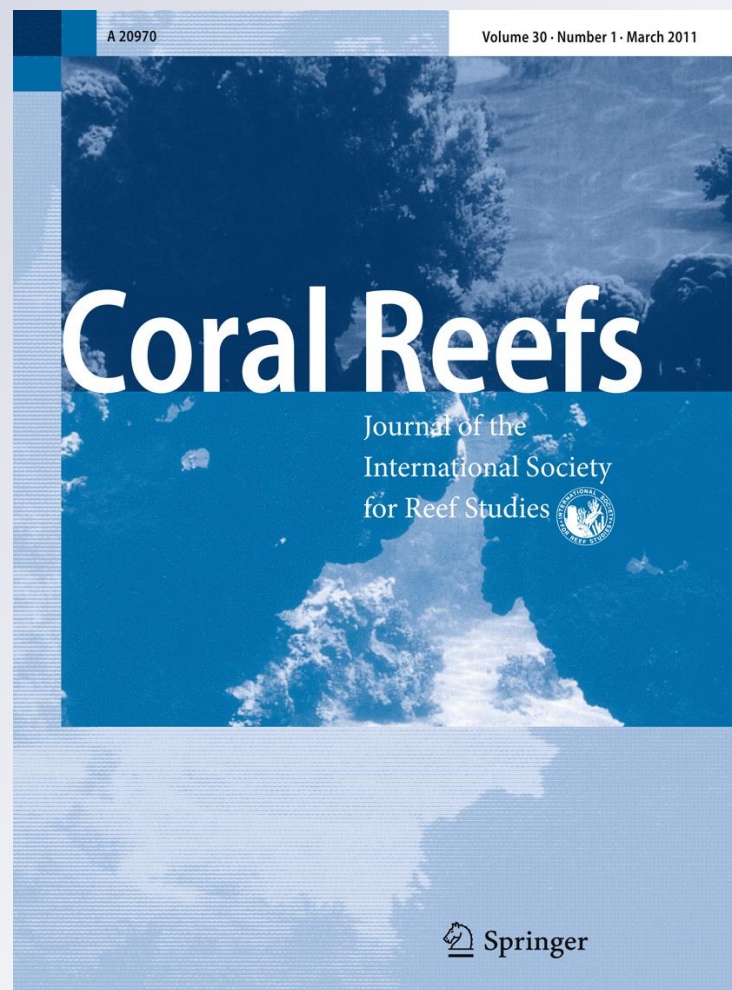


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# Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean

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**Abstract** Grey reef sharks (*Carcharhinus amblyrhynchos*) are apex predators found on many Indo-Pacific coral reefs, but little is known about their movement patterns and habitat requirements. We used acoustic telemetry to determine movements and habitat use of these sharks at the isolated Rowley Shoals atolls, 250 km off the coast of north-western Australia. We equipped 12 male and 14 female sharks ranging from 0.79 to 1.69 m in total length

with transmitters that were detected by an array of 11 strategically placed receivers on two atoll reefs. Over 26,000 detections were recorded over the 325 days of receiver deployment. No sharks were observed to move between reefs. Receivers on the outer slopes of reefs provided nearly all (99%) of the detections. We found no differences in general attendance parameters due to size, sex or reef, except for maximum period of detection where larger sharks were detected over a longer period than smaller sharks. Male and female sharks were often detected at separate receivers at the outer slope habitat of one reef, suggesting sexual segregation, but this pattern did not occur at the second reef where males and females were detected at similar frequencies. We identified two patterns of daily behaviour: (1) sharks were present at the reef both day and night or (2) sharks spent more time in attendance during day than at night. Fast Fourier transforms identified 24-h cycles of attendance at the reef and a secondary peak of attendance at 12 h for most sharks, although no individuals shared the same attendance patterns. Our study provides baseline data that can be used to optimise the minimum area and habitat requirements for conservation of these apex predators.

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· Marine protected areas · Grey reef shark

## Introduction

Marine biodiversity is under ever-increasing threat, primarily as a result of over-harvesting, pollution and the direct and indirect impacts of climate change (Roberts and Hawkins 1999; Jackson et al. 2001). Due to their life history traits of slow growth and relatively low reproductive

output, apex predators are at particular risk from these processes (Pauly et al. 1998; Myers and Worm 2003, 2005; Field et al. 2009a), and their loss can elicit trophic cascades and destabilise the relative abundance of smaller species by removal of top-down control (Myers et al. 2007). Additionally, predators alter diversity and size distributions of their prey, and their mere presence can affect the foraging behaviour of prey in ways that alter ecosystem functions like nutrient recycling and structural habitat complexity (Roberts 1995; Stevens et al. 2000; Heithaus et al. 2007; Ritchie and Johnson 2009; Ferretti et al. 2010). Ultimately, the loss of apex marine predators, including elasmobranchs and large teleosts, can lead to permanent shifts in communities and alternate equilibrium states (Cortés 1999; Friedlander and DeMartini 2002; Bascompte et al. 2005; Myers et al. 2007).

Sharks are apex predators within most coral reef ecosystems (Friedlander and DeMartini 2002). There is growing concern over the status and trends of global populations of these animals (Robbins et al. 2006; Heupel et al. 2009) because the tropical Indo-Pacific Oceans have seen a boom in fishing exploitation fuelled by an increasing demand for shark products from South-East Asian markets (Clarke et al. 2006; Field et al. 2009b). In conjunction with destruction and degradation of habitats, this problem could severely threaten shark populations in reef ecosystems (Last and Compagno 2002). One of the most common strategies designed to mitigate the loss of apex predators within these environments has been to set aside habitats as marine protected areas. Unfortunately, these measures are often imposed without detailed knowledge of the spatial dynamics of their inhabitants, a problem that might render the conservation measure sub-optimal if they do not protect a large part of the target species' home ranges (Robbins et al. 2006).

