12-9-2017

Habitat Use of Blacktip Sharks (Carcharhinus limbatus) at Fishing Piers

Kelsey L. Spencer
Coastal Carolina University

HABITAT USE OF BLACKTIP SHARKS (*CARCHARHINUS LIMBATUS*) AT FISHING PIERS

by

Kelsey L. Spencer

Submitted in Partial Fulfilment of the

Requirements for the Degree of Master of Science in

Coastal Marine and Wetland Studies in the

School of Coastal and Marine Systems Science

Coastal Carolina University

2017

Dr. Daniel C. Abel
Major Professor

Dr. Derek P. Crane
Major Professor

Dr. Neil Hammerschlag
Committee Member

Dr. Erin J. Burge
Committee Member

Dr. Michael Roberts
Dean of College of Science

Dr. Richard Viso
SCMSS Assistant Director

Acknowledgments

This project would not have been possible without the aid of numerous people, whom I would like to acknowledge. A tremendous amount of gratitude goes to both of my advisors: Drs. Dan Abel and Derek Crane for their unwavering support and encouragement. I am extremely grateful for the enthusiasm Dr. Abel had for my project and his belief in me and my abilities to complete all the tasks he sent my way. I will never forget his lessons on the power of words. Without the extensive statistical knowledge of Dr. Crane, the quality of this project would be nowhere near what it is today. I have truly grown in the area of statistics and I owe it all to Dr. Crane. I would also like to thank my committee members Drs. Neil Hammerschlag and Erin Burge. Dr. Hammerschlag kept me focused on the task at hand and his encouragement pushed me to continue to improve. Dr. Burge has always been a great inspiration with his expertise in ichthyology and his extensive knowledge of the Myrtle Beach area was paramount for my research.

I would like to extend my appreciation to Ann Wilson, Jerry Ives, and all the staff at Myrtle Beach State Park. Ann was instrumental in my cooperation with Myrtle Beach State Park and secured their support to purchase five of my tags. Additionally, I would like to thank the owners and operators of Pier 14, 2nd Avenue Pier, and Garden City Pier for housing my monitoring equipment. Special thanks to all the help I received from Danielle Viso and Steve Luff for assisting in the deployment of my receivers.

I owe my gratitude to the CCU boat captains and the charter boat captains at YKnot Fishing Charters and Careyon Charters, who generously devoted their time to take me shark fishing. I also could not have done this without the help of my father-in-law, Tim Martin, and his enthusiasm to drive eight hours to deliver his boat so that I might use it to tag my last shark.

Numerous others dedicated their time and energy, for which I offer my sincere thanks. These include: my fellow graduate students Caroline Collatos and Matt Larsen for their eagerness to help with all aspects of my research even though they had their own research to worry about, Dr. Var Limpasuvan for assisting with the algorithm for the fast Fourier transformation analyses, the South Carolina Department of Natural Resources and many other researchers for sending me detection data, my volunteer interns: Whitney Davis, Krissy Hogge, Jessica Holdorff, Simone O'Dowd, and Hunter Sheets, and all other CCU volunteers who aided with either shark fishing or pier surveys.

Financial support for this project was provided by the Coastal Marine and Wetland Studies graduate program and Essex County Turtle Back Zoo. Support in the form of acoustic telemetry equipment was also provided by The Ocean Tracking Network and Myrtle Beach State Park.

Finally, for their never-ending love and support throughout this somewhat bumpy venture, I would like to thank my husband, Josh Martin, and dedicate this thesis to my parents, Dennis and Jean Spencer.

