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Habitat use and movement patterns of juvenile and neonate blacktip sharks, *Carcharhinus limbatus* in nursery areas on San Cristobal Island, Galapagos

"Uso de habitat y patrones de movimiento de tiburones juveniles punta negra, *Carcharhinus limbatus* en la Isla San Cristóbal, Galápagos"

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Resumen

Movimientos a corto plazo y la preferencia de hábitat de tiburones juveniles de la especie punta negra fueron estudiados en áreas de crianza en la isla San Cristóbal, Galápagos. Mediante el método del seguimiento continuo usando telemetría acústica, se registraron los movimientos de 8 tiburones juveniles. Seis individuos mostraron una alta fidelidad a su área de crianza principal, mientras que dos de los tiburones viajaron a otro área de crianza ubicada a una distancia de 6,5km. Todos los animales menos dos neonatos realizaron viajes frecuentes afuera de las bahías protegidas. Estos movimientos de exploración eran o altamente direccionales siguiendo la línea de la costa en búsqueda de otro sitió protegido o en direcciones al azar hacia aguas de mayor profundidad. Debido a la gran variación del tamaño al nacer, no se encontró una correlación entre la extensión del rango de actividad o la tasa de movimiento y la longitud total de los tiburones. Tampoco se evidenció ningún cambio diurno del comportamiento de movimiento, pero los tiburones exhibieron una tasa de movimiento mucho más alta afuera de las áreas de crianza que adentro. Su considerable fidelidad a los áreas de crianza se reflejo en la mayor concentración de los movimientos en áreas núcleos, los cuales tenían una extensión similar para todos los individuos y se ubicaron dentro de las bahías protegidas. Los tiburones juveniles punta negra mostraron una preferencia para aguas someras con sustratos de arena y de arena con rocas. La alta dependencia de las crías de esta especie a áreas de crianza se demostró por una gama de análisis espaciales, por lo tanto nuestros resultados podrían guiar el establecimiento de una nueva zonificación de la Reserva Marina de Galápagos, que protege estas zonas cruciales para la salud de la población de los tiburones punta negra.

Abstract

Short-term movements and habitat preference of juvenile blacktip sharks were studied in nursery areas on San Cristóbal Island, Galapagos. We actively tracked a total of 8 individual sharks. Six blacktip sharks showed high site fidelity to their primary nursery area, while two sharks traveled to another nursery area at a distance of 6,5km. Regular trips outside the nurseries were made by all individuals with the exception of two neonate sharks. These exploratory movements were either highly directional along the coast in search of a suitable adjacent refuge or with random directionality towards deeper water. Due to high variation of body length at birth, there was no correlation between activity space size or swimming speed and total length of the sharks. No significant difference in dial behavior was observed, but sharks had a much higher average swimming speed outside nursery areas than within them. High site fidelity was also reflected by the concentration of movements within similar-sized core areas inside the protected bays. Juvenile sharks had a strong preference for sandy and mixed sand/rock substrates in shallow water. Strong site attachment to nursery areas was evident for the entire sample across a variety of analyses, and may be used as a spatial guide to include nurseries as protected areas in the zoning scheme of the Galapagos Marine Reserve.

Table of Contents

Tables and Figures

Tables: Appendix I

Table 1: Summary of shark movement patterns and home range estimators.

Table 2: Difference of ranks and results for multiple comparisons of habitat preference.

Figures: Appendix II

Figure 1: 95% and 50% kernel density estimators for shark #1.

Figure 2: 95% and 50% kernel density estimators for shark #9.

Figure 3: 95% and 50% kernel density estimators for shark #3.

Figure 4: Habitat map showing the bathymetry of the nursery area.

Figure 5: Habitat map showing the different substrate types of the nursery area.

Introduction

Within the marine realm, elasmobranchs (sharks and rays) represent a key target group for the conservation of marine biodiversity because of their ecological importance as keystone predators and their role as umbrella species for biodiversity hotspots (Hearn et al. 2010; Sergio et al. 2008).

At the same time, these large predators are particularly exposed to a wide range of human induced threats (Baum et al. 2003). The decline of apex predators, such as sharks can have cascading top-down effects on the populations of lower trophic levels, causing changes in the structure of entire marine communities (Baum & Worm 2009; Ferretti et al. 2008). Despite the important role that elasmobranchs play for the health of marine ecosystems, large gaps remain in the scientific information needed to guide their conservation (Baum et al. 2003).

Worldwide, shark populations have been declining at an alarming rate (Dulvy et al. 2008). At regional levels, population declines of some species have been estimated to be as high as 90% and more (Baum et al. 2003). Bull, dusky, and smooth hammerhead sharks for example are suggested to have declined by over 99% in the eastern United States (Myers et al. 2007). Among other causes, shark populations are directly threatened by fisheries seeking to sell shark fins for high profit in Asian markets and indirectly due to a very high by-catch rate in longline fisheries and shrimp trawlers (Cosandey-Godin & Morgan, 2011; Baum et al. 2003). In addition to fishing pressures, elasmobranchs are also threatened by habitat destruction and pollution (Ferretti et al. 2008).

In particular, coastal shark habitats, such as nursery areas are threatened due to their proximity to human populations and the resulting increase in fishing pressure,

habitat degradation and pollution (Knip, Heupel, & Simpfendorfer 2010; Speed et al. 2010). For instance, high mortality rates have been estimated for blacktip sharks (*Carcharhinus limbatus*) when incidentally caught in gillnet fisheries (Hueter et al. 2006). At the same time, the nursery habitats of sharks have a high potential for protection in marine protected areas due to the restricted activity space and high site fidelity of juveniles (Garla et al. 2006).

Acoustic telemetry has become a widely preferred research technique for studying the movements of marine organisms in relation to marine protected areas (Lindholm 2005). Nevertheless, few studies have used this technique to evaluate the effectiveness of existing protected areas in preserving shark populations (Chapman et al. 2005; Heupel & Simpendorfer 2005; Garla et al. 2006).

