is high, then effectiveness is compromised (Holland et al., 1996). Consequently, how much time targeted organisms spend within protected-area boundaries (Heupel and Simpfendorfer, 2005) is one of the most important criteria for reserve design; for this reason, such information is of great value for management.

One method to collect these data is through the use of acoustic telemetry, which can quantify movement patterns and estimate home range size. For example, this approach has been used to estimate spatial habitat use by several species of teleosts (Holland et al., 1996; Afonso et al., 2009; Wetherbee et al., 2004). It is essential that data on long-term (>1 year) patterns of movement and habitat use by many individuals of a target species are collected. Acoustic monitoring, where a network of underwater receivers are placed to capture seasonal shifts in movement (e.g. Egli and Babcock, 2004), is useful in this regard.

There has been a persistent global decline in many populations of tropical reef sharks (Ward-Paige et al., 2010; Robbins et al., 2006; Friedlander and DeMartini, 2002; Ferretti et al., 2010; Field et al., 2009), and marine parks have been suggested as one potential solution to slow this process at local scales (e.g., Bond et al., 2012). However, there have only been a few quantitative assessments of the effectiveness of protected areas for this role because the necessary movement data are generally only available for a few species and size classes (e.g. Heupel and Simpfendorfer, 2005, Bond et al., 2012, Chapman et al., 2005, Garla et al., 2006, Knip et al., 2012, da Silva et al., 2013 and Barnett et al., 2011). Studies suggest that reef sharks typically restrict their movements to within a range of <100 km^2 and show fidelity to specific sites (Chapman et al., 2005; Garla et al., 2006; Speed et al., 2010; Field et al., 2011; Speed et al., 2011; Papastamatiou et al., 2009; DeAngelis et al., 2008; Gruber et al., 1988; Chapman et al., 2009). In some instances, larger movements have been observed by smaller species (<2 m length) such as grey reef (*Carcharhinus amblyrhynchos*) and blacktip reef sharks (*Carcharhinus melanopterus*) (e.g. Heupel et al., 2010 and Chin et al., 2013), although such movements are common in large species (>4 m) such as tiger sharks (*Galeocerdo cuvier*) (Heithaus et al., 2007; Meyer et al., 2009).

Benefits of marine protected areas are likely to be greater for juvenile sharks because these life stages tend to have smaller home ranges and show greater site fidelity than adults (Garla et al., 2006; Gruber et al., 1988; Chapman et al., 2009; Heupel et al., 2010), and home range generally increases with body size (Speed et al., 2010). However, patterns in habitat use are not necessarily constant. For example, both the juveniles and adults of some species can spend more time in refugia during the day before moving more widely at night (Garla et al., 2006; Speed et al., 2011; Papastamatiou et al., 2009; McKibben and Nelson, 1986; Klimley and Nelson, 1984; Barnett et al., 2012), while grey reef sharks can be present on the reef both day and night at isolated atolls (Field et al., 2011). In a more connected network of habitats, the same species can move routinely between patches of reef over scales of 30–40 km, and can even make large movements of up to 134 km (Heupel et al., 2010). The ability of adult sharks to move over these broad spatial scales suggests that no single reserve is likely to be of sufficient size to offer complete protection throughout all life stages (Dale et al., 2011). However, designing reserves to reduce negative impacts on the most vulnerable life history stages is still possible. To optimise this process, we require data on the movement and residency patterns of reef sharks across spatial and temporal scales.

Ningaloo Reef is the largest fringing reef in Australia (260 km long) and is protected by the multiple-use Ningaloo Marine Park established in 1987 (DEC, 2005). Commercial fishing is prohibited and there are 18 marine protected areas that cover 34% of the park's area (combined protected areas = 883.65 km^2). Although many species of reef sharks are common within the park, including *C. melanopterus*, *C. amblyrhynchos*, whitetip reef *Triaenodon obesus*, and sicklefin lemon *Negaprion acutidens* sharks (Stevens et al., 2009), the zoning plan for the park was not developed with the sole aim of conserving populations of these animals. Therefore, it is not known to what extent spatial management of the reef aids the conservation of these species.

This study addresses the lack of data currently available for reef shark management and conservation planning. The overlap of shark movement patterns with the spatial coverage of a protected area (Mangrove Bay Sanctuary) within Ningaloo Marine Park was determined. The hypotheses of the study are: (1) juveniles have a smaller range of movement than adults and will therefore be afforded more protection by the MPA; (2) due to increased nocturnal movement rates, sharks should be detected within the Mangrove Bay array more frequently during the day than at night, provided they are resident to the area; and (3) the range of movements of *C. amblyrhynchos* should be larger than *C. melanopterus* and juvenile *N. acutidens* given their larger body size.

2. Material and methods

2.1. Study area

Data were collected at Ningaloo Reef between November 2007 and August 2010 (Fig. 1). The primary study site was at Mangrove Bay (21° 58′ 14″S, 113°56′ 34″E), although extensive work was done in a parallel study at Coral Bay (23° 7′ 36″S, 113° 46′8″E) (Speed et al., 2011). Both Mangrove and Coral Bay encompass protected areas within them and are managed under the Ningaloo Reef Marine Park by the Western Australia Department of Parks and Wildlife. Mangrove Bay can be characterised as an open, sandy lagoonal habitat that encompasses small mangrove-lined inlets and creeks.

2.2. Acoustic monitoring and shark tagging

Acoustic receivers (VR2W and VR3, Vemco©, Halifax, Canada) were deployed along the reef to record long-term movements of tagged individuals. The network of receivers consisted of three curtains that ran at right angles to the reef towards the edge of the continental shelf, and two main arrays, one of which was in Coral Bay and the other in Mangrove Bay (Fig. 1). The southern curtain consisted of 18 receivers; the central curtain had 13, and the northern curtain had seven. The Coral Bay array had nine receivers, while the Mangrove Bay array had 56. Receivers were fixed in position with either with steel pickets, or tyres filled with cement (Speed et al., 2011). Approximate mean maximum detection range of receivers was 300 m (Speed et al., 2011).

