

# Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll

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**Abstract.** The effects of habitat on the ecology, movements, and foraging strategies of marine apex predators are largely unknown. We used acoustic telemetry to quantify the movement patterns of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll National Wildlife Refuge, in the Pacific Ocean. Sharks had relatively small home ranges over a timescale of days to weeks ( $0.55 \pm 0.24 \text{ km}^2$ ) and showed strong site fidelity to sand-flat ledges within the west lagoon over a three-year period. Sharks showed evidence of diel and tidal movements, and they utilized certain regions of the west lagoon disproportionately. There were ontogenetic shifts in habitat selection, with smaller sharks showing greater selection for sand-flat habitats, and pups (total length 35–61 cm) utilizing very shallow waters on sand-flats, potentially as nursery areas. Adult sharks selected ledge habitats and had lower rates of movement when over sand-flats and ledges than they did over lagoon waters. Fractal analysis of movements showed that over periods of days, sharks used patches that were 3–17% of the scale of their home range. Repeat horizontal movements along ledge habitats consisted of relatively straight movements, which theoretical models consider the most efficient search strategy when forage patches may be spatially and temporally unpredictable. Although sharks moved using a direct walk while in patches, they appeared to move randomly between patches. Microhabitat quantity and quality had large effects on blacktip reef shark movements, which have consequences for the life-history characteristics of the species and potentially the spatial distribution of behaviorally mediated effects on lower trophic levels throughout the Palmyra ecosystem.

**Key words:** acoustic telemetry; blacktip reef sharks; foraging behavior; fractal analysis; habitat utilization; nursery areas; Palmyra Atoll; predator-dominated ecosystems.

## INTRODUCTION

Apex predators are thought to exert top-down control on marine ecosystems through both density- and trait-mediated interactions (Bascompte et al. 2005, Preisser et al. 2005). While an understanding of ecological processes requires knowledge of predator diets, of equal importance is an understanding of activity patterns, habitat utilization, and foraging strategies. Foraging theory predicts that animals will select habitats that provide the greatest return in some form of currency such as prey encounter rate (Stephens and Krebs 1986). However, for many animals it is difficult to distinguish habitat selection for foraging purposes from those associated with mating or predator avoidance. Most adult apex predators do not have to invest much energy into antipredatory behavior, and since most reproductive behavior is seasonal, it is possible to separate foraging

from these other behaviors. Ontogenetic shifts in habitat selection can further contribute to an understanding of why animals select the habitats they use.

Many species of shark are considered apex predators, but there may be large geographic differences in their ecological significance (e.g., Stevens et al. 2000, Bascompte et al. 2005). The current worldwide decline in many shark populations further highlights the importance of understanding their ecological significance in multiple habitats and locations (e.g., Stevens et al. 2000). While shark movements and habitat utilization have been studied in several locations (e.g., McKibben and Nelson 1986, Rechisky and Wetherbee 2003), there are precious few studies that have quantified fine spatial scale habitat selection in relation to foraging strategies (Morrissey and Gruber 1993b, Heithaus et al. 2002, 2006). There are presently no studies that have quantified both high spatial (at the scale of meters) and temporal scale (over the scale of years) movement patterns for any shark species.

The blacktip reef shark (*Carcharhinus melanopterus*, Quoy and Gaimard 1824) is a common shark species

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found on coral reefs of the Indo-Pacific (Compagno et al. 2005), and qualitative observations suggest that they occupy shallow reefs and sand-flats at both atolls and high islands (Hobson 1963, Stevens 1984). Blacktip reef sharks are one of the most abundant apex predators at many atolls (Stevens 1984, Compagno et al. 2005), although human impacts have reduced their numbers at many locations (e.g., Sandin et al. 2008). Dietary analysis suggests that *C. melanopterus* are tertiary predators and feed primarily on teleosts, crustaceans, cephalopods, and, in some areas, reptiles (Cortes 1999). These factors raise the possibility that blacktip reef sharks could exert top-down control on many coral reef ecosystems. However, currently no detailed analysis of blacktip reef shark movement patterns, space utilization and habitat selection exists.

Palmyra Atoll is part of the Line Island chain in the central Pacific Ocean, and has been a U.S. National Wildlife Refuge since 2001, essentially making the atoll a no-take marine reserve. There are high densities of apex predators at Palmyra, with sharks making up almost 60% of the fish biomass, and recent studies suggest that these high densities are a consequence of reduced human impacts (DeMartini et al. 2008, Sandin et al. 2008). Diver observations show that blacktip reef sharks are the most abundant predator in the inner lagoons and sand-flats at Palmyra (Hobson 1963, Friedlander et al. 2007, DeMartini et al. 2008). However, the ecological impacts of blacktip reef sharks are partially a function of which habitats the sharks select for, and how they behave in such habitats. Knowledge of habitat selection is particularly crucial for understanding predator-dominated coral reef ecosystems, where the behavioral response of prey to predators appears to largely dictate resulting ecosystem trophic structure (Knowlton and Jackson 2008).

We used acoustic telemetry to quantify the movement patterns, habitat utilization, and foraging strategies of blacktip reef sharks at Palmyra. Our specific objectives were: (1) determine the degree of site fidelity shown by the sharks to sand-flats within a lagoon at Palmyra Atoll over different temporal and spatial scales, (2) determine if there are any diel or tidal changes in movement patterns, (3) quantify the selection or avoidance for microhabitats in the lagoon over the scale of hours to days, and (4) use fractal analysis to quantify the movement path structure and subsequent foraging strategies of blacktip reef sharks at Palmyra over short time periods (hours to days).

## METHODS

### *Study site*

Palmyra Atoll (5°53' N, 162°05' W) is part of the Line Island chain located just north of the equator (Fig. 1). Two primary lagoons (west and east) are linked by a small channel, and a larger channel links the west lagoon to the outer reefs (Fig. 1). The lagoons have a maximum depth of 50 m, with a mud/sand substratum causing low

water visibility, while the outer fore-reefs are characterized by steep slopes with high coral cover and high visibility. Due to Palmyra's location in the Inter-tropical Convergence Zone, the atoll receives up to 500 cm of rainfall per year, and consequently terrestrial habitat is largely rain forest (Fig. 1). In addition to Palmyra's refuge status, only a small crew of up to 17 refuge staff and scientists inhabit the atoll, hence human influences are maintained at a low level.

