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Diel habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high use area exposed to dive tourism

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ABSTRACT

Knowledge of the diel spatial ecology of wild animals is of great interest to ecologists and relevant to resource management and conservation. Sharks are generally considered to be more active during nocturnal periods than during the day; however, few studies have empirically evaluated diel variation in shark habitat use and how anthropogenic disturbances may influence these patterns. In the western central Atlantic Ocean, tiger sharks (*Galeocerdo cuvier*) are highly abundant in the shallow waters of the Little Bahama Bank, Bahamas. Within the northwest edge of the Bank, there is an area nicknamed "Tiger Beach," where tiger sharks are provisioned year-round at spatially discrete ecotourism dive sites spanning ~1.5 km^2. In this study, we used an array of acoustic receivers encircling an area of 102.4 km^2 to evaluate for potential differences in diel spatial habitat use patterns for 42 tagged tiger sharks at Tiger Beach and the surrounding area. Using tracking data from 24 June 2014 to 13 May 2015, we evaluated spatial and diel patterns of shark activity space, centers of activity, residency and the daily proportion of sharks detected within the array. Sharks were detected during both day and night with no significant diel differences in habitat use metrics across the array, although spatial differences in residency existed. Four sharks accounted for 53.8% of residency data throughout the tracking period, with the majority of sharks primarily entering and exiting the array, except during summer months when the most of the tagged tiger sharks were absent from the array. We also found limited empirical support for hypothesized effects of provisioning tourism on tiger shark habitat use. However, additional research at finer, individual scales, may be needed to better resolve the potential influence of provisioning on tiger sharks at Tiger Beach.

1. Introduction

Given large space and high energetic requirements of apex predators, ecosystems can generally support a relatively low density of these enigmatic animals (Colinvaux, 1978). Thus, identifying high use areas by apex predators and understanding the patterns and drivers of their habitat use is of ecological and conservation significance given widespread population declines of many species (Brook et al., 2008; Ripple et al., 2014) and the potential for trophic cascades (Estes et al., 2011; Ritchie and Johnson, 2009). Such knowledge is particularly important in the case of critical habitats, such as feeding areas or gestation grounds, where individuals may be disproportionately vulnerable to exploitation, or that can conversely serve as effective protected areas (Newton, 2008; Queiroz et al., 2016). Sharks are predators in almost all marine environments, and as a group are highly threatened with overfishing (Worm et al., 2013). While large sharks often migrate over expansive areas, some species also exhibit periods of high residency in space and time (Chapman et al., 2015; Speed et al., 2010; Graham et al., 2016).

It is widely assumed and commonly reported that elasmobranchs are more nocturnally active than during diurnal periods; however, few studies have specifically investigated for potential diel patterns in habitat use (reviewed by Hammerschlag et al., 2017a). There is evidence of increased movements of some sharks during nocturnal and/or crepuscular periods (e.g. increased rate of night movement, Campos et al., 2009; deeper night dives, Howey-Jordan et al., 2013; increased crepuscular horizontal movement Papastamatiou et al., 2015), but these patterns are not ubiquitous (Hammerschlag et al., 2017a). Given

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increased anthropogenic impacts on the oceans, there is growing concern as to the potential impacts of humans (noise pollution, light, fishing) on diel patterns of fish habitat use, and the implications this may have on their life histories and ecological roles (reviewed by Hammerschlag et al., 2017b).

One factor that can impact the spatial behavior of sharks is food provisioning from dive tourism, although evidence for this is mixed and appears to be context-dependent (Brena et al., 2015; Gallagher et al., 2015). Some studies have indeed found evidence of habituation and/or increased residency patterns of elasmobranchs at sites exposed to provisioning dive tourism (e.g. Fitzpatrick et al., 2011), while other studies suggest minimal impacts (e.g. Brunnschweiler and Barnett, 2013). In the Cayman Islands, Corcoran et al. (2013) used acoustic telemetry to compare habitat use patterns of Southern stingrays (*Dasyatis Americana*) at sites where provisioning by tourists was present versus absent. Stingrays from the tourism sites demonstrated a reversal of diel activity, with increased activity during the day and minimal nocturnal movements, compared to nocturnally active stingrays from non-feeding sites. Stingrays at tourism sites also utilized significantly smaller activity spaces, which overlapped with the provisioning sites compared to conspecifics from adjacent habitats (Corcoran et al., 2013). Given that changes in diel behavior resulting from provisioning tourism may impact energetics in large elasmobranch fishes (Barnett et al., 2016) and subsequently alter their fitness, it is particularly important to investigate such effects on individuals during important life-history stages (e.g. gravid) and within critical habitats (e.g. gestation grounds) (Gallagher et al., 2015), especially since dive tourism is of growing socio-economic importance to numerous countries around the world (Gallagher and Hammerschlag, 2011).

In the western central Atlantic Ocean, tiger sharks (*Galeocerdo cuvier*) exhibit frequent use of the northern waters of Little Bahama Bank, Bahamas (Hammerschlag et al., 2012; Fig. 1). The area is dominated by female tiger sharks of mixed age classes (Sulikowski et al., 2016). Young female tiger sharks may use the area as a refuge to reach maturity, without the threat of harassment by male sharks, whereas gravid sharks may use the area as a gestation ground, benefiting from year-round calm warm waters that accelerate embryo development (Sulikowski et al., 2016). The northwest edge of the Bank is a popular location for shark diving tourism, nicknamed “Tiger Beach”, where tiger sharks are provisioned year-round by dive-tourists during the day at spatially explicit dive sites spanning an area of 1.5 km^2. Satellite tracking of tiger sharks from the area has suggested that these dive tourism activities do not significantly impact the long-term migration patterns of the tracked animals (Hammerschlag et al., 2012, 2015); however, the potential influences of the tourism activities on diel habitat use patterns of tiger sharks within Tiger Beach and adjacent areas of Little Bahama Bank remains unknown.

Given a general lack of knowledge on diel shark habitat use patterns (Hammerschlag et al., 2017a), paired with a high density of large tiger sharks at Tiger Beach and adjacent area (Hammerschlag et al., 2012), potentially for reproductive purposes (Sulikowski et al., 2016), the primary objective of the present study was to evaluate temporal variability in the spatial patterns of tiger sharks in this area. Moreover, since tiger sharks in the area are exposed to spatially explicit provisioning dive tourism, a second objective was to evaluate if diel habitat use patterns of sharks differed at the dive tourism sites compared to adjacent locations where dive tourism is absent.

To accomplish these two objectives, we used passive acoustic telemetry to test the null hypothesis [H0] that tiger sharks exhibit uniform patterns of spatial habitat use by day and night. Additionally, we tested the following alternative hypotheses: [H1] sharks are more active during night than by day as generally assumed, exhibiting larger nocturnal space use patterns as have been reported for some elasmobranch species (e.g., Papastamatiou et al., 2015); [H2] sharks exhibit increased use of dive tourism sites compared to adjacent areas by both day and night as has been found for elasmobranchs exhibiting habituation/conditioned responses to provisioning tourism sites (e.g. Corcoran et al., 2013) or [H3] sharks exhibit increased use of dive sites compared to adjacent areas only by day (the time in which provisioning occurs) (e.g. Fitzpatrick et al., 2011). We acknowledge that due to the nature of the study system, it is not feasible to experimentally manipulate provisioning activities by dive operators, and accordingly evaluate responses of sharks. Similarly, shark movement data were not available prior to tourism or provisioning commencing. Therefore, we cannot fully resolve the effects of tourism provisioning on tiger shark behavior. However, our experimental approach can provide evidence to support or refute patterns of tiger shark habitat use consistent with known tourism effects on elasmobranch behavior [H2, H3], providing insights into possible tourism effects and avenues for future directed research.