Table of Contents

List of Tables

List of Figures

Habitat use of Blacktip Sharks (*Carcharhinus limbatus*)

at Fishing Piers

Abstract

Blacktip sharks (*Carcharhinus limbatus*) can be observed near fishing piers throughout the summer along the northeast coast of South Carolina. These piers attract and support a wide variety of potential prey and sharks are able to forage on fishers' discards with minimal energetic cost. I tagged 12 blacktip sharks with acoustic transmitters, monitored piers with acoustic receivers, and conducted pier-creel surveys to determine the habitat use of blacktip sharks at fishing piers, factors that influenced residence time and presence/absence at piers, and any cyclical patterns in visits to piers. Data were analyzed with pier association indices (PAI), mixed models, and fast Fourier transformation analyses. While the majority of monitored sharks were infrequently detected at piers, four (33.3%) displayed a high degree of fidelity at piers. Two sharks (16.7%) were detected only at the pier where they were tagged, whereas two other individuals were detected at all monitored piers in 2017. The most likely model for shark residence time at piers included terms for pier location and diel cycle (w_i = 0.52), while the most likely model explaining presence/absence of sharks at piers included terms for tidal height and diel cycle (w_i = 0.95). Sharks did not display cyclical patterns in detections at piers. To my knowledge, this is the first study to specifically examine the habitat use of blacktip sharks at fishing piers. My data suggests that fidelity of sharks at piers is a phenomenon for some of the tagged sharks, but not all.

Introduction

Coastal anthropogenic structures, such as fishing piers, bridge pilings, and docks, attract and support a wide variety of coastal fishes (Burchmore *et al*. 1985, Barwick *et al*. 2004). Fish will congregate around these physically complex structures that disrupt predator foraging efficiency to increase their chances of survival (Glass 1971, Savino & Stein 1982). Pelagic teleost species utilize low light levels at the edges of piers to ambush unsuspecting prey (Able *et al*. 2013), concurrently putting these pelagic species at risk for predation from large coastal sharks (Ellis & Musick 2007).

One of the most commonly observed shark species around fishing piers along the northeast coast of South Carolina is the blacktip shark (*Carcharhinus limbatus*; K. Spencer unpubl. data). Blacktip sharks seasonally migrate in the western Atlantic (Castro 1996, Kajiura & Tellman 2016). From May until early November, they are one of the most common large coastal shark species along the North Carolina, South Carolina, and Georgia shorelines (Table 1; Trent *et al*. 1997, Thorpe *et al*. 2004, Ulrich *et al*. 2007). Despite the seasonal abundance of this species and its anecdotally documented presence at fishing piers, no scientific studies address the associative behavior or habitat use of blacktip sharks, or indeed any other shark species, specifically at fishing piers.

Associative behavior, which can be defined as the association between an animal and inanimate objects or topographic structures (Fréon & Dagorn 2000), has been studied using acoustic telemetry for a variety of shark species (Heupel & Hueter 2002, Lowe *et al*. 2006, Heupel *et al*. 2010, Espinoza *et al*. 2011, Kock *et al*. 2013, Chapman *et al*. 2015, Watwood 2015). In adult sharks, this behavior is speculated to be advantageous for either feeding, mating, pupping, and/or resting (Speed *et al*. 2010). In northeast SC, sharks are commonly observed feeding on discarded fish and entrails at piers, and display conditioned responses to a splash in the water (K. Spencer unpubl. data), thus suggesting that sharks may in part congregate around fishing piers primarily to feed.

Although not intentional, the provisioning of sharks with food at fishing piers could unwittingly influence their behavior. Burgess (1998) commented that the feeding of sharks could increase local populations since food is readily available with minimal energetic cost. The aggregations of blacktip sharks around fishing piers could potentially make them vulnerable to exploitation (Kajiura & Tellman 2016); however, little is known about the factors influencing habitat use of blacktip sharks at piers.

Understanding the advantages and environmental correlates of shark aggregations are important in determining their ecological role in a given system (Heupel & Simpfendorfer 2005). Blacktip sharks are thought to respond to environmental cues to govern their movement patterns (Heupel *et al*. 2004). Their movements have been previously correlated with changes in diel cycle (Heupel & Simpfendorfer 2005), tidal cycle (Steiner *et al*. 2007), and water temperature (Castro 1996, Kajiura *et al*. 2016). Literature is insufficient on the lunar cycle effects on blacktip shark movements, however, the school shark (*Galeorhinus galeus*) has been observed displaying lunar shifts in vertical migration patterns in coastal waters (West & Stevens 2001).

