Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll

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ABSTRACT

Animal movements, residence times, and subsequently foraging strategies, should vary with habitat quality. We used acoustic and satellite telemetry, as well as stable isotopes, to look at movement patterns, macro-scale habitat use, and trophic ecology of blacktip reef sharks, *Carcharhinus melanopterus*, between two lagoons (eastern and western) at Palmyra Atoll, a US National Wildlife Refuge in the central Pacific. Sharks in the Palmyra lagoons have relatively small home ranges and appear to obtain most of their energy from the lagoon ecosystem. Sharks showed low levels of migration between lagoons over periods of several years, and individuals in the larger western lagoon tended to have longer residence times than those in the smaller eastern lagoon. Furthermore, for sharks in the western lagoon, there was no relationship between total length (TL) and δ^{15}N, ^{13}C relative isotope concentrations, or a Body Condition index (BC). For sharks in the eastern lagoon, TL was positively related to δ^{15}N and negatively related to δ^{13}C and BC. These results suggest that there are low levels of mixing of sharks between lagoons, and these are leading to differences in trophic ecology and potentially foraging success. Although the causative factors behind these differences are unknown, shark home range location can potentially lead to variation in trophic ecology, even over small spatial scales.

1. Introduction

Animal movements and habitat selection are influenced by a wide range of biotic and abiotic factors, and ultimately determine how successful the individual is at acquiring food, potential mates, and obtaining safety from predators (e.g. Stephens and Krebs, 1986; Lin and Batzli, 2001). Therefore, it is expected that animals will regulate home range size, and residence times within habitats; dependent on feeding strategies, habitat quality, and levels of intra and inter specific competition; potentially over small spatial scales (e.g. Gittleman and Harvey, 1981, Lin and Batzli, 2001). Theoretical models predict that animal turnover rates and residence times within habitats are influenced by habitat quality, with lower turnover rates in optimal habitats (e.g. Winker et al., 1995, Griffen and Drake, 2008). Understanding such patterns for apex predators is particularly important as the relationship between home range size, habitat selection, and trophic ecology can lead to spatially explicit differences in top down control and other cascading processes (e.g. Dill et al., 2003; Whitehead and Rendell, 2004; Heithaus and Dill, 2006).

Many species of sharks are apex predators, yet currently there are few studies that have explored the relationship between movements and foraging in elasmobranchs (e.g. Heupel and Hueter, 2002; Heithaus and Dill, 2006; Sims et al., 2006). These relationships also have conservation implications as some shark species are declining world-wide due to over fishing, and it is unclear as to the ecological consequences of these declines (e.g. Heithaus et al., 2008). An important tool in the conservation of shark populations, is the establishment of Marine Protected Areas (MPAs). However, the establishment of effective MPAs requires a detailed understanding of predator movement patterns and how these vary seasonally and with habitat (e.g. Heupel et al., 2004; Meyer et al., 2007; Papastamatiou et al., 2009a). Furthermore, if we are to develop mechanistic home range models (where animal home range in a particular location can be predicted) an understanding of how foraging ecology influences movement parameters is essential (e.g. Moorcroft and Barnett, 2008).

Island or atoll scale MPAs are often characterized by high shark population densities, making them ideal locations for understanding these parameters under "baseline" conditions (e.g. DeMartini et al., 2008; Sandin et al., 2008). Palmyra Atoll is a US National Wildlife Refuge, located in the Central Pacific Ocean, with a large population of sharks

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that constitutes up to 60% of the total fish biomass (DeMartini et al., 2008; Sandin et al., 2008). Within the lagoons and over the sand-flats of Palmyra, the dominant predator is the blacktip reef shark, *Carcharhinus melanopterus* (Papastamatiou et al., 2009a,b). Palmyra is composed of two large lagoons and active and passive tracking of blacktip movements indicated that sharks show strong site fidelity to core sand-flats over time scales of days to weeks, and sometimes years (Papastamatiou et al., 2009a,b). Deployment of a small number of long term coded transmitters, as well as mark and recapture data, suggested that there were low rates of movement of sharks between the two lagoons (Papastamatiou et al., 2009a,b). However, the degree of mixing of sharks between lagoons is unknown, as are seasonal changes in lagoon use. Furthermore, it is unknown if differences in home range location (lagoon) leads to differences in the trophic ecology of the sharks (e.g., trophic positions, foraging location, foraging success). Due to differences in the size of lagoons, we hypothesize that residence time, and movement patterns may differ for sharks in the two lagoons. We used a combination of acoustic and satellite telemetry, as well as stable isotopes to determine how residence times and movements varied between sharks within the two lagoons, and how this correlated with trophic ecology. Telemetry and stable isotopes are powerful tools for exploring the relationships between movements and foraging in fishes, although currently few studies have applied the dual techniques to marine settings (Cunjak et al., 2005). Specifically, we aimed to 1) determine levels of inter-lagoon movements, 2) determine differences in residence times between sharks in the two lagoons, 3) determine seasonal patterns of movement and how this varied between individuals, and 4) use stable isotopes and a body condition index to investigate difference in trophic ecology of sharks between lagoons.

2. Methods

2.1. Study site

Palmyra Atoll is located in the northern Line Islands (N 5°53′, W 162°05′), approximately 1000 km south of the Hawaiian Islands (Fig. 1). The atoll consists of two lagoons, which are connected by a small shallow channel, which experiences strong tidal currents. The western lagoon has a maximum depth of 50 m, an area of 3 km², and is connected to the outer reef by a dredged 5 m deep, 1.7 km long channel. The eastern lagoon has a maximum depth of 30 m and an area of 1 km², but is only connected to the outer reefs via shallow sand-flats. Both lagoons consist of a mud/silt benthic substratum, and consequently have low water visibility. Extensive sand-flats in both lagoons are exposed to air during extreme low tides, and connect to the lagoons by steep coral ledges. The outer fore-reefs are characterized by steep slopes, high coral cover and good water visibility. Palmyra was inhabited during World War II by the US military, which led to large scale structural changes to the interior of the atoll. Palmyra has been largely uninhabited since 1944, and became a US National Wildlife Refuge in 2001, with only a small group of up to 17 staff and researchers inhabiting the atoll at any one time. Consequently, anthropogenic impacts at Palmyra have been maintained at low levels.