Sharks were tagged with V13-1H (dB 153) and V16-5H (dB 165) coded transmitters (VEMCO©, Halifax, Canada), which were inserted into the peritoneal cavity (Speed et al., 2011). Due to comparatively lower output strength of the V13 tags compared to V16 tags, the detection range would be slightly reduced for sharks fitted with V13 tags, although V13 tags have been found to be comparable in previous tests at Ningaloo (Speed et al., 2009). As part of a parallel study, sharks were also tagged at Coral Bay

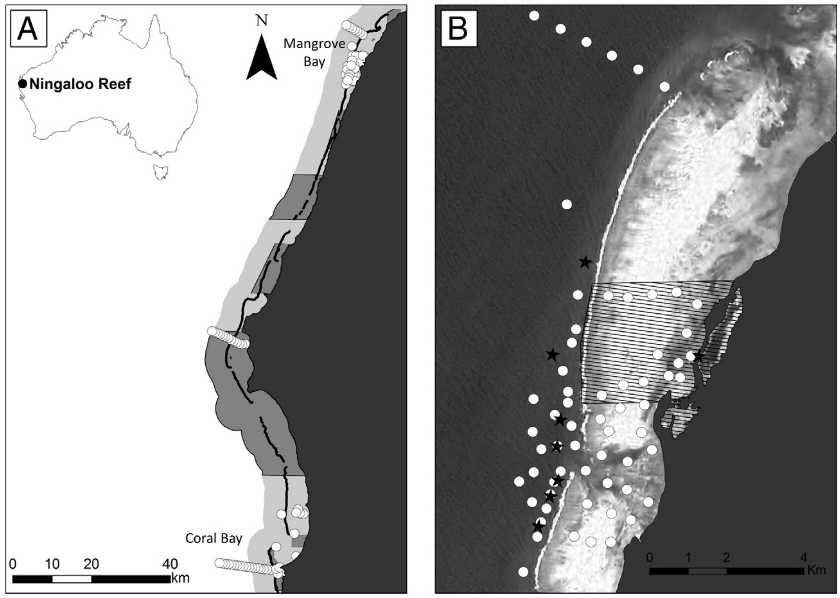

Fig. 1. Map of the study area showing: (A) Ningaloo Reef, and (B) Mangrove Bay array. Protected areas are shown in map A as ■, and receivers are shown in all maps as ○. Shark tagging locations in map B are represented as ★.

with Jumbo Rototags in the dorsal fin (Dalton Supplies, Henley-on-Thames, United Kingdom) for rapid visual re-identification. Most tagging was done in Mangrove Bay in Feb 2008, although further tagging was done in November 2009. External tags were not used at Mangrove Bay because only one tagging trip was initially planned for this study, and therefore, the likelihood of recapture was considered to be low. Sharks were caught on handlines from beaches within the Mangrove Bay MPA. Long-lines were also set outside the reef adjacent to Mangrove Bay in 10–15 m depth with baited hooks set at 10 m intervals for 100 m (Fig. 1(B)). Soak time for each line was approximately one hour.

2.3. Use of protected area

Mangrove Bay was chosen as the ideal location at which to examine the overlap between shark movement patterns and zoning protection at Ningaloo due to the large number of receivers in the array, which covered ≈24 km^2 and included a protected area (Mangrove Bay Sanctuary Zone, 11.35 km^2, DEC, 2005). To determine how much of the spatial range of the monitored sharks was covered by the protected area, a subset of animals tagged at Mangrove Bay that had consistent detections for more than six months was selected. This timeframe largely accounted for seasonal changes of movement patterns within the array.

Because some of the receivers within the array had overlapping detection ranges, a centre-of-activity algorithm that provided average positions every 30 min was used to account for any multiple detections of the same individual (Simpfendorfer et al., 2002). Total half-hourly individual centre-of-activity positions within the array were used to calculate the percentage that occurred within the protected area, equivalent to the total time each individual spent within the protected area. The total monitoring area within and outside of the protected area was estimated using a 300-m buffer around each receiver, which equated to approximate mean maximum detection ranges (Speed et al., 2011). The density of centre-of-activity positions within and outside of the protected area was a function of total centre-of-activity positions divided by total area, which gives centre-of-activity positions in km^2.

Kernel densities of centre-of-activity positions were estimated using Hawth's Tools (Beyer, 2004) in ArcGIS version 9.3 (ESRI, 1999). The bandwidth selection method was chosen a priori based on expected space use by animals (Gitzen et al., 2006), which was determined in a previous study (Speed et al., 2011). Individual kernel densities per species were then combined to provide an overall approximation of space use at Mangrove Bay and other high-use areas. Calculation of home range size was not possible due to movements of tagged animals beyond the detection ranges of our array, therefore an activity space was calculated (e.g. McKibben and Nelson, 1986). Activity space per individual was calculated based on centre-of-activity positions, using minimum convex polygons in Hawth's Tools (Beyer, 2004).

2.4. Long-distance movements

Long-distance movements were estimated by calculating the minimum linear dispersal, the straight-line distance between the two most distant receivers at which a shark was detected (Chapman et al., 2005). Based on published data, 'long-distance' was defined as those movements ≥ 10 km, (e.g. Field et al., 2011, Heupel et al., 2010, McKibben and Nelson, 1986 and Papastamatiou et al., 2010a). Only detections that were recorded on the same receiver multiple times within periods of < h^{-1} were used in order to minimise the likelihood of false detections (Pincock, 2008). Detections from all receivers within arrays and curtains along the reef were included in this analysis. To complement detections of animals that had moved large distances, recorded information based on opportunistic recaptures of animals by recreational fishers was also incorporated.

