Vol. 623: 85–97, 2019
https://doi.org/10.3354/meps13010

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 30

Fine-scale movements of juvenile blacktip reef sharks *Carcharhinus melanopterus* in a shallow nearshore nursery

Lachlan W. George[1,2,*], Ana P. B. Martins[1,2], Michelle R. Heupel[3], Colin A. Simpfendorfer[1]

[1]Centre for Sustainable Tropical Fisheries and Aquaculture & College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

[2]AIMS@JCU, Division of Research & Innovation, James Cook University, Townsville, QLD 4811, Australia

[3]Australian Institute of Marine Science, Townsville, QLD 4810, Australia

ABSTRACT: Limited information is available on the fine-scale movements and habitat use of juvenile sharks in very shallow (<1 m) nearshore areas and the factors that drive these behaviours. Active acoustic tracking was used to investigate movements and habitat use of juvenile (683 ± 58 mm total length; mean ± SD) blacktip reef sharks *Carcharhinus melanopterus* at Orpheus Island, Australia. Six juveniles were tracked by foot and boat for over 62 h. Juveniles moved in synchrony with tidal cycles, always remaining within very shallow (<1 m) sandy reef flat or reef crest waters during outgoing, low and incoming tides, and using inundated mangrove habitat during higher tides, indicating that tidal fluctuations were a major driver of movement and habitat use. Individuals never left the bay where they were captured or entered deep water beyond the fringing reef, restricting their movements within water <60 cm deep. In general, linearity and rate of movement were significantly higher during incoming or outgoing tides, whereas these measures were significantly lower during higher tide heights when juveniles were occupying mangrove habitats. The observed behaviour was most likely a predator-avoidance strategy, highlighting the importance of mangrove root habitat use by juvenile blacktip reef sharks in coastal nursery areas and indicating that this may be an essential habitat for the young of this species.

KEY WORDS: Active acoustic telemetry · Fine-scale movements · Nursery area · Predator avoidance · Tidal variation · Habitat use

1. INTRODUCTION

Nearshore areas support a wealth of marine biodiversity due to their high productivity and offer a variety of unique habitats that can be used by individuals and/or populations (Beck et al. 2001, Spalding et al. 2007, Knip et al. 2010). Due to the abundance of potential prey items and a diversity of habitat types, nearshore areas are often inhabited by numerous shark species, providing them with potential foraging and/or nursery grounds (Beck et al. 2001, Heupel et al. 2007, Adkins et al. 2016). The use of nearshore areas as a nursery for juvenile sharks has been suggested to improve their chances of survival through access to prey and increased protection from predators (Branstetter 1990, Heithaus 2007). Research on shark nursery areas has identified nurseries for individual (Cartamil et al. 2010, Froeschke et al. 2010) and multiple species (Simpfendorfer & Milward 1993, Parsons & Hoffmayer 2007), described resource partitioning within communal nurseries (Kinney et al. 2011, Heupel et al. 2019) and has helped to better understand the ecology of juveniles within these areas, especially for members of the families Carcharhin-

*Corresponding author: lachlan.george@my.jcu.edu.au

idae and Sphyrnidae (e.g. Simpfendorfer & Milward 1993, Rechisky & Wetherbee 2003, Knip et al. 2010).

The high productivity of nearshore areas is largely due to the fact that they are highly dynamic environments with constantly changing environmental (abiotic and biotic) conditions that occur at different temporal scales (Knip et al. 2010). This high variability makes living in such environments challenging. Studies have shown that a number of abiotic factors such as temperature (Cartamil et al. 2010, Matich & Heithaus 2012), salinity (Heupel & Simpfendorfer 2008, Ubeda et al. 2009), tidal movement (Ackerman et al. 2000, Conrath & Musick 2010) and depth (Wetherbee et al. 2007, Guttridge et al. 2012) influence the behaviour of juvenile sharks in nearshore waters. Biotic factors such as the presence of prey (Curtis et al. 2013) and predators (Heupel & Hueter 2002, Wetherbee et al. 2007) are also documented as drivers of juvenile shark movements within nursery areas. To access the benefits of nursery areas in nearshore environments, inhabitants must deal with the dynamic nature and challenges presented by these areas.

Understanding how sharks respond to environmental changes has largely been achieved by monitoring their movements with the use of passive acoustic telemetry (Schlaff et al. 2014). Although this method has enabled researchers to track the movements of many different shark species and assist in the process of determining the drivers responsible for their movements, passive acoustic telemetry has its limitations (Heupel et al. 2006), especially in nearshore nursery areas which, in some cases, present unique challenges. To understand how some environmental factors influence the movement and habitat use of sharks, detailed information is required at a much finer scale (on the scale of metres) than can be achieved using passive acoustic telemetry, due to the physical attributes (e.g. very shallow water, complex habitats) of the environment (Heupel et al. 2006). Consequently, limited information is available on fine-scale movements of juvenile sharks in very shallow (<1 m) nearshore nursery areas and how they deal with the dynamic nature of nearshore environments.

The blacktip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) is a widely distributed whaler shark occurring throughout the tropics; from the Red Sea and western Indian Ocean to the western and central Pacific (Last & Stevens 2009). This species is commonly observed in clear shallow waters on and around coral reefs (Heupel 2005, Last & Stevens 2009). However, it has also been found to inhabit turbid nearshore environments that lack coral reef habitat and are predominantly comprised of mangroves, seagrass beds and mudflats (Lyle 1987, Chin et al. 2012). Studies have since shown that this species regularly occurs within non-reef areas which may be important for reproduction and early life stages, with juveniles sometimes using these habitats as a nursery, before undergoing ontogenetic shifts in habitat use (Chin et al. 2013a). Although long-term studies investigating the space use and movements of juvenile blacktip reef sharks in nearshore environments have been conducted (Stevens 1984, Papastamatiou et al. 2009, Chin et al. 2013a, Schlaff et al. 2017), fine-scale space use and factors that influence their movement and habitat use, other than those investigated by Schlaff et al. (2017), in shallow (<1 m) environments have not previously been examined.

The principal objective of this study was to examine the movements and habitat use of juvenile blacktip reef sharks within a nearshore intertidal nursery area. In this study, we (1) quantified fine-scale movements, (2) examined tidal fluctuation as a driver of movement and (3) investigated patterns of habitat use. Knowledge on fine-scale movements will improve our understanding of the spatial ecology and importance of habitat types to this species and will advance our knowledge on the use of coastal nurseries and the ecology and behaviour of juvenile sharks within these areas. Understanding space and habitat use can contribute to successful management, as the identification of important areas (i.e. foraging or nursery) and key habitats can inform conservation practices where necessary (Simpfendorfer & Heupel 2012). This is important for nearshore areas which are increasingly exposed to high levels of anthropogenic impacts such as fishing pressure (Jackson et al. 2001, Knip et al. 2010, Dulvy et al. 2014), coastal development and habitat loss (Lotze et al. 2006), all of which can negatively affect the survival rate and essential habitats important to juvenile sharks in nursery areas (Jennings et al. 2008).

