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Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery

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Abstract. The benefits of marine protected areas are difficult to estimate for mobile species, but their effectiveness can be increased if essential habitats, such as nursery areas, are protected. In the present study we examined movements of juvenile blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks in a coastal nursery in northern Australia. Telemetry-derived data were modelled using Brownian bridges and overlaid with maps of habitats and no-take zones. Juvenile *N. acutidens* were typically residents ($\geq$30 days) of the nursery with small areas of core space use ($<$1.9 km^2), whereas juvenile *C. melanopterus* were non-residents ($<$30 days) and used larger areas ($<$5.6 km^2). Both species exhibited positive selection for sandflats and mangroves, and avoidance of deeper lagoonal and slope habitats. Monthly patterns were examined only for resident *N. acutidens*, and residency decreased with increasing shark length and varied seasonally for males but not females. Space use showed weak declines with increasing tidal range, and slight increases with mean air pressure, rainfall and shark length. Protecting sandflat and vegetated habitats may increase the efficacy of no-take zones for juvenile *N. acutidens*, because they exhibit residency and affinity to these features. Conversely, such protection will be of limited benefit for juvenile *C. melanopterus*, because they exhibit low residency and broader movements.

Additional keywords: conservation, elasmobranchs, marine, modelling, protected areas.

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Introduction

Marine protected areas (MPAs) are important tools for addressing the rapid loss of biodiversity resulting from various stressors, including overexploitation by fisheries and habitat degradation (Worm *et al.* 2006). Benefits of MPAs to species are maximised where no-take zones are well enforced, old (>10 years since establishment), large in area (>100 km^2) and isolated. When these criteria are met, MPAs can support 5-fold more large fish and 14-fold more shark biomass than fished areas (Edgar *et al.* 2014). Small-scale MPAs may also be effective for species that have restricted ranges or key life stages linked to predictable or fixed habitat features (Garla *et al.* 2006; Schofield *et al.* 2013). Because many sharks are highly mobile and tend to make large-scale movements (>100 km; Heupel *et al.* 2010), MPAs are often too small (median size 4.6 km^2; Wood *et al.* 2008) to encompass the range of movements of larger individuals and adults (Green *et al.* 2015). Small MPAs may offer protection for smaller-bodied species that have restricted movements over their full life cycle (Escalle *et al.* 2015; Munroe *et al.* 2015) or species that occupy coastal nurseries for their early life history stages (Heupel *et al.* 2007) but disperse more widely on reaching maturity. This is particularly important for the resilience of shark species, because most tend to grow slowly, mature late and produce few young (Cortés 2002; Heithaus 2007).

Young sharks typically segregate from adults in shallow, coastal nurseries, which are defined as areas that: (1) support higher abundances of neonates (age <1 year); (2) are used over extended periods of time; and (3) are used over multiple years (Heupel *et al.* 2007). Such nurseries are thought to promote the survivorship of young sharks through protection from predators and increased foraging success (Cortés 2002; Heithaus 2007;

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Guttridge *et al.* 2012). The former may be facilitated by the increased availability of microhabitats, such as mangroves, sandflats and seagrass beds, in inshore nurseries (Chin *et al.* 2012; Munroe *et al.* 2014; Escalle *et al.* 2015). The use of these shallow habitats may also contribute to the foraging success of sharks, with ebbing high tides forcing smaller fish and other prey off intertidal sandflats (Papastamatiou *et al.* 2009, 2015). For many species, the use of nurseries coincides with warmer water temperatures (e.g. Grubbs and Musick 2007; Conrath and Musick 2008), which may also assist with thermoregulation and increased foraging or digestive efficiency (DiGirolamo *et al.* 2012). Aggregation by juveniles (Guttridge *et al.* 2009) in a nursery may also improve foraging success through social learning (Guttridge *et al.* 2013) or dilution of predation risk (Heupel and Simpfendorfer 2005). Tide-mediated selection for these shallow habitats has also been proposed as a strategy for predator avoidance (Wetherbee *et al.* 2007; Guttridge *et al.* 2012). However, competition for limited food resources could result in habitat partitioning within and between species in communal nurseries (Papastamatiou *et al.* 2006; Kinney *et al.* 2011). Given the susceptibility of inshore coastal habitats to anthropogenic effects and climate change (Field *et al.* 2009; Chin *et al.* 2010), improved knowledge of ecological factors that affect the use of coastal nurseries is required to enhance the management and conservation of sharks.

Although nurseries for coastal sharks have been identified and characterised in the north-western Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Keeney *et al.* 2005; Chapman *et al.* 2009; Conrath and Musick 2010; Norton *et al.* 2012), very limited information about nurseries exists for the Indian Ocean. Ningaloo Reef in the eastern Indian Ocean is the world's largest fringing coral reef system and a United Nations World Heritage Site that supports a wide variety of habitats and is a global hot spot of shark diversity (Lucifora *et al.* 2011). Extensive surveys indicate that Mangrove Bay, a shallow (water depth <10 m), mangrove-lined tidal embayment in the north of the Ningaloo Reef Marine Park (NMP), had the highest sighting rates for six species of shark and rays within the NMP (Stevens *et al.* 2009). There is some evidence that Mangrove Bay is a communal nursery for juveniles, but the delineation of nursery habitats within the Bay remains unclear (Cerutti-Pereyra *et al.* 2014; Speed *et al.* 2016). Furthermore, the zoning plan of the NMP was not developed to protect these species (Escalle *et al.* 2015; Speed *et al.* 2016) and therefore existing spatial management strategies may not be suitable for conservation and management of shark and ray nurseries.

The present study addresses these issues using acoustic telemetry to examine spatial and temporal patterns in the movements of young blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks at Mangrove Bay. We hypothesised that: (1) both species would exhibit patterns of long-term residency (>6 months) and restricted space use, consistent with the use of Mangrove Bay as a shark nursery; (2) residency would decrease and space use increase with increasing shark size, thus decreasing the degree of protection afforded to both species by existing no-take MPAs; (3) because factors such as temperature (Conrath and Musick 2008; Froeschke *et al.* 2010), proximity to tidal inlets (Froeschke *et al.* 2010) and barometric pressure (Heupel *et al.* 2003; Udyawer *et al.* 2013) are known to be important determinants of habitat use by juvenile sharks, the presence of young sharks in Mangrove Bay would be affected by environmental variables (tides, water temperatures, air pressure, wind, etc.); and (4) given the similarities in their dependency on coastal producers (Speed *et al.* 2012), young sharks of these species would be likely to partition habitats within the nursery to coexist and decrease interspecies competition.

Materials and methods

Study site

Ningaloo Reef (21.9°S, 113.9°E) extends for 320 km along the north-west coast of Western Australia (WA) and has been protected by the multiple-use NMP, covering a total area of 4566 km^2, since 1996 (Fig. 1; Leprovost Dames and Moore 2000; CALM and MPRA 2005). Commercial fishing is prohibited within the NMP, but recreational fishing is allowed in all zones with the exception of no-take zones, which comprise 34% of the NMP. Shark capture and tagging for the present study was concentrated at Mangrove Bay within the NMP (Fig. 1), a tidal embayment encompassing small mangrove-lined inlets and a fringing reef at the seaward edge. The bay contains the Mangrove Bay Sanctuary Zone, a no-take area ~11.4 km^2 in size, established to protect a small area of mangrove forest within the NMP and its associated ecosystems (CALM and MPRA 2005; Smallwood *et al.* 2012). Habitats within Mangrove Bay include coral reefs, bare rocky reefs, mangroves, algae and turf-covered reefs interspersed with sandflats (Fig. 1; Bancroft 2003). The mean monthly tidal range is ~2.0 m, with the Bay drying at lowest tide levels. The prevailing wind is from south to south-west (Table 1) and the region is periodically subjected to severe cyclonic wind and floods (Lovelock *et al.* 2011). Mean monthly water temperature is ~25.3°C (Table 1).

Shark tagging and receiver array

Blacktip reef (*C. melanopterus*) and sicklefin lemon (*N. acutidens*) sharks were captured from shore within the Mangrove Bay Sanctuary zone using gill nets or handlines with barbless, 6/0 circle hooks baited with pilchard or squid. Captured sharks were transferred to a holding tank filled with seawater and identified to species, sexed, measured, photographed, assessed for clasper calcification and examined for umbilical scar condition and wounds. We measured fork length (FL; the distance from the snout to the fork of the tail) and stretched total length (TL; the distance from the snout to the tip of the upper lobe of the caudal fin) to the nearest centimetre and classified sharks as either neonate based on the presence of umbilical scars (Chin *et al.* 2015) or juvenile using length-at-age data (Last and Stevens 2009). In total, 13 *C. melanopterus* (8 females, 5 males; Table 2) and 23 *N. acutidens* (11 females, 12 males) were implanted with a uniquely coded microchip (Trovan FDX-A; Microchips Australia Pty Ltd, Melbourne, Vic., Australia) at the base of the left dorsal fin to minimise the possibility of double-tagging with acoustic tags. Sharks were then inverted to induce tonic immobility (Kessel and Hussey 2015) and an acoustic tag (V13-1H; Vemco, Halifax, NS, Canada) was implanted into the abdominal cavity through a 2-cm incision made using a scalpel along the ventral midline that was subsequently closed with

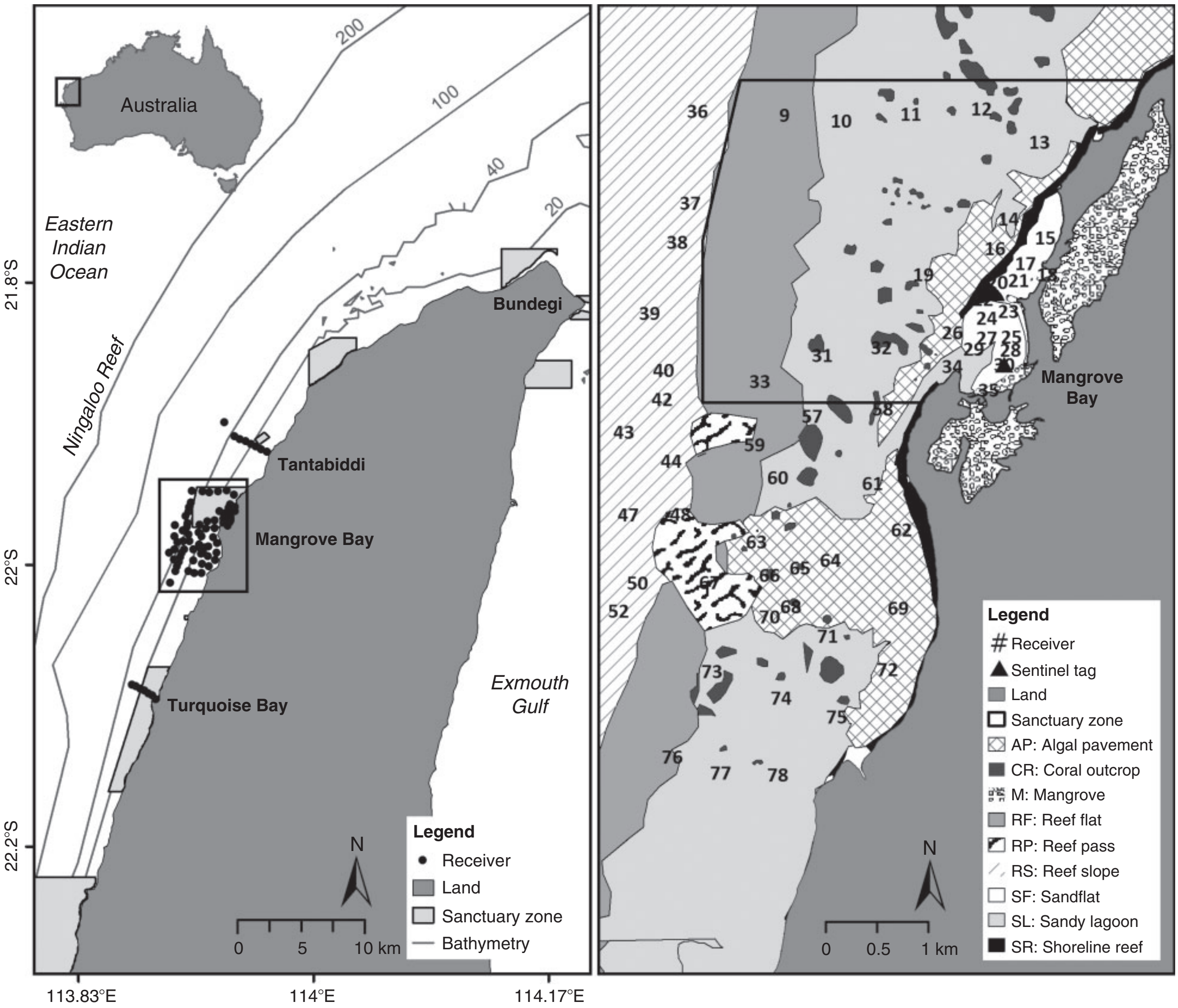

Fig. 1. Map of Mangrove Bay, in the northern Ningaloo Reef Marine Park, showing the location of acoustic receivers (points on the left plot and numbers on the right plot), bathymetry (grey lines), sanctuary zones (solid lines) and inset map of Australia. Benthic habitats are shaded by habitat type.