2.5. Temporal patterns

Residency for tagged animals at Mangrove Bay was calculated by dividing the number of days each animal was present within the array by the total number of monitoring days. An animal was considered to be present within the array if it had >1 detection d^{-1} (Speed et al., 2011). Further, individuals were classified as being either inside (centre-of-activities per day >50% inside the MPA) or outside (centre-of-activities per day >50% outside the MPA) for ease of interpretation of daily spatio-temporal movement patterns. Detections per individual of ≥ 1 detection h^{-1} within the receiver array were used to describe hourly patterns of presence by sharks at Mangrove Bay throughout the monitoring period. Total

Table 1
List of reef sharks tagged with acoustic transmitters and monitored for more than six months. Residency to array = the % of days detected within the array out of the monitoring period, MPA use = the % of centres of activity that fell within the MPA, MPA density = the number of COA estimates that fell within the MPA per km^2, Activity space = MCP.

Date	Tag #	Species	TL (cm)	Sex	Class	Tagging location	Residency to array (%)	MPA use (%)	MPA density (km^2)	Activity space (km^2)
24/02/2008	8 229	*C. amblyrhynchos*	146	F	A	Off shore	90.05	<1	0.3	21.82
23/02/2008	8 230	*C. amblyrhynchos*	150	F	A	Off shore	96.20	<1	15.5	17.30
27/02/2008	8 217	*C. melanopterus*	121	F	A	Off shore	19.73%	99	1040.2	10.12
25/02/2008	8 218	*C. melanopterus*	134	F	A	Off shore	66.91%	<1	1.9	21.00
26/02/2008	8 234	*C. melanopterus*	130	F	A	Off shore	48.15	0	0.0	10.80
23/02/2008	8 252	*C. melanopterus*	90.1	F	J	Shore	33.01	98	277.0	8.50
27/02/2008	8 255	*C. melanopterus*	100	F	A	Shore	50.06	28	130.8	18.37
28/02/2008	8 256	*C. melanopterus*	78	M	J	Shore	12.61	84	216.0	5.84
23/11/2009	60 969	*C. melanopterus*	97	F	A	Shore	84.57[a]	>99	470.5	3.56
23/02/2008	8 246	*N. acutidens*	73	M	J	Shore	41.60	>99	1038.8	0.70
22/02/2008	8 342	*N. acutidens*	82	F	J	Shore	52.57	98	913.0	0.55
23/11/2009	60 979	*N. acutidens*	101	F	J	Shore	93.71[a]	>99	229.7	0.57

[a] Sharks only monitored for approximately 6 months (24/11/09–17/05/10).

standardised detections per hour were calculated throughout the 24-hour cycle by dividing the total number of detections per hour by the number of individuals present within the same hour for each species (Speed et al., 2011).

3. Results

3.1. Shark tagging

A total of 25 sharks from three species were tagged with acoustic transmitters at Mangrove Bay: *C. melanopterus* ($n = 10$), *C. amblyrhynchos* ($n = 10$), and *N. acutidens* ($n = 5$). Three of these sharks were never detected by any receiver (*C. melanopterus* [$n = 1$] and *C. amblyrhynchos* [$n = 2$]).

Size classes tagged at Mangrove Bay were compared with those tagged as part of a parallel study at Coral Bay (Speed et al., 2011), to provide context for the Ningaloo region. The most common size class of *C. melanopterus* caught at both Mangrove Bay and Coral Bay was 121–140 cm total length (L_T), indicating that adults had predominantly been sampled (Fig. 2(A)). Similarly, mainly adults of *C. amblyrhynchos* were caught at both of these locations, with the most common size classes being 141–160 cm L_T at Mangrove Bay, and 141–160 cm and 161–180 cm L_T at Coral Bay (Fig. 2(B)). All *N. acutidens* that were tagged were juveniles, with larger individuals (121–160 cm L_T) only being caught at Coral Bay (Fig. 2(C)).

3.2. Use of protected area

Approximately half (55% $n = 12$) of the individuals detected by the array were suitable for long-term assessment of spatial movements using detection data due to regular detections throughout the monitoring period (Table 1). Of these individuals, two were adult *C. amblyrhynchos*, seven were *C. melanopterus* (2 juveniles and 5 adults), and three were juvenile *N. acutidens*. Residency within Mangrove Bay was highest for the two adult C. *amblyrhynchos* (90.1% and 96.2%), and lowest overall for the two juvenile *C. melanopterus* (33.0% and 12.3%).

Even though residency was greatest for *C. amblyrhynchos*, both of these individuals were tagged outside the protected area and the percentage of centre-of-activity positions that occurred within the protected area was <1% of the total centre-of-activity positions calculated within the Mangrove Bay array. Two *C. melanopterus*, also tagged outside the protected area, had <1% of centre-of-activity positions within the MPA, although the other five individuals of this species had centre-of-activity positions within the protected area that ranged from 28 to >99%. One of these five individuals was also tagged offshore outside the protected area (Table 1). All of the *N. acutidens* had >98% of centre-of-activity positions calculated within the protected area.