### *Active tracking*

Blacktip reef sharks were attracted to the Banjos, Nursery, or Channel sand-flats using squid bait (Fig. 1). We then concealed a V13 acoustic transmitter (dimensions 13 × 30 mm, carrier frequencies 62–78 kHz; Vemco, Halifax, Nova Scotia, Canada) in a piece of squid, and allowed one of the sharks to voluntarily consume the transmitter containing bait. To facilitate longer tracks, we also caught some individuals and surgically implanted the transmitters into the body cavity. In those cases, we caught sharks on barbless hooks and brought them alongside the boat where they were restrained, inverted, and placed in tonic immobility; a trance-like state. A small incision was then made through the shark's abdominal wall, and a transmitter was implanted into the body cavity. The wound was closed with a single suture and the shark was released. We waited a minimum of 48 h before initiating tracks of sharks that were surgically fitted with transmitters, to remove the influence of surgery on movements. A polyvinyl chloride (PVC) pipe of known length placed on the sand-flat enabled us to estimate shark total length in instances when the shark was fed a transmitter. For sharks fed transmitters, we discarded the first 2 h of data so as to remove the influence of feeding and odors on movement patterns. Continuous tracking was conducted using a kayak technique (Meyer and Holland 2001) and an RJE PRS 275 handheld underwater receiver (RJE International, Irvine, California, USA), which enabled us to track the sharks in very shallow water. All sharks were tracked continuously during daytime hours with GPS positions taken every 15 min. During tracking we maintained a minimum 10–30 m distance from the shark, but when GPS positions were taken we would move to the exact location of the shark, so that we could quantify habitat use. If the shark was over a sand-flat, we were able to determine the exact location of the shark because the shallow water over the flats enabled us to visually track the shark and determine which habitat it was occupying. If the shark was over a ledge or in deeper lagoon waters, we would get an accurate fix by positioning the kayak until the acoustic signal strength was the same in all directions, indicating that we were directly above the animal. Notes were taken while tracking to indicate which habitat sharks occupied when positional fixes were obtained, to ground-truth the GPS data. Due to safety regulations, continuous tracking could not be conducted at night. During the night we

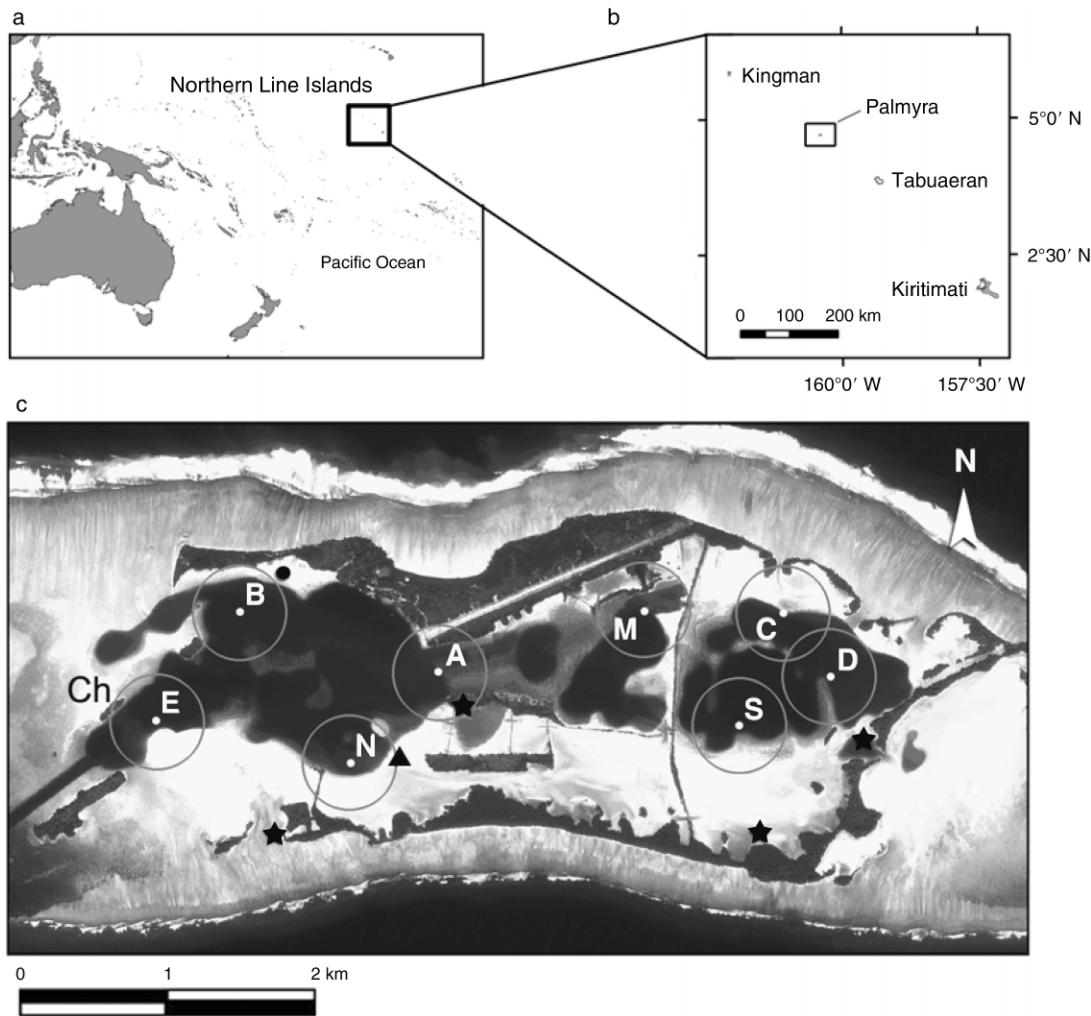


FIG. 1. (a) Map of the Line Islands relative to the central Pacific Ocean. (b) Islands of the Northern Line Islands, including Palmyra Atoll. (c) VR2 receiver positions and detection radii within Palmyra Atoll. VR2 receivers in the west lagoon are Banjos (B), Eddies (E), Nursery (N), Airport (A), and Midchannel (M); those in the east lagoon are Sixes (S), Cookies (C), and Downeast (D). The locations of Banjos (black circle), Nursery (black triangle), and the main Channel (Ch) sand-flats are also shown. Black stars show the known locations of blacktip reef shark pup aggregations.

either obtained single location checks every two hours, or we tracked continuously for one hour, every two hours. We estimated positional accuracy of shark locations to be  $\pm 7\text{--}8$  m (based on GPS accuracy).

#### *Nursery delineation*

Neonate and young-of-the-year (YOY) blacktip reef sharks were only observed in very shallow sand-flat habitats, close to shore. As it relates to ontogenetic shifts in habitat use, and because blacktip shark pups were too small to carry acoustic transmitters, we sampled these sharks at locations where they were aggregating. Sharks were caught using a 30 m long seine net that was positioned perpendicular to the shoreline. We then herded the sharks into the net where they were measured, sexed, weighed, and released.

#### *Data analyses*

*Home range.*—All spatial analyses of movement data were conducted in ArcView GIS version 3.2 (ESRI 1999) layered over geo-referenced IKONOS images of Palmyra Atoll. For all shark tracks longer than 24 h, we calculated two estimates of home range. The kernel utilization distribution (KUD; Worton 1989) is a probability distribution that represents the area where there is a 95% and 50% chance of finding the individual tracked. The 95% KUD is considered a measure of the overall home range of the animal, and the 50% KUD is more representative of the area of core use (e.g., Heupel et al. 2004). A minimum convex polygon (MCP) is the area of a polygon formed by connecting the outer position fixes of an animal's movements. Both estimates were calculated using the Animal Movements extension with

ArcView GIS version 3.2 (Hooge and Eichenlaub 1997). Areas of the KUD and MCP that extended onto land were manually removed. Multiple regression analyses were used to determine the influence of shark total length (TL) and water temperature on 95% KUD area. As a quantitative measure of the shape of the shark's home range, we determined the index of eccentricity (ECC),  $ECC = l/w$ , where  $l$  is the maximum length of the animal's activity space, and  $w$  is the maximum width of the activity space. A circular activity space will produce  $ECC = 1$ , while ECC values greater than 1 indicate an asymmetrical shaped activity space (Morrissey and Gruber 1993a, Rechisky and Wetherbee 2003).