2. MATERIALS AND METHODS

2.1. Study site

Research was conducted at Orpheus Island on the central Great Barrier Reef (Fig. 1a), specifically in Pioneer Bay (Fig. 1b). The bay has an area of approximately 0.80 km^2. The shoreline of Pioneer Bay is dominated by non-estuarine mangrove stands, predominantly *Rhizophora* spp., although a number of other species such as *Avicennia marina* and *Osbornia*

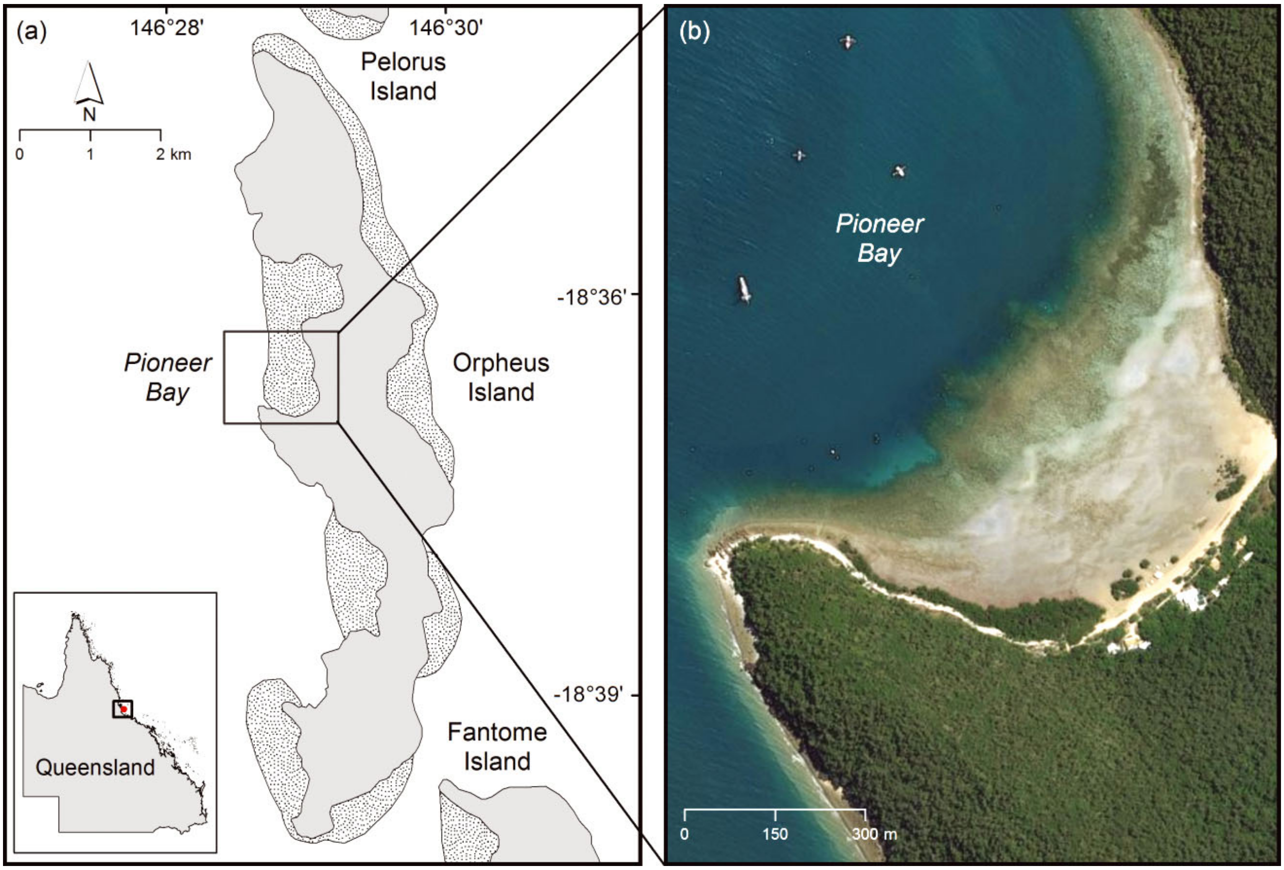

Fig. 1. Study site. (a) Orpheus Island located in the Palm Island group in the Great Barrier Reef World Heritage Area (insert shows the location of the study site within Queensland, Australia). Light grey stippling represents reef flat habitat. (b) Pioneer Bay at Orpheus Island

octodonta are also present (S. Cannici pers. comm.). The bay is characterised by a sandy flat extending from the shoreline transitioning into a reef flat comprised of dead microatolls and sand which is bordered by a fringing reef that falls to a sandy substrate in deeper water of approximately 10 m. Tidal variation within Pioneer Bay is large (~4 m range); during high tide, the intertidal reef flat and mangrove stands are flooded, whilst during low tide they are generally void of water.

2.2. Field methods

Field work was carried out between April and August 2017. Sharks were caught using 3 different methods: rod and reel, seine and gillnet. Sharks caught on rod and reel were captured using size 8/0 Mustad hooks and pilchards (*Sardinops* sp.) as bait. Seine netting (20 m long, 1 cm mesh size and 2 mm line) was used in shallow waters when sharks were swimming along the shoreline or amongst mangroves. The gillnet used was 60 m long and 2.5 m deep with a mesh size of 10 cm and 0.18 mm line. Soaking times varied between 1 and 2 h, with the net checked constantly and generally set during incoming and outgoing tides. Once caught, sharks were sexed, measured to the nearest mm (total length, TL) with a measuring tape and tagged with a small Dalton Rototag on the first dorsal fin. A Vemco V9 (9 × 29 mm) acoustic transmitter was attached to the Rototag using small cable ties. Each transmitter was coded with a unique frequency ranging between 75 and 84 kHz and pinged continuously. Handling time for each shark was <10 min, and sharks were released at the site of capture.