Over the last three decades, the development of acoustic tracking and passive monitoring equipment (e.g. Heupel et al. 2006) has increased the tractability of monitoring large numbers of marine predators over spatial scales relevant to management and conservation (1–100 km, e.g. Australian Animal Tracking And Monitoring System, Integrated Marine Observing System 2009). To date, studies of sharks using these techniques have largely focused on shallow, inshore, coastal or estuarine environments (Speed et al. 2010), and there have been fewer attempts to monitor these predators in coral reef ecosystems (McKibben and Nelson 1986; Economakis and Lobel 1998; Chapman et al. 2005; Garla et al. 2006; Skomal et al. 2007; Papastamatiou et al. 2009).

Here, we use acoustic telemetry techniques to monitor patterns of movement and habitat use of grey reef sharks (*Carcharhinus amblyrhynchos*) at two of the remote coral reefs atolls of the Rowley Shoals, 250 km off the coast of

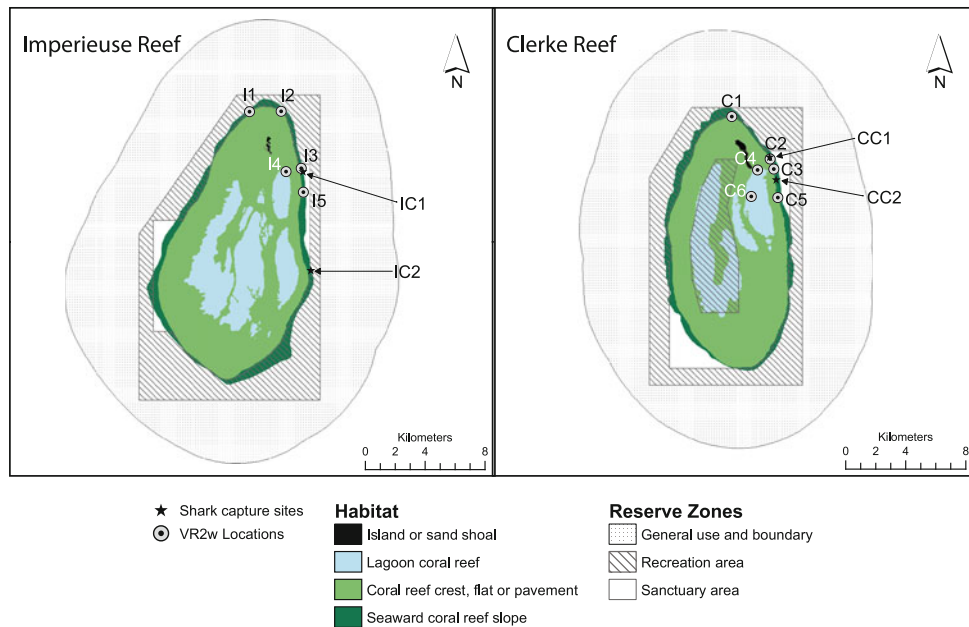
north-west Australia (Electronic Supplemental Material, ESM Fig. S1). Imperieuse and Clerke Reefs are 50 km apart in 350 m of water (Petkovic and Buchanan 2002) close to the edge of continental shelf. Our study species is the most abundant shark on many coral reefs of the Indo-Pacific but, in common with others, is now declining over large parts of its range, probably due to over-exploitation (Robbins et al. 2006). The Rowley Shoals are an isolated group of reefs managed as marine reserves (established in 1990), where no commercial and only limited recreational fishing (mostly catch and release) is permitted. For this reason, they are one of the best examples of pristine reef habitat that remains in the Indian Ocean, and they support a diverse and abundant fauna of apex predators dominated by grey reef sharks (Meekan et al. 2006). As such, these reefs provide a unique opportunity to generate baseline information on the movement and habitat use of these sharks in a coral reef environment little modified by human activity. Furthermore, the area covered by our receiver array, although not covering the entire reef, can be considered similar to that of other small MPAs on coral reefs in many parts of the world. Our specific aims were to (1) compare patterns of reef attendance and habitat use at these sites, (2) determine movement patterns between similar habitats of the two reef atolls, (3) describe daily patterns of behaviour and (4) assess the long-term patterns of attendance and correlations among individuals.

## Methods

VEMCO VR2w receiver stations (VEMCO, Halifax, Nova Scotia, Canada) were deployed on reefs, and V13 transmitters were attached to sharks at Imperieuse (17°35'S, 118°56'E) and Clerke (17°19'S, 119°20'E) Reefs in the Rowley Shoals from December 2007 to November 2008. These reefs are large (approximately 20 × 10 km), and our study was limited to north-eastern sections of the reefs that were the sites of long-term monitoring programmes of coral and fish communities (Gilmour et al. 2007). The coverage of our study combined with the long-term monitoring is therefore likely to enable comparisons with other similar-sized reefs. These parts of the reefs were also areas of relatively lower wave action and turbulence, allowing relatively easy access to receiver stations.

Each transmitter fitted to a shark produced a unique coded pulse nominally every three minutes that was detected when the sharks were within a range of approximately 350 m of the receiver (range testing is described in the ESM). Five receivers were deployed and 13 sharks fitted with transmitters at Imperieuse Reef, while at Clerke Reef, six receivers were deployed and 16 sharks fitted with transmitters. At both reefs, the receivers were moored at





**Fig. 1** Maps of the Imperieuse and Clerke Reefs, *left* and *right* panels, respectively, showing the VR2w receivers and shark capture locations at each reef, habitat and Western Australia reserve zoning for Imperieuse and Clerke Reefs, respectively

locations within the lagoons and around the entrance channels on the outer slope (Fig. 1). This allowed for both within- and between-reef comparisons of movement, migration and habitat use by grey reef sharks over 11 months.

