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Importance of environmental and biological drivers in the presence and space use of a reef-associated shark

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ABSTRACT: As coral reef ecosystems come under increasing pressure from fisheries and climate change, understanding how species that rely on these habitats respond to changes within their environment is increasingly important. The presence and movement of 28 grey reef sharks *Carcharhinus amblyrhynchos* were monitored for 15 mo in the southern Great Barrier Reef in relation to environmental conditions and biological factors. Twenty-eight models including water temperature, atmospheric pressure, wind speed, rainfall and time (week or month), size and sex were tested against presence and activity space data and compared using Akaike information criterion (AIC). Model results for presence of individuals in relation to environmental conditions indicated that temperature and wind speed had weak effects, likely related to detectability. Models using 3 different measures of activity space indicated no relationship between shark activity space and environmental parameters. Week was a significant factor in the top performing activity space models, with males showing increased activity space during weeks in September, when mating is believed to occur. These results suggest changes in movement were biologically rather than environmentally driven. It appears that *C. amblyrhynchos* are adapted to a wide range of environmental conditions in coral reef habitats and that movement between or away from reef platforms is likely related to biological factors such as prey density, competition, reproduction or dispersal rather than environmental or seasonal changes.

KEY WORDS: *Carcharhinus amblyrhynchos* · Acoustic monitoring · AATAMS · Coral reef

INTRODUCTION

Coral reef ecosystems are some of the most fragile systems in the world and are under increasing threat, with many showing increased degradation through time (De'ath et al. 2012). Despite a long history of research and known impacts of natural and anthropogenic stressors affecting coral reefs (Gardner et al. 2003, Bellwood et al. 2004, De'ath et al. 2012) our understanding of how changes in environmental conditions affect coral reef fish species is limited. Most research has centred around the role that climate change will have on coral reef teleosts (Munday et al. 2008) and sharks (Chin et al. 2010). The effects of environmental factors are especially difficult to determine for highly mobile members of coral reef ecosystems such as large fish and sharks. As coral reefs receive increasing attention (Chin et al. 2011) and conservation concern (Bellwood et al. 2004), understanding how environmental factors affect reef residents will be of increasing importance to ensure effective management, such as through improved design of marine protected areas.

Reef sharks have been the focus of research throughout their range for several decades (e.g. Randall 1977, McKibben & Nelson 1986, Wetherbee et al.

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1997, Chapman et al. 2005, Papastamatiou et al. 2010). However, despite a range of studies on the presence and movement of various reef shark species, little data is available regarding long-term space use, seasonal trends in movement, or environmental drivers for habitat use. Many previous studies agree that reef sharks often show a high degree of site fidelity, including Caribbean reef sharks (Garla et al. 2006), grey reef sharks (Field et al. 2011, Barnett et al. 2012), whitetip reef sharks (Barnett et al. 2012) and blacktip reef sharks (Papastamatiou et al. 2010). However, patterns of movement within reef systems and the amount of space used have not been correlated to seasonal or environmental changes. In contrast, several authors have reported broad movement of some reef shark species (e.g. Chapman et al. 2005, Heupel et al. 2010, Speed 2011), but like research reporting site fidelity, these studies have not attempted to correlate movement with environmental conditions. Technological limitation of some studies (e.g. extent of acoustic monitoring arrays) has also constrained the understanding of how far reef sharks may move.

Evidence of the effects of environmental factors on location and presence is reported for numerous shark and ray species. For example, many coastal shark species undertake seasonal migrations, presumably to avoid undesirable water temperatures (e.g. Grubbs & Musick 2007, Heupel 2007). Evidence also suggests that female sharks may seek out warmer waters to help speed gestation and thus base their presence and movement patterns on availability of warm water (Hight & Lowe 2007, Knip et al. 2012). In addition to temperature, salinity also plays a role in the presence and movements of elasmobranch species. There is evidence that bonnethead *Sphyrna tiburo* and pigeye *Carcharhinus amboinensis* sharks move away from freshwater incursions (Ubeda et al. 2009, Knip et al. 2011a) and juvenile bull sharks *Carcharhinus leucas* and smalltooth sawfish *Pristis pectinata* follow salinity gradients (Heupel & Simpfendorfer 2008, Simpfendorfer et al. 2011). These studies all indicate that elasmobranch species may seek out or avoid specific environmental conditions, presumably to optimise fitness.

Given that environmental drivers are important in the movement of sharks in other habitats, and with predictions that reef sharks are at moderate risk from changes in environmental conditions that will result from climate change (Chin et al. 2010), the purpose of this study was to look for evidence that environmental drivers affect reef shark movements. Specifically, we examined 2 measures of grey reef shark *Carcharhinus amblyrhynchos* use of Heron Island Reef in the southern Great Barrier Reef to investigate different scales of possible movement in relation to environmental and biological parameters. Firstly, the presence of sharks at the reef was assessed to determine whether environmental drivers result in sharks moving away from the reef (i.e. inter-reef movements). Secondly, the size of activity space was assessed to define effects of environmental drivers on intra-reef movements.