We calculated two measurements of site fidelity for blacktip reef sharks. We calculated the linearity index  $L_i$ , which varies between 0 (strong site fidelity) and 1 (nomadic behavior), and the index of reuse (IOR), which can range from 0 (no overlap in daily activity spaces, suggesting nomadic behavior) to 1 (100% overlap in daily activity spaces, suggesting site fidelity; Appendix A) (Morrissey and Gruber 1993a, Rechisky and Wetherbee 2003). In order to determine if blacktips showed daily shifts in core areas, we also calculated IOR values between daily 50% KUD areas.

To test for diel behavior, we compared daytime and nighttime activity space size (using the MCP measurement) for each shark using a Student's  $t$  test. We also determined rate of movement (ROM) for each shark during day and night periods, with ROM defined as the distance moved by the shark between two points, divided by the time taken to swim between the points. To evaluate the effects of diel and tidal periods on shark ROM, we categorized all ROM values into (1) day vs. night and (2) tidal period (high slack, low slack, flood, ebb). We tested diel and tidal effects simultaneously by dividing ROM data into eight diel and tidal groupings and using a one-way ANOVA with a Tukey-Kramer a posteriori test. ROM data were converted to body lengths per minute (BL/min) to control for shark total length. Data were square root-transformed to meet the assumptions of normality (Shapiro-Wilk  $W$  test). ROM data represents speed over ground; hence, an animal swimming in a straight line will have higher ROM than an animal foraging over a small area (see Phillips et al. 2004).

**Habitat utilization.**—The inner lagoons at Palmyra consist of four microhabitat types: sand-flats, reef ledges, deeper sand-flats, and lagoons. Sand-flats are extensive areas with water depth  $< 2$  m and benthic habitat of sand/coral rubble, while deeper sand-flats are areas in the center of lagoons where water depth is 2–5 m. Lagoons comprised all other regions within the atoll where water depth exceeds 5 m and benthic substratum is primarily fine sand/mud. Ledges are located at the boundary between sand-flats and lagoons. Based on results of fractal analysis, we considered ledge habitats to include the area within 10 m of either side of the drop off. For each shark, we determined the number of position fixes that occurred in each of these habitat

types. We then calculated the area of each of these habitats in the west lagoon, as a percentage of the total area, using the geo-referenced IKONOS image of Palmyra. We used a chi-squared test to determine if habitats utilized by the sharks differed significantly from expected based on overall habitat available. We then used the modified Strauss linear index of food selection,  $L = r_i - p_i$ , where  $L$  is the habitat selection value,  $r_i$  is the percentage use of habitat  $i$ , and  $p_i$  is the percent availability of habitat  $i$  (Morrissey and Gruber 1993b). Values of  $L > 0$  suggest selection for a particular habitat, while values of  $L < 0$  suggest avoidance of a habitat. We determined habitat selection values for all sharks combined, but then performed least-squared linear regression analysis between individual shark length and habitat selection values for sand-flat, ledge, and lagoon habitats. In order to evaluate the effect of habitat type on speed over ground, we also quantified ROM for each shark while they were moving over ledge, sand-flat, and lagoon habitats and utilized an ANCOVA test using ROM as the dependent variable, habitat as an independent variable, and shark total length as a covariate. A Tukey's test was then used to determine the location of pairwise differences. For habitat analysis, ROM data were log-transformed to meet the assumptions of normality.

**Fractal analysis.**—A fractal dimension is a measure of tortuosity of a movement path, and can range from 1 for a straight line to 2 for a path so tortuous that it completely covers a plane (Nams 1996, 2005). Fractal measures of animal movements are generally scale dependent, as the tortuosity of a path will vary based on the spatial scale at which it is viewed. Therefore, by examining how the fractal value ( $D$ ) varies with scale for a movement path, we can quantify the spatial scales at which the animal views its environment and also detect patch use (Nams 2005). For a more detailed description of the use of fractal analysis in animal ecology see Nams (1996, 2005), and Doerr and Doerr (2004). However, a caveat of using fractal analysis to describe animal movements is that, if the animal is moving using a correlated random walk (CRW), then the changes in fractal  $D$  with scale may not be caused by a change in tortuosity with scale (Nams 1996, 2005). A CRW occurs when an animal moves randomly but consecutive steps are correlated, leading to directional bias. We used the  $CRW_{Diff}$  statistic in Fractal 5.0 software (V. O. Nams, Nova Scotia Agricultural College, Nova Scotia, Canada), which determines if an animal's net dispersal is greater or more constrained than that predicted by the CRW model (Nams 2006; see Appendix B).

Two fractal measures were used to analyze the movement patterns of blacktip reef sharks. Fractal mean was used to estimate an overall fractal  $D$  value for each blacktip reef shark by using the traditional divider method (Doerr and Doerr 2004; see Appendix C). To measure the change in fractal  $D$  with scale, we used the VFrac estimator described by Nams (1996). VFracal

calculates the fractal values based on the turning angle between consecutive locations, and its associated error estimator (Nams 1996). We used the VFractal estimator in Fractal, version 5.0, for divider sizes ranging from 10 m to 1000 m. The 95% confidence intervals were calculated using a bootstrapping procedure, which randomly selects turning angles from the movement path to calculate VFractal, with 1000 replicates (Nams 1996).

To detect patch use, we determined the correlation in tortuosity between adjacent path segments for a range of divider sizes. If the divider size is below the size of a patch used by the animal, then it is likely that consecutive path segments will be either inside or outside the patch; hence, the tortuosity correlation between adjacent path segments should be positive. As divider size approximates patch size, then it's likely that one path segment will be inside the patch (with high tortuosity), while the adjacent segment is outside the patch (with low tortuosity); hence, the correlation should be negative. Therefore, a positive correlation followed by a negative correlation is indicative of patch use and size (Nams 2005). If there is no patch use, then there should be no correlation between patch segments and the correlation should be zero regardless of whether the animal is moving in a random or directed manner (Nams 2005). All fractal measures and correlation statistics were calculated in Fractal version 5.0.

#### *Long-term movements*

To quantify longer term site fidelity of blacktip reef sharks to different reef flats, we established an array of eight omni-directional automated underwater acoustic receivers (model VR2, Vemco, Halifax, Nova Scotia) throughout the west (five receivers) and east lagoon (three receivers; Fig. 1). The receivers were moored to the mud/silt lagoon substratum in depths of 10–30 m, with the receivers suspended 10–15 m below the surface. We surgically implanted nine blacktip reef sharks within the west lagoon with Vemco V8SC-2L transmitters (8 mm diameter  $\times$  20 mm length; Appendix G). Each transmitter produces a unique pulse code that can be detected by the VR2 receivers when a tagged shark is within range (300 m) of the receiver. These transmitters had a nominal battery life of one year (for additional methods, see Appendix D). VR2 receivers were retrieved, downloaded, and redeployed every 4–6 months.