absorbable surgical sutures (Ethicon 2–0; Johnson and Johnson, Livingstone International Pty Ltd, Sydney, NSW, Australia). Each tag transmitted a unique identification code with a transmission delay that varied randomly from 110 to 250 s and a battery life of 514–540 days. Sharks were held for 5–10 min from capture to completion of surgery, after which individuals were monitored until recovery (i.e. the individual could swim away from gentle restraint, usually 5–15 min) and released at the site of capture. All procedures were permitted under Department of Parks and Wildlife licences (SF009588, 163165, CE004244), Department of Fisheries WA exemptions (2150, 2355) and the University of Western Australia Animal Ethics Committee (UWA AEC; RA 3/100/1168).

An array of 85 acoustic receivers (VR2 and VR2W; Vemco) deployed as part of a national network of receivers (https://animaltracking.aodn.org.au/, accessed 9 March 2016) was used to monitor movements of sharks tagged in Mangrove Bay (Fig. 1; see Table S1, available as Supplementary material for this paper). The array consisted of 71 receivers at Mangrove Bay and two cross-shelf lines of 8 receivers at Tantabiddi and 7 receivers at Turquoise Bay (Fig. 1). Receivers were secured to metal pickets either hammered directly into the reef or mounted in custom-built cement blocks (0.013 m^3) deployed on the reef. The receivers were placed within movement corridors including inlets, natural constrictions and channels. Various factors can affect spatial and temporal variability in the detection range of receivers, including depth, temperature wind and ambient noise (Kessel *et al.* 2014; Huveneers *et al.* 2016). To establish the effective detection range of receivers in intertidal areas of Mangrove Bay, receivers were anchored in a straight line at ~0, 50, 100, 150, 175, 200, 225, 250 and 275 m away from a submersed, fixed-delay interval V13-1H range-test tag (with a mean transmission interval of 10 s). Range tests were conducted in the intertidal zone of Mangrove Bay in March 2013, when wind speeds ranged from 0 to 47.9 km h^{-1} (median 20.3 km h^{-1}), and in the lagoon in August 2012 following the

Table 1. List of explanatory variables included in models of residency index (RI) and core and total kernel areas (50 and 95% KAs respectively) of *Negaprion acutidens* at Mangrove Bay

Details include description, source, range of values calculated from monthly values from March 2013 to May 2015, unit of measure for each continuous variable or category levels for categorical predictors (marked with an asterisk). All variables were included as fixed effects apart from tag number, which was included as a random effect in all models

Variable	Description	Source	Units or levels	Range
Environmental				
PressAV	Mean air pressure	Milyering weather station	hPa	1004.1–1017.1
PressR	Air pressure range	Milyering weather station	hPa	0–14.8
TempAV	Mean water temperature	Temperature logger	°C	23.0–28.2
TempR	Water temperature range	Temperature logger	°C	2.4–7.4
TideAV	Mean tidal height	Regional Oceanic Modelling System	m	1.42–1.66
TideR	Tidal height range	Regional Oceanic Modelling System	m	1.78–2.17
WspeedAV	Mean wind speed	Milyering weather station	km h^{-1}	0–22.7
WspeedR	Wind speed range	Milyering weather station	km h^{-1}	0–49.0
WdireAV	Mean wind direction	Milyering weather station	Degrees	0–257.2
RainAV	Mean cumulative rainfall	Milyering weather station	mm	0–17.8
Biological				
TL	Stretched total length	Observer	mm	63.0–116.9
Tag*	Tag identification number	Observer; Vemco Ltd (Halifax, NS, Canada)	B1–13; L1–23	–
Sex*	Sex	Observer	Female, male	–
Temporal				
Month	Month	Calendar	Month	1–12

methods described by Pillans *et al.* (2014). The detection probability of a receiver was calculated by dividing the number of detections by the expected mean number of transmissions (given a mean transmission interval of 10 s) over the range-testing period. The effective detection range was defined as the distance at which detection probability was 50% (D_{50}) and estimated using a LOESS smoother fitted in R, ver. 3.3.1 (R Foundation for Statistical Computing, Vienna, Austria, see http://www.r-project.org). Range testing showed that the effective detection range (D_{50}) for the receivers in the intertidal bay was 175 m (see Fig. S1) and in the lagoon was 300 m (Pillans *et al.* 2014). Receivers were spaced 150–300 m apart in the intertidal zone adjacent to mangroves (2-m depth) and 200–800 m apart in the lagoon (2–10-m depth), channel (10–15-m depth) and open shelf (15–40-m depth; Fig. 1). Receivers were downloaded every 6–9 months and acoustic monitoring of tagged sharks occurred from March 2013 to May 2015.

To assess temporal variation in receiver performance (Payne *et al.* 2010), we deployed a V13-1H sentinel tag (with a transmission delay of 550–650 s) at fixed distances from two receivers (1 and 153 m) located in areas of greatest shark activity between November 2013 and January 2015 (Fig. 1). We assessed the effect of environmental variables on detection probability of these two receivers using generalised additive models (see the Methods section and Table S2 in the Supplementary material).

Residency and space use

Prior to analysis, false detections were removed from the dataset. False detections were defined as single detections recorded within a 24-h period, or when two detections recorded by different receivers were within too short a time frame for an individual to travel the distance separating the receivers (Pincock 2012). To examine patterns of residency, a shark was considered as present if two or more detections were recorded on a receiver on a given day (Papastamatiou *et al.* 2010). A residency index (RI) was calculated as the number of days a shark was present within the full array as a proportion of the total number of days monitored. Because individuals were released on different days, the projected battery life of each tag was used as a standard reference value for the total number of days monitored. All sharks were likely to have survived the tagging process (Buray *et al.* 2009; Chin *et al.* 2015) and thus sharks not detected by the array were assumed to have departed. RI values ranged from 0 (no residency) to 1 (high residency). Drawing upon descriptions of one of the criteria for a shark nursery (Heupel *et al.* 2007), we classified individuals as either non-residents that were present within the array for days to weeks ($<$30 days; RI $<$ 0.06) or residents that were predictably present within the array for months to years ($\geq$30 days; RI $\geq$ 0.06).

To investigate space use patterns the mean geographic position of each shark was estimated every 15 min using the centre of activity (COA) algorithm developed by Simpfendorfer *et al.* (2002). Only sharks that were detected for at least 5 days were included in this analysis to minimise the effect of short detection times on results. The COA positions provide a more accurate representation of movement than the raw receiver locations, and were used in subsequent analysis of kernel utilisation distributions (KUDs) to quantify the spatial area used by tagged sharks. Receiver locations were collected in World Geodetic System 1984 (WGS84) geographic coordinates, but subsequent spatial analysis was conducted in a Lambert conformal conic projection (m). KUD was estimated using the Brownian bridge kernel method in the *adehabitatHR* package (Calenge 2015) in R (R Foundation for Statistical Computing), which applies a conditional random walk to model both the shark positions and the expected path travelled between

Table 2. Tagging and detection details of 13 *Carcharhinus melanopterus* and 23 *Negaprion acutidens* monitored at Mangrove Bay from March 2013 to May 2015

Details include sex (F, female; M, male), life stage (N, neonate; J, juvenile), stretched total length (TL), residency category (RC; R, resident; NR, non-resident), total monitoring days (TMD), days detected (DD), consecutive days detected (CDD), the number of receivers on which a tagged shark was detected, residency index (RI) and core and total kernel areas (50 and 95% KA respectively). Sharks L5 and L19 were moving around the array until 26 May 2013 and 20 January 2014 respectively. After these dates, the tags were stationary close to one receiver. The RI for these sharks was calculated from data before the tags became stationary. Shark L3 was recaptured by fishermen in the recreational-use zone within the array on 21 July 2013 and its tag was subsequently implanted into Shark L9. NA, not available

Tag	Sex	Stage	TL (cm)	RC	Date tagged	Date last detected	TMD	DD	CDD	Number of receivers	RI	50% KA	95% KA
C. melanopterus													
B1	F	N	88	R	27 November 2013	16 February 2015	540	395	148	39	0.73	1.70	22.89
B2	F	N	56	R	4 December 2013	31 May 2015	540	407	90	5	0.75	0.16	0.95
B3	M	N	74	R	2 December 2013	4 November 2014	540	45	6	13	0.08	4.14	27.21
B4	F	N	53.5	NR	25 November 2013	2 December 2013	540	8	8	15	0.01	0.36	1.41
B5	F	J	107	NR	29 November 2013	4 December 2013	540	6	6	10	0.01	5.51	31.47
B6	F	N	55.5	NR	14 December 2013	15 December 2013	514	2	2	13	0.00	0.65	2.76
B7	F	N	55	NR	15 December 2013	12 January 2014	514	9	4	2	0.02	0.07	0.33
B8	F	N	51	NR	17 December 2013	23 December 2013	514	7	7	16	0.01	3.00	18.72
B9	F	N	55.5	NR	17 December 2013	21 December 2013	514	5	5	8	0.01	4.89	17.92
B10	M	N	56	NR	27 November 2013	NA	NA	NA	NA	NA	NA	NA	NA
B11	M	N	59	NR	5 December 2013	23 December 2013	514	16	11	4	0.03	0.09	0.45
B12	M	N	52	NR	10 December 2013	3 January 2014	514	12	10	15	0.02	1.05	7.80
B13	M	N	68	NR	17 December 2013	11 January 2014	514	9	8	12	0.02	0.15	0.94
N. acutidens													
L1	F	N	70.5	R	21 March 2013	17 October 2013	540	185	156	18	0.34	0.20	1.18
L2	F	N	67	R	21 March 2013	29 June 2013	540	101	101	29	0.19	0.12	1.10
L3	F	N	70	R	24 March 2013	21 July 2013	120	105	57	17	0.88	0.19	2.15
L4	M	N	75	R	21 March 2013	12 November 2013	540	230	223	12	0.43	0.11	0.57
L5	M	N	65	R	21 March 2013	2 August 2013	65	65	67	19	1.00	0.86	11.33
L6	M	N	69.5	R	22 March 2013	5 August 2013	540	136	135	30	0.25	0.33	2.77
L7	M	N	63	R	23 November 2013	8 January 2014	540	47	8	8	0.09	0.13	0.70
L8	M	N	72	R	26 November 2013	23 December 2014	540	391	327	17	0.72	0.43	2.22
L9	M	N	70	R	27 November 2013	1 August 2014	248	75	11	9	0.30	0.73	7.29
L10	M	N	81	R	27 November 2013	21 May 14	540	159	80	20	0.29	0.99	5.60
L11	M	N	90	R	30 November 2013	11 April 2014	540	131	129	16	0.24	0.19	1.06
L12	M	N	90.5	R	11 December 2013	27 May 15	514	512	470	21	1.00	0.34	2.40
L13	F	N	75.5	R	25 November 2013	5 August 2014	540	236	112	30	0.44	1.81	13.91
L14	F	N	74.5	R	28 November 2013	27 July 2014	540	242	242	15	0.45	0.20	0.75
L15	F	N	101	R	2 December 2013	10 March 2015	540	440	370	20	0.81	0.63	3.76
L16	F	N	69	R	17 December 2013	31 May 15	514	517	123	15	1.00	0.32	1.71
L17	F	N	73	NR	12 December 2013	3 January 2014	514	23	23	16	0.04	0.42	1.94
L18	F	N	64.5	NR	12 December 2013	15 December 2013	514	4	4	14	0.01	0.23	1.47
L19	F	N	74	NR	16 December 2013	5 June 2014	514	37	37	4	0.07	0.13	0.86
L20	F	N	91.5	NR	16 December 2013	24 December 2013	514	8	6	16	0.02	2.19	13.02
L21	M	N	85	NR	25 November 2013	30 November 2013	540	4	3	8	0.01	0.58	2.01
L22	M	N	66.5	NR	10 December 2013	24 February 2014	514	28	7	19	0.05	2.50	24.15
L23	M	N	72	NR	14 December 2013	23 December 2013	514	10	10	16	0.02	0.59	1.97

