Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2015) **87**, 323–341
doi:10.1111/jfb.12724, available online at wileyonlinelibrary.com

Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters

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(Received 1 December 2014, Accepted 10 May 2015)

This study used a network of acoustic receivers deployed around a no-take zone in Mangrove Bay, within the Ningaloo Reef Marine Park in Western Australia, to study residency and habitat preference of a small coastal shark, the nervous shark *Carcharhinus cautus*. Twelve *C. cautus* were tagged with acoustic tags and monitored for up to 579 days. Based on individuals detected within the receiver array for at least 2 months, *C. cautus* had small core (50% kernel utilization distribution, KUD) and home ranges (95% KUD) of 0·66 and 3·64 km^2, respectively, and showed a strong habitat preference for mangroves, which are only found in the no-take zone. This resulted in *C. cautus* spending most of their detected time within the no-take zone boundaries (mean = 81·5%), showing that such a protected area could be beneficial to protect this species from extensive fishing pressure and local depletion, where required. Not all *C. cautus* remained within the acoustic array, however, suggesting that individual variations occur and that not all individuals would benefit from such protection. This study provides important information about the habitat, residency and movements of *C. cautus* that can be used for management and conservation. The strong affinity and residency of *C. cautus* within a mangrove-fringing coastline, emphasizes the importance of mangrove habitat to the species and suggests that such preferences can be used to design appropriate no-take zones for this species or others with similar habitat preferences.

Key words: AATAMS; acoustic telemetry; habitat; marine protected area; residency.

INTRODUCTION

Coastal habitats such as bays, lagoons and estuaries are highly productive environments that support high abundances and diversities of fishes (Blaber *et al.*, 1989).

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Many sharks use these habitats for mating, foraging, as a nursery or a refuge against predators (Blaber *et al.*, 1985; Knip *et al.*, 2010; Speed *et al.*, 2010). Because human settlements tend to be clustered around the shorelines of these environments, sharks within these habitats may be susceptible to both direct (*e.g.* fishing) and indirect (*e.g.* habitat destruction and pollution) anthropogenic pressures (Field *et al.*, 2009).

Marine protected areas (MPA) are seen as a potentially useful tool to mitigate these threats (Speed *et al.*, 2010), although the effectiveness of MPAs, and particularly no-take zones, relies on the overlap between the spatial distribution of the target population and the location of the no-take zone, in addition to the focal species spending a large portion of their lives within boundaries of the no-take zone (Kramer & Chapman, 1999). As such zones are often small in size (median = $4 \cdot 6$ km^2; Wood *et al.*, 2008), they are generally thought to be most useful for the protection of sedentary species or specific habitat types. Because many sharks are very mobile and have wide home ranges (many km^2) and can undertake long (10–1000 s of km) migrations, the benefits of no-take zones for these predators are less obvious (Russ & Alcala, 2004; Chapman *et al.*, 2005), although there is some evidence that they can provide at least a partial refuge from fishing pressure (Garla *et al.*, 2006; Bond *et al.*, 2012; Knip *et al.*, 2012*a*).

Despite a lack of conclusive evidence for effect, the establishment of shark sanctuaries has recently become popular, particularly around islands and in developing nations in the Pacific. This has led to debates over the rationale for the use of MPAs in this context and implied that such sanctuaries may only be ‘paper parks’ (Davidson, 2012; Chapman *et al.*, 2013). Given the increasing threats to coastal ecosystems (Jackson *et al.*, 2001) and shark populations worldwide (Worm *et al.*, 2013; Dulvy *et al.*, 2014), more information is now required on the ability of no-take zones to contribute towards the conservation and management of sharks in coastal environments.

Here, this issue is addressed for the nervous shark *Carcharhinus cautus* (Whitley 1945). The species provides a good model, as it is a medium-bodied whaler shark (family Carcharhinidae) that attains 150 cm total length (L_T) and spends most of its life cycle in shallow inshore waters, particularly in areas adjacent to mangroves (Lyle, 1987; White & Potter, 2004). The conservation status of *C. cautus* is currently listed as data deficient by the International Union for the Conservation of Nature (IUCN) Red List (www.iucnredlist.org; Bennett & Kyne, 2003) and little is known about their residency and movement patterns. Acoustic telemetry was used to record habitat use and residency patterns of *C. cautus* in a fringing coral reef and mangrove system that included a small no-take zone at Mangrove Bay Sanctuary in Ningaloo Marine Park, Western Australia. The principal aims of this study were to assess the importance of mangrove habitat to the species, to determine patterns of residency and to examine the overlap of *C. cautus* home ranges with the spatial coverage of the no-take zone.

MATERIALS AND METHODS

STUDY SITE

This study focused on Mangrove Bay (21° 58′ 14″ S; 113° 56′ 34″ E), Ningaloo Reef, between February 2008 and May 2010 (Fig. 1). This bay is a small, mangrove-lined tidal inlet (112 ha) and the only significant area of mangrove forest within the Ningaloo Reef Marine Park established in 2005 (Department of Conservation and Land Management, 2005). It contains a no-take area, the Mangrove Bay Sanctuary Zone (*c.* $11 \cdot 35$ km^2; Department of Conservation and Land