### Shark capture and transmitter deployments

Sharks were equipped with VEMCO V13-1H transmitters (36 mm length  $\times$  13 mm width; VEMCO, Halifax, Nova Scotia, Canada). These tags continually transmitted an individual coded pulse, randomly within 120- and 240-s intervals, producing a nominal transmission (power output 158 dB) around 180 s apart at a frequency of 69 kHz, with an expected battery life of over 500 days. With one exception, all of the sharks were large enough to support a transmitter mounted on a dorsal fin tag. The smallest individual (less than 1 m total length) had a transmitter surgically implanted in the inter-peritoneal cavity (Heupel and Hueter 2001).

We caught sharks using handlines with baited barbless hooks for tagging. Fishing effort was indiscriminate of shark size, and all sharks were considered for tagging (ESM Fig. S2). We set hooks on the bottom, in intermediate water or at the surface depending on the tides and depth sounder images of the individual location. Once hooked, the sharks were brought to the surface alongside the research vessel and a tail rope attached. For external attachment of tags, the sharks were then manoeuvred next

to an inflatable rubber boat moored alongside the research vessel and into a canvas stretcher that restrained and supported sharks without removing them from the water. This gave access to the sharks for measurement, determination of sex and attachment of the tag-mounted transmitter to the dorsal fin. Each transmitter was mounted (glued and cable tied) on a jumbo rototag that was then pinned to the dorsal fin using a pre-cut hole made by a hole punch. For implantation of the transmitter, we followed the procedures of Heupel and Hueter (2001) where the shark was placed upside down in a cradle that allowed sea water to flow into the shark's mouth and around the gills. No sharks were killed or harvested during the study.

### Receiver deployments

Before deployment, the receivers were wrapped in tape and painted with anti-foulant. We moored all receivers to the reef using two star pickets, cable ties and stainless steel wire in water depths of 10–17 m. The receiver head was positioned on a star picket at least 1 m above the reef. Receivers at Imperieuse Reef were retrieved after 323 days of deployment and after 312 days of deployment at Clerke Reef. The receivers were deployed in similar lagoon and outer-reef slope environments with the exception that receivers at I3 at Imperieuse Reef, and C2 and C3 at Clerke Reef were within 200 m of the outer edge of the lagoon channel mouths (Fig. 1). We assessed the detection range of the receivers following the technique of VEMCO (2010)

and detection efficiency (Simpfendorfer et al. 2008), and the procedures and analyses are outlined in ESM. The mean maximum detection range for all receivers was 348 m and ranged from 250 to 454 m (ESM Table S1). No range-testing data were available for I1 (comprehensive range testing was attempted at almost all receiver sites, but due to time constraints, it was not possible for this receiver); the detection range for I1 was therefore assumed to be at least 250 m.

## Analysis

To determine shark attendance patterns at the focal areas of the reefs, we calculated the maximum number of days over which the sharks were detected and a daily detection rate that was the proportion of monitoring days during which each shark was detected. For the latter variable, a '1' indicates at least one detection every day and a '0.5' indicates detection on half of the deployment days. We also calculated the mean number of daily detections for each shark. To determine whether there were broad habitat differences, we calculated the daily number of detections on the outer slope of the reef as a proportion of total detections and the mean daily number of receivers at which each shark was detected. In the text and tables, these are reported  $\pm$  one standard deviation.

We compared these patterns of reef attendance and broad habitat areas between sexes and among sizes of sharks using general linear models (Gaussian normal error distribution, link function = identity) that included 'reefs' as a factor to compare between reefs. Akaike's information criterion (corrected for sample size) weights ( $wAIC_c$ ) were used to provide a measure of the strength of evidence for each model. These were calculated as the change in  $AIC_c$  relative to the top-ranked model. Model goodness-of-fit was assessed as the percentage of deviance explained (%DE) in the response. Evidence ratios ( $ER = AIC_c$  weight of slope model  $\div$   $AIC_c$  weight of intercept-only model (see Burnham and Anderson 2002)) were used to compare models and are useful even for a comparison of a null model to a single alternative, in a concept akin to Bayesian odds ratios (McCarthy 2007). For example, an  $ER$  of 10 indicates that a hypothesised model is 10 times more likely to be a better biased-corrected model than the null, given the available data. The  $ER$  is preferable to a classic null-hypothesis significance test because the likelihood of the alternative model is explicitly evaluated (not just the null).

To examine the concordance in daily patterns in reef attendance among individuals, we grouped individuals by the proportion of time spent at the reefs. This was done by binning the time spent in range of a receiver (data pooled among all receivers) into hourly intervals for each

individual. We then used hierarchical clustering, based on Euclidean distance dissimilarity matrices, to group the sharks based on the proportion of time spent within the different daily hour bins. The optimal number of groups was determined using  $k$ -means clustering and the Calinski–Harabasz criterion (the F-ratio of ANOVA for the predictor variables). The groupings were then plotted as a dendrogram and as the mean proportions of time spent in each hour bin to show how patterns of attendance varied among sharks. We used a permutational multivariate analysis of variance (formerly known as a nonparametric MANOVA) to test whether these two groups were different, based on 9999 permutations of a Euclidean distance dissimilarity matrix of the proportion of each day spent in each hour bin, using the *adonis* function in the *vegan* package in R (Anderson 2001; R Development Core Team 2010), directly analogous to a MANOVA test.

The spatial differences in habitat used by the sharks were described by the amount of detections at the different receivers at each of the reefs. To determine whether there were any effects of size or sex, we used the *adonis* function in the *vegan* package (Anderson 2001; R Development Core Team 2010), which considers categorical and continuous variables together. This analysis compared the proportion of detections at each of the receivers for each of the sharks over their period of duration. We treated the two reefs separately due to the different spatial pattern of the receiver arrays.