MATERIALS AND METHODS

Study site

Movements of the grey reef shark *Carcharhinus amblyrhynchos* were examined in the southern Great Barrier Reef, Australia. The study site included Heron Island Reef and Sykes Reef (23.45° S, 151.55° E) located 72 km offshore from Gladstone, Queensland, Australia (Fig. 1). Heron Island Reef is ca. 10 km long and 5 km wide and includes an emergent cay and large lagoon. Depths in channels adjacent to the reef reach up to 40 m. Sykes Reef is approximately 3 km from the eastern end of Heron Island Reef and the 2 platforms are connected by sandy shoal habitat. Depths around Sykes Reef are 12 to 16 m. Sykes Reef is smaller than Heron Island Reef with a length of 5 km and a maximum width of 2 km. Tidal range is approximately 3 m with the reef crest on Heron Island Reef drying at lowest tidal levels, isolating the lagoon.

Field methods

An array of 30 VR2W acoustic receivers (Vemco) deployed around Heron Island and Sykes Reefs were used to monitor the presence and movements of individuals within the region. Receivers were deployed around the reef rim of both Heron Island and Sykes Reefs and 5 units were located within the Heron Island Reef lagoon (Fig. 1). Receivers were deployed on long star pickets driven into the seabed in depths from 10 to 20 m. Permanent sentinel transmitters at 6 locations around the study site monitored the acoustic receivers, which had a detection range of >200 m in this environment (M. R. Heupel unpubl. data). Downloading of acoustic receiver data occurred twice per year.

Sharks were captured by rod and reel or long-line fishing. Long-lines were comprised of a 400 m bot-

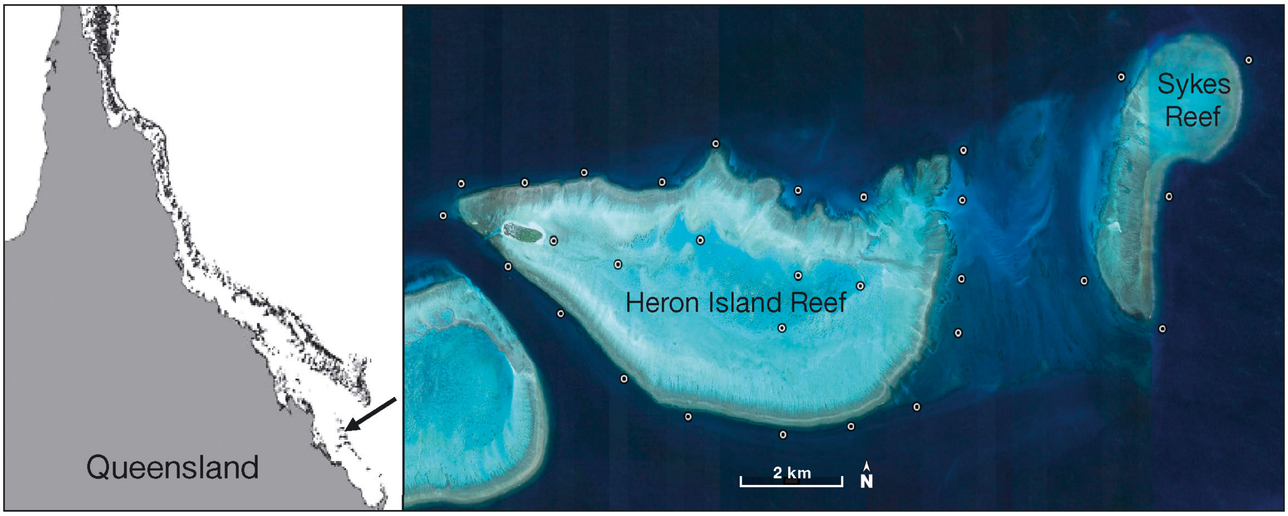

Fig. 1. Study site: Heron Island Reef and Sykes Reef, Great Barrier Reef, Queensland, Australia. Circles indicate acoustic receiver locations

tom-set mainline (8 mm nylon rope) anchored at both ends and soaked for 1 h. Gangions consisted of 1 m of 5 mm nylon cord and 1 m of wire leader. Size 14/0 Mustad tuna circle hooks were baited with squid and 25 to 40 hooks were attached to the mainline. Individuals collected by rod and reel were captured on 8/0 or 14/0 hooks baited with pilchard or squid. All captured individuals were measured to the nearest cm fork length (FL), sexed, tagged with an external identification tag and internally fitted with a 16 mm × 65 mm acoustic transmitter (V16P-4H, Vemco). Acoustic transmitters pulsed on a pseudo-random repeat rate of 50 to 100 s with an estimated battery life of 824 d. Each transmitter emitted a unique identification code and the depth of the individual in the water column, with a maximum depth rating of 68 m. Transmitters were surgically implanted into the abdominal cavity of sharks using the same procedure in all years (see Heupel & Hueter 2001 for detailed methods). All surgical procedures were conducted following protocols approved by James Cook University Animal Ethics and sharks were retained for a maximum of 10 min during measuring and tagging procedures.

Data on environmental factors were taken from real-time monitoring at Heron Island Reef as part of the Facility for Automated Intelligent Monitoring of Marine Species sensor network and Great Barrier Reef Ocean Observing System mooring (www.imos.org.au) that recorded air and water conditions every 5 to 10 min. Environmental data from January 2011 to June 2012 were used in the analysis (Fig. 2). Water temperature was taken from a mooring close to the reef (GBRHIN), and atmospheric pressure, wind speed and rainfall were taken from a weather station on Heron Island. Mean values of environmental parameters were calculated for weeks and months during the study, and were merged with occurrence and activity space data for the corresponding time periods.