2. Methods

2.1. Study area and Tiger Beach

The shallow banks of the Bahamas Archipelago are mostly composed of underwater carbonate platforms. The Little Bahama Bank extends off Grand Bahama Island. The environment is a shallow (average 5 m deep), and mostly homogenous sand flat, with irregular seagrass patches, and infrequent small patches of coral.

The area known as Tiger Beach is frequented by shark diving operations, and is located within the northwest edge of the Little Bahama Bank (26.86° N, 79.04° W). Here, up to four dive operators may concurrently conduct tiger shark diving activities spanning an area of 1.5 km^2. Tiger shark diving occurs primarily during the day, where sharks are attracted to divers using submerged crates of minced fish (i.e. chumming). During diving activities, tiger sharks are also irregularly fed fish carcasses (Hammerschlag et al., 2012).

To evaluate patterns of tiger shark habitat use in the study area, we used passive acoustic telemetry, whereby sharks were tagged with acoustic transmitters and tracked via an array of stationary hydrophones (detailed in Sections 2.2 and 2.3 below).

2.2. Shark capture and acoustic tagging

Tiger sharks were captured using standardized circle-hook drumlines as described in Gallagher et al. (2014). Briefly, the gear consisted of a submerged weight base tied to a line running to the surface by means of an attached, inflatable buoy float, with a baited circle hook attached to the weight. Once hooked, each shark was slowly brought to the boat and restrained on a dive platform partially submerged in the water. To facilitate respiration, a hose was immediately inserted into the shark's mouth that actively pumped water over the shark's gills. This capture and handling method was selected to promote shark vitality and reduce stress levels during sampling (Gallagher et al., 2014). For each individual captured, sex was recorded and total length (TL) was measured to the nearest cm over a straight line along the axis of the body.

Acoustic transmitters (Vemco V16, 69 kHz, 68 × 16 mm) were surgically implanted into the intracoelomic cavity of sharks through a small incision in the abdominal wall above the pelvic fins. After tag insertion, the incision was closed with several simple interrupted nylon sutures. Twenty tiger sharks were tagged between 18 and 20 October 2013, thirteen sharks were tagged between 12 and 14 May 2014, and nine sharks were tagged between 14 and 16 November 2014 (Table 1). Sharks were then released at their location of capture. When sharks came within detection range of the hydrophones (described below), the tag number and time of detection was recorded on the corresponding receiver.

2.3. Telemetry array

To record the movements of acoustically tagged sharks, an array of

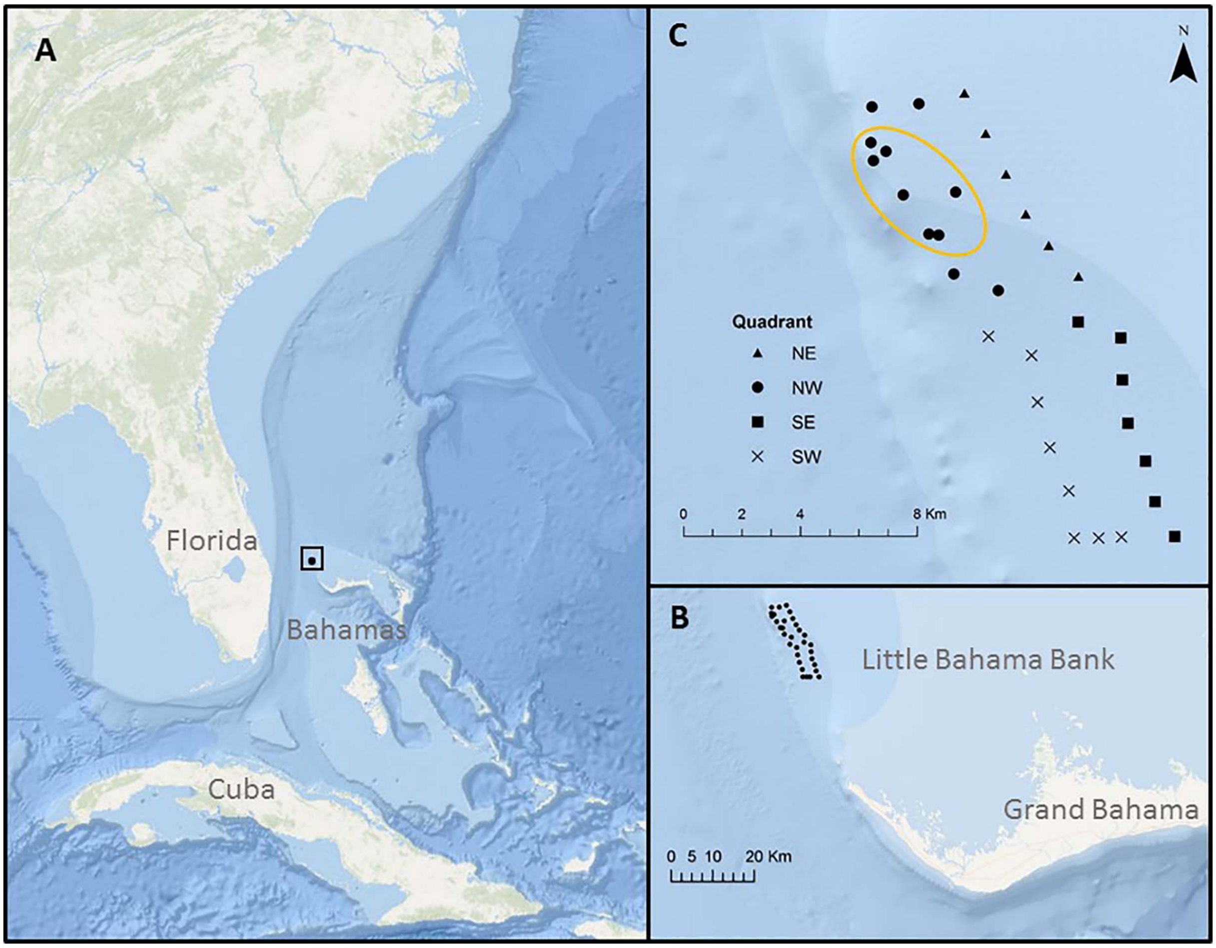

Fig. 1. (A) The location of the study area in the northern Bahamas indtified with a black square and positioning of the telemetry array on the northwestern edge of the Little Bahama Bank (B), off Grand Bahama Island. The 32 recievers are arranged in a roughly 12 km × 3 km rectangle (C) with the western line inshore of the bank edge. Symbols denote the designated quadrant of the telemetry receivers. The NW quadrant is known as Tiger Beach. Receivers nearest the primary shark provisioning dive sites are circled in orange.