successive positions. We set two smoothing parameters: sig1, which controlled the width of the 'bridge' connecting successive positions; and sig2, which was related to the imprecision of the positions (Horne *et al.* 2007). Values of sig1 were selected using the *liker* function (Calenge 2015), which implemented the maximum likelihood approach (Horne *et al.* 2007). A fixed sig2 value of 175 m was used as the mean positional error around each receiver location and calculated from the effective detection range (D_{50}) established from range tests (see Fig. S1). Utilisation distribution increases with increasing sig2 values (positional error), with low and high values under- and overestimating space use (Calenge 2015; see Table S2). Therefore, we used the mean positional error for sig2 because it is considered the best trade-off to over- and underestimation and is likely to be more robust to variations in detection range that are likely in shallow environments and allowed for a more conservative assessment of the relative use of a MPA by tagged sharks. We subtracted the area where the 50 and 95% KUD contours overlapped with land to determine core and total space use (50 and 95% kernel areas respectively) over the total period each shark was detected. Individual kernel areas were then overlaid in ArcGIS, ver. 10.3 (ESRI, Redlands, CA, USA), to produce relative densities (i.e. the sum of the number of individuals in each overlapping area) of core kernel area and contours of total kernel area per species. Kernel areas were then overlaid with shapefiles of no-take zones and benthic habitat categories (Bancroft 2003) in ArcGIS, ver. 10.3 (ESRI), to calculate the relative proportion (0–1) of total space use within no-take zones and each benthic habitat type respectively (Fig. 1). Chi-squared goodness-of-fit and multiple comparison tests with Bonferroni corrections were used to assess whether sharks used any habitat type significantly more often than expected based on availability. To determine whether individuals were selecting or avoiding habitats, selectivity indices (S_i) were calculated for each habitat type as:

$$S_i = o_i - \pi_i$$

where o_i is the proportion of habitat type i used by each individual and π_i is the proportion of habitat type i used by all sharks, as described by (Strauss 1979). Selection was indicated with values greater than zero, whereas avoidance was indicated by values less than zero.

We first tested for differences in shark length and number of days detected between species (*C. melanopterus* and *N. acutidens*) and sexes using generalised linear models (GLMs) and an information theoretic approach to model selection (Burnham and Anderson 2002). For each response variable (shark length and number of days detected), a Gaussian error distribution with identity link was used and the slope model was compared with the intercept-only (null) model according to Akaike's information criterion corrected for small sample size and corresponding AIC_C weight (wAIC_C), which assigns relative strengths of evidence to the different competing models. The information theoretic approach uses a multimodel framework to provide a more robust method than standard regression techniques for comparing alternative hypotheses (Burnham and Anderson 2002) and was used in all subsequent model evaluation. The residuals of the models within 2 AIC_C points of the top-ranked model were examined to verify that the appropriate distribution was applied.

A suite of generalised additive models (GAMs) was used to evaluate the effects of shark length and sex and possible two-way interactions on three response variables, namely RI and, core and total kernel area (50 and 95% KA respectively), separately for each species. RI was modelled as the frequency of presence (i.e. the number of days a shark was present or absent) using a binomial error distribution with logit link and 50 and 95% KA using Gaussian error distributions with identity link. For the GAMs of RI, both binomial and β error distributions were tested with diagnostic plots showing that the former was more appropriate. Shark TL was modelled using a cubic regression spline (bs = 'cr'), with the basis dimension 'k' restricted to <4 to avoid overfitting. A maximum of one term per model was specified for *C. melanopterus* due to the small sample size ($n = 10$) and three terms were specified for *N. acutidens* due to the relatively larger sample size ($n = 21$). Hence, a candidate set of three models was used for *C. melanopterus* and five models were used for *N. acutidens* that included all possible combinations of variables, which were ranked according to AIC_C and wAIC_C (Table 3). For each response variable, a confidence set of models that were within 2 AIC_C points of the top-ranked model were considered equivalent and if these models did not include the null model, we used model averaging to calculate relative variable importance (RVI; Burnham and Anderson 2002) from the sum of wAIC_C across the confidence set. Models containing only highly influential variables (i.e. determined as those preceding a sharp decline in RVI) were used for graphical representation of variable effects.

Monthly patterns of residency and space use

Monthly metrics of residency and space use were calculated and analysed only for *N. acutidens* that were resident within the receiver array for over 30 days ($n = 16$). It was not possible to perform temporal analysis for *C. melanopterus* due to the low number of resident individuals ($n = 3$). To examine biological and environmental effects on monthly patterns of residency and space use, a suite of relevant explanatory variables was compiled, including water temperature, air pressure, rainfall, tidal height, wind speed and direction, month, sex and the TL of shark (Table 1). Multicollinearity was assessed between pairs of variables using Pearson correlation coefficients (r) and one variable was retained from correlated pairs ($r > 0.6$) to minimise the possibility of over-fitting models (Dormann *et al.* 2013). To account for the growth of tagged sharks over the monitoring period, monthly TL was estimated based on the initial size at capture and published growth rates of juvenile *N. acutidens* reported in the Indian Ocean (Stevens 1984). Water temperature was recorded at Tantabiddi using data loggers (U22-001; HOBO Data Loggers Australia, Adelaide, SA, Australia) calibrated at the Australian Institute of Marine Science (AIMS) and sampling at 30-min intervals, which were periodically downloaded and replaced every 3–12 months. Daily values for air pressure (hPa), rainfall totals (mm) and wind speed (m s^{-1}) and direction (degrees) were obtained from a weather station at Milyering (10 m elevation; 22.03°S, 113.92°E) situated 6.8 km south of Mangrove Bay (http://data.aims.gov.au/, accessed 7 October 2015). Predicted tidal height data were obtained through the Regional Oceanic Modelling System (https://www.myroms.org/, accessed 4 November 2015). Monthly mean values and range were computed for all variables from March 2013 to May 2015 and chronologically matched with shark movement data across the monitoring period.

Generalised additive mixed-effect models (GAMMs) with binomial error distributions and logit link were used to model RI. To model square root-transformed (to normalise distribution) 50 and 95% KAs, GAMMs with Gaussian error distributions and identity link were used. To account for repeated observations made for each shark, tag number was included as a random effect in the models (Bolker *et al.* 2009). All explanatory variables were modelled with a cubic regression spline, except for month and wind direction, which were modelled with a cyclic cubic regression spline (i.e. a penalised cubic regression spline whose ends match, up to second derivative). Because the latter smoother includes shrinkage by default, the shrinkage version of the cubic regression spline was also implemented here. The basis dimension 'k' was restricted to <4 to avoid overfitting. A maximum of four fixed effects per model was specified due to small sample sizes and the rule of marginality was applied such that interactions were included only in models

Table 3. Ranked additive models (m1, model 1, etc.) of residency index (RI), core and total kernel area (50 and 95% KA respectively) and the proportion of total kernel area within no-take zones (p95% KA in no-take) of *Carcharhinus melanopterus* and *Negaprion acutidens* explained by the biological variables (see Table 1 for explanations of each variable)

All models fitted for each response are shown; the best-supported model is highlighted in bold. Details include the estimated degrees of freedom (d.f.$_e$), Akaike's information criterion corrected for small sample size (AICc), increase in AIC$_C$ relative to the model with the lowest AIC$_C$ value (ΔAIC$_C$), relative AIC$_C$ weight (wAIC$_C$) and goodness of fit (adjusted R^2). TL, total length; sqrt, square root

Model number	Response	Model	d.f.$_e$	AIC$_C$	ΔAIC$_C$	wAIC$_C$	Adjusted R^2
C. melanopterus							
m3	RI	TL	3.00	331.26	0.00	1	88.0
m2	RI	Sex	1.00	1471.35	1140.09	0	6.1
m1	RI	1	0.00	1665.93	1334.67	0	0.0
m1	sqrt (50% KA)	1	0.00	26.20	0.00	0.90	0.0
m2	sqrt (50% KA)	Sex	1.00	30.60	4.40	0.10	9.3
m3	sqrt (50% KA)	TL	2.78	36.08	9.88	0.01	54.2
m1	sqrt (95% KA)	1	0.00	43.85	0.00	0.86	75.3
m2	sqrt (95% KA)	Sex	1.00	48.20	4.35	0.10	8.7
m3	sqrt (95% KA)	TL	2.92	49.94	6.09	0.04	0.00
m3	p95% KA in no-take	TL	2.99	159.68	0.00	1	59.7
m2	p95% KA in no-take	Sex	0.00	456.49	296.81	0	10.8
m1	p95% KA in no-take	1	1.00	463.76	304.08	0	0.0
N. acutidens							
m5	RI	Sex × TL	6.96	3526.32	0.00	1	0.7
m4	RI	Sex + TL	4.00	4244.19	717.87	0	4.0
m3	RI	TL	3.00	4244.21	717.89	0	1.8
m2	RI	Sex	1.00	4906.25	1379.93	0	4.2
m1	RI	1	0.00	4946.41	1420.09	0	0.0
m1	sqrt (50% KA)	1	0.00	21.84	0.00	0.33	0.0
m3	sqrt (50% KA)	TL	0.00	21.84	0.00	0.33	0.0
m5	sqrt (50% KA)	Sex × TL	2.67	23.25	1.42	0.16	16.1
m2	sqrt (50% KA)	Sex	1.00	24.50	2.66	0.09	4.8
m4	sqrt (50% KA)	Sex + TL	1.00	24.50	2.66	0.09	4.8
m1	sqrt (95% KA)	1	0.00	69.02	0.00	0.35	0.0
m3	sqrt (95% KA)	TL	0.00	69.02	0.00	0.35	0.0
m2	sqrt (95% KA)	Sex	1.00	71.46	2.44	0.10	3.7
m4	sqrt (95% KA)	Sex + TL	1.00	71.46	2.44	0.10	3.7
m5	sqrt (95% KA)	Sex × TL	1.87	71.55	2.53	0.10	3.8
m5	p95% KA in no-take	Sex × TL	5.59	630.86	0.00	1	23.8
m4	p95% KA in no-take	Sex + TL	3.85	664.67	33.81	0	20.9
m3	p95% KA in no-take	TL	2.69	667.37	36.51	0	13.2
m1	p95% KA in no-take	1	0.00	676.48	45.62	0	0.0
m2	p95% KA in no-take	Sex	1.00	677.49	46.63	0	5.0

with both main effects. This resulted in a set of 96 candidate models, with model selection and averaging undertaken using the same approach described for GAMs. Standard diagnostic plots were made to assess the validity of the models in the confidence set and we checked for temporal autocorrelation in the residuals. The top six models for each response were then presented, except when more than six models were within 2 AIC$_C$ points, in which case all models within the confidence set were presented. All models were implemented using the *lme4, MuMIn*, *mgcv* and *gamm4* packages in R (R Foundation for Statistical Computing). Unless specified otherwise, all data are presented as the mean (±s.d) values.