Data analysis

Position estimates

Two approaches to positioning were taken. The first used a centre-of-activity approach (COA) (Simpfendorfer et al. 2002) that produced mean locations from detections every hour that were weighted by the number of detections at each receiver in the array during that period. Since all sharks were fitted with depth-sensing transmitters, the mean depth during 1 h periods was also calculated, providing COA with 3 dimensions. Latitude and longitude were converted to universal transverse mercator projection to ensure that the units of all 3 dimensions were the same (metres). The second approach was to consider Heron Island Reef as a linear system (e.g. Simpfendorfer et al. 2008). Such an approach to representing geographic location was valid since *Carcharhinus amblyrhynchos* were normally associated with the reef edge and rarely, if ever, entered the lagoon (M. R. Heupel unpubl. data). To implement the linear positioning, the far western tip of the reef edge was designated as the starting point and position around the reef was calculated as the distance from that point.

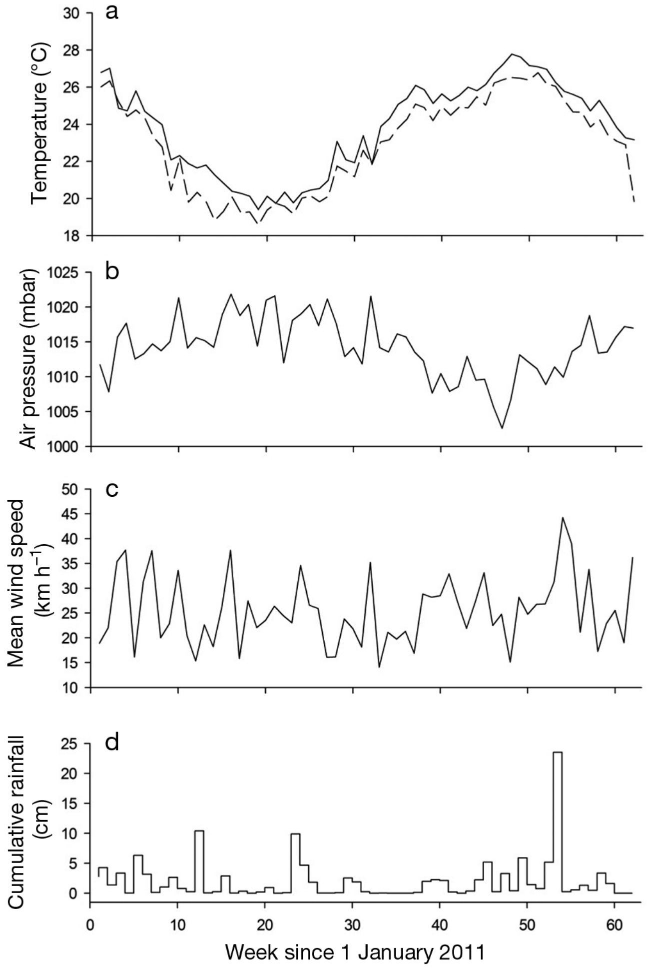

Fig. 2. Weekly environmental values for Heron Island Reef: (a) mean water (solid line) and air (dashed line) temperature, (b) mean air pressure, (c) mean wind speed and (d) cumulative rainfall

The distance between the starting point and a detection was calculated by summing the distance between each of the acoustic receivers from the receiver on which a detection occurred to the starting point (in an anticlockwise direction around the reef). The values of reef distance and depth were then averaged over a 1 h period to produce a 2-dimensional representation of location on a similar time scale to that of the COAs.

Activity space estimators

Three separate activity space estimates were calculated for individual sharks on both weekly and monthly time steps. Two-dimensional kernel utilisation distributions (KUD) were calculated in the horizontal (hKUD) and vertical (vKUD) plane. The hKUD represented the traditional home range estimate, while the vKUD incorporated depth data to define use of the water column along the edge of the reef. Finally, a 3-dimensional KUD activity space (3D KUD) was calculated to incorporate vertical and horizontal components of movement (Simpfendorfer et al. 2012).

All KUDs were initially calculated using the R package *ks* (Duong 2007) using a plug-in bandwidth selector. To ensure comparability between individuals within each measure of activity space, a bandwidth value that most appropriately represented shark locations (i.e. uncertainty around points matched the known performance of the system) was selected from the individual values, and the analyses rerun. Areas or volumes of activity space were calculated for the 50% and 95% KUDs to represent the core and extent of activity space, respectively. Since COAs could not be determined when sharks moved beyond the outer baseline of the receiver array, activity space estimates underestimated true levels.

Drivers of occurrence

To investigate the drivers of occurrence, a set of 28 candidate generalised linear mixed models were constructed with different combinations of biological (size, sex), environmental (water temperature, atmospheric pressure, rainfall, wind speed) and temporal (week or month) factors (Table 1). Models were tested against weekly presence or absence using a logistic regression approach. To account for the repeated-measures nature of the data, individual was treated as a random factor within the models. Models were implemented in the *nlme* package (Pinheiro et al. 2012) for R (R Development Core Team 2012). Candidate models were compared using the Akaike information criterion (AIC). The factors in the model with the lowest AIC value were considered to be the most significant drivers of occurrence. If the null model had the lowest AIC value then the data were considered to be random relative to the tested factors. Since sharks were released over a 12 mo period from March 2011, data from the first month were excluded from the analysis to allow sufficient sample sizes of animals. In addition, weeks or months that had <10 position estimates for an individual were excluded because these consistently underestimated activity space. Models M8 and M9 were modified to remove interactions because the binary data were unable to be fitted to these complex models. Presence or absence of individuals was coded as a binary variable, and models run using the *lme4* package (Bates 2012) in R.