32 hydrophones were deployed in the study area (Fig. 1). We used VR2W receivers (VEMCO Division, AMIRIX Systems), which are single-channel, fully submerged, omnidirectional battery-operated hydrophones designed to detect uniquely coded acoustic transmissions from animals tagged with compatible transmitters (Lacroix and Voegeli, 2000). The 32 receivers were spaced at approximately 750 m intervals, and were deployed such that they formed a ca. 12 × 3.2 km rectangle covering the northwestern area of Little Bahama Bank, with the western line of receivers deployed along the inshore edge of the Bank following the depth contour (mean depth ± S.D. = 6.32 ± 0.94 m). In addition, receivers were also placed at the four primary sites used by dive tourism operators for shark diving activities located within the northwest portion of the array (i.e., the area known as Tiger Beach, Fig. 1).

To anchor receivers into the substrate, we used a hardware and anchoring system modified from Reyier et al. (2014). Briefly, VR2W data loggers were secured to custom-built stainless steel units that were mounted to a steel anchor deeply embedded in the seafloor. The mounting hardware was protected from electrolytic corrosion by a large sacrificial zinc anode attached near the bottom. The receivers were secured, such that the mounting hardware and zinc anode were below the hydrophone to prevent any potential acoustic shadowing. In areas where sand and/or gravel were at least 73 cm deep, the anchor was screwed securely into the sea floor. In areas where there was insufficient sand and gravel, the loose material was excavated to expose the limestone rock substrate and a hole was drilled into the substrate and secured with underwater epoxy. The bottom 25 cm of the anchor shank was driven into the hole and bonded with the epoxy. All 32 receivers were in place by 25 June 2014.

Diurnal range testing revealed a detection radius of 1.6 km, suggesting that the receivers (placed 750 m apart) maintained full coverage along the perimeter of the receiver placement. Comparable nocturnal range testing was not done, but given the oligotrophic waters and lack of any obvious day-night differences in sources of interfering environmental noise (e.g., snapping shrimp, boat traffic), acoustic detection was unlikely to differ markedly between night and day. Receivers were retrieved on two occasions (9/10 November 2014, and 12/13 May 2015) in order to download the data.

2.4. Data analyses

Given acoustic technology is subject to code collisions (two or more coded transmissions collide and produce an incomplete or incorrect code) and environmental noise, the data were checked and filtered prior to analysis. Specifically, data were filtered to remove non-tiger shark tag codes and incomplete tag-to-receiver transmissions that may have resulted from code collisions or environmental noise (Heupel et al., 2006). Furthermore, a coded transmission was only considered valid if accompanied by one or more identical coded transmissions, i.e., ≥ 2 detections/receiver were required before a tagged animal could be considered present at a receiver. Any time drift on receivers was corrected using the software program VUE (VEMCO Division, AMIRIX Systems). Data that were recorded simultaneously on two or more receivers were treated as a single detection, whereby the first detection in the database was retained and the others discarded. Once filtering and quality control measures were taken, data were imported into the R Statistical Environment (R Core Team, 2016).

Table 1
Details on the tiger sharks tagged at the study area within Little Bahama Bank, Bahamas. Presented are the total residency events as well as minium, maximum and median residency time for each sharks from 25 June 2015 to 13 May 2015. Shark data in the table are first sorted by sex and then by total residency events. Residency time is in minutes (min.).

ID	Tagging date	PCL	FL	TL	Sex	Total # residency events	Median residency time (min)	Min. residency (min)	Max. residency (min)
26755	18-Oct-13	243	271	322	F	943	9.6	0.6	579.6
26750	17-Oct-13	200	223	273	F	601	11.4	0.6	150.0
26753	18-Oct-13	248	281	331	F	518	9.0	0.6	230.9
26756	18-Oct-13	225	253	325	F	450	11.4	0.6	415.0
24659	14-May-14	277	300	366	F	370	7.1	0.6	143.0
26760	19-Oct-13	290	313	380	F	298	8.3	0.6	109.0
26761	18-Oct-13	242	273	344	F	246	10.5	0.6	327.5
26754	19-Oct-13	190	212	260	F	208	10.7	0.7	81.8
26764	17-Oct-13	303	323	378	F	198	8.8	0.6	82.8
24645	12-May-14	188	210	262	F	195	9.8	0.6	81.9
26766	20-Oct-13	281	308	369	F	181	7.3	0.7	148.0
24,658	14-Nov-14	259	282	336	F	180	7.2	0.8	100.4
24652	13-May-14	294	324	383	F	128	5.2	0.6	48.2
23343	16-Nov-14	267	294	355	F	75	11.0	0.7	141.3
24656	13-May-14	272	297	358	F	64	8.7	0.9	44.4
24662	13-May-14	194	210	264	F	53	13.0	1.3	61.6
24657	15-Nov-14	259	282	342	F	52	11.5	1.2	55.0
24644	12-May-14	296	311	349	F	51	7.6	0.8	32.5
24654	12-May-14	203	223	273	F	46	14.4	1.0	122.1
24651	13-May-14	175	192	242	F	45	9.3	0.7	56.3
26767	20-Oct-13	272	298	357	F	43	8.1	1.5	44.7
24648	12-May-14	275	309	356	F	40	12.1	1.0	51.5
24647	12-May-14	152	174	213	F	32	13.1	0.7	41.9
24650	12-May-14	274	292	352	F	16	4.6	1.4	28.1
26757	18-Oct-13	281	317	373	F	15	3.4	1.2	11.1
24646	12-May-14	246	266	324	F	14	3.4	0.9	33.4
26768	20-Oct-13	273	295	357	F	12	8.2	2.2	24.0
23341	16-Nov-14	207	231	283	F	9	15.3	3.1	43.0
26758	19-Oct-13	278	306	357	F	8	15.3	3.4	39.0
24653	13-May-14	226	247	301	F	6	8.2	1.2	18.1
26751	17-Oct-13	233	259	307	F	2	5.1	1.1	9.0
26762	19-Oct-13	265	295	360	F	1	34.7	34.7	34.7
23346	16-Nov-14	169	182	236	F	0	NA	NA	NA
26749	17-Oct-13	182	203	245	F	0	NA	NA	NA
26752	18-Oct-13	266	293	353	F	0	NA	NA	NA
26759	19-Oct-13	286	315	368	F	0	NA	NA	NA
26763	19-Oct-13	222	244	292	F	0	NA	NA	NA
23340	14-Nov-14	NA	NA	356	F	240	10.2	0.7	414.2
26765	20-Oct-13	269	300	356	M	171	5.0	0.6	75.6
24649	15-Nov-14	99	111	144	M	16	27.8	4.2	81.4
24643	16-Nov-14	264	289	346	M	13	3.6	0.6	10.5
23345	14-Nov-14	263	290	352	M	3	11.0	8.3	11.4

Diel period (day/night) was calculated based on the daily sunrise and sunset times from the nearest town to the study area, Freeport, Grand Bahama Island. Day was considered as the period between 1 h after sunrise and 1 h before sunset. Likewise, night was considered the period between 1 h after sunset and 1 h before sunrise. We excluded crepuscular periods due to relatively small contribution of data (∼14% of detections for sunrise and sunset, respectively) which would have also resulted in an unequal sampling period and data variance.

To monitor for spatial patterns in habitat use, receivers were designated into four distinct quadrants based on the arrangement of the telemetry array and the locations of the shark dive operations. These quadrants included the Northwest (NW, characterized by edge of the reef drop-off and the primary site of dive tourism activities, eleven receivers; Tiger Beach), Northeast (NE, characterized as the northern sand flat, six receivers), Southeast (SE, characterized as the southern sand flat, seven receivers), and the Southwest (SW, characterized by the southern reef drop-off, eight receivers). Given an unequal number of receivers per quadrant, we tested for correlations between total residency versus the number of receivers and the daily proportion detected, and found no statistical differences. Therefore, we were able to subsequently compare shark habitat use patterns between quadrants.