Results

Tagged sharks were monitored for 2–544 days between March 2013 and May 2015 (Table 2; Fig. 2). All the tagged sharks were neonates with umbilical scars in various stages of healing (age <1 year), with the exception of one *C. melanopterus* that was a juvenile female. The mean TL of *N. acutidens* was slightly larger than that of *C. melanopterus* (75.2 ± 10.0 ($n = 23$) *v.* 63.9 ± 16.7 cm ($n = 13$) respectively), with higher statistical support for the generalised linear model (GLM) that included species (wAICc = 0.59) than the intercept-only model (wAIC$_C$ = 0.41). We found no evidence for a difference in TL between sexes for either *C. melanopterus* (65.2 ± 20.6 and 61.8 ± 9.0 cm in females and males respectively; wAIC$_C$ = 0.89 for the intercept-only model) or *N. acutidens* (75.5 ± 11.0 and 75.0 ± 9.5 cm in females and males respectively; wAIC$_C$ = 0.77 for the intercept-only model).

Residency and space use

Nine *C. melanopterus* and five *N. acutidens* were detected within the array between 2 and 23 days after tagging, but ceased to be detected after January 2014 (Table 2). The remaining three

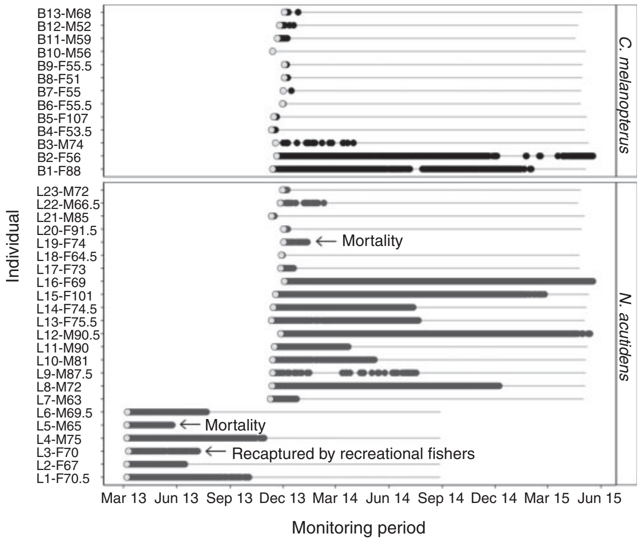

Fig. 2. Daily presence of individual *Carcharhinus melanopterus* (black circles) and *Negaprion acutidens* (dark grey circles) released with acoustic transmitters in Mangrove Bay from March 2013 to May 2015. Individuals are identified by species (B, blacktip reef shark; L, sicklefin lemon shark), tag identification number, sex (M, male; F, female), followed by stretched total length (cm). The tagging dates are indicated by light grey circles and grey lines represent the availability of the shark for detection based on tagging date and battery life of the tag.

C. melanopterus were detected for a maximum of 45–407 days (77 ± 152 days) and 18 *N. acutidens* were detected for between 47 and 517 days (166 ± 160 days), with higher statistical support for the model that included species (wAICc = 0.84) relative to the intercept-only model ($\mathrm{wAIC_C} = 0.16$). We found no evidence for differences in the number of days detected between the sexes in both species ($\mathrm{wAIC_C} = 0.80$ and 0.77 for the intercept-only model for *C. melanopterus* and *N. acutidens* respectively). One of the tagged *C. melanopterus* (B10) was not detected following its release (Fig. 2). Two of the 18 *N. acutidens* (L5 and L19) were assumed to have died close to a receiver after 65 and 37 days respectively, resulting in the tag being continuously detected by one or more overlapping receivers (Fig. 2). We retrieved a tag from one *N. acutidens* (L3) that was recaptured by a recreational fisher outside the Mangrove Bay no-take zone, and subsequently deployed it into another *N. acutidens* (L9). Throughout the detection period, 74% of tagged sharks were detected on more than 10 receivers (15 ± 8 receivers; Table 2). One *C. melanopterus* (B1) and three *N. acutidens* (L13, L15 and L22) were detected by the receiver curtains off Tantabiddi (~10 km north) and Turquoise Bay (~15 km south), a part of the array that was designed to detect such long-range movement (Fig. 1). We found strong evidence for an effect of species on RI, with the slope model having highest statistical support (wAICc = 1) and *N. acutidens* having higher residency than *C. melanopterus* (0.42 ± 0.34 *v.* 0.17 ± 0.30 respectively).

For *C. melanopterus* residency, the additive model including TL had the highest statistical support (GAM, $\mathrm{wAIC_C} = 1$; Table 3) and accounted for 88% of the variance in the response, indicating a positive trend in residency when TL increased from 60 to 90 cm (Fig. 3*a*). For *N. acutidens* residency, we found highest support for the model including sex, TL and the interaction between sex and TL (GAM, $\mathrm{wAIC_C} = 1$; Table 3), indicating increased residency among smaller (≤70 cm TL) neonate females and decreased residency with increasing TL of larger (>70 cm TL) neonate females (Fig. 3*b*). In contrast, there was no apparent change in residency with increasing TL for males (Fig. 3*c*), but this model accounted for less than 1% of the variance in the response ($R^2 = 0.7$).

Core and total kernel areas (50 and 95% KA respectively) of 10 *C. melanopterus* and 21 *N. acutidens* largely overlapped within nearshore waters of Mangrove Bay (Fig. 4). We found evidence that 50% KAs differed between species, with the slope model having higher statistical support (wAICc = 0.72) than the intercept-only model ($\mathrm{wAIC_C} = 0.28$; mean (±s.d.), 1.6 ± 2.0 and 0.6 ± 0.7 km^2 for *C. melanopterus* and *N. acutidens* respectively; Table 2). There was also evidence for a species difference in 95% KAs, with the slope model having higher statistical support (wAICc = 0.66) than the intercept-only model ($\mathrm{wAIC_C} = 0.34$). The 95% KAs were larger for *C. melanopterus* than for *N. acutidens* (11.2 ± 12.5 *v.* 4.8 ± 6.1 km^2 respectively).

We found no evidence for a difference in overall core space use of *C. melanopterus* with either shark sex or TL with the intercept-only model having majority support ($\mathrm{wAIC_C} = 0.80$). Similarly, there was little evidence for an effect of TL or sex on total space use, because the intercept-only model ranked highest (Table 3). There was also no evidence for a difference in core and total space use of *N. acutidens* in response to either shark sex or TL, with the intercept-only model most parsimonious (Table 3). The proportion of total space use within no-take zones was higher for *N. acutidens* relative to *C. melanopterus* (0.86 ± 0.19 *v.* 0.71 ± 0.30 respectively), with the slope model having complete support ($\mathrm{wAIC_C} = 1$) over the intercept-only model.

In terms of the proportion of 95% KA within no-take zones, the additive mixed model including TL had the highest statistical support for *C. melanopterus* ($\mathrm{wAIC_C} = 1$; Table 3). This model accounted for 60% of the variance in the response, and indicated a negative trend in the protection of total space use when TL exceeded 60 cm for *C. melanopterus* (Fig. 3*d*). For *N. acutidens,* the highest statistical support was for the model including sex, TL and the interaction between sex and TL ($\mathrm{wAIC_C} = 1$; Table 3) and accounted for 24% of the variance. The proportion of total space use within no-take zones was marginally higher for females between 65 and 75 cm TL, but was consistent for males across the range of TL sampled (Fig. 3*e, f*). There was no difference in the proportion of habitat types used between species (50% KA, $\chi^2_8 = 1.14$, $P = 1.00$; 95% KA, $\chi^2_8 = 13.21$, $P = 0.10$) and across space use metrics within species (*C. melanopterus*, $\chi^2_8 = 5.22$, $P = 0.73$; *N. acutidens,* $\chi^2_8 = 1.71$, $P = 0.99$). Core and total space use of both species primarily focused on sandflats (>34 and >21% respectively) and sandy lagoon habitats (>30 and >26% respectively). We found that neonates selected disproportionately for inshore sandflats, followed by mangroves, algal pavement and shoreline reefs (*C. melanopterus*, $\chi^2_8 = 29.57$, $P < 0.001$; *N. acutidens*, $\chi^2_8 = 106.78$, $P < 0.001$; Fig. 5). Mean selection values revealed that reef slope and sandy lagoon habitats were consistently avoided by *C. melanopterus* and *N. acutidens* (Fig. 5).

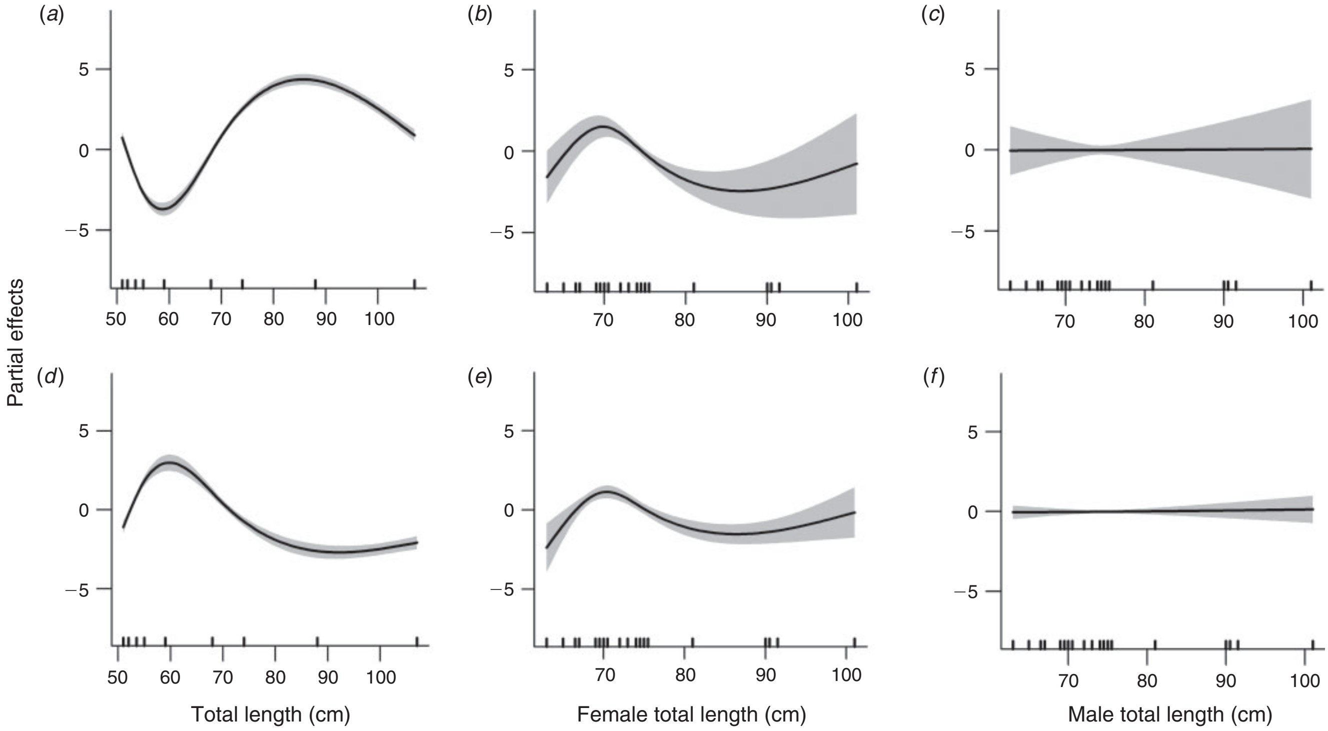

Fig. 3. Partial residual plots showing the relationships of the dependent variables of (*a–c*) residency index and (*d–f*) the relative proportion of 95% kernel area in no-take marine protected areas with that of the independent variable of total length in the top-ranked additive models for *Carcharhinus melanopterus* (*a*, *d*) and *Negaprion acutidens* (*b*, *c*, *e* and *f*). Black lines represent the fitted line and grey shaded areas represent 95% confidence intervals.