Sharks were tracked on foot or from a small dinghy using a VR100 ultrasonic acoustic receiver and handheld directional hydrophone (Vemco). At 5 min intervals, a GPS point was recorded by the tracking team using a handheld GPS, with this location assumed to be the location of the shark (Rechisky & Wetherbee

2003). GPS points were recorded when the shark was visibly sighted or when the strongest signal was recorded at the lowest gain setting on the receiver. The activity, habitat and substrate type, depth and important surroundings (e.g. potential predators, prey, feeding attempts) were also recorded. When tracking on foot, the tracking team consisted of 2 people, one recording GPS points and taking notes, the other manoeuvring the hydrophone and towing the VR100 on a small surf ski. As with any study that requires an observer to be present, such as during active tracking, there is the possibility of altering the animal's behaviour. Therefore, to minimise disturbance that may have influenced the animal's behaviour, tracking was conducted in a quiet and calm manner and all movements were ceased when the animal was in sight or approaching the tracking team. When tracking from a boat, the engine was immobilised once the general location of the animal was established (Curtis et al. 2013). Only 1 shark was tracked at a time. Individuals were tracked for as long as possible during daylight hours, with tracks only ceasing due to limited light or loss of signal. When a track was suspended, the animal was relocated the following day if possible and tracked again, resulting in multiple tracks for the same individual. Upon completion of the study, Rototags and acoustic tags remained on the sharks. If recaptured, the acoustic tag was removed from the Rototag if it had expired; however Rototags were left in place as they are a useful tool to identify individuals in the future.

2.3. Data analysis

Tracks were analysed in the statistical software R (Version 3.5.0) (R Development Core Team 2016) using the package 'adehabitatLT' (Calenge 2015). Latitude and longitude were converted to Universal Transverse Mercator (UTM) so that distance measures were in metres. If tracks contained missing values due to issues such as signal loss, the data were formatted so that observations were regular (Calenge 2015). If the signal was lost for more than 60 min and then re-acquired, it was considered a new track in the analysis.

2.3.1. Segmenting movements

Movement paths were segmented into intervals of homogenous behaviour using the Lavielle method (Calenge 2015), a function within the 'adehabitatLT' package to determine the frequency at which the juvenile sharks changed their movement behaviour during a track. The Lavielle method selected the segmentation of a time series, using speed and residence time as parameters, searching for the best path from the first to last observation in a contrast matrix. It used an algorithm that finds the most appropriate path through the matrix (Calenge 2015). Segments were then chosen from a graphical illustration. To understand how behaviour may have been influenced by tide height, the mean tide height of a segment was calculated (using local tide charts) and plotted against segment length to determine if a correlation was present.

2.3.2. Linearity

Tortuosity of a movement path can be described as the degree of convolution or straightness of a path (Bascompte & Vilà 1997). One method of estimating the tortuosity of a movement track is to use an index of linearity (Benhamou 2004). The linearity index (L) is given by the equation:

$$L = (F_n - F_1) / D \quad (1)$$

where $F_n - F_1$ is the distance from the first point to the last point, and D is the summed distance between all points (Bell & Kramer 1979). Linearity values range from 0 to 1, with values near 0 indicating random movement and values of 1 representing linear movement (Bell & Kramer 1979). Linearity was calculated as a moving 5-point value, whereby the first 5 points of a track were used to calculate the first value of linearity for the track. The first value in the sequence of 5 was then removed and the next position added to the remaining values and linearity calculated again. This process was repeated until all locations in the track were included in the analysis. The effect of tidal height on linearity was examined using a generalised linear mixed effects model with the 'glmmTMB' package in R (Magnusson et al. 2017), with individual as a random factor. A third-order polynomial natural spline (df = 3) was then applied to model the effect of tide height. A third-order natural spline was chosen, as it was found to be the best fit for tide height. Using the 'expand.grid' function within R, a new data frame containing all possible combinations of variables was created to predict over the mixed effects model to show the effect of tide height on linearity.

2.3.3. Rate of movement

Rate of movement (ROM) was determined for each 5 min period as distance travelled per minute (m min^{-1}). To investigate if ROM varied with tide height, a polynomial function was fitted to the data using the same procedures as were used for linearity. Data were not normally distributed and natural log transformed prior to statistical testing.

2.3.4. Habitat use

To understand the importance of habitat and to help infer how drivers influence juvenile movements, particularly tide height, habitat use was also examined. As Pioneer Bay is tidally influenced, many habitats were not always accessible to the juvenile sharks. During periods of high tide, the bay is flooded, submerging the fringing mangroves. However, during low tide, water recedes from the bay, leaving the mangrove stands and much of the reef flat dry. Consequently, mangrove habitat could only be used by juveniles during certain tidal heights. Using tracking data and observational notes recorded during tracking, we estimated that juveniles could only access mangrove habitat when the tide height was ≥185 cm (±34 cm, SD). To determine if there was a correlation between tide height and the use of mangrove habitat, observational notes were used to calculate the time juveniles spent within the mangrove stands, as well as the time they occurred outside of the mangrove habitat when it was accessible (i.e. tide height ≥185 cm) and compared to the corresponding average tide height for that period.

3. RESULTS

Six juvenile blacktip reef sharks were actively tracked in Pioneer Bay during the study, with 3 individuals tracked in April–May, 1 in July and 2 in August. Two females and 4 males were tracked (Table 1). Size ranged from 618 to 770 mm (TL), with all individuals considered juveniles based on their size (Chin et al. 2013b). The 6 individuals generated 18 tracks which varied in duration from 1 h to 7 h 35 min. All tracks of all individuals were retained for analysis as we found no obvious effect of tagging on shark ROM between tracks immediately after release and later tracks (ANOVA with Tukey post hoc test, $p > 0.05$). Variation in track duration was predominantly a result of signal loss due to being obscured by complex habitats such as mangrove roots and coral, accessibility to habitat due to tidal stage and daylight. Individual R07869 was tracked longer than all other individuals (8 d) to investigate inter-day variability in movement and habitat-use patterns.

Table 1. Details of 6 actively tracked juvenile blacktip reef sharks in Pioneer Bay, Orpheus Island, Australia. If possible, sharks were tracked for more than 1 d, resulting in multiple tracks for individuals. A total of 18 tracking sessions were carried out. TL: total length

Tag ID	Sex	Size (mm TL)	Date caught	Track	Date of track	Duration of track (h:min)	Total time tracked (h:min)
R07854	F	710	24/04/17	1	24/04/17	01:50	04:40
				2	25/04/17	02:50	
R07858	M	620	27/04/17	1	27/04/17	01:00	10:05
				2	28/04/17	04:15	
				3	29/04/17	04:50	
R07856	M	618	30/04/17	1	02/05/17	03:25	06:20
				2	03/05/17	01:45	
				3	05/05/17	01:10	
R07870	M	680	08/07/17	1	09/07/17	04:35	04:35
R07869	F	700	17/08/17	1	17/08/17	01:35	31:10
				2	18/08/17	03:50	
				3	19/08/17	03:35	
				4	20/08/17	02:45	
				5	23/08/17	03:10	
				6	24/08/17	03:30	
				7	25/08/17	07:35	
				8	26/08/17	05:10	
R07868	M	770	21/08/17	1	22/08/17	05:20	05:20