2.5. Habitat use metrics and data analyses

To facilitate hypothesis testing, we calculated the following four metrics of shark habitat use within the array: (1) activity space, (2) centers of shark activity, (3) daily proportion detected and (4) residency (total residency and total daily residency). Calculations of these habitat use metrics are described in the following paragraphs. Metrics of activity space and centers of activity were calculated across all sharks detected, separately by day versus night. The daily proportion detected and residency metrics were calculated across sharks, separately within each quadrant, during both day and night. Metrics and associated data analyses were only calculated for sharks when the entire set of 32 receivers were in place beginning 25 June 2014 and ending in 13 May 2015 when the last data were downloaded.

Activity space (in hectares, ha) within the receiver array was estimated using 95% minimum convex polygons (MCPs) calculated from the R package adehabitatHR (Calenge, 2006). For this analysis, tagged animals were required to be detected on a minimum of five unique receivers within the specified diel period. MCPs were generated for each shark individually by day/night.

Center of activity (density per ha) was calculated by day/night period for each individual following methods described by Simpfendorfer et al. (2002). The resultant centers of activity were plotted as point densities (circle radius = 1 km) in ArcGIS version 10.1

(Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA). The daily proportion detected within a given quadrant by day or night was calculated as the number of sharks detected relative to the number of tagged sharks within each 24 hour period.

Tiger shark residency was estimated using the R package VTrack (Campbell et al., 2012). Here, a residency event at a given receiver began when a tagged animal was recorded ≥ 2 times and terminated when 30 min had passed without a detection at the given receiver, or the animal was detected on another receiver. A 30-minute period was considered ample time for a transient tiger shark to swim outside the detection range of one receiver.

To evaluate our null hypothesis of uniform distribution in diel habitat use [H0], we tested for differences in the daily proportion of sharks detected within each quadrant by day and night. To accomplish this, the daily proportion detected in a particular quadrant per diel period was modeled using a generalized linear model (GLM), where the outcome was assumed to be a binomial distribution. The model included diel period (day versus night), quadrant, and their statistical interaction (diel period × quadrant) as fixed factors.

Additionally, we also tested for differences in tiger shark residency within each quadrant by day and night. Tiger shark residency was analyzed using normally-distributed linear mixed models (LMM). Here, total residency (average total hours resident throughout the tracking period per shark) and total daily residency (average total hours resident per day per shark) was calculated for each quadrant and diel period. Fixed factors included quadrant, diel period and their interaction. Transmitter ID was included as a random intercept to account for variation in residency from individual tiger sharks. Residency was $\log_e^{-}$ transformed to obtain homogeneity of variance. If sharks were exhibiting space use behavior consistent with [H0] then we would expect to find no significant differences in either the daily proportion detected or residency patterns within each quadrant and/or between day and night.

To examine the first alternative hypotheses of increased horizontal movement and larger space use at night [H1] we tested for statistical differences in activity space by day and night. Activity space (ha) within the array was analyzed using a bivariate normally distributed LMM. The model included diel period (day versus night) as a fixed factor and transmitter ID as a random intercept to account for the variation among individuals in movement. Quadrant was not included in this analysis because activity spaces often extended into multiple quadrants within the telemetry array. Activity space size was $\log_e$-transformed to obtain homogeneity of variance in the residuals. If sharks were exhibiting space use behavior consistent with [H1] then we would expect find significantly larger (more dispersed) activity space at night compared to day.

To evaluate both the second and third alternative hypothesis of either [H2] increased use of dive tourism sites during both day and night, or [H3] increased use of dive tourism sites only during the day when provisioning occurs, we tested for significant spatial and temporal differences in the daily proportion detected by quadrant and diel period using a GLM as described above. Likewise, we also tested for differences in tiger shark residency metrics within each quadrant by day and night using a LMM as described above. Both models included diel period (day versus night), quadrant, and their statistical interaction (diel period × quadrant) as fixed factors as well as transmitter ID as a random intercept to account for potential variation from individual tiger sharks. To investigate for any linear relationship between residency at a receiver and its distance from the dive sites, we regressed average shark residency per receiver against its distance to the nearest dive site. To test for potential diel differences in patterns of residency versus distance from dive sites, we applied analysis of covariance (ANCOVA) to these data. Finally, we graphically compared centers of shark activity by night and day. If sharks were exhibiting space use behavior consistent with [H2] then we would expect to find that the daily proportion detected and their residency patterns would be significantly higher by both day and night in the NW quadrant of the array (Tiger Beach) where dive tourism occurs as compared to the other quadrants. Similarly, average residency per receiver should increase with proximity to dive sites by day and night. Likewise, centers of activity should be focused over the NW quadrant by both day and night as compared to the other quadrants. If sharks were exhibiting space use behavior consistent with [H3] then we expect to find that the daily proportion detected and their residency patterns would be significantly higher only by day in the NW quadrant as compared to the other quadrants. Similarly, average residency per receiver should increase with proximity to dive sites during the day, but not during the night. Likewise, centers of activity should be focused over the NW quadrant only during the day as compared to the other quadrants.

Backwards model selection and log-likelihood tests were used to determine the statistical significance of interactions between the main effects of diel period and quadrant in GLM and LMM (Chambers et al., 1992). Under this model selection strategy, insignificant terms were dropped beginning with interactions (Zuur et al., 2009). Binomial GLMs were validated by checking the residuals for over-dispersion (i.e., greater variance than is expected by a statistical model; Bolker et al., 2009) and by plotting the Pearson and deviance residuals of each covariate and against the fitted values. Gaussian LMMs were validated by plotting the normalized residuals against each covariate and the fitted values. Model fit for LMMs was estimated following Nakagawa and Schielzeth (2013). Daily proportion detected and residency data were modeled using the R packages lme4 and nlme, respectively (Bates et al., 2011; Pinheiro et al., 2014).

3. Results

3.1. Shark detections

During the tracking period, which began on 25 June 2014 (32 receivers deployed) until 13 May 2015 (32 receivers downloaded), a total of 55,847 detections were recorded from 39 of the 42 tagged tiger sharks (Table 1). During this period, 37 tiger sharks recorded at least one residency event, defined as occurrence of a tagged animal being recorded ≥ 2 times and up to when 30 min had passed without a detection at the given receiver or the animal was detected on another receiver (Table 1).

3.2. Daily proportion detected & shark residency

The daily proportion of detected sharks varied seasonally, decreasing in all quadrants during the summer months (Fig. 2). Rarely was more than one tagged animal simultaneously detected within the array between June and October 2014 (median = 1, range = 1–3). For any day/night period, total detections were highest in the NW quadrant, where the most receivers were deployed for a given quadrant (11 receivers, 34.8% of the data). However, backwards model selection indicated the interaction between diel period and quadrant was not significant in the GLM (*L-Lik* = 0.118, d.f. = 3, $P = 0.99$, Table S1). Differences in the daily proportion detected were small and non-significant (Fig. 4). The largest difference in the daily proportion detected occurred between the NW quadrant during the day (mean = 0.046, [0.043, 0.050, 95% CI]) and the SW during the night (mean = 0.036, [0.032, 0.039, 95% CI], Fig. 2).