2.2. Long-term movements: passive telemetry

We surgically implanted 49 blacktip reef sharks with long-life ID coded acoustic transmitters. Sharks were caught in both the western and eastern
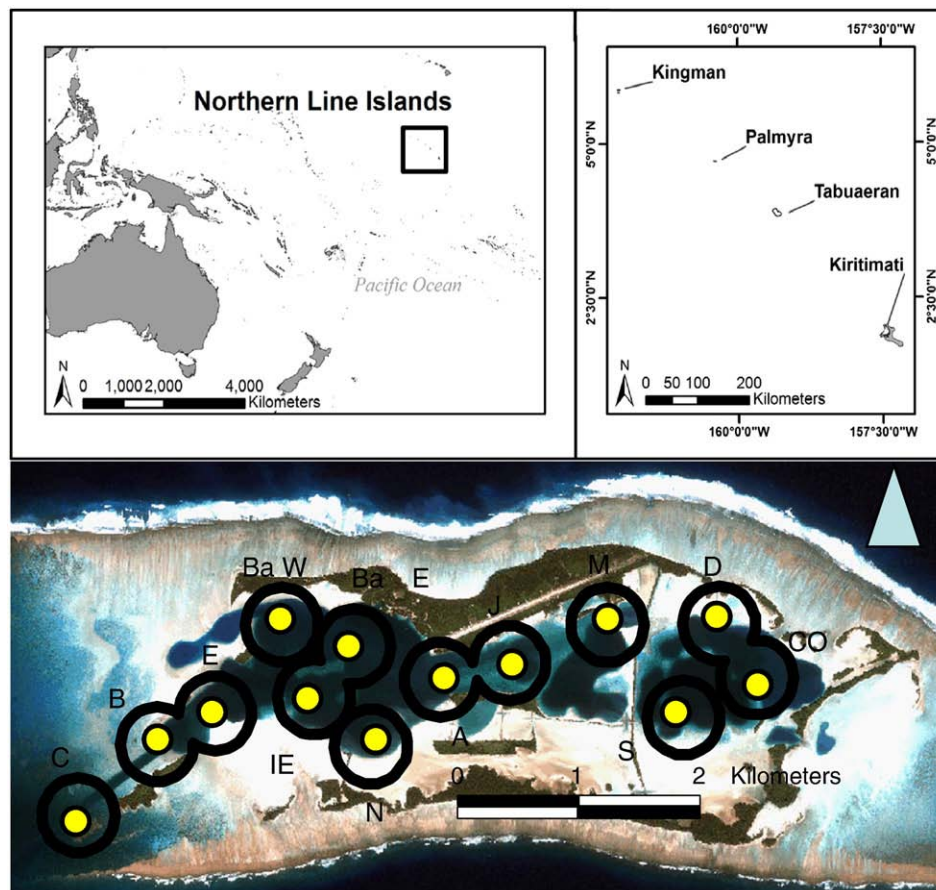

Fig. 1. Map of Palmyra Atoll, and its location within the Line Island chain. Yellow circles show the location of VR2 receivers, while the black circles in the aerial image represent detection radius of VR2 receivers (for V8 and V9 transmitters) deployed throughout the lagoons (radius 300 m). VR2s are Outer Channel (C), Barge (B), Eddies (E), Inner Eddies (IE), West Banjos (Ba W), East Banjos (Ba E), Nursery (N), Airport (A), Jenns (J), Mid-channel (M), Sixes (S), Downeast (D), and Cookies (CO). Sixes, Downeast and Cookies are all located in the eastern lagoon, all other receivers are in the western lagoon.

lagoons using barbless hooks and brought alongside the boat where they were restrained and turned on their backs, placing them in tonic immobility, a trance like state (e.g. Papastamatiou et al., 2009a). A small incision (2 cm) was made through the abdominal wall, the transmitter inserted into the body cavity, and a single suture was used to close the wound. The shark was then measured, sexed, and released. We tagged 16 sharks with Vemco V8SC-2L-R04K transmitters (8 mm diameter × 20 mm length, 136 dB, Nova Scotia, Canada) in 2004–2005, and 29 sharks with V9-2L-R04K transmitters (9 mm × 20 mm, 142–150 dB) in 2006–2007 (battery life approximately 1 year). Four sharks were also fitted with more powerful V16-2L-R04K transmitters (16 mm × 20 mm, 150–165 dB), as these have a battery life of up to 3 years. Transmitters emit acoustic pulse trains of approximately 3.5 s in duration at frequencies of 69 kHz, with a unique code so that individual sharks can be identified. A semi-randomized delay of 30–90 s occurs between pulse trains and reduces the chance for acoustic collisions between pulse trains from other neighboring transmitters.

Transmitters were detected by an array of 13 underwater listening stations (omni-directional Vemco VR2 receivers), which can record the presence of transmitters every time a shark swims within range (approximately 300 m for V8s, 500 m for V9s, and 800 m for V16s, Fig. 1). For each valid acoustic detection, the receivers record the time, date, and transmitter number. Receivers were suspended below floats anchored to the mud/silt lagoon floor by sand-screws, typically 5–10 m below the surface, depending on the location. We retrieved and downloaded receivers every 6–9 months, over a period of four years. We deployed eight receivers in 2004, and an additional five in 2006 (13 total).

We analyzed data separately for sharks tagged in 2004–2005 ($n = 20$) from those tagged in 2006–2007 ($n = 29$), due to the different transmitter specifications and number of receivers deployed during each tagging season. We used a site fidelity index (I_t) to assess the degree of site fidelity shown by each shark where % I_t = (number of days detected/actual detection span)*100. We used two metrics to quantify the amount of time sharks spent within detection range of each VR2. For each shark and each VR2, we determined the number of days each shark was actually detected, and the percentage number of detections. A shark spending several hours at one VR2 can have a lot of detections, even though it visited the VR2 on one day only. We transformed the data ($\log(x + 1)$ for number of days detected, and arcsine square root for % detections) and generated a Bray–Curtis similarity matrix between sharks. We then used a one-way ANOSIM test (Primer ver. 5) to quantify spatial overlap between sharks of the eastern and the western lagoons. ANOSIM calculates overlap between factors (lagoon where sharks were caught) and compare them against 999 random permutations, to generate a Global R statistic ($-1 > R < 1$, Clarke and Gorley, 2001) and a p value. Statistical significance in the ANOSIM test ($\alpha \leq 0.05$) indicates that factors did not overlap with each other. Further classifications based on the R value were, $R > 0.75$ well separated, $R > 0.5$ overlapping but clearly separate, and $R < 0.25$ no separation (Clarke and Gorley, 2001). Non-metric multidimensional scaling ordinations (nMDS) were used to graphically demonstrate any difference in space utilization.