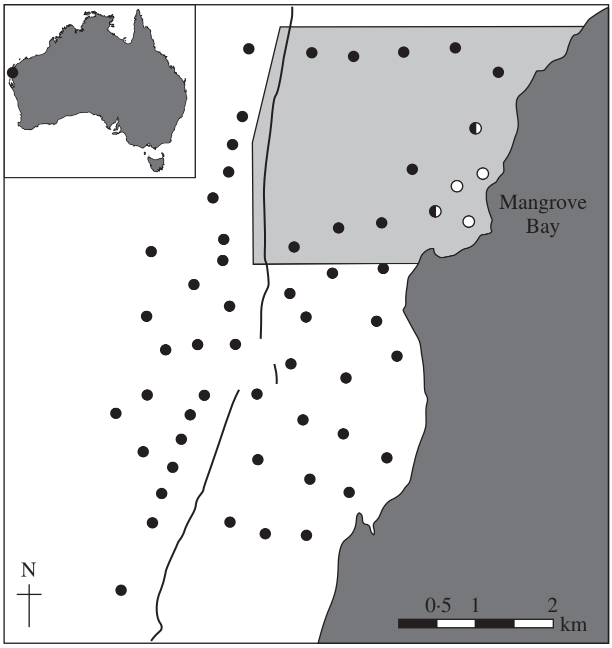

Fig. 1. Map of Mangrove Bay, Ningaloo Reef showing the location of the sanctuary zone (■) and acoustic receivers. The colour of the receiver symbols represents habitat type: (●) receivers located in reef slope, reef pass (— shows the reef crest) and lagoon, (○) receivers located in mangrove and (◐) receivers in mixed lagoon–mangrove habitat. Inset shows location of Ningaloo Reef relative to Australia.

Management, 2005) that was primarily established to protect mangroves and the ecosystem they support. The Mangrove Bay Sanctuary Zone is situated within the shallow (3–10 m) lagoon running *c*. 10 km inside and parallel to the reef crest of Ningaloo Reef. It is part of the multiple-use Ningaloo Marine Park in which commercial fishing is prohibited. While various kinds of recreational fishing are permitted and inshore shark species are sometimes caught (Smallwood & Beckley, 2012), *C. cautus* are not known to be targeted by recreational fishers.

ACOUSTIC TELEMETRY: RECEIVERS AND TAGGING

Fifty-seven passive acoustic receivers (VR2W and VR3, Vemco; www.vemco.com) were deployed in February 2008 (Fig. 1), providing an array *c*. 28 km^2 in extent (including 14 receivers deployed within the Mangrove Bay Sanctuary Zone) (Pillans *et al.*, 2014). The acoustic array was designed to monitor tagged animals in Mangrove Bay and to detect animals leaving or entering the no-take zone and the marine park. Distances between consecutive receivers ranged from 200 to 1000 m, with a mean of *c*. 500 m. The study area encompassed the no-take sanctuary zone as well as surrounding recreation zones, and included lagoon, reef pass and reef slope habitats. Range testing of receivers showed that the mean maximum detection range of receivers was 300 m (Pillans *et al.*, 2014). All receivers formed part of the Ningaloo Reef Ecosystem Tracking Array (NRETA) established as part of the Australian Animal Tracking and Monitoring System Facility (AATAMS; www.imos.org.au), and were also used to monitor other elasmobranchs and teleosts (Pillans *et al.*, 2011, 2014; Cerutti-Pereyra *et al.*, 2014).

Eleven of the 12 *C. cautus* tagged were caught in February 2008, with the last *C. cautus* tagged in November 2009. All but one were captured inside the no-take zone using handline or gillnet (#8250 was caught 800m south of the no-take zone boundary; detected 8 days and showing a similar pattern of residency as the other *C. cautus* captured inside the no-take zone). After capture, *C. cautus* were inverted to induce a state of tonic immobility and tagged internally with V13-1H acoustic transmitters (Vemco). Transmitters were surgically implanted into the peritoneal cavity following the methods of Heupel *et al.* (2006*a*). The interval between signal transmissions for these tags was 120–240 s, resulting in an expected battery life of 520 days. L_T over the curvature of the body (Francis, 2006) was then measured to the nearest mm and sex was determined by the presence or absence of claspers. Life-history stage (juvenile or adult) was determined using L_T and previously calculated size-at-maturity data (White *et al.*, 2002). All individuals were released within 10 min of capture.

DATA ANALYSIS

False detections were removed from data sets prior to analysis. These were defined as single detections recorded within a 24 h period, or when two detections obtained by different receivers were too close in time for an individual to be able to travel the distance separating the receivers (Pincock, 2012).

Receivers were assigned to five habitat categories: lagoon (28 receivers), reef slope (23), mangroves (three), reef pass (one) and mixed lagoon and mangrove, where receivers were located between these two habitats (two). Habitat preference was determined for each *C. cautus* by calculating electivity using Chesson's index (Lechowicz, 1982): $\alpha = [(r_i p_i{}^{-1})][\sum(r_i p_i{}^{-1})]^{-1}$, where r_i was the proportion of time spent in habitat i obtained by estimating the proportion of detections in habitat i, and p_i the proportion of habitat i available in the study site or the proportion of the receivers in each habitat. The electivity index varied from 0 to 1, with a value of 0 indicating avoidance and a value of 1 indicting affinity.

To limit biases in estimations of residency, site fidelity was quantified using two residency indices (I_R). The overall residency index (I_{Ro}) was calculated by dividing the number of days an individual was present by the monitoring period, which assumed that *C. cautus* not detected within the array had left the area. The monitoring period was considered to be 520 days based on the estimated life of tag batteries. Although two *C. cautus* were detected for a greater period of time (up to 579 days), detections beyond 520 days were excluded from the analysis. The detected residency index (I_{Rd}) accounted for uncertainty in the fate of *C. cautus* after last detections. It was calculated by dividing the number of days an individual was present by the period during which this *C. cautus* was detected (*i.e.* period between first and last detection). As false detections were already accounted for, an individual was considered present within the array if it was detected within a 24 h period. An I_{Rd} value of 0 indicated no residency and a value of 1 permanent residency (Bryars *et al.*, 2012; La Mesa *et al.*, 2012). Correlation between L_T and I_{Rd} was examined using a Spearman or Pearson correlation test, depending on whether the data were normally distributed as determined by a Shapiro test.

For each *C. cautus*, the extent of movement was assessed using two parameters averaged across days detected: (1) the mean distance from tagging location and (2) the mean number of receivers detecting transmissions. Distances from tagging location were assessed by calculating the distance between each receiver and tagging location using Google Earth.

