

Biological and environmental effects on activity space of a common reef shark on an inshore reef

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ABSTRACT: Proximity to land and sources of freshwater expose fishes residing on inshore reefs to fluctuating environmental conditions (e.g. high freshwater run-off/low salinity events). However, site attachment in many reef residents, such as reef sharks, could mean that relocation in response to unfavourable environmental conditions may not be feasible. Passive acoustic telemetry was used to monitor movement and space use of 18 blacktip reef sharks *Carcharhinus melanopterus* on an inshore reef off the coast of Queensland, Australia, to determine their response to environmental change. Activity space of sharks was modelled against combinations of environmental (wind speed, rain, salinity and water temperature) and biological (size, sex) factors. Size was the most influential predictor of space use, with larger sharks having larger activity spaces. Sex also appeared in top-performing models, showing that juvenile males use more space than juvenile females, although effects were marginal. Model results also indicated a relationship between shark activity space and salinity, where space use increased with decreasing salinity. A similar but weaker relationship was observed with water temperature. These results show that blacktip reef sharks respond to minor changes in salinity, suggesting that they may be able to relocate when conditions are unfavourable, and help define the resilience of this species to disturbance and change.

KEY WORDS: Salinity · Spatial ecology · Blacktip reef shark · *Carcharhinus melanopterus* · Climate change · Acoustic monitoring · Coral reef · IMOS Animal Tracking Facility

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INTRODUCTION

Environmental factors play an important role in the spatial ecology of many elasmobranch species. Studies have documented changes in movement patterns and habitat use of elasmobranchs in response to a variety of factors such as temperature, salinity and tides (Schlaff et al. 2014). As drivers of movement, environmental factors have the potential to alter the distribution of individuals or populations over both short and long temporal scales, which could significantly influence entire ecosystems. To date, most studies linking environmental factors to movement of

elasmobranchs have focussed primarily on estuarine species or nearshore species occupying coastal embayments (e.g. Hopkins & Cech 2003, Heithaus et al. 2009, Froeschke et al. 2010) and on pelagic species (Vaudo et al. 2016). In order to more fully understand the role environmental factors play in the spatial ecology of elasmobranchs, it is important to examine environmental effects on movement and space use of species from a broader range of habitats.

Little information is currently available on the effects of environmental change on reef sharks. An integrated risk assessment of elasmobranchs in Australia's Great Barrier Reef World Heritage Area

determined that reef-associated sharks were among the most vulnerable to climate change, with changes in temperature, freshwater input and ocean circulation predicted to have widespread effects on these species (Chin et al. 2010). For reef sharks, vulnerability was driven by habitat degradation and an associated loss of overall resiliency based on their site attachment to coral reefs and adjacent (e.g. reef flat) habitats (e.g. Gruber et al. 1988, Barnett et al. 2012, Bond et al. 2012, Heupel & Simpfendorfer 2015). Unlike for species that use continuous coastal habitats and have the ability to relocate should environmental conditions deteriorate, movement away from patchily distributed coral reef habitat may not be a viable option for reef sharks because of the risk of not finding new suitable habitat.

In those studies that have documented environmental effects on the spatial ecology of reef sharks, the factors most commonly reported to influence movement and space use are temperature (Economakis & Lobel 1998, DiGirolamo et al. 2012, Guttridge et al. 2012, Speed et al. 2012b) and tide (Wetherbee et al. 2007, Papastamatiou et al. 2010, Guttridge et al. 2012, Filmlalter et al. 2013). In contrast, recent, long-term monitoring revealed that space use of grey reef sharks on the Great Barrier Reef (GBR) was not related to environmental factors (Heupel & Simpfendorfer 2014, Espinoza et al. 2015), but rather was likely biologically driven (e.g. prey density, reproduction). Common to all of these studies, however, is that they were conducted on offshore reefs where conditions are expected to be more stable than on inshore reefs. By comparison, inshore regions are highly dynamic and are characterised by environmental fluctuations such as high freshwater run-off/low salinity events (King et al. 2002, Devlin & Brodie 2005, Devlin & Schaffelke 2009) and large and/or rapid changes in temperature (Mann 2000). For sharks resident on inshore reefs, frequent exposure to variable environmental conditions may result in different movement patterns compared to individuals found farther offshore.

The blacktip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard 1824-25) is a medium-bodied predator, common to reefs throughout the Indo-West and Central Pacific. In Australia, its distribution ranges from Moreton Bay (Queensland) north and west to Shark Bay (Western Australia) (Last & Stevens 2009). It is the third most commonly encountered shark on the GBR after the grey reef shark *C. amblyrhynchos* and the whitetip reef shark *Triaenodon obesus* (Heupel et al. 2009, Last & Stevens 2009). Blacktip reef sharks are site-attached, with

several studies documenting comparatively small home ranges and localised movement across a wide range of habitats and life history stages (Stevens 1984, Papastamatiou et al. 2011, Speed et al. 2011, Chin et al. 2013c, 2016). Investigations into catch and occurrence of reef sharks within the GBR lagoon showed that blacktip reef sharks dominate the catch (60.2%), making it the most common reef shark found in inshore habitats (Chin et al. 2012). Inshore populations are more regularly exposed to environmental variability, making this species an excellent case study on the effects of environmental factors on the spatial ecology of a reef shark.

The purpose of this research was to examine the response of blacktip reef sharks to environmental changes within an inshore reef environment. Examining how resident sharks respond to fluctuations in their environment will help determine how resilient populations are to disturbance and change. We tested the hypothesis that movement patterns of blacktip reef sharks on an inshore reef will reflect changes in the local environmental conditions (e.g. temperature, salinity). In addition, previous research has documented sex (Papastamatiou et al. 2009a, Speed et al. 2011, Chin et al. 2016) and ontogenetic (Papastamatiou et al. 2009b, Speed et al. 2011, 2016, Chin et al. 2016) differences in movement and space use of blacktip reef sharks believed to be due to sex- and size-specific differences in energetic costs (e.g. reproduction, growth) and habitat requirements (e.g. prey availability, predator avoidance). As biological mechanisms may alter responses to environmental drivers, we also tested the hypotheses that environmental factors influencing movement and space use will differ between sexes and size classes.