The primary objective of this study was to monitor the habitat use of blacktip sharks at specific fishing piers along the northeast coast of South Carolina (Fig. 1). I used a combination of environmental data and pier creel surveys to investigate the effects of pier location, diel cycle, tidal height, water temperature, lunar cycle, and the relative abundance of prey on the habitat use of blacktip sharks at fishing piers. Specifically, I focused on the following five objectives: 1) assessing the fidelity of blacktips sharks at fishing piers, 2) characterizing if sharks exhibited high use at a particular pier, 3) identifying possible factors influencing the residence time of sharks at piers, 4) identifying possible factors influencing presence/absence of sharks at piers, and 5) identifying potential periodic or cyclical patterns in visits to fishing piers.

Materials and Methods

Receiver configuration and range testing

Sharks were caught on or near fishing piers in 2016 and 2017 along the Grand Strand in northeastern South Carolina. The Grand Strand is a 93 km long region with a shallow sloping coastal zone and several small and some large tidal inlets and swashes separated by predominately wave-dominated and welded barrier islands and barrier spits (Baldwin *et al*. 2004).

Prior to Hurricane Matthew in October 2016, ten fishing piers existed in this zone (Fig. 1). Acoustic receivers (VR2W 69 kHz, Vemco) were placed at four of these: Pier 14, 2nd Avenue, Myrtle Beach State Park (MBSP), and Garden City Piers (2017 only; Fig. 1) to passively detect and record transmissions from transmitters within their detection ranges. Additionally, detections from receivers at two additional piers, Apache and Springmaid Piers (Fig. 1) were provided by the South Carolina Department of Natural Resources (SCDNR), who was monitoring movement patterns of Atlantic (*Acipenser oxyrinchus*) and shortnose (*A. brevirostrum*) sturgeon until those piers were damaged by Hurricane Matthew. Thus, five piers were monitored in 2016 (Apache, Pier 14, 2nd Avenue, Springmaid, and MBSP Pier) and four were monitored in 2017 (Pier 14, 2nd

Avenue, MBSP, and Garden City Pier). Piers were selected based on proximity to one another. The longest and shortest distances between two adjacent piers were 11.6 km (between Apache Pier and Pier 14) and 1.4 km (between Springmaid Pier and MBSP Pier).

Receivers that I deployed were fastened via six heavy-duty, 45 cm zip-ties to a half-inch braided nylon and polyester rope that was tied around a stainless steel hitch ring mounted to one of the horizontal supporting (collar) beams of the piers. Receivers were mounted on specific collar beams to ensure that they would not get entangled around a pylon. Receivers were anchored in the water, about 2 – 3 m from the bottom, with chain secured to the bottom of the rope. A similar configuration was used for SCDNR receivers. Individual receiver deployment varied throughout the monitoring period, with some gaps in deployment due to equipment malfunction and Hurricane Matthew (Fig. 2).

Range testing was conducted to determine detection efficiency and maximum distance from the receiver at different distances from the MBSP Pier receiver. Limited detection range was desired to ensure that detected sharks could be considered to be associated with piers. Starting 50 m east of the pier, I anchored a transmitter (V9-2L 69 kHz, 15 s repeat rate, power output 145 dB re 1 μPa at 1 m) into the water approximately 2 – 3 m from the bottom for 25 min to allow for 78 signal transmissions (Welsh *et al.* 2012). Then, I repeated the procedure at 100, 150, 200, 250, and 300 m from the receiver. The detection efficiency of the receiver at each distance was calculated by dividing the number of recorded detections by the number of expected detections over the deployment period (Welsh *et al.* 2012).

Tagging

Blacktip sharks were captured and tagged at two different locations within the Grand Strand: 2nd Avenue pier and MBSP Pier. Second Avenue Pier was the middle of monitored piers in 2016, whereas MBSP pier became the middle pier in 2017 with the inclusion of Garden City Pier. The middle pier was selected based on the assumption that tagged sharks travelling to other piers might have a higher likelihood of encountering a monitored pier and thus be detected.