We determined the number of detections at each VR2 receiver for each shark as a percentage of the total number of detections. To determine if sharks were disproportionately using certain areas more than others, we compared proportion of detections between the different VR2 receivers. The data did not conform to the assumptions of parametric statistics despite transformation and a nonparametric Kruskal-Wallis rank sum test was utilized. To examine temporal patterns of movement, we used a fast Fourier transformation (FFT). An

FFT decomposes time series data into component frequencies, and then searches the data set for cyclical patterns. Cyclical patterns with dominant frequencies can be identified as peaks in a power spectrum. As such, FFT analysis can identify diel, tidal, or seasonal patterns in animal movements (e.g., Meyer et al. 2007). We binned the number of VR2 detections in every hour for each day of the VR2 deployments and smoothed the data using a Hamming window before applying the FFT. A Hamming window reduces the effects of adjacent spectral components, which can potentially generate biologically meaningless frequency peaks.

## RESULTS

### *Active tracking*

*Home range.*—We actively tracked 14 blacktip reef sharks (total length [TL]  $100 \pm 17$  cm [mean  $\pm$  SD]) for periods ranging from 4 h to 72 h, between February 2005 and September 2007 (Appendix E). Although this represents continuous tracking times, we would also periodically relocate sharks up to 14 days following the start of the track. Ten sharks were fed transmitters, while four animals had transmitters surgically implanted. There was no significant difference in overall ROM between sharks that were fed transmitters ( $11.3 \pm 8.7$  m/min) and those that had them surgically implanted ( $11.4 \pm 9.4$  m/min,  $t = 1.97$ ,  $P = 0.77$ ). Sharks moved over a limited area, with repeated use of core locations on a daily to weekly basis (Fig. 2). Home range estimates were small, with average 95% KUD areas of  $0.55 \pm 0.24$  km<sup>2</sup>, and MCP areas of  $0.33 \pm 0.26$  km<sup>2</sup>, while the maximum linear dimension of the home range was  $1.4 \pm 0.3$  km (Appendix F). The 95% KUD estimates were larger than MCP estimates for five of the six sharks examined, although the difference was not significant ( $t$  test paired for means,  $t = 1.45$ ,  $P = 0.76$ ; Appendix F). There was no effect of shark TL, water temperature, or the interaction term on 95% KUD area ( $F = 0.11$ ,  $P = 0.77$ ). Blacktip reef sharks tended to have activity spaces that were asymmetrical and oblong in shape, as indicated by the high ECC values ( $4.8 \pm 2.3$ ; Appendix F), and there was no influence of shark TL on ECC ( $F = 1.1$ ,  $df = 13$ ,  $P = 0.30$ ).

The repeated use of core areas by blacktip reef sharks was also apparent based on the low  $L_i$  values ( $0.121 \pm 0.096$ ; Appendix F). The highest  $L_i$  value (0.280) was for the shortest tracks (9 and 4 h), but much lower values were obtained from sharks tracked for longer periods. For example, shark number 9 was tracked for 72 h and had  $L_i = 0.007$ , and shark number 4 tracked for 48 h had  $L_i = 0.028$  (Appendix F). There was no influence of shark TL on  $L_i$  ( $F = 0.002$ ,  $df = 13$ ,  $P = 0.89$ ). IOR values ( $0.19 \pm 0.11$ ) were lower than expected based on the low  $L_i$  values (Appendix F). However, the lower IOR values in general were due to low overlap in consecutive 50% KUD activity spaces. The IOR between 50% KUD for day 1 and 2 for blacktip number 9 was 0.005, for blacktip number 4 was 0.189, blacktip number 2 was

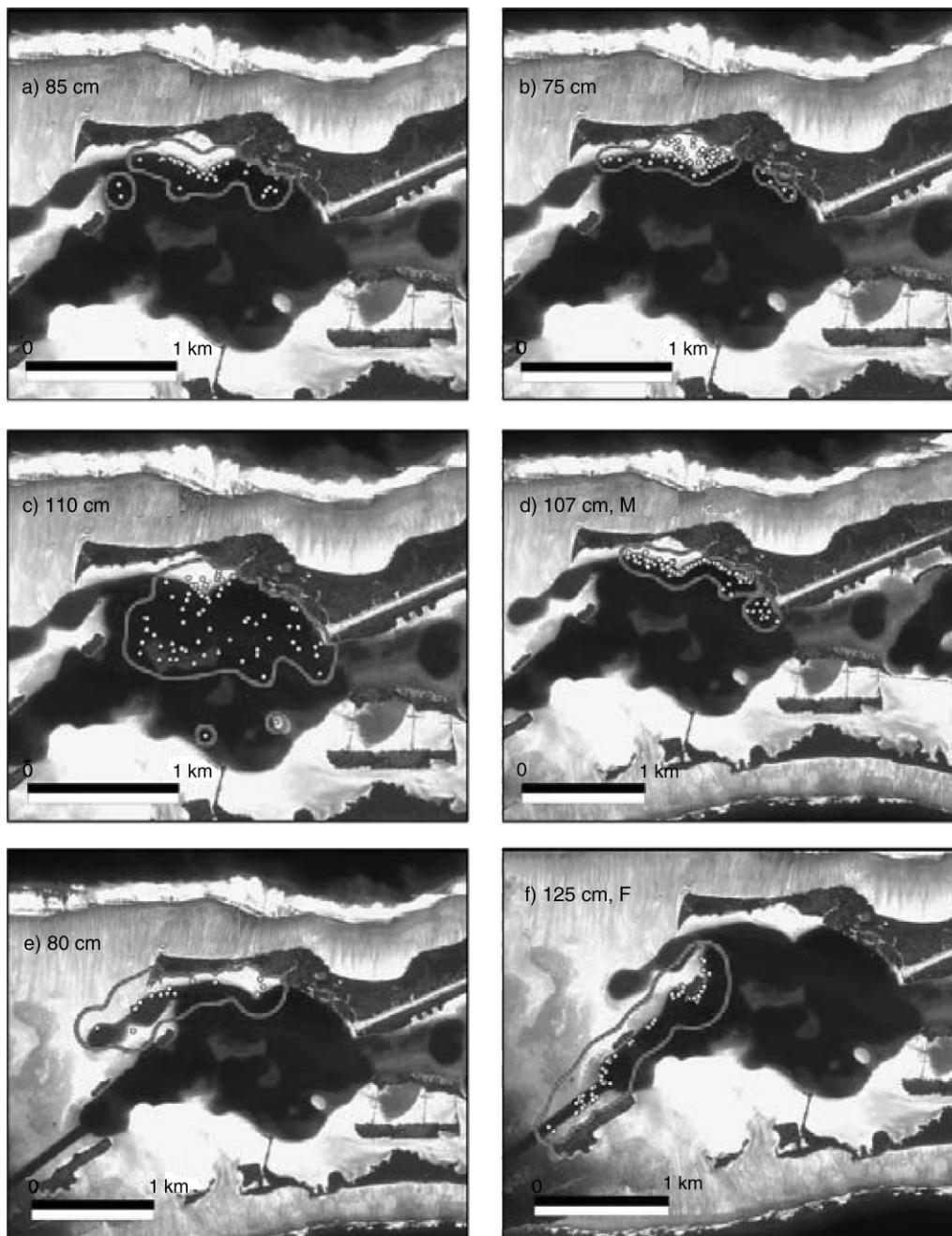


FIG. 2. Home range of six blacktip reef sharks at Palmyra Atoll. Polygons are 95% kernel utilization distributions (KUDs), and dots are shark locations. The total length and sex (where known; M, male, and F, female) of each shark is given in the figure.