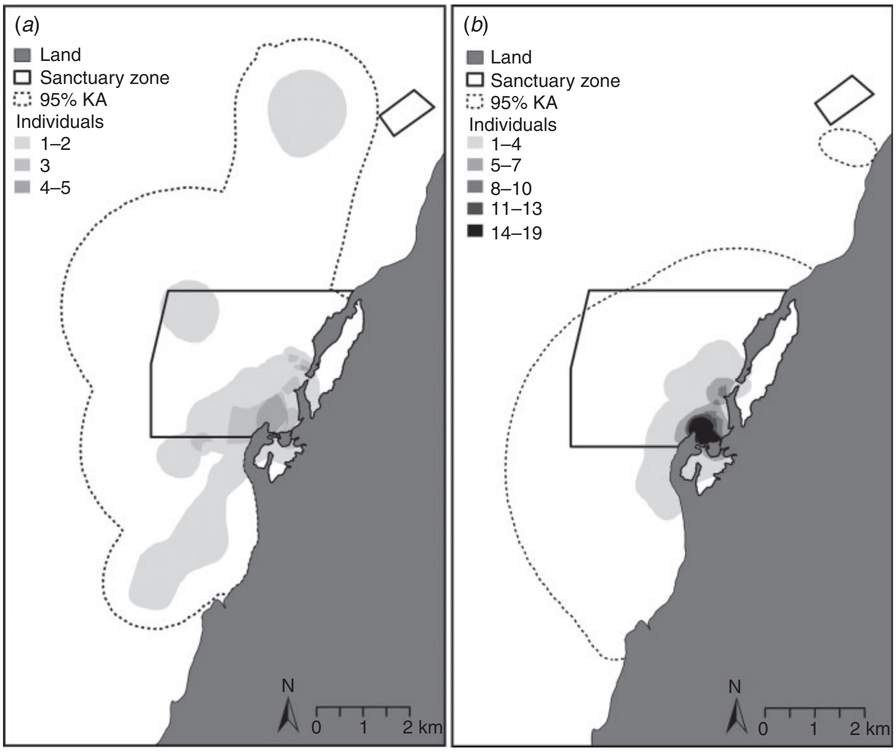

Fig. 4. Maps of 50 and 95% kernel areas (KAs) for (*a*) *Carcharhinus melanopterus* and (*b*) *Negaprion acutidens* monitored within Mangrove Bay for at least 5 days. Contours of 95% KA (dashed lines) and relative densities of 50% KA (shaded areas) are shown for combined individuals.

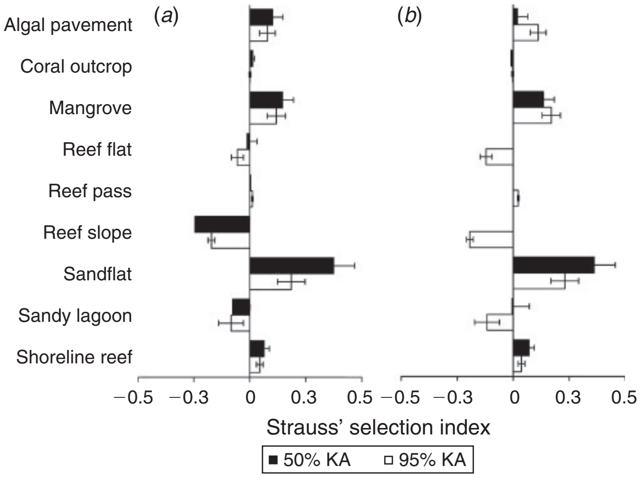

Fig. 5. Mean (±s.e.) Strauss' selection index values based on 50 and 95% kernel areas (KAs) of (*a*) *Carcharhinus melanopterus* and (*b*) *Negaprion acutidens* across the habitat types detailed in Fig. 1.

Monthly patterns of residency and space use

A detection span sufficient (>30 days) to allow the estimation of monthly RI and space use (50 and 95% KAs) was obtained for three *C. melanopterus* and 16 *N. acutidens* (Table 2). However, the GAMMs described were only fitted for *N. acutidens* and not *C. melanopterus* due to the small sample size. Mean values of water temperature were strongly correlated with those of tidal height ($r = 0.86$), and mean values of air pressure was strongly correlated with those of wind direction ($r = -0.73$). Therefore, predictors from each correlated pair ($r > 0.6$) were used in separate candidate models. The modelling revealed that the confidence set (<2 ΔAIC_C) included one model where RI was the response, 13 models where 50% KA was the response and two models where 95% KA was the response (Table 4). For RI, the model containing TL and the interaction between month and sex had the highest statistical support ($wAIC_c = 1$, $R^2 = 4.8\%$; Figs 6, 7*a–c*). We found only weak relationships between 50% KA and explanatory variables for all 13 models within the confidence set (R^2 ranging from 0.2 to 2.8%; Table 4). Of these,

Table 4. Ranked additive mixed models (m1, model 1, etc.) of monthly residency index (RI), core and total kernel area (50 and 95% KA respectively) of *Negaprion acutidens* explained by the independent variables

The top six models for each response are shown; if more than six models are within 2 Akaike's information criterion corrected for small sample size (AICc) points, all these models are shown. Tag number was treated as a random effect in all models; the model(s) containing the most influential variables and used for graphical representation are highlighted in bold. Details for each model include the estimated degrees of freedom (d.f.$_e$), AIC_C, increase in AIC_C relative to the model with the lowest AIC_C value (ΔAIC_C), relative AIC_C weight ($wAIC_C$) and goodness of fit (adjusted R^2). TL, total length; sqrt, square root; PressAV, mean air pressure; PressR, air pressure range; TideR, tidal height range; WdireAV, mean wind direction; RainAV, mean cumulative rainfall

Model number	Response	Model	d.f.$_e$	AIC_C	ΔAIC_C	$wAIC_C$	Adjusted R^2
50% KA							
m11	RI	TL + month × sex	17.88	592.67	0.00	1.00	4.8
m7	RI	TL + month	11.81	661.58	68.91	0.00	4.3
m10	RI	TL + sex	12.81	663.47	70.80	0.00	4.5
m12	RI	Month + sex × TL	14.43	666.71	74.04	0.00	4.4
m23	RI	TL + pressAV	4.90	696.62	103.95	0.00	4.1
m43	RI	Sex × TL + pressAV	5.90	698.58	105.91	0.00	4.2
50% KA							
m84	sqrt (50% KA)	TempAV + tideR	3.62	−236.03	0.00	0.06	0.6
m19	sqrt (50% KA)	TideR	2.65	−235.98	0.05	0.06	0.2
m13	sqrt (50% KA)	PressAV	1.21	−235.61	0.42	0.05	1.5
m66	sqrt (50% KA)	PressAV + tideR	3.39	−235.43	0.60	0.05	1.2
m4	sqrt (50% KA)	Month	3.04	−235.24	0.79	0.04	2.0
m29	sqrt (50% KA)	TL + tideR	3.41	−235.17	0.86	0.04	2.8
m79	sqrt (50% KA)	RainAV + tideR	3.59	−235.12	0.91	0.04	1.1
m7	sqrt (50% KA)	TL + month	3.98	−235.06	0.97	0.04	1.5
m23	sqrt (50% KA)	TL + pressAV	3.17	−234.97	1.06	0.04	1.8
m92	sqrt (50% KA)	TideR + wdireAV	3.39	−234.80	1.24	0.03	0.4
m2	sqrt (50% KA)	TL	2.37	−234.72	1.31	0.03	2.4
m64	sqrt (50% KA)	PressAV + pressR	2.95	−234.45	1.58	0.03	1.5
m63	sqrt (50% KA)	PressAV + rainAV	3.09	−234.15	1.88	0.03	2.4
95% KA							
m25	sqrt (95% KA)	TL + rainAV	3.07	129.39	0.00	0.26	8.2
m45	sqrt (95% KA)	TL + sex + rainAV	4.08	130.83	1.44	0.13	12.7
m15	sqrt (95% KA)	RainAV	1.58	131.65	2.26	0.08	2.4
m35	sqrt (95% KA)	Sex + rainAV	2.58	133.14	3.75	0.04	6.2
m76	sqrt (95% KA)	RainAV + tempAV	2.3	133.16	3.77	0.04	3.2
m79	sqrt (95% KA)	RainAV + tideR	2.13	133.61	4.22	0.03	2.9

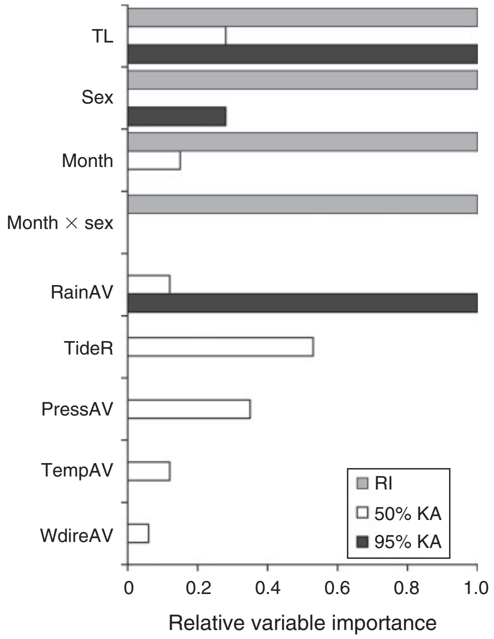

Fig. 6. Relative variable importance values of the independent variables in additive mixed models of monthly patterns of residency index (RI) and 50 and 95% kernel areas (KAs) of *Negaprion acutidens*. Variables that were common within the confidence set (i.e. models with values <2-point change in Akaike's information criterion corrected for small sample size) have a relative variable importance value of 1.0. RainAV, mean rain accumulation; TideR, tidal height range; PressAV, mean air pressure; TempAV, mean water temperature; WdireAV, mean wind direction.

relative variable importance (RVI) values derived from model averaging indicated that tidal height range, mean air pressure and TL had the most effect on core space use (Fig. 6) and the models containing these variables (Models 19, 13 and 2; Table 4) are shown in Fig. 7*d*–*f*. For 95% KA, model averaging indicated that TL and mean rain accumulation had the most effect on total space use (Fig. 6) and the model containing these variables (Model 25; wAICc = 0.26, R^2 = 8.2%; Table 4) is shown in Fig. 7*g*, *h*. Estimated TLs of *N. acutidens* at the end of the detection period ranged from 64.8 to 114.8 cm, indicating that all resident individuals were still immature. There was a negative trend in the monthly residency of immature *N. acutidens* across the range of TL sampled (Fig. 7*a*). Monthly residency indices of *N. acutidens* were sex specific (Fig. 7*b*, *c*). Females were resident throughout the year (Fig. 7*b*), whereas males were found to have longer residency in winter and spring (June–September) than in summer and autumn (Fig. 7*c*). Core space used by *N. acutidens* increased by 0.02 km^2 when mean air pressure was greater than 1012 hPa, and decreased by 0.05 km^2 when monthly tidal height range exceeded 2.0 m (Fig. 7*d*, *f*). Core and total space used by *N. acutidens* increased by 0.1 and 0.5 km^2 respectively when TL exceeded 88 cm (Fig. 7*e*, *h*). Total space use of *N. acutidens* increased marginally as mean rainfall increased from 0 to 7 mm and then stabilised (Fig. 7*g*).