We used a General Linear Model (GLM) to evaluate the influence of lagoon, shark size, and sex on the length of time sharks were detected. The dependent variables were either: number of days detected, or duration of detections. Shark size was also set as a covariate in the model, and interaction effects were included. Both number of days detected and duration of detections were log transformed to conform to the assumption of homogeneity of variance. GLMs were run separately for batch 1 (2004/2005) and 2 (2006/2007) sharks.

We used time series analysis to detect diel or tidal movement patterns for each shark by calculating the number of detections that occurred during each hour of every day for the duration that each shark was detected. We then used a Fast Fourier Transformation (FFT) with Hamming window smoothing to search for cyclical patterns in the data set. The FFT converts time series data into frequencies and searches for cyclical patterns, which can be identified as peaks in a power spectrum (see Meyer et al., 2007, Papastamatiou et al., 2009a). All FFT analysis was done using Statistica (ver. 6, Statsoft).

To detect seasonal movement patterns, we determined the number of days that each shark was detected each month. However, we only did this for sharks that were detected for a minimum of a year duration, which removes the possibility that transmitter battery characteristics could produce a false seasonal peak. For example, if sharks are detected for a number of days in the months preceding tagging, but not subsequently detected, then it is impossible to know if the seasonal spike is a true behavioral response, or a function of the transmitter battery life.

2.3. Long-term movements: satellite telemetry

In order to quantify the movements of blacktip reef sharks when they were outside of the VR2 array, we equipped four sharks with SPOT 5 satellite transmitters (Wildlife Computers). Sharks were caught on hook and line, and transmitters were attached to the dorsal fin. Satellite tags transmit to Argos satellites every time the dorsal fin breaks the surface. A geo-location estimate is then obtained with a location accuracy class which ranges from 3 to 1 (best to worst). The following root mean squares errors are provided by the Argos tracking and environmental monitoring system (www.argos-system.org), Class $3 < = 150$ m, Class $2 = 150–300$ m, and Class $1 = 350–1000$ m. Class A, B, and Z hits can also be obtained, but the errors on these locations are greater than the scale of the atoll itself; subsequently we only analyzed data with Class 3, 2, and 1 location accuracies. We estimated shark activity space size by calculating the 95% and 50% Kernel Utilization Distribution (KUD, see Papastamatiou et al., 2009a) using the Animal Movements extension in Arview GIS (v. 3.2).

2.4. Stable isotopes and body condition indices

The composition of heavy isotopes in an animal's tissue reflects the concentration in its food and the isotopic signature of the primary producers in the ecosystem. The $^{15}N{:}^{14}N$ ratio is an indicator of a predator's trophic position in the food web, while the $^{13}C{:}^{12}C$ ratio highlights the source of carbon for the primary producers at the base of the food chain from which the predator is feeding (e.g. coastal or pelagic, France, 1995; Post, 2002). We caught sharks in both lagoons as described above. We made a small incision in the flank of the shark and used a biopsy sampler to remove a small piece of epaxial white muscle tissue. Samples were frozen until they were processed at the stable isotope laboratory at the University of Hawaii at Manoa. Samples were dried in a 60 °C drying oven for at least 48 h or until the sample was completely dried out, and then ground into a fine powder and weighed out into micro sampling dishes. We used a carbon–nitrogen analyzer (Finnigan ConFlo II/Delta-Plus, Bremen, Germany) to determine the relative concentration of heavy ^{15}N and ^{13}C in each sample. Values were presented as ‰, relative to standards of V-PDB and atmospheric N_2 for ^{13}C and ^{15}N respectively. Measurement accuracy was improved by also comparing measurements during each analysis against a glycine standard. All sharks sampled in this study had C:N ratios of 3.36 ± 0.09 (mean ± 1 SD, range 3.26–3.60) suggesting that tissues were primarily composed of protein with little variation between individuals, so no lipid extraction was performed in the present study (e.g. Post et al., 2007). We used separate GLMs to analyze isotope data, with $\delta^{15}N$ and ^{13}C as dependent variables, and shark length (TL), location (eastern or western lagoon) and sex as independent variables. Interaction functions were included in the model and shark length was set as a covariate. Samples for isotopic analysis were collected in September through November in 2006 and 2007, precluding any tests of seasonal changes.

Body condition indices were calculated for sharks in both lagoons, by dividing shark total length by girth (defined as the perimeter of the

animal, measured directly behind the pectoral fins). We used a GLM as described above to determine the effects of shark TL, sex and location on body condition index. In this case, shark TL was normalized using a square root transformation.

3. Results

3.1. Long-term movements: passive telemetry

We acoustically tagged 49 blacktip reef sharks between March 2004 and May 2007 (S1). We detected 38 of the 49 individuals (78%) for durations of 9–1260 d (median 133 d, S1). Tagged sharks were detected at all receivers within the array, although there were intraspecific differences in the number of receivers visited by each individual shark (Table 1). The total number of detections for each shark ranged from 15 to 163,592 (median 732). Sharks spent from 7.0–100% of their time within the VR2 array (median $I_t = 56.6\%$, S1), and shark length was not a predictor of I_t ($F = 1.46$, $p = 0.96$, d.f. = 37). There were a greater number of detections for batch 1 transmitters (2004/2005 tags, median 1211) than for batch 2 transmitters (2006/2007 tags, median 165, Mann–Whitney U test, $w = 279$, $p = 0.03$).

Visual examination of the data shows that sharks in the western and eastern lagoons, were primarily detected in the lagoons in which they were tagged. Of the 38 sharks for which data were obtained, 12 (32%) showed movements between lagoons, although these inter-lagoon movements were brief and did not occur often (Table 1). Of the 25 sharks tagged in the western lagoon, 8 (32%) moved between lagoons, while of the 13 sharks tagged in the eastern lagoon, 4 (31%) moved between lagoons. For sharks tagged in the western lagoon, 0–0.1% of detections occurred in the eastern lagoon. For sharks tagged in the eastern lagoon, 0–0.9% of detections (median) occurred in the western lagoon.