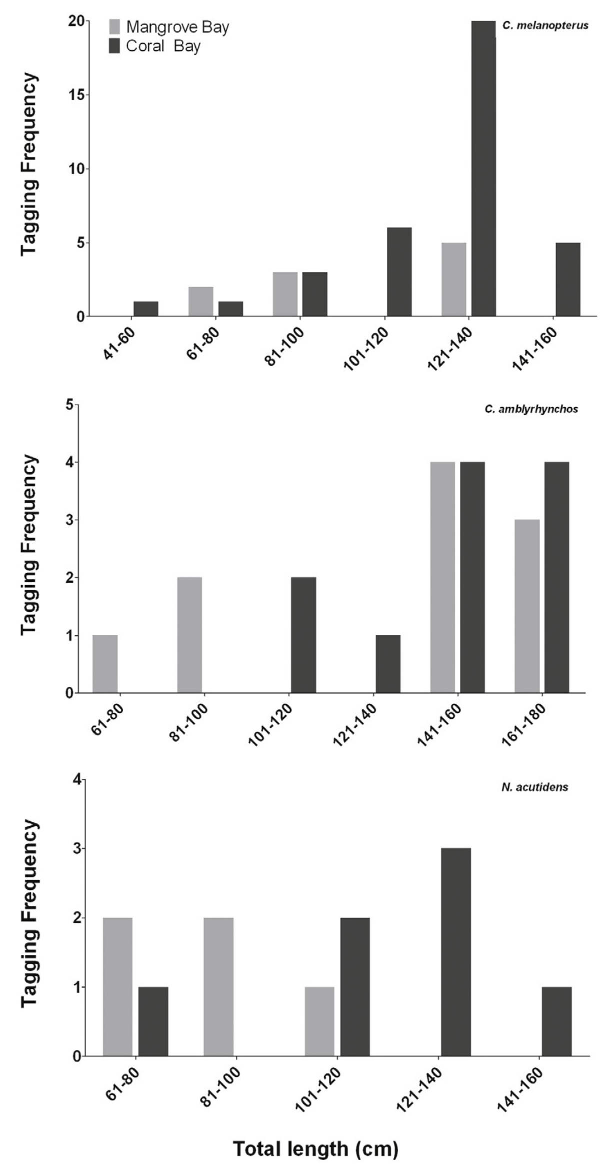

Fig. 2. Size-frequency histograms of sharks tagged with acoustic transmitters at Coral Bay and Mangrove Bay for: (A) *C. melanopterus*, (B) *C. amblyrhynchos*, and (C) *N. acutidens*.

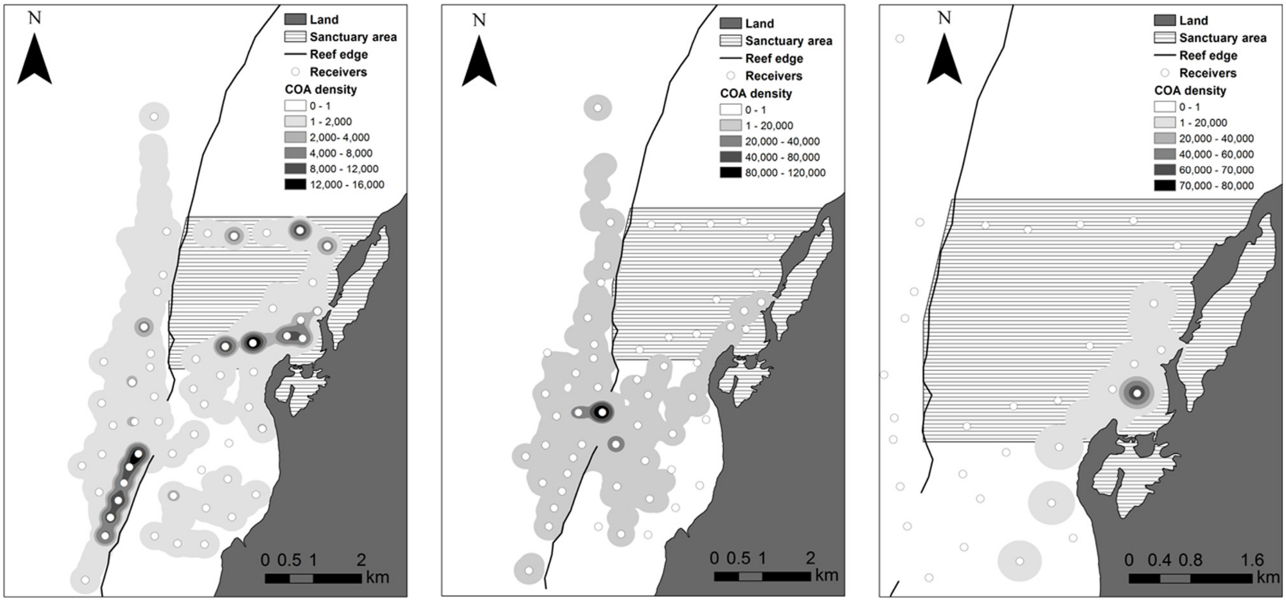

Fig. 3. Kernel density activity centres for sharks tagged with acoustic transmitters at Mangrove Bay for: (A) *C. melanopterus*, (B) *C. amblyrhynchos*, and (C) *N. acutidens*.