Table 1. Effect of biological and environmental factors on grey reef shark *Carcharhinus amblyrhynchos* presence (pa) at Heron Island Reef. Akaike's information criterion (AIC) values from 28 candidate models with best fit model result in **bold**. AIC values marked with * are those that a likelihood ratio test showed as significantly different from the null model (M1). FL: fork length; wk: week; temp: water temperature; wind: wind speed; rain: rainfall; pres: atmospheric pressure

Model (all include animal ID as a random factor)	df	AIC
M1 pa ~ 1	2	396.1
M2 pa ~ Sex	3	398.0
M3 pa ~ FL	3	396.5
M4 pa ~ wk	48	406.9
M5 pa ~ wk×Sex	95	458.8
M6 pa ~ Sex×FL	5	399.3
M7 pa ~ wk+FL	49	407.8
M8 pa ~ Sex+FL+wk	50	409.8
M9 pa ~ temp	3	377.1*
M10 pa ~ wind	3	396.6
M11 pa ~ rain	3	398.1
M12 pa ~ pres	3	409.5
M13 pa ~ temp+wind	4	**373.0***
M14 pa ~ temp+rain	4	377.7*
M15 pa ~ temp+pres	4	404.4
M16 pa ~ wind+pres	4	410.3
M17 pa ~ temp+wind+rain	5	375.0*
M18 pa ~ Sex+temp+wind+rain	6	377.0*
M19 pa ~ FL+temp+wind+rain	6	375.5*
M20 pa ~ Sex+temp	4	379.1*
M21 pa ~ Sex+wind	4	398.4
M22 pa ~ Sex+rain	4	399.9
M23 pa ~ FL+rain	4	398.5
M24 pa ~ FL+wind	4	397.0
M25 pa ~ FL+temp	4	377.6*
M26 pa ~ Sex×FL+temp	6	379.4*
M27 pa ~ Sex×FL+rain	6	401.2
M28 pa ~ Sex×FL+wind	6	399.8

Drivers of activity space size

To determine if the activity space size of *Carcharhinus amblyrhynchos* was influenced by biological or environmental factors, the same set of 28 candidate models were tested against KUD estimates with individual as a random effect. Raw activity space data were skewed, and several different transforms (log, square-root and arcsine) were tested to normalize the data. The square-root transform provided the best outcomes across the range of metrics, and was used for all data. The same model interpretation approach was used as for the drivers of occurrence.

To examine if the magnitude of changes in environmental parameters (from week to week), rather than their absolute value, caused changes in activity space the week to week difference in 50% and 95% vKUD was tested against the week to week differences in environmental parameters. This examination used the same modelling approach (i.e. 28 candidate models) as for the absolute values of the parameters.

RESULTS

Data from 28 *Carcharhinus amblyrhynchos* (11 female, 17 male) captured and released at Heron Island Reef between March 2011 and February 2012 were examined in relation to environmental parameters. Individuals ranged in size from 59 to 150 cm FL (female: mean = 113 cm, range = 69 to 150 cm; male: mean = 121 cm, range = 59 to 144 cm) and included both immature and mature individuals of both sexes that were present in the study site for periods of 6 to 62 wk. There were no coincident periods of absence to indicate seasonal or environmental factors causing coordinated movement away from the study reefs (Fig. 3).

Occurrence

Thirteen *Carcharhinus amblyrhynchos* were not detected for periods of 1 wk or longer during the study period. A total of 75 wk of absences occurred across these individuals with total absences ranging from 1 to 15 wk. Analysis of the 28 candidate models (Table 1) indicated that only a few produced results that were better than the null model. The model with the lowest AIC value had both temperature and wind as factors in *C. amblyrhynchos* presence. No biological factors were included in the best fit model.

Activity space

Testing of 28 candidate models for 50 and 95% vKUD, hKUD and 3D KUD estimates indicated no relationship between size of activity space and environmental parameters. Instead, the best fit model in all cases included size (FL), week, sex and their interactions as factors (Table 2). The second-best fitting model included sex and week as factors. High consistency between models across all activity space metrics suggests that the results are robust and not related to the type of activity space measure employed. Examination of monthly activity space estimates and environmental parameters revealed the same result, with environmental factors playing no significant role in the amount of space used.