A considerable number of telemetry studies on elasmobranchs have been conducted relating movement behavior to a wide range of physical and biotic factors (Sundstroem et al. 2001). Several studies have determined movement behavior and site fidelity of juvenile sharks (Garla et al. 2006; Holland et al. 1993; Morrissey & Gruber 1993; Rechisky & Wetherbee 2003), but very few have correlated shark movement behavior to habitat preferences (Franks 2007; Morrissey & Gruber 1993a). Passive acoustic monitoring has been used to investigate residency and home ranges of juvenile Blacktip sharks (*C. limbatus*) in a nursery area in Florida, yet home range estimation was limited by the coverage of the fixed acoustic stations (Heupel, Simpfendorfer, & Hueter 2004). Furthermore, Heupel & Hueter (2002) investigated the relationship between spatial distribution of *C. limbatus* and prey densities found within the nursery, but the effects of other abiotic factors were left unstudied.

Within the Galapagos Marine Reserve (GMR) sharks are generally protected, yet there still exists a large volume of incidental shark by-catch by the local fishery and even illegal fishing directed at sharks. In particular, the juveniles of several shark species are threatened by the local mullet fishery, which takes place in the mangrove fringed bays that also appear to be important habitats for juvenile sharks

(Andrade & Murillo 2002, Llerena 2009). Also, information on the distribution, abundance and movement behavior of juvenile sharks is generally lacking for the Galapagos Marine Reserve (Hearn et al., 2008). In 2009, the Galapagos National Park Services identified 5 nursery areas for San Cristobal Island, all of which lie within zones that are currently open to the artisanal fisheries (Heylings, Bensted-Smith & Altamirano 2002; Llerena 2009).

Our study uses acoustic telemetry to shed light on the home range and site attachment of juvenile blacktip sharks in their nursery areas in order to provide site-specific management tools. We sought to examine possible differences in movement patterns such as swimming speeds among dial periods and different locations within the sharks' home ranges in order to increase our understanding of their behavior in relation to the current zoning scheme of the GMR. Additionally, we investigated the preference of juvenile *C. limbatus* for distinct habitats in order to emphasize the importance of nursery areas within the Galapagos Islands. Finally we quantified the spatial distribution of shark movements that may provide baseline information for the design of no-take fishing zones that protect critical habitats for juvenile Blacktip sharks.

Field Methods

Study Site

Puerto Grande (0°48'4.50"S, 89°28'9.00"W) is a small mangrove-fringed bay with a maximum depth of 8m located on the eastern side of San Cristobal Island, and is considered as the island's most important nursery area (Llerena 2009). The Galapagos Archipelago is characterized by two distinct seasons that are created by the shifts in strength of the different ocean currents hitting the Galapagos platform. The cool, dry season is caused by the cold and productive Humboldt Current, which prevails from June to November. The warm and rainy season in turn is driven by the warm Panama Current and lasts from December to May (Houvenaghel 1984).

Active tracking of juvenile and neonate *C. limbatus* in this study was conducted in two phases. (1) In the transition from the warm to the cold season from April to August 2012 and (2) from November 2012 to January 2013, during the transition from the cold to the warm season. An average of 1 field trip per month was conducted in both periods.

Shark Tagging

Juvenile Blacktip sharks were captured using a 20m long gill net (mesh size 3in) in shallow waters close to mangrove stands (Holland et al. 1993). Upon capture, sharks were handled on a large measuring table aboard the tracking vessel to take standard measurements and apply acoustic transmitters. The sharks' size (total, fork, precaudal and interdorsal length, measured to the closest 0.5cm) weight (to the closest 0.01kg) was recorded and sex was determined. In order to limit variation in movement behavior due to ontogenetic shifts and the possible impact of externally attached transmitters, only neonates (identified by the presence of an open umbilicus or umbilical scar) of a minimum size of approximately 64 cm and juveniles less than 73 cm total length (TL) were used for the tracking study (Barry & Condrey 2008). According to the average published size of neonates of 60,5 cm (Castro 1996; Killiam & Parsons 1989) and the minimum growth rate of 12,5 cm/yr (Barry & Condrey 2008) for juveniles of 0+ and 1+ years for this species, we assumed that all sharks within this range were less than one year of age.

After taking the standard measurements, a hose connected to a bilge pump was placed into the animal's mouth in order to pass fresh seawater through the gills and provide the shark with oxygen during the transmitter application procedure (Garla et al. 2006). Acoustic transmitters (Vemco Ltd., V9, 24 mm length, 2.2 g in water) were externally attached to the sharks' first dorsal fin by adapting the technique used by Wetherbee et al. (2007): Before application, the transmitters were glued into a piece of flexible PCV tube cut in half and secured using plastic zip ties. Absorbable surgical strings (Ethicon, Vicryl 0.0) were used to attach the transmitters with two stitches through the base of the first dorsal fin and loopholes in the extending plastic

tube at each end of the transmitter. The entire procedure, including the time from retrieving the animals out of the net until returning them into the water, lasted an average of 9:45 min, thus minimizing physical stress to the animals. When returning the shark into the water, swimming movements were imitated with the shark until they started to swim on their own (Morrissey & Gruber 1993b).

Active Tracking

Telemetry equipment consisted of a directional hydrophone (Vemco Ltd., VH110) connected to an acoustic receiver (Vemco Ltd., VR100), which was installed on a 4,5m skiff. The acoustic receiver was connected to an 80Ah car battery to keep it powered for extended tracking (Holland et al. 1992). Transmitters had pulse intervals of 1.0 and 2.0 s, a battery life of 7-10 days, and were coded by the manufacturer at frequencies between 63 and 84 kHz. Active tracking of the juvenile sharks was intended to last for 48 hours in order to capture enough movement and possible variability for home range analysis but keep logistics at a reasonable level (Rechisky & Wetherbee 2003; Sundström et al. 2001). A small zodiac was used to exchange the two tracking teams of 3-4 people each every 8 hours and to provide fuel, charged car batteries and food supplies.

In order to keep the position of the boat as close to the animals as possible without interfering with their natural behavior, the tracking vessel was moved towards the sharks when the received signal was less than 80dB, but kept in position at signal strengths between 80-105 dB. Throughout the entire tracking sessions, detailed field notes about shark behavior and boat movement were taken in order to facilitate data processing and interpretation.