The absolute or relative number of detections could not be used to compare the amount of time spent inside and outside the Mangrove Bay Sanctuary Zone due to differing number of receivers deployed in each area and the overlapping detection ranges in some parts of the study site (largely within Mangrove Bay itself). Therefore, a centre-of-activity (COA) algorithm (using weighted means) was used to account for any multiple detections of the same *C. cautus* and estimate the time each *C. cautus* spent inside and outside of the no-take zone. COAs are the average positions of *C. cautus* based on multiple detections by different receivers calculated every 30 min (Simpfendorfer *et al.*, 2002), which has been shown to give successful resolution of reef-shark movements (Speed *et al.*, 2011). For each *C. cautus*, the number of COA estimates inside and outside the sanctuary zone was calculated. The number of COA in each zone was then standardized by the area monitored by the receivers to account for the larger number of receivers deployed outside the sanctuary zone, which was divided by the total number of COAs standardized and expressed as a percentage, providing the percentage of detections within and outside of the no-take zone. The area monitored was estimated using a circle of detection range around a receiver (radius of 300 m) and the number of receivers deployed in each zone.

Home ranges were calculated using 50 and 95% kernel utilization distributions (KUDs) and minimum convex polygon (MCP) from COAs with the package *adehabitatHR* in R (Calenge, 2006). MCP is the area formed when connecting the outermost COAs of an animal (after the removal of 5% of extreme points using the mcp function that automatically excludes outliers); while KUD represents the area with 50 or 95% probability of finding an individual. Home ranges were only calculated for *C. cautus* detected for >2 months, which was deemed to provide sufficient temporal resolution to estimate home ranges. The correlation between home range size (KUD 50%) and L_T was tested using the Spearman or Pearson correlation test, depending on whether the data were normally distributed as determined by a Shapiro test.

All analyses were conducted using R 2.15.2 (R Development Core Team; www.r-project.org). Values provided in the results are mean ± S.E.

RESULTS

TAGGED *C. CAUTUS*, HABITAT SELECTIVITY AND RESIDENCY

Twelve *C. cautus* with L_T ranging from 770 to 1170 mm were tagged and monitored in Mangrove Bay between February 2008 and May 2010. Based on published size-at-maturity data (White *et al.*, 2002), five individuals were juveniles (four females and one male) and seven were adults (six females and one male). The last detection of the 11 *C. cautus* tagged in February 2008 was in September 2009, 579 days after tagging. The lack of detections after this date was probably due to failure of transmitter batteries. From November 2009, the only detections in the array were from the last *C. cautus* tagged in that month (Fig. 2 and Table I). The number of days between the first and last detection ranged from 4 to 579 days, with five individuals detected <20 days, six detected for > 5 months and one *C. cautus* detected for slightly > 2 months (Fig. 2 and Table I).

The electivity index of *C. cautus* detected for >2 months showed a high affinity of *C. cautus* to mangroves (0·64 ± 0·12), but avoidance of the reef slope (0), reef pass (0) and lagoon habitats (0·05 ± 0·02) (Table I). A low electivity index was also found for mixed lagoon and mangrove habitats (0·30 ± 0·10). Most individuals were associated

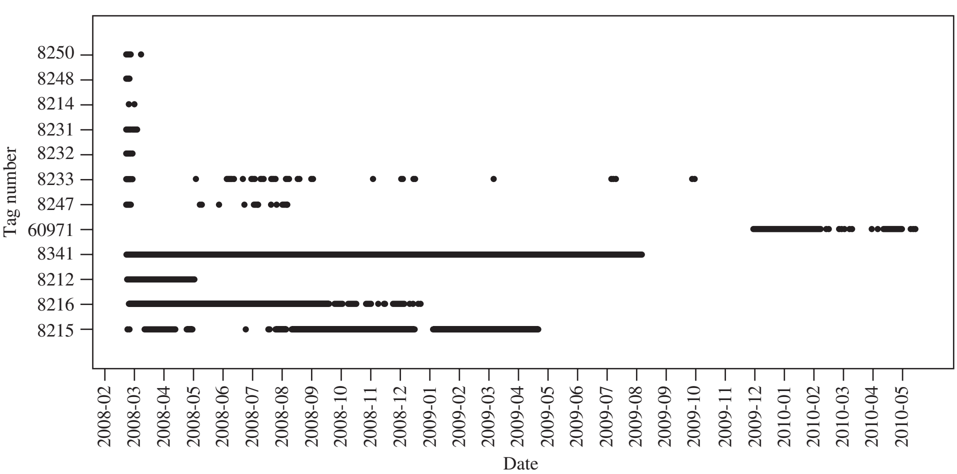

FIG. 2. Daily presence of tagged *Carcharhinus cautus* in mangrove from February 2008 to May 2010.