There was significant spatial separation (no overlap) in the number of days sharks were detected at specific VR2s, for sharks tagged during 2004/2005 in the western and eastern lagoons (ANOSIM, $R = 0.97$, $p = 0.001$), while there was some overlap but still clear separation for those tagged in 2006/2007 ($R = 0.62$, $p = 0.01$), which was apparent in the nMDS plots (Fig. 2). Western and eastern lagoon sharks also separated based on percentage detections at specific VR2s for the 2004/2005 tagging period ($R = 1.0$, $p = 0.02$). Again, there was some overlap in the percentage detections between sharks of the western and eastern lagoons for the 2006/2007 tagging period, but the groups were still clearly separate ($R = 0.68$, $p = 0.01$). In other words, sharks tagged in the western or eastern lagoons were detected on different sets of VR2s.

Table 1

Number of days blacktip reef sharks were detected at VR2s throughout the Palmyra lagoons. W 04 and W 06 are sharks tagged in the western lagoon during 2004/2005 and 2006/2007 respectively. E 04 and E 06 are sharks tagged in the eastern lagoon during 2004/2005 and 2006/2007. All receivers are located in the western lagoon except for Sixes, Downeast, and Cookies, which are in the eastern lagoon. Values are median number of days detected and numbers in parentheses are third quartiles.

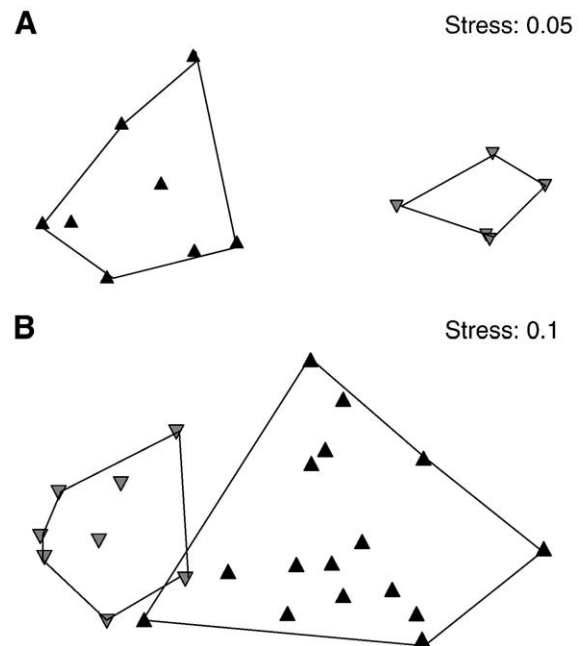| Lagoon	Location	W 04	W 06	E 04	E 06
East	Sixes	2 (16)	0 (3)	12 (28)	27 (89)
	DownEast	0 (5)	0 (2)	24 (46)	1 (17)
	Cookies	0 (4)	0 (3)	42 (112)	2 (26)
West	Mid-channel	24 (86)	1 (24)	0 (2)	0 (1)
	Jens	–	0 (17)	–	0 (0)
	Airport	133 (312)	16 (63)	0 (1)	0 (1)
	Nursery	10 (58)	4 (9)	0 (0)	0 (0)
	Banjos East	–	5 (37)	–	0 (0)
	Banjos West	123 (526)	3 (15)	0 (0)	0 (0)
	Inner Eddies	–	0 (6)	–	0 (0)
	Big Eddies	2 (164)	2 (12)	0 (3)	0 (0)
	Barge	–	1 (9)	–	0 (0)
	Outer Channel	–	0 (4)	–	0 (0)

Fig. 2. Non-metric multidimensional scaling ordination of space utilization between sharks tagged in the western (black triangles) and the eastern (grey triangles) lagoons during A) 2004/2005, and B) 2006/2007.

The GLM revealed that sharks tagged in the western lagoon in 2004/2005, were detected for a greater number of days (west: 430 ± 305 d, east: 63 ± 58 d (± 1 SD), d.f. = 12, $F = 17.21$, $p = 0.02$) and duration (west: 795 ± 309 d, east: 127 ± 179 d, d.f. = 12, $F = 33.7$, $p < 0.001$) than those tagged in the eastern lagoon. There were no effects of sex, shark TL or interactions (for numbers of days: sex $p = 0.63$, TL $p = 0.43$, location×TL $p = 0.58$. For duration: sex $p = 0.14$, TL $p = 0.19$, location TL $p = 0.59$). There was no difference in the amount of time when sharks tagged during 2006/2007 were detected for either the number of days detected (west: 126 ± 143, east: 89 ± 135, d.f. = 23, $F = 0.02$, $p = 0.889$) or duration (west: 219 ± 155, east: 127 ± 131, d.f. = 23, $F = 0.00$, $p = 0.971$). There was however, a significant effect of shark TL on the duration over which sharks were detected (d.f. = 23, $F = 5.34$, $p = 0.03$).

Of the 29 sharks with enough data to run FFT time series analysis, 20 (69%) showed 24 h (diel) peaks, and 15 (52%) showed 6, 8, or 12 h (tidal) peaks. Of the 17 sharks tagged in the western lagoon, 11 (65%) showed diel peaks and 7 (41%) had tidal peaks. Of the 12 sharks from the eastern lagoon, 9 (75%) showed diel peaks and 6 (50%) had tidal peaks. Three sharks in the east lagoon also had peaks at periods of 4 and 2.5 h.

There were three apparent seasonal patterns in the number of days per month that sharks were detected (Fig. 3). Of the 13 sharks which were detected in excess of one year, 4 (31%) showed no seasonal patterns, with relatively consistent numbers of days detected per month (Fig. 3 A, B). All four sharks were tagged in the western lagoon. Seven sharks (54%, a mixture of males, females, and eastern and western lagoon sharks) showed seasonal movements where they were detected within the VR2 array for a greater number of days during the winter months (Fig. 3 C, D). Finally, two sharks (15%, both males) showed the opposite pattern, being detected within the array predominantly during the summer months (Fig. 3 E, F).