Data Analysis

Data Filtering

Location data from tracking was filtered in a 2-step process: First, the raw data was filtered to exclude data points with signal strengths lower than 70dB with exception

of detections that were lower than 70dB due to tracking in very shallow water or obstacles such as rocky outcrops between the tracking vessel and the shark. These exceptions were justified using the detailed chronological field notes.

Secondly, we established a fixed time interval of two minutes in order to filter the remaining data. The regression of empirical measurements of the signal strength versus the distance between the tracking vessel and acoustic transmitters rendered a distance of 49.15 +/-14.5m (r2=0,82; df=8) at 80dB signal strength. Therefore we estimated the maximum error of the recorded geographical positions of the sharks to be within a circle of r=50m (A=7954m^2). This sets the scale at which we can detect changes in behavior or a preference for a certain area. We calculated the time it would take a juvenile *C. limbatus* to cross a circle of r=50m at a maximum sustained swimming speed (U_{ms}) of 1.10 Ls^{-1} (body lengths per second) which was adapted from available data of U_{ms} for juveniles of similar total length of other shark species (Graham et al. 1990). For the sharks tracked in this study with an average body length of 69cm (sd±3.0cm) it would take them approximately two minutes if they were merely passing through the defined area at U_{ms}. This would result in only one position within the area versus two or more positions if the individual would spend more time in an area of the defined spatial scale. Therefore in this study a time interval of two minutes is the best to detect possible preferences for certain areas at the set scale.

Movement Patterns

The geographic positions at two-minute intervals were plotted for each shark using ArcView GIS 10 (Environmental Systems Research Institute Inc., Redlands, California). The rate of movement over ground (ROM, reported in ms^{-1}) was calculated by dividing the distance traveled between successive positions through the time interval. We averaged ROM across all positions and across all nighttime (19:00 - 06:00) and daytime (06:00 - 19:00) positions for each track. The total distance traveled by each animal was calculated by adding the distances between all consecutive positions of each track.

Movements of all sharks that swam into less protected waters outside the nursery (n=5, out of eight individuals tracked) were divided into two behavioral groups. 1) Nursery Restricted Movement (NRM), which includes all movement within the nursery area and 2) Exploratory Behavior (EB), which incorporates all movement made outside the nursery. The Wilcoxon signed-rank test was then used to compare over-ground swimming speed of the two different groups.

Finally, we calculated the linearity index (LI) as a measure of site attachment for each shark using the formula: $LI = (F1 - Fi)/D$. We measured the distance between the last geographic position taken for an individual (Fi) and the start location of the track ($F1$) and then divided it by the total distance traveled by the animal (D). A value of 1 indicates highly directional movement without revisitation of the same sites, versus a highly tortuous track around the same area would result in a value close to 0 (Morrissey & Gruber 1993b).

Home Range Estimators

Since all of the methods used here to describe home range are estimations based on short-term data, we use the term *activity space* instead. The minimum convex polygon home range estimator (MCP) is biased towards an overestimation of activity space due to the inclusion of areas that were not actually visited by an animal (Nilsen, Pedersen, & Linnell 2007). Nevertheless, MCP was chosen as a home range estimator in order to preserve the comparability of our study to others and to include the entire extent home ranges in our analyses (Nilsen et al. 2007). MCP's were calculated using the Geospatial Modeling Environment (GME) 0.7.2, RC2 for ArcGIS 10.0 for the entire track and for all daytime and nighttime positions of each shark (Beyer 2012). Afterwards, each MCP was reduced to remove areas coinciding with landmasses (Morrissey & Gruber 1993b).

Two commonly used kernel density estimators (95% and 50% KDE) were calculated with the GME software using a manually selected fixed smoothing factor (*h*). Fixed KDEs are a good choice if accuracy in the tails of the density estimation is not

needed for statistical comparison. In our case, the fixed manually selected value for *h* best represented core areas of high probability densities across the entire sample (Beyer 2012; Worton 1989).

Linear correlations were performed in order to investigate the effect of shark total length on rate of movement (ROM) and home range (MCP) size before conducting comparisons of these parameters. Due to the low sample size and the high variation of values for MCP and ROM in the nighttime and daytime groups, we conducted a Wilcoxon signed-rank test to test for significant dial change in behavior.

Habitat Preference

Based on the scale at which we can detect the preference for certain areas in this study, we established a minimum size of habitat units (area of circle with r=50m) to measure habitat preferences.

To investigate preferences for different depths, a total of 174 manual depth measurements were taken with a random distribution throughout Puerto Grande bay using a CTD profiler (YSI Inc., CastAway™-CTD). The tide level at the time of each depth measurement in the field was determined using tide level predictions made by the program xtide (based on data provided by the NOAA, National Ocean Service, available online: www.flaterco.com/xtide). Depths were standardized to a mid-tide level of +1m by adding or subtracting the predicted difference. Standardized data points were then interpolated using Arc GIS 10 (Environmental Systems Research Institute Inc, Redlands, California) to create bathymetry maps of the bay with depth categories equal to or larger than the minimum habitat unit size.

In order to map substrate type in the nursery area, we used high-resolution satellite imagery of the study site and verified the substrate types observed in the images by sampling the different types at several depths throughout the bay before creating polygons of equal to or larger than the established minimum habitat unit size in Arc GIS 10.

Using the habitat maps generated by this method, 9 habitat categories (sandy bottom, mixed sand/rock, and rocky substrates at each interval of 0-2, 2-4, 4-8m depth) were established to examine shark preference for the different habitats using Johnson's (1980) resource preference method.

By defining the habitats available to an organism, we automatically assume that the organism has complete knowledge of these habitats to be able to make a choice between habitats (Fauchald & Tveraa 2003). We considered the availability of habitats to the sharks by looking at the data of the smallest neonate shark tracked (CL9, TL=64cm) during this study. We assumed that all sharks in this study had similar knowledge of the availability of all habitats in the nursery used by this individual. Because two of the tracked animals left the nursery during the first night, resulting in a small percentage of detections in the bay we excluded both individuals from the analysis.