0.024, and blacktip number 13 was 0.0. When sharks were relocated on subsequent days, they were located within or near the original 50% KUD, which resulted in low  $L_t$  values.

Blacktip reef sharks did not exhibit any detectable diel shifts in activity space size or location (day  $0.17 \pm 0.15$  km<sup>2</sup>, night  $0.14 \pm 0.16$  km<sup>2</sup>, paired  $t$  test for mean,  $t = 0.42$ ,  $df = 12$ ,  $P = 0.68$ ). However, there were significant differences in ROM values when data were separated by

diel tidal periods (ANOVA,  $F_{7,257} = 2.63$ ,  $df = 257$ ,  $P = 0.012$ ). Sharks swam with a greater speed over ground during ebb tides at night ( $18.1 \pm 8.2$  BL/min) compared with flood tides at night ( $8.5 \pm 9.5$  BL/min). Flood and ebb nighttime ROM values did not differ from any of the other categories. However, it should be noted that, because not all sharks were continuously tracked during nighttime periods, the smallest ROM samples sizes were for nocturnal flood and ebb tides.

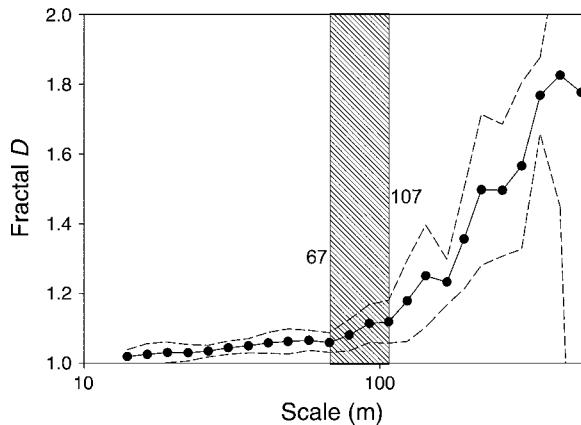


FIG. 3. Changes in VFracal with scale for movements of all blacktip reef sharks combined. The solid line indicates the mean, while dashed lines are upper and lower 95% confidence intervals. The  $x$ -axis is on a log scale. The box shows the location of discontinuities in  $D$ . The numbers are  $x$ -axis values at the locations of the discontinuities.

**Habitat utilization.**—The observed use of habitats by sharks differed significantly from expected based on available area of each habitat type ( $\chi^2 = 16.1$ ,  $P = 0.01$ ). When data from all sharks were combined, high  $L$  values (selection) were obtained for ledge habitats ( $L = 0.59$ ), while lower  $L$  values (avoidance) were obtained for sand-flat ( $L = -0.14$ ) and lagoon habitats ( $L = -0.38$ ; Appendix I). Sharks showed neither avoidance nor selection for deeper sand-flat habitats. As sharks increased in size, their selection for sand-flat habitats decreased ( $L$  decreased,  $F = 5.52$ ,  $df = 13$ ,  $P = 0.04$ ,  $r^2 = 0.36$ ,  $L = -0.008TL + 0.75$ ; Appendix I). There was no significant relationship between  $L$  for ledge or lagoon habitats and shark TL ( $F = 0.062$ ,  $P = 0.81$ ).

Both shark TL (ANCOVA,  $F_{2,15} = 7.38$ ,  $df = 15$ ,  $P = 0.017$ ) and habitat type ( $F = 11.83$ ,  $df = 15$ ,  $P = 0.001$ ) influenced ROM, although there was no significant interaction on ROM ( $F = 0.82$ ,  $P = 0.46$ ). As sharks increased in size, ROM also increased, and sharks swam with the greatest speed over ground when over lagoon habitats, and the lowest when over sand-flats. Sharks moved slower over sand-flat habitats ( $7.6 \pm 1.4$  m/min) than they did over lagoon ( $16.8 \pm 6.6$  m/min,  $P = 0.0007$ ) and ledge ( $11.7 \pm 2.3$  m/min,  $P = 0.022$ ) habitats. Sharks had higher ROM when over lagoon rather than ledge habitats ( $P = 0.049$ ).

**Fractal analysis.**—Blacktips showed more constrained movements than predicted by the correlated random walk (CRW) model (CRW<sub>diff</sub> =  $-0.128$ ,  $df = 11$ ,  $P = 0$ ), making fractal analysis an appropriate technique for analyzing shark movements. The relatively high  $D$  values ( $1.25 \pm 0.08$ ) indicate that sharks had tortuous movement patterns, characterized by repeated back and forth movements along the reef ledges (Fig. 2, Appendix F).

Results from fractal analysis suggest that sharks view their environment at a minimum of three different scales

(Fig. 3). When data from all sharks were combined, discontinuities in  $D$  existed at 15–66 m, 67–107 m, and  $>107$  m (Fig. 3). At scales between 15 and 66 m movements appeared to be scale invariant, as there were no changes in  $D$  with scale.  $D$  started to slowly increase at scales  $>67$  m and increased more rapidly at scales  $>107$  m. At scales  $>400$  m, the confidence intervals were too wide for any conclusions to be made with regard to movement structure. However, fractal analysis of individual animals indicates that there are some individual differences in the scale of patch use (Fig. 4). Both changes in VFracal and correlation coefficients show that shark number 2 differentially selected patches at scales of 32–76 m (Fig. 4a, b). The shark swam in relatively straight paths (low  $D$ ) up to scales of 30 m, after which movements became more tortuous, especially at scales  $>150$  m. Shark number 9 also swam in a fairly direct manner up until a scale of 30 m, after which a discontinuity and increase in  $D$  occurred, with progressively more tortuous movement paths at scales from 30–400 m (Fig. 4c). Correlation coefficients show patch use at scales of 30–40 m and 115–200 m (Fig. 4d). In general, blacktip reef sharks in the west lagoon used patches at scales of 30–40 m, 60–90 m, and 115–200 m, which approximate 3%–17% of the scale of their home range length (Appendix F).

#### Nursery delineation

In over 500 hours of tracking and fishing for sharks on sand-flats, ledges, and lagoons, neonate and YOY sharks were only seen and captured on sand-flats very close to the shoreline ( $<1$  m), often in water no more than 10 cm deep. In these areas, we caught 43 neonate and YOY blacktip reef sharks (TL  $46 \pm 5$  cm, range 34–61 cm, mass  $393 \pm 169$  g, 25 females, 18 males; Fig. 1). These potential nursery areas were always located interior from the reef ledge, although it is unknown where the sharks went during extreme low tides (when sand-flats are exposed). Nursery locations only represent areas where we sampled. YOY were observed in areas where we did not sample, and they were always found in the same habitat type (very shallow water over sand-flats, close to the shoreline).