Table I. Summary of *Carcharhinus cautus* tagged in Mangrove Bay

Tag number	L_T (mm)	Sex	Class	Tagging date	Number of days detected	Number of days monitored	Overall I_{Ro}	Detected I_{Rd}	Number of detections	Distance*(m)	Number of receivers per day	α lagoon	α mangrove	α mixed habitat
8341‡	77·0	F	J	23 February 2008	500	524	0·96	0·95	12 115	353·83	2·63	0·03	0·65	0·32
8247‡	74·9	F	J	23 February 2008	19	165	0·04	0·12	456	217·95	1·75	0·07	0·63	0·30
8248	74·0	M	J	24 February 2008	4	4	0·02	1·00	109	769·48	2·75	0·01	0·92	0·06
8250	79·8	F	J	24 February 2008	8	17	0·02	0·47	87	1936·12	1·88	0·02	0·83	0·15
8232	109·9	F	A	24 February 2008	7	7	0·01	1·00	226	335·94	2·71	0·01	0·63	0·36
8233‡	107·9	F	A	25 February 2008	37	579	0·07	0·06	835	707·94	2·14	0·17	0·04	0·79
8231	114·3	F	A	25 February 2008	11	12	0·02	0·92	122	117·58	1·73	0·00	0·64	0·36
8215‡	117·0	F	A	26 February 2008	253	420	0·49	0·60	19 566	964·90	4·52	0·03	0·97	0·00
8212‡	110·0	F	A	26 February 2008	67	69	0·13	0·97	6384	865·28	3·55	0·02	0·45	0·52
8216‡	104·5	F	A	27 February 2008	220	300	0·42	0·73	14 947	1228·63	4·05	0·03	0·83	0·14
8214	90·5	F	J	27 February 2008	2	10	0·004	0·20	13	871·28	6·50	0·00	1·00	0·00
60971‡	96·0	M	A	23 November 2009	92	173	0·178	0·53	917	675·24	2·31	0·00	0·94	0·06

L_T, total Length; F, female; M, male; J, juvenile; A, adult; I_R, residency index.
*Mean distance from tagging location averaged across day detected.
αChesson's index. Corresponds to electivity for the three habitats where *C. cautus* was detected.
‡Individuals detected for >2 months.

with mangroves with nine *C. cautus* having an electivity index for this habitat above 0·63 (range: 0·63–1·00; Table I). All *C. cautus* showed some avoidance of the lagoon, with electivity indices ranging from 0 to 0·17. Two *C. cautus* had low affinity or avoidance of mangroves (#8212 $\alpha = 0{\cdot}45$ and #8233 $\alpha = 0{\cdot}04$), but were associated with mixed mangrove and lagoon habitats (0·79 and 0·52, respectively). It appears unlikely that these associations were an artefact of differences in detection probability among habitats, since detection probabilities in shallow habitats such as mangroves are typically lower than those in deeper lagoon, reef pass and reef slope habitats (Cagua *et al.*, 2013).

The I_{Ro} was $0{\cdot}20 \pm 0{\cdot}08$ (range: 0·00–0·95), while the I_{Rd} was higher $0{\cdot}63 \pm 0{\cdot}10$ (range: 0·06–1·00) (Table I). For individual *C. cautus*, three patterns of residency could be distinguished (Fig. 2). Five *C. cautus* (8215, 8212, 8216, 8341 and 60971) were detected regularly throughout the period of monitoring, with I_{Rd} ranging from 0·53 to 0·97. Five other *C. cautus* (8250, 8248, 8214, 8231 and 8232) were only detected for a few days after tagging, with the maximum number of days monitored being 17. The remaining *C. cautus* (8233 and 8247) were recorded for long periods (579 and 165 days, respectively), but only infrequently during this time (I_{Rd} of 0·06 and 0·12). There was no correlation between I_{Rd} and the L_T of *C. cautus* (Pearson correlation test: $r = 0{\cdot}04$, $P > 0{\cdot}05$).

EXTENT OF MOVEMENT, TIME SPENT IN THE SANCTUARY ZONE AND HOME RANGE

Detections from all *C. cautus* were close to the tagging location ($753{\cdot}7 \pm 143{\cdot}8$ m), with the highest daily mean distance from tag detected location being *c.* 1940 m. The extent of movements between detections was small, with *C. cautus* being detected on $3{\cdot}0 \pm 0{\cdot}4$ receivers per day (Table I).

The number of COA estimates for individuals detected inside and outside the no-take zone ranged from 3 to 3622 and 0 to 1058, respectively (Table II). When *C. cautus* were detected within the acoustic array, it was mostly within the no-take zone (range: 82–100%, $94{\cdot}2 \pm 1{\cdot}8$%).

The size of home ranges of tagged *C. cautus* detected in Mangrove Bay ranged from 0·18 to 1·40 km^2 for the core (KUD 50%) ($0{\cdot}66 \pm 0{\cdot}17$ km^2) and from 0·72 to 7·19 km^2 for the maximum extent (KUD 95%) ($3{\cdot}64 \pm 0{\cdot}85$ km^2) (Table II). MCPs ranged from 0·36 to 5·56 ($1{\cdot}66 \pm 1{\cdot}44$ km^2). The core ranges of all *C. cautus* were all within the Mangrove Bay Sanctuary (Fig. 3). All home ranges were smaller than the dimension of the receiver array (16·1 km^2) and the overall studied area (*c.* 28 km^2). Size of the home range was not significantly correlated with L_T of the *C. cautus* (Pearson correlation test: $r = 0{\cdot}37$, $P > 0{\cdot}05$).

DISCUSSION

Residency of early life-history stages within mangrove or near-shore environments is typical of many shark species. Occupancy of these habitats is thought to increase survival as they may provide a refuge from predation and increased prey availability for juveniles (Branstetter, 1990; Heupel & Simpfendorfer, 2005). In this study, both large juveniles and adult *C. cautus* had a preference for mangrove habitats, suggesting that

TABLE II. Number of centre-of-activity (COA) detected inside and outside the sanctuary zone and home range size of *Carcharhinus cautus* in Mangrove Bay

Tag number	COA in	COA out	Total COA	% In*	% Out*	MCP (km^2)	KUD 50%	KUD 95%
8341‡	3622	1058	4680	91·2	8·8	2·20	0·24	1·97
8247‡	131	0	131	100·0	0·0	0·36	0·18	0·72
8248	34	0	34	100·0	0·0			
8250	18	11	29	83·2	16·8			
8232	68	1	69	99·5	0·5			
8233‡	186	20	206	96·6	3·4	5·22	1·40	7·19
8231	74	0	74	100·0	0·0			
8215‡	3259	365	3624	96·4	3·6	5·56	0·69	3·49
8212‡	1123	34	1157	99·0	1·0	0·95	0·39	2·02
8216‡	2028	940	2968	86·7	13·3	3·06	1·11	4·68
8214	3	2	5	81·9	18·1			
60971‡	366	51	417	95·6	4·4	5·70	0·63	5·39
Total	10 912	2482	13 394	94·2	5·8	1·66	0·66	3·64