3.2. Long-term movements: satellite transmitters

We tagged 3 sharks in the western lagoon and one in the eastern lagoon with SPOT transmitters (Table 2). All sharks were monitored for 1–1.5 months, after which funding constraints prohibited further
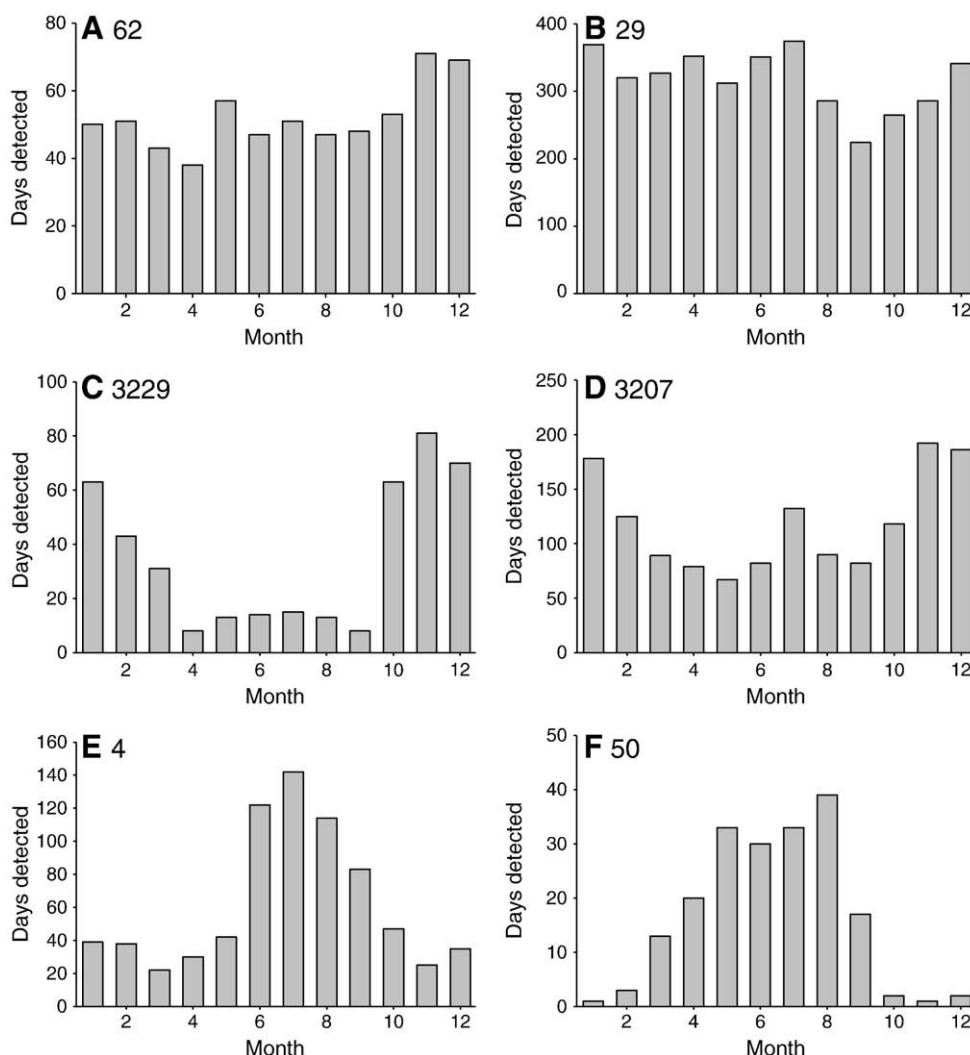
Fig. 3. Bar charts of the number of days per month sharks were detected by VR2s. Shark transmitter number is given on each figure. Three behaviors are exhibited: no seasonal changes (A,B), winter increase in number of days within array (C,D), and summer increase in number of days detected (E,F). For months, Jan = 1, Dec = 12.

detections. Sharks were primarily detected over the sand-flats and occasionally on the outer reefs. Only one shark was detected moving into an adjacent lagoon (BT2, Fig. 4A) and only 5 out of 152 detections (3%) and all on the same day, were in the eastern lagoon (Table 2). Sharks had activity space KUDs that varied from 7.97 to 12.08 km^2 and had maximum lengths of 4.31–7.71 km (Table 2, Fig. 4).

3.3. Stable isotopes

We obtained muscle tissue from 63 sharks, (39 from the western and 24 from the eastern lagoons) which ranged in TL from 75–130 cm. There was no difference in TL between western (102.4 ± 12.6 cm) and eastern lagoon sharks (98.6 ± 12.1 cm, $t = 1.19$, $d.f. = 50$, $p = 0.24$). There was a negative relationship between δ^{15}N relative concentration and δ^{13}C ($F = 25.5$, $d.f. = 62$, $r^2 = 0.28$, $p < 0.001$) when samples from all sharks were combined, and also when analyzed separately for sharks of the

western ($r^2 = 0.22$, $p = 0.001$, $d.f. = 38$) and eastern lagoons ($r^2 = 0.36$, $p = 0.001$, $d.f. = 23$).

The GLM revealed a significant effect of the interaction between TL and location ($F = 8.91$, $d.f. = 62$, $p = 0.04$) on δ^{15}N, leading us to analyze δ^{15}N separately for the eastern and western lagoons using multiple regressions. Shark TL did not influence δ^{15}N for western lagoon sharks ($F = 0.10$, $d.f. = 38$, $p = 0.76$), but did for sharks caught in the eastern lagoon ($F = 19.54$, $d.f. = 23$, $r^2 = 0.42$, $p < 0.001$, Fig. 5B). There was no effect of sex for either western ($F = 0.03$, $p = 0.86$) or eastern ($F = 2.72$, $p = 0.11$) lagoon sharks. Sex ratios of sharks do not differ between lagoons, and are therefore unlikely to influence results (Papastamatiou et al., 2009b). Overall however, there was no difference in δ^{15}N between western (14.64 ± 0.52‰ [mean ± 1 SD]) and eastern lagoon sharks (14.54 ± 0.67‰, $t = 0.65$, $d.f. = 39$, $p = 0.52$). In other words, the absolute values did not differ between the lagoons, but the relationship between shark TL and δ^{15}N did.

Table 2
Summary information for blacktip reef sharks tagged with SPOT satellite tags. TL Total length, KUD 95% Kernel Utilization Distribution. Maximum length of activity space is also given.