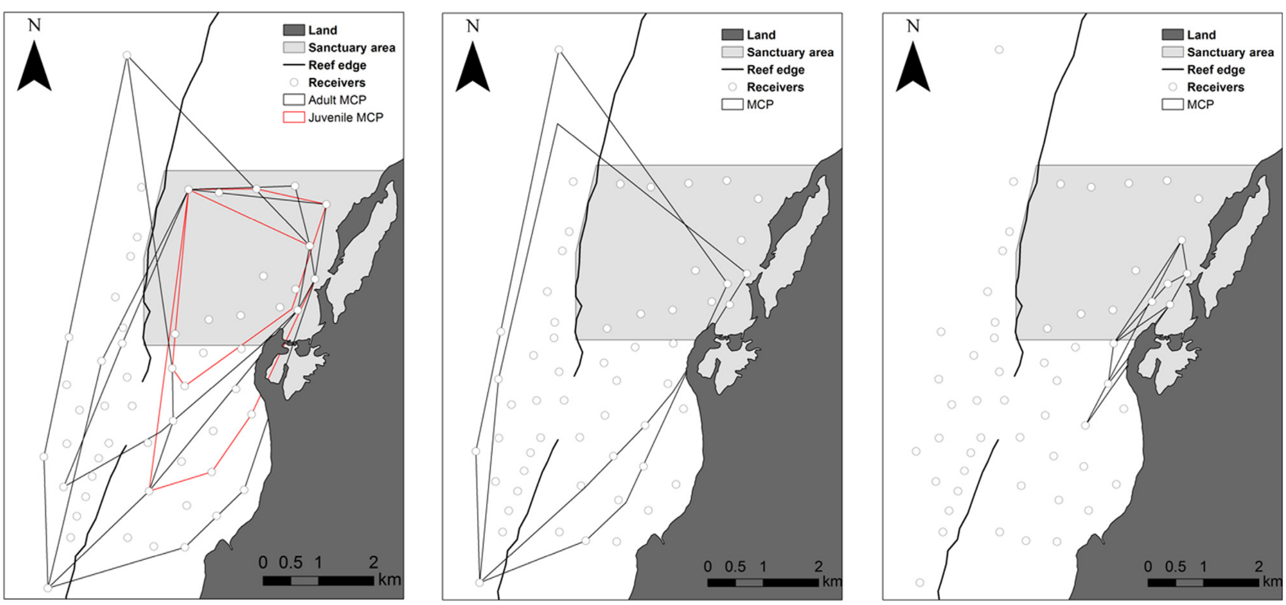

Fig. 4. Activity spaces (Minimum convex polygons) for sharks tagged with acoustic transmitters at Mangrove Bay for: (A) *C. melanopterus*, (B) *C. amblyrhynchos*, and (C) *N. acutidens*.

There were two main concentrations of centre-of-activity density for *C. melanopterus*: one outside the reef edge to the south of Mangrove Bay, and the other within the protected area (Fig. 3(A)). The main concentration for *C. amblyrhynchos* was to the south of the protected area in the channel between the lagoon and the reef edge (Fig. 3(B)). The centre-of-activity density concentration for *N. acutidens* was within the protected area (Fig. 3(C)), close to where all of these individuals were tagged.

The average size of activity spaces (minimum convex polygon) for adult *C. melanopterus* was 12.8 km^2 ($\pm$3.12 SE), which was larger than the average juvenile activity space of only 7.2 km^2 ($\pm$1.33) (Table 1 and Fig. 4(A)). *C. amblyrhynchos* had the largest mean activity space of the three species (19.56 km^2 $\pm$ 2.26) (Fig. 4(B)), while juvenile *N. acutidens* had the smallest (0.61 km^2 $\pm$ 0.04) (Fig. 4(C)).

3.3. Long-distance movements

Five adult female *C. melanopterus* tagged in Coral Bay in a parallel study (Speed et al., 2011) were subsequently detected by the Mangrove Bay array in this study (Table 2). All individuals were detected in summer (Dec–Feb) for periods ranging from 1 to 27 days. Detections were only recorded on receivers inside the lagoon, most of which were inside the protected area. All sharks made return trips to Coral Bay, and one went farther south before being caught by a recreational fisher. With the exception of one shark (# 53349), all individuals made at least one of their excursions (i.e., Coral Bay to Mangrove Bay) in less than one week. One (# 53347) went even farther north than Mangrove Bay, and was detected by the northern line of acoustic receivers (Table 3). This was the longest minimum linear dispersal at 137.8 km, and a return trip of 275.6 km. Other long-distance movements were

Table 2
Individuals that were tagged in Coral Bay and were subsequently detected within the Mangrove Bay array.

Date tagged	Tag number	Species	Sex	Size class	# of detections	Date of detections	Returned?
25/11/2007	8 329	*C. melanopterus*	F	A	4	10/01/2008	Yes[a]
24/11/2008	14 502	*C. melanopterus*	F	A	9	6/01/10 and 02/02/10	Yes
20/11/2008	53 347	*C. melanopterus*	F	A	12	18/01/2010	Yes
19/11/2008	53 349	*C. melanopterus*	F	A	1186	11/12/2008–07/01/2009	Yes
15/11/2008	53 361	*C. melanopterus*	F	A	17	26/12/2009	Yes

[a] This animal was not detected by the Coral Bay array after being detected in Mangrove Bay, although it was recaptured south of Coral Bay.

Table 3
List of long-distance movements (>10 km) based on minimum linear dispersal (MLD).

Tag #	Species	Station name	Latitude	Longitude	Station name	Latitude	Longitude	MLD (km)
8 229	*C. amblyrhynchos*	Central line 6	−22.6027	113.6278	MBJH2A	−21.9263	113.9114	80.5
8 218	*C. melanopterus*	North Line 1	−21.8990	113.9367	MB1A	−22.0128	113.8986	13.2
53 344	*C. melanopterus*	Skeleton South	−23.1301	113.7700	Stan p north	−22.9874	113.7999	16.1
53 347	*C. melanopterus*	Skeleton South	−23.1301	113.7700	North line 2	−21.8948	113.9302	137.8
53 351	*C. amblyrhynchos*	Skeleton South	−23.1301	113.7700	South line 17	−23.1178	113.6454	12.8
53 355	*C. amblyrhynchos*	Skeleton South	−23.1301	113.7700	South line 15	−23.1196	113.6602	11.3
53 361	*C. melanopterus*	Skeleton South	−23.1301	113.7700	Central line 9	−22.5930	113.6070	61.8
53 414	*C. amblyrhynchos*	Skeleton South	−23.1301	113.7700	Central line 9	−22.5930	113.6070	61.8

also recorded along the south, mid and north lines of receivers, and were all movements made by either *C. melanopterus* or *C. amblyrhynchos*. Most of these movements were minimum linear dispersals of <80 km.