Sharks were captured on baited longlines and drum-lines set from a small boat near 2nd Avenue Pier and MBSP Pier, and by hook-and-line directly from MBSP Pier. All boat-based fishing methods utilized 30-minute soak times to reduce the stress and mortality of any ram-ventilating species. A 150 m bottom longline with 25 size 16/0 circle hooks (Abel *et al*. 2007) was baited with Boston mackerel (*Scomber scombrus*) and anchored approximately 200 m east of the piers (the closest I judged to safely set lines). Baited drum-lines, anchored approximately 100 m north or south of the pier (again, for safety), consisted of a 1 m monofilament gangion with a size 16/0 circle hook secured to 9 m of rope with a buoy and anchor at each end. Global Positioning System (GPS) location, time, and depth were recorded for each longline and drum-line. Captured sharks were secured to the side of the boat with a tail-rope prior to implantation of the transmitter. Nine sharks were captured via a boat-based method.

Pier-based hook-and-line fishing was conducted using single 16/0 or 12/0 circle hooks or a rig with three treble hooks baited with either Boston mackerel, pinfish (*Lagodon rhomboides*), Florida pompano (*Trachinotus carolinus*), or southern kingfish (*Menticirrhus americanus*). Of the three sharks that were caught from the pier, one was caught on the circle hook rig and two on the treble hook rig. Hooked sharks were brought alongside the pier, were maneuvered into a net, and were lifted onto the pier. Sharks were then placed in a 1.2 m diameter holding pool half filled with seawater at ambient temperature and salinity.

Sharks were fitted with coded acoustic transmitters (V9-2L 69 kHz, Vemco), with a battery life up to 1.5 yr, to determine fidelity and record visits made to piers. Prior to implantation of the transmitter, captured sharks were identified to species, were sexed, and were measured. Precaudal length (PCL), fork length (FL), and stretched total length (TL) were recorded for each individual. Animals were then inverted and placed in tonic immobility. A 2 cm incision was made in the abdominal wall 2 cm off-center and midway between the pelvic and pectoral fins (Holland *et al*. 1999). Coated transmitters (9 x 29 mm, 2.9 g) were placed internally through the incision and two braided polyester sutures were used to close the wound. Transmitters were coated with a combination of 70% paraffin wax and 30% beeswax to reduce immune response (Holland *et al*. 1999, Lowe *et al*. 2006). Transmitters had a nominal delay of 70 s, but were set with random repeat code, or RCODE, which varies transmissions from 45-95 s. Tags with RCODE vary the silent period between transmissions via a pseudo-random number generator which ensures that if transmissions from two transmitters collide on one occasion, their transmissions will separate on the following transmission (Voegeli *et al*. 2001). Following surgery, sharks were then righted and tagged with a unique color-coded ROTO tag, or tags (*e.g.*: blue-blue), that was easily recognizable from fishing piers. Upon release, the total time alongside the boat or on the pier was recorded and the health of the shark was evaluated as either poor, moderate, or strong.

Environmental data

I collected environmental data to analyze the possible effects of physical variations in the environment on shark habitat use at fishing piers. Although several abiotic factors were recorded from the monitoring station previously mentioned at 2nd Avenue and Apache Piers, only the following factors were explored due to prior observed influences on blacktip shark movements or anecdotal observations suggesting an influence on their association with piers. Tidal cycle and lunar cycle were recorded as both categorical and quantitative variables for use in separate models. Tidal cycle was categorized as either "falling" or "rising." Falling was defined as the six-hour time block beginning 1 h after high tide and ending 1 h after low tide, whereas rising began 1 h after low tide and ended 1 h after high tide. This categorization ensured that all of high tide (one-hour on either side of the time for high tide) and all of low tide (one-hour on either side of the time for low tide) were included in the same category. High and low tide times were based on the National Oceanic and Atmospheric Administration (NOAA) predictions at each pier.