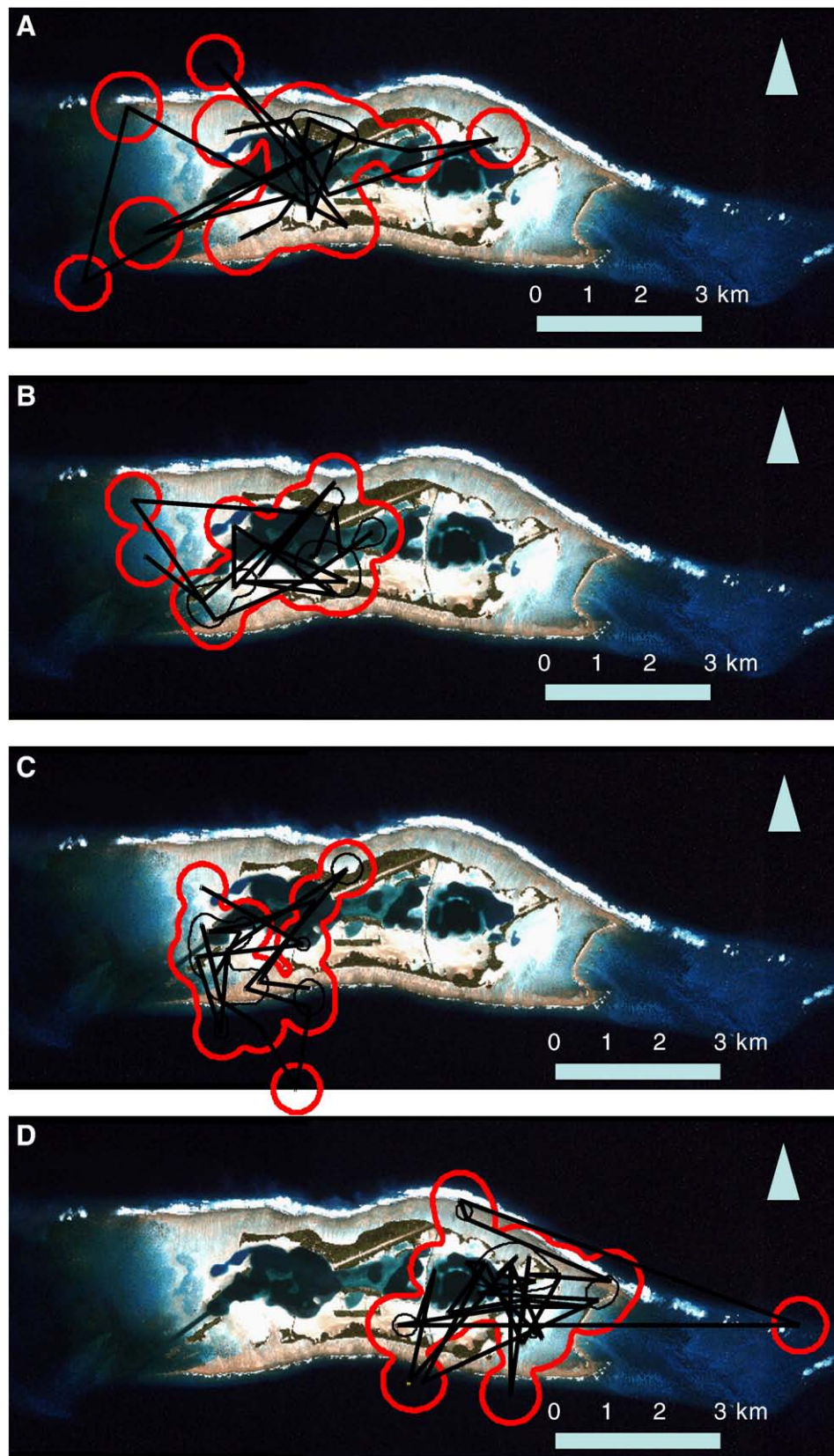| Shark #	Lagoon	Sex	TL (cm)	Date 1st detected	Date last detected	# detections	KUD (km^2)	Max. length (km)
BT1	W	F	123.3	16 Dec 08	12 Jan 09	147	7.97	4.31
BT2	W	F	120.1	20 Dec 08	31 Jan 09	152	12.08	7.71
BT3	E	F	121.5	24 Dec 08	23 Jan 09	242	11.17	7.62
BT4	W	F	119.0	20 Dec 08	31 Jan 09	133	8.98	5.14