Four animals (4.2% animals tagged with Rototags, $n = 94$) were recaptured by recreational fishers from the shore, outside of protected areas at Ningaloo Reef. Three of the recaptures were adult *C. melanopterus* tagged in Coral Bay (Speed et al., 2011). One of these was caught approximately 1 km north of its tagging location, and was subsequently released. The other two were captured and retained. One of these was captured approximately 40 km south of Coral Bay, and the other was captured approximately 100 km south of Coral Bay. This animal (# 8329) was also one of the five *C. melanopterus* detected in Mangrove Bay. The fourth recapture was a juvenile *N. acutidens* that was tagged in Mangrove Bay and recaptured approximately 10 km to the south. That animal was also not released.

3.4. Temporal patterns

Two *C. amblyrhynchos* were detected throughout the entire monitoring period (>2 years), while the other six were only detected for the first 1–2 months (Fig. 5). No *C. melanopterus* was detected as frequently as the two *C. amblyrhynchos*, although three of the individuals were detected almost until the end of the second year of monitoring (Feb–Apr 2010). The juvenile *C. melanopterus* and *N. acutidens* tagged in November 2009 were both detected frequently until the end of the study. Two of the juvenile *N. acutidens* tagged in 2008 were detected frequently up until mid-2009.

Standardised detections for *C. amblyrhynchos* while within Mangrove Bay were most frequent during the daytime and peaked at 0900 h (Fig. 6(A)). Similarly, detections of *C. melanopterus* were highest during the daytime and peaked around 1200 and 1300 h (Fig. 6(B)). Detections of the juvenile *N. acutidens* showed an inverse relationship with both other species, with a peak at 0200 h (Fig. 6(B)).

4. Discussion

The effective use of static protected areas to conserve wide-ranging species is notoriously difficult due to movement of animals across boundaries (Sergio et al., 2005; Woodroffe and Ginsberg, 1998). This is a common problem identified for both terrestrial (Woodroffe and Ginsberg, 1999; Loveridge et al., 2007; Linnell et al., 2001; Forbes and Theberge, 1996) and marine species (Meyer et al., 2007a,b; Flores and Bazzalo, 2004). In particular, this issue has been identified for many species of shark such as: juvenile blacktip (*C. limbatus*) (Heupel and Simpfendorfer, 2005), hammerhead (*Sphyrna lewini*) (Ketchum et al., 2009; Hearn et al., 2010), Caribbean reef (*Carcharhinus perezi*), nurse (*Ginglymostoma cirratum*) (Chapman et al., 2005), pigeye (*Carcharhinus amboinensis*) and spottail (*Carcharhinus sorrah*) (Knip et al., 2012), and smoothhound sharks (*Mustelus mustelus*) (da Silva et al., 2013).

Similar to previous studies, we found that all tagged animals were detected outside of the protected area (Mangrove Bay MPA) at some point during the study. In fact, the average residency of individuals within the array was ≈57% of days monitored, suggesting that the size of the protected area was too small to protect most of the resident animals. Furthermore, the large activity spaces suggest that this protected area by itself only provides limited protection for adult *C. melanopterus* and *C. amblyrhynchos* from recreational fishing pressure at Ningaloo Reef. However, it is important to consider the entire network of MPAs ($n = 18$) within Ningaloo Marine Park, of which the average size is ≈49 km^2 (DEC, 2005). Considering that estimated activity spaces for all individuals monitored were less than 22 km^2, albeit these are likely underestimates for adult reef sharks, it is reasonable to assume that individuals in and around MPAs at Ningaloo are afforded some protection throughout the year. The effectiveness of the entire network of MPAs within Ningaloo Reef needs to be assessed in future studies of large, mobile animals.

For *C. amblyrhynchos* tagged at Mangrove Bay, 75% of animals left the array after a short period. It was more likely that *C. melanopterus* would remain in the array; nevertheless 33% of tagged adult individuals were resident for <6 months. Residency for both species was higher at Coral Bay (Speed et al., 2011), despite the Coral Bay receiver array being less extensive, making it more likely that tagged animals would be missed. Long-distance movements were observed in ≈15% of tagged *C. melanopterus* and ≈19% of tagged *C. amblyrhynchos*, underscoring the observation that some individuals of this species regularly use large areas of the reef.

Of the individuals assessed for long-term movements, *C. amblyrhynchos* had the highest residency of all species, although the highest density of detections for this species was south and outside of the protected area, within the channel between the lagoon and the reef edge. Channels connecting lagoons with outer reef habitat and exposed reef slopes have been previously