The majority of residency data (53.8%) were generated from four sharks (#26755, #26750, #26756, #26753). The fitted model for tiger shark total residency did not contain a significant interaction between diel period and quadrant (*L-Lik* = 5.718, d.f. = 1, $P = 0.127$). Model fit was estimated at 0.04 and 0.26 for marginal and conditional R^2, respectively. The fitted values showed that tagged animals spent significantly more cumulative time per receiver in the NE quadrant (Fig. 4). No overall differences were evident between day and night total residency across all quadrants in the array (Fig. 4, Table S1).

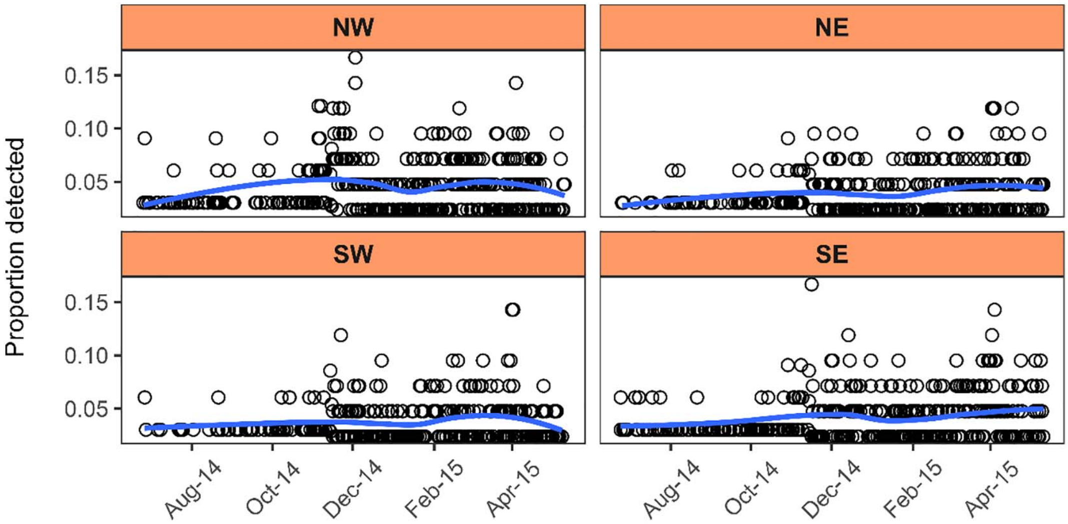

Fig. 2. Proportion of tagged tiger sharks detected daily in the acoustic array. Proportions are based on the known number of tagged tiger sharks on a given day. Points are fitted with a Loess smoother. Values on the X-axis indicate calendar month and year (YY).

The model for total daily residency per receiver contained a significant interaction (*L-Lik* = 38.8, d.f. = 3, $P < 0.001$). Model fit was 0.05 and 0.12 for marginal and conditional R^2, respectively (Table S1). This model illustrated that average total daily residency per receiver was highest in the NE quadrant by both day and night, except for values in the NE quadrant were comparable to those in the NW quadrant during day (Fig. 5). Additionally, total daily residency was significantly higher during the day versus the night in the NW quadrant, whereby the model estimated tiger shark daily residency per receiver was 1.5 times greater during the day (12.5 min, [11.6, 13.6, 95% CI]) than at the night (8.4 min, [7.6, 9.2, 95% CI], Fig. 5, Table S1).

Linear regression between average residency per receiver and its distance from the nearest dive site revealed no significant relationships by day ($R^2 = 0.09$, $P = 0.08$) or by night ($R^2 = 0.0001$, $P = 0.97$; Fig. 6). Moreover, ANCOVA revealed no diel differences in patterns of residency per receiver versus distance from nearest dive site ($P = 0.33$).

3.3. Activity space & center of activity within array

Activity space estimates (95% MCP) within the array could be generated from 34 individuals that provided ≥ 5 detections at unique receivers during either the day ($n = 105$ MCP estimates) or night ($n = 90$ MCP estimates) in the telemetry array (Table 2). However, the majority of MCP estimates (60.1%) came from five individuals during both the day and night (#26755, #26750, #26753, #24659, #26756; Table 1), and of these, three sharks (#26755, #26750, #26753) accounted for 46.7% of all MCP estimates (Fig. 7). Ten of the 34 sharks provided only a single activity space estimate for either the day or night during the monitoring period. There were no significant differences in the activity space areas at night (median 418.6 ha, min. = 3.87 ha, max. = 3715 ha) versus during the day (median 460.8, min. = 3.87 ha, max. = 2841.4 ha; paired *t*-test, 33.4, $t172 = 0.368$, $P = 0.71$, Table S1). Random effects accounted for 2.4% of the variability observed.

Table 2
Summary statistics for 95% minimum convex polygon estimates of activity space (ha) from tagged tiger sharks ($n = 34$) that provided ≥ 5 detections at unique receivers during either the day or night in the telemetry array.

Summary stat	Day: area (ha)	Night: area (ha)
Min	3.87	3.87
1st quartile	208	208
Median	460	418
Mean	607	653
3rd quartile	781	889
Max	3841	3715

Tiger shark daily centers of activity were produced for 34 animals over 228 days beginning 24 June 2014. Although 16 sharks provided ≥ 10 point estimates, four sharks were responsible for a large proportion of these (48.1%, 399/830). Estimates were generated during the day (365 estimates from 32 sharks) and night (417 estimates from 30 sharks). A high point density per hectare was observed in both the NW and NE quadrant during day and night (Fig. 3). Generally, the centers of activity tended to be slightly shifted to the northeastern side of the array at night (Fig. 8).

4. Discussion

Our results did not support our null hypothesis that tiger sharks exhibit uniform patterns in diel spatial habitat use within the study area. While we did not find any differences in the daily proportion of shark detected or in their residency patterns by diel period throughout the array, there was a significant difference in the daily proportion of sharks detected over the study period, and in shark residency patterns within quadrants, with a significant interaction between quadrant and diel period. We do, however, caution extrapolating our general findings to all tiger sharks in the study area of the Little Bahama Bank given that ~50% of residency data came from four individuals. The majority of sharks left the array during the summer months; rarely was more than one tagged shark detected within the array between June and September. Based on previous satellite tagging of tiger sharks from south Florida and the northern Bahamas, including Tiger Beach, most tiger sharks migrate north to coastal waters off the US eastern seaboard between Georgia and North Carolina during summer months, possibly to feed on aggregations of nesting loggerhead sea turtles (*Caretta caretta*; Hammerschlag et al., 2015).