Fig. 4. Movements of 4 blacktip reef sharks as determined using SPOT tags. A) BT2, B) BT4, C) BT1, D) BT3. All sharks were tagged in the western lagoon except for BT3 (D) which was tagged in the eastern lagoon. Polygons are Kernel Utilization Distributions (KUD). Thick outer red lines are for 95% KUD, while thin inner black lines are for 50% KUD. Note the lack of movement between lagoons.
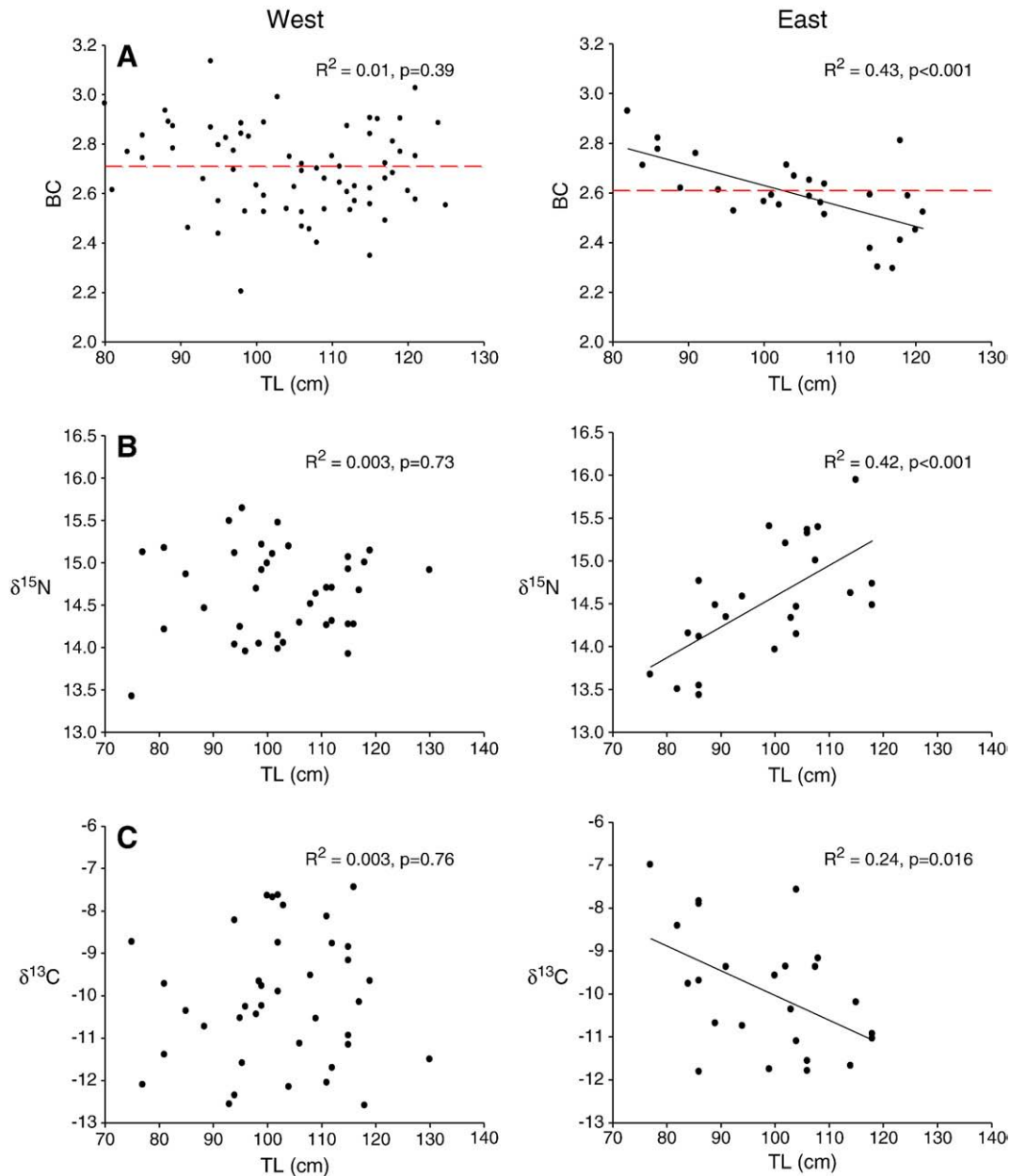
Fig. 5. Effect of shark total length (TL) on A) body condition index (BC, length/girth) B) δ^{15}N C) δ^{13}C heavy stable isotopes. Sharks have been separated based on lagoon where they were caught (western or eastern). The red dashed line in A) represents the mean BC value for each lagoon.

There was a high degree of variability among individuals in δ^{13}C (-10.045 ± 1.482, range -12.6 to -7.0). Similarly, the GLM revealed a marginally significant interaction between location and TL ($F = 4.05$, $d.f. = 62$, $p = 0.049$) on δ^{13}C, and consequently we analyzed data for each lagoon separately. There was no effect of shark TL on δ^{13}C for sharks in the western lagoon ($F = 0.19$, $d.f. = 38$, $p = 0.67$), but there was a negative relationship for sharks in the eastern lagoon ($F = 7.35$, $d.f. = 23$, $r^2 = 0.24$, $p = 0.013$, Fig. 5C). Sex had no effect on δ^{13}C for either western ($F = 0.71$, $p = 0.41$) or eastern ($F = 0.69$, $p = 0.41$) lagoon sharks. Again however, there was no overall difference in δ^{13}C between western (-10.10 ± 1.52‰) and eastern lagoon sharks (-9.95 ± 1.44‰, $t = -0.39$, $d.f. = 50$, $p = 0.70$).

3.4. Body condition indices

Body condition indices (BC) were obtained from 103 sharks, of which 74 were from the western and 29 from the eastern lagoons.

There were no significant interaction effects ($F = 2.68$, $d.f. = 102$, $p = 0.11$), so they were removed from the model. The GLM revealed a significant effect of location ($F = 8.31$, $p = 0.005$) on BC, but no effect of sex ($F = 1.94$, $p = 0.17$) or TL ($F = 2.59$, $p = 0.11$). When analyzed separately for each lagoon, there was no effect of sex ($F = 1.14$, $p = 0.29$) or TL ($F = 0.33$, $p = 0.57$) on BC for sharks in the western lagoon. For sharks in the eastern lagoon, sex had no effect ($F = 0.13$, $p = 0.72$) but TL had a negative influence on BC ($F = 13.91$, $r^2 = 0.43$, $p = 0.001$, Fig. 5A). BC indices were higher for sharks in the western lagoon (2.71 ± 0.21) than those in the eastern lagoon (2.60 ± 0.15, $t = -3.0$, $d.f. = 72$, $p = 0.004$).

4. Discussion

Active, passive, and satellite telemetry all suggest that blacktip reef sharks in the lagoons of Palmyra Atoll have relatively small core home ranges, show high levels of site fidelity to core areas, but make occasional

longer range excursions. However, the degree of site fidelity and residence time varies with habitat, with disproportionate use of areas within lagoons, and differences in residence times between the two lagoons (present study, Papastamatiou et al., 2009a,b). Unsurprisingly, activity space estimates using satellite transmitters over the scale of months, were larger than the previous estimates over days, although there are also going to be larger positional errors associated with satellite tracking (Papastamatiou et al., 2009a). In addition, we obtained less acoustic detections than expected on VR2s, and there are several potential explanations for the low detection efficiencies. Active and satellite tracking of blacktips has shown that they show strong habitat selection for sand-flat ledges, followed by the sand-flats themselves (this study, Papastamatiou et al., 2009a). Detection efficiency of VR2 receivers on the ledges and sand-flats is very poor, due to the shallow water at these locations (Friedlander et al., unpublished data). Further evidence of this is seen from sharks implanted with more powerful V16 transmitters (and subsequent greater detection radii), which were detected within the array for a high percentage of time (79–95%) despite being detected over several years. Technical issues with transmitters may also explain low detection rates. Batch 2 transmitters produced far less detection than batch 1, and performed somewhat below their expected battery lives (which may also explain why no significant difference in residence time between the two lagoons was detected for sharks tagged during 2006/ 2007). However, we also acknowledge that sharks could have shifted their home range outside of the array where they would not be detected. It is also unclear if the 22% of sharks that were not heard from was due to mortality following surgery, transmitter failure, or if they had a home range outside of the VR2 array. Finally, the VR2 array only covered ~2% of the habitat useable by blacktip reef sharks at Palmyra Atoll. Considering the size of the atoll, it is not surprising that sharks were only detected as little as they were, which may also suggest that home range estimates are still underestimates.

