

Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators

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ABSTRACT: Coastal habitats provide important functions for many species and may serve as nursery grounds for teleost fishes and sharks and rays. However, the importance of these habitats in sustaining marine species at seascape scales is debated, and their significance to reef shark populations is poorly understood. The blacktip reef shark *Carcharhinus melanopterus* is a widely distributed mobile marine predator; we explored its use of shallow, turbid coastal habitats in the Great Barrier Reef using tagging and acoustic telemetry. Residency and movement patterns of 23 individuals were monitored for up to 28 mo, revealing different patterns between sexes and sizes. Neonate/juveniles were short-term residents; adult females were long-term residents and preliminary data suggest that adult males were vagrants. Adult females and neonate/juveniles had small activity spaces (50% kernel utilisation distribution, KUD < 5 km²) and shared the same habitats and locations while adult males (when present) had larger activity spaces (50% KUD up to 14 km²). Population organisation, movement patterns and biological data suggest that blacktip reef sharks may use turbid coastal habitats for reproduction. This study reveals a new variation in coastal habitat use by sharks with habitat use patterns differing from those observed in other coastal sharks, and from conspecifics on coral reefs. These patterns do not conform to the characteristics of classical shark nurseries, and highlight the species' ecological flexibility. The study also demonstrates that shark behaviour and habitat use patterns can affect their vulnerability to fishing, habitat loss and climate change, and can affect the efficacy of marine protected areas.

KEY WORDS: Coastal habitats · Fish community · Fish behaviour · Fisheries · Marine protected area · Marine predator · Nursery · Shark

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INTRODUCTION

There is increasing recognition of the need to identify and protect key coastal habitats and to understand how mobile marine species use these habitats, in order to better manage and conserve coastal resources (Knip et al. 2010, Mee 2012). Shallow coastal and estuarine habitats are vital to many species and there is a growing body of knowledge about coastal habitats and estuaries, their social, cultural

and economic values, and their ecological significance to marine and terrestrial fauna (Faunce & Serafy 2006, Nagelkerken 2009, Barbier et al. 2011). In particular, shallow coastal habitats such as mangroves, seagrass beds and intertidal foreshores perform important ecosystem roles such as acting as foraging grounds and nursery areas (Beck et al. 2001, Blaber 2007, Nagelkerken 2009). Coastal habitats may also be intricately linked to populations and ecosystems further offshore, as illustrated by the connec-

tivity and ontogenetic movements of fishes between coastal mangroves and coral reefs in the Caribbean (Mumby et al. 2004, Nagelkerken et al. 2008b), Gulf of Mexico (Jones et al. 2010) and Great Barrier Reef (Russell & McDougall 2005, Chin et al. 2013a). Inversely, degradation and loss of coastal habitats has been linked to decreased abundance and diversity of fishes (Taylor et al. 2007), providing corroborating evidence of the importance of coastal ecosystems to fish communities. The importance of coastal ecosystems in conserving marine species is widely acknowledged and has been explicitly considered in seascape-level planning of marine protected areas (MPAs) (Mumby 2006). Some coastal habitats have been afforded special protection, e.g. Essential Fish Habitats in the United States, and Fish Habitat Areas in Queensland, Australia (Zeller 1998). Nevertheless, direct evidence demonstrating the connectivity role of coastal habitats in sustaining marine species by acting as coastal nurseries that supplement habitats offshore is limited (Gillanders et al. 2003, Sheridan & Hays 2003), leading to debate concerning the role and function of these systems (Sheaves et al. 2006, Blaber 2007, Kimirei et al. 2013).

Coastal habitats are important to a wide range of elasmobranchs (sharks and rays), with a growing number of studies documenting the value of these systems (e.g. Vaudo & Heithaus 2009, Knip et al. 2010, Pierce et al. 2011). Coastal areas may have high productivity which can reduce inter- and intra-specific competition and provide abundant resources to support shark populations (Simpfendorfer & Milward 1993, Wiley & Simpfendorfer 2007, Kinney et al. 2011). Coastal habitats may also function as important nursery areas. Springer (1967) provided one of the earliest accounts of coastal shark nurseries and proposed a model of social organisation in shark populations based on size and sex segregation and movement patterns. Springer's model proposes that adult female sharks seasonally visit shallow coastal environments to give birth and then depart, leaving the neonates to mature in the relative safety of the nursery grounds. Meanwhile, adult males are transient visitors that seasonally enter shallow habitats to mate, and depart once mating is complete (Springer 1967). Numerous sharks and teleost fishes in both temperate and tropical waters have since been found to conform to this model (e.g. Castro 1993, Ebert & Ebert 2005, Russell & McDougall 2005, Grubbs et al. 2007, DeAngelis et al. 2008, Conrath & Musick 2010). Heupel et al. (2007) proposed that shark nurseries can be defined by 3 criteria: (1) neonate and juvenile sharks are more commonly encountered in the area

than other areas, (2) sharks have a tendency to remain or return for extended periods, and (3) the area or habitat is repeatedly used across years. The model proposes that coastal nurseries enhance growth and survival of neonate and juvenile sharks by providing abundant prey and/or reducing competition and predation pressures by adult conspecifics or larger sharks (Springer 1967, Branstetter 1990, Heupel et al. 2007). By enhancing neonate and juvenile growth and survival, coastal habitats play an important role in supporting marine ecosystems further offshore and may be crucial to continued recruitment into offshore populations and fisheries (Beck et al. 2001, Nagelkerken et al. 2008b, Jones et al. 2010).

While coastal habitats provide important ecosystem functions for mobile marine species, the use of these habitats may also increase their exposure and vulnerability to environmental stressors such as decreased salinity and increased turbidity from flood and weather events. Globally, coastal habitats are also under increasing pressure from human activities with many areas affected by fishing, pollution, habitat loss and degradation (Lotze et al. 2006, Mee 2012). Shark and ray populations are in decline in many parts of the world and pressures in the coastal zone may exacerbate these declines (Simpfendorfer 2000, Fowler et al. 2005, White & Kyne 2010). Furthermore, the effects of climate change are predicted to be greatest on sharks in the coastal zone (Chin et al. 2010). The combination of pressures in the coastal zone and concerns over declining shark populations, juxtaposed against the important ecological functions coastal habitats provide, is stimulating debate about the contribution coastal habitats and movement corridors may make to the conservation of mobile marine species such as sharks and rays (Chapman et al. 2005, Knip et al. 2010, 2012a, Pendoley et al. 2014).