MATERIALS AND METHODS

Study area

Field work was conducted around Orpheus Island (18.37° S, 146.30° E), part of the Palm Island Group of the GBR approximately 16 km off the coast of Queensland, Australia (Fig. 1a). Orpheus Island is 12 km long, 1 to 2.5 km wide and surrounded by fringing reef, with depths ranging from 8 to 20 m. Several bays are located around the island, which are characterised by sand and/or coral rubble intertidal flats with most containing sections of non-estuarine mangrove habitat (dominated by *Rhizophora* spp.). Average depth in the bays is less than 5 m, and maximum tidal range reaches 4 m. Because of its close

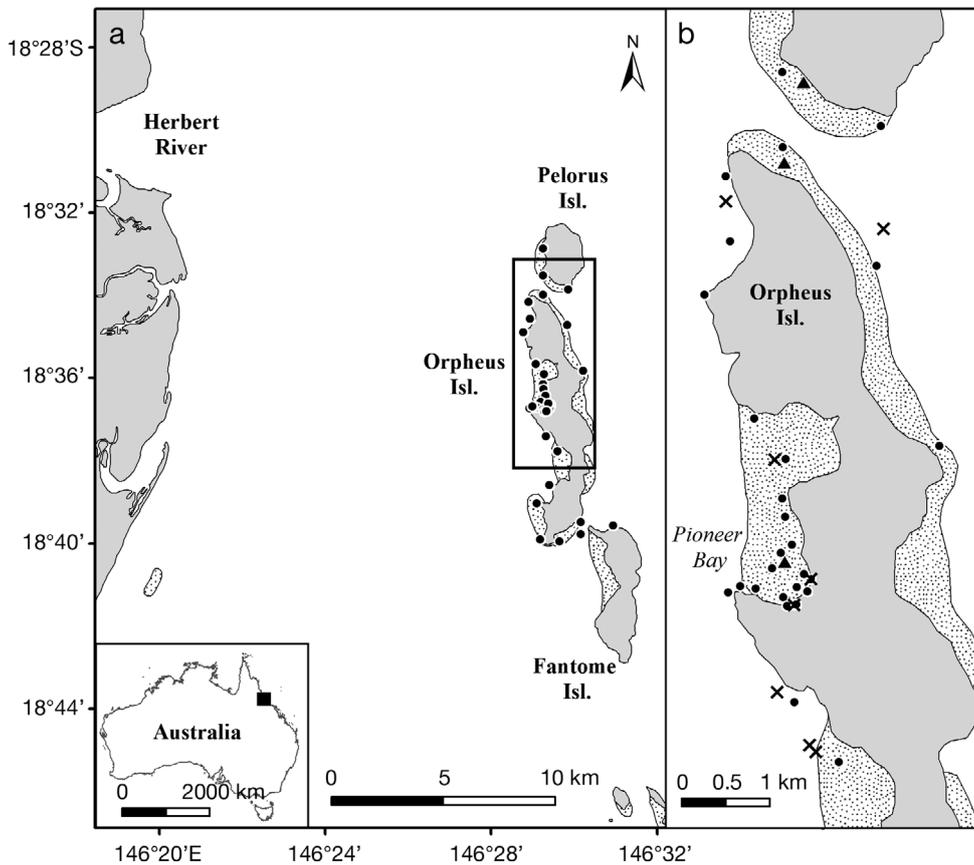


Fig. 1. Study site. (a) Orpheus Island, Palm Islands, Queensland, Australia (insert shows the location of the study site within Australia). (b) Close-up of Orpheus Island, showing weather stations (triangles) and fishing locations (crosses). In both panels, the positions of acoustic receivers at Orpheus, Pelorus and Fantome Islands are marked with circles. Light grey stippling indicates reef flat habitat

proximity to the mainland, Orpheus Island is directly affected by run-off from several rivers along the north Queensland coast, including the Herbert and Burdekin Rivers (King et al. 2002), resulting in a variable inshore environment.

Field methods

Movement patterns and space use of blacktip reef sharks were examined using passive acoustic telemetry. Thirty-six VR2W acoustic receivers (Vemco) were deployed around the study site to monitor the movement of tagged individuals (Fig. 1). While the majority of receivers were distributed around Orpheus Island, some were deployed on the adjacent Pelorus ($n = 3$) and Fantome ($n = 2$) Islands to track movements of individuals between islands. Receivers were positioned 2 to 3 m above the seabed, fastened to a nylon rope with a float and anchored to the reef using stainless steel chain shackled to a coral head. Receivers placed in areas without reef substrate ($n = 12$) were attached to star pickets embedded into the sea floor. Receivers closest to shore ($n = 8$) within Pioneer Bay, an intertidal reef flat located on the west-

ern side of Orpheus Island, became completely exposed at tidal heights of 160 cm or less, relative to the lowest astronomical tide (LAT) and at 140 cm or less, relative to LAT for mid-bay receivers. Detection range of receivers was ~ 125 m within shallow inshore bays around the island (Welsh et al. 2012), with the detection range likely larger in deeper habitats around the island. Data from receivers were downloaded twice a year.

Tagging took place between December 2011 and February 2013 at several locations around Orpheus Island (Fig. 1b). Sharks were captured using multi-hook long-lines or rod and reel. Long-lines consisted of a 500 m mainline (8 mm nylon rope) anchored at both ends and left to soak for 1 h. Gangions (1 m of 5 mm nylon cord with 1 m wire trace and size 14 Mustad tuna circle hooks) were attached at 8 to 10 m intervals along the mainline and baited with either frozen butterfly bream (*Nemipterus* sp.) or squid (*Loligo* sp.). Individuals collected by rod and reel were captured on 8/0 Mustad hooks baited with pilchard (*Sardinops* sp.) or squid. All captured individuals were measured to the nearest millimetre, sexed and tagged with a rototag in the first dorsal fin for identification prior to release. V13P acoustic

transmitters (69 kHz; 13 mm diameter × 45 mm length; Vemco) were surgically implanted into the body cavity via a small incision (3–4 cm) following the methods of Heupel & Hueter (2001). Transmitters emitted a unique pulse series (i.e. ID code) specific to the individual tagged, as well as depth (maximum depth: 50 m), on a pseudorandom repeat every 120 to 200 s and had an estimated battery life of 374 d. Sharks were retained for a maximum of 10 min during measuring and tagging procedures, with all surgical procedures conducted according to protocols approved by James Cook University's Animal Ethics committee (permit A1566).

The Integrated Marine Observing System's (IMOS) Facility for Automated Intelligent Monitoring of Marine Systems manages a network of sensor equipment around Orpheus and Pelorus Islands (Fig. 1b) that

record real-time data on 12 environmental parameters (e.g. barometric pressure, rainfall). These data are publicly available from IMOS (www.imos.org.au) or Australian Institute of Marine Science (www.aims.gov.au) websites. Environmental data for the period between December 2011 and the end of January 2014 were downloaded and used in analyses (Fig. 2). Salinity measurements were taken at the Pelorus Island weather station (at a depth of 14.6 m), and temperature measurements from the northernmost Orpheus Island station (at a depth of 7.6 m). The weather station within Pioneer Bay measured both temperature and salinity, but was not operational for the full period of the study. Variation in salinity and temperature data between these 2 weather stations and the third station within Pioneer Bay was limited (average of ± 0.23 ppt; $\pm 0.25^\circ\text{C}$) when all 3 stations were active;

as such, data from the 2 northern stations were selected for use in further statistical analyses as these data sets were the most complete. Given the complex topography at Orpheus Island along with the large tides, it is unlikely that an environmental gradient would develop within the study area. However, it is possible that variability in abiotic conditions exists around the islands that could not be measured. Environmental parameters were recorded at 1 h intervals and were filtered and later processed to provide summary data at the same time scale as that used for activity space estimates. Data were then centred to have a mean of 0 (Becker et al. 1988) before being tested for correlation. Where environmental parameters of interest were found to be highly correlated ($R > 0.70$), 1 of each pair of correlated co-variables was removed, leaving water temperature, salinity, rainfall and average wind speed to be included in the final analyses.