Individual attendance data over the entire study were visualised using Eonfusion (Myriax Pty. Ltd. Hobart, Australia) and assessed using spectral analysis and then compared among sharks using cross-correlation. Not all sharks were detected each day, so we only used data from sharks that had a proportion of days detected  $>0.5$ , as they were present at least every other day. For each shark, we created an hourly time series for the entire study period by pooling the number of detections for all receivers and calculating the number of minutes each hour that the shark was at the reef. To determine the primary frequencies within the data, we used a fast Fourier transformation of the time series and applied a hamming window to reduce the effects of adjacent spectral components that might contribute to erroneous peaks (Chatfield 1996). To determine whether individuals were associated with each other when they appeared at the reef, we converted the hourly binned data to presence–absence values and cross-correlated these records among individuals. For these analyses, positive cross-correlation coefficients ( $R$ ) indicated that time series of attendance overlapped,  $R = 0$  indicated that there was no correlation and negative coefficients indicated that attendance was in opposite phase. All mean values are presented with one standard deviation (mean  $\pm$  SD) unless otherwise stated.

**Results**

Reef attendance

Receivers recorded a total of 26,733 detections from 26 of the 29 grey reef sharks that were tagged (Table 1). The mean maximum period of detection for the sharks was 230 days and ranged from 51 to 323 days (Fig. 2). Over the course of the study, the mean daily detection index was  $0.5 \pm 0.3$ , indicating that sharks were recorded at the monitored sections of the reefs on half of the days while they were detected during the study period, although they might have been at the reef outside of the array when not detected. Over the entire deployment, the mean number of detections per shark was  $1,028 \pm 1,327$  and the mean number of daily detections was  $3 \pm 4$  and ranged from 0 to 17. Nearly all of the detections ( $99 \pm 0.7\%$ ) were recorded at receivers on the outside slopes of the reefs. Models indicate that there is little evidence for differences in the daily detection index, the number of detections per shark, or the proportion of detections on the outside of the reefs among sizes or sexes of sharks. There was, however, evidence for an effect of shark size, with larger sharks tending to be detected over a longer period than smaller sharks (Table 2), and a small reef effect with sharks at Imperieuse Reef being detected for  $241 \pm 86$  days compared to  $222 \pm 87$  days at Clerke Reef (evidence ratio [ER] = 2.4; DE = 36%; ESM Fig. S3 and Table S3).

Hierarchical clustering identified two groups of daily attendance patterns (Fig. 3) that were confirmed by permutational multivariate analysis of variance ( $F_{2,12} = 3.13$ ,  $P = 0.021$ ). The first group consisted of sharks that were recorded equally by receivers both during the day and night, while the second consisted of sharks that spent more

time at the monitored sections of the reefs during the day than at night. Of the 13 sharks that had a detection index of  $>0.5$ , 10 (76%) showed evidence for 24-h cycles in reef attendance, and of these, six also had a secondary peak in attendance cycles at 12 h (ESM Fig. S4). The remaining three sharks had a primary visiting frequency at 12 h and a secondary peak at 24 h. Five sharks (38%) had a minor 8 h peak. Cross-correlation analyses found no coefficients  $>0.2$  or  $<-0.2$ , indicating that there was little correlation among individual patterns of attendance on the reef.

Habitat use

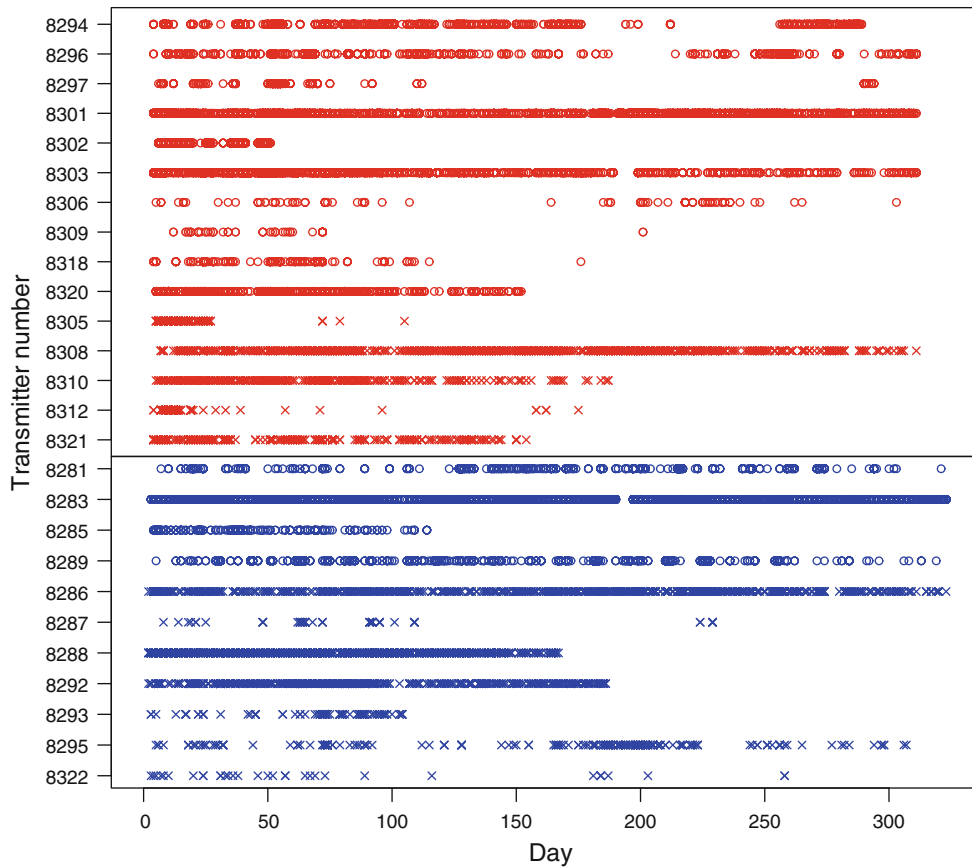
No sharks were detected moving between monitored sections of the reefs. Although not a direct measure of distance travelled, the greatest distance moved was around 6.8 km between a shark's capture and release site (IC2), at the northern extent of the receiver array, and its subsequent detection at I3 (Table 3; Fig. 1) in the middle of the array at Imperieuse Reef. Within a reef, detections were not evenly distributed between lagoon and outer slope habitats, with 99% being received at the outer-reef slope receivers I3 and I5 on Imperieuse Reefs and 99% of detections at outer slope receivers C2, C3 and C5 on Clerke Reef (Fig. 1). On days when the individual sharks were detected, they were typically at only one receiver, with 75% of each individual's detections occurring at one receiver over the period of monitoring (Table 3), which was not necessarily at the receivers closest to their capture sites.