MCP, minimum convex polygon; KUD, kernel utilization distribution (50 and 95%).
*Standardized percentages of COA inside and outside the sanctuary zone.
‡*Carcharhinus cautus* detected for >2 months.

these environments can also play an important role in the adult lives of some species (Knip *et al.*, 2012*b*). Although there was some individual variation, over 75% of the tagged *C. cautus* showed a strong affinity for mangroves while within the study area and avoided lagoon, reef slope and reef-pass habitats, a preference consistent with earlier studies (White & Potter, 2004). Two *C. cautus* that were exceptions to this pattern had a preference for mixed habitat that encompassed both mangroves and the lagoon and one of these (8233) had the largest home range and a relatively low residency index.

Residency of *C. cautus* was variable among individuals, with some *C. cautus* displaying high residency within Mangrove Bay (high I_{Rd} and I_{Ro}), similar to many other reef-associated species such as Caribbean reef *Carcharhinus perezi* (Poey 1876) (Bond *et al.*, 2012), spottail *Carcharhinus sorrah* (Müller & Henle 1839) (Knip *et al.*, 2012*c*) and blacktip reef *Carcharhinus melanopterus* (Quoy & Gaimard 1824) (Papastamatiou *et al.*, 2009) sharks (see Table III). Other *C. cautus* had consistently low I_{Rd} and I_{Ro} and were not considered resident within the study site. In addition, some *C. cautus* had a high I_{Rd} but low I_{Ro}, thus were detected frequently, but only for a short period of time immediately after tagging. The fate of these *C. cautus* is unknown and might include death due to post-release stress following handling and tagging (Garla *et al.*, 2006; Heupel *et al.*, 2006*b*), capture by recreational fishers (Garla *et al.*, 2006; Knip *et al.*, 2011*a*) or emigration (Carlson *et al.*, 2008; Heupel *et al.*, 2010*b*; Knip *et al.*, 2012*b*).

Some degree of residency within a study area appears typical of most shark species. In previous studies, up to 80% of 49 populations of 32 different species have shown some residency within the study site (Table III). Conversely, variability in residency within species is common in other carcharhinids, both among reef habitats [*e.g.* grey reef shark *Carcharhinus amblyrhynchos* (Bleeker 1856), Heupel *et al.*, 2010*a*; *C. sorrah*, Knip *et al.*, 2012*b*], and within the Ningaloo Marine Park [*C. melanopterus*,