Data on shark activity space were inconsistent with our first alternative hypothesis of increased nocturnal horizontal movement or larger space use within the array at night. During both the day and night, tiger sharks frequently moved throughout the receiver array which enclosed an area of 102.4 km^2. Sharks did not exhibit larger space use in the array at night; they had relatively large (mean > 600 ha) and comparable activity spaces by day and night within the array (Table 2). This finding is consistent with a recent review of studies on elasmobranch behavior during nocturnal and crepuscular periods which found limited evidence for increased activity at night despite this common assumption (Hammerschlag et al., 2017a). While some sharks are indeed more active during dark periods (e.g., Campos et al., 2009; Howey-Jordan

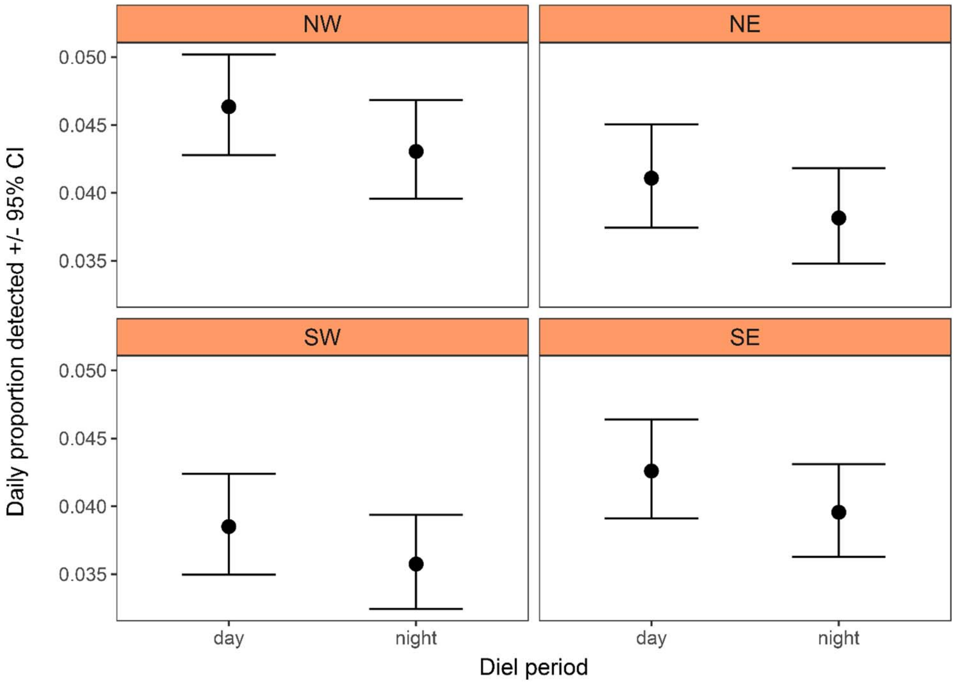

Fig. 3. Fitted values and 95% confidence limits for the daily proportion of tagged tiger sharks detected by diel period on receivers designated within the four quadrants of the array.

et al., 2013; Papastamatiou et al., 2015; Fallows et al. 2016), our results support the notion that generalizations about increased elasmobranch activity during dark periods are unsupported and investigations of nocturnal shark behavior is an area of much needed further research (Hammerschlag et al., 2017a, 2017b).

Our analysis also did not reveal any significant differences in the daily proportion detected in the NW quadrant during day and night, leading us to reject our second alternative hypothesis. Similarly, analysis of total residency and total daily residency also failed to support this [H2], as the highest residency patterns (both total and daily residency) during day and night occurred within the NE quadrant of the array where dive tourism is absent. Likewise, centers of activity were not restricted to the NW quadrant by both day and night, which would be expected if tourism caused habituation or conditioning of tiger sharks to the dive sites, as has been found in the case of Southern Stingrays conditioned by provisioning tourism (Corcoran et al., 2013).

Consistent with our third alternative hypotheses [H3], total daily residency of tiger sharks were similar during day and night in all quadrants, except for the NW, where sharks spent significantly more time during the day compared to night. However, total daily residency was highest in the NE quadrant where dive tourism was absent. Patterns of total residency and the daily proportion detected were also inconsistent with our third alternative hypothesis. While, sharks did exhibit among the highest mean values of daytime residency at the receivers closest to the tourism sites (Fig. 6), daytime residency was also high at the receivers farthest away from the provisioning sites. Similarly, while centers of activity clustered within the NW quadrant during the day, they were not restricted within the NW quadrant compared to the other

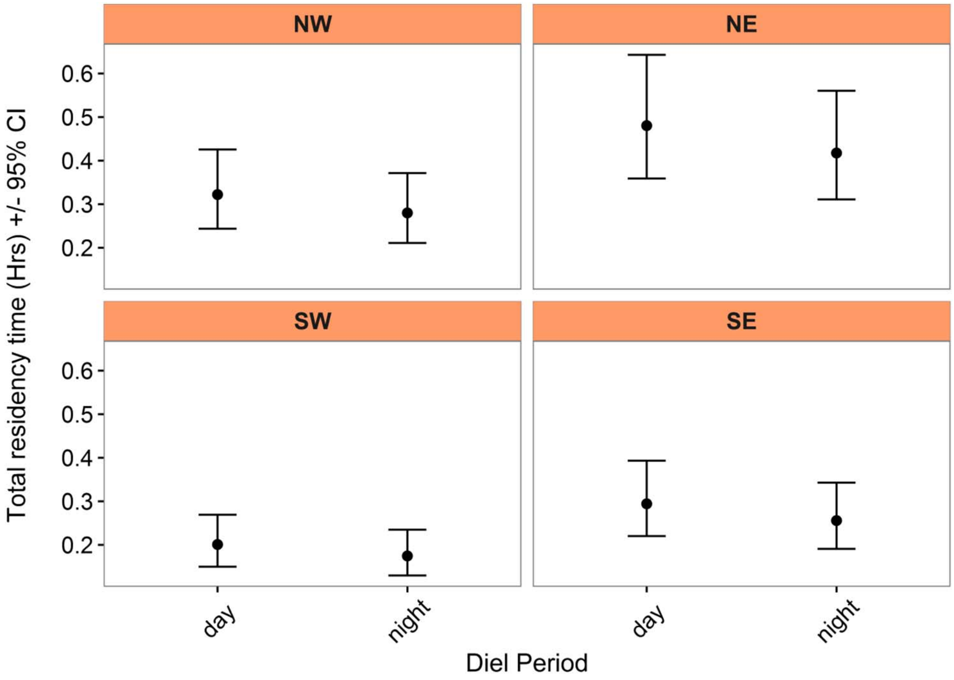

Fig. 4. Fitted values and 95% confidence limits for total residency on receivers in a given quadrant for tiger sharks detected within the telemetry array. Total residency was calculated for each individual within each diel period and quadrant. Fitted value estimates are shown for all fixed effects.