The method proposed by Johnson (1980) uses ranks instead of raw data to measure the usage and availability of certain resources by the animals, and thus is less susceptible to over or underestimation of the availability of resources. It also provides the possibility to calculate an average across all individuals and to subsequently test for significance of the preference of certain habitat types versus others (Johnson 1980). We first defined the availability of each habitat category by calculating the percentage of the category in relation to the total area deemed available to the sharks. The usage of that category by an individual was rendered by the number of positions within the habitat as a percentage of the total positions counted in the entire area deemed available. The percentage values were then ranked for both the availability and usage of a habitat. The difference between the rank of usage and the rank of availability then presents the relative preference (negative values) or avoidance (positive values) for a certain habitat. Preference values for a habitat were then averaged across the sample size, and we ran an ANOVA to test the null hypothesis that all habitat categories are equally preferred.

To determine significant differences between all combinations of the 9 habitat types we conducted a multiple comparison with the Tukey post-hoc test.

Results

A total of six young-of-the-year (YOY) and two neonate Blacktip sharks were tracked throughout the study period (n=8, TL= 64.0-72.0cm; Table 1). One older neonate (umbilicus almost closed) was lost 4 hours after its release and was relocated 10 hours later in a nearby nursery. Therefore it was not included in the analysis. The smallest neonate trapped in the gill net during this study had a total length of 60,5cm (total neonates captured during study: n=6, mean TL=64.3cm, s=3,5cm). This reconfirms that all sharks tracked in our study were most likely less than one year of age even if growth rates are very low similar to the lowest reported for this species (12,5 cm/yr; Barry & Condrey 2008). The total tracking duration for each shark ranged from 27 to 45 hours (Table 1). Some of the tracks were interrupted over a short period of time ranging from one to three hours either because of short-term losses of the signal or, in the case of Shark #8, due to the malfunctioning of a car battery. These gaps were subtracted from the overall track duration and were accounted for in the analysis. No effect of the tagging procedure on shark behavior could be observed either in the field or in the resulting data. There was no sign of a general increase or decrease in swimming speeds of juvenile *C. limbatus* after release as compared to changes in behavior reported for both, juvenile hammerhead and adult common thresher sharks (Cartamil et al. 2010; Holland et al. 1993). None of the individuals in this study seemed to avoid proximity to the tracking vessel after release. Shark #4, which was released just before dusk, immediately increased activity, while sharks released during midday exhibited lower activity in the center of the bay.

Movement Patterns

The total distance traveled over ground for all sharks ranged between 13.66km for the shortest and 46.89km for the longest track (mean=28.20km, s=10.3km). Overall rate of movement (ROM) ranged between 0.17 and 0.38ms^{-1} (mean=0.20ms^{-1}, s=0.08ms^{-1}; Table 1). Neither distance traveled nor ROM was correlated with shark total length (r^2=0.124, p=0.05 and r^2=0.004, p=0.05, respectively). All but two individuals (#4 and #7) stayed within the nursery or returned to the nursery after excursions outside the bay and therefore have an extremely low value for the linearity index (mean=0,006, s=0.004), indicating a very strong site fidelity (Morrissey & Gruber 1993b).

Home Range Estimators

Minimum convex polygons (MCP) had a wide range over the sample size (8.76-8.76 km2). Neonate sharks had the smallest MCP values and never moved outside of the bay, but there was no correlation found between TL and MCP size over the entire sample. Shark #3 (TL=68cm) made large excursions outside of the bay during two consecutive nights, resulting in the second largest MCP. Two out of eight individuals (#4 and #7) moved away from the nursery area of Puerto Grande along the coast towards the southeast, resulting in larger MCP's (4.76km^2 and 8.76km^2 respectively). Both individuals displayed highly directional movement during the first night, always staying in shallow water close to shore until reaching a small bay 6,5 km away that had been suggested as a nursery area for *C. limbatus* by Llerena (2009). Throughout the rest of the tracking session, both individuals displayed very restricted movements in the small mangrove fringed bay.

Dial Behavior

Sharks ventured furthest from the nursery area during the night. Individual #3 traveled up to 2.9 km from the shoreline before returning to Puerto Grande. Both sharks that left the study site and traveled to the adjacent nursery moved highly directional for several hours at night. Generally, mean nighttime ROM (0.24ms^{-1},

s=0.12ms^{-1}) seemed to be higher than daytime ROM (0.17 ms^{-1}, s=0.05ms^{-1}), but due to the high variability and low sample size, this difference is not statistically significant (Wilcoxon signed rank test: n=8, w= 8, 0.10 < p < 0.20).

Likewise, the maximum extent of the estimated home range appeared to be generally larger at night (mean MCP=2.25km^2, s=2.60km^2) than during the daylight (mean MCP=0.63km^2, s=1.22km^2), but was not significant (Wilcoxon signed rank test: n=8, w=6, 0.10 < p < 0.20).

Behavioral Differences

Five of the six young-of-the-year Blacktips made explorations outside of their nursery ground. Three of these individuals (#3, #6, #8) displayed high site fidelity (LI= 0,007, 0,002, and 0,01 respectively; table 1) returning to the nursery after longer excursions. Comparison of the exploratory behavior (EB: Mean ROM=0.44ms^{-1}, s=0.09ms^{-1}) outside the sheltered bay versus nursery-restricted movement (NRM: Mean ROM=0.18ms^{-1}, s=0.05ms^{-1}) revealed a highly significant difference in mean speed over ground (Wilcoxon signed rank test, n=5, w=0, p < 0.001).

Kernel Density Estimators

Kernel density estimators of 95% shown in table 1 were highly variable between all sharks, ranging from 0.09 to 1.26km^2 (mean= 0.38, s=0.39), and were strongly correlated with the MCP home range estimator (r^2= 0.626, p<0,02). In contrast, 50% KDE varied little between individuals (examples: figure 1 and 2), and reflected the high density of movement inside the nursery areas within a confined mean area of 0.03 km^2 (s=0.03km^2). Only individual #3 had a higher 50% KDE due to the extended excursions outside the bay, resulting in a highly disbursed distribution of geographic positions over a wide area, with several revisits of the same area approximately 2,4km from the nursery area, which is reflected in the size and distribution of the 50% KDE (Figure3).