There were also differences in detection patterns within arrays at the two monitored sections of the reefs (Table 3; Fig. 4). At Clerke Reef, males and females had similar proportions of detections at the same receivers, and we

**Table 1** Attendance metrics for grey reef sharks (*Carcharhinus amblyrhynchos*) caught and instrumented at the Rowley Shoals

Attendance metric	All sharks (n = 26)			Female (n = 14)			Male (n = 12)		
	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD
Total length (m)	0.79	1.69	1.36 ± 0.25	1.00	1.69	1.46 ± 0.22	0.79	1.60	1.26 ± 0.25
Maximum period of detection	51	323	230 ± 86	51	323	248 ± 91	104	323	209 ± 77
Total number of days detected	20	312	120 ± 91	25	312	130 ± 96	20	265	109 ± 89
Daily detection rate	0.09	0.97	0.51 ± 0.29	0.12	0.97	0.53 ± 0.28	0.09	0.96	0.51 ± 0.33
Total number of detections per shark	34	5,366	1,028 ± 1,327	48	5,366	1,285 ± 1,647	34	2,414	728 ± 787
Daily number of detections per shark	0	17	3 ± 4	0	17	4 ± 5	0	7	2 ± 2
Proportion of total daily detections by receivers on the outer slopes	0.89	1.00	0.98 ± 0.03	0.89	1.00	0.98 ± 0.03	0.96	1.00	0.99 ± 0.01
Mean daily number of receivers visited per shark	1	2	1 ± 0	1	2	1 ± 0	1	2	1 ± 0

Mean values are presented with one standard deviation (SD)



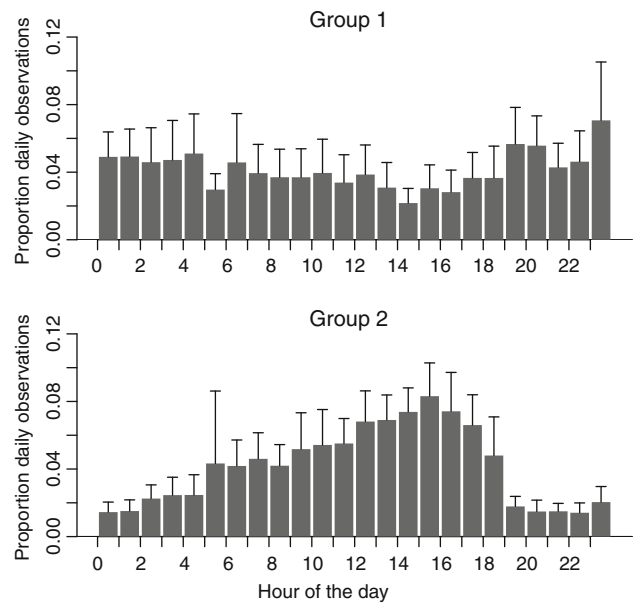
**Fig. 2** Daily detections of male (*multi symbol*) and female (*open circle*) grey reef sharks at Clerke and Imperieuse Reefs (*top and bottom panel*, respectively) over the entire study period for all VR2w receivers

**Table 2** Ranked general linear models of maximum period of detection explained by grey reef shark total length (TL), sex and reef (*n* = 26)

Model	<i>k</i>	LL	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	wAIC <sub>c</sub>	%DE
TL + reef	3	-146.241	301.573	0.000	0.620	36.01
TL	2	-148.405	303.332	1.759	0.257	24.42
TL + sex	3	-148.381	305.852	4.279	0.073	24.56
intercept only	1	-152.044	308.255	6.682	0.022	0.00
sex	2	-151.308	309.138	7.565	0.014	5.50
reef	2	-151.881	310.284	8.711	0.008	1.24
sex + reef	3	-150.797	310.686	9.113	0.007	9.14

Shown are the number of parameters (*k*), maximum log-likelihood (LL), Akaike's information criterion corrected for small samples (AIC<sub>c</sub>), change in AIC<sub>c</sub> relative to the top-ranked model (ΔAIC<sub>c</sub>), ΔAIC<sub>c</sub> model weights (wAIC<sub>c</sub>), and the percentage deviance explained in the response (%DE)

found no evidence of size differences on the proportion of detections for each shark at the different receivers. At Imperieuse Reef, however, male and female sharks were detected more frequently at different receivers (permutational multivariate analysis of variance:  $F_{2,10} = 8.79$ ,



**Fig. 3** Time-of-day attendance patterns for the two groups of grey reef sharks determined by hierarchal clustering of the daily aggregated hourly binned time data shown as a histogram of the number of minutes individual sharks were detected by all the receivers each hour



**Table 3** Number of detections for each grey reef shark at each receiver over the course of the study period at the Rowley Shoals