The blacktip reef shark *Carcharhinus melanopterus* is a widely distributed reef shark that is often reported in the clear-water coral reef habitats of the Indo-Pacific (Last & Stevens 2009). As a medium sized shark, individuals only grow to 1.5 m total length, but the species has relatively slow growth and low fecundity compared to other coastal sharks, with annual to biennial reproduction over the summer months that usually produces 1 to 4 pups (Chin et al. 2013b). While considered to be a reef shark, *C. melanopterus* also frequent turbid coastal habitats such as mangroves, seagrasses and inter-tidal sand and mud foreshores (Chin et al. 2012), and there are indications that these habitats may be important to reproduction (Chin et al. 2013c). Blacktip reef sharks

are taken in numerous coastal fisheries throughout their range including fisheries in Africa, India, Thailand, Indonesia, Malaysia and Australia (Marshall 1996, Heupel 2005, Teh et al. 2007, Chin et al. 2012), and their use of shallow coastal habitats may expose them to increased pressure from fishing, habitat loss, potential impacts from climate change, as well as the cumulative effects of these individual pressures (Chin et al. 2012). Meanwhile, their use of turbid coastal habitats and the importance of these habitats in sustaining populations are poorly understood. This study used tagging and long-term acoustic telemetry to determine the residency and movement patterns of blacktip reef sharks within a tropical coastal bay over multiple years. The study specifically examined how long-term residency and movement patterns differed between sexes and size classes, and explored how these patterns could affect the management and conservation of other mobile marine predators.

MATERIALS AND METHODS

Study area

This study was carried out in Cleveland Bay (19° 14' S, 146° 53' E), a coastal region of the Great Barrier Reef World Heritage Area (GBRWHA) adjacent to the city of Townsville in North Queensland, Australia (Fig. 1). Cleveland Bay is a shallow embayment (<10 m depth) comprised of a diverse range of habitat types including subtidal fringing coral reefs, intertidal rubble, sand and mud foreshore habitats, fringing mangroves, and intertidal and subtidal seagrass beds. The Bay is a tropical environment with water temperatures fluctuating between 20.7°C (winter) and 30.6°C (summer) (A. Chin unpubl. data). Substrate types are predominantly fine mud sediments, and waters are highly turbid with turbidity levels regularly reaching 50 mg l⁻¹ (Browne et al. 2010). The Bay also receives inputs of terrestrial sediments via flood waters during monsoon rains. Summer monsoonal rains produce floodwater plumes that increase turbidity, introduce fine sediments and can cause salinity to fall from a mean of 32 ± 4.5 to 16.2 ppt (A. Chin unpubl. data). Cleveland Bay is located within the Great Bar-

rier Reef Marine Park and is managed through a spatial zoning system. The Bay includes 2 'Conservation Park' zones where net fishing is prohibited and line fishing is limited to 1 line angler⁻¹ with 1 hook line⁻¹, as well 6 'Green Zones' in 6 small bays around Magnetic Island where fishing is prohibited.

Field sampling and telemetry

Blacktip reef sharks were sampled in Cleveland Bay between January 2008 and March 2011 as part of a long-term shark tagging and sampling program operating throughout the region (Harry et al. 2011, Kinney et al. 2011, Chin et al. 2012). Targeted sampling for blacktip reef sharks was also carried out from October 2008 to May 2011 at Cackle Bay on the southwestern side of Magnetic Island (Fig. 1) where blacktip reef sharks were locally abundant (Chin et al. 2013c). Sharks were captured using 500 m long bottom-set longlines made from 8 mm diameter

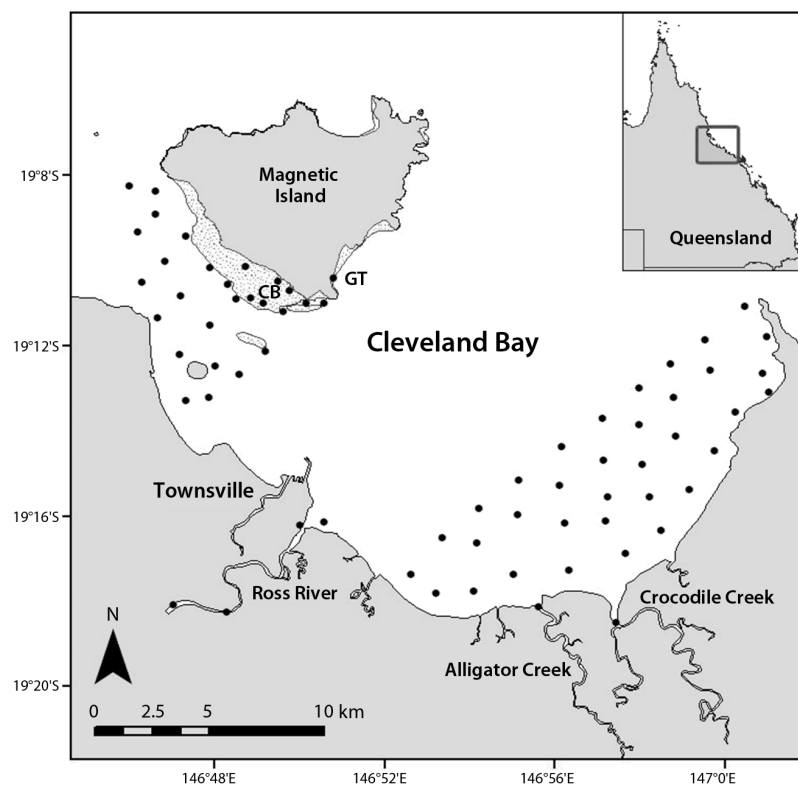


Fig. 1. Study site showing Cleveland Bay, Magnetic Island and Cackle Bay (CB); inset shows location of Cleveland Bay on the Queensland east coast. Light grey stippling: intertidal habitats (mud and sand foreshores, rubble banks and seagrass beds) around Magnetic Island and Cackle Bay. Black dots: locations of Vemco acoustic receivers deployed in a grid pattern array that covered approximately 140 km²; GT: location of the gate receiver (see 'Materials and methods')

nylon rope and anchored with 3.6 kg Danforth anchors. Gangions were 2.5 m long and constructed from a 1.5 m length of 4 mm braided cord, a 1 m length of nylon coated stainless wire leader and 14/0 Mustad tuna circle hooks. Hooks were baited with butterfly bream *Nemipterus* spp., sea mullet *Mugil cephalus*, diamond scale mullet *Liza vaigiensis* and blue threadfin *Eleutheronema tetradactylum* with different bait types randomly mixed between hooks. Upon capture, all sharks were measured and tagged with Dalton Rototags® on the first dorsal fin. A selection of blacktip reef sharks including neonates, juveniles and adults of both sexes were inverted to induce tonic immobility (Henningsson 1994) and internally tagged with Vemco V16 coded acoustic transmitters (Vemco) with a pseudo-random ping rate of 45 to 75 s for long-term acoustic monitoring. A small incision (3 to 4 cm) was made in the abdomen, and the transmitter surgically inserted into the abdominal cavity to ensure retention of the transmitter. The incision was closed with surgical sutures in both the muscle and skin layer. Surgical procedures were approved under James Cook University animal ethics guidelines, and promote rapid recovery and survival of tagged animals (Chin et al. 2015). Following the procedure, animals were revived and released at the site of capture.

