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Fine-scale movement and activity patterns of Caribbean reef sharks (*Carcharhinus perezi*) in the Bahamas

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Abstract Knowledge of the spatial ecology and movement of animals contributes to our understanding of intra- and inter-specific interactions and ecosystem dynamics, and can inform conservation actions. Here we assessed the space use and activity levels of a marine predator, the Caribbean reef shark (*Carcharhinus perezi*), in coastal regions of Eleuthera, The Bahamas over a 60-day period using acoustic telemetry. Of the 14 adult sharks (eight males, six females) tagged with acoustic transmitters (equipped with accelerometer sensor), nine were detected in a 14 km^2 gridded receiver array. Male sharks were significantly less likely to be detected over time relative to females. Given post-release survival is typically high in *C. perezi*, this finding may indicate that males have larger home ranges and may exhibit lower site fidelity compared to females. Patterns of space use indicated *C. perezi* primarily occupied the outer reef shelf and were rarely detected on the interior of the reef. Shark activity levels (inferred from acceleration profiles) were highest in close proximity to the reef shelf. Our findings indicate *C. perezi* individuals frequently occupy deeper water habitats, but make forays into reef shelf habitats where high activity levels are likely related to foraging.

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Introduction

Patterns of animal space use and activity have important implications for fundamental ecology by informing species interactions, population and ecosystem dynamics (Tilman and Kareiva 1997; Morales et al. 2010), as well as conservation through management of habitats and human activities (Sutherland 1998; Buchholz 2007). Elasmobranch fishes exhibit diverse patterns in space use and behaviour, playing important ecological roles in marine ecosystems (Ferretti et al. 2010; Schlaff et al. 2014). However, they also face numerous threats to their conservation (Knip et al. 2010; Dulvy et al. 2014). Recent advances in biotelemetry and biologging devices have enabled much deeper insights into the movement, behaviour, and physiology of elasmobranch fishes (Hammerschlag et al. 2011; Hussey et al. 2015). Acceleration sensors are particularly useful for characterizing patterns in activity, as well as bioenergetics (Whitney et al. 2007, 2010; Gleiss et al. 2009, 2010; Wilson et al. 2015; Cooke et al. 2016). When paired with positioning technology, acceleration patterns can inform behavioural ecology and habitat function (Payne et al. 2011; Brownscombe et al. 2017).

The Caribbean reef shark (*Carcharhinus perezi*) is a medium-bodied requiem shark, found across the tropical and sub-tropical western Atlantic (Rosa et al. 2006). *C. perezi* forms a considerable proportion of predator biomass in this region (Brooks et al. 2011, 2013), and is integral to the health and vitality of coral reef systems (Rosa et al. 2006; Maljković and Côté 2011). The Bahamas is one nation particularly reliant upon healthy *C. perezi* populations, due to the significant economic return from shark diving ecotourism (Maljković and Côté 2011; Haas et al. 2017), as well as ecosystem benefits (i.e. top-down control) critical to maintaining ecosystem health (Roff et al. 2016). Despite exhibiting high site fidelity to distinct bioregions (Garla et al. 2006; Chapman et al. 2007), *C. perezi* individuals are known to associate with multiple habitats such as coral reefs and open-ocean/deepwater (Chapman et al. 2007; Shipley et al. 2017). Although *C. perezi* is well known to The Bahamas (Brooks et al. 2011, 2013), key space-use patterns are poorly documented compared to other locales such as Brazil (Garla et al. 2006) and Belize (Chapman et al. 2005). Furthermore, there is currently no information pertaining to the activity levels of *C. perezi* in the scientific literature, nor how activity varies with diel period.