#### Long-term movements

We deployed long-term transmitters in nine sharks ( $114 \pm 10$  cm TL, five males and four females; Appendix G) between February 2004 and February 2005. Between February 2004 and October 2007, all eight (100%) of our receivers detected seven of the nine tagged sharks (78%) for periods of 444–1160 d (median 926 d; Appendix G). There were significant differences in the percentage detections by each VR2 receiver (Kruskal-Wallis,  $H = 19.84$ ,  $df = 7$ ,  $P = 0.006$ ), with a greater proportion of detections of tagged sharks at the Banjos (median 33.5%) and Airport (median 15.2%) receivers than any of the other locations (see Appendix H). Sharks showed site fidelity to a small area as  $81\% \pm 12\%$  of detections

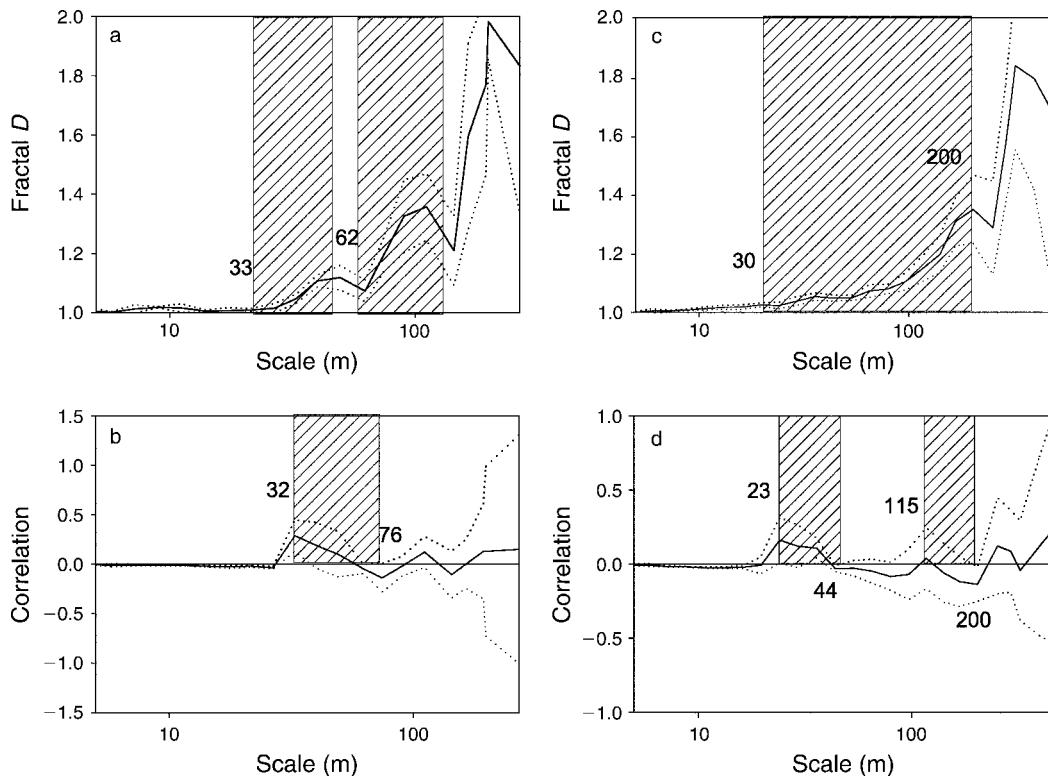


FIG. 4. Fractal analysis of blacktip reef shark movement patterns at Palmyra Atoll (a, b) for a 75-cm total length (TL) individual (shark number 2), and (c, d) for a 110-cm female shark (shark number 9). The upper panels show change in VFractal with scale, while lower panels show change in correlation in fractal values between adjacent steps. The solid lines show mean values, while dotted lines show upper and lower 95% confidence intervals. Striped rectangular bars show areas of discontinuity in VFractal (upper panels) or scales of patch use (lower panels). Scale values at these locations are given on the figure. The x-axis is on a log scale.

occurred at one core receiver for each shark (Appendix H). Detected movements were mostly confined to the west lagoon, with only 0%–4.3% of detections occurring in the east lagoon (median 0.1%). Distinct seasonal changes in movements were only apparent in two individuals (29%), which showed movements to the east lagoon (Appendix K). Both sharks (one male, one female), made annual movements to the east lagoon starting in late December, over a three-year period. The excursions were brief and occurred periodically over a two-month period, with both sharks returning to the west lagoon daily after excursions.

Spectral analysis showed evidence of diel and tidal effects (Fig. 5). Five of the six (83%) sharks showed 24-h peaks in the time frequency spectrum, and four (67%) showed 12-h, 6-h, or 8-h peaks associated with tidal movements (Appendix H). However, the spectral density of the peaks was low, indicating that diel or tidal behavior did not occur daily, and that there were periods of no detections.

#### DISCUSSION

##### *Home range size and site fidelity*

Coastal sharks in tropical areas appear to have relatively small home ranges and show some degree of

site attachment (McKibben and Nelson 1986, Holland et al. 1993, Morrisey and Gruber 1993a). In agreement with studies of other tropical species, blacktip reef sharks at Palmyra Atoll utilize small home ranges over the scale of weeks to years. Furthermore, the blacktips at Palmyra appear to have smaller home ranges than recorded for any other adult species of shark (McKibben and Nelson 1986, Holland et al. 1993, Rechisky and Wetherbee 2003). Blacktip reef sharks tracked at Aldabra Atoll, Indian Ocean, also showed limited movements, but moved up to 2.5 km in 7 h, although Aldabra (34 km length) is significantly larger than Palmyra (12 km; Stevens 1984). Many factors can regulate home range size, including shark size, water temperature, habitat quality, and population and social factors. In the present study we found no effect of shark size and water temperature on home range size. Theory predicts that as an animal increases in size, energetic requirements and consequently area over which resources are obtained (home range) also increases (see review in Lowe and Bray 2006). While a number of studies have shown an ontogenetic expansion in home range with shark length (e.g., Heupel et al. 2004, Garla et al. 2006), only juvenile lemon sharks (*Negaprion brevirostris*) in the Bahamas have been shown to display a linear