Residency and movements of blacktip reef sharks were monitored for up to 2.3 yr through passive acoustic telemetry using 69 Vemco VR2 and VR2W acoustic receivers deployed throughout Cleveland Bay (Fig. 1) and covering approximately 140 km² (e.g. Knip et al. 2012a,b). No receivers could be placed in the middle of Cleveland Bay due to the presence of a designated shipping lane leading to Townsville Port, and seasonal trawling for penaeid prawns. Ten of these receivers were deployed in Cockle Bay on the southwest side of Magnetic Island (Fig. 1) to specifically monitor blacktip reef shark movements in this area. This included a 'gate' receiver explicitly located to detect whether animals were leaving the array by travelling around the headland to the east of Cockle Bay (Fig. 1). Receiver performance was examined for different parts of the array, and detection range was established at approximately 900 m for the majority of receivers (Knip et al. 2012b). Given the shallow, structurally complex environs of Cockle Bay, receiver performance in this location was determined separately. Receiver performance testing involved determining the effective detection range of receivers as well as examining diagnostic data on receiver performance recorded by the receivers during their deployment.

Range testing was conducted using moored acoustic transmitters that were activated and deployed at different locations within Cockle Bay at varying distances from receivers for up to 4 wk. Analysis of detection data revealed detection ranges of between 300 and 676 m, although detection range reached 1001 m on one occasion. Diagnostic data on receiver performance for 10 receivers deployed in Cockle Bay were analysed using methods described in Sempendorfer et al. (2008) and are presented in Supplement 1 at www.int-res.com/articles/suppl/m544p197_supp.pdf.

Data analysis

Telemetry data were analysed to determine residency (temporal patterns) as well as movement and activity space (spatial patterns) of neonate, juvenile and adult blacktip reef sharks. Residency patterns were indicated using a Residency Index (Res) calculated as $Res = D_d / D_m$, where D_d is the number of days an individual was detected in the receiver array and D_m is the number of days monitored, between the date the animal was first detected after release and 28 February 2012 (the end date of the study at which time conservative estimates suggested that the transmitter batteries of earliest released individuals would be exhausted). An individual was considered to be present within the array on a given day when a minimum of 2 detections were recorded within a 24 h period. Res values ranged from 0 to 1, with 0 indicating low residency and 1 representing high residency. Individuals were highly likely to have survived the tagging processes (Chin et al. 2015), and thus all tagged individuals were assumed to have been available in the study area for detection by the receiver array between the time of release and the study end date. This approach allowed permanent departures from the array to be considered in the analysis, and provided a consistent approach to comparing residency over the study period between individuals (Chin et al. 2013a).

Drawing upon descriptions used in ornithological studies (Robinson et al. 2004, Craig et al. 2011), Res values were used to assign individuals into 1 of 3 residency categories: vagrant, short-term resident or long-term resident. Vagrants were temporary occupants that only occurred in an area for days to weeks (1 to 31 d); short-term residents (analogous to migrants) were predictably found in an area for a period of months (32 to 365 d); and long-term residents remained in an area for periods that covered

multiple seasons (>365 d) and rarely left the area. Because individuals were released on different days (and thus had different monitoring periods over which they could be detected), a standard reference value for the monitoring period was calculated to enable comparisons of residency between individuals. The median monitoring period (time between release date and study end date) was 744 d. Using 744 d as the standard monitoring period, vagrants were defined as individuals with a Res of 0.00 to 0.04 (present for 1 to 31 d); short-term residents as individuals with a Res of 0.05 to 0.46 (present for 32 to 356 d); and long-term residents as individuals with a Res of 0.47 to 1.00 (present >365 d).

Movement patterns were described using a Roaming Index (Rom) which indicated the extent of an individual's movements within the receiver array. Rom was calculated using the equation $Rom = R_d/R_a$, where R_d is the number of receivers an individual was detected on during the monitoring period and R_a is the number of receivers deployed during the monitoring period. Rom values ranged from 0 to 1, with values close to 0 indicating low roaming (individual detected on only a few receivers) and 1 representing high roaming (individual is detected on every receiver). Res and Rom were plotted together to compare residency and movement patterns for neonate/juveniles, adult males and adult females.

Activity space (home range) was derived using kernel utilisation distributions (KUDs). Estimated locations of individuals were calculated at 30 min intervals using an algorithm that provided estimated centres of activity (COA) within the receiver array (Simpfendorfer et al. 2002, Knip et al. 2011). The total activity space/home range of an individual over the entire monitoring period was derived from COA estimates using 50% (core home range) and 95% (home range extent) KUDs (Worton 1989). KUDs were plotted using ArcGIS 9.3 (ESRI) to illustrate patterns in home range size and location between neonate/juvenile, adult male and adult female blacktip reef sharks. All analyses for residency, roaming and activity space/home range were performed with the program R (R Development Core Team 2012), with home range analysis using the R package 'adehabitat'.

RESULTS

Across Cleveland Bay, 120 blacktip reef sharks were tagged with Rototags® and released between 8 October 2008 and 25 March 2011. The population showed a bimodal structure comprised of neonates

and juveniles, and adult females. The adult population also showed strong sex bias with a sex ratio of 7:1 adult females to adult males (Chin et al. 2013c). Sampling throughout Cleveland Bay indicated that blacktip reef sharks were highly localised to Cackle Bay, and that the population was comprised almost exclusively of neonates, juveniles and adult females with a noticeable paucity of adult males and intermediate-sized individuals between 850 and 1050 mm stretched total length (L_{ST}) (Chin et al. 2013c). Of the 120 individuals tagged and released, 27 were fitted with acoustic transmitters between 16 October 2009 and 13 April 2010 and monitored until 28 February 2012. Individuals fitted with transmitters ranged from neonates to mature adults (655 to 1550 mm L_{ST}). Telemetry data from 4 individuals (3 juveniles and 1 neonate) suggested that these animals had been depredated ($n = 3$) or had lost their tag ($n = 1$) and were omitted from analyses. The remaining 23 individuals (Table 1) included 4 adult males, 10 adult females, 1 neonate male, 6 juvenile males and 2 juvenile females. These sharks were monitored for 663 to 844 d (mean \pm SE: 761 \pm 11.69 d).