The waters of South Eleuthera, The Bahamas, are characterized by large coral heads and a narrow continental shelf, which runs adjacent to a deep-water inlet of the Atlantic Ocean, the Exuma Sound. The walls of the Sound drop rapidly to approximately 400 m shallow before sloping gradually to roughly 1600 m at its centre (Ball et al. 1969). The unique bathymetry of the Exuma Sound and surrounding neritic waters allow for the examination of elasmobranch behaviour occurring at the interface between shallow and open-ocean/deep-water habitats. As such, we quantified short-term movements and activity patterns of *C. perezi* in south Eleuthera, The Bahamas, to provide the first indication of key space-use areas, and diel patterns in activity for individuals at this locale.

Methods

Animal capture and tagging

This study was conducted between June and August 2009 in the waters surrounding South Eleuthera, The Bahamas (24.837° N, 76.342° W).

Thirty-two VR2 acoustic receivers (VEMCO, Nova Scotia, Canada) were deployed in a 14km^2 grid in the waters off southwest Eleuthera, The Bahamas (24.77° N, 76.21° W). All receivers were placed no further than 500 m apart, in areas were obstruction by large coral heads would not cause significantly variability in detection ranges; however, the use of sentinal tags and range testing were not performed. *C. perezi* individuals were captured using stationary mid-water longlines equipped with 30–50 gangions baited with bonito (*Sarda sarda*) (see Brooks et al. 2013 for detailed methodology). Animals were secured alongside the research vessel, and a V9-AP-2 L coded sensor acceleration-pressure sensing transmitter (45 s average delay (range = 30–60 s); 82 day duration; VEMCO Inc., Canada), was attached to the dorsal fin prior to release. Each V9AP was secured to an acrylic mount. Two small holes were then made through the middle of the dorsal fin using a sterile scalpel, and the mount secured either side of the dorsal fin using surgical suture. The entire workup procedure lasted no longer than 15 min per animal. The accelerometer sensor had a 5 Hz sampling frequency and measured acceleration (g) in three axes (x,y,z). Prior to transmission, the route mean square (RMS) was calculated as $RMS = \sqrt{A_x^2 + A_y^2 + A_z^2}$. The mean RMS was calculated for 27 s sampling periods and stored on board prior to transmission. The pressure sensor was rated to a depth of 200 m. The transmitters were programmed to transmit a single pressure sensor reading for every two acceleration readings.

Statistical analysis

Data were analysed using RStudio version 0.99.896 (R Core Team 2013). *C. perezi* post-release detection probability was modelled with Cox proportional hazards regression with sex and length as predictors and days detected post-release as a response variable. Data were checked for the assumption of proportional hazards prior to analysis. To identify spatial preference across the array, the log-transformed numbers of detections and mean acceleration values were examined for each individual VR2 receiver. A generalized additive mixed effects model was fit to log-transformed shark acceleration with time of day as a predictor, days post-release as a smoother, and individual as a random effect. The model was validated following the protocol outlined in Zuur et al. (2009). After deploying these tags a parallel study on Caribbean reef sharks in this region revealed that they make sporadic excursions into deep-water (> 200 m) (Shipley et al. 2017). Therefore all depth data collected during this study were removed from analyses due to the malfunctioning of integrated depth sensors after all tagged animals exceeded the depth rating of sensors (max depth = 200 m).

Results

Fourteen (eight male, six female) *C. perezi* individuals encompassing immature and mature individuals (139–217 cm STL) were captured and tagged over the course of this study. Five were not detected after tagging (Table 1). The remaining nine sharks generated a total of 10,862 detections across the array, with days at liberty ranging from 1 to 61 between individuals respectively (Table 1). Only three sharks exhibited significant presence around the array for the entire deployment duration (1,074,441, 1,074,437 and 1,074,447) despite that all sharks were captured and released within the footprint of the array. The time between release and first detection was highly variable between animals (7:20 h to 614:28 h, Table 1), however all animals remained undetected for at least 7 h post-release before being detected.