Habitat Preference

GIS-rendered habitat maps of substrate type and bathimetry, which served as a basis for the analysis of habitat preferences, are shown in figure 4. Sandy and mixed rock/sand substrates are found at meduim depth in the northern center of the bay and the very shallow northern tip. Rocky substrates are more concentrated in the shallow waters of the southern end and in the mid and deeper water of the bay opening (refer to figures 4 and 5).

Difference of ranks showed the relative preference of each individual seperately for the 9 habitat categories (Table 2). Analaysis of Variance between the mean values of prefernce for each habitat resulted in a highly significant value ($F_{(8,53)}=84.75$, $p<0.001$). Therefore, we can adopt the alternative hypothesis that not all habitat types are equally preferred. Examining the average of the difference of ranks across all individuals, a clear preference for sandy and mixed sand/rock substrates at the shallow water interval between 0 and 2m depth is evident. On the other hand, sharks seem to avoid the sandy patches at water depths between 4 and 8m in the center of the bay opening as well as rocky substrates at shallow (0 to 2m deep) and mid-deep water (2 to 4m; table 2).

Results of the post-hoc test (significance level $p=0.05$) also shown in table 2 revealed no significant difference between the two most preferred habitat types (sandy and mixed substrate in shallow water) which can be found in the most secluded tip of the bay. These two differed from all other habitat types. Rocky and mixed substrates at deeper water (up to -8m) as well as mixed and sandy bottom at mid deep water showed no significant difference of perference, but were different as compared to deep sandy and shallow rocky substrates. Finally, sharks seemed to avoid rocks at mid deep water, which can be found at the southern end of the bay and the center of the bay opening, significantly more than any other substrate (refer to figures 4 and 5).

Discussion

Transmitter Application

The external tag application method proved to be fast and effective. Only one individual lost the attached transmitter before the end of the intended 48 hours of tracking, probably due to improperly tightened surgical knots. Juvenile hammerhead sharks studied by Holland (1993) were force-fed acoustic transmitters. In their tracking study, and a considerable amount of tracks were terminated due to the sharks regurgitating transmitters (Holland, 1993). In short-term tracking studies, we recommend the method used here as opposed to surgical implantation of transmitters, which is believed to have a greater effect on shark behavior. Methods used to avoid the effect of surgery on study subjects include keeping them in captivity for recovery before studying their movements in the wild, or studying their movements for extended periods (Garla et al. 2006a; Morrissey & Gruber 1993b).

One individual tracked in our study was recaptured after a 40-hour tracking session. After the removal of the transmitter, only four faint points where the needle penetrates the dorsal fin could be seen as well as a slight irritation of the skin, where the transmitter had been attached. Furthermore, several sharks with attached transmitters were observed leaping out of the water during feeding activity, suggesting that the transmitters had no effect on their natural behavior (Bigelow & Schroeder 1948).

General Movement Patterns

All juvenile sharks tracked in this study concentrated their movements within Puerto Grande bay or inside another nearby nursery area. The two neonates were the only sharks to never leave the bay to explore less protected areas, resulting in the smallest home ranges for these individuals. Excursions made outside of the bay by individuals who then returned to the same nursery area ranged from a few minutes

up to 10 hours. Two individuals, shark #4 and #7, left the study site during the first night and followed the coastline until they reached another protected bay, which had been identified as a nursery area by Llerena (2009). It took them 05:10 hours and 02:47 hours respectively to cover the 6,5 km distance. After arriving, they displayed a high site fidelity to the sheltered bay during the rest of the track.

The overall rate of movement of juvenile blacktip sharks studied here, was somewhat higher than that reported for juvenile and neonate hammerhead pups of slightly smaller size (Holland et al. 1993). The unusually higher than average ROM of shark #3 can be explained by its extensive nighttime excursions.

The lack of correlation between shark total length and swimming speed or home range is most likely an artifact of the limited overall range of sharks tracked in this study. The great variation of total length found for neonate sharks caught in this study (range: TL=60,5-71,5cm) suggests a high variation of size at birth for the Galapagos subpopulation of blacktip sharks, similar to neonate *C. limbatus* studied on the southeast coast of the United States. For the latter, a total length of 65,3cm was reported for the smallest free-swimming neonate, while the largest embryo carried by a female was 74,2cm (TL). Therefore, our results suggest that an increase in swimming speed and activity space might rather be a result of experience due to age than body length in juveniles less than one year of age. In Florida, use of passive acoustic monitoring had shown that blacktip sharks, which had been tagged as neonates in April expanded their activity space after three to four months, indicating a small-scale ontogenetic shift (Heupel et al. 2004). This increase in activity space and exploratory behavior can possibly be attributed to intraspecific competition and increasing energetic demands (Sims 2010).

Studies on lemon sharks in the Bahamas that included a wider range of age classes (Franks 2007; Morrissey & Gruber 1993b) showed a significant increase of MCP size with increasing body size. Further investigation that incorporates older juvenile individuals could possibly detect an ontogenetic shift in the movement behavior of blacktip sharks. On the other hand, actively tracked juvenile and neonate sandbar

sharks tracked in Delaware Bay, were found to have a very low correlation between body length and MCP, and there was no difference between home range sizes of neonates and juveniles (Rechisky & Wetherbee 2003).

Dial Behavior

Increased activity spaces for blacktip sharks were expected at night compared to daytime movement as found in juvenile hammerhead sharks (Holland 2003). Even though there was a general trend towards increased swimming speed (ROM) and larger activity space (MCP) at night there was no significant difference due to the great variation of both measures within groups of a small sample size. Additional data is needed to investigate the hypothesis of increasing crepuscular or nighttime activity found in many shark species (Barry & Condrey 2008).