Residency and roaming patterns

Almost all individuals were recorded on receivers within minutes to hours after release and displayed active swimming patterns (Chin et al. 2015). Over the longer term, plots of daily residency showed 3 main patterns: (1) individuals that were detected consistently throughout the monitoring period, (2) individuals that were detected consistently for an intermediate period of time (32 to 265 d) before detections permanently ceased, and (3) individuals that were intermittently detected for short periods (<31 d) (Fig. 2). Only 2 individuals left for an extended period (>1 mo) and then returned (adult female 59599 and adult male 59591; Fig. 2). Residency patterns differed between adult females, adult males and neonate/juveniles. Adult females were highly resident while adult males tended to show low residency (Fig. 2, Table 2, Supplement 2 at www.int-res.com/articles/suppl/m544p197_supp.pdf) although there was high variability between individual adult males (Fig. 2). Neonate/juveniles had intermediate residency but also exhibited high variability in residency between individuals (Fig. 2, Table 2). Adult females had significantly higher Res values than juveniles, but other pair-wise comparisons of Res values between adult males and other animals showed no significant differences (Table 3). Applying Res values to residency

Table 1. Biological, residency and movement characteristics of 23 blacktip reef sharks *Carcharhinus melanopterus* fitted with Vemco V16 transmitters monitored for up to 844 d. Activity space and residency patterns varied between neonate/juveniles, adult males and adult females. Activity space is represented by kernel utilisation distribution (KUD); length is stretched total length (L_{ST}); dates are given as dd/mm/yyyy

Tag ID	Biological details			Residency				Activity space and home range		
	Maturity	Sex	Size (mm L_{ST})	Date of first detection	Monitoring period (d)	No. of days detected	Residency index	Roaming index	50% KUD (km ²)	95% KUD (km ²)
59590	Adult	F	1550	17/10/2009	844	747	0.88	0.39	5.04	38.11
59593	Adult	F	1420	04/11/2009	826	522	0.63	0.33	9.19	37.1
59594	Adult	F	1360	22/10/2009	839	619	0.74	0.39	4.17	28.63
59595	Adult	F	1454	18/12/2009	782	740	0.95	0.29	3.58	17.28
59596	Adult	F	1480	18/12/2009	782	748	0.96	0.23	3.56	16.8
59597	Adult	F	1420	18/12/2009	782	423	0.54	0.28	3.54	15.41
59598	Adult	F	1075	18/12/2009	782	776	0.99	0.17	4.07	17.84
59599	Adult	F	1400	18/12/2009	782	16	0.02	0.04	2.54	11.21
59607	Adult	F	1232	16/02/2010	722	722	1.00	0.19	4.04	15.4
63645	Adult	F	1400	02/02/2010	736	721	0.98	0.19	3.12	13.74
59591	Adult	M	1358	29/10/2009	832	69	0.08	0.06	2.56	12.94
59592	Adult	M	1210	26/10/2009	835	1	0.00	0.06	4.49	38.1
59604	Adult	M	1271	21/12/2009	779	11	0.01	0.09	3.16	19.34
63648	Adult	M	1340	16/04/2010	420	663	0.63	0.64	14.56	74.01
59602	Juvenile	F	730	21/12/2009	779	442	0.57	0.23	3.28	14.12
63646	Juvenile	F	735	04/03/2010	706	48	0.07	0.14	3.98	22.69
59600	Neonate	M	709	21/12/2009	779	309	0.40	0.25	2.46	10.94
59603	Juvenile	M	780	21/12/2009	779	42	0.05	0.29	3.28	28.28
59605	Juvenile	M	665	02/02/2010	736	2	0.00	0.07	3.27	30.1
59617	Juvenile	M	721	03/03/2010	707	50	0.07	0.12	3.29	14.35
63647	Juvenile	M	889	13/04/2010	666	371	0.56	0.26	4.54	26.42
63649	Juvenile	M	811	13/04/2010	666	230	0.34	0.17	2.96	13.47
63650	Juvenile	M	752	17/02/2010	721	715	0.99	0.12	2.83	14.2

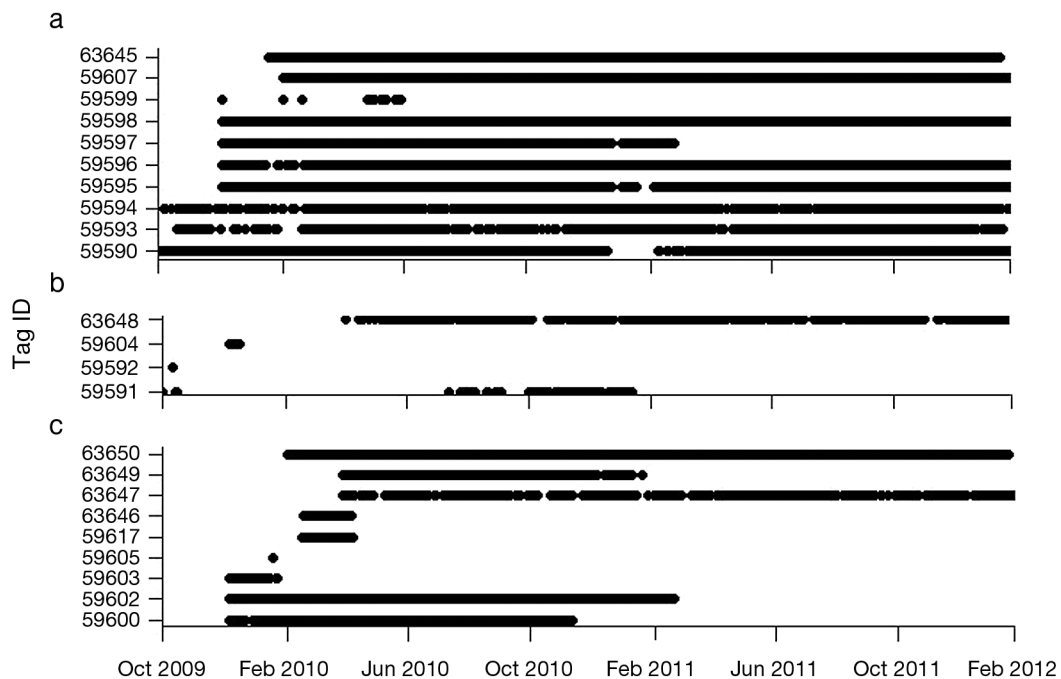


Fig. 2. Residence plot from acoustic telemetry data showing difference in residency patterns between (a) 10 adult female, (b) 4 adult male and (c) 9 neonate/juvenile blacktip reef sharks

Table 2. Differences in residency and activity space between neonate/juvenile, adult male and adult female blacktip reef sharks *Carcharhinus melanopterus*. Activity space is represented by kernel utilisation distribution (KUD)

	n	Residency index			Roaming index			50% KUD (km ²)			95% KUD (km ²)		
		Min.	Max.	Mean±SE	Min.	Max.	Mean±SE	Min.	Max.	Mean±SE	Min.	Max.	Mean±SE
Adult females	10	0.02	1.00	0.77±0.10	0.04	0.39	0.25±0.03	2.54	9.19	4.29±0.58	11.21	38.11	21.2±3.10
Adult males	4	0.00	0.63	0.18±0.15	0.06	0.64	0.21±0.14	2.56	14.56	6.19±2.82	12.94	74.01	36.1±13.72
Neonate/ juveniles	9	0.00	0.99	0.34±0.11	0.07	0.29	0.18±0.03	2.46	4.54	3.32±0.21	10.94	28.28	19.4±2.47