Shark transmitter	Release location	Sex	TL (m)	Period of detection (d)	Receiver stations						Total detections
					C1	C2	C3	C4 <sup>×</sup>	C5	C6 <sup>×</sup>	
<b>Clerke</b>											
8294	CC2	F	1.69	289	0 (0)	745 (43.3)	<b>904 (52.6)</b>	0 (0)	71 (4.1)	0 (0)	1,720
8296	CC2	F	1.69	311	0 (0)	126 (11.5)	<b>842 (76.7)</b>	88 (8)	6 (0.5)	36 (3.3)	1,098
8297	CC1	F	1.54	294	0 (0)	<b>40 (19.1)</b>	<b>123 (58.9)</b>	0 (0)	46 (22)	0 (0)	209
8301	CC1	F	1.49	311	0 (0)	<b>91 (2.2)</b>	<b>3,994 (97.5)</b>	0 (0)	11 (0.3)	0 (0)	4,096
8302	CC1	F	1.00	51	0 (0)	<b>2 (0.5)</b>	<b>18 (4.6)</b>	0 (0)	370 (94.4)	2 (0.5)	392
8303	CC1	F	1.61	311	0 (0)	<b>146 (5.5)</b>	<b>2,100 (79.6)</b>	9 (0.3)	383 (14.5)	0 (0)	2,638
8306	CC1	F	1.66	303	0 (0)	<b>10 (11.2)</b>	<b>14 (15.7)</b>	0 (0)	65 (73)	0 (0)	89
8309	CC1	F	1.58	201	0 (0)	<b>23 (47.9)</b>	<b>10 (20.8)</b>	3 (6.3)	12 (25)	0 (0)	48
8318	CC1	F	1.37	176	0 (0)	<b>22 (14.6)</b>	<b>127 (84.1)</b>	2 (1.3)	0 (0)	0 (0)	151
8320	CC1	F	1.45	152	0 (0)	<b>28 (2.9)</b>	<b>64 (6.7)</b>	0 (0)	868 (90.4)	0 (0)	960
8305	CC1	M	1.23	105	0 (0)	<b>48 (15.4)</b>	<b>113 (36.2)</b>	12 (3.8)	139 (44.6)	0 (0)	312
8308	CC1	M	1.49	311	0 (0)	<b>56 (3.5)</b>	<b>246 (15.4)</b>	4 (0.3)	1,285 (80.7)	2 (0.1)	1,593
8310	CC1	M	1.52	187	0 (0)	<b>6 (1)</b>	<b>5 (0.9)</b>	0 (0)	570 (98.1)	0 (0)	581
8312	CC1	M	1.19	175	0 (0)	<b>3 (1.1)</b>	<b>252 (95.1)</b>	3 (1.1)	0 (0)	7 (2.6)	265
8321	CC1	M	1.22	154	0 (0)	<b>36 (8.9)</b>	<b>258 (63.9)</b>	0 (0)	110 (27.2)	0 (0)	404
Total detections per receiver					0	1,382	9,070	121	3,936	47	
					I1	I2	I3	I4 <sup>×</sup>	I5		
<b>Imperieuse</b>											
8281	IC1	F	1.55	321	0 (0)	32 (7.8)	<b>314 (76.6)</b>	2 (0.5)	<b>62 (15.1)</b>		410
8283	IC1	F	1.49	323	0 (0)	21 (0.4)	<b>5,249 (97.8)</b>	56 (1)	<b>40 (0.7)</b>		5,366
8285	IC1	F	1.14	114	0 (0)	0 (0)	<b>108 (43.9)</b>	1 (0.4)	<b>137 (55.7)</b>		246
8289	IC1	F	1.12	319	0 (0)	0 (0)	<b>455 (80)</b>	14 (2.5)	<b>100 (17.6)</b>		569
8286	IC1	M	1.05	323	0 (0)	0 (0)	<b>32 (1.8)</b>	0 (0)	<b>1,764 (98.2)</b>		1,796
8287	IC2	M	0.79	229	0 (0)	0 (0)	29 (46)	0 (0)	34 (54)		63
8288	IC1	M	1.08	167	0 (0)	0 (0)	<b>635 (26.3)</b>	0 (0)	<b>1,779 (73.7)</b>		2,414
8292	IC1	M	1.53	186	0 (0)	0 (0)	<b>64 (7)</b>	0 (0)	<b>851 (93)</b>		915
8293	IC1	M	1.02	104	0 (0)	0 (0)	<b>43 (36.8)</b>	0 (0)	<b>74 (63.2)</b>		117
8295	IC1	M	1.35	307	0 (0)	0 (0)	<b>175 (70.9)</b>	0 (0)	<b>72 (29.1)</b>		247
8322	IC2	M	1.60	258	0 (0)	0 (0)	10 (29.4)	0 (0)	24 (70.6)		34
Total detections per receiver					0	53	7,114	73	4,937		

Also shown in brackets are the percentages of the total number of detections for each shark at each receiver

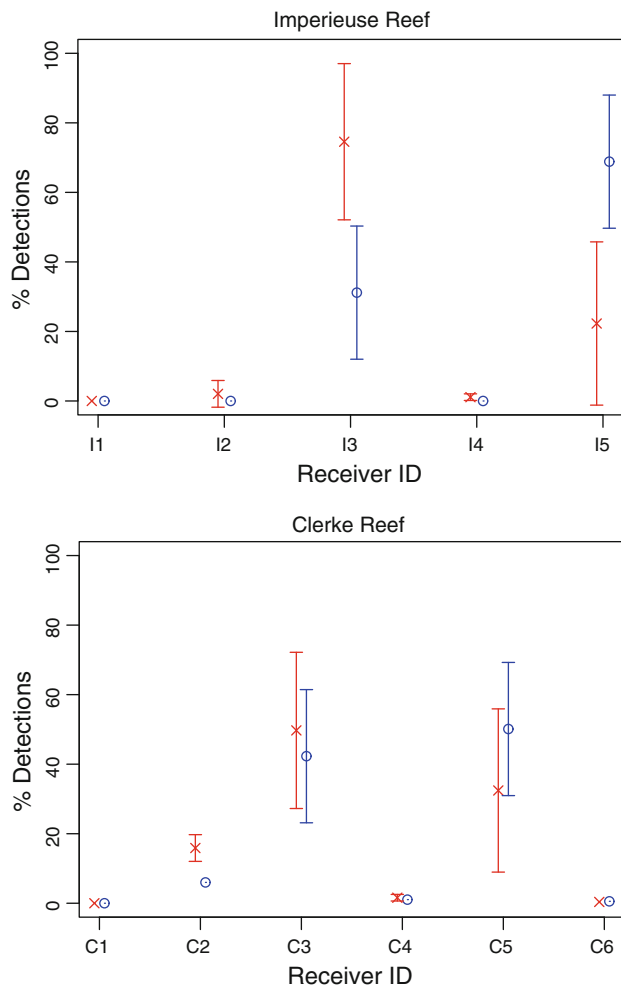
<sup>×</sup> denotes receivers located in the lagoons, and values in bold indicate detections by a receiver within 1 km of a shark's capture location