Hourly tidal height by mean sea level (MSL) accessed online via NOAA's website (tidesandcurrents.noaa.gov) at Springmaid Pier was used for quantitative tidal cycle data. Following the destruction of Springmaid Pier by Hurricane Matthew, NOAA's predicted tidal height data were used when verified tidal height data were no longer available. The monitoring station was rebuilt on MBSP Pier in early 2017 with renewed access to NOAA's online database.

I categorized lunar cycle using percent illumination, gathered by the United Stated Naval Observation (USNO; aa.usno.navy.mil), which records the fraction of the moon illuminated for each day. Lunar cycle was noted as either, "new," "1st quarter," "full," or

"3rd quarter." Percent illumination data from USNO were also used for quantitative lunar cycle data. Diel cycle was recorded as either "day" or "night" based on USNO times for sunset and sunrise (aa.usno.navy.mil). Sea surface temperature data were gathered from a monitoring station at 2nd Avenue Pier as part of the Long Bay Hypoxia Monitoring Consortium (Libes & Kindelberger 2010) and accessed online (www.sutronwin.com). Following Hurricane Matthew, the water temperature monitoring equipment on 2nd Avenue Pier could not be reinstalled until early 2017. As a result, water temperature data were utilized from a similar monitoring station at Cherry Grove Pier (Fig. 1) when data at 2nd Avenue Pier were no longer available.

Pier Surveys

I used angler catch per unit effort (CPUE) from fishing piers to provide an index of the relative prey availability near piers. Surveys of fishing effort and catch were conducted by trained volunteers at five piers from July through October in 2016 and June through September in 2017 (Fig. 1). Apache, Pier 14, 2nd Avenue, Springmaid, and MBSP Piers were surveyed with the inclusion of Garden City Pier in 2017 due to the absence of Springmaid Pier. A simple random sampling design with replacement was used to determine both the time and pier surveyed each day. Sampling with replacement resulted in slight differences between the number of surveys conducted at each pier (Table 2); however, because I was unable to test between pier differences over the analysis periods, species composition and abundance were assumed to be consistent between piers. One two-hour window was randomly selected from 07:00 to 21:00 each day at a single pier resulting in seven surveys per week. The time, date, weather, and wind speed and direction were noted at the beginning of the survey. In 2017, visual observation of large coastal sharks was also recorded. Additionally, the tide that occurred during the majority of the survey was recorded as either “falling,” “rising,” “high,” or “low.” Both high and low tide were treated as a one-hour time block on either side of the predicted time for high tide and low tide by NOAA (see *Environmental data*). For example, if the survey occurred from 10:00 to 12:00 and high tide was at 11:30, the tide was recorded as “high.”

For estimating the relative prey abundance near piers, fishing effort was recorded as the average of the number of rods actively fishing at the beginning and end of the survey. Catch was recorded and tallied to the lowest practical taxonomic level throughout the survey. Only potential prey species for blacktip sharks (Table 3; Castro 1996, Walls *et al*. 2002, Bethea *et al*. 2004, Compagno *et al*. 2005) were included in CPUE analysis (see Table S1 for a comprehensive list of all species observed during pier surveys). Prey CPUE was defined as the number of fish caught per rod. Potential prey species observations (Table 3) were pooled together to serve as an index of prey availability throughout the region over two-week time periods. I used a two-week time period to ensure that at least four surveys made up each CPUE value, despite some surveys being missed and pier closures due to Hurricane Matthew (n = 38 for 2016; n = 29 for 2017).

Data Analysis

Detection data from 2016 and 2017 study periods were combined for analyses. The 2016 study period spanned from July 14 to November 6. The end date was the date of last detection for all tagged sharks. The 2017 study period spanned from June 1 to September 1. All statistical analyses were performed using RStudio within R statistical software (R version 3.4.2; RStudio Team 2015). All mixed models were conducted using the *lme4* package (Bates *et al*. 2017).