The Importance of Nurseries

Data presented here identifies Puerto Grande bay as a nursery area for *C. limbatus*, meeting all three criteria established by Heupel et al. (2007): (1) The high abundance of juveniles reported for this bay in 2009 and during this study distinguishes it from other coastal areas. Knowledge on the absence of juvenile *C. limbatus* from other areas is, nevertheless, based on anecdotal knowledge on the catch rates obtained from local artisanal fishermen (Llerena 2009). (2) Movement behavior of all 8 sharks analyzed shows that blacktips have a high tendency of remaining in or returning to the area. (3) Puerto Grande had been identified as a shark nursery several years before by Llerena (2009) and was reconfirmed in this study.

Analysis of *C. limbatus* movements especially focuses on the hypothesis stated in (2), that the juvenile sharks remain in the study site for prolonged periods or return frequently. Site fidelity reported with the linearity index for juvenile and neonate blacktip sharks remaining within or returning to the same nursery was even lower than for juvenile lemon sharks (mean LI=0,04), which were considered to have a

strong site attachment (Morrissey & Gruber 1993b). The high preference for a limited area was also reflected by the 50% kernel densities, which were very similar for all individuals (with the exception of shark #3) over the entire study period. Both neonate blacktips tracked in this study had much lower 95% KDE areas, compared to young-of-the-year individuals. This trend is in accordance with the results to the 95% and 50% KDEs of juvenile *C. limbatus* studied in Terra Ceia bay, Florida, which were tagged with an open umbilical scar in April. In this study, 95% KDEs increased between June and October, while 50% KDEs stayed very constant over months and across years (Heupel et al. 2004).

One third of the blacktip sharks monitored in Terra Ceia Bay, using fixed receivers within the nursery area remained in the same area for over 100 days, but a large proportion of individuals left the bay within 60 days of monitoring (Heupel 2004). The presented findings suggest that the juveniles leave the nursery area in order to find areas of similar conditions, probably to avoid intraspecific competition (Sims 2010). Juvenile blacktip sharks in Florida left their nursery more frequently with increasing age possibly due to changes in foraging behavior (Heupel 2004). Insight on the movement patterns outside the sheltered nurseries was gained through this study. The high swimming speed, and the lack of a common direction or area of high movement densities all indicate the random and exploratory nature of the excursions into open water. No feeding behavior was observed during these exploratory movements, but on many occasions within the bay. Feeding activity mainly occurred just after sunrise and before and after sunset, as had been suggested in other studies (Barry 2003). Nevertheless, juvenile blacktip sharks have a wide variety of prey items and therefore our observation might be biased towards feeding on small schooling fish (Barry 2003). A fast ontogenetic shift in feeding ecology was proposed by Barry (2003), who found a higher percentage of empty stomachs for neonate versus juvenile blacktip sharks. This could explain the increase in activity space of the young-of-the-year, shifting towards a more generalized diet (Barry 2003). In contrast, predator avoidance seems to be more important for neonates, which have a much higher mortality rate than young-of-the-year older than 15 weeks and are

also believed to be less efficient predators (Heupel & Simpfendorfer 2002; Wourms 1977).

Habitat Preference

The preference of juvenile blacktip sharks for shallow water in the northern extreme of the bay can most likely be attributed to a predator avoidance behavior of both juvenile and neonate individuals. The lack of correlation between the amount of time juvenile *C. limbatus* spent within different areas of a nursery habitat and measured prey densities suggests that predator avoidance behavior is to the main factor driving habitat preference (Heupel & Hueter 2002; Heupel & Simpfendorfer 2005). This could be reflected by the equal preference of shallow sandy and sand/rock-mix bottoms found in this study, which differs from the low usage of rocky bottom at shallow depths. The avoidance of shallow rocks might be explained due to the increased exposure to wave action and/or the proximity to the bay entrance where larger predators might be more common (Heupel & Simpfendorfer 2005). Additionally, water in these areas was observed to be much clearer than in shallow water over sandy and mixed substrates. Hammerhead pups studied by Holland et al. (1993) were supposed to aggregate in turbid water as a mean of predator avoidance. Juvenile blacktip sharks in the Terra Ceia nursery aggregated during daytime and dispersed at night (Heupel & Simpfendorfer 2005). Similarly, aggregations of 5 to 7 individuals were observed around 16:00 and 06:00 over mid-deep sandy and mixed substrates in the center of the bay during this study. Aggregating individuals, displayed a slow circling movement and did not appear to be feeding which supports the hypothesis of Heupel & Simpfendorfer (2005) that this behavior might rather be attributed to a predator avoidance strategy than to foraging. Research on juvenile lemon sharks showed a selection of warmer near shore shallows with a sandy and rocky bottom similar to the results presented here. Nevertheless, these sharks simultaneously preferred areas that had low predation risk and high prey availability, contrasting to the behavior of blacktip sharks (Franks 2007; Heupel & Hueter 2002; Morrissey & Gruber 1993a).

Conclusions

Movement patterns and habitat preference both indicate the importance of nursery areas to *C. limbatus* during their first year. Kernel density estimators and analysis of the movement behavior identify the high concentration of shark movements within a very restricted area, and thus their vulnerability to fisheries inside the protected bay (Heupel & Simpfendorfer 2002). The random direction of exploratory behavior results in low probability densities (95% KDE) and thus limits the likelihood of being caught by artisanal fisheries targeting mullets (Mugilidae) outside the nurseries (Andrade & Murillo 2002). The similar size and location of 50% KDEs across all individuals suggests the use of these core zones throughout the entire year, which would increase the effectiveness of protection measurements for juvenile sharks (Garla et al. 2006). These results offer spatial data that can guide the protection of precisely defined no-take zones, thus avoiding overstressing the local artisanal fisheries. Additional data is currently being generated on the residency time and site fidelity of juvenile blacktip sharks in several nurseries of the Galapagos using passive acoustic monitoring techniques. Furthermore, the identification of nursery habitats of this species is being conducted on the mayor islands of the archipelago by the Galapagos National Park Services (GNPS personal communication). The resulting information can then be combined with the presented findings to design no-takes zones across the entire archipelago that particularly protect the juvenile life-stages of *C. limbatus*. Since neither industrial fishing nor long-line fisheries are allowed in the GMR, the closure of the shark nurseries would ensure the protection of all life stages and their habitats, which would be crucial to ensuring effective conservation management (Kinney & Simpfendorfer 2009).