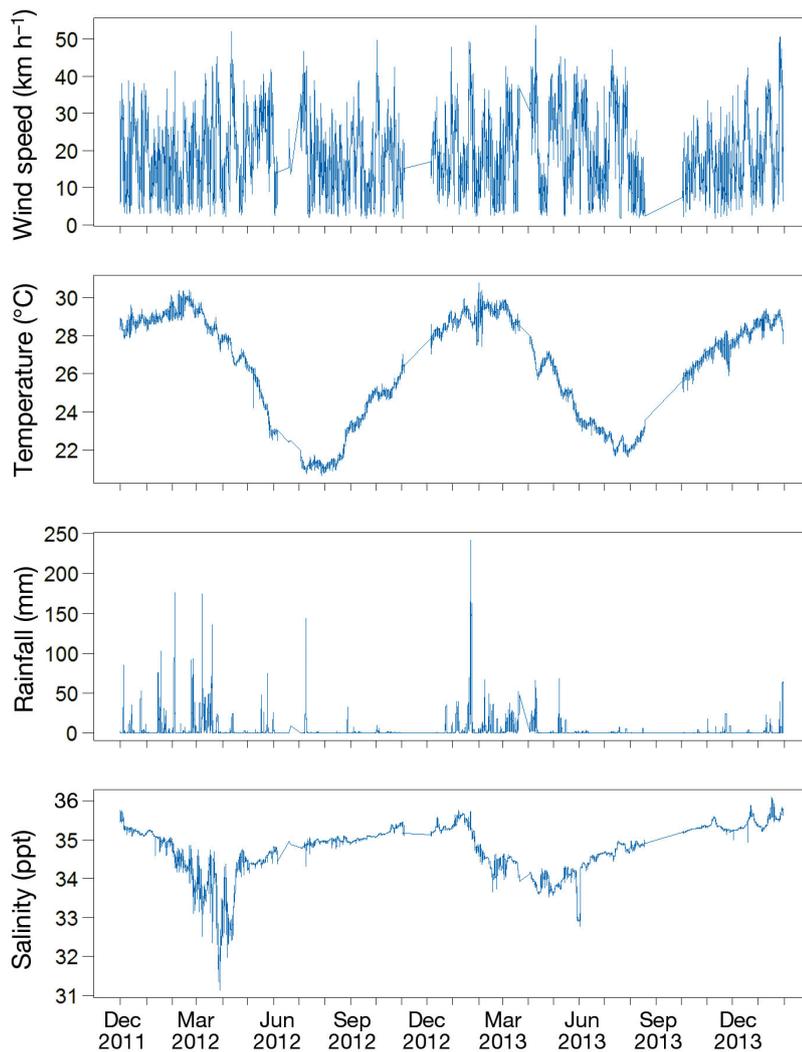


Fig. 2. Environmental measurements for Orpheus and Pelorus Islands from December 2011 to the end of January 2014

Data analysis

Data from acoustic receivers were examined to investigate changes in activity space and movement patterns of blacktip reef sharks in response to environmental conditions. To be included in the analyses, sharks had to

be detected within the array for ≥ 30 d and at least twice on a single receiver on any given day to reduce the chance of including false detections. Residency of individuals was calculated as the ratio of days detected within the acoustic array to days at liberty, with values ranging from 0 to 1 for low to high residency, respectively. 'Days at liberty' represented the total detection days possible and was defined as the number of days from initial tagging and transmitter activation to the date when the battery was expected to expire (i.e. predicted tag life) for individuals tagged in December 2011/2012 or until the end of the study for sharks tagged in February 2013.

Position estimates

Customised R scripts were used to provide a 'centre of activity' (COA) estimate for each individual over a 30 min time period (Simpfendorfer et al. 2002). COA locations represented the mean position of each shark for the given time step weighted by the number of detections at each receiver within the array. Following the methods of Simpfendorfer et al. (2008) and Heupel & Simpfendorfer (2014), the acoustic array was treated as a linear system. Using this approach, the receiver located on the northwest side of Pelorus Island was designated as the starting point, and position of individuals was calculated as the distance from that point. Reef distance values were then combined with mean tag depth values from the same time period to generate a 2-dimensional representation of location averaged over a 30 min time period.

Activity space

Weekly activity spaces of individuals were calculated using 50 and 95% vertical kernel utilization distributions (vKUDs) based on COA estimates using the *ks* package in R (Duong 2007). Vertical activity space estimates provided information on depth use with distance along the reef for each individual. Areas of core use (50% vKUD) and extent (95% vKUD) were examined over weekly intervals to investigate changes in movement and space use over time. Weeks with <10 position estimates for an individual resulted in that week being excluded from subsequent analyses for that individual to avoid inaccurate estimates of activity space. Unless otherwise indicated, analyses were conducted in the R environment (R Development Core Team 2013).

Factors influencing activity space size

Linear mixed effects models were used to examine activity space data for size, sex and environmental effects using the *nlme* package in R (Pinheiro et al. 2012). Individual (animal 'ID' code) was incorporated as a random factor within these models to account for the repeated-measures nature of the data (Bolker et al. 2009). Before running models, activity space estimates were first checked for normality and square root transformed if required (Heupel & Simpfendorfer 2014). Models were also tested for collinearity by calculating the variance inflation factors among the covariates using the R package *car* (Fox & Weisberg 2011). An information theoretic model selection process was used to investigate the effects of fixed (environmental variables, stretch total length [STL], sex) and random (individual) factors on weekly 50 and 95% vKUDs of individuals (Burnham & Anderson 2003). The 'dredge' function in the *MuMIn* package in R (Barton 2013) was used to generate a series of candidate models that were compared to each other using Akaike's information criterion corrected for small-sample bias (AICc). Candidate models were constructed against all possible combinations of environmental and biological factors and the null model (global model: \sim water temperature + salinity + rainfall + wind speed + STL + sex \times week + [1|ID]). Maximum likelihood ratio tests were used to compare candidate models against the null model and test for significant differences ($\alpha = 0.05$). Model averaging was conducted on the top candidate models ($\Delta\text{AICc} < 2$) for 50 and 95% vKUD, which weighted environmental and biological parameters with respect to AICc weight. Parameter estimates were then averaged over the subset of candidate models, a process that allowed for incorporation of model uncertainty. Cumulative AICc weights ($0 \leq w_i \leq 1$) were calculated to evaluate strength of evidence for each activity space-modelled covariate within averaged models (Burnham & Anderson 2003). Following Barbieri & Berger (2004), covariates with $w_i > 0.5$ were considered significant drivers of activity space.