Sharks were tracked either immediately after capture and tagging or located the following day, depending on the time of capture. Individuals were generally found close to the site of capture or at least on the same side of the bay if tracking was initiated the following day or within the same area where a previous track was terminated. Tracking revealed that most juveniles remained on the same side of the bay on which they were originally caught during any one tidal cycle, making occasional expeditions into the centre of the bay but never crossing to the other side. However, the individual tracked for 8 d used both sides of the bay over the period of tracking (Fig. 2). Some juveniles repeated their movement paths from the previous day, mov-

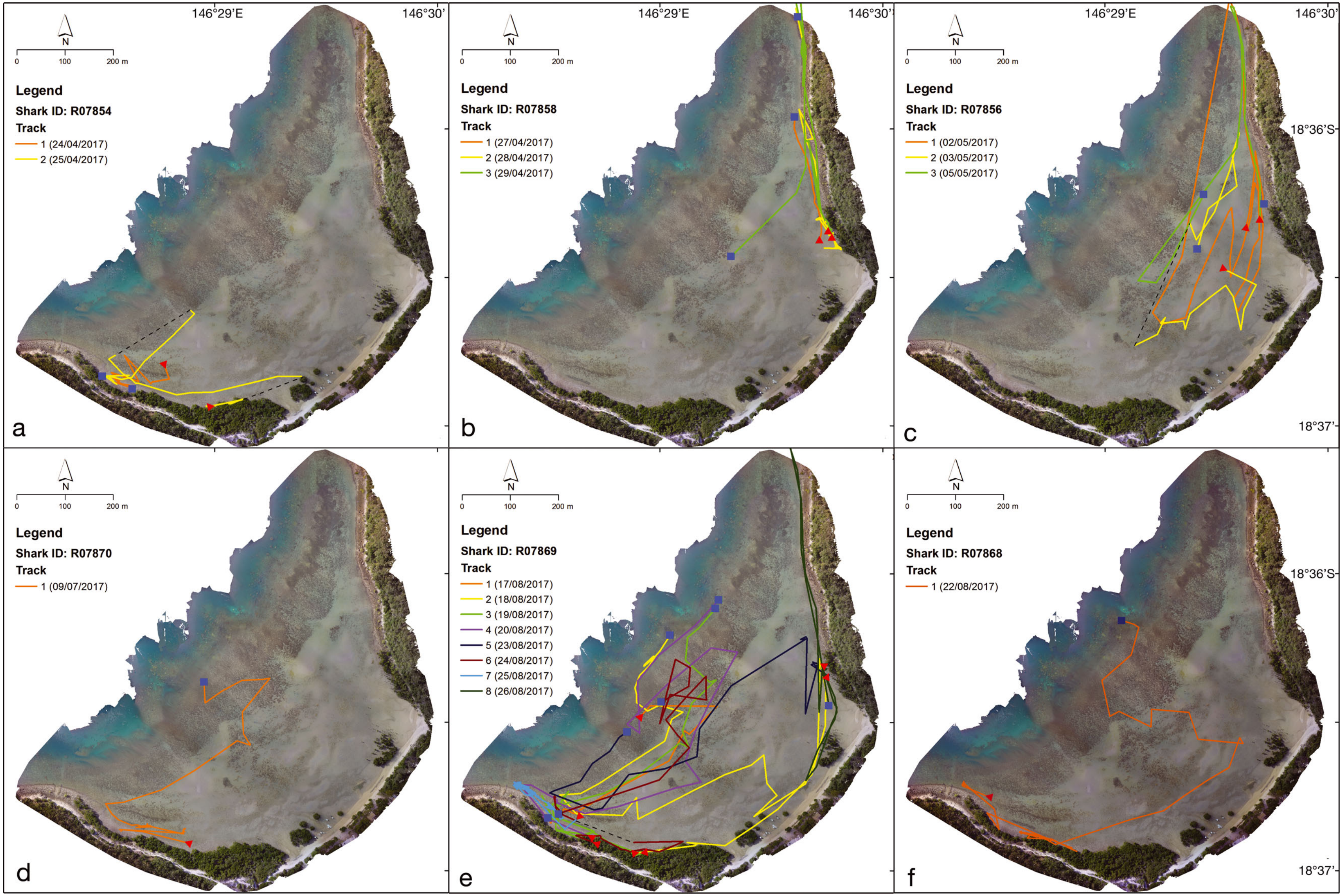

Fig. 2. Movement paths of manually tracked juvenile blacktip reef sharks in Pioneer Bay, Orpheus Island. Red triangles represent the beginning of a track and blue squares represent the end of a track. Dashed lines correspond to the loss of signal for more than 60 min when tracking. Dates represent the date of the track. All sharks remained within Pioneer Bay, moving over the intertidal reef flat during outgoing and incoming tides

ing along a near-identical path. Other sharks also occasionally mirrored previous tracks from other juveniles when occupying the same side of the bay.

Tracking occurred over a range of tidal heights, during neap and spring tides, with juveniles predominantly restricting their movements to fringing mangroves (swimming amongst the complex root system) inside the bay during high tide before moving out onto the reef flat as the tide dropped and eventually moving to the edge of the fringing reef. During neap high tides, sufficient water remained in the bay submerging mangrove roots and allowing juvenile sharks to enter the root system. All sharks remained inside Pioneer Bay, with none tracked further than the fringing reef (Fig. 2). During low tide, sharks were tracked on the fringing reef but were never observed to leave the reef crest and enter deeper water, with spring low tides exposing the reef flat and forcing individuals further onto the reef crest, closer to deeper, open water. Juveniles repeatedly swam in depths of approximately 40 to 60 cm during outgoing or incoming tides and were rarely observed moving into water >1 m. When observed attempting to catch prey, juveniles were occasionally sighted moving into water <10 cm deep.