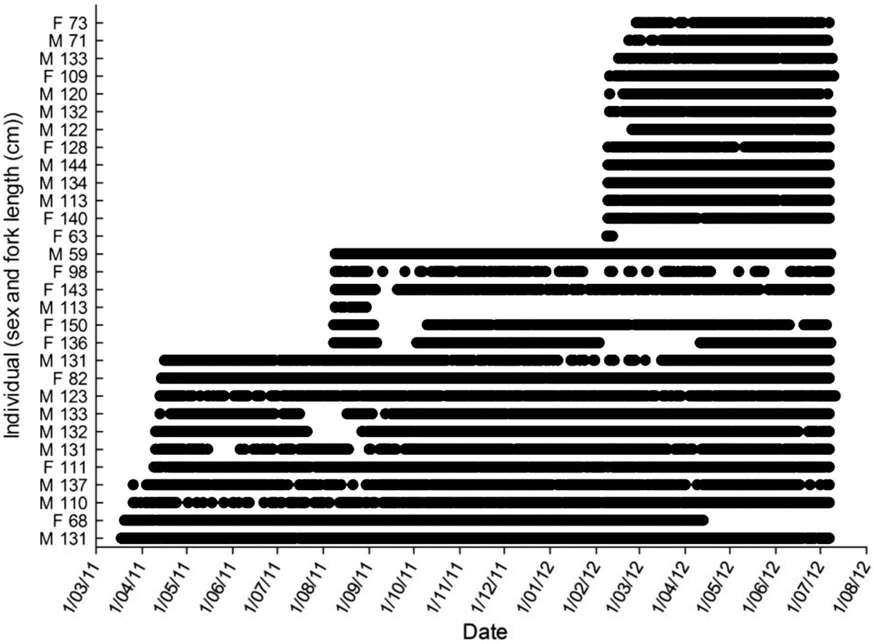

Fig. 3. *Carcharhinus amblyrhynchos.* Presence plot for 28 grey reef sharks captured and released at Heron Island Reef from March 2011 to February 2012

Table 2. Candidate models and AIC values for drivers of activity space (as) size in *Carcharhinus amblyrhynchos*. Three activity space metrics were used: vertical 2-dimensional kernel utilisation distribution (vKUD), horizontal 2-dimensional kernel utilisation distribution (hKUD) and 3-dimensional kernel utilisation distribution (3D KUD). Effects on core activity space (50%) and activity space extent (95%) were tested. Best fit model result is indicated by **bold**. AIC values marked with * are those that a likelihood ratio test showed as significantly different from the null model (M1). sqrt: square root; see Table 1 for other definitions

Model (all include animal ID as a random factor)	df	50% vKUD AIC	95% vKUD AIC	50% hKUD AIC	95% hKUD AIC	50% 3D KUD AIC	95% 3D KUD AIC
M1 sqrt(as) ~ 1	3	5373.7	5808.1	6547.9	7259.8	7709.3	8391.4
M2 sqrt(as) ~ Sex	4	5369.0*	5803.5*	6540.4*	7250.7*	7699.1*	8379.6*
M3 sqrt(as) ~ FL	4	5374.3	5805.4*	6548.2	7257.7*	7705.4	8381.7*
M4 sqrt(as) ~ wk	49	5061.5*	5528.2*	6100.6*	6746.2*	7154.3*	7797.2*
M5 sqrt(as) ~ wk×Sex	96	4804.9*	5225.2*	5632.9*	6214.1*	6607.0*	7178.7*
M6 sqrt(as) ~ Sex×FL	6	5372.4	5799.1*	6539.3	7245.1*	7691.2*	8361.0*
M7 sqrt(as) ~ wk×FL	96	5127.2*	5552.8*	5992.6*	6569.3*	6913.1*	7493.3*
M8 sqrt(as) ~ Sex×FL×wk	190	**4793.7***	**5147.5***	**5282.2***	**5739.3***	**6030.7***	**6482.3***
M9 sqrt(as) ~ temp	4	5330.3*	5791.5*	6509.7*	7229.7*	7677.1*	8364.6*
M10 sqrt(as) ~ wind	4	5378.0	5812.0	6547.2	7258.0	7705.0*	8387.7
M11 sqrt(as) ~ rain	4	5376.4	5810.1	6546.0	7254.3*	7705.5	8384.4*
M12 sqrt(as) ~ pres	4	5343.3*	5802.1*	6521.9*	7242.0*	7685.1*	8377.9*
M13 sqrt(as) ~ temp+wind	5	5334.2*	5794.5*	6509.5*	7224.3*	7674.8*	8360.3*
M14 sqrt(as) ~ temp+rain	5	5329.3*	5791.8*	6503.6*	7218.5*	7671.7*	8353.2*
M15 sqrt(as) ~ temp+pres	5	5330.2*	5793.5*	6505.7*	7226.0*	7670.7*	8359.1*
M16 sqrt(as) ~ wind+pres	5	5347.6*	5806.0	6521.5*	7240.0*	7681.2*	8374.2*
M17 sqrt(as) ~ temp+wind+rain	6	5333.8*	5795.3*	6503.5*	7216.1*	7668.6*	8349.4*
M18 sqrt(as) ~ Sex+temp+wind+rain	7	5329.4*	5790.6*	6495.9*	7207.0*	7658.4*	8337.5*
M19 sqrt(as) ~ FL+temp+wind+rain	7	5319.4*	5788.6*	6499.0*	7201.8*	7653.0*	8336.8*
M20 sqrt(as) ~ Sex+temp	5	5325.9*	5786.9*	6502.1*	7220.6*	7666.9*	8352.8*
M21 sqrt(as) ~ Sex+wind	5	5373.3	5807.4	6539.6*	7248.9*	7694.7*	8375.9*
M22 sqrt(as) ~ Sex+rain	5	5371.8	5805.5	6538.5*	7245.2*	7695.2*	8372.7*
M23 sqrt(as) ~ FL+rain	6	5385.3	5813.7	6551.5	7255.3*	7703.6*	8375.9*
M24 sqrt(as) ~ FL+wind	6	5383.9	5815.9	6554.1	7261.2	7700.9*	8380.9*
M25 sqrt(as) ~ FL+temp	6	5338.8*	5788.4*	6513.5*	7229.3*	7673.1*	8355.1*
M26 sqrt(as) ~ Sex×FL+temp	7	5328.5*	5782.1*	6500.5*	7214.3*	7658.5*	8333.7*
M27 sqrt(as) ~ Sex×FL+rain	7	5375.1	5801.2*	6537.3*	7239.6*	7687.3*	8353.9*
M28 sqrt(as) ~ Sex×FL+wind	7	5376.6	5803.0*	6538.5*	7243.3*	7686.8*	8357.2*