Table 3. Kolmogorov-Smirnov test statistics for differences in residency and roaming (Res and Rom) values between juvenile, adult male and adult female blacktip reef sharks *Carcharhinus melanopterus*. *Statistically significant difference at $\alpha = 0.05$

	df	Residency index		Roaming index	
		D-score	p-value	D-score	p-value
Neonate/juveniles × adult males	12	0.3889	0.7964	0.3689	0.2083
Neonate/juveniles × adult females	18	0.6889	0.0223*	0.3889	0.4708
Adult males × adult females	13	0.7000	0.1216	0.6500	0.1787

classifications revealed that different sizes and sexes tended to fall into different residency categories (Fig. 3). Neonates and juveniles were mostly classified as short-term residents while almost all adult females were classified as long-term residents (Fig. 3). Adult males displayed a mix of residency

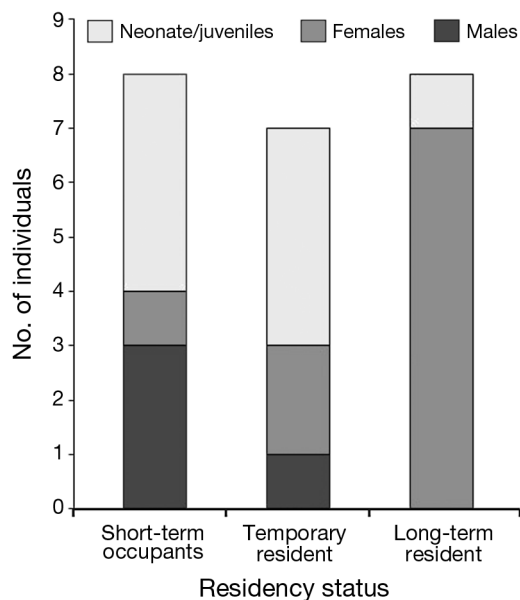


Fig. 3. Residency classifications of neonate/juvenile, adult female and adult male blacktip reef sharks monitored for periods ranging from 663 to 844 d

patterns, with 2 individuals classed as vagrants, 1 classed as a short-term resident and 1 as a long-term resident (Fig. 3).

Roaming patterns also differed with sex and size. Adult males were detected on the greatest number of receivers, resulting in relatively high Rom values (Table 2). In contrast, neonate/juveniles and adult females visited fewer receivers and had lower Rom values (Table 2). Nevertheless,

differences in Rom values were not statistically significant between neonate/juveniles, adult males and adult females (Table 3). However, it should be noted that comparisons of Res and Rom between adult males and other animals were compromised by the small number of adult males ($n = 4$) available to include in the analysis and the high variability in Res and Rom values between these 4 individuals.

Plotting Res and Rom values together illustrated differences in residency and roaming patterns between groups, with neonate/juveniles, adult males and adult females tending to fall in different sectors (Fig. 4). Both neonate/juveniles and adult females showed low roaming, but neonate/juveniles showed a range of residency patterns while adult females were slightly more likely to roam. Almost all males were low residents and low roamers. However, it should be noted that Rom values only reflect movement within the array and thus the combination of low Res and low Rom values may reflect broader movements outside detection range of the receiver array.

Activity space and home range

Analysis of activity space data showed 2 distinct patterns: neonate/juveniles (short-term residents) and adult females (long-term residents) had small

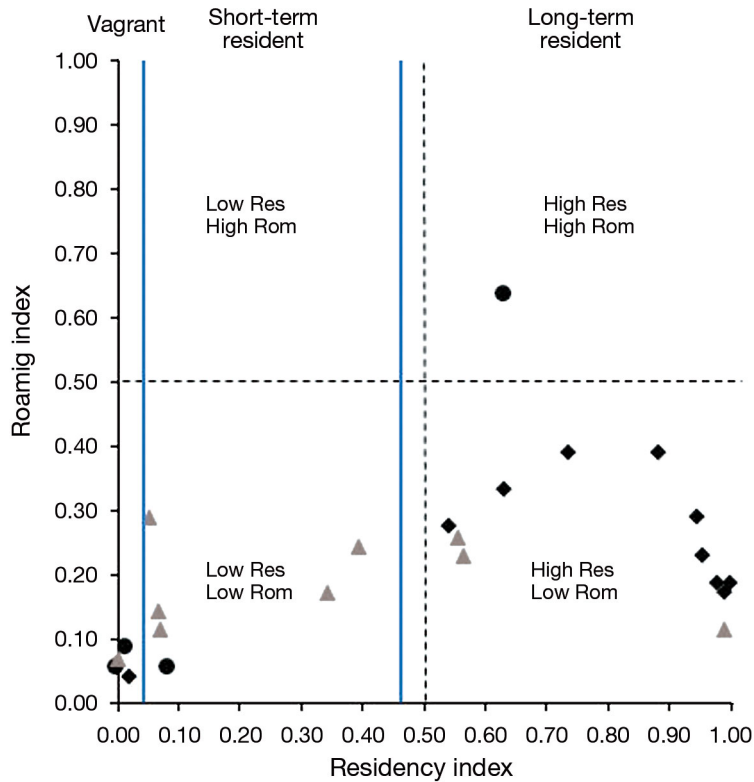


Fig. 4. Residency (Res) and roaming (Rom) plot showing the relationship between residency status and movement patterns for neonate/juvenile (▲), adult male (●) and adult female (◆) blacktip reef sharks. Blue lines delineate Res categories

home ranges and were highly resident to a specific location, while adult males (vagrants) used larger areas and were detected in different areas of the Bay. Neonate/juvenile individuals and adult females had mean 50% KUDs of 3.32 and 4.29 km² respectively (Table 2). Sizes of 95% KUDs were also similar between these 2 groups, with means of 19.4 and 21.2 km² for neonate/juveniles and adult females respectively (Table 2). As KUD values were not normally distributed ($\chi^2 = 20.511$, $p < 0.001$), KUD size comparisons between groups were performed using Kolmogorov-Smirnov tests. Neonate/juveniles and adult females had similar 50 and 95% KUD sizes (Table 4) although adult females showed more variation in activity space size between individuals (Table 2). Adult males appeared to have larger activity spaces with mean 50% KUD of 6.19 km² and mean 95% KUD of 36.1 km². While adult male KUD sizes were not statistically different from those of neo-

nate/juveniles or adult females (Table 4), the low residency and high variability between individual adult males (Table 2) made it difficult to estimate KUDs for these individuals. Transient, vagrant males appeared to have wider-ranging movements and the Rom values and activity space (KUD) estimates generated for these individuals only represent their limited movements within the detection range of the Cleveland Bay receiver array. However, the only long-term resident adult male had the largest activity space recorded in the study, with 50 and 95% KUDs of 14.56 and 74.2 km² respectively (Table 2). Neonate/juvenile individuals and adult females showed high affinity to the same confined area of Cockle Bay (Fig. 5). In contrast, the single resident adult male had 2 core use areas; one centred around Cockle Bay and the other around a subtidal shoal (Virago Shoal) close to the mainland (Fig. 5). That male's 95% KUD encompassed the whole area of the receiver array between Magnetic Island and the mainland, and also included some of the eastern side of Cleveland Bay.