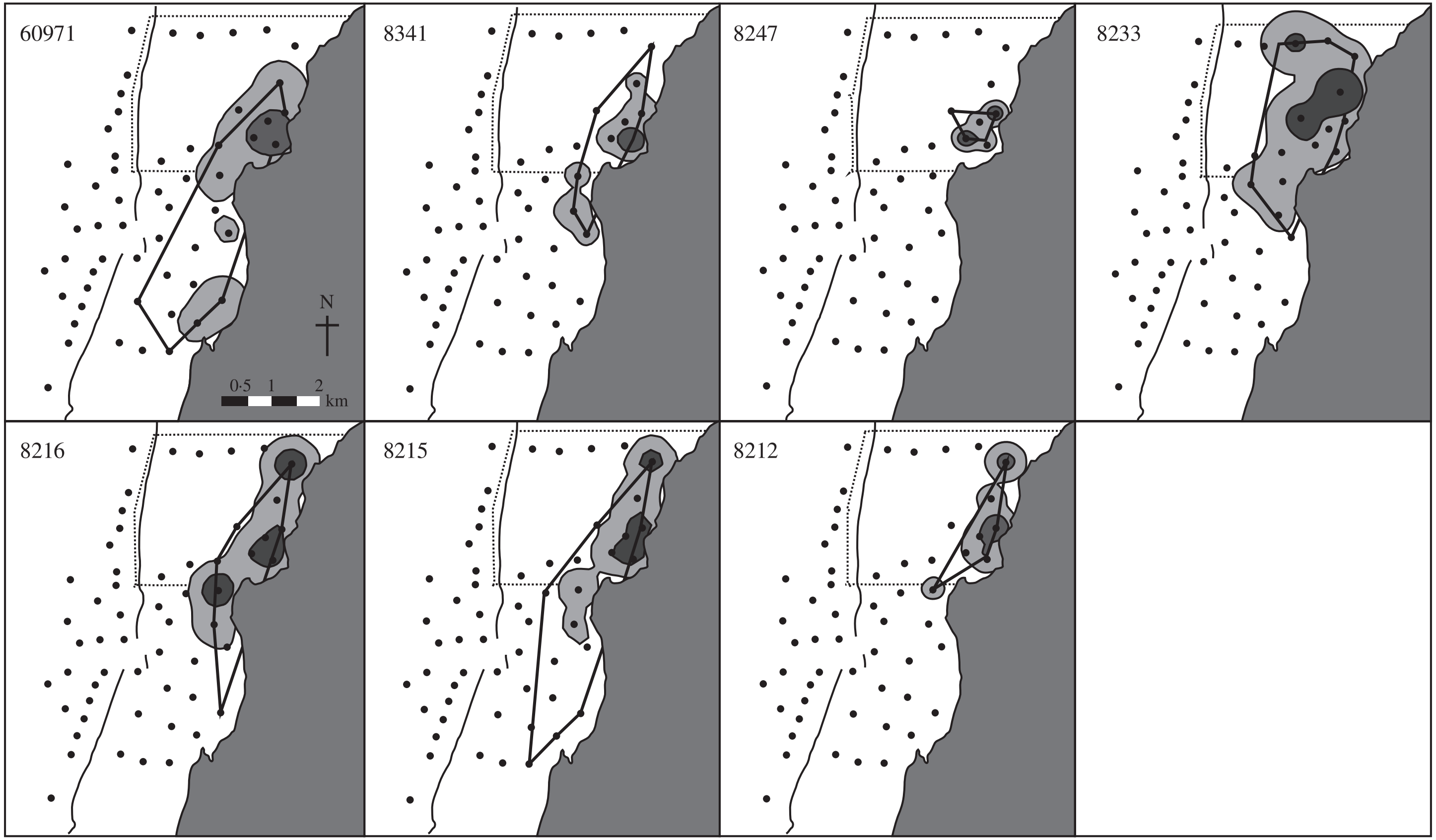

Fig. 3. Maps of *Carcharhinus cautus* home range in Mangrove Bay for individuals present for >2 months (60971, 8341, 8247, 8233, 8216, 8215 and 8212). Boundaries of the sanctuary zone (.......); acoustic receivers (●); KUD = kernel utilization distribution (■, KUD 50%; ■, KUD 95%); MCP = minimum convex polygon (—).

TABLE III. Summary of studies using acoustic telemetry to assess Level of residency is reported using the residency index, when calculated, or based on the conclusion of the authors

Species	Author	Sample size	Habitat	Class	Size (cm)	Residency index	Home range (km*)	Suitability of MPA
Carcharhinidae								
Carcharhinus albimarginatus	Barnett *et al.* (2012)	4	Coral reef, sand	A	157–230	High site fidelity		Yes†
Carcharhinus amboinensis	Knip *et al.* (2012*a*)	20	Mud, coral reef, mangrove	J		0·23* (MPA)		Yes; recommend onion-ring design
Carcharhinus amboinensis	Knip *et al.* (2011*b*)	32	Mud, coral reef, mangrove	J	63–100		Weekly KUD 95% = 29·05	
Carcharhinus amboinensis	Knip *et al.* (2011*a*)	43	Mud, coral reef, mangrove	J	63–129		Monthly KUD 50% = 7·66 Monthly KUD 95% = 37·8	
Carcharhinus amblyrhynchos	Heupel *et al.* (2010*b*)	10	Coral Reef	J	~90	High site fidelity, but also range widely		Yes for juveniles
				A	95–167			
Carcharhinus amblyrhynchos	Speed *et al.* [in press]	2	Lagoon, coral reef, mangrove	J	141–180	0. 12–0·33	MCP = 19·6	No
				A		0·90–0·96		
Carcharhinus amblyrhynchos	Speed *et al.* (2011)	11	Coral reef, sand	J + A	123–240	High site fidelity		
Carcharhinus amblyrhynchos	Field *et al.* (2011)	26	Coral reef	A	79–169	High site fidelity		No
Carcharhinus amblyrhynchos	Barnett *et al.* (2012)	18	Coral reef, sand	J + A	80–182	High site fidelity		Yes†
Carcharhinus cautus	This study	12	Lagoon, coral reef, mangrove	J + A	77–117	0·63	MCP = 1·66 KUD 50% = 0·66 KUD 95% = 3·64	Yes, but temporal variation
Carcharhinus leucas	Yeiser *et al.* (2008)	19	Estuary	J	91–180		Weekly MCP = 2–44 Weekly KUD 50% = 5·1 Weekly KUD 95% = 31·5	
Carcharhinus leucas	Heupel *et al.* (2010*b*)	67	Estuary	J		High site fidelity	Monthly HR = 0·9–5·6§	

Table III. Continued

Species	Author	Sample size	Habitat	Class	Size (cm)	Residency index	Home range (km*)	Suitability of MPA
Carcharhinus limbatus	Heupel *et al.* (2004)	33	Mangrove fringed bay	J		High site fidelity	Daily KUD 95% = 0·7–1·2	
Carcharhinus melanopterus	Speed *et al.* (2011)	36	Coral reef, sand	A	103–129	0·38–0·72		
Carcharhinus melanopterus	Speed *et al.* [in press]	7	Lagoon, coral reef, mangrove	J A	121–140	<0·01–0·99* (MPA)	MCP = 7·21 MCP = 12·8	No
Carcharhinus melanopterus	Papastamatiou *et al.* (2009)	14	Lagoon, coral reef	J + A	83–117	Site attachment	MCP = 0·26 KUD 95% = 0·55	
Carcharhinus perezi	Bond *et al.* (2012)	34	Lagoon, coral reef	J + A	66–197	0·43 (MPA) but long migration		Yes
Carcharhinus perezi	Chapman *et al.* (2005)	5	Lagoon, coral reef	J + A	117–215	0·70 (MPA)		Yes, recommend larger MPA
Carcharhinus perezi	Garla *et al.* (2006)	22	Coral reef	J + A	78–224	High site fidelity		Yes, for juvenile
Carcharhinus sorrah	Knip *et al.* (2012*a*)	20	Mud, coral reef, mangrove	A		0·32* (MPA)		Yes, recommend onion-ring design
Carcharhinus sorrah	Knip *et al.* (2012*b*)	20	Mud, coral reef, mangrove	A	95–127	0·64	Monthly KUD 50% = 9·08 Monthly KUD 95% = 39·8	
Carcharhinus sorrah	Knip *et al.* (2012*c*)	29	Mud, coral reef, mangrove	A	95–127	0·64		
Negaprion acutidens	Speed *et al.* (2011)	7	Coral reef, sand	J	1·03–1·21	0·67–0·99		
Negaprion acutidens	Speed *et al.* [in press]	3	Lagoon, coral reef, mangrove	J	121–160	>0·98* (MPA)	MCP = 0·61	No
Negaprion acutidens	Filmalter *et al.* (2013)	19	Lagoon, coral reef		139–202	High site fidelity, but individual variations		Yes†
Negaprion brevirostris	Edren & Gruber (2005)	33	Mangrove, coral reef	J	<150	High site fidelity	KUD 90% = 0·90	
Negaprion brevirostris	Yeiser *et al.* (2008)	5	Estuary	J	187–230		Weekly MCP = 2–56 Weekly KUD 50% = 5·6 Weekly KUD 95% = 31·3	