RESULTS

Between December 2011 and February 2013, we tagged 34 blacktip reef sharks with acoustic transmitters at Orpheus Island. No attempt was made to control the number of males and females, and transmitters were fitted to animals regardless of sex. Nineteen sharks were tagged in December 2011 (10 fe-

Table 1. Details of acoustically tagged blacktip reef sharks *Carcharhinus melanopterus* (ID code) with stretch total length (STL), sex, release date (dd/mm/yyyy) and overall 50 and 95% vertical activity space (vKUD) estimates. Residency index was calculated as the ratio of days detected within the array to days at liberty, with values ranging from 0 to 1 for low to high residency

ID code	STL (mm)	Sex	Release date	Days at liberty	Days detected	Residency index	Overall 50% vKUD (m ²)	Overall 95% vKUD (m ²)
6523	685	F	10/12/2011	374	268	0.72	796	8000
6525	570	M	10/12/2011	374	203	0.54	370	695
6526	510	M	10/12/2011	374	144	0.39	237	1095
6527	1050	F	11/12/2011	374	367	0.98	1055	10730
6531	770	M	13/12/2011	374	369	0.99	2841	29163
6532	1070	F	13/12/2011	374	373	1.00	982	22245
6533	1030	F	13/12/2011	374	369	0.99	1160	22852
6534	1070	F	13/12/2011	374	374	1.00	2813	31471
6535	750	M	13/12/2011	374	367	0.98	808	10328
6539	1350	F	13/12/2011	374	374	1.00	2538	17390
6540	1260	F	14/12/2011	374	374	1.00	4120	34322
7950	584	F	20/12/2012	374	104	0.28	314	871
7955	812	M	22/12/2012	374	332	0.89	4186	17679
7956	588	F	22/12/2012	374	345	0.92	366	937
7957	559	M	26/12/2012	374	52	0.14	328	2416
7958	593	M	13/02/2013	341	51	0.15	174	1218
7959	610	M	13/02/2013	341	199	0.58	137	2250
7962	559	M	16/02/2013	338	134	0.40	89	1883

male, 9 male), 1 in March 2012 (female), 8 in December 2012 (3 female, 5 male) and 6 in February 2013 (3 female, 3 male). Sixteen individuals were subsequently either never detected within the array ($n = 2$) or had limited data ($n = 14$) and were excluded from analyses. Of the 18 individuals included in the study, the smallest shark (510 mm STL) had a partially open umbilical scar identifying it as a neonate, while the

largest shark tagged measured 1350 mm STL (Table 1). As age and growth studies for this species have reported average size at maturity to be 1050 mm STL for males and 1335 mm STL for females (Chin et al. 2013b), only a single mature adult was included in final analyses (female, 1350 mm STL).

Minimum detection time of sharks was ~2 mo, with half ($n = 9$) present for the full period of predicted tag

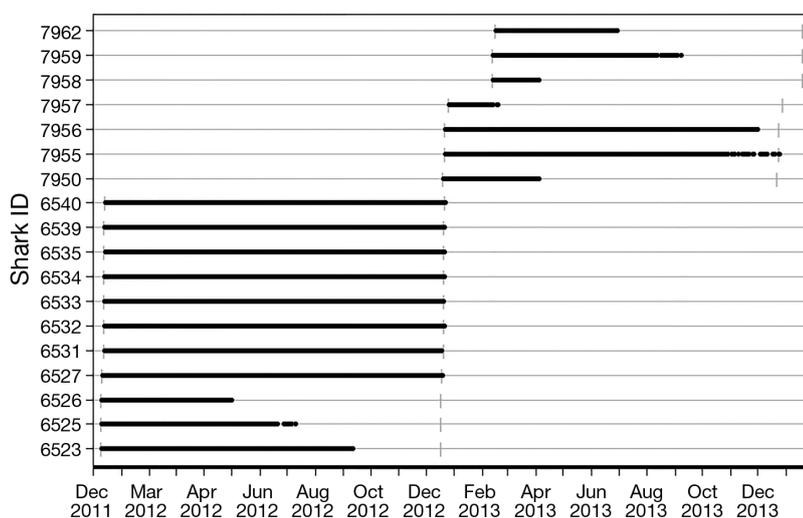


Fig. 3. Presence plot for 18 blacktip reef sharks *Carcharhinus melanopterus* captured and released at Orpheus Island from December 2011 to the end of January 2014; black circles indicate presence at the site and light grey vertical bars indicate predicted tag life

life (Fig. 3). Remaining sharks ($n = 9$) either departed from the monitored area permanently, died outside of the array or experienced tag failure. The timing of detection loss was random and did not appear to be coordinated among individuals or with environmental changes. One individual was detected exclusively on a single receiver for a period of ~5.5 mo prior to tag expiry and was presumed to have died (these months were excluded from analyses). Blacktip reef sharks showed site-attachment to reef habitats with high residency indices (≥ 0.70) calculated for 11 individuals (Table 1). Four individuals were detected within the array every day for the duration of the study. It is important to note that, due to the way in which 'days at liberty' were deter-

mined (i.e. using predicted tag life, not when individual tags were last detected), residency values may be underestimated as individuals go undetected, although present, when using habitats outside of the listening range of the acoustic array.

Results from modelling indicated that both biological (size, sex) and environmental (salinity, temperature) effects influenced the activity space of monitored sharks. The best-fit model (i.e. lowest AICc value) for 95% vKUD included STL, sex, salinity and temperature (Table 2) while the best-fit model for 50% vKUD included STL, sex, salinity and week (Table 3). Neither best-fit model for 50 or 95% vKUD had overwhelming support (i.e. similar low AICc weights among the top 15 models), and all candidate models were significantly better than the null models (maximum likelihood ratio test, $p < 0.01$). Cumulative AICc weights for averaged models (both 50 and 95% vKUD) supported dredge outputs, with all environmental and biological parameters included in best-fit models shown to influence activity spaces of tagged sharks ($w_i > 0.5$; Table 4). STL had the highest cumulative AICc weight across both metrics of vKUD, indicating that it had the most influence on activity space. After size, salinity had the most significant influence on 95% vKUD of sharks followed by water temperature and sex. Week was the second-most influential factor affecting 50% vKUD, followed by sex and salinity.

Model averaging showed that larger sharks had larger activity spaces, with 50 and 95% vKUDs increasing with size (Fig. 4a,c; Table 4; ANOVA, $p < 0.01$). Average weekly 50% vKUD of the smallest individual (male, 510 mm STL) was less than 10% that of largest (female, 1350 mm STL), ranging from 117 ± 91 (SE) m^2 to $1496 \pm 97 m^2$, respectively; weekly 95% vKUD ranged from an average of $2270 \pm 488 m^2$ to $12\,101 \pm 492 m^2$, with the largest individual using over 5 times more space than the smallest. Although not signifi-

Table 2. Top-ranked candidate models examining the effects of environmental and biological factors on extent of blacktip reef shark *Carcharhinus melanopterus* vertical activity space (95% vKUD; square-root transformed). The best-fit model with the smallest Akaike's information criterion corrected for small-sample bias (AICc) is shown in **bold**. Maximum likelihood ratio tests showed all models to be significantly better than the null model. $\Delta AICc$ is the Akaike difference and w is the Akaike weight. STL: stretch total length; as: activity space; wk: week; sal: salinity; temp: water temperature; rain: rainfall; wind: average wind speed