DISCUSSION

Coastal blacktip reef sharks displayed 3 broad patterns of movement and habitat use: (1) limited occurrence of adult males that, when present, tended to show wide ranging, transient movements (short-term residents or vagrants), (2) adult females that were long-term residents with movements concentrated in a small area, and (3) neonate/juveniles (both sexes) that were short-term residents with movements concentrated in a similarly small area. Importantly, adult females, neonates and juveniles all used the same

Table 4. Kolmogorov-Smirnov test statistics for differences in activity spaces (50 and 95% kernel utilisation distribution, KUD) between neonate/juvenile, adult male and adult female blacktip reef sharks *Carcharhinus melanopterus*. No results were statistically significant ($\alpha = 0.05$)

	df	50% KUD		95% KUD	
		D-score	p-value	D-score	p-value
Neonate/juveniles × adult males	12	0.3000	0.9191	0.5000	0.4042
Neonate/juveniles × adult females	18	0.5778	0.0846	0.3560	0.4922
Adult males × adult females	13	0.3000	0.9191	0.4500	0.4995

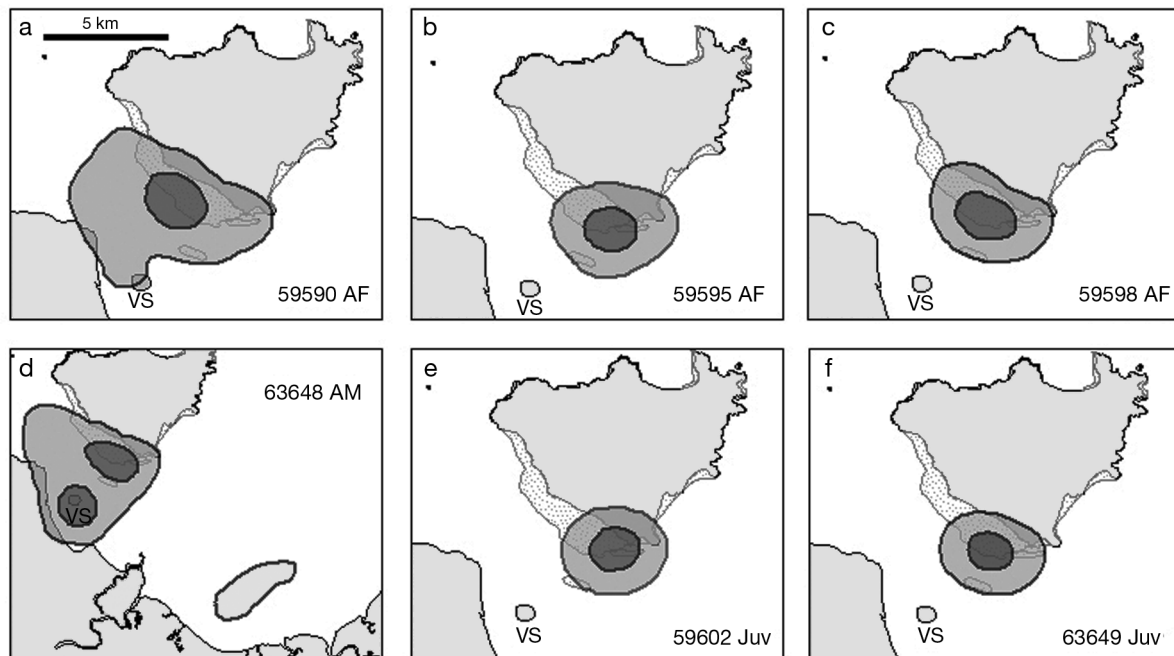


Fig. 5. Kernel utilisation distributions (KUDs) of (a–c) 3 adult female (AF), (d) 1 adult male (AM) and (e–f) 2 juvenile (Juv) blacktip reef sharks, selected as representatives for these population groups. Dark grey: core use areas (50% KUD); light grey: home range extent (95% KUD); VS: Virago Shoal

habitat and location within Cockle Bay. These residency and movement patterns provide a new variation of coastal habitat use by sharks, as well as having implications for reef shark management and conservation.

Movement patterns and population organisation

The movement patterns and population organisation of blacktip reef sharks observed in this study contrast with patterns observed in other reef sharks. While blacktip reef sharks in French Polynesia, Palmyra Atoll (Central Pacific) and Western Australia showed similar scales of movement to this study (Papastamatiou et al. 2009, 2010, Speed et al. 2011, Mourier & Planes 2013), blacktip reef sharks in Cleveland Bay had different movement patterns. In the present study, we found that adult females were long-term residents with limited movement over multiple years, they shared the same space with neonates and juveniles, and juveniles appeared to disperse at the onset of maturity (Chin et al. 2013a). Males were rarely encountered in Cleveland Bay, and when present, displayed much larger movements than the resident females. In contrast, at Aldabra Atoll adult males and females had broadly similar movement patterns (Stevens 1984), and in French Polynesia adult females

moved from their normal area of residence to other locations to give birth, and this movement pattern accounted for genetic dispersal within the population (Mourier & Planes 2013). In Western Australia, adult female blacktip reef sharks also showed wide-ranging movements with seasonal migrations into shallow coastal sand flats and fringing reefs during spring, at which time some were also pregnant (Speed et al. 2011).

Blacktip reef sharks in Cleveland Bay also differ in population structure from conspecifics in other regions. Catch data from sampling throughout Cleveland Bay showed a strong sex bias with a ratio of 7:1 adult females to males (Chin et al. 2013c), contributing to the evidence that males are transient. This extent of sex structuring was not reported in blacktip reef sharks at Aldabra Atoll (Stevens 1984) or at Palmyra Atoll (Papastamatiou et al. 2009). While populations in French Polynesia showed some sex structuring (Mourier et al. 2013), sex segregation occurs at a much smaller scale than in the present study, possibly due to the limited habitat available in isolated atoll habitats. In Western Australia and Palmyra, neonates and juveniles were separated from adults at a micro-habitat scale (Papastamatiou et al. 2009, Speed et al. 2011) whereas in this study, adult females and juveniles co-occurred within the same small area (<5 km²) over periods of months to

years, and adult females, neonates and juveniles were regularly captured on the same longline (A. Chin unpubl. data). The population structure and movement patterns from Cleveland Bay also differ from the grey reef shark *Carcharhinus amblyrhynchos*, Caribbean reef shark *C. perezi* and whitetip reef shark *Triaenodon obesus*, all of which show wide-ranging movements and the lack of a strong female sex bias (Chapman et al. 2005, Pikitch et al. 2005, Heupel et al. 2010, Whitney et al. 2012).