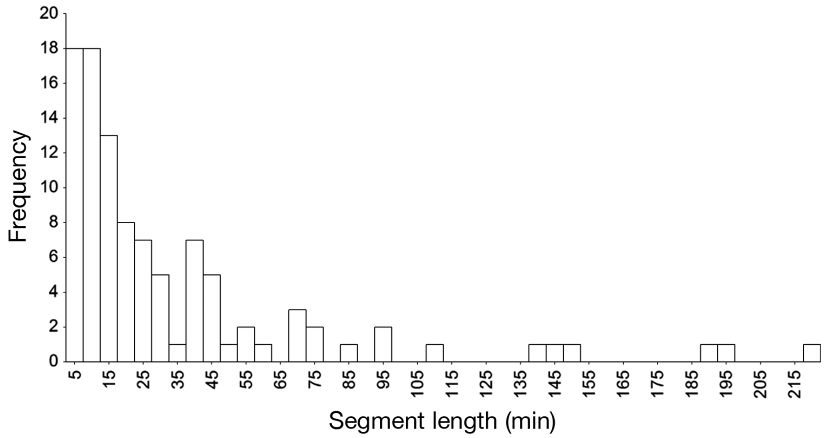

Fig. 3. Frequency of segment lengths (intervals of homogenous behaviour) calculated by the Lavielle method (see Section 2.3.1) for actively tracked juvenile blacktip reef sharks

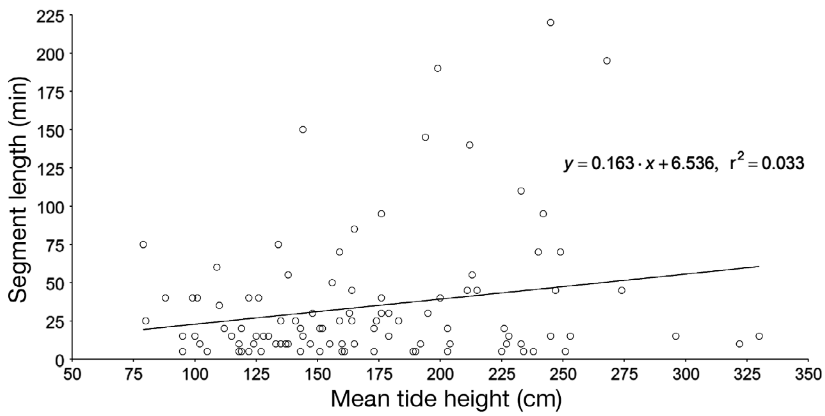

Fig. 4. Segment length calculated by the Lavielle method as a function of mean tide height. Line represents a regression line, where *y* is segment length and *x* is mean tide height

3.1. Segmented movements

Segments of consistent behaviour defined by the Lavielle method ranged in length from 5 to 220 min (Fig. 3). More than 80% of segment lengths were <50 min, with 5 and 10 min segments occurring most frequently (17.8%), followed by 15 min segments (12.8%). Only 7 segments were >100 min, with the longest being 220 min. The high number of small segments suggests that during a track, juveniles rarely maintained a constant behaviour for long periods of time. A weak, but significant, correlation was found between segment length and mean tide height (r^2 = 0.03, p = 0.04), with segment length increasing as mean tide height increased (Fig. 4). The majority of long segment lengths (>100 min) occurred when juveniles were tracked in mangrove habitat during high tide.

3.2. Linearity

Linearity of tracks ranged from 0.28 to 0.79, with mean linearity of each track being 0.50 (±0.13, SD). Linearity differed significantly with tide height (Table S1 in the Supplement at www.int-res.com/articles/suppl/m623p085_supp.pdf), with juveniles showing more linear movements during lower tide heights while displaying more random movements during higher tide heights (Fig. 5a). Highest average linearity values were recorded during tide heights between 100 and 150 cm, and the lowest average values were recorded during tide heights >300 cm.

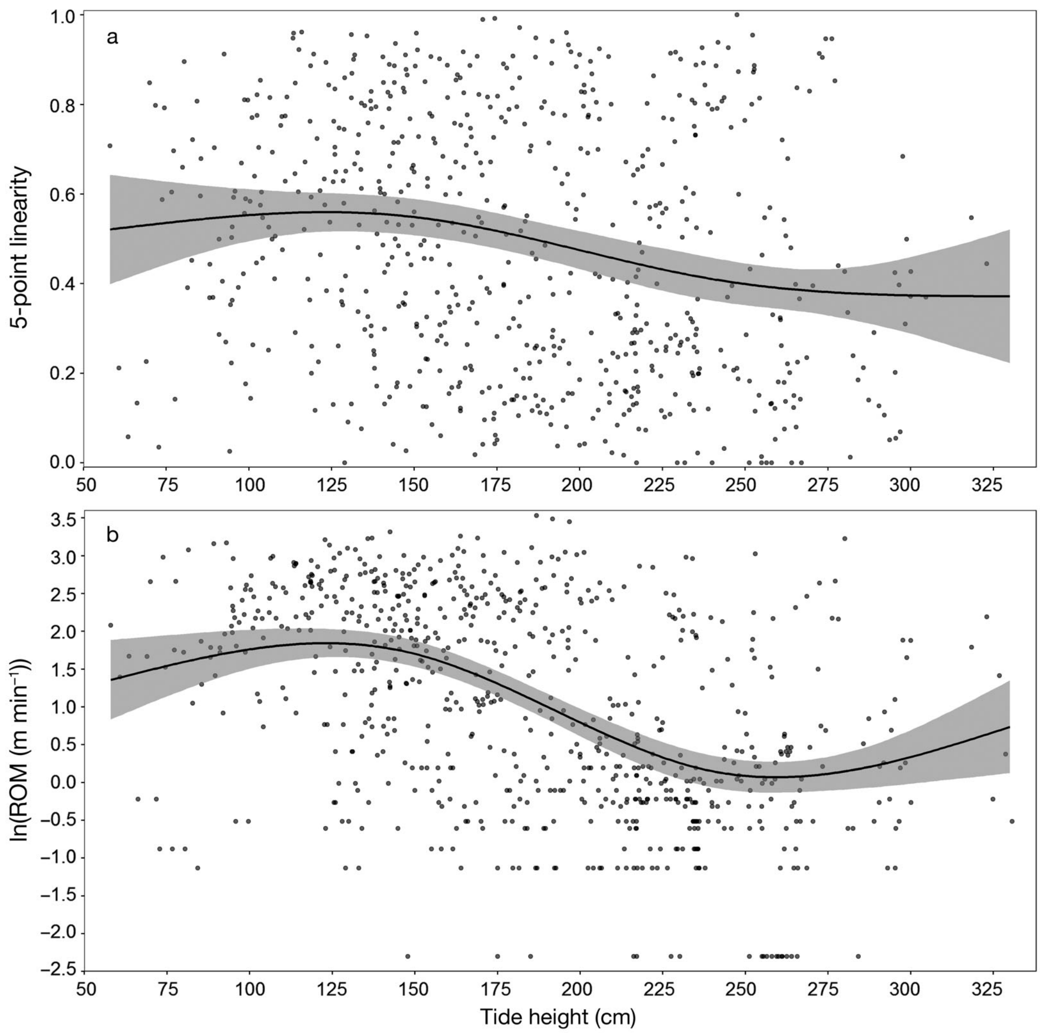

Fig. 5. Predicted trends in (a) linearity and (b) rate of movement (ROM) of actively tracked juvenile blacktip reef sharks in relation to tide height. Grey shading represents 95% confidence intervals and points represent raw data. ROM data were not normal and therefore natural-log transformed

3.3. ROM

Mean ROM for tracked sharks was (mean ± SD) 7.23 ± 3.59 m min^{-1} (range = 1.82–16.77 m min^{-1}). Tide height had a significant effect on ROM (Table S2). ROM was highest during lower tide heights (Fig. 5b). The highest average ROM occurred between tide heights of 100 and 150 cm, whereas the lowest average ROM was recorded between tide heights of 225 and 275 cm.