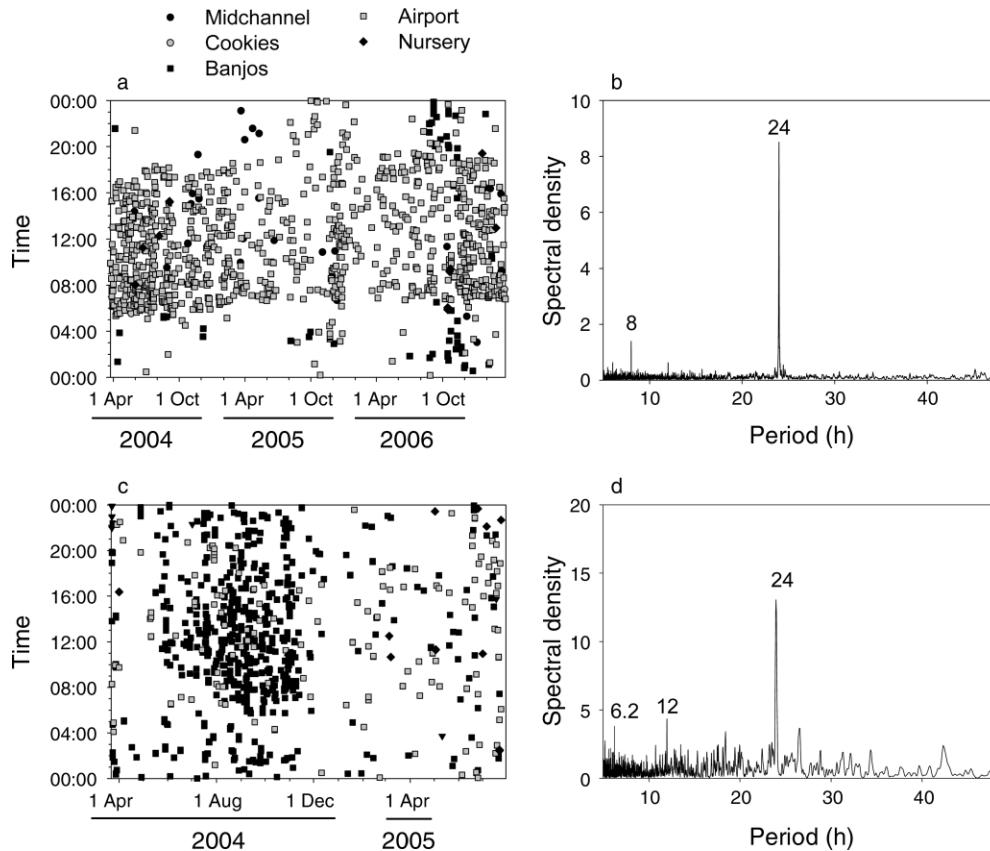


FIG. 5. Examples of long-term movements of two acoustically tagged blacktip reef sharks. (a) Scatter plot showing movements for shark number 62 and (b) associated spectral analysis (FFT). The periods with dominant peaks in the FFT have been labeled with the exact value. (c) Scatter plot for shark number 56 and (d) associated spectral analysis. Note the use of different scales on the y-axis for (b) and (d).

increase in home range size with shark length over the smaller size ranges (47–100 cm pre-caudal length [PCL]; Morrissey and Gruber 1993a).

Blacktip reef sharks showed a high degree of site fidelity to the west lagoon, in particular, to core areas within the lagoon for periods over several years. While the active tracking indicated strong fidelity to the Banjos and Channel sand-flat ledges, acoustic monitoring data also showed that blacktip reef sharks consistently utilized these areas of the west lagoon for multiple years, although they occasionally make brief excursions to other locations within the west lagoon or to the east lagoon. Further evidence for strong site fidelity is the fact that the majority of detections (mean 81%) for each shark were on one core receiver. Tag and recapture data of blacktips at Aldabra Atoll also indicated high site fidelity as 81% of recaptures occurred within 1 km of the tagging location (Stevens 1984). Similar levels of site attachment have been seen in both juvenile and adult species of sharks from tropical islands and atolls (McKibben and Nelson 1986, Chapman et al. 2005, Garla et al. 2006), although those species tended to move over a larger area than the blacktips in the present study. Our data provides the longest time frame over

which site fidelity to a small area has been quantified for any species of shark. Similarly sized coastal sharks from sub-tropical and temperate bays, show less site attachment and perform extensive seasonal migrations, which are most likely attributed to the much greater seasonal variation in environmental conditions in those areas (e.g., Rechisky and Wetherbee 2003, Heupel et al. 2004). The repeated use of ledge habitats suggests that blacktip reef sharks at Palmyra are able to meet most of their energetic needs in relatively small areas, at least on the edges of certain sand-flats. The sharks also showed daily shifts in 50% KUDs within their home range, which has also been seen in juvenile lemon sharks and may be related to behaviorally mediated resource depletion (Morrissey and Gruber 1993a, Brown et al. 1999).

#### *Diel and tidal effects on behavior*

Several shark species show increased rates of movement and size of activity space at night, suggesting nocturnal foraging (Nelson and Johnson 1980, McKibben and Nelson 1986, Garla et al. 2006). Blacktips at Palmyra show some degree of diel behavior, although there are intraspecific differences in the magnitude and consistency of the behavior between sharks. Although there are

numerous explanations for diel behavior including feeding, predator avoidance, reproduction, and energetic advantages (Lowe and Bray 2006), it is unclear as to what factors regulate this behavior for blacktips at Palmyra.

Tidal stage has been shown to effect shark behavior in several locations, with individuals moving onto previously exposed sand or mud flats at high tide to forage (e.g., Nelson and Johnson 1980, Wetherbee et al. 2007). Results from both passive and active tracking suggest a tidal component to blacktip movements at Palmyra, although there were intraspecific differences in the magnitude of the response. Sharks had significantly lower rates of movement during the nocturnal flood tide than the ebb tide. The reduced rates of movements for the sharks at Palmyra with the flood tides corresponds with the influx of cooler water and subsequent decrease in water temperature (up to 3°C, NOAA Coral Reef Ecosystem Division: Appendix J). There are three potential explanations for reduced swimming speeds during this time period: (1) reduced metabolic rates caused by lower temperature, (2) reduced swim speeds due to foraging in small patches, and (3) decreased swim speeds from reduced search behavior and foraging. Based on endogenous rhythms in gastric motility and pH in captive blacktip reef sharks, it was previously hypothesized that individuals would preferably forage during times of low water temperature, as the natural delay in gastric motility following feeding (gastric accommodation) would coincide with times of increased water temperature (Papastamatiou et al. 2007). The hypothesis would fit well with explanation 2, but presently all three explanations are plausible. Changes in rate of movement have also been shown to effect detection frequency by acoustic monitors (Topping et al. 2006), which may also explain the tidal peaks in the VR2 detections. Previous studies of sand flat associated fishes at Palmyra (e.g., bonefish, jacks) have shown that these many fishes invade sand flats during flooding tides, but leave during falling tides via discrete corridors (Friedlander et al. 2007). It is likely that, at times, blacktip movements may be linked with these tidally driven prey migrations. Finally, qualitative data also suggests that blacktip reef shark pups and YOY show tidally mediated movements. These sharks occupy areas (shallow sand-flats) that are inaccessible during low tide; hence, some movements correlated with tidal flow must exist (similar behavior is seen in juvenile lemon sharks; Wetherbee et al. 2007).

#### *Habitat utilization*

Although we found no influence of shark length on home range area, there were ontogenetic shifts in habitat selection, with smaller sharks showing stronger selection for sand-flat habitats. Sand-flat habitats are characterized by shallow waters and would provide small sharks with protection from larger predators. Neonatal and YOY blacktip pups were only found in very shallow water, very close to shore. These smaller sharks could potentially have a number of predators, including adult

blacktip reef sharks, gray reef sharks (*Carcharhinus amblyrhynchos*), tiger sharks (*Galeocerdo cuvier*), and large teleosts. While the use of coastal bays as nursery areas is well documented in elasmobranchs (e.g., Heupel et al. 2007), far less is known about the use of small-scale nursery zones (on the scale of meters) at atolls and islands (Garla et al. 2006, Wetherbee et al. 2007). There should be strong selection for the utilization of shallow (safe) habitats by shark pups in predator-dominated ecosystems. Similarly, juvenile lemon sharks select for shallow inshore mangrove habitats or tidal pools to obtain protection from predation by larger sharks (Morrissey and Gruber 1993b, Wetherbee et al. 2007).