Discussion

The present study is the first to quantify long-term residency and patterns of space use of neonate *C. melanopterus* and *N. acutidens* in the eastern Indian Ocean. Differences in the residency patterns between these species imply that for *N. acutidens*, the nearshore waters of Mangrove Bay meet the proposed criteria of Heupel *et al.* (2007) for a nursery, but it is apparent that additional data are required for *C. melanopterus.* Neonates of *N. acutidens* had small activity spaces (mean 95% KA = 4.5 km^2), which is consistent with patterns in earlier studies both at Ningaloo (Speed *et al.* 2011, 2016) and elsewhere (Filmalter *et al.* 2013). We also found evidence of ontogenetic expansions in space use among neonates of this species.

Although the present study does not provide quantitative data on increased neonate abundance in Mangrove Bay (one of the criteria for a nursery area), our high capture rates and extensive in-water surveys from Stevens *et al.* (2009) suggest that Mangrove Bay supports a higher abundance of both species. The presence of open and partially healed umbilical scars (age <1 week; Chin *et al.* 2015) on both *C. melanopterus* and *N. acutidens* captured between November and March over two seasons indicates that neonates of these species are pupped in or near to Mangrove Bay in autumn and summer, and some remain there for up to 17 months. We found highly variable patterns in the residency of neonate and juvenile *C. melanopterus* (mean RI (±s.d.), 0.14 ± 0.3), consistent with reported variability in the residency of juveniles of this species (0.3 ± 0.3) in eastern Australia (Chin *et al.* 2016). The findings for *C. melanopterus* in the present study contrast with patterns of long-term residency observed in *N. acutidens*, and corroborate increasing evidence that although extended residency in shark nurseries is common (DeAngelis *et al.* 2008; Chapman *et al.* 2009; Knip *et al.* 2011; Legare *et al.* 2015), it is not universal in juvenile sharks (Chin *et al.* 2016; Munroe *et al.* 2016). The results of the present study suggest that although Mangrove Bay may provide suitable pupping grounds for *C. melanopterus*, it does not appear to function as a long-term nursery habitat for this species. Prolonged residency and site attachment has been recorded for adult *C. melanopterus* on isolated coral atolls (Papastamatiou *et al.* 2009; Mourier *et al.* 2012), whereas large-scale dispersal (>80 km) has been documented for neonates and juveniles in archipelagic systems (Chin *et al.* 2013, 2016). The shallow depth of the lagoon at Mangrove Bay (<4 m) and availability of contiguous reef habitat along Ningaloo Reef may facilitate the dispersal of neonate *C. melanopterus* along the reef system. Two of the nine *C. melanopterus* (B5 and B9) that permanently departed the array were last recorded on the receivers at the northern limit of the array at Tantabiddi, indicating a minimum linear dispersal distance of 10 km. Alternatively, or in addition, low apparent residencies of neonate *C. melanopterus* could also reflect high mortality rates of juveniles, as have been documented in populations of blacktip (Heupel and Simpfendorfer 2002), lemon (Gruber *et al.* 2001) and scalloped hammerhead (*Sphyrna lewini*) (Duncan and Holland 2006) sharks elsewhere. In contrast, 70% of tagged *N. acutidens* had high residency and exhibited repeated use of nearshore, shallow sandflats, consistent with patterns reported for this species at atolls in the western Indian Ocean (Filmalter *et al.* 2013) and habitat selection in other similar-sized carcharhinids (Papastamatiou *et al.* 2009; Chin *et al.* 2012; Rizzari *et al.* 2014).

As expected, our temporal models revealed a progressive decline in monthly residency and increase in monthly space use

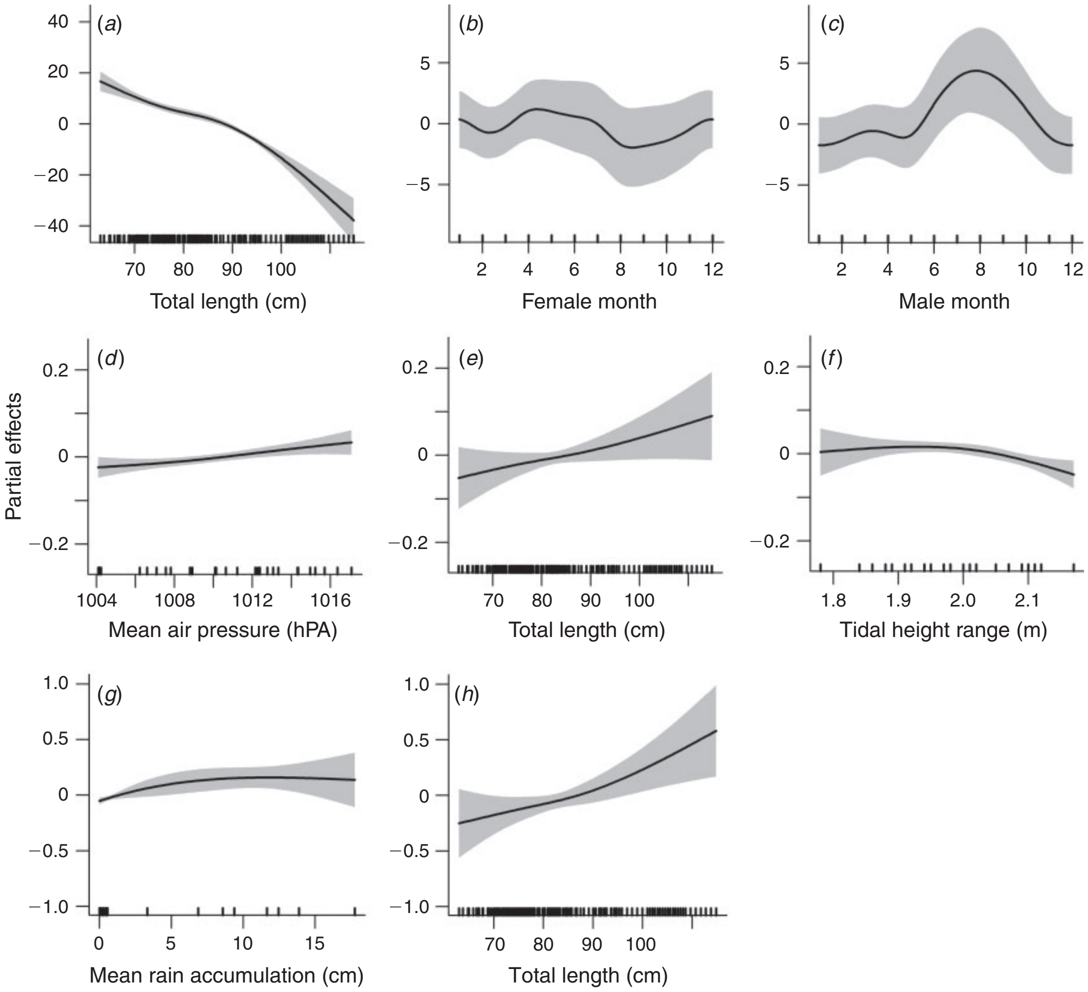

Fig. 7. Partial residual plots relative to the independent variables in the top-ranked additive mixed models for (*a–c*) residency index, (*d–f*) 50% kernel area (KA) and (*g*, *h*) 95% KA of *Negaprion acutidens* (see Table 4 for an explanation of each model). Each vertical plane represents the effect of a variable on each response. Black lines represent fitted lines and grey shaded areas represent 95% confidence intervals.

with ontogeny for resident individuals of *N. acutidens*. Ontogenetic expansion in space use (Garla *et al.* 2006; Dicken *et al.* 2007; Knip *et al.* 2011), followed by reduced nursery residency (Hussey *et al.* 2009; Conrath and Musick 2010) has been observed in many sharks, and is thought to reflect foraging optimisation in association with reduced predation risk as sharks grow in size (Heupel *et al.* 2004; Matich and Heithaus 2015). The relationship between TL and overall residency of *N. acutidens* showed the opposite trend to monthly residency, with an increase in overall residency for the larger neonates. These differences may suggest that other factors in addition to ontogeny drive residency, but it would seem that our temporal modelling approach, which incorporated monthly increases in shark TL, was more appropriate for examining the relationship between ontogeny and residency.

Estimates of total space use by neonate and juvenile *C. melanopterus* in Mangrove Bay (95% KA; 0.3–31.5 km^2) were consistent with estimates in east Australia (95% KA; 10.9–30.1 km^2; Chin *et al.* 2016) and larger than those found in older juveniles (minimum convex polygons (MCP); 5.8–8.5 km^2) and adults (MCP; 3.5–21.8 km^2) in this region (Speed *et al.* 2016). The findings of the present study support recent evidence that coastal habitat use by *C. melanopterus* (Chin *et al.* 2016) differs from conspecifics on coral reefs (Papastamatiou *et al.* 2011; Mourier *et al.* 2013*b*) and does not conform to the characteristic patterns of classical nursery use where neonates demonstrate highly restricted movements before undergoing ontogenetic expansions in space use. The results of the present study, combined with previous studies, reflect the ecological flexibility of *C. melanopterus* in being able to adapt movement patterns to optimise the use of local environments and suggest that this behaviour may be innate. In any event, the results of the present study must be treated with caution because of the low sample size ($n = 10$) of tagged *C. melanopterus* and the fairly short duration of monitoring.

Consistent with previous observations of overlap in nursery habitat use by *C. melanopterus* and *N. acutidens* in the Pacific Ocean (Papastamatiou *et al.* 2009; Mourier *et al.* 2013*a*), both species in the present study showed positive selection for nearshore sandflat and vegetated (mangrove and algal pavement) habitats, indicating low levels of habitat partitioning. This absence of habitat partitioning and space use overlap between and within species may reflect opportunistic use of abundant refuges or prey resources (Frisch *et al.* 2016) within sandflats and vegetated habitats where parturition occurs (Papastamatiou *et al.* 2009; Mourier *et al.* 2013*a*). Alternatively, strong selection for inshore sandflats and mangroves may relate to reduced predation risk within physical refuges (Guttridge *et al.* 2012), increased chances of finding prey on shallow sandflats (Papastamatiou *et al.* 2009) or behavioural thermoregulation (Papastamatiou *et al.* 2015). Avoidance of deeper lagoonal and reef slope habitats by neonate sharks may reduce predation risk or competition with other species, because larger predators, such as adult *C. melanopterus*, grey reef Carcharhinus *amblyrhynchos* and tiger sharks *Galeocerdo cuvier*, frequent these habitats (Ferreira *et al.* 2015; Speed *et al.* 2016).

Our modelling of temporal patterns indicated that environmental variables affected the space use of *N. acutidens* on a monthly basis, but had no effect on monthly residency. Along with expansions in space use with ontogeny, we found a weak negative effect of tidal range on core space use of neonate *N. acutidens,* consistent with the hypothesis of tide-mediated selection of shallow or familiar habitats as a strategy for predator avoidance, as seen in juvenile lemon sharks *Negaprion brevirostris* (Wetherbee *et al.* 2007; Guttridge *et al.* 2012). At Mangrove Bay, the high-use area at the southern part of the Bay contained a shallow sandflat adjacent to a mangrove-fringed inlet that remained flooded at low tides. Our telemetry data and capture locations confirmed that at high tide neonate *N. acutidens* often remained within the complex of mangrove root systems that probably afforded a physical refuge for these juveniles from larger predators. Alternatively, or in addition, reduced space use may be a strategy for optimising foraging efficiency as a consequence of tidally driven prey migrations via discrete corridors (Friedlander and Monaco 2007; Papastamatiou *et al.* 2009). We detected slight increases in core space use of *N. acutidens* with increases in barometric pressure, which is consistent with evidence of behavioural responses of a range of Carcharhinid shark species to changing barometric pressure (Heupel *et al.* 2003; Udyawer *et al.* 2013). Increases in total space use of *N. acutidens* with increasing rainfall may reflect avoidance of freshwater inflows or the redispersion of prey from core parts of the habitat. Alternatively, freshwater inflows were hypothesised to contribute to increased niche separation of juvenile sharks from adults (Heupel and Simpfendorfer 2008) and to expand available habitat for juvenile bull sharks *Carcharhinus leucas* (Matich and Heithaus 2015). The minimal effect of environmental variables on residency suggests that local conditions and the availability of prey resources may be favourable year-round for this species in the nursery. The lack of seasonality in the residency of neonate *N. acutidens* females was consistent with patterns seen in older juveniles (Filmalter *et al.* 2013), but we found increases in the residency of neonate *N. acutidens* males in winter months. Differences in residency patterns between sexes in adults sharks may be driven by sex-specific differences in thermoregulatory requirements (Hight and Lowe 2007), avoidance of sexual harassment in females (Wearmouth *et al.* 2012) or sex-specific dietary preferences (McCord and Campana 2003), and the results of the present study suggest that sex-specific behaviour may be innate. The latter hypothesis could be verified by future studies examining differences in diet between the sexes.