3.4. Habitat use

Juvenile sharks spent 15 min to >3 h in mangrove habitat during tracking (Fig. S1). Although there were no apparent trends in the amount of time spent in mangrove habitat, it is clear that in some cases juveniles spent a considerable amount of time within this habitat. On 3 occasions, juveniles were tracked in mangrove habitat for periods between 121 and 125 min, and the 2 longest recorded times a juvenile spent in mangrove habitat were 170 and 185 min. When accessible (i.e. tide height ≥185 cm), juveniles spent 70% of the recorded time in the mangroves, with limited time spent outside during this period (Fig. 6). The greatest length of time spent outside of the mangroves when they were accessible was 230 min. This instance was during the track of individual R07869 which was nearly 8 h in length and included numerous observations of circling and feeding on bait fish that were schooling outside of the mangroves at high tide.

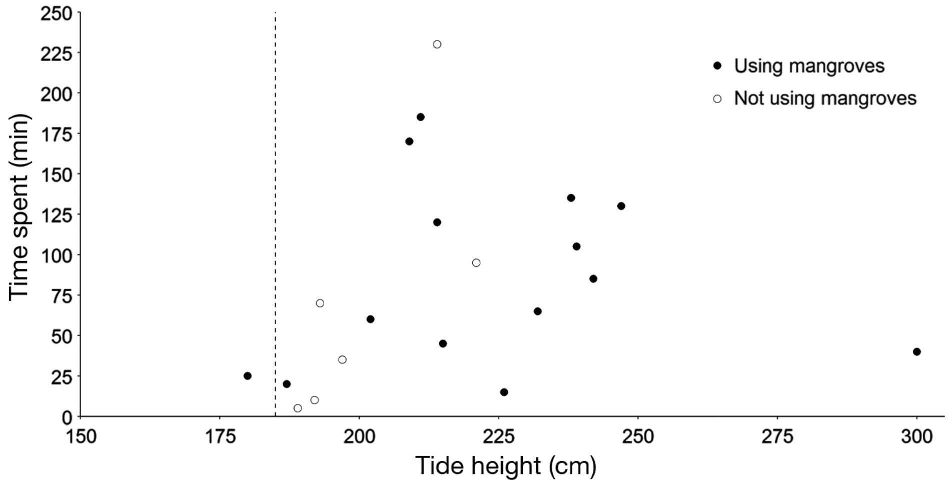

Fig. 6. Use of mangrove habitat by juvenile blacktip reef sharks in Pioneer Bay when mangroves were accessible. Points represent the duration of time during a track that a juvenile shark spent either using or not using the mangrove habitat. Dashed line represents tide height at which mangrove habitat was accessible to juvenile sharks (185 ± 34 cm, mean ± SD)

4. DISCUSSION

Active tracking data from this study revealed that small juvenile blacktip reef sharks in Pioneer Bay were strongly influenced by tidal cycles. Daily tide fluctuations were found to regulate juvenile movements and habitat use, suggesting that tide height is one of the main environmental drivers of movement for these individuals. Juveniles moved in synchrony with tidal cycles, remaining within very shallow waters during outgoing, low and incoming tides, while using submerged mangrove habitat during high tides. Other juvenile sharks have also been recorded moving with the tide, including lemon *Negaprion brevirostris* (Wetherbee et al. 2007, Guttridge et al. 2012), sandbar *Carcharhinus plumbeus* (Medved & Marshall 1983, Rechisky & Wetherbee 2003) and pigeye *C. amboinensis* sharks (Knip et al. 2011). In all cases, movements allowed juvenile sharks to remain in the shallowest possible water. Therefore, tidal variation and access to key habitats appear to be integral components of the movement strategy of many juvenile sharks inhabiting very shallow regions.

The movements exhibited by juvenile blacktip reef sharks in the current study were very similar to those of juvenile mangrove whiprays *Urogymnus granulatus* studied in the same location by Davy et al. (2015). Rays were observed to occupy mangrove habitat during high tide, before exiting with the outgoing tide, following the shallow edge of the water and returning to the mangroves with the incoming tide. Simpfendorfer et al. (2010) also reported similar movement patterns in juvenile smalltooth sawfish *Pristis pectinata*, whereby individuals moved with the ebb and flow of the tide, continuously tracking the shallow edges of the water. Davy et al. (2015) concluded that the behaviour demonstrated by the rays was most likely due to predator avoidance. This cyclic movement by the juvenile blacktip reef sharks may also be a predator-avoidance strategy based on use of the reef flat by larger sharks at high tide (L. George pers. obs.).

The use of shallow-water environments by juvenile blacktip reef sharks may be a common survival strategy, since this behaviour has also been documented at Aldabra Atoll (Stevens 1984), Palmyra Atoll (Papastamatiou et al. 2009) and Ningaloo, Western Australia (Speed et al. 2011, Oh et al. 2017). Juveniles in the present study were never tracked further than the reef crest or observed entering deep water beyond the fringing reef. This provides evidence of selection for shallow waters and suggests that these areas provide the necessary resources for small juvenile blacktip reef sharks since they do not appear to use deeper-water areas, despite the potential for increased prey availability. Avoiding deep-water environments has been observed in other juvenile shark populations inhabiting tidally influenced environments. For example, Wetherbee et al. (2007) found that juvenile lemon sharks at Atol das Rocas in Brazil restricted their movements to shallow tidal pools during low tide, avoiding deeper areas. It is also possible that this behaviour may be beneficial to juveniles for locating prey. As fish move within the shallows during the incoming and outgoing tide, they may be easier for juvenile sharks to prey upon due to the lack of escape routes. Juveniles may therefore be moving within the shallows of the fluctuating tides not only to avoid predators, but also to follow and potentially consume prey (Papastamatiou et al. 2009, Knip et al. 2011). During high tide, juveniles were frequently tracked within mangroves, with some individuals spending extended periods of time within this habitat before exiting with the outgoing tide. A similar pattern was observed in actively tracked juvenile lemon sharks where juveniles often penetrated dense mangrove habitat (Morrissey & Gruber 1993a). Likewise, Guttridge et al. (2012) reported that juvenile lemon sharks used a shallow mangrove inlet during high tide to avoid sub-adult conspecifics. Therefore, heavy use of mangrove habitats appears to be similar among juveniles of species that occur near these habitats.