Larger sharks showed a clear habitat preference for reef ledges, often spending their time patrolling back and forth along the reef ledge (also indicated by the relatively high fractal values and the oblong shaped activity spaces used by the sharks). Use of edges as foraging sites appears to be a common feature of top-level predators in both terrestrial and marine systems (e.g., Phillips et al. 2004, Heithaus et al. 2006). Ledge or edge habitat use has been seen in several elasmobranchs (e.g., Morrissey and Gruber 1993a, Rechisky and Wetherbee 2003, Heithaus et al. 2006), but only one other study has quantified ledge use (Heithaus et al. 2006). We have conducted dives on the steep ledges in the lagoons at Palmyra, and they appear to support a high abundance of potential prey items, so we propose that blacktip reef sharks either obtain a higher forage base over the ledges, or obtain greater encounter rates with prey (possibly prey moving off the flats). The reduced swim speeds over ledge and sand-flat habitats are most likely a consequence of the sharks foraging in patches in these locations. Although adult sharks spent less time than expected (based on available area) over sand-flats, all adult sharks made brief excursions onto the flats. The increased rates of movement over lagoon waters are a consequence of straight-line swimming, suggesting that these habitats are mainly used to transit between ledges and sand-flats. Large tiger sharks are occasionally seen in the west lagoon, and it is also possible that adult blacktip reef sharks reduce predation risk by avoiding deeper lagoon habitats.

The results from both active and passive tracking indicate that sand-flats within the west lagoon may differ in quality, as sharks showed strong fidelity to the Banjos, Channel, and Airport receiver areas, but much lower fidelity to the habitat surrounding the Nursery receiver even though these locations are only a few hundred meters apart. All sharks tagged and actively tracked at the Nursery's ledge had left the area after 24 hours, and could not be relocated there over several days. Between 0% and 4% of detections occurred at the Nursery's receiver for acoustically tagged sharks, even though four of the six sharks were tagged on the Nursery's sand-flats. The Nursery's sand-flat does not have a coral ledge, unlike the other flats, and therefore supports a lower biomass of potential prey items (Y.

Papastamatiou, *personal observation*). Therefore, the ledge at Nursery's most likely represents an area of low habitat quality that may be driving the low level of site attachment shown by the sharks. Clearly, habitat quality is important for regulating the levels of site attachment, even over small spatial scales.

The lack of movement of sharks from the west to the east lagoon is also striking and may further be a function of habitat quality. However, the east lagoon serves some purpose for the life history of at least some individuals as indicated by the highly seasonal and synchronous migrations by two individuals. The reproductive cycle of blacktip reef sharks varies by location and can occur either annually (Porcher 2005) or every other year (Stevens 1984). The reproductive cycle of blacktips at Palmyra is unknown, but it is possible that the seasonal movements observed for some individuals may be related to mating behavior.

We were not able to quantify habitat use on the outer reefs at Palmyra, where conditions are very different from the inner lagoons. Although we observed blacktip reef sharks when diving on the outer reefs, the dominant predator is the gray reef shark, and therefore the ecological importance of blacktips may be reduced. However, there can be differences in behavior of sharks on ocean ledges versus lagoons (e.g., McKibben and Nelson 1986).

#### *Movement path structure and foraging strategy*

Fractal analysis is a powerful tool in the study of animal movement paths, although the majority of its application to date has focused on terrestrial animals (e.g., Doerr and Doerr 2004, Nams 2005). However, the technique is gaining popularity for use with marine animals and has been used to look at seasonal changes in movement path structure and to identify Area Restricted Search zones (Laidre et al. 2004, Tremblay et al. 2007). The overall movement paths of blacktip reef sharks at Palmyra could not be modeled with a correlated random walk, but instead, they showed directed movements within patches, while moving randomly between patches. By using fractal analysis we were able to detect patch use by blacktip reef sharks, with sharks using small-sized patches (most of a scale between 30 m and 100 m, or approximately 3%–17% of the scale of the shark's home range) on ledges and sand-flats. Movements within the 15–66 m scale range are largely scale-invariant, suggesting that sharks move using a directed walk while in patches by orienting to ledges (Nams 2006). The directed walk within patches appears to be a common behavior amongst all sharks, as indicated by the narrow confidence intervals at those scales. Shark movements became more tortuous at scales between 60 m and 107 m, which is most likely a function of more tortuous movements in larger patches. The final domain occurred at scales >107 m, with  $D$  rapidly increasing at larger scales indicating that the sharks may use a random walk to move between patches while

confined between the boundaries of their home range or sand-flat (e.g., Doerr and Doerr 2004). Habitat is also likely to affect an animal's movement structure and tortuosity (e.g., Philips et al. 2004), but due to the short amount of time sharks spent over lagoons and sand-flats, we were not able to analyze habitat effects.

The small home ranges utilized suggest that blacktip reef sharks should have good information about the spatial distribution of patches within their home range. However, patches are still likely to be spatially and temporally dynamic, and theoretically, highly correlated random walks, leading to almost straight movements, are thought to be the most efficient search strategy within a heterogenous environment (e.g., Zollner and Lima 1999, Philips et al. 2004). The repeated and tortuous searching and patch use on ledge habitats, where search paths by necessity are relatively straight, should enable blacktip reef sharks to maximize search efficiency. Excursions and patch use on to the sand-flats were also made by some sharks, although at present we can only speculate that these are for foraging purposes. Short track time (maximum three days) is a limitation of active telemetry tracking, and it would certainly be desirable to analyze movement path structure over the scale of months to years. However, presently there is no other technique for obtaining high spatial resolution movement data from fish predators, especially those that confine their movements to small areas.

Clearly, our results cannot be directly extrapolated to blacktip reef shark populations worldwide, but they do show how microhabitat quality and quantity can effect movements, behavior, and life history of top-level predators. The design of efficient marine reserves to conserve shark populations is particularly difficult due to the wide-ranging movements of these animals. However, by using the analytical framework presented here, and by quantifying the scales at which sharks view and respond to their environment, we will be able to improve models used to predict population level dispersal at other locations. Furthermore, the mounting evidence for shifting baselines at predator-depleted atolls (Sandin et al. 2008) is making it increasingly important to quantify predator behavior in the few remaining pristine atolls like Palmyra.

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#### APPENDIX A

Description of site fidelity tests (*Ecological Archives* E090-064-A1).

#### APPENDIX B

Description of test used to determine if sharks are moving with a correlated random walk (*Ecological Archives* E090-064-A2).

#### APPENDIX C

Description of fractal analysis (*Ecological Archives* E090-064-A3).

#### APPENDIX D

Description of passive telemetry techniques used to quantify long-term movements of sharks (*Ecological Archives* E090-064-A4).

#### APPENDIX E

Table showing details of blacktip reef sharks actively tracked at Palmyra Atoll (*Ecological Archives* E090-064-A5).

#### APPENDIX F

Table showing movement statistics for blacktip reef sharks actively tracked at Palmyra Atoll (*Ecological Archives* E090-064-A6).

#### APPENDIX G

Table of details for blacktip reef sharks fitted with long-life acoustic transmitters at Palmyra Atoll (*Ecological Archives* E090-064-A7).

#### APPENDIX H

Table showing percentage detections by VR2 receivers at eight locations throughout the Palmyra lagoons (*Ecological Archives* E090-064-A8).

#### APPENDIX I

Figure showing habitat selection statistics for blacktip reef sharks actively tracked at Palmyra Atoll (*Ecological Archives* E090-064-A9).

#### APPENDIX J

Figure showing diel changes in tidal height and water temperature at Palmyra Atoll (*Ecological Archives* E090-064-A10).

#### APPENDIX K

Figure showing seasonal movements of two blacktip reef sharks passively tracked at Palmyra Atoll (*Ecological Archives* E090-064-A11).