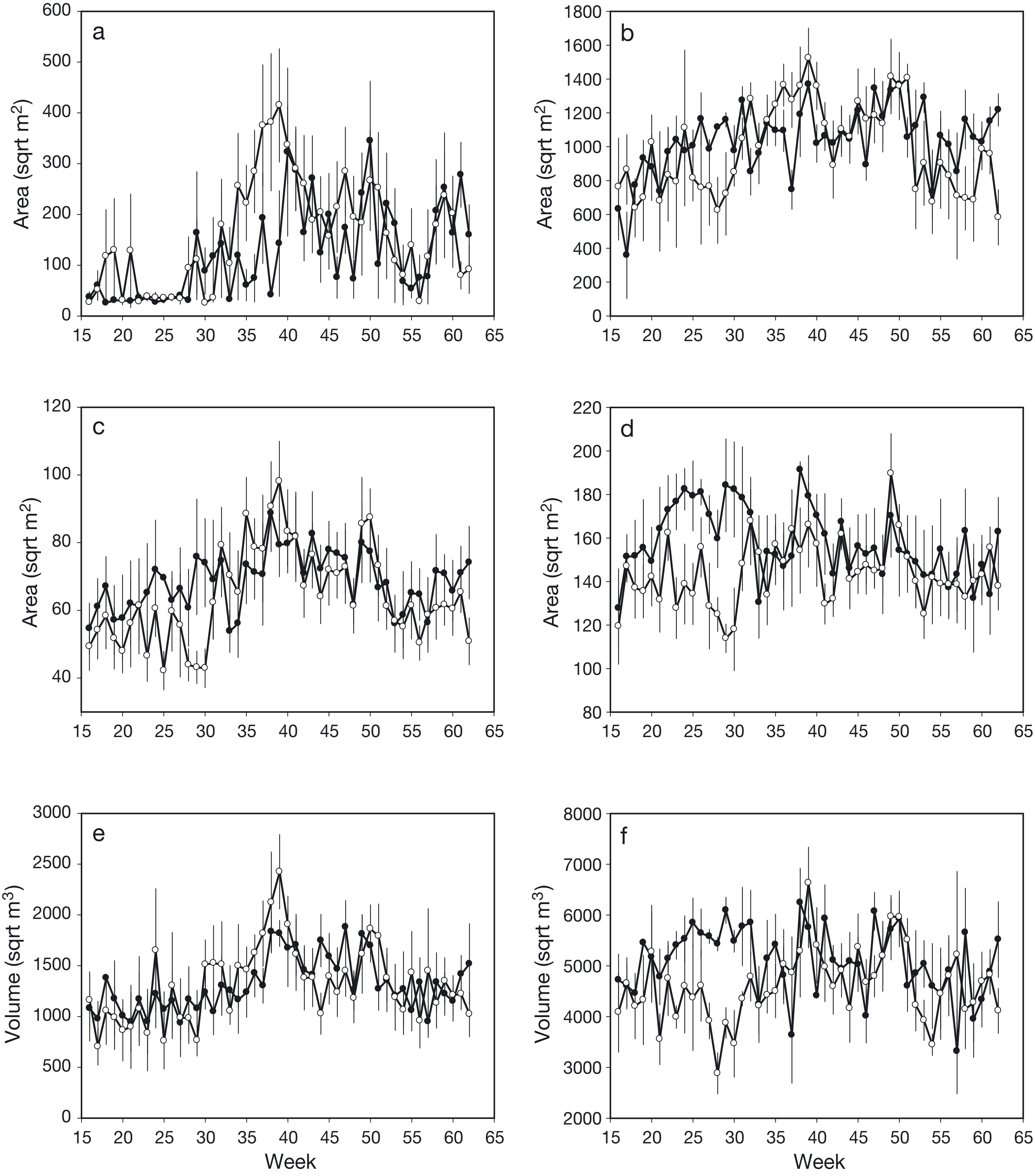

Fig. 4. Interaction plots for male and female *Carcharhinus amblyrhynchos* activity space (represented as square root of area or volume) by week, with Week 16 representing 11 Apr 2011. The left column (a,c,e) includes 50% KUD and the right (b,d,f) 95% KUD estimates; rows indicate activity space estimators including hKUD (a,b), vKUD (c,d) and 3D KUD (e,f); sex is represented by black (female) and white (male) symbols; bars indicate SE

Table 3. Effect of change in environmental factors on the change in size of activity space (Δas) of *Carcharhinus amblyrhynchos* at Heron Island Reef. Resulting AIC values from 28 candidate models, with best fit model result in **bold**. Based on likelihood ratios tests, no models were significantly better than the null model (M1)