There was no significant effect of body size on the probability of being detected post release (Cox Proportional Hazards; $z = 0.17$, $p = 0.86$). There was a significant effect of sex ($z = 2.2$, $p = 0.03$), whereby males were significantly less likely to be detected in the array post-release than females (Fig. 1a). For those sharks that were detected within the array ($n = 9$), there was a significant effect of diel period on mean acceleration (GAMM; $F_{1,10,860} = 9.2$, $p < 0.001$). *C. perezi* individuals were more active at night, with activity levels peaking around 12 am (Fig. 1b).

Examining spatial distributions, *C. perezi* individuals primarily occupied the edge of the Exuma Sound throughout the entire deployment duration and did not move onto the shallower regions of the shelf closer to South Eleuthera (Fig. 2). The majority of detections occurred northwest of Cape Eleuthera in the northeast region of the Exuma Sound, and in the southern region of the array. *C. perezi* activity levels were generally higher in close proximity to the reef shelf, with high activity in diverse regions along the shelf at night (Fig.

Table 1 Summary information for *C. perezi* individuals tagged with V9 acoustic transmitters. Days at liberty is defined as the total duration each individual was detected on the array

Shark No.	Tagging date	Sex	STL	Time to first detection (hours)	Total no. of detections	Days at liberty	No. of days detected
1,074,441	9/6/2009	F	183	20:20:00	876	61	58
1,074,442	10/6/2009	M	180	–	–	–	–
1,074,438	11/6/2009	M	161	7:02:00	1	2	1
1,074,439	11/6/2009	M	172	189:22:00	45	6	4
1,074,437	12/6/2009	F	161	19:19:00	8738	61	58
1,074,447	12/6/2009	F	150	19:11:00	1053	61	56
1,074,449	12/6/2009	M	172	–	–	–	–
1,074,443	13/6/2009	M	172	71:41:00	6	11	1
1,074,450	13/6/2009	M	139	–		–	–
1,074,451	13/6/2009	F	217	614:28:00	27	10	7
1,077,440	13/6/2009	F	149	–		–	–
1,074,446	17/6/2009	M	178	22:09:00	68	27	9
1,074,445	18/6/2009	F	144	20:06:00	48	50	13
1,074,452	27/6/2009	M	168	–	–	–	–