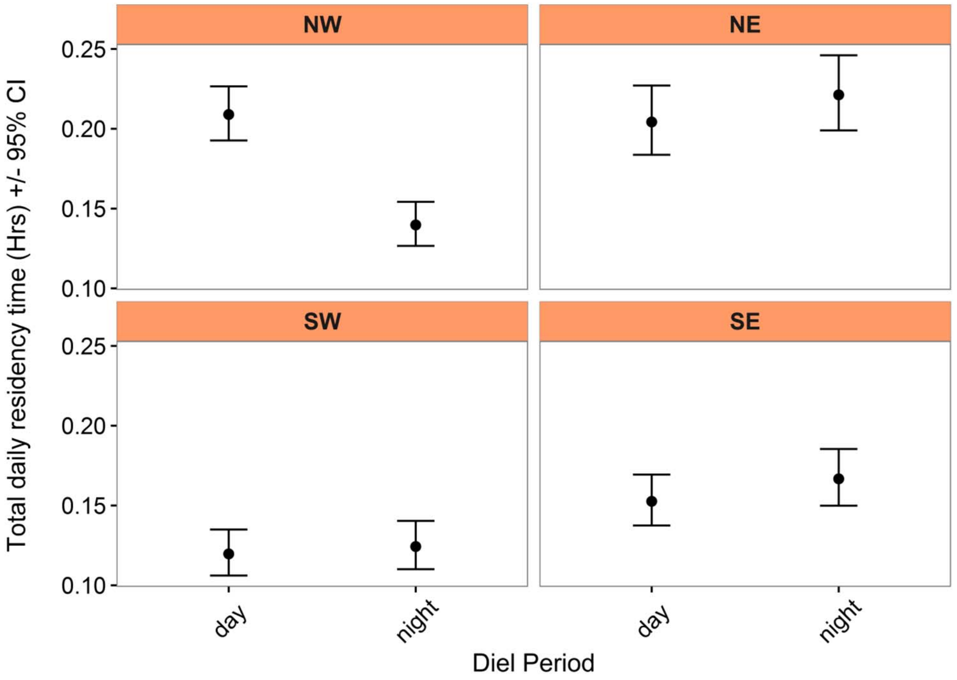

Fig. 5. Fitted values and 95% confidence limits for total daily residency on receivers in a given quadrant for tiger sharks detected within telemetry array. Total residency was calculated by diel period (day versus night) and quadrant. Fitted value estimates are shown for all fixed effects.

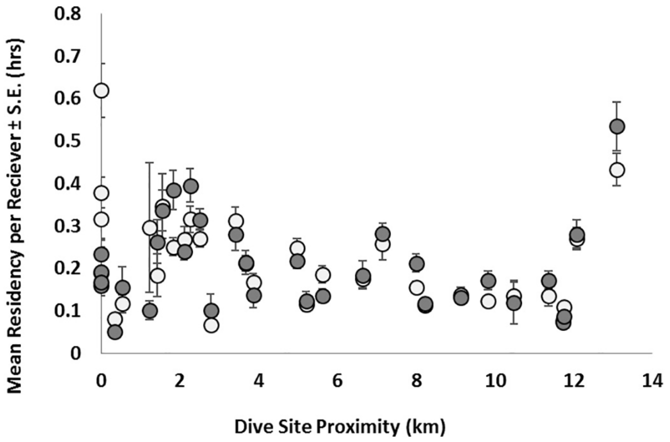

Fig. 6. Tiger shark residency per receiver (hrs) versus its proximity to dive tourism sites (km). Values and error bars are mean ± standard errors (S.E.).

quadrants, which would be expected if sharks restricted their movements to dive tourism sites during the time periods when provisioning occurred, similar to the response of whitetip reef sharks (*Trianodon obesus*) to provisioning tourism (Fitzpatrick et al., 2011). Indeed, centers of activity during the day also showed a cluster within the SE quadrant of the array, which is farthest away from the provision sites. These results lead us to reject our third alternative hypothesis.

Our results provide little empirical support for hypothesized effects of dive tourism on tiger shark habitat use patterns within the study area. However, in the absence of a study design where tourism activities can be manipulated or where shark habitat use data is available for comparison prior to wildlife tourism and provisioning, we cannot fully resolve the effects of dive tourism on shark behavior. While large-scale, unreplicated natural experiments (LUNEs) have their experimental limitations, in the absence of alternatives, they can provide a unique power to test hypotheses at ecologically relevant scales as we have done so here (Barley and Meeuwig, 2017).

It is possible that diel patterns of total daily residency in the NW quadrant could be related to shark provisioning activities, which occur there during the day, and are mostly absent at night. However, total residency in the NW quadrant was lower than in the NE quadrant. It is plausible that pre-provisioning residency was similarly high during day and night in both quadrants (although naturally higher in the NE), but as a result of the onset of day-time provisioning in the NW quadrant, sharks residency has increased there during the day relative to the night. That said, limited differences among some biological and physical factors (water clarity, substrate type, depth) suggest other factors, such as prey availability, may contribute to the habitat use patterns observed. As suggestive by the center of activity data, differences in diel total daily residency in the NW quadrant could be an artifact of individuals moving eastward at night, which may be related to feeding on nocturnal prey emerging in the inshore shallow banks such as lobsters and crabs. On several occasions during the tagging procedure, tiger sharks regurgitated spiny lobsters (*Panulirus argus*) and stone crabs (*Menippe mercenaria*) that were relatively fresh and undigested (Authors, direct observation). However, this hypothesis needs further exploration, which could be investigated through prey availability surveys, combined with active tracking of sharks, animal borne-video, and/or accelerometry (Watanabe and Takahashi, 2013; Meyer, 2017).

Other studies have also found minimal or no detectable effects of shark diving operations on shark habitat use. For example, the seasonal fluctuations in numbers of Galapagos (*Carcharhinus galapagensis*) and sandbar sharks (*C. plumbeus*) at diving operation in Hawaii are consistent with the seasonal migration patterns for these shark species (Meyer et al., 2009). The habitat use of bull sharks (*C. leucas*) at coral reefs in Fiji are similar in the presence or absence of dive provisioning activities (Brunnschweiler and Barnett, 2013). However, other studies have found small-scale influences of shark diving operations on shark behavior and habitat use. For example, white sharks (*Carcharodon carcharias*) in Australia show increased residency patterns and changes in diel behavior in areas of dive provisioning activities, as well as reductions in swimming depth, horizontal movement range, and swimming speed in proximity to cage divers (Bruce and Bradford, 2013; Huveneers et al., 2013). In the present study, sharks did not exhibit habitat use patterns consistent with hypothesized effects of provisioning tourism. Tiger sharks were detected throughout the array, with large activity spaces found by day and night (median > 400 ha, maximum > 3700 ha; Table 2). Moreover, only four sharks remained within the array for most of the tracking period, which would not be expected if sharks were restricting their movements to the dive sites as a result of provisioning. Taken together, these data are suggestive that