Model rank	Model	df	— 95% vKUD — AICc	$\Delta AICc$	w
1	sqrt(as) STL+sex+sal+temp	9	4783.54	0.00	0.11
2	sqrt(as) STL+sal+temp	8	4783.65	0.11	0.10
3	sqrt(as) STL+sex+sal	8	4785.40	1.86	0.04
4	sqrt(as) STL+sal	7	4785.52	1.98	0.04
5	sqrt(as) STL+sex+sal+temp+wind	10	4785.59	2.05	0.04
6	sqrt(as) STL+sex+sal+temp+rain	10	4785.61	2.07	0.04
7	sqrt(as) wk+STL+sex+sal+temp	10	4785.61	2.07	0.04
8	sqrt(as) STL+sal+temp+wind	9	4785.69	2.16	0.04
9	sqrt(as) STL+sal+temp+rain	9	4785.71	2.18	0.04
10	sqrt(as) wk+STL+sal+temp	9	4785.71	2.18	0.04
11	sqrt(as) STL+sex+sal+rain	9	4786.73	3.19	0.02
12	sqrt(as) STL+sal+rain	8	4786.82	3.29	0.02
13	sqrt(as) STL+sex+temp	8	4786.87	3.34	0.02
14	sqrt(as) STL+temp	7	4787.01	3.48	0.02
15	sqrt(as) STL+sex+sal+wind	9	4787.47	3.93	0.02

Table 3. Top-ranked candidate models examining the effects of environmental and biological factors on core vertical activity space (50% vKUD; square-root transformed) of blacktip reef sharks *Carcharhinus melanopterus*. The best-fit model with the smallest AICc is shown in **bold**. Maximum likelihood ratio tests showed all models to be significantly better than the null model. Abbreviations as in Table 2

Model rank	Model	df	— 50% vKUD — AICc	$\Delta AICc$	w
1	sqrt(as) wk+STL+sex+sal	9	4138.29	0.00	0.07
2	sqrt(as) wk+STL+sex+sal+wk×sex	10	4138.60	0.32	0.06
3	sqrt(as) wk+STL+sal	8	4138.63	0.34	0.06
4	sqrt(as) wk+STL+sex	8	4138.70	0.41	0.06
5	sqrt(as) wk+STL+sex+wk×sex	9	4139.00	0.71	0.05
6	sqrt(as) wk+STL	7	4139.08	0.79	0.05
7	sqrt(as) wk+STL+sex+sal+temp	10	4139.97	1.68	0.03
8	sqrt(as) wk+STL+sex+sal+wind	10	4140.00	1.71	0.03
9	sqrt(as) wk+STL+sex+sal+rain	10	4140.04	1.75	0.03
10	sqrt(as) wk+STL+sex+sal+temp+wk×sex	11	4140.14	1.86	0.03
11	sqrt(as) wk+STL+sal+temp	9	4140.29	2.01	0.03
12	sqrt(as) wk+STL+sal+wind	9	4140.33	2.04	0.02
13	sqrt(as) wk+STL+sex+sal+wind+wk×sex	11	4140.33	2.04	0.02
14	sqrt(as) wk+STL+sex+sal+rain+wk×sex	11	4140.35	2.06	0.02
15	sqrt(as) wk+STL+sal+rain	9	4140.35	2.06	0.02

cant, male sharks used marginally larger activity spaces than females (Fig. 4a,c). However, as only a single adult female was detected upon release, sex-specific differences in space use must be interpreted with caution. Interaction plots for sex and STL from averaged models showed juvenile males to be driv-

Table 4. Cumulative Akaike's information criterion (AIC) weights (w_i), parameter estimates and p-values calculated from an averaged subset ($\Delta AIC_c < 2$) of candidate models showing the relative influence of biological and environmental parameters on vertical activity space (50 and 95% vKUD; square-root transformed) of blacktip reef sharks *Carcharhinus melanopterus*. Cumulative weights and parameters considered influential drivers of activity space are shown in **bold**. Abbreviations as in Table 2

Parameter	Estimate \pm SE	p	w_i
50% vKUD			
STL	0.056 \pm 0.013	<0.001	1.00
sex	8.621 \pm 7.829	0.271	0.77
wk	0.103 \pm 0.039	0.009	1.00
wk:sex	-0.027 \pm 0.056	0.626	0.30
sal	-0.550 \pm 0.576	0.340	0.67
temp	-0.034 \pm 0.165	0.838	0.13
wind	-0.026 \pm 0.200	0.895	0.06
rain	-0.034 \pm 0.270	0.900	0.06
95% vKUD			
STL	0.130 \pm 0.035	<0.001	1.00
sex	12.673 \pm 17.683	0.474	0.51
sal	-1.906 \pm 0.831	0.022	1.00
temp	-0.969 \pm 0.838	0.247	0.72

ing observed sex-based patterns in activity space, and therefore data may not reflect true biological trends at the higher end of the size spectrum. In addition, the lower cumulative AICc weight of sex for both 50% ($w_i = 0.77$) and 95% ($w_i = 0.51$) vKUDs indicated that this factor was of less importance to observed patterns in activity space than STL. The sex \times week interaction term was not included in either of the best-fit models during model selection nor shown to be important ($w_i < 0.5$; Table 4), suggesting that patterns in activity space over time did not differ between males and females.

Models incorporating salinity consistently ranked high during the model selection process (Tables 2 & 3). However, cumulative AICc weights from averaged models suggested that salinity was more important to 95% vKUD ($w_i = 1.00$) than to core space use ($w_i = 0.67$), where it had a marginal effect (Table 4). During the study, salinity levels ranged from 31.1 ppt (March 2012) to 36.1 ppt (January 2014). The general trend was for 95% vKUD to increase with decreasing salinity (Fig. 4d, Table 4; ANOVA, $p = 0.02$), with increased depth use, increased use of horizontal