Analysis of movements based on acoustic telemetry requires several assumptions to be made regarding equipment performance and cessation of detections from tagged animals. In contrast with other studies (Gjelland and Hedger 2013; Mathies *et al.* 2014; Huveneers *et al.* 2016), we found no evidence of temporal variations in receiver performance due to ambient noise from wind or rain or changes in air pressure or water temperature. Because movement and behaviour were not observed directly, an abrupt end in detections could have resulted from premature transmitter failure, tagging-associated mortality (predation or transmitter expulsion), natural or fishing mortality and dispersal of the tagged animal from the study area. Characteristic detection patterns indicated natural mortality of two *N. acutidens*, which were assumed to have died or been consumed close to a receiver after 65 and 17 days of tagging, resulting in the tag being continuously detected by one or more overlapping receivers. There was also one instance of fishing mortality, with one *N. acutidens* recaptured by recreational fishers. High rates of wound healing and survival of internally tagged individuals of our two focal species (Buray *et al.* 2009; Filmalter *et al.* 2013; Chin *et al.* 2015) and multiple recaptures of sharks between 2 and 19 days from release (17%) indicated that declines in detections of tagged sharks likely reflect dispersal to other sites, high rates of natural or fishing mortality or a combination of both, rather than tagging mortality.

Conservation and management

No-take zones in the present study encompassed large proportions (>70%) of total space use areas for neonate populations of *N. acutidens* and, to a lesser extent, *C. melanopterus* and provide some support for the use of small-scale no-take MPAs for effective management of the vulnerable, early life stages of carcharhinids (Garla *et al.* 2006; Heupel *et al.* 2010). To effectively protect mobile species, no-take zones should ideally be at least twice the size of the 95% KA of focal species (Green *et al.* 2015). Although total space use estimates of both species are largely encompassed by existing no-take zones, there was evidence of short-term residency and declining spatial protection for neonate *C. melanopterus* when their TL exceeded 60 cm, thus supporting our hypothesis of lower protection for larger-sized sharks of this species. Conversely, protection afforded by no-take zones was fairly consistent with increasing TL of neonate *N. acutidens.* A previous study suggested considerable rates of recapture (4.2%) of tagged reef sharks by recreational fishers in the NMP (Speed *et al.* 2016), indicating that areas within (Smallwood *et al.* 2012) or adjacent to no-take zones may still be vulnerable to anthropogenic effects. A southward extension of the Mangrove Bay no-take zone would enhance protection for neonate populations of *C. melanopterus* and *N. acutidens*. The results of the present study indicate that similar scale no-take zones may provide some protection for other neonate populations of *C. melanopterus* along the Ningaloo Reef coast and increase species resilience at seascape scales (Mumby 2006).

Given that Ningaloo Reef extends over 320 km of coastline, it is unlikely that Mangrove Bay is the only potential nursery, although equivalent habitats with fringing mangroves are rare along this coastline (Smallwood *et al.* 2012). Future work should focus on the identification of other potential nursery or pupping locations and possible connectivity between these nurseries.

The short-term residency and higher dispersal capacity of *C. melanopterus* seen in this study and elsewhere (Chin *et al.* 2013, 2016) suggest that this species is able to use a wider variety of habitats for development than *N. acutidens*, particularly shallow reef environments within the region (Vanderklift *et al.* 2014). In contrast, the intensive use of small areas by *N. acutidens* has implications for the vulnerability of the species due to increased exposure to coastal threats, such as fisheries, pollution and habitat loss or degradation (Knip *et al.* 2010). The International Union for the Conservation of Nature has currently classified *C. melanopterus* as 'Near Threatened' globally (Heupel 2009) and *N. acutidens* as 'Least Concern' in Australia but 'Vulnerable' globally (Pillans 2003), providing opportunity to protect one of the last strongholds for the species. Although we have identified potential drivers of space use and residency for *C. melanopterus* and *N. acutidens* in their natal environments, further studies of reef shark movement and behaviour involving an expanded acoustic array, active tracking in shallow microhabitat, standardized surveys and genetic assessment of parentage (Mourier and Planes 2013; Mourier *et al.* 2013*b*) will help clarify the significance of particular nursery habitats for population maintenance in contiguous coastal systems.

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Supplementary material

Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery

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Methods

Variables influencing receiver efficiency

To examine environmental effects on monthly patterns of detection efficiency of two acoustic receivers placed 1 and 153 m from a V13–1H sentinel transmitter, we compiled a suite of explanatory variables including water temperature, air pressure, rainfall, tidal height, wind speed and direction, month, sex and total length of shark (Table 1 in the main paper). Water temperature was recorded at Tantabiddi using HOBO Pro V2 data loggers (U22-001; HOBO Data Loggers Australia, Adelaide, South Australia) calibrated at the Australian Institute Marine Science; AIMS and sampling at 30-min intervals, which were periodically downloaded and replaced every 3–12 months. Daily values for air pressure (hPa), rainfall totals (mm), wind speed (m s^{-1}) and direction (degrees) were obtained from a weather station at Milyering (10-m elevation; 22.03°S, 113.92°E) situated 6.8 km south of Mangrove Bay (http://data.aims.gov.au/, accessed 7 October 2015). Predicted tidal height data were obtained through the Regional Oceanic Modelling System (https://www.myroms.org/, accessed 4 November 2015). Values of monthly mean and range were computed for all variables from November 2013 to January 2015 and chronologically matched with detection data of the sentinel tag across the monitoring period. We used generalized additive mixed models (GAMMs) with binomial error distributions to model detection probability. We modelled month as a random effect in all models and fitted all environmental variables with a cubic regression spline, restricting the basis dimension ‘k’ to < 4 to avoid overfitting. A maximum of one fixed term per model was specified due to fairly small sample sizes ($n = 12$). This resulted in a set of 11 candidate models (Table S2) which were ranked according to the sample-corrected Akaike’s Information Criterion (AIC_C) and relative AIC_C weight ($wAIC_C$).

Results

Variables influencing receiver efficiency

Atmospheric pressure, water temperature, rainfall, wind speed and direction were not found to be important drivers of receiver performance (Table S2). Therefore, we found no evidence that the monthly patterns in residency and space use of tagged sharks in our study were an artefact of ambient noise from wind or rain or changes in air pressure or water temperature. We found the highest statistical support for model 7 ($wAIC_C = 1$), which showed a negative influence of tidal height on detection probabilities of the station located 1 m from the sentinel tag, and model 8 ($wAIC_C = 1$), which showed negative influence of tidal range on detection probabilities of the station located 153 m from the sentinel tag (Table S2; Fig. S2).

Table S1. Summary of the location, habitat type and detections of the acoustic receivers deployed in the Mangrove Bay array

Receiver	Longitude	Latitude	Deployment		Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
			Start	End					
Tantabiddi									
1	–21.899	113.937	01-Mar-14	01-Jun-15	Coral reef		1	1	0.00
2	–21.909	113.944	19-Mar-13	01-Jun-15	Coral reef		1	17	0.00
3	–21.911	113.948	19-Mar-13	01-Jun-15	Coral reef		1	4	0.00
4	–21.915	113.956	01-Mar-14	19-Oct-14	Sandflat		1	0	0.00
5	–21.912	113.952	19-Mar-13	01-Jun-15	Rocky reef		1	1	0.00
6	–21.916	113.959	19-Mar-13	01-Jun-15	Sandflat		1	4	0.00
7	–21.918	113.963	19-Mar-13	01-Jun-15	Rocky reef		1	4	0.00
8	–21.920	113.967	19-Mar-13	01-Jun-15	Rocky reef		1	12	0.00
Mangrove bay									
9	–21.948	113.921	19-Mar-13	01-Jun-15	Coral reef	SZ	2	20	0.00
10	–21.949	113.926	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	0	0.00
11	–21.948	113.933	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	0	0.00
12	–21.948	113.939	19-Mar-13	01-Jun-15	Coral reef	SZ	2	0	0.00
13	–21.950	113.944	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	65	0.01
14	–21.957	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	970	0.19
15	–21.959	113.944	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	1845	0.36
16	–21.960	113.940	25-Mar-13	01-Jun-15	Algal reef	SZ	2	764	0.15
17	–21.961	113.943	25-Mar-13	31-May–15	Rocky reef	SZ	2	2322	0.46
18	–21.962	113.945	26-Mar-13	31-May–15	Rocky reef	SZ	2	4615	0.91
19	–21.962	113.934	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	231	0.05
20	–21.963	113.940	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	6707	1.33
21	–21.963	113.942	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	30593	6.05
22	–21.964	113.939	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	2018	0.40
23	–21.965	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	4006	0.79
24	–21.966	113.939	08-Dec-14	31-May–15	Rocky reef	SZ	2	112	0.02
25	–21.967	113.941	19-Mar-13	31-May–15	Rocky reef	SZ	2	5673	1.12
26	–21.967	113.936	19-Mar-13	01-Jun-15	Algal reef	SZ	2	2729	0.54

Receiver	Longitude	Latitude	Deployment		Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
			Start	End					
27	–21.968	113.939	19-Mar-13	01-Jun-15	Sandflat	SZ	2	4407	0.87
28	–21.969	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	39054	7.72
29	–21.969	113.938	19-Mar-13	31-May–15	Sandflat	SZ	2	135477	26.79
30	–21.974	113.941	19-Mar-13	31-May–15	Sandflat	SZ	2	75768	14.98
31	–21.969	113.925	19-Mar-13	01-Jun-15	Coral reef	SZ	2	1582	0.31
32	–21.969	113.930	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	156	0.03
33	–21.972	113.919	19-Mar-13	01-Jun-15	Coral reef	SZ	2	92	0.02
34	–21.970	113.936	19-Mar-13	01-Jun-15	Sandflat	SZ	2	161182	31.87
35	–21.972	113.939	26-Mar-13	31-May–15	Mangrove	SZ	2	18401	3.64
36	–21.948	113.914	19-Mar-13	01-Jun-15	Coral reef		3	1	0.00
37	–21.956	113.913	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
38	–21.959	113.912	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
39	–21.966	113.910	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
40	–21.971	113.911	19-Mar-13	01-Jun-15	Coral reef		3	2	0.00
41	–21.972	113.902	19-Mar-13	24-May–13	Rocky reef		3	0	0.00
42	–21.973	113.911	19-Mar-13	01-Jun-15	Coral reef		3	1	0.00
43	–21.976	113.907	08-Mar-14	24-Oct-14	Rocky reef		3	0	0.00
44	–21.979	113.912	19-Mar-13	01-Jun-15	Coral reef		3	5	0.00
45	–21.980	113.902	08-Mar-14	01-Jun-15	Rocky reef		3	1	0.00
46	–21.984	113.904	08-Mar-14	24-Oct-14	Rocky reef		3	0	0.00
47	–21.983	113.908	08-Mar-14	01-Jun-15	Coral reef		3	0	0.00
48	–21.983	113.912	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
49	–21.989	113.902	19-Mar-13	02-Mar-14	Rocky reef		3	26	0.01
50	–21.989	113.909	19-Mar-13	22-Oct-14	Coral reef		3	1	0.00
51	–21.991	113.898	19-Mar-13	19-Oct-14	Rocky reef		3	6	0.00
52	–21.992	113.907	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
53	–21.998	113.905	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
54	–22.001	113.903	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
55	–22.005	113.902	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00