$P = 0.026$ ), although there was no effect of size on detections. At this reef, females were detected more frequently at I3, whereas males were detected more frequently at I5. Both of these receivers were on the outer slope of the reef face with I3 close to the channel in the reef and I5 about 1.5 km farther south.

**Discussion**

Our study is the longest and most comprehensive to date of the residency and habitat-use patterns of grey reef sharks, one of the common apex predators found on coral reefs

throughout the Indo-Pacific. Knowledge of the extent of movements and the degree of site fidelity of sharks are essential for appropriate management and conservation (Heupel et al. 2004; Heupel and Simpfendorfer 2005; Field et al. 2009a; Speed et al. 2010), and without this information, protection strategies could be imposed over areas that ultimately prove to be insufficient for persistence of populations. Although the distribution and area covered by our receivers do not encompass entire reefs, our results are relevant for the movement and residency patterns of reefs sharks in relation to the size and positioning of MPAs within similar reef systems. Our data are limited to relatively small monitored sections of these large reefs, so our



**Fig. 4** The proportion of detections at each of the receivers at Imperieuse and Clerke Reefs (*top* and *bottom* panel, respectively) by male (*multi symbol*) and female (*open circle*) sharks

results probably underestimate the sharks' spatial use patterns, especially at sites where detections were temporally sporadic. Nonetheless, the patterns described indicate clear behavioural patterns that can be used to determine range requirements at both local and broader spatial scales (Speed et al. 2010).

Grey reef sharks at the Rowley Shoals spent most of their time on the outer slopes of the reefs, with individuals detected infrequently inside the lagoons. Such patterns confirm earlier suggestions that these sharks mainly select areas of rugged terrain with strong currents (Hobson 1963; Wass 1971; Johnson 1994; Wetherbee et al. 1997). Data from surveys using fishing and visual census techniques also support this hypothesis; grey reef sharks are often associated with reef crests, outer-reef slopes and steep drop-offs on coral reefs (Wetherbee et al. 1997; Robbins 2006). However, on occasion, grey reef sharks do participate in aggregations in shallow lagoons and reefs (McKibben and Nelson 1986; Economakis and Lobel

1998). Shark aggregations are often composed of pregnant females that use warm shallow waters as a means of increasing gestation rates or by young juveniles to increase growth rates (Economakis and Lobel 1998; Hight and Lowe 2007). We recorded no evidence of this behaviour, although logistic constraints limited the deployment of receivers across entire lagoons of reefs.

Grey reef sharks at the Rowley Shoals tended to be detected at only one or two receivers, indicating that they inhabit a relatively small area. Furthermore, these receivers were within a few kilometres of the large reef channels and closer to the capture sites than the receivers at the northern extents of the reefs which had few, if any, detections. However, detections were only possible within a limited area (i.e. when sharks were within the detection range of the receivers). The effects of tag loss were also considered when checking and processing our data, and combined with anecdotal sightings of tagged sharks in the years after the deployment and study period from tourist operators visiting the reefs, would indicate little or no influence. It is possible that sampled sharks moved outside the array, so we were unable to estimate the spatial extent of their home ranges, although we observed evidence of site fidelity and segregation within our receiver array.

Site fidelity is a common feature of many other shark species that inhabit coral reefs; the behaviour has been observed in juvenile blacktip and lemon sharks in the Virgin Islands (DeAngelis et al. 2008), juvenile and adult lemon sharks at Bimini Islands (Gruber et al. 1988; Morrissey and Gruber 1993a; Edrén and Gruber 2005), juvenile and adult blacktip reef sharks at Palmyra Atoll (Papas-tamatiou et al. 2009), and juvenile Caribbean reef sharks (*Carcharhinus perezi*) in Fernando de Noronha Archipelago, Brazil (Garla et al. 2006). Fidelity might reflect specific habitat and environmental requirements, prey availability and foraging strategies, territoriality and social interactions, or some combination of these factors (Speed et al. 2010). At the broadest scale, over half of the sharks we tagged were detected for >150 days, indicating that most exhibited some site fidelity to the reef. At the finer within-array scale at each reef, most sharks were detected at only one or two receivers. Furthermore, most of the sharks were detected at receivers close to where they were tagged, suggesting that they did not disperse widely. Strong site fidelity in grey reef sharks has also been recorded by McKibben and Nelson (1986) who found that sharks tagged at lagoon reefs or ocean pinnacles at Enewetak Atoll often returned to the same site every day. The degree of site fidelity varied among individuals, with those sharks tagged at ocean reefs being more nomadic and moving larger distances along the reef (McKibben and Nelson 1986). An alternative interpretation might be that, due to the low number of daily detections for individuals, sharks were

detected while continuously travelling or moving between sites. Our data cannot provide conclusive evidence either way, but regular and multiple detection of sharks within the monitored sections of the reefs does suggest site fidelity. Heupel et al. (2010) found that nine grey reef sharks monitored on the Great Barrier Reef and in the Coral Sea showed only limited site fidelity at fine scales (individual receivers; >1 km), but there was greater support at local scales (within and between reefs; <20 km), with individuals frequently moving between local reefs. This result probably reflects the spatial context of tagging studies; Heupel et al. (2010) monitored sharks within the archipelagic Great Barrier Reef where neighbouring reefs are separated by only some few hundreds of metres. In this system, sharks crossed the narrow passes between reefs many times, effectively treating the group of reefs in their study area as a single, continuous habitat. In our study, isolated reefs were separated by far greater distances (tens of km) of deep water, and these might have provided greater barriers to routine movements.