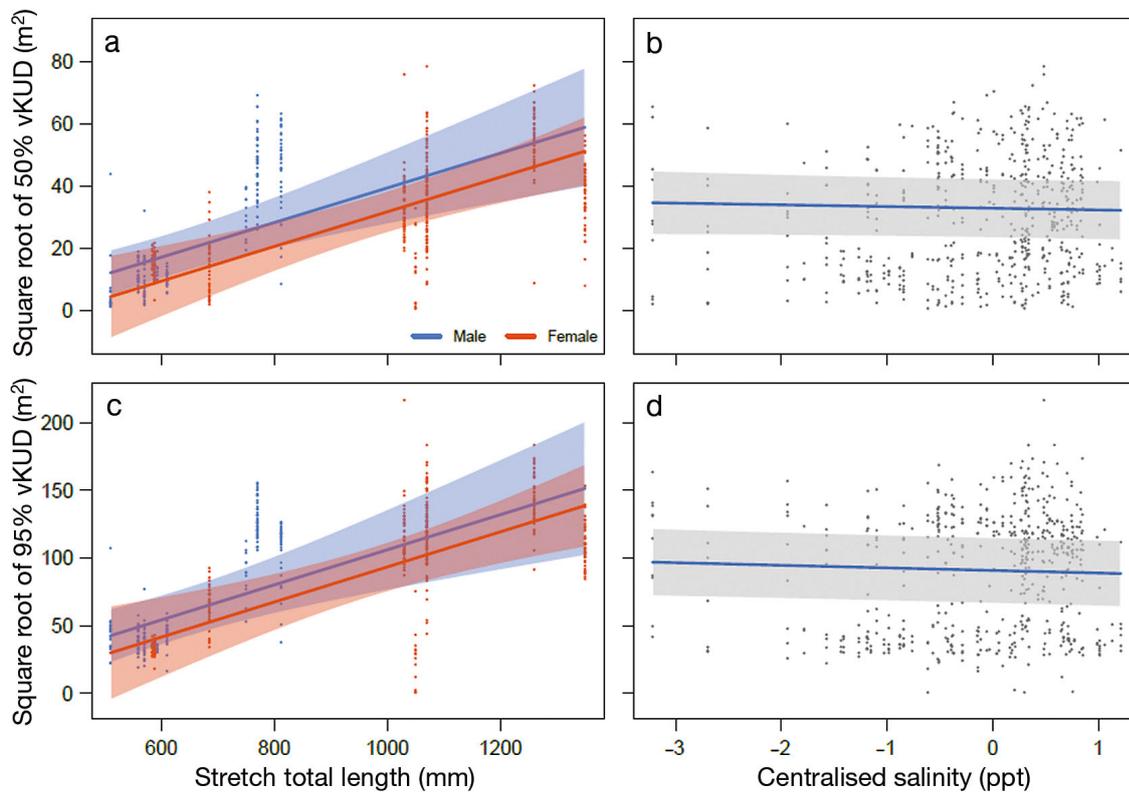


Fig. 4. Interaction plots from averaged models showing effects of biological and environmental factors on blacktip reef shark *Carcharhinus melanopterus* vertical activity space (vKUD; square-root transformed). The left column shows changes in (a) 50% and (c) 95% vKUD with increasing size (stretch total length, STL) for females (red) and males (blue). The right column indicates changes in (b) 50% and (d) 95% (d) vKUD with changes in salinity. Shaded areas indicate 95% confidence intervals and points are raw data for STL and centralised raw data for salinity

space or a combination of both accounting for these changes; the marginal effect of salinity on 50% vKUD indicated that core activity spaces were more stable (Fig. 4b, Table 4). Temperature was also included in the best-fit model for 95% vKUD. Results from model averaging showed the estimated size of activity space to decrease with increasing temperature (Table 4). Cumulative AICc weights for 95% vKUD suggested that temperature was less important ($w_i = 0.72$) as a predictor of activity space size than salinity—an observation supported by its low relative importance ($w_i = 0.13$) and lack of inclusion in the best-fit model for 50% vKUD. It is worth noting that, given the design of the acoustic array, observed patterns in space use were over relatively coarse spatial scales and may not reflect fine-scale movement and behavioural responses to temperature change.

DISCUSSION

The results of this research demonstrated that both biological and environmental factors influence how blacktip reef sharks occupy space within inshore reef habitats. Size was the most influential predictor of space use, with activity space positively correlated with this factor. Similar patterns were observed for this species in coastal habitats in Western Australia, where larger activity spaces were observed for adults (Speed et al. 2016). Ontogenetic shifts in movement, behaviour and habitat use have been recorded for several reef-associated sharks (Garla et al. 2006, Wetherbee et al. 2007, Grubbs 2010, Heupel et al. 2010), including blacktip reef sharks (Papastamatiou et al. 2009b, Chin et al. 2013a, 2016, Speed et al. 2016). Many of these studies showed that juvenile sharks primarily use shallow-water habitats (e.g. mangrove stands, sand flats), which differ from movements of adults that use both shallow intertidal and adjacent deep reef habitats (Wetherbee et al. 2007, Papastamatiou et al. 2009b, Knip et al. 2011a, DiGirolamo et al. 2012). Studies suggest that juvenile sharks expand their space use as they grow, with broader movements of adults likely related to energetic requirements and the need to find adequate resources (Lowe & Bray 2006, Tamburello et al. 2015). Thus, activity spaces of blacktip reef sharks at Orpheus Island are likely increasing with animal size as a response to growing energetic demands as well as a more developed ability to capture larger and faster-moving prey in varied habitats. Observations from stable isotope studies on this species show evidence of size-based differences in diet, with larger

individuals feeding higher in the food web (Speed et al. 2012a).

A marginal influence of sex was observed on space use in the present study, where juvenile males displayed larger activity spaces than juvenile females. Previously, studies on adult grey reef sharks in Australia have documented sex-dependent activity spaces and movements by mature males during the mating season, most likely to find suitable mates (Heupel & Simpfendorfer 2014, 2015). Similarly, adult female blacktip reef sharks utilising a shallow, turbid coastal habitat were highly resident while males had larger activity spaces and were transient (Chin et al. 2016). While these studies suggest that differences in space use between males and females may be related to reproductive requirements, in the present study only a single adult female was obtained, making it impossible to examine changes in activity space in response to seasonal biological processes (e.g. mate-searching, breeding, parturition). Nevertheless, activity spaces of juvenile male sharks at Orpheus Island were larger than those of juvenile females, indicating that movement drivers in juveniles may be more complex. Responses to environmental factors among juvenile blacktip reef sharks was not expected to differ given the similar energy requirements and associated space use of both sexes. However, as sex-specific costs in reproduction have different energetic demands, it is possible that further research will reveal differences in response to environmental drivers between sexes.

Our results indicated that salinity plays an important role in the spatial ecology of blacktip reef sharks on inshore reefs. Of the 4 environmental factors modelled (wind speed, rain, salinity and water temperature), salinity had the greatest influence on activity space, with 95% vKUDs increasing with decreasing salinity. Most sharks, including blacktip reef sharks, are stenohaline and occupy a narrow salinity range (Pang et al. 1977). When salinity levels fall outside of individual tolerances, sharks may use movement to avoid physiological stress and possible mortality (Heupel & Simpfendorfer 2008, Simpfendorfer et al. 2011). As such, one explanation for changes in activity space with salinity was that sharks moved to avoid unfavourable environmental conditions and that their corresponding space use increased as they sought more suitable conditions. In nearshore regions, seasonal fluctuations in rates of freshwater inflow and associated changes in salinity levels have been linked to movement of elasmobranchs as individuals avoid areas of high freshwater inflow and decreased salinity (Collins et al. 2008, Knip et al.

2011b, Francis 2013). A similar movement response based on freshwater inflow has been reported for bonnethead sharks *Sphyrna tiburo*, where sharks left the area at lower salinity levels (Heupel et al. 2006). It is also possible that activity spaces of sharks increased as individuals actively sought out a preferred salinity range within the study area in an effort to reduce the energetic costs associated with osmoregulation, a behavioural strategy observed in other elasmobranch species (Simpfendorfer et al. 2005, Froeschke et al. 2010). In addition, response by sharks to salinity changes may be due to the effects of this factor on resource distribution as opposed to physiological limitations, although this was not possible to measure in the current study.