TABLE III. Continud

Species	Author	Sample size	Habitat	Class	Size (cm)	Residency index	Home range (km*)	Suitability of MPA
Rhizoprionodon terraenovae	Carlson *et al.* (2008)	56	Seagrass	J	40–59	Multiple residency; homing for some sharks	Daily KUD 50% = 0·88–1·64 Daily KUD 95% = 5·1–8·4	
Rhizoprionodon taylori	Munroe *et al.* (2014)	40	Seagrass, coral reef/sand	A	48–77	0·00–0·56	Monthly KUD 50% = 11·3 Monthly KUD 95% = 51·0	
Triaenodon obesus	Speed *et al.* (2011)	4	Coral reef, sand	A	86–181	High site fidelity		
Triaenodon obesus	Barnett *et al.* (2012)	18	Coral reef, sand	A	112–150	High site fidelity		Yes†
Dasyatidae								Yes
Pastinachus atrus	Cerutti-Pereyra *et al.* (2014)	6	Lagoon, coral reef, mangrove	J	46–84	High site fidelity, but seasonal variation		Yes
Urogymnus asperrimus	Cerutti-Pereyra *et al.* (2014)	4	Lagoon, coral reef, mangrove	J	54–75	High site fidelity, but seasonal variation		Yes
Himantura uarnak	Cerutti-Pereyra *et al.* (2014)	1	Lagoon, coral reef, mangrove	J	76	High site fidelity, but seasonal variation		
Echinorhinidae								
Echinorhinus cookei	Dawson & Starr (2009)	15	Marine canyon	SA	170–270	High site fidelity	KUD 50% = 0·11	
Ginglymostomatidae								
Ginglymostoma cirratum	Chapman *et al.* (2005)	25	Lagoon, coral reef	J + A	136–240	Partial site fidelity 0·70 (MPA)		Yes; recommend larger MPA
Hexanchidae								
Hexanchus griseus	Andrews *et al.* (2010)	39	Estuary	J	150–200	High site fidelity		
				A	>200			
Notorynchus cepedianus	Williams *et al.* (2012)	32	Estuary	J + A	100–250	High site fidelity		

TABLE III. Continud

Species	Author	Sample size	Habitat	Class	Size (cm)	Residency index	Home range (km*)	Suitability of MPA
Myliobatidae								
Rhinoptera bonasus	Collins *et al.* (2007)	21	Estuary	J A	<70 70–90		KUD 50 = 3·3 KUD 95 = 22·6	
Odontaspididae								
Carcharias taurus	Kneebone *et al.* (2012)	73	Estuary	J	78–108	0·82		
Pristidae								
Pristis pectinata	Simpfendorfer *et al.* (2010)	22 + 12‖	Mud/mangrove	J	78–200	High site fidelity	KUD 50 = 0·4–7 KUD 95 = 4–104	
Rhinobatidae								
Glaucostegus typus	Cerutti-Pereyra *et al.* (2014)	5	Lagoon/coral reef/mangrove	J	72–119	High site fidelity, but seasonal variation		Yes
Rajidae								
Raja clavata	Wiegand *et al.* (2011)		Estuary	J + A	<90	Seasonal site fidelity		No
Sphyrnidae								
Sphyrna tiburo	Heupel *et al.* (2006*b*)	36	Estuary	J + A	61–107		Daily KUD 50 = 1·64 Daily KUD 95 = 8·31	
Sphyrna lewini	Hearn *et al.* (2010)	61	Volcanic island		120–230	Seasonal site fidelity		
Stegostomatidae								
Stegostoma fasciatum	Dudgeon *et al.* (2013)	10	Rocky reef	A	198–230	Seasonal site fidelity		
Triakidae								
Mustelus californicus	Espinoza *et al.* (2011)	22	Estuary	J + A	50–101	0·12	MCP = 0·6 KUD 50 = 0·006–0·13 KUD 95 = 0·06–0·78	
Mustelus lenticulatus	Francis (2013)	10	Mud/Sand	J	34–58	High site fidelity	4–7§	Yes; needs to cover large area†
Mustelus mustelus	Da Silva *et al.* (2013)	24	Lagoon/Sand	J + A	81–147	High site fidelity, but seasonal variation		Yes; could be associated to fishing restriction during the season sharks disperse

A, adult; J, juvenile; SA, sub-adult; KUD, kernel utilization distribution; MCP, minimum convex polygon, MPA indicated that the study was undertaken within an MPA.

*Estimated using time spent inside the MPA instead of the proportion of day present within the monitored area.

†Unlike the other studies, these studies did not assess the efficiency of a current MPA, but investigated whether the use of potential MPA would be beneficial to the species.

§Home range size was estimated on the extent of movement, but was not calculated using MCP or KUD.

‖In this study, 12 of the 34 monitored animals were actively tracked instead of being monitored using passive acoustic telemetry.

C. amblyrhynchos, sicklefin lemon *Negaprion acutidens* (Rüppell 1837) and whitetip reef shark *Triaenodon obesus* (Rüppell 1837); Speed *et al.*, 2011]. Such differences in residency patterns have obvious implications for the efficiency of MPAs and no-take zones (Babcock *et al.*, 2012), with shark species that are most resident within habitats likely to derive the greatest protection from these management strategies.