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Receiver	Longitude	Latitude	Deployment Start	 End	Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
56	–22.013	113.899	19-Mar-13	26-Oct-14	Coral reef		3	0	0.00
57	–21.975	113.924	19-Mar-13	01-Jun-15	Coral reef		4	763	0.15
58	–21.974	113.930	19-Mar-13	01-Jun-15	Algal reef		4	3144	0.62
59	–21.977	113.919	19-Mar-13	01-Jun-15	Coral reef		4	23	0.00
60	–21.980	113.921	19-Mar-13	01-Jun-15	Coral reef		4	13	0.00
61	–21.980	113.929	19-Mar-13	01-Jun-15	Sandflat		4	2119	0.42
62	–21.985	113.932	19-Mar-13	01-Jun-15	Coral reef		4	509	0.10
63	–21.986	113.919	19-Mar-13	01-Jun-15	Coral reef		4	1	0.00
64	–21.987	113.925	19-Mar-13	01-Jun-15	Coral reef		4	12	0.00
65	–21.988	113.923	02-Mar-14	01-Jun-15	Coral reef		4	0	0.00
66	–21.989	113.920	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
67	–21.989	113.915	19-Mar-13	01-Jun-15	Coral reef		4	2	0.00
68	–21.991	113.922	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
69	–21.991	113.931	19-Mar-13	01-Jun-15	Algal reef		4	183	0.04
70	–21.992	113.920	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
71	–21.994	113.925	19-Mar-13	01-Jun-15	Algal reef		4	13	0.00
72	–21.997	113.931	19-Mar-13	01-Jun-15	Rocky reef		4	45	0.01
73	–21.997	113.915	19-Mar-13	01-Jun-15	Coral reef		4	15	0.00
74	–21.999	113.921	19-Mar-13	01-Jun-15	Coral reef		4	6	0.00
75	–22.001	113.926	19-Mar-13	01-Jun-15	Coral reef		4	5	0.00
76	–22.005	113.912	19-Mar-13	01-Jun-15	Coral reef		4	4	0.00
77	–22.006	113.916	19-Mar-13	01-Jun-15	Rocky reef		4	12	0.00
78	–22.006	113.921	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
Turquoise bay									
79	–22.085	113.871	19-Mar-13	01-Jun-15	Rocky reef		6	0	0.00
80	–22.086	113.874	19-Mar-13	01-Jun-15	Rocky reef		6	0	0.00
81	–22.088	113.877	19-Mar-13	01-Jun-15	Coral reef		6	0	0.00
82	–22.089	113.880	19-Mar-13	01-Jun-15	Coral reef	SZ	5	0	0.00
83	–22.091	113.883	19-Mar-13	01-Jun-15	Coral reef	SZ	5	0	0.00

Receiver	Longitude	Latitude	Deployment		Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
			Start	End					
84	–22.093	113.886	19-Mar-13	01-Jun-15	Coral reef	SZ	5	4	0.00
85	–22.095	113.888	19-Mar-13	01-Jun-15	Coral reef	SZ	5	3	0.00

Table S2. Summary of the effects of environmental variables on detection probabilities recorded on acoustic receivers placed 1 m (receiver #30) and 153 m (receiver #28) from a sentinel transmitter used to monitor detection efficiency in Mangrove bay

Month was treated as a random effect in all models (m1, model 1; etc.); details for each model include the estimated degrees of freedom (d.f.$_e$), the Akaike's Information Criterion for small sample size (AIC$_C$), relative AICC weight (wAIC$_C$) and goodness of fit (Adjusted R^2). PressAV, mean air pressure; RainAV, mean cumulative rainfall; TempAV, mean water temperature; TempR, water temperature range; TideAV, mean tidal height; TideR, tidal height range; WdireAV, mean wind direction; WspeedAV, mean wind speed; WspeedR, wind speed range

Model number	Model	Receiver #30				Receiver #28			
		d.f.$_e$	AIC$_C$	wAIC$_C$	Adjusted R^2	d.f.$_e$	AIC$_C$	wAIC$_C$	Adjusted R^2
m1	1	0.00	5244.06	0	0	0	3938.69	0	0
m2	days.detected	9.87	4768.45	0	2.6	9.22	3853.48	0	21.4
m3	pressAV	2.76	5065.04	0	7.8	2.83	3892.54	0	5.1
m4	rainAV	1.90	5209.43	0	0.6	2.19	3852.26	0	0
m5	tempAV	2.89	5026.28	0	12.4	2.45	3931.24	0	1.8
m6	tempR	2.91	5189.72	0	0.4	0.43	3940.56	0	0.1
m7	tideAV	2.92	4185.76	0	27.6	2.96	3724.17	1	5.4
m8	tideR	2.92	3860.27	1	31.8	2.7	3770.69	0	2.4
m9	wdireAV	1.95	5186.17	0	0.8	1.74	3934.78	0	5.4
m10	wspeedAV	2.66	5238.57	0	0.4	2.9	3809.00	0	8.6
m11	wspeedR	2.31	5206.21	0	0.7	2.84	3925.91	0	0

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Table S3. Summary of the effects of varying sig2 values on estimates of 50 and 95% kernel areas of one *N. acutidens* individual

Monthly tracks of the shark #L1, which had the median value for 50% kernel area, were used to estimate kernel area range

Sig2 value	Detection probability	Kernel area (KA) range	
		50% KA (km^2)	95% KA (km^2)
285.2	0.20	0.24–0.51	0.96–1.84
263.2	0.25	0.22–0.49	0.9–1.75
252.3	0.30	0.21–0.47	0.84–1.67
229.8	0.40	0.18–0.44	0.73–1.51
175.0	0.50	0.12–0.36	0.51–1.56
129.6	0.60	0.08–0.34	0.36–2.77
106.7	0.70	0.07–0.34	0.34–3.85
97.0	0.75	0.07–0.34	0.34–4.33
87.5	0.80	0.06–0.34	0.33–4.8

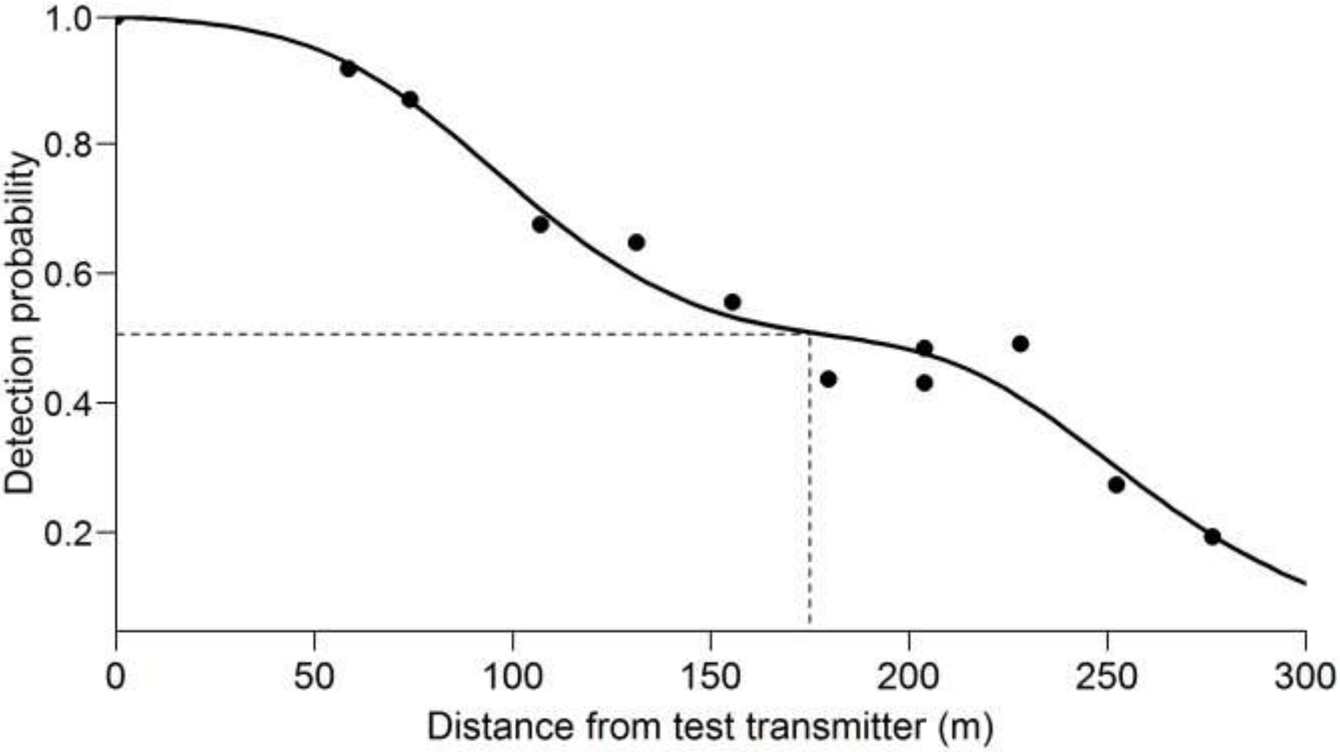

Fig. S1. Detection probabilities recorded on acoustic receivers placed at increasing distances from a test transmitter at Mangrove Bay in March 2013. Data were fitted using a loess smoothing curve and dashed lines represent the effective detection range at which 50% of the transmissions were detected (D_{50} = 175.0 m).

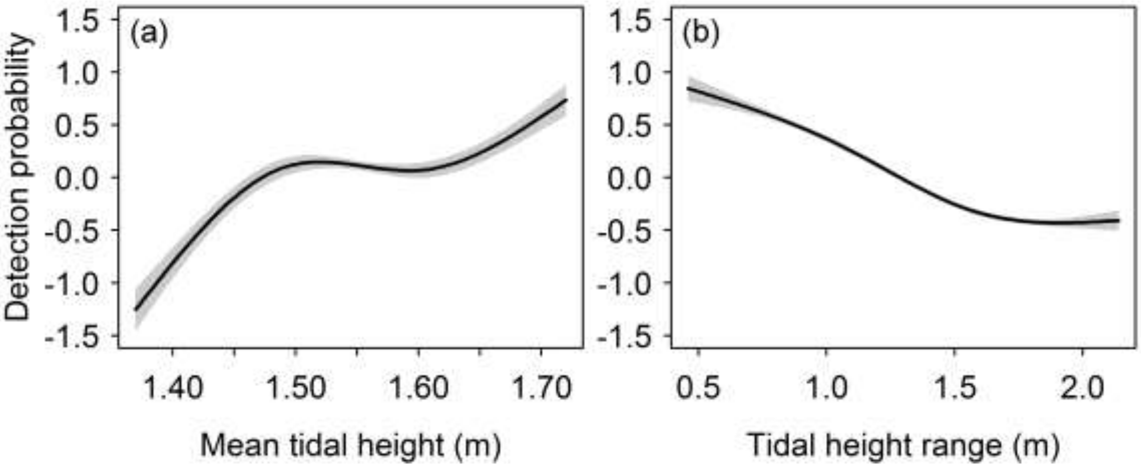

Fig. S2. Summary of the effects of explanatory variables on detection probabilities recorded on acoustic receivers located (*a*) 1 m and (*b*) 153 m from a sentinel tag placed within an area with highest shark activity. Dashed lines and error bars represent 95% confidence intervals.