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Appendix I: Tables

Table 1. Summary of movement patterns and home range estimators of 8 *C. limbatus* tracked.

Shark ID	Sex	Age class	TL (cm)	Hours Tracked (h)	ROM (ms^{-1})	Distance (km)	LI	MCP (km^2)	95% KDE (km^2)	50% KDE (km^2)
1	M	YOY	67.5	45	0.26	38.38	0.002	0.32	0.20	0.04
3	F	YOY	70	35	0.38	46.89	0.007	7.39	1.26	0.10
4	F	YOY	66	27	0.14	13.66	0.464	4.76	0.31	0.01
5	F	NEO	64	42	0.18	27.13	0.009	0.20	0.10	0.02
6	F	YOY	72	45	0.16	27.16	0.002	2.07	0.24	0.02
7	F	YOY	68.5	42	0.18	27.81	0.234	8.76	0.59	0.02
8	M	YOY	72	40	0.17	23.65	0.010	0.88	0.25	0.02
9	M	NEO	71.5	34	0.17	20.89	0.008	0.12	0.09	0.02
Mean:			69	-	0.20	28.20	0.006	3.06	0.38	0.03
SD:			3.0	-	0.1	10.3	0.004	3.47	0.39	0.03

Tab.1. ROM= Rate of movement, LI= Linearity index, MCP= Minimum convex polygon, KDE= Kernel density estimator.

Table 2. Difference of ranks and results for multiple comparisons of habitat preference.

| Habitat	Shark ID						Mean	Conclusion	
	1	3	5	6	8	9			
Sand (0-2)	-4	-3	-5	-4	-6	-4	-4	Preferred	
Mix (0-2)	-3	-5	-4	-4	-4	-4	-4	Preferred	
Rock (4-8)	-1	-2	-1	-1	-2	0	-1	Preferred	
Mix (2-4)	-1	-1	0	-1	0	-1	-1	Preferred	
Sand (2-4)	0	0	0	0	1	0	0	Neutral	
Mix (4-8)	-1	0	1	1	0	0	0	Neutral	
Sand (4-8)	2	2	3	1	2	2	2	Avoided	
Rock (0-2)	3	3	3	3	2	1	3	Avoided	
Rock (2-4)	5	6	3	5	7	6	5	Avoided	

Tab 2. Difference of ranks for each habitat and each individual shark. The conclusion for the entire sample is based on average difference of ranks for all sharks. Results for multiple comparison using Tukey's post-hoc test: Habitat types underlined by the bar of the same color are not significantly different (p<0.05). Habitat types lacking a common bar are significantly different from each other.
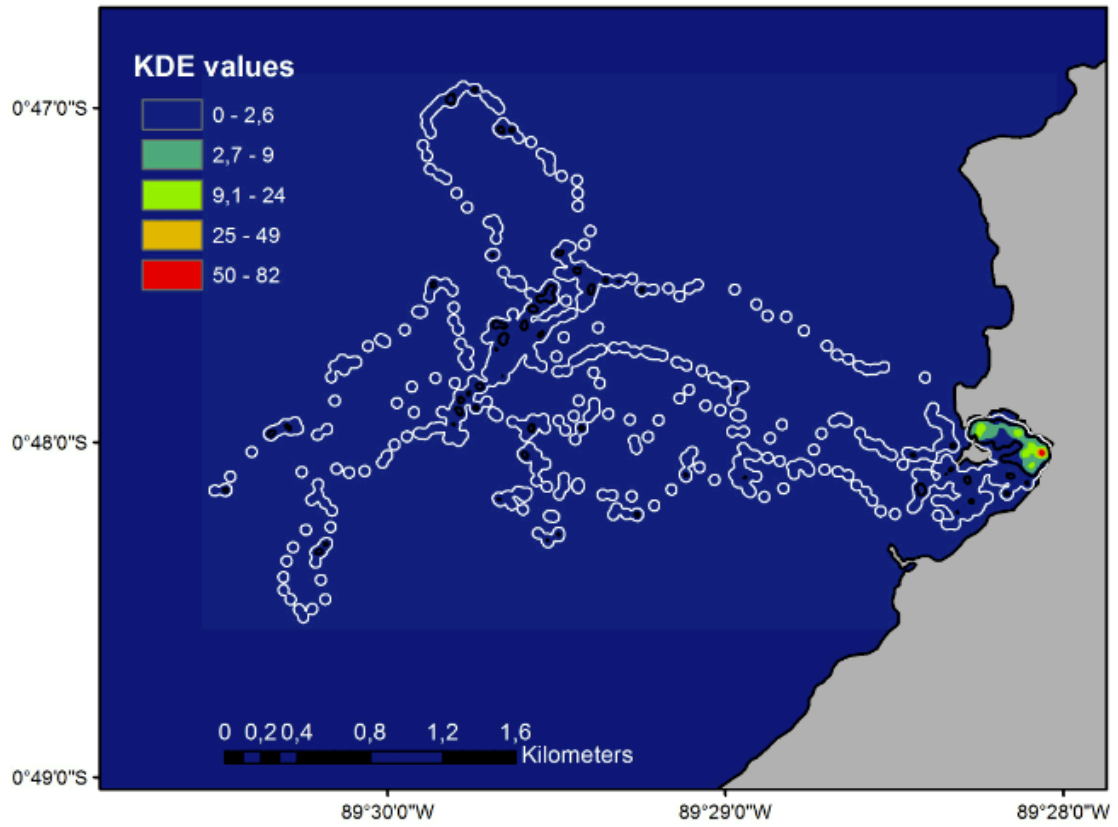
Appendix II: Figures