While blacktip reef sharks reacted to salinity decreases by increasing their activity space, they did not permanently leave the study site during these periods. This suggests that this species may be somewhat resilient to environmental fluctuations, an observation supported by research showing that blacktip reef sharks may be more tolerant of the effects of a tropical cyclone than other inshore shark species (Udyawer et al. 2013). The failure to move under cyclonic and low-salinity conditions may also serve to highlight the importance of coral reef habitat to this species. Resilience to environmental changes may allow individuals to remain in reef habitats and be able to access the key ecosystem services reefs provide until conditions recover. Similarly, neonate sawfish *Pristis pectinata* were observed to remain in shallow water estuarine habitats longer than older juveniles when salinity levels increased, possibly due to the improved chance of survival gained from remaining in these protected habitats outweighing the energetic costs of osmoregulation (Simpfendorfer et al. 2011) or because they are better adapted to survive in these conditions. It is also possible that salinity conditions at Orpheus Island simply did not reach a level that would cause emigration. Salinity levels declined to below 16 ppt before bonnethead sharks emigrated from a Florida (USA) estuary (Heupel et al. 2006). Similarly, catch data from an inshore reef at Magnetic Island, approximately 100 km south of Orpheus Island, reported a substantial decline in catch rate of blacktip reef sharks when salinity decreased to 16 ppt following a heavy rainfall event (A. Chin pers. comm.). In comparison, salinity fluctuations at Orpheus Island were quite small (range: 31–36 ppt) and thus may not have been low enough to cause sharks to depart the reef despite altering their movement patterns.

Our study indicates that temperature may have an effect on activity space of sharks, although less pronounced than salinity. Previous studies have shown temperature to be an important driver of movement and space use for this species (Speed et al. 2011, 2012b, Papastamatiou et al. 2015). The lack of variation in salinity experienced in offshore (Papastamatiou et al. 2015) or freshwater-limited (Speed et al. 2011, 2012b) areas may mean that temperature plays a greater role for those populations than salinity, although this has not been tested. In comparison, Orpheus Island is only 16 km from the mainland and the catchments which affect salinities can experience rainfall of up to 600 ml over only a few days causing large and rapid changes (Bureau of Meteorology 2015). Freshwater plumes associated with wet season flooding have been shown to regularly extend offshore past Orpheus and the Palm Islands, with salinity levels decreasing to at least 30 ppt (Wolanski & Jones 1981, King et al. 2002, Devlin & Brodie 2005, Devlin & Schaffelke 2009). Blacktip reef sharks resident to these inshore reef systems have likely developed mechanisms to cope with fluctuations in salinity in order to remain in coral reef habitat. Given that previous studies documenting temperature effects on space use of blacktip reef sharks looked at fine-scale (i.e. diel) changes in movement and behaviour, it is also possible that the coarser resolution of the data in the present study (i.e. over larger temporal scales) may have masked temperature effects.

CONCLUSION

This study demonstrated the importance of biological and environmental factors on movement and activity space of a common reef shark on inshore reefs. Size had the greatest effects on space use, with larger sharks using larger activity spaces, presumably due to growing energetic demands and the need to find adequate resources. Sex effects were also observed, with juvenile males using marginally more space than juvenile females; reasons for this are not immediately clear and results should be treated cautiously due to limitations in the data (i.e. only 1 adult tagged). After size, salinity was the best predictor of activity space of juvenile blacktip reef sharks at Orpheus Island. Sharks increased their activity spaces as salinity levels decreased; however, further study is required to determine if response was due to a physiological limitation, individuals actively seeking out more favourable conditions (i.e. behavioural osmoregulation) or some other factor (e.g. movement

of prey species; Heupel & Simpfendorfer 2014). Water temperature had a similar but weaker effect on activity space size. Results add to previous studies on this species that have documented environmental effects on space use and serve to highlight how site-specific differences in physical structure and conditions can drive movement. While sharks reacted to salinity decreases by increasing their activity space, they did not permanently leave the study site, which suggests that this species may be somewhat resilient to environmental change or that conditions did not reach a level that would cause departure. Furthermore, blacktip reef sharks appear to use more than just reef environments (Chin et al. 2012, 2016), displaying an ecological flexibility that may have allowed them to seek out higher-salinity areas within the study region during low-salinity events.

Both the frequency and intensity of tropical storms are projected to increase in the future (Emanuel 2005, Webster et al. 2005), leading to associated increases in the number of high rainfall/freshwater run-off events. Practically, this means that sharks resident on inshore reefs will encounter greater and more frequent fluctuations in local salinity levels than they do currently and will need to develop mechanisms to cope if they are to survive on inshore reefs. As reef sharks are site-attached to reef habitats, they may be limited in their ability to avoid unfavourable conditions. While the current study shows that these sharks are able to handle salinity fluctuations to some degree, should conditions deteriorate past a physiological threshold or persist for an extended period of time, they may be forced to leave, risking decreased fitness or, at worst, mortality. As salinity is predicted to have some of the greatest effects on reef sharks under future climate change scenarios (Chin et al. 2010) and given current and projected declines in coral reef habitat (Hoegh-Guldberg et al. 2007, Diaz-Pulido et al. 2009), an examination of the effects of salinity on movement and activity space of reef sharks is timely and will help to better predict how they may respond in the future.

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LITERATURE CITED

- ✦ Barbieri MM, Berger JO (2004) Optimal predictive model selection. *Ann Stat* 32:870–897
- ✦ Barnett A, Abrantes KG, Seymour J, Fitzpatrick R (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PLOS ONE* 7:e36574
- ✦ Barton K (2013) MuMIn: multi-model inference. R package version 1.9.5. <http://CRAN.R-project.org/package=MuMIn>
- Becker RA, Chambers JM, Wilks AR (1988) The new S language: a programming environment for data analysis and graphics. Wadsworth and Brooks/Cole Advanced Books & Software, Monterey, CA
- ✦ Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- ✦ Bond ME, Babcock EA, Pikitch EK, Abercrombie DL, Lamb NF, Chapman DD (2012) Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PLOS ONE* 7:e32983
- ✦ Bureau of Meteorology (2015) Flood warning system for the Herbert River. www.bom.gov.au/qld/flood/brochures/herbert/herbert.shtml (accessed 1 August 2015)
- Burnham KP, Anderson D (2003) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY
- ✦ Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Glob Change Biol* 16:1936–1953
- ✦ 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 MR, Simpfendorfer CA, Tobin AJ (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
- ✦ Chin A, Tobin AJ, Heupel MR, Simpfendorfer CA (2013c) Population structure and residency patterns of the blacktip reef shark *Carcharhinus melanopterus* in turbid coastal environments. *J Fish Biol* 82:1192–1210
- ✦ Chin A, Heupel MR, Simpfendorfer CA, Tobin AJ (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. *Mar Ecol Prog Ser* 544:197–211
- ✦ Collins AB, Heupel MR, Simpfendorfer CA (2008) Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. *Estuaries Coasts* 31:1174–1183
- ✦ Devlin MJ, Brodie J (2005) Terrestrial discharge into the Great Barrier Reef Lagoon: nutrient behavior in coastal