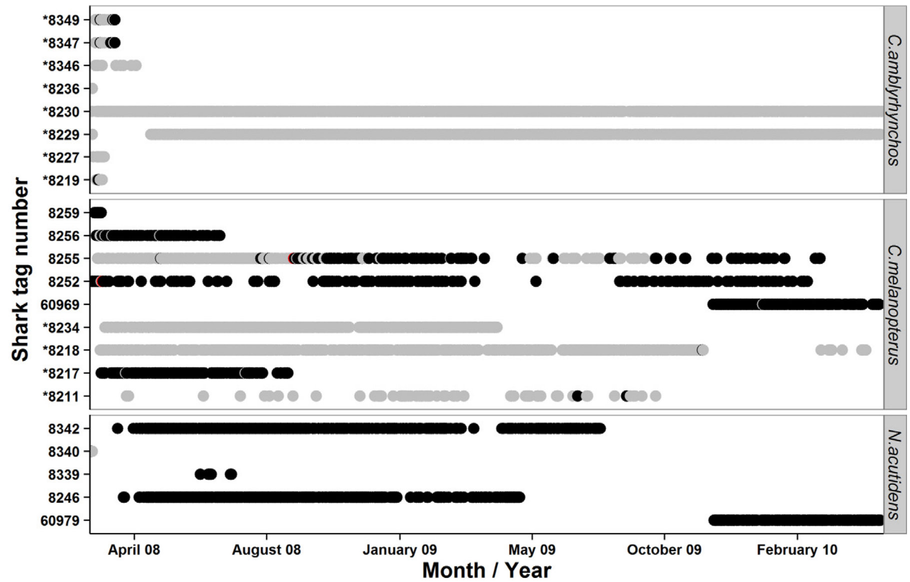

Fig. 5. Daily detections for every individual tagged at Mangrove Bay with acoustic tags. An animal was considered present if it had >1 detection per day within the array. Inside = ●, Outside = ●, and 50/50 = ●. Individuals were classified as 'inside' the MPA if >50% of centre-of-activities were within the MPA per day were, and were classified as 'outside' the MPA if >50% of centre-of-activities were outside the MPA per day. Tag numbers preceded by an asterisk (∗) denote sharks that were tagged outside of the Mangrove Bay MPA.

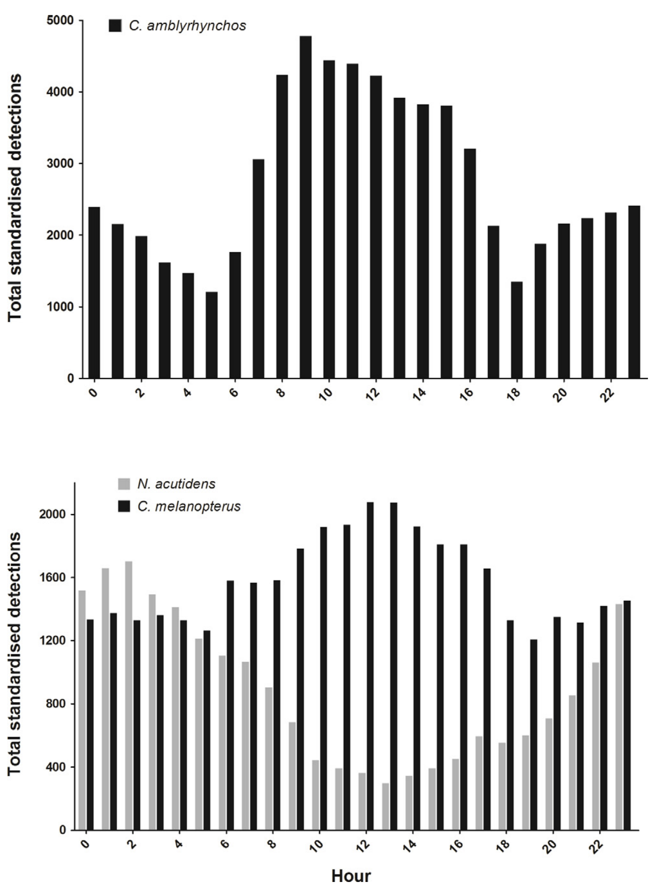

Fig. 6. Total hourly standardised detections based on acoustic detections of sharks tagged at Mangrove Bay.

identified as high-use areas for this species (Field et al., 2011; Speed et al., 2011; McKibben and Nelson, 1986; Barnett et al., 2012; Economakis and Lobel, 1998), as well as for other reef sharks such as *G. cirratum* and *C. perezi* (Chapman et al., 2005). These habitats are not represented within the Mangrove Bay protected area. The habitat use of adult *C. melanopterus* was concentrated south of the protected area, outside the reef edge, similar to *C. amblyrhynchos*, although there was more activity within the protected area by *C. melanopterus* than *C. amblyrhynchos*. Mean activity space sizes were larger for adults of *C. amblyrhynchos* than *C. melanopterus*, as well as juvenile *C. melanopterus* and *N. acutidens*, thus confirming our hypothesis that adult *C. amblyrhynchos* would have the greatest range of movements due to their larger body size. Mean activity space sizes for both adults in our study were consistent with earlier studies that have estimated home range sizes, where *C. melanopterus* varied from ≈0.5 km^2 (Papastamatiou et al., 2009) to 12.08 km^2 (Papastamatiou et al., 2010a), while *C. amblyrhynchos* varied from 0.19 to 53 km^2 (McKibben and Nelson, 1986). Our activity space estimates for *C. melanopterus* were relatively large, from 3.5 to 21 km^2 (average 12.8 $km^2 \pm 3.12$ SE) and the difference between our results and those of previous studies probably reflects variation in monitoring duration or structure of the environment (e.g., atolls versus fringing reefs) among study sites.

Adult *C. melanopterus* had larger mean activity spaces (12.8 $km^2 \pm 3.12$ SE) than juveniles of the same species (7.2 km^2). Such ontogenetic differences in space use might arise partially from a sampling bias, given that more adults ($n = 5$) were tagged than juveniles ($n = 2$), although increases in range with increasing body size is a common trait of many shark species (Speed et al., 2010). The extensive use of sand flats interspersed with reef patches within the lagoon was also behaviourally consistent with previous observations for *C. melanopterus* and other reef species (Papastamatiou et al., 2009; McKibben and Nelson, 1986; Nelson and Johnson, 1980). Juvenile *C. melanopterus* and *N. acutidens* remained largely within the Mangrove Bay protected area (84%–99% of detections), most likely because of the availability of suitable sand flat and mangrove habitats (White and Potter, 2004). These results suggest that current protected-area zoning at Mangrove Bay provides reasonable protection for juveniles, thus supporting our hypothesis of greater protection for juveniles due to their restricted movements, albeit this conclusion is based on a small sample size. In contrast, the boundaries would need to be extended considerably should the protection of adults become a management priority. This is due in part to the limited spatial extent of current boundaries, but also the absence of reef slope areas within the protected area at Mangrove Bay. The addition of the channel from the lagoon and the reef slope areas within the protected area could provide increased protection for adult reef sharks.