Model (all include animal ID as a random factor)	df	50% vKUD AIC	95% vKUD AIC
M1 Δas ~ 1	3	1860.6	**1706.0**
M2 Δas ~ Sex	4	1864.7	1708.4
M3 Δas ~ FL	4	1873.2	1715.9
M4 Δas ~ wk	49	1885.7	1744.9
M5 Δas ~ wk×Sex	50	1889.4	1747.3
M6 Δas ~ Sex×FL	5	1877.2	1718.2
M7 Δas ~ wk+FL	50	1898.2	1754.8
M8 Δas ~ Sex+FL+wk	51	1901.8	1757.1
M9 Δas ~ Δtemp	4	**1859.4**	1708.9
M10 Δas ~ Δwind	4	1871.5	1717.1
M11 Δas ~ Δrain	4	1869.7	1714.4
M12 Δas ~ Δpres	4	1868.5	1714.9
M13 Δas ~ Δtemp+Δwind	5	1868.4	1717.3
M14 Δas ~Δ temp+Δrain	5	1866.4	1717.7
M15 Δas ~Δ temp+Δpres	5	1879.3	1725.9
M16 Δas ~ Δwind+Δpres	6	1879.0	1728.5
M17 Δas ~ Δtemp+Δwind+Δrain	7	1883.0	1730.8
M18 Δas ~ Sex+Δtemp+Δwind+Δrain	7	1891.5	1738.2
M19 Δas ~ FL+Δtemp+Δwind+Δrain	5	1863.4	1711.2
M20 Δas ~ Sex+Δtemp	5	1875.5	1719.5
M21 Δas ~ Sex+Δwind	5	1873.7	1716.9
M22 Δas ~ Sex+Δrain	5	1882.2	1724.4
M23 Δas ~ FL+Δrain	5	1884.0	1727.0
M24 Δas ~ FL+Δwind	5	1872.0	1718.6
M25 Δas ~ FL+Δtemp	7	1885.4	1729.0
M26 Δas ~ Sex×FL+Δtemp	7	1895.7	1735.0
M27 Δas ~ Sex×FL+Δrain	7	1897.5	1737.6
M28 Δas ~ Sex×FL+Δwind	3	1860.6	1706.0

Although week was a significant factor in the top 2 performing models, the lack of temperature, wind or rainfall as significant covariates suggested that the observed change in activity space was biologically rather than environmentally based. The high variability in activity space by week suggests other untested factors may be important in determining its extent. Larger sharks tended to have smaller activity spaces, although there was a relatively weak negative correlation (50% vKUD $r = -0.21$, $p < 0.0001$; 95% vKUD $r = -0.42$, $p < 0.0001$). Sex was also a factor in increased size of activity space with males consistently using greater area during Weeks 25 to 30 (September). The short duration of this change and failure of females to follow this pattern provides further evidence that this change in amount of space used was unlikely to be the result of seasonal environmental changes (Fig. 4).

Analysis of the weekly differences in 50% and 95% vKUD and environmental factors rather than absolute values indicated that activity space was not related to any of the factors tested, with no model having a significantly lower AIC value (Table 3). These results indicate that the magnitude of changes in environmental parameters during the study period did not influence the amount of space used by *Carcharhinus amblyrhynchos* at Heron Island Reef.

DISCUSSION

The results of this study demonstrated that environmental factors had little role in shaping the size of activity space in *Carcharhinus amblyrhynchos* at Heron Island Reef. Three different indices of activity space all showed that while biological factors (sex and size) were important, environmental factors were not—at least at the reef scale. This result is unlike existing evidence from other elasmobranch species where there is increasing evidence of the influence of environmental conditions on the presence and movement of coastal shark and ray species. For example, factors such as temperature, tidal state and day length have been linked to shark presence and movement on daily and seasonal time scales (e.g. Ackerman et al. 2000, Grubbs & Musick 2007, Heupel 2007). One possible explanation for the lack of change in activity space by *C. amblyrhynchos* is the high level of isolation that coral reef platforms usually present. Sharks living in coastal habitats can often move alongshore without having to cross deep water or risk increased exposure to predators. Reef resident species, however, may have to cross large expanses of deep water to reach other coral reef habitats (e.g. Heupel et al. 2010). High dependence on this habitat as well as the potentially widespread nature of reefs may have resulted in lower movement potential in reef species through greater environmental tolerances, compared to shark species in other habitats. Thus reef resident sharks may be more tolerant of the conditions in their environment due to potential isolation from other suitable habitat.

In addition, conditions in coastal regions are more variable than those at most reefs; for example, freshwater influences are rarely present in most coral reef systems. Highly variable and potentially extreme conditions may force coastal species to move away from the source of change (e.g. Ubeda et al. 2009, Knip et al. 2011a) or risk suffering mortality (Matich & Heithaus 2012). Movement is an option for coastal species that can travel to or through contiguous coastal habitat to find a suitable short or long-term site of residence. In contrast, reef sharks may have adapted to a wide range of local environmental conditions to avoid movement. Support for this concept may be found in a recent study by Udyawer et al. (2013) who found that several coastal shark species fled an inshore bay during the approach of Cyclone Yasi, while resident blacktip reef sharks *Carcharhinus melanopterus* did not leave the region. The failure of *C. melanopterus* to move from the path of an oncoming storm may be the result of an innate need to remain in suitable habitat rather than risk movement and subsequent failure to find another reef. This strategy is aided by the fact that conditions at offshore reef sites are typically stable which would allow individuals to adapt to these conditions without needing to migrate seasonally or undertake other movements.