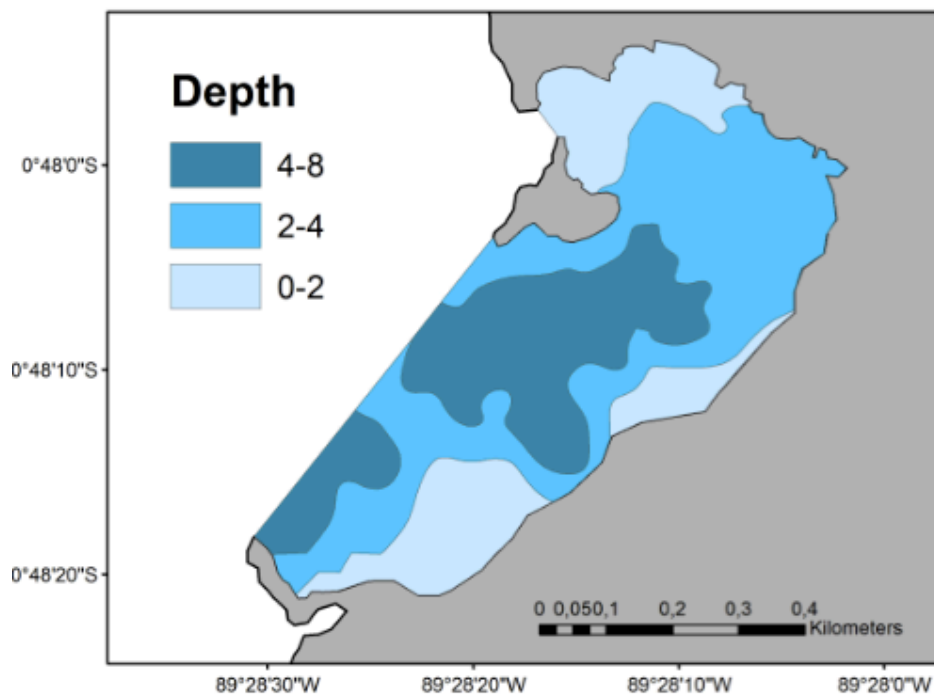**Figure 1.** 95% KDE (white outline) and 50% KDE (black outline) for shark #1.
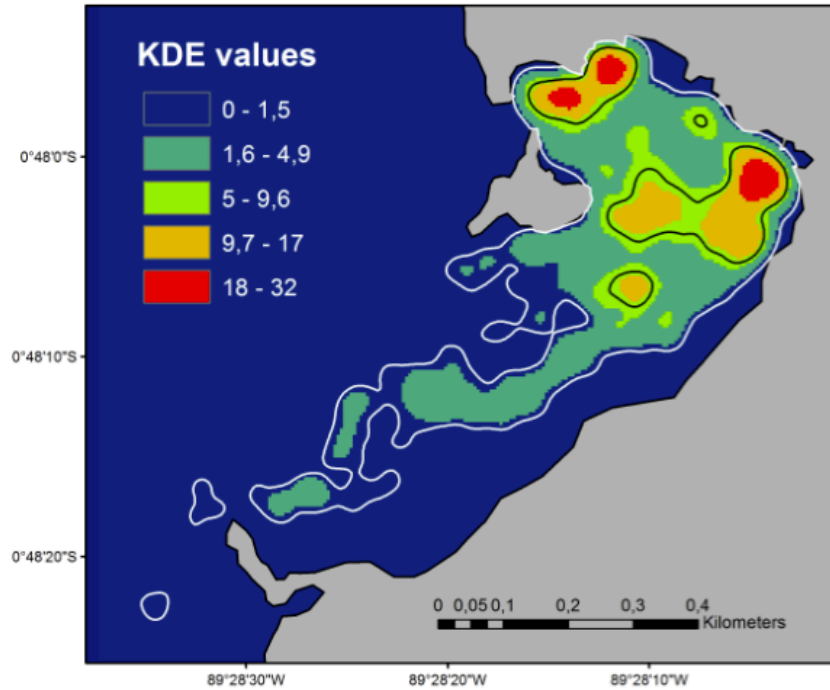
Figure 2. 95% KDE (white outline) and 50% KDE (black outline) for shark #9.
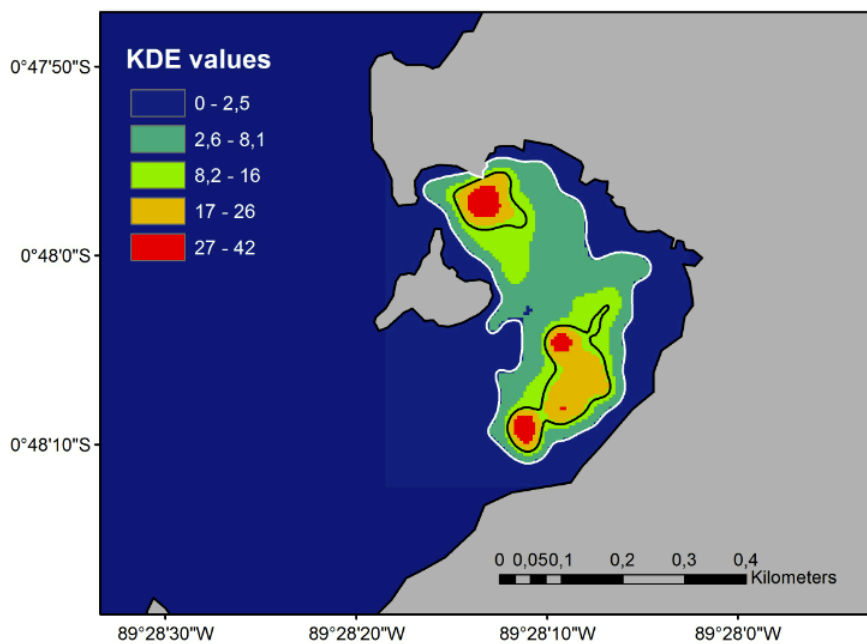
Figure 3. 95% KDE (white outline) and 50% KDE (black outline) for shark #3.

Figure 4. Habitat map showing the bathymetry of the nursery area.

Figure 5. Habitat map showing the different substrate types of the nursery area.