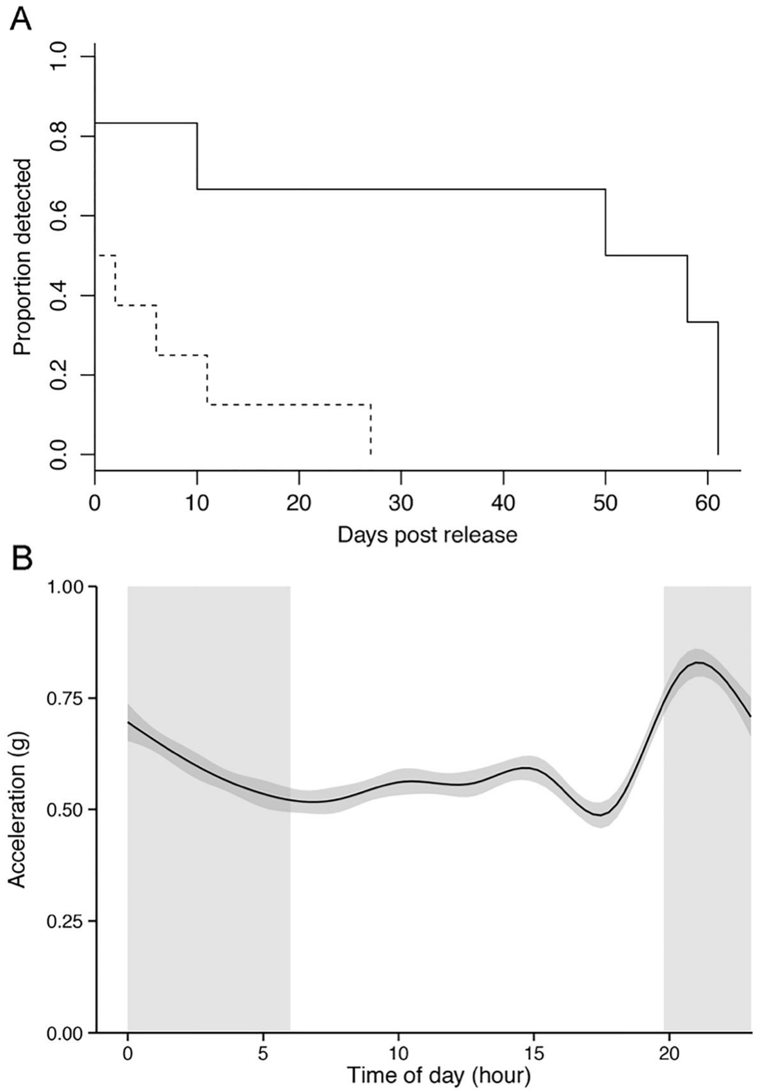

Fig. 1 **a** Proportion of male (dashed line) and female (solid line) *C. perezi* individuals detected by number of days post release, **b** *C. perezi* acceleration (g) by time of day fit with a gam smoother

2). Sharks were also active in particular regions along the shelf during the day, with especially high levels of activity in the southern portion of the array where the shelf is close to shore (Fig. 2).

Discussion

Acoustic telemetry with accelerometer transmitters provided novel information regarding space-use and activity of *C. perezi* in south Eleuthera, The Bahamas. Time to first detection was highly variable between individuals, who all remained absent from the array for at least seven hours post-release. This behaviour could indicate stress-induced behavioural modification (Hoolihan et al. 2011), whereby animals may flee a considerable distance from the sampling area to recover from physical and physiological stress induced during the initial capture and tagging event. Females had a greater detection probability over the deployment duration than males (Fig. 2). *C. perezi* is known to be resilient to experimental longline capture (Brooks et al. 2012), and previous work has demonstrated low levels of post-release mortality regardless of sex (Shipley et al. 2017). It is therefore most likely that the majority of undetected fish exited the study region. Based on this assumption, male