Ontogenetic and sexual segregation of individuals in space and time is common in many sharks (Springer 1967), particularly in other carcharhinids (Castro 1993). It is thought to have evolved as a consequence of competition for resources or predation (Sims 2003). Segregation can also be a reflection of differing physiological tolerances to environmental and other abiotic conditions that could provide gradients to separate juvenile and adult habitats (Morrissey and Gruber 1993b; Wetherbee et al. 1997; Pikitch et al. 2005; Carraro and Gladstone 2006; McAuley et al. 2007; Meyer et al. 2009). We found that larger individuals were detected for longer periods and with adequate monitoring of the lagoon areas where juvenile sharks could have been spending relatively more time (cf. Meyer et al. 2009). Therefore, we can only suggest limited ontogenetic variation in habitat use despite the lack of a size (and therefore age) effect on the spatial pattern of habitat use. Recently, ontogenetic differences in site fidelity were observed in grey reef sharks on the Great Barrier Reef, with smaller individuals having greater site fidelity than larger individuals (Heupel et al. 2010). At Imperieuse Reef, we observed possible evidence of sexual segregation, with male and female sharks detected more frequently at different receivers on the outer slopes. The reason for this is unclear because within a similar habitat on Clerke Reef, we found no segregation of males and females. Virtually, all the sharks we tagged were adults (mean size at maturity is between 1.1 and 1.4 m for both sexes; Last and Stevens 1994), and so our results cannot provide much to corroborate ontogeny in patterns of segregation.

We did not find any evidence of inter-reef (>50 km) or long-range (>10 km) movements within the same reef. The greatest movement we recorded was around 6.8 km

between a shark's capture/release point and the farthest receiver it visited, although the lack of long-range movement detections might only reflect the limited number of receivers that we were able to deploy around the perimeter of these large reefs. There is also a possibility that the sharks we monitored moved greater distances outside of the detection ranges of our receivers or dispersed to unmonitored regions. Active tracking by McKibben and Nelson (1986) found that grey reef sharks moved up to 16 km along reefs and over areas of up to 53 km<sup>2</sup> in periods of days to weeks. Long-distance dispersal in this species has also been recorded by Heupel et al. (2010) who found that a single tagged shark travelled 134 km between a reef in the Coral Sea and the outer barrier reefs of the Great Barrier Reef. Furthermore, tagged grey reef sharks at Ningaloo Reef in Western Australia are capable of moving 60 km along the reef front over 3 months (Speed et al., pers. comm.). Thus, it is likely that we have underestimated the potential for larger-scale movements by grey reef sharks at the Rowley Shoals.

General patterns in attendance at the reef varied among sharks. One group of individuals was detected predominantly during the day, while a second group was detected both day and night. These patterns were not correlated with sex or size of the sharks. Varying patterns of detection among individual grey reef sharks were also observed by Heupel et al. (2010) who found that two individuals were detected more during the day and one individual was detected more at night, while three others had no pattern of differential day or night detections. Others have found patterns where reef sharks were only detected during the day (Economakis and Lobel 1998); however, this occurred when sharks aggregated in shallow water, a behaviour that was not observed at the Rowley Shoals. McKibben and Nelson (1986) found that some grey reef sharks used different reef habitats during the night and day, which might account for the detection of some sharks only during the day in our study. If this is the case, it is not a behaviour that is shared by all members of the population at the Rowley Shoals because other sharks were present in the area of the receivers both day and night.

Most (75%) of the tagged sharks had strong 24-h cycles in frequency of detections, and over 50% of the sharks had 12-h cycles of detection within receiver ranges. The presence of a minor 8-h cycles could suggest the influence of the tidal cycle, but without further investigation, this remains unclear. These observations along with the two groups of daily activity suggest that the sharks might have a diel or crepuscular pattern to their behaviour of visiting the section of the reef where the receivers were placed. Similar cycles in frequencies of attendance have been recorded in blacktip reef sharks (Papastamatiou et al. 2009) and were thought to reflect diel and tidal influences. At the

Rowley Shoals where cycles did not necessarily coincide among individuals, this could suggest that there was not a clear environmental signal that entrained these patterns in a manner consistent among all sharks. Rather, these out-of-phase cycles might reflect individual foraging or other behavioural strategies that avoid intra-specific interaction and competition. The influence of environmental condition (tides, currents, daylight and other stochastic events) remains unclear on individual strategies of reef attendance and requires further testing.

Our study provides the first long-term data (almost a year) on site fidelity and movement patterns in grey reef sharks on a relatively pristine coral reef in the Indian Ocean. It confirms earlier suggestions that these sharks show strong patterns of site fidelity at local scales and remain close to where they were captured and could be year-round residents within relatively small areas of reef. Segregation and site fidelity patterns were evident although not fully explained with the available data. For protected areas to be of a sufficient size to ensure that a large proportion of the population will persist, these behavioural patterns will need better quantification. Because sharks were not detected all the time, it is likely that they are using either larger areas of the reef outside the limited spatial extent of our receivers or habitats in deeper water, including the outer-reef slope. Future work now requires the monitoring of other life stages, particularly juveniles, and a wider deployment pattern of receivers over the entire reef along with monitoring of other ecosystem and environmental influences. This would ensure that movement patterns and all life history stages of the population could be incorporated into spatial management plans.

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