Sharks tracked for consecutive days often showed consistent patterns within their movements, restricting their activity to a particular side of the bay. Although movement paths were different between individuals in relation to the side of the bay they were tracked in and their exact path of movement, individuals generally repeated the same or similar movement path from the previous day and some carried out very similar movements to other individuals that were tracked in the same location. Similar movements between tracks have been observed in Hawaii, where juvenile scalloped hammerheads *Sphyrna lewini* schooled during the daytime before dispersing to forage at night and then returning to the same core area the following day (Holland et al. 1992, 1993). The authors attributed this behaviour to predator avoidance. Morrissey & Gruber (1993b) also reported repeated lap-like movements of juvenile lemon sharks in the shallows along the shoreline in Bimini, Bahamas, while Simpfendorfer et al. (2010) documented repeated use of a mangrove drainage creek by a juvenile smalltooth sawfish, with the individual returning to the same location during each high-tide period. Like the juvenile lemon sharks monitored by Guttridge et al. (2012), the juveniles in our study may have used repeated movements based on success in avoiding predation or capturing prey. Interestingly, the blacktip reef shark that was tracked for a period of 8 d used both sides of the bay and generally did not repeat movement paths the following day, something that may have been observed in the other juveniles had they been tracked longer. This difference in pattern suggests that further study is required to more fully understand movement patterns within the broader population.

When transitioning between mangrove habitat and the fringing reef during outgoing and incoming tides, juveniles moved with direction and at higher speeds than other times. Davy et al. (2015) also documented this trend in actively tracked juvenile mangrove whiprays. This behaviour suggests that the juvenile sharks were moving with a purpose. Although moving with direction, segment lengths were very short during this tidal period, indicating that individuals were changing their behaviour frequently. During outgoing and low tides when the juveniles are moving into shallower water, they may be susceptible to stranding as the water recedes, explaining their more directed and higher rates of movement as well as regular changes in behaviour. A need to move with the pace of the dropping tide may explain the observed direct and high ROM, whereas the constant change in behaviour may be a result of the sharks trying to avoid becoming trapped in tidal pools or feeding. During large tide fluctuations, Pioneer Bay is generally devoid of water. The shallow, consistent nature of the sand flats precludes the creation of tide pools that individuals could use; they must therefore move to the reef crest to avoid stranding. In some instances, juveniles were observed to chase prey during lower tides (L. George pers. obs.), which may also explain some of the changes in behaviour.

During high tide, random movements at low speed were more typical and segment length was longer, indicating that the behaviour of the juveniles remained unchanged for extended periods. Juveniles often entered mangrove habitats during higher tides and therefore the need to move with direction and speed to avoid becoming stranded was no longer an issue due to the large volume of water and the protection offered by the mangrove roots. The juvenile sharks in this study appeared to be carrying out repeated lap-like movements while in the mangrove habitat waiting for the tide to recede.

Movement within and direct use of mangrove habitats by juvenile blacktip reef sharks has not previously been investigated. Earlier studies in nearshore areas have documented the presence of juveniles near mangrove habitats (Chin et al. 2013a), suggesting they may play a role in the early life stages of this species, but have not documented use. A number of habitats are available in Pioneer Bay during high tide; however, juveniles regularly used mangroves lining the shore, penetrating their complex root system and only spending a small proportion of time outside of this habitat when it was accessible. The use of mangrove habitat by juvenile elasmobranchs has previously been documented in a number of nearshore environments (Morrissey & Gruber 1993a, Simpfendorfer et al. 2010, Davy et al. 2015, Escalle et al. 2015), with studies suggesting that the mangrove habitat was used by juveniles as a means of predator avoidance. Potential predators of juvenile blacktip reef sharks include any larger shark. Adult blacktip reef and sub-adult sharptooth lemon sharks *N. acutidens* were regularly observed entering Pioneer Bay and patrolling mangrove edges during high tide (L. George pers. obs.), while other large sharks present within the area may also enter the bay, but are observed less often. Due to the density of the mangrove prop roots in the bay, potential predators and also competitors (e.g. large fish) would have difficulty penetrating the mangrove habitat system, which therefore acts as a refuge for small juvenile blacktip reef sharks.

Other studies have suggested that the use of mangrove habitat by juvenile elasmobranchs may increase their access to prey (e.g. Morrissey & Gruber 1993a, Simpfendorfer et al. 2010). Mangrove habitats are also commonly used by teleost fish as refuges from predators (Verweij et al. 2006) and to forage for prey (Chittaro et al. 2005), and in some cases, they act as nurseries (Nagelkerken et al. 2000, Mumby et al. 2004). Barnes et al. (2012) examined the use of mangrove habitat by coral reef fish in Pioneer Bay and found that 38 species occurred within the mangroves. The high abundance of fish within this habitat may also be drawing juvenile blacktip reef sharks into the mangroves. Dietary analysis of blacktip reef sharks has found that teleost fish are the predominant prey (Stevens 1984, Lyle 1987). It is therefore possible that juveniles are entering the mangroves during high tide and spending the majority of their time within them not only to avoid predators, but also to access the high abundance of potential prey. Further research into the use of mangrove habitat by small juvenile blacktip reef sharks will provide greater understanding of their use and importance. These future studies should aim for larger sample sizes to provide more conclusive generalisations in regards to movement patterns and incorporate night time tracks to help understand if the juveniles exhibit diel changes in behaviour. However, it appears that protecting mangrove habitat in coastal areas will be beneficial to juvenile blacktip reef sharks, as it plays an important role in their predator-avoidance strategy within nursery areas.

Acknowledgements. We thank the staff and students of the Fishing and Fisheries Research Group at James Cook University (JCU) for their support and assistance in the field: K. Potgieter, I. Bouyoucos, E. Higgins, S. Mukherji and D. Tonnet. We also thank E. Lédée and S. Bierwagen for support with ArcGIS, J. Smart for assistance with data analysis and K. Joyce for providing high-resolution imagery of Pioneer Bay. This project was funded by the JCU College of Science and Engineering, with additional funds from AIMS@JCU. Research was conducted under Great Barrier Reef Marine Park Authority Permit G15/37987.1, Queensland General Fisheries Permit 187250 and JCU Animal Ethics Committee Permit A2310.