Although conditions at offshore reefs may be more stable than those of coastal ecosystems, variability in conditions still exist across the range of the species. Broadly distributed species with high site fidelity, such as *Carcharhinus amblyrhynchos,* may experience limited ranges of environmental variables, but over their entire range experience a wide range of values. One example of how sharks respond to these wide ranges is to vary their growth latitudinally (e.g. *Sphyrna tiburo*, Lombardi-Carlson et al. 2003). By varying their biological response to environmental values individuals are able to maximise their fitness. This suggests that species must adapt to a range of environmental conditions within their distribution such that fitness and survival are maximised. Adaptation to environmental factors may be even more crucial for habitat dependent species that cannot easily move to colonise new regions. The results presented here represent the situation for a population of *C. amblyrhynchos* toward the southern extent of their range, and most likely demonstrate the behavioural response toward their limit of tolerance. As such, if edge effects based on environmental change were driving fitness, survival, or movement, these would likely be more apparent in this region than in more central portions of their range distribution.

There was a weak effect of temperature and wind speed on the presence of *Carcharhinus amblyrhynchos* for periods of 1 wk or longer. A subset of tracked sharks left the reef for longer than 1 wk, indicating that these environmental factors did not act across the whole population. Absences were likely the result of 2 processes: (1) the movement of sharks away from Heron Island Reef, and (2) the inability of the equipment to detect the presence of sharks due to the interference of these environmental factors (Heupel et al. 2006). The latter of these explanations is less likely because of the selection of week-long periods for the examination of presence and absence; and also that the periods of absence were not aligned between individuals of particular sizes or sexes. It is thus possible that the movement of some individuals away from the reef was associated with environmental factors. However, it is possible that longer periods of high wind speed may have reduced the ability of the receivers to detect some sharks, as has been reported in other studies (Hobday & Pincock 2012, Gjelland & Hedger 2013, Udyawer et al. 2013).

To date, there have been limited data available on the importance of size or sex on the activity space of *Carcharhinus amblyrhynchos*. Field et al. (2011) reported that total length was a significant factor explaining the long-term presence of this species at isolated atolls in northwestern Australia. However, this study found no effect of sex on presence. In a study on the depth use of *C. amboyrhynchos*, Vianna et al. (2013) did not report size as a factor in depth use. Increasing activity space with size has been observed in a range of coastal elasmobranch species, including *Pristis pectinata* (Simpfendorfer et al. 2011) and pigeye sharks (Knip et al. 2011b). Limitations on size and sex based movement for *C. amblyrhynchos* have mostly resulted from limitation in the ability to provide sufficient spatial coverage in reef habitats to adequately determine activity space, or because of size or sex bias in samples.

Stability of conditions in most coral reef ecosystems and the lack of increased activity space size or movement based on environmental parameters suggest that it would require an extreme fluctuation beyond the species' tolerance level for an environmental factor to cause *Carcharhinus amblyrhynchos* to move from a reef platform. No such conditions were experienced during the study period. Large changes such as hurricane or cyclone events may cause sharks to be displaced or change their movement patterns (Heupel et al. 2003, Udyawer et al. 2013), although data from Udyawer et al. (2013) also suggest that even these extreme events may not alter the presence of reef species. Unfortunately, in this study there was no data to test this theory. Lack of correlation between presence and movement in relation to environmental conditions has also been reported for Caribbean reef sharks *Carcharhinus perezi* monitored via acoustic telemetry, satellite tracking and baited remote underwater visual surveys (Bond et al. 2012). Garla et al. (2006) also reported *C. perezi* to be present year round with no evidence of seasonal migration.

However, several studies have revealed that reef sharks move between reef platforms and also move large distances (Chapman et al. 2005, Heupel et al. 2010, Speed 2011, Mourier & Planes 2012). Evidence of these movements without an apparent environmental driver suggests that the reasons for movement are primarily biological. Movement of individuals between closely spaced reef platforms may indicate that individuals see these regions as more or less continuous habitat (e.g. movement between Heron Island and Sykes Reef; Heupel et al. 2010, Barnett et al. 2012). Use of adjacent reefs may be a means of maximising habitat use and foraging opportunities, especially if inter-reef movements are spontaneous and not obviously seasonal or diurnal in nature. Increased movement and activity space by males in September may be the result of a biological factor such as mating, which is documented to occur during this period on the Great Barrier Reef (Robbins 2006). Increased activity space use of males may be a tactic to improve their ability to locate responsive females for mating. Failure of females to follow this pattern suggests this is a uniquely male behaviour and as such could be related to mating. Larger scale movements of reef sharks such as those described previously (e.g. Chapman et al. 2005, Heupel et al. 2010, Speed 2011) may also be a means of dispersal and reducing competition at individual reef platforms. The wide-ranging distributions of these species suggest that at least some large-scale movement must occur (as suggested by Randall 1977), and seem unlikely to be the result of changes in environmental conditions unless perhaps conditions are so extreme as to no longer support local populations.

CONCLUSIONS

Results of this long-term analysis of the activity space of *Carcharhinus amblyrhynchos* reveal that environmental conditions did not play a role in the presence, amount of space used and behaviour of individuals. These results suggest this species is adapted to survival in reef regions and tolerant of seasonal and episodic environmental changes. Therefore, movement between or away from individual reef platforms is likely driven by other factors such as prey density, competition, reproduction or dispersal.

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