Regardless of these issues, shark migration rates between the eastern and western lagoons appear to be low. Why such infrequent and brief migration rates occur between lagoons is unclear, although physical characteristics of the lagoons may play a role. Access between the lagoons either requires swimming through a shallow 18 m wide channel with strong tidal currents, or traversing several kilometers of shallow sand-flats around the islands surrounding the lagoons (see Fig. 1). Blacktips are certainly capable of swimming in very shallow water, but the physical characteristics of the lagoons may reduce the chance that sharks from one lagoon visit the other. It is possible that some sharks moved between lagoons and were not detected; however, it is likely they did not travel far within the other lagoon or else their probability of detection on another VR2 would have increased. It is also possible that sharks swim around the back reef portions of the atoll and not through the lagoons.

A previous study had shown that sharks in the western lagoon show diel and tidal movements, and we show here that similar patterns are seen for sharks in the eastern lagoons, although there were intra-specific differences in the magnitude and consistency of these behaviors (present study, Papastamatiou et al., 2009a). Additionally, some sharks in the eastern lagoon also showed cyclical patterns of detections with periods of 2.5 and 4 h, which were not seen for sharks in the western lagoon. These shorter cycles may be related to small differences in tidal flow characteristics between the two lagoons. Sharks also showed some degree of seasonal movement patterns, although there were again, individual differences. While some sharks did show winter or summer shifts in the amount of time spent within the array, they must still have been close to the array during their "absence" period as all sharks were detected at all times of the year. Alternatively, these seasonal signals could represent an expansion and subsequent contraction of the shark's home range. It is unknown if these movements are related to mating, or if some other factors are responsible. Individual differences in seasonal movements have been seen in other shark and teleost top-predators in tropical

ecosystems, and may be related to temporally or spatially separate mating/spawning aggregations, although this has yet to be verified (e.g. Meyer et al., 2007, 2009).

The interpretation of stable isotope data is complicated, as an animal's isotopic signatures can vary considerably based on diet, season, ontogeny, body condition, and differences in the signature of primary producers (Post, 2002). Variations in baseline isotope signatures can vary over small spatial and temporal scales, and could be problematic when comparing absolute values for sharks of the two lagoons. However, the consistent difference in the relationship between isotopes and Body Condition index (BC) with shark size, for the two lagoons, suggests that there is a genuine size related difference in the trophic ecology of sharks in the two lagoons (these differences are independent of baseline isotopic signatures). For sharks in the eastern lagoon, $\delta^{15}N$ increases with shark size, potentially an indicator of larger sharks occupying higher trophic positions. However, there is some evidence that fasting animals increase the concentration of ^{15}N in their tissues (e.g. Hobson et al., 1993). The increase in ^{15}N with shark size, and the concurrent decrease in BC could be an indicator that larger sharks in the eastern lagoon are in nitrogen deficit and for some reason have a harder time obtaining adequate resources than smaller individuals. However, a more appropriate body condition index would include body mass, and more definitive measures of the changes in isotopic signatures of primary producers and consumers are required before this hypothesis can be verified (e.g. Post, 2002; Schulte-Hostedde et al., 2008).

The primary energy source for blacktip reef sharks caught in the lagoon appears to be prey that forage on benthic algae in the lagoon (when compared to isotope values for turf algae, lagoon and fore-reef phytoplankton, and secondary consumers, obtained from Palmyra, D.J. McCauley unpublished data), but the high inter individual variability in ^{13}C suggests a range of dietary inputs, although confirming this will require a more detailed examination of isotopic signatures of prey species (e.g. Urton and Hobson, 2005; Woo et al., 2008). The depleted ^{13}C signal for some sharks indicates a somewhat greater (although still marginal) reliance on more pelagic prey, due to differences in ^{13}C between coastal benthic algae and pelagic phytoplankton (e.g. France, 1995). Heavy carbon isotopes of primary producers can also vary greatly temporally (see Post, 2002), and sharks were generally sampled during two sampling periods (in May and November). Some of the variability in ^{13}C may be explained by seasonal fluctuation although our sample sizes were not large enough to test this. However, elasmobranch muscle tissue has slow turnover rates, and should be fairly stable over the scale of months to years, and sharks from eastern and western lagoons were sampled at the same time, so these should not greatly affect the observed relationships (Post, 2002; MacNeil et al., 2006). No sharks have been tagged or sampled on the fore-reefs, and it is not known if sharks seen during observation dives show site fidelity to the fore-reef (where they subsequently forage), or if they are lagoon based sharks making occasional excursions off-shore.

Numerous factors could explain the observed differences in trophic ecology between the two lagoons. These could include variation in environmental conditions, tidal currents, safety from predators, and varying degrees of intra and inter specific competition. There do not appear to be differences in abundance of blacktips between the lagoons (based on Catch Per Unit Effort (CPUE), Papastamatiou et al., 2009b), which would imply that population densities between the lagoons may differ. Utilizing CPUE to infer abundance is problematic; however, more accurate assessments of shark abundance are needed to verify differences in population densities.

Regardless of the causative factors leading to these differences, the consistent distinction in the ontogenetic trophic relationship of sharks between the two lagoons, in conjunction with the telemetry results, suggests that sharks are primarily staying in one lagoon, and some habitat quality characteristic is leading to variation in the trophic ecology between lagoons. These may also translate to differences in foraging success and residence times of sharks within the lagoons, although additional studies

are needed to confirm this. Our study highlights the importance of the interactions between habitat, movements and trophic ecology for a population of marine apex predators in a nearly intact ecosystem. Future studies should determine if similar responses to habitat are seen in sharks in areas with lower population densities, or if these results are partially driven by interference from intra-specific competition.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2010.02.009.

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