The *C. cautus* that remained within the array for extended periods had extremely small home (average 3·6 km^2) and core (average 0·7 km^2) ranges calculated from COAs, compared with other tropical carcharhinids (Table III). For example, *C. melanopterus* and *C. amblyrhynchos*, two common reef sharks in Mangrove Bay, had core range sizes around Mangrove Bay that were >20 times larger at 13 and 20 km^2, respectively [Speed *et al.*, in press]. While the different ecologies, trophic positions and preferred habitats of *C. melanopterus* and *C. amblyrhynchos* (Papastamatiou *et al.*, 2009; Speed *et al.*, 2011) might explain their larger home ranges, the core range of *C. cautus* was also an order of magnitude smaller than that of *C. sorrah* (9·08 km^2; Knip *et al.*, 2012*b*), a species that also remains within near-shore regions (Knip *et al.*, 2012*a*, *b*) and has a similar trophic position to *C. cautus* (Last & Stevens, 2009; Knip *et al.*, 2012*a*). With the exception of some scyliorhinids, such small core and home ranges are not common in tropical Carcharhiniformes but have been observed previously in other species such as *C. melanopterus* at a Pacific Ocean atoll and grey smooth-hound shark *Mustelus californicus* Gill 1864, which had home range sizes of 0·55 and 0·6 km^2, respectively (Papastamatiou *et al.*, 2009; Francis, 2013) (Table III). At Mangrove Bay, the small home range of *C. cautus* might reflect the relatively limited availability of mangroves and turbid water, so that in other environments where these habitats are more widespread, the species may have larger range sizes. Alternatively, food resources may be very plentiful at Mangrove Bay, so that individuals are able to forage within very small home ranges.

Carcharhinus cautus with low residency at Mangrove Bay might have been tagged on the southern limit of their home range, with their core to the north of the study site where no receivers were deployed. Differences in the location of home range cores have been argued to account for variability of residency in other sharks and fishes [*e.g.* bonnethead shark *Sphyrna tiburo* (L. 1758), Heupel *et al.*, 2006*b*; western blue groper *Achoerodus gouldii* (Richardson 1843), Bryars *et al.*, 2012]. Alternatively, individuals might have differed in patterns of habitat use, with some staying in a relatively small area and others moving further away to access other habitats (Carlson *et al.*, 2008; Yeiser *et al.*, 2008; Knip *et al.*, 2012*b*). Such variation in habitat use is thought to explain differences in residency among individuals of the inshore species *C. sorrah* in Cleveland Bay, a tropical estuarine habitat in north Queensland, Australia (Knip *et al.*, 2012*b*). A teleost inhabiting Mangrove Bay, the spangled emperor *Lethrinus nebulosus* (Forsskål 1775), had a similar home range size (average KUD 95% of 8·6 km^2) to that of *C. cautus*, but displayed high variability in home range stability (Pillans *et al.*, 2014). One year after tagging of this species, >60% of *L. nebulosus* had moved outside of the array. In contrast, little variation was detected in home range size of *C. cautus* within the same array.

A large proportion of tagged *C. cautus* home ranges and 80% of their detections were within the no-take zone at Mangrove Bay, suggesting that the current zoning pattern is likely to provide some protection to the species from recreational fishing pressure in this environment. The level of risk that recreational fishing at Ningaloo Reef presents to this species is unknown, although reef sharks are targeted and caught by recreational fishers

(Smallwood & Beckley, 2012). Other research programmes have recorded capture rates of 4·2% of tagged reef sharks by recreational fishermen [Speed *et al.*, in press] and there are anecdotal reports of increasing catches of reef sharks by recreational fishers at Ningaloo Reef (P. Barnes, pers. comm.). For this reason, the results of this study suggest that the no-take zone of the marine park at Mangrove Bay may serve a useful function in protecting *C. cautus* from fishing pressure.

In other regions, evidence for the value of no-take zones as a strategy for protecting reef sharks varies both among locations and even between studies at the same location. Among the studies that examined the suitability of no-take zones for sharks, 65% found that these could be of benefit (Table III; Chapman *et al.*, 2005; Heupel *et al.*, 2010*a*; Bond *et al.*, 2012; Knip *et al.*, 2012*a*; Francis, 2013), while 35% suggested that the no-take zone was too small to offer protection for the target species because of the spatial scale of their movements (Table III; Chapman *et al.*, 2005; Field *et al.*, 2011; Wiegand *et al.*, 2011; Francis, 2013). Clearly, the benefits that a reserve may offer will depend on the amount of time that a species spends within reserve boundaries and the number of life-history stages catered for by the reserve. For example, Knip *et al.* (2012*c*) concluded that a no-take zone of the Great Barrier Reef Marine Protected Area had conservation benefits for populations of both *Carcharhinus amboinensis* and *C. sorrah* because large numbers of individuals spent a significant amount of time (up to 70%) in the protected zone and because both juveniles and adults were found in the zone so that it offered protection for a large part of the life cycle of the species (Knip *et al.*, 2012*a*).

This study provides some of the first information on the movement, habitat choice and residency patterns of the nearshore tropical shark *C. cautus*. The affinity of both juvenile and adult *C. cautus* to mangrove habitats and the small home ranges, limited large-scale movements (> 5 km), and high residency rates of at least some individuals within the population suggests that no-take zones could be an effective means of conserving populations of this Data Deficient species in tropical coastal environments.

C.H. was partly funded by Marine Innovation South Australia (MISA). Receiver data were provided through the Australian Animal Tracking and Monitoring System (AATAMS), a facility of Integrated Marine Observing System (IMOS). AATAMS also provided in-kind support and technical assistance. Field work was carried out in compliance with research permits supplied by the Department of Environment and Conservation and the Western Australian Department of Fisheries (SF7536, CE002881 and 1719-2010-39) and was funded by the Australian Institute of Marine Science. Animal ethics for all animal handling was approved by the Charles Darwin University Animal Ethics Committee (A07035). We thank J. Stevens, R. McAuley, F. McGregor and J. Chidlow for assistance with field work. We thank two anonymous reviewers for their constructive comments on earlier versions of the manuscript.

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