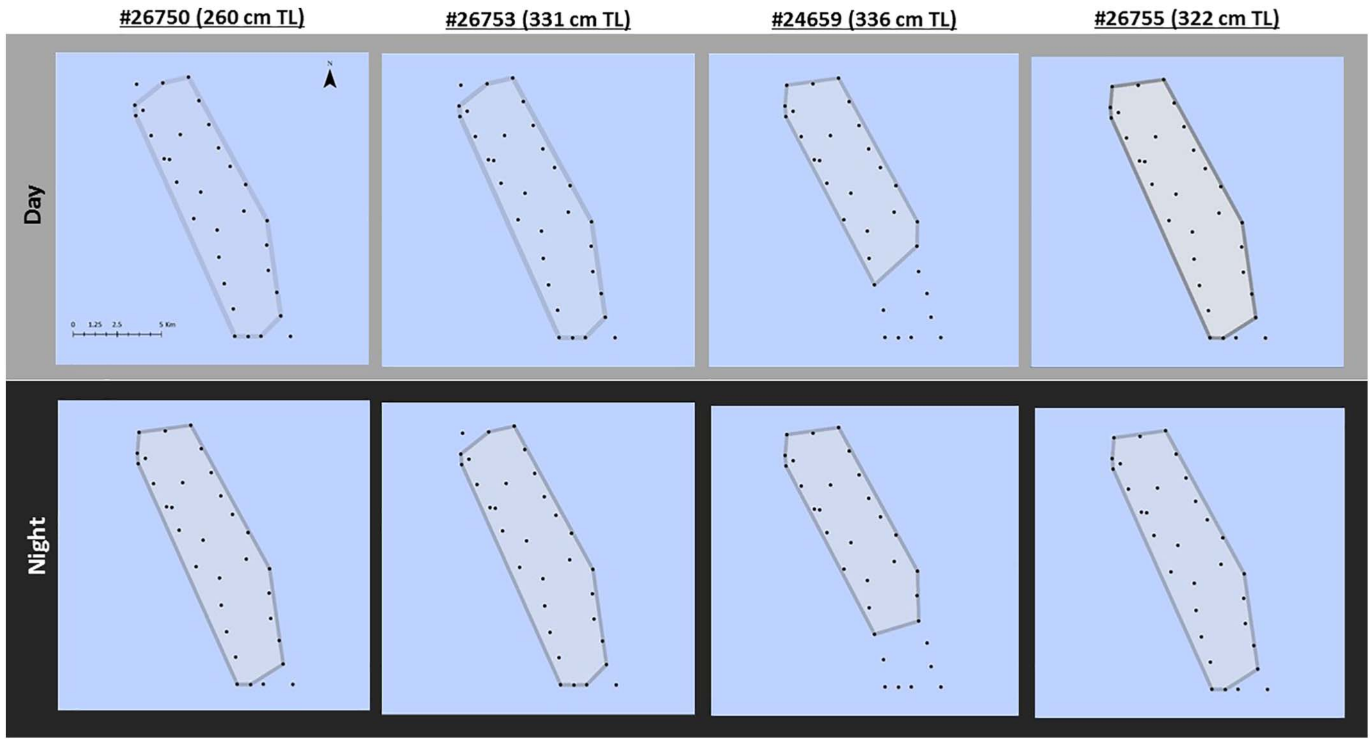

Fig. 7. Activity space (95% MCP, grey polygons) during daytime (top panel) versus nighttime (bottom panel) of four sharks accounting for majority (~50%) of both MCP and residency estimates. The black circles indicate acoustic receivers; TL = shark total length.

dive operations are likely not the primary driver of habitat use patterns for the majority of tagged tiger sharks in the study area. However, further research is needed to fully resolve possible tourism effects on shark behavior, including investigating how changes in daily patterns in dive tourism activities may relate to shark habitat use.

While not directly investigated here, it is plausible that tourism activities may have a larger effect on the habitat use of some individuals than others. Indeed, four sharks accounted for about 50% of activity space and residency data. Based on a dedicated investigation of the reproductive biology of tiger sharks at our study site (Sulikowski et al.,

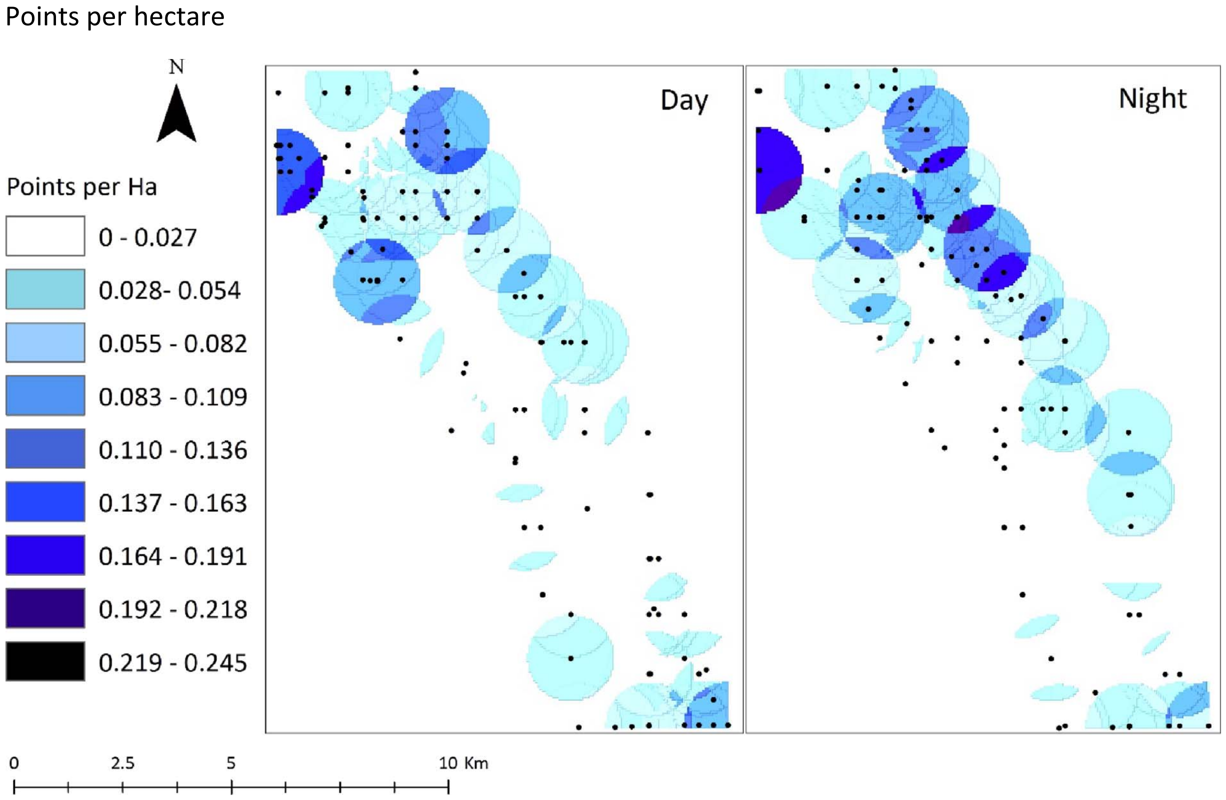

Fig. 8. Point densities (points/ha) of tiger shark centers of activity calculated for the day and night within the acoustic telemetry array.

2016), we were able to identify the life-history/reproductive states of the four females that contributed most of the activity space and residency data: #26750 was immature (270 cm TL), #26755 was mature but non-gravid (322 cm TL), #26753 was gravid (331 cm TL), and #24659 was mature but non-gravid (366 cm TL). Given that these four sharks were of mixed size classes, life-history and reproductive stages, it is unclear why these individuals spent more time in the array than others. However, it could be related to a number of factors, including individual differences in nutritional state (Gallagher et al., 2017) or individual preferences (Matich and Heithaus, 2015). Future work will seek to evaluate intra-specific variation in habitat use associated with factors such as life-history and nutritional state, and if population-level conclusions can be inferred.

In summary, we found the tagged tiger sharks utilized the entire region covered by the acoustic array. Sharks were detected in the array during both day and night with relatively minimal overall differences in patterns of diurnal versus nocturnal habitat use, although spatial differences in residency existed. The majority ($>$ 50%) of activity space and residency data came from four individuals that remained in the array throughout much of the tracking period, while the majority of sharks left the array during the summer months, with only infrequent movements in and out. Although additional data is needed to resolve and further understand the potential influence of dive tourism on tiger sharks, we found limited empirical evidence of shark habitat use patterns consistent with hypothesized effects of provisioning tourism on sharks. These findings are of particular relevance at this time given the ecological and conservation importance of characterizing habitat use patterns of marine apex predators at high use areas, and understanding the potential impacts of human activities when occupying these locations.

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