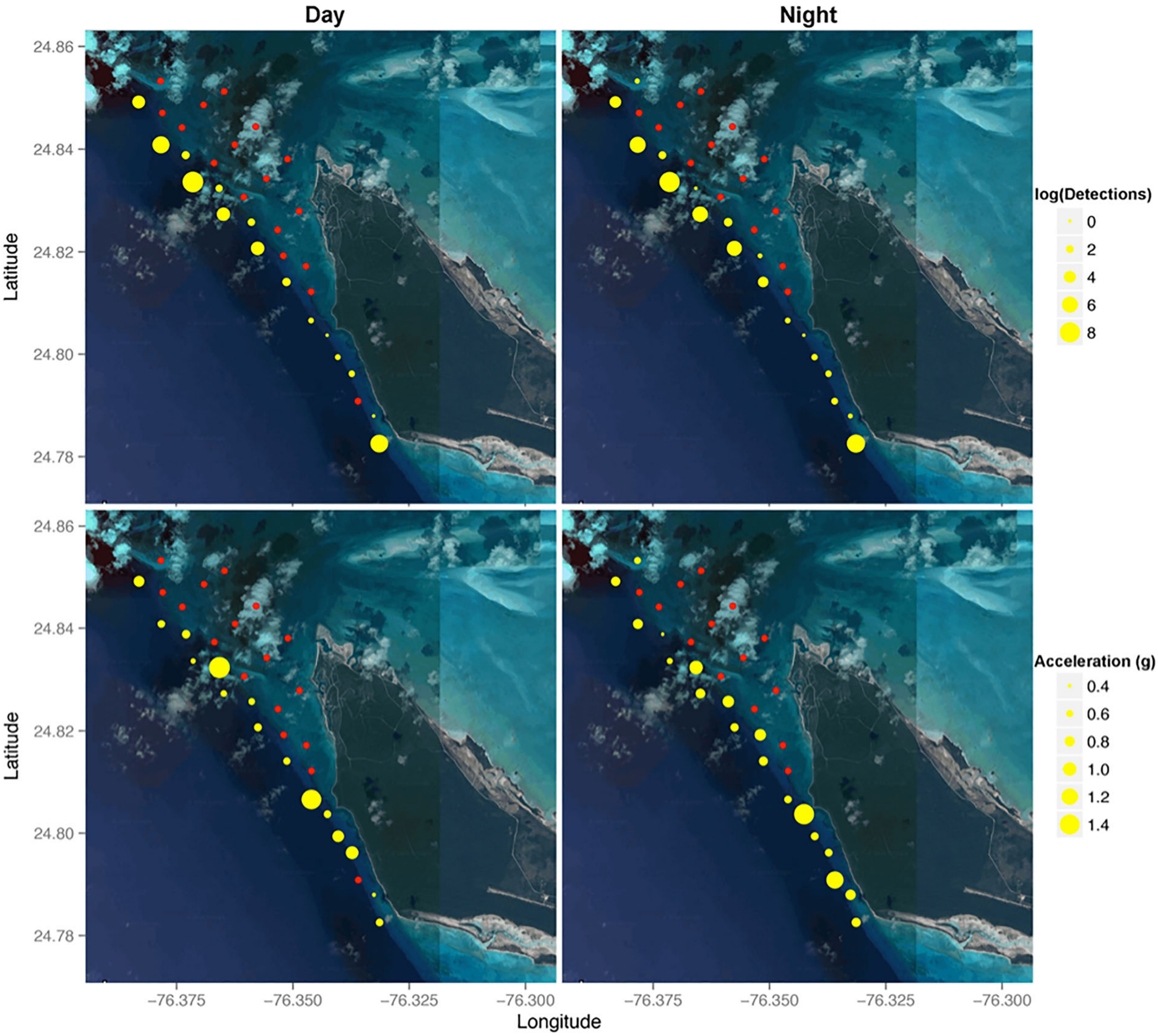

Fig. 2 Top panels: Fixed kernel-density estimates of log-transformed number of detections for *C. perezi* individuals at each acoustic receiver; red dots indicate no detections, bottom panels: Mean acceleration values for *C. perezi* individuals at each acoustic receiver; red dots indicate no detections

C. perezi could have larger home ranges than females, however rigorously testing this hypothesis this would require quantifying movements across a larger number of individuals and life history stages, and significantly increasing array coverage, which extended beyond the scope of this study. Further, extending sampling across an increased temporal window may elucidate seasonal changes in habitat use, as some individuals may move further offshore, and away from south Eleuthera during summer and fall (Shipley et al. 2017). Despite these caveats, sexual segregation in space-use is known for many elasmobranchs; for example spottail sharks (*Carcharhinus sorrah*; Knip et al. 2012), blue sharks (*Prionace glauca*), and shortfin mako sharks (*Isurus oxyrinchus*; Mucientes et al. 2009). These observations therefore imply that when designing and designating MPAs, the potentially variable home range sizes between male and female *C. perezi* should be considered. Although alternate tracking methodologies, such as satellite telemetry may offer insight into broad-scale movements and the interaction of animals with national boundaries, finer scale observations are of particular importance when informing current national conservation strategies in the Caribbean. The Caribbean challenge initiative, for example, focuses on the protection of distinct habitattypes, in which participating nations including The Bahamas, are aiming to protect 20% of coastal resources by 2020 (Moultrie 2012). In such cases, an understanding of organismal fine-scale habitat use is paramount to developing the most efficient, and informed placement of future MPAs.