LITERATURE CITED

Ackerman JT, Kondratieff MC, Matern SA, Cech JJ (2000) Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environ Biol Fishes 58:33–43

Adkins ME, Simpfendorfer CA, Tobin AJ (2016) Large tropical fishes and their use of the nearshore littoral, intertidal and subtidal habitat mosaic. Mar Freshw Res 67: 1534–1545

Barnes L, Bellwood DR, Sheaves M, Tanner JK (2012) The use of clear-water non-estuarine mangroves by reef fishes on the Great Barrier Reef. Mar Biol 159:211–220

Bascompte J, Vilà C (1997) Fractals and search paths in mammals. Landsc Ecol 12:213–221

Beck MW, Heck KL Jr, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Bell WJ, Kramer E (1979) Search and anemotactic orientation of cockroaches. J Insect Physiol 25:631–640

Benhamou S (2004) How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? J Theor Biol 229:209–220

Branstetter S (1990) Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In: Pratt HL, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech Rep NMFS 90, p 17–28

Calenge C (2015) Analysis of animal movements in R: the adehabitatLT package. R Package Version 0.3.23. https://CRAN.R-project.org/package=adehabitatLT

Cartamil D, Wegner NC, Kacev D, Ben-aderet N, Kohin S, Graham JB (2010) Movement patterns and nursery habitat of juvenile thresher sharks *Alopias vulpinus* in the Southern California Bight. Mar Ecol Prog Ser 404: 249–258

Chin A, Tobin A, Simpfendorfer C, Heupel M (2012) Reef sharks and inshore habitats: patterns of occurrence and implications for vulnerability. Mar Ecol Prog Ser 460: 115–125

Chin A, Heupel M, Simpfendorfer C, Tobin A (2013a) Ontogenetic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. Aquat Conserv 23: 468–474

Chin A, Simpfendorfer C, Tobin A, Heupel M (2013b) Validated age, growth and reproductive biology of *Carcharhinus melanopterus*, a widely distributed and exploited reef shark. Mar Freshw Res 64:965–975

Chittaro PM, Usseglio P, Sale PF (2005) Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. Environ Biol Fishes 72:175–187

Conrath CL, Musick JA (2010) Residency, space use and movement patterns of juvenile sandbar sharks (*Carcharhinus plumbeus*) within a Virginia summer nursery area. Mar Freshw Res 61:223–235

Curtis TH, Parkyn DC, Burgess GH (2013) Use of human-altered habitats by bull sharks in a Florida nursery area. Mar Coast Fish 5:28–38

Davy LE, Simpfendorfer CA, Heupel MR (2015) Movement patterns and habitat use of juvenile mangrove whiprays (*Himantura granulata*). Mar Freshw Res 66:481–492

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. eLife 3:e00590

Escalle L, Speed CW, Meekan MG, White WT, Babcock RC, Pillans RD, Huveneers C (2015) Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters. J Fish Biol 87: 323–341

Froeschke JT, Stunz GW, Sterba-Boatwright B, Wildhaber ML (2010) An empirical test of the 'shark nursery area concept' in Texas bays using a long-term fisheries-independent data set. Aquat Biol 11:65–76

Guttridge TL, Gruber SH, Franks BR, Kessel ST and others (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris.* Mar Ecol Prog Ser 445:279–291

Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. Am Fish Soc Symp 50: 3–13

Heupel M (2005) Species status reports: blacktip reef shark *Carcharhinus melanopterus*. In: Fowler SL, Cavanagh RD, Camhi M, Burgess GH and others (eds) Sharks, rays and chimaeras: the status of the chondrichthyan fishes. Status survey. IUCN/SSC Shark Specialist Group, Gland, p 296–297

Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Mar Freshw Res 53:543–550

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277–289

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Heupel MR, Munroe SE, Lédée EJ, Chin A, Simpfendorfer CA (2019) Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage. Mar Biol 166:68

Holland K, Lowe C, Peterson J, Gill A (1992) Tracking coastal sharks with small boats: hammerhead shark pups as a case study. Mar Freshw Res 43:61–66

Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead shark pups on their natal grounds. Copeia 1993:495–502

Jackson JB, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Jennings DE, Gruber SH, Franks BR, Kessel ST, Robertson AL (2008) Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. Environ Biol Fishes 83: 369–377

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. Mar Ecol Prog Ser 439:263–276

Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: models, importance, and consequences. Mar Ecol Prog Ser 402:1–11

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Mar Ecol Prog Ser 425:233–246

Last PR, Stevens JD (2009) Sharks and rays of Australia. CSIRO Publishing, Collingwood

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Lyle JM (1987) Observations on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzroyensis* (Whitley) from Northern Australia. Aust J Mar Freshw Res 38:701–710

Magnusson A, Skaug H, Nielsen A, Berg C and others (2017) glmmTMB: generalized linear mixed models using a template model builder. R package version 0.2.1.0. https://CRAN.R-project.org/package=glmmTMB

Matich P, Heithaus MR (2012) Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas.* Mar Ecol Prog Ser 447:165–178

Medved RJ, Marshall JA (1983) Short-term movements of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae). Bull Mar Sci 33:87–93

Morrissey JF, Gruber SH (1993a) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris.* Environ Biol Fishes 38:311–319

Morrissey JF, Gruber SH (1993b) Home range of juvenile lemon sharks, *Negaprion brevirostris.* Copeia 1993: 425–434

Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC and others (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533–536

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, Van't Hof T, den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51:31–44

Oh BZL, Thums M, Babcock RC, Meeuwig JJ, Pillans RD, Speed C, Meekan MG (2017) Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery. Mar Freshw Res 68:1501–1517

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996–1008

Parsons GR, Hoffmayer ER (2007) Identification and characterization of shark nursery grounds along the Mississippi and Alabama gulf coasts. Am Fish Soc Symp 50:301–316

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fishes 68:113–128

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24:1089–1103

Schlaff AM, Heupel MR, Udyawer V, Simpfendorfer CA (2017) Biological and environmental effects on activity space of a common reef shark on an inshore reef. Mar Ecol Prog Ser 571:169–181

Simpfendorfer CA, Heupel MR (2012) Assessing habitat use and movement. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, p 579–601

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ Biol Fishes 37:337–345

Simpfendorfer CA, Wiley TR, Yeiser BG (2010) Improving conservation planning for an endangered sawfish using data from acoustic telemetry. Biol Conserv 143:1460–1469

Spalding MD, Fox HE, Allen GR, Davidson N and others (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583

Speed CW, Meekan MG, Field IC, McMahon CR and others (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. Mar Ecol Prog Ser 429:261–275

Stevens JD (1984) Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proc R Soc B 222:79–106

Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. Environ Biol Fishes 84:293–303

Verweij MC, Nagelkerken I, de Graaff D, Peeters M, Bakker EJ, van der Velde G (2006) Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Mar Ecol Prog Ser 306: 257–268

Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. Mar Ecol Prog Ser 343:283–293

Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA

Submitted: December 17, 2018; Accepted: May 27, 2019
Proofs received from author(s): July 22, 2019