- waters. *Mar Pollut Bull* 51:9–22
- Devlin M, Schaffelke B (2009) Spatial extent of riverine flood plumes and exposure of marine ecosystems in the Tully coastal region, Great Barrier Reef. *Mar Freshw Res* 60: 1109–1122
- Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R and others (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLOS ONE* 4:e5239
- DiGirolamo AL, Gruber SH, Pomory C, Bennett WA (2012) Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery. *J Fish Biol* 80:1436–1448
- Duong T (2007) ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. *J Stat Softw* 21:1–16
- Economakis A, Lobel P (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environ Biol Fishes* 51: 129–139
- Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436:686–688
- Espinoza M, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Residency patterns and movements of grey reef sharks (*Carcharhinus amblyrhynchos*) in semi-isolated coral reef habitats. *Mar Biol* 162:343–358
- Filmlalter JD, Dagorn L, Cowley PD (2013) Spatial behaviour and site fidelity of the sicklefin lemon shark *Negaprion acutidens* in a remote Indian Ocean atoll. *Mar Biol* 160: 2425–2436
- Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks, CA
- Francis MP (2013) Temporal and spatial patterns of habitat use by juveniles of a small coastal shark (*Mustelus lenticulatus*) in an estuarine nursery. *PLOS ONE* 8:e57021
- Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. *Mar Ecol Prog Ser* 407:279–292
- Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. *Mar Biol* 149:189–199
- Grubbs RD (2010) Ontogenetic shifts in movements and habitat use. In: Carrier J, Musick JA, Heithaus M (eds) *Sharks and their relatives. II: Biodiversity, adaptive physiology, and conservation*. CRC Press, Boca Raton, FL, p 319–350
- Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bull Mar Sci* 43:61–76
- 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, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. *Limnol Oceanogr* 54:472–482
- Heupel MR, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In: Sibert J, Nielsen J (eds) *Electronic tagging and tracking in marine fisheries*. Kluwer Academic Publishers, Dordrecht, p 217–236
- 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, Simpfendorfer CA (2014) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. *Mar Ecol Prog Ser* 496:47–57
- Heupel MR, Simpfendorfer CA (2015) Long-term movement patterns of a coral reef predator. *Coral Reefs* 34:679–691
- Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environ Biol Fishes* 76:47–67
- Heupel MR, Williams AJ, Welch DJ, Ballagh A and others (2009) Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. *Fish Res* 95: 350–361
- Heupel MR, Simpfendorfer CA, Fitzpatrick R (2010) Large-scale movement and reef fidelity of grey reef sharks. *PLOS ONE* 5:e9650
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS and others (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Hopkins TE, Cech JJ (2003) The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environ Biol Fishes* 66:279–291
- King B, McAllister F, Done TJ (2002) Modelling the impact of the Burdekin, Herbert, Tully and Johnstone River plumes on the central Great Barrier Reef. *Tech Rep* 44. CRC Reef Research Centre, Townsville
- Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011a) 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
- Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011b) Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. *Mar Freshw Res* 62:658–667
- Last PR, Stevens J (2009) *Sharks and rays of Australia*. CSIRO Publishing, Collingwood
- Lowe CG, Bray RN (2006) Fish movement and activity patterns. In: Allen LG, Horn MH, Pondella DJ (eds) *The ecology of California marine fishes*. University of California Press, Berkeley, CA, p 524–553
- Mann KH (2000) *Ecology of coastal waters: with implications for management*. Blackwell Science, Malden, MA
- Pang PKT, Griffith RW, Atz JW (1977) Osmoregulation in elasmobranchs. *Am Zool* 17:365–377
- Papastamatiou YP, Caselle JE, Friedlander AM, Lowe CG (2009a) Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra Atoll: a predator-dominated ecosystem. *J Fish Biol* 75:647–654
- Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009b) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology* 90:996–1008
- Papastamatiou YP, Friedlander AM, Caselle JE, Lowe CG (2010) Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll. *J Exp Mar Biol Ecol* 386:94–102
- Papastamatiou YP, Cartamil DP, Lowe CG, Meyer CG, Wetherbee BM, Holland KN (2011) Scales of orientation,

- directed walks and movement path structure in sharks. *J Anim Ecol* 80:864–874
- ✦ Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? *PLOS ONE* 10:e0127807
- ✦ Pinheiro J, Bates D, DebRoy S, Sarkar D (2012) nlme: Linear and nonlinear mixed effects models. R package 3.1-109. <http://CRAN.R-project.org/package=nlme>
- R Development Core Team (2013) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ 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
- ✦ Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Can J Fish Aquat Sci* 59:23–32
- Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. *Estuaries* 28:78–85
- ✦ Simpfendorfer CA, Heupel MR, Collins AB (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Can J Fish Aquat Sci* 65:482–492
- ✦ Simpfendorfer CA, Yeiser BG, Wiley TR, Poulakis GR, Stevens PW, Heupel MR (2011) Environmental influences on the spatial ecology of juvenile smalltooth sawfish (*Pristis pectinata*): results from acoustic monitoring. *PLOS ONE* 6:e16918
- ✦ 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
- ✦ Speed CW, Meekan MG, Field IC, McMahon CR, Abrantes K, Bradshaw CJA (2012a) Trophic ecology of reef sharks determined using stable isotopes and telemetry. *Coral Reefs* 31:357–367
- ✦ Speed CW, Meekan MG, Field IC, McMahon CR, Bradshaw CJA (2012b) Heat-seeking sharks: support for behavioural thermoregulation in reef sharks. *Mar Ecol Prog Ser* 463:231–244
- ✦ Speed CW, Meekan MG, Field IC, McMahon CR and others (2016) Reef shark movements relative to a coastal marine protected area. *Reg Stud Mar Sci* 3:58–66
- ✦ Stevens JD (1984) Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. *Proc R Soc Lond B Biol Sci* 222:79–106
- ✦ Tamburello N, Côté IM, Dulvy NK (2015) Energy and the scaling of animal space use. *Am Nat* 186:196–211
- ✦ Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Mar Ecol Prog Ser* 480:171–183
- ✦ Vaudo JJ, Wetherbee BM, Wood AD, Weng K, Howey-Jordan LA, Harvey GM, Shivji MS (2016) Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature. *Mar Ecol Prog Ser* 547:163–175
- ✦ Webster PJ, Holland GJ, Curry JA, Chang HR (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309:1844–1846
- ✦ Welsh JQ, Fox RJ, Webber DM, Bellwood DR (2012) Performance of remote acoustic receivers within a coral reef habitat: implications for array design. *Coral Reefs* 31:693–702
- ✦ 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
- ✦ Wolanski E, Jones M (1981) Physical properties of Great Barrier Reef lagoon waters near Townsville. I. Effects of Burdekin River floods. *Mar Freshw Res* 32:305–319

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