The blacktip reef shark's range of population organisation and movement patterns across different habitats and locations suggest that the species is ecologically flexible and can adopt population structures and behaviours that optimise the use of local conditions. Indeed, the Cleveland Bay population experiences high turbidity, complex bathymetry and habitat types, freshwater flows and extreme salinity changes that are not present in coral reef habitats. In addition, coastal habitats support high biological productivity (Blaber et al. 1989, Nagelkerken et al. 2008a). These dynamic conditions can affect shark behaviour and distribution (Schlaff et al. 2014) as well as community structure (Sheaves & Johnston 2009). The blacktip reef shark's ecological flexibility may enable the species to exploit shallow, turbid coastal habitats and take advantage of increased resource opportunities resulting from the diversity and productivity of coastal habitats.

Interestingly, the blacktip reef sharks' intensive use of a small area of Cockle Bay does not appear to be linked to the availability of specific habitat types. There are extensive areas of mangroves and mudflats along the northwest coast of Magnetic Island, and extensive fringing reef habitat and sand, mud and rubble flats along the island's southeast coast. However, blacktip reef sharks from Cockle Bay did not appear to use these adjacent locations and were not detected on the 'gate' receiver specifically deployed to detect such movements. The blacktip reef sharks' attachment to Cockle Bay was also particularly strong. Individuals elected to stay in Cockle Bay during a category 5 cyclone while other sharks in adjacent locations departed prior to the storm's arrival (Udyawer et al. 2013). Furthermore, extensive catch sampling using longlines and mesh nets over several years throughout Cleveland Bay showed that blacktip reef sharks were only captured at Cockle Bay and occasionally at Virago shoal, providing additional evidence of the site attachment to these confined areas (Chin et al. 2013c). Intensive use of Cockle Bay suggests that this location may feature environmental variables that confer advantages in

provisioning and/or survival that outweigh the potential risks from intra-specific competition and predation between adult females and neonates/juveniles, as well as potential impacts from extreme weather events. Blacktip reef shark movements have been attributed to behavioural patterns that reduce competition and/or predation (e.g. Papastamatiou et al. 2009), but while these factors may shape the movement patterns and site attachment of blacktip reef shark in Cleveland Bay, the causative factors behind these patterns remain unstudied.

The role of coastal habitats in supporting reef sharks

The blacktip reef sharks' population organisation and movement patterns, taken together with data showing mating and pupping over multiple years (see Chin et al. 2013c) suggest that turbid coastal habitats like Cockle Bay may be important to reef shark reproduction. Sex segregation may reduce harassment and injury to females, while size segregation reduces predation on neonates and juveniles (Wearmouth & Sims 2008). The high productivity, prey availability and diversity of coastal ecosystems may also increase provisioning and facilitate resource partitioning that maximises juvenile survival (Simpfendorfer & Milward 1993, Kwak & Klumpp 2004, Kinney et al. 2011). Indeed, the shallow intertidal flats of Cockle Bay support a diverse community of fishes and decapods (Kwak & Klumpp 2004) that are potential prey for neonate and juvenile blacktip reef sharks, which were regularly observed actively feeding on these flats (A. Chin pers. obs.). Additionally, inter-specific predation on juvenile sharks may be reduced in the shallow intertidal foreshores as larger shark species that could potentially prey upon neonate/juvenile blacktip reef sharks were rarely encountered during 3 yr of sampling in these habitats (A. Chin unpubl. data), whereas sampling in adjacent areas captured a range of these potential predators (Kinney et al. 2011, Knip et al. 2011).

Nevertheless, the co-occurrence of adult females with neonates and juveniles contradicts conventional nursery theory. It is possible that the specific environmental conditions present in shallow turbid coastal habitats make this population organisation possible. The high turbidity of these systems could help neonates and juveniles evade adult females, as turbidity can reduce predation success in some fishes (Sweka & Hartman 2003, Radke & Gaupisch 2005). Prey availability and reduced predation pressure may

lead to increased neonate and juvenile growth and survival compared to clear water island lagoons where juvenile survival may be reduced by resource limitations (Lowe 2002). Increased provisioning for adult females could also potentially assist embryo development. Indeed, previous research revealed that the size at birth and growth rates of juveniles at Cockle Bay were greater than reported for conspecifics elsewhere (Chin et al. 2013c). While the factors and processes that may attract blacktip reef sharks to these habitats are unknown, their strong site attachment to this area, data showing active mating and pupping over multiple years (Chin et al. 2013b), and a population structure and ontogenetic movements that indicate patterns consistent with nursery functions (Chin et al. 2013a,c) suggest that their attachment to this location may be linked to reproductive processes.

Variations from classical coastal nurseries

The turbid coastal habitats in this study appear to support reproduction in reef sharks, however in this example, they should not be considered as conventional nursery grounds. The coastal shark nursery model suggests that adult females enter coastal nursery areas to mate and/or pup and then depart, leaving an aggregation of neonates and juveniles to mature in the nursery ground without interference from adults or large sharks (Springer 1967, Heupel et al. 2007). The absence of adults in nursery grounds is thought to reduce competition with and predation on neonates and juveniles (Simpfendorfer & Milward 1993, Wearmouth & Sims 2008). Additionally, the movement of adult females to and from nursery grounds provides an important vector for genetic dispersal (e.g. Mourier & Planes 2013) as juveniles may stay close to natal grounds even after leaving a nursery (Chapman et al. 2009). In contrast, this study revealed that adult females did not leave the natal area as predicted, and instead were permanent residents while the juveniles dispersed over large distances (Chin et al. 2013a). Furthermore, neonates and juveniles shared the same space as adult females until they departed (Chin et al. 2013a). Thus, while this study appears to conform to the definition of a nursery ground (Heupel et al. 2007), the co-occurrence of adult females, neonates and juveniles in a confined area deviates from these criteria. Consequently, while these habitats are crucial to reproductive functions, they are not classical nursery grounds.