Due to the extensive coverage of the array along the length of Ningaloo Reef, several long-distance movements (>10 km) were recorded for *C. melanopterus* and *C. amblyrhynchos*. Few studies to date have observed long-distance movements by either of these species, although a 134-km excursion has been reported for *C. amblyrhynchos* on the Great Barrier Reef (Heupel et al., 2010). Others have observed more restricted movements for *C. amblyrhynchos*: up to 16 km at Enewetak Atoll (McKibben and Nelson, 1986) and 6.8 km at the Rowley Shoals, an atoll off the coast of north-western Australia (Field et al., 2011). Although long-distance movements or migrations are common in some sharks, they are generally attributed to reproductive behaviour, seasonal movements of prey, or changing water temperature (Speed et al., 2010). Indeed, one of the only studies that has observed long-distance movements of *C. melanopterus* was done using microsatellite DNA and parentage analysis, where the authors found that in French Polynesia female *C. melanopterus* migrate away from their home range to give birth at an island up to 50 km away (Mourier and Planes, 2013). Juvenile *C. melanopterus* monitored on the east coast of Australia undergo ontogenetic movements (>80 km) between nursery areas and offshore reefs (Chin et al., 2013). All of the movements observed between Coral Bay and Mangrove Bay were made by adult female *C. melanopterus* during the summer months. Given that neonate and juvenile *C. melanopterus* are common near shore in the Mangrove Bay protected area, and pupping occurs in November in northern Australia (Last and Stevens, 2009), it seems plausible that these long-distance movements might have been related to reproduction.

The use of external tags enabled the collection of information from sharks that were recaptured by recreational fishers along Ningaloo Reef. This recapture rate (4.2%) was higher than expected due to the absence of any commercial fisheries operating within the Marine Park, although perhaps not surprising given the popularity of shore-based recreational fishing at Ningaloo Reef (Sumner et al., 2002). Others have also reported comparable and even higher recapture rates for reef sharks: 15.3% ($n = 22$) for *C. perezi* off the coast of Brazil (Garla et al., 2006), and 5.4% ($n = 73$) for *C. galapagensis* in Hawaii (Dale et al., 2011). Such susceptibility to fishing underlines the need for management strategies to address protection for all size and age classes of reef sharks, particularly for species such as *C. melanopterus* that inhabit shallow inshore habitats, where recreational fishers tend to focus at Ningaloo.

Several individuals of all study species were present within the Mangrove Bay array throughout the two years of our study, suggesting some sharks exhibit site fidelity. This behaviour is common in reef sharks (e.g. Garla et al., 2006, Field et al., 2011, Speed et al., 2011, Papastamatiou et al., 2009, Gruber et al., 1988, Chapman et al., 2009, McKibben and Nelson, 1986, Barnett et al., 2012, Papastamatiou et al., 2010b, Mourier et al., 2012 and Filmalter et al., 2013) and is useful for management and conservation where sanctuaries encompass a substantial proportion of the animal's home range (e.g. Parsons et al., 2003). However, this is not likely to be the case at Mangrove Bay, where regular movements of sharks outside of the protected area suggest that it cannot provide adequate protection for all size classes. In comparison, a study of two species of coastal sharks (*C. amboinensis* and *C. sorrah*) found that these species spent on average 22% and 32% of their time, respectively, within protected areas (Knip et al., 2012). The authors therefore suggested that this management approach still provides some benefits for these species. By contrast, a recent study on *Mustelus mustelus* in coastal South Africa reported that they spend on average 79% of their time in a protected area, and therefore are provided a high degree of protection (da Silva et al., 2013).

Daylight peaks in detections for both *C. melanopterus* and *C. amblyrhynchos* imply that animals move out of the array at night, possibly to forage, thus providing support for our hypothesis. An increase in nocturnal foraging by several species of reef sharks has been observed previously (Garla et al., 2006; Speed et al., 2011; Papastamatiou et al., 2009; McKibben and Nelson, 1986; Klimley and Nelson, 1984). In contrast, juvenile *N. acutidens* were detected less frequently during the day, which contrasts findings of a recent study of sub-adults monitored in the Seychelles (Filmalter et al., 2013). This finding might have been an artefact of sampling in our study because the mangrove area was exposed during low tides. The inability to monitor intertidal areas surrounding the mangroves at Mangrove Bay where young-of-the-year *C. melanopterus* and *N. acutidens* were common during high tide (CW Speed and O O'Shea, unpublished data) was one of the unavoidable shortcomings of our acoustic monitoring approach. This problem might also have contributed to the low residency observed for juvenile *C. melanopterus*. Tracking and monitoring of these size classes will require separate, intensive studies in future.

4.1. Conclusions

Acoustic monitoring of long-term movements of reef sharks has provided an initial assessment of the effectiveness of current protection for these animals at Ningaloo Reef. The protected area at Mangrove Bay provides adequate protection for juvenile *C. melanopterus* and *N. acutidens*; however, adult *C. melanopterus* and *C. amblyrhynchos* have activity spaces that extended well beyond the protected area, and frequently use areas outside of the protected area. Movements of *C. melanopterus* females from Coral Bay to Mangrove Bay might have been to give birth in the mangrove habitat. Should reef shark conservation become a priority for Ningaloo, an extension of the current Mangrove Bay protected area to the south could provide greater protection for adult size classes.

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