C. perezi individuals were exclusively detected along continental drop-off for the entire deployment duration, and were not detected on receivers located further inshore. This likely represents ontogenetic segregation in habitat-use between differing size-class individuals; whereby smaller individuals reside further inshore, compared to larger sharks, which foray along escarpments and drop-offs (Pikitch et al. 2005; Brooks et al. 2013; Shipley et al. 2017). Specific depth estimates could not be retrieved from the integrated pressure sensors, as individuals moved to depths (max = 200 m), which exceeded the maximum capacity of the sensor. This suggests animals were active well below 200 m; behaviour documented in some *C. perezi* individuals (Chapman et al. 2007; Shipley et al. 2017). Sharks were commonly detected in two distinct areas along the drop-off of the northeast Exuma Sound. Firstly, a large number of detections were observed in the northern region of the array, as well as a peak in detections on a single receiver in the southern region, near Deals Point. Further, animals did not differentiate space use in relation to time of day, as high space use along the drop-off was homogenous during day and night time periods. These observations are in support of previous findings, as *C. perezi* individuals tagged at other locales have been observed to associate with highly specific areas of reef crest, and exhibit limited horizontal displacement (Chapman et al. 2005; Brooks et al. 2013). This suggests that patterns of detections observed in this study are largely driven by site fidelity exhibited by a single individual.

Importantly, spatial and temporal variability in detection frequency with acoustic telemetry systems can bias ecological interpretation of data (Kessel et al. 2014). This study did not employ range testing or sentinel tags to track detection range or efficiency, which must be considered when interpreting findings. Detection efficiency is generally lower and more temporally variable (due primarily to tides, wind, reef noise) in shallow water habitats (Gjelland and Hedger 2013; Kessel et al. 2014). We received zero detections of Caribbean reef sharks on the shallow reef region, which regardless of detection efficiency, suggests limited use of this area. These movement patterns are also consistent with data from other locales, such as Belize (e.g. Chapman et al. 2005). Detection efficiency also often decreases in reef habitats at night (Kessel et al. 2014), which may have resulted in reduced detections at night in our study, especially at receivers in close proximity to the reef.

Diel-variability in the activity of *C. perezi* was observed, as individuals exhibited greater activity during the night compared to the day, with a peak activity occuring around 12 am. Although species- and habitat-specific, some elasmobranch species are known to increase activity during the night in association with increased feeding (Gleiss et al. 2013; Papastamatiou et al. 2015; Barnett et al. 2016). Activity levels were also generally highest in close proximity to the reef shelf, which likely represents important foraging habitat for this species (Chapman et al. 2007). The proximity of the study location to open-ocean, and mesophotic reef habitat adjacent to the drop-off, may provide *C. perezi* access to a diverse number of prey-rich resource pools, as reef sharks are known to exploit both pelagic and mesophotic habitats to sustain energetic requirements (McCauley et al. 2012; Papastamatiou et al. 2015). *C. perezi* individuals are also known to perform deep vertical excursions (> 200 m), with a high frequency during the night (Chapman et al. 2007; Shipley et al. 2017), which is supportive of increased nighttime activity of individuals observed in this study. We therefore conclude such observations are likely driven by increased foraging behaviour during this period. Although beyond the scope of this study, 12 am could represent the time of highest lunar intensity, which may dictate periods of high activity, as seen in other reef-associated fishes (Koenig et al. 2017).

Novel insights from accelerometers highlight the distinct movement and activity patterns of *C. perezi* off South Eleuthera, The Bahamas. Based on our findings, male *C. perezi* may exhibit larger home ranges than females, but this hypothesis requires further testing. Regardless, such behavior illustrates the inherent complexity of shark behaviour, and may complicate the designation of future MPAs. Fringing coral reefs and continental drop-offs were identified as key habitat-use areas by immature and mature sharks, which may represent key foraging habitats, and may be exploited at higher frequency during the night. These findings provide insight into the spatial and behavioural ecology of *C. perezi*, which may have important implications for design and placement MPAs, as well as characterizing species interactions and community ecology in coastal marine systems.

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