While turbid shallow habitats in the GBRWHA may not conform to classical definitions of nursery grounds, they are still important habitats to blacktip reef sharks. The long-term residency of adult females and the co-occurrence of adult females, neonates and juveniles in small areas of turbid coastal habitat represent a new variation of how reef sharks use coastal habitats, and highlights juvenile dispersal as an important driver of genetic mixing in reef sharks across regional scales. Coastal habitats also support permanent groups of reproductively active adult females that may be the key population component driving population dynamics in these long-lived fishes (Prince 2005). Groups of resident adult females may be visited by transient males during the summer mating season (Chin et al. 2013c) and after pupping, shallow coastal habitats may enhance the growth and survival of neonates and juveniles until they depart from their natal grounds (Chin et al. 2013a). Meanwhile, coastal habitats provide the necessary resources and security for adult females to regain fitness for successive breeding events.

Implications for management and conservation of mobile marine species

The residency and movement patterns described in this study have several implications for the management of mobile marine species, and show how habitat use patterns can affect species-specific risk portfolios. A species' vulnerability can be assessed by considering the interactions of 3 separate components: (1) exposure to risks, (2) sensitivity to exposure, and (3) the species' adaptive capacity to compensate for impacts (Australian Greenhouse Office 2005, Chin et al. 2010). Data on movement and behaviour patterns can address these 3 components by describing a species' exposure to risk (overlap between risks and species distribution), sensitivity (expressed through movement and habitat use patterns of key components of the population), as well as its capacity to adapt (expressed as ecological flexibility, mobility and distribution) (Chin et al. 2010).

For coastal blacktip reef sharks, intensive use of small areas can greatly affect their vulnerability. The high residency of blacktip reef sharks in turbid coastal habitats increases their exposure to coastal fisheries, pollution and habitat loss and degradation. Additionally, since the blacktip reef shark uses both coastal and coral reef environments in the GBRWHA, it is also exposed to the cumulative pressures from fishing, habitat loss and climate change in both

coastal and coral reef environments (Chin et al. 2010, 2012). The blacktip reef shark may also be highly sensitive to this exposure. The use of specific coastal habitats for key reproductive stages suggests increased sensitivity at local scales since reliance on specific habitats and locations can increase localised risk (Yates et al. 2012). The species' biology also suggests that it is at a higher risk compared to other marine species and coastal sharks since it grows slowly and has low reproductive output (Tobin et al. 2010, Chin et al. 2013b), which suggests that protecting adult females may be especially important to sustaining viable populations. As such, the intensive use by breeding females of coastal habitats with high exposure to pressures increases the species' sensitivity as these areas are used for important life history events—mating, pupping and juvenile growth. Hypothetically, intensive fishing pressure within a 5 km² area of Cockle Bay could cause localised depletion of breeding females, and also remove a source of blacktip reef shark recruits to other areas along the coast and offshore coral reefs.

Nevertheless, it is essential to consider management objectives and the effects of scale when assessing vulnerability of mobile marine species and the effectiveness of management tools such as marine parks. For example, at regional scales, the blacktip reef sharks' exposure and sensitivity may be moderated by its abundance and adaptive capacity, which increases population-level resilience and may buffer localised impacts. The occurrence of the species in both coral reef and coastal environments suggests an inherent ecological flexibility such that habitat losses in one area could be offset by movement of individuals to new locations (Yates et al. 2012, Chin et al. 2013a). The species' wide distribution and mobility means that recruitment from other locations through juvenile dispersal and male migrations could help to replenish locally depleted populations and maintain genetic diversity (Chin et al. 2013a). Additionally, seascape-scale spatial management such as the Great Barrier Reef Marine Park zoning could reduce the exposure of mobile marine species while enhancing their adaptive capacity. This study revealed that blacktip reef sharks use a small area in Cockle Bay that lies entirely within a Conservation Park zone which prohibits commercial net fishing. Marine Park regulations and water quality management plans also place some controls on pollution in Cleveland Bay (see Supplement 3 at www.int-res.com/articles/suppl/m544p197_supp.pdf). These protections may help to sustain healthy habitats and populations of breeding females that supply recruits to other loca-

tions. Similar conservation and 'no take' zones along the GBRWHA coast may provide comparable protection for other blacktip reef shark populations, thus reducing the species' exposure at seascape scales while preserving dispersal and recruitment processes. Collectively, these findings suggest that the blacktip reef shark may be vulnerable to localised pressures, but may be resilient at seascape scales such as the GBRWHA. This example also illustrates the importance of carefully specifying spatial scales and management objectives when assessing species vulnerability or management effectiveness.

The population organisation and movement patterns of blacktip reef sharks in Cleveland Bay described here provide a different view of how sharks use coastal habitat and illustrate how habitat use can affect conservation and management; however, the study's limitations must be acknowledged. This study occurred in one area of the GBRWHA, and while there is evidence that localised populations of blacktip reef sharks exist in other areas of the GBRWHA, the residency and movements of these sharks in other turbid coastal regions have yet to be examined. Furthermore, the contributions of coastal habitats to the larger GBRWHA population will depend on the extent to which these habitats improve survival and recruitment of juveniles into the adult population compared to other locations and habitat types (e.g. offshore coral reefs). This information is currently unknown, and comparative studies with blacktip reef sharks in coral reefs on the GBRWHA have not been carried out. Additionally, the movement and habitat use data have only been qualitatively applied to a vulnerability framework; a more rigorous assessment (e.g. Chin et al. 2010) is required to fully describe the cumulative risk faced by blacktip reef sharks in coastal regions. Lastly, the limitations of the acoustic telemetry methods employed should be kept in mind. Residency and roaming analyses rely on the assumption that zero detection data (i.e. periods when tagged animals are not detected) indicates that the animal is absent. However, it is also possible that the tagged individuals had died, or were still present within the array but were undetected. While it is unlikely that tagged animals died after release (Chin et al. 2015), it is impossible to distinguish whether zero data indicates that an animal was absent, or it was present but undetected. Thus, it is possible that some individuals were present more often than detected. This is especially important for adult males, for which only limited data ($n = 4$) were available. Consequently, while catch and telemetry data both suggest that adult males are transient vagrants in

Cleveland Bay, more data are needed to verify these findings. It is also possible that the sharks used areas in Cleveland Bay that were outside receiver range. In particular, animals could also be using areas to the SE of Cockle Bay which would extend the KUD boundaries in that direction. While none of the resident individuals from Cockle Bay were detected on the gate receiver, and tag–recapture data suggest that blacktip reef sharks are unlikely to frequent that area (Chin et al. 2013c), it is possible that they used areas to the SE of Cockle Bay but were undetected. In this case, these animals could be exposed to additional risks such as net fishing. Further studies of reef shark movements in turbid coastal habitats, such as an expanded network of telemetry arrays, active tracking and expanded catch sampling and conventional tagging programs may resolve some of these uncertainties, providing a clearer understanding of the role turbid coastal habitats play in reef shark population dynamics and improving the rigour of risk assessments for coastal sharks and other mobile marine species.

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