To investigate habitat use at piers, I evaluated receiver data for each shark based on the “total number of days detected at piers,” “number of days monitored,” “number of days detected at each individual pier,” and “detection events.” Data gathered in the first 12 hours were not included in analyses to allow sharks to resume normal activity following release. The monitoring period was defined as the number of days from release date (plus 12 h) to the date of last detection for each individual. A pier association index (PAI) value was generated for each shark by dividing the number of days detected at piers by the monitoring period. The proportion spent at each pier was calculated for each shark by dividing the number of days spent at each pier by the total number of days detected. I considered a shark as exhibiting high use of a pier if an individual spent greater than 50% of their days detected at a specific pier.

I used a general linear mixed model (GLM) to assess if pier location, lunar cycle, tidal cycle, diel cycle, water temperature, and prey CPUE influenced shark residence time at piers (Papastamatiou *et al*. 2010). I defined detection events as a minimum of two detections within a 30-minute period from a single individual (Topping & Szedlmayer 2011, Hammerschlag *et al*. 2017a). Prior to analysis, a log10 transformation of residence time was required to correct skewed data. Categorical tidal and lunar cycle were used because some detections spanned considerable periods of time. For example, detection events spanned 24 hours for one individual on several occasions. Therefore, the tidal, lunar, and diel cycle that occurred throughout the majority of the event was used. The average hourly water temperature was used at the beginning of the event for analysis.

I used a binomial generalized linear mixed model (GLMM) to assess the potential influence of water temperature, tidal height, diel cycle, lunar cycle (percent illumination), and prey CPUE on presence versus absence of individual sharks at piers. Environmental data and prey CPUE were assigned for each hour on the hour. Any detection recorded was given a “1” for that hour and individual, while no detections recorded were given a “0.” Quantitative tidal and lunar cycle was utilized for the GLMM. In order to account for pseudoreplication resulting from multiple detections being recorded for each individual, transmitter number was assigned as a random intercept variable for both the GLM and GLMM. All possible subsets were also used in both models to identify key variables affecting each response. Because the objective of these analyses were explanatory and not predictive, it was not necessary to break data into training and testing data sets to test model performance. I used Bayesian information criterion (BIC; Schwarz 1978), information loss (ΔBIC; Raftery 1995), and Schwarz weights (w_i; Burnham & Anderson 2004) to select the most likely model for each analysis. Finally, I calculated coefficient estimates (95% CI) for variables contained in the most likely GLM and coefficient estimates and odds ratios (95% CIs) for variables contained in the most likely GLMM. About 5% (n = 720) of data points from the GLMM and about 3% (n = 15) of data points from GLM had to be removed due to missing water temperature data because of sensor failure or removal of equipment prior to Hurricane Matthew.

Time series analyses were used to identify possible cyclical patterns in shark detections. Detections for individuals with greater than 200 observations were first summed into hourly bins (Papastamatiou *et al*. 2010). I then conducted a fast Fourier transformation (FFT) with hamming window smoothing (Papastamatiou *et al*. 2010), which converts detections into component frequencies and then searches the data set for cyclical patterns (Papastamatiou *et al*. 2009). Shark periodicity is represented as peaks in a power spectrum. If power spectrum graphs had definite peaks, as in Papastamatiou *et al*. (2010), then sharks were said to have displayed periodicity in visits to piers. Spectral analyses were performed using the Interactive Data Language (IDL) v. 4 (Exelis Visual Information Solutions, Boulder, Colorado).

Results

Receiver performance

Range testing confirmed that detections only from individuals <100 m from piers, arbitrarily defined as close proximity to the pier, were recorded. At a distance of 50 m from the receiver, a total of 55 of 78 possible test detections were recorded, resulting in a test detection efficiency of 0.71. Only two test detections were recorded at 100 m, resulting in a test detection efficiency of 0.03. Additional information on tag performance over a 24-hour period was provided by the opportunistic use of a deceased shark less than 50 m from the receiver. Of 1,152 transmissions from this animal, 1,069 were recorded, resulting in a detection efficiency of 0.93. The number of detections per hour were visually assessed with tidal height, diel cycle, and water temperature (Fig. 3). Environmental parameters did not appear to affect receiver performance (Fig. 3).

Pier surveys and environmental data

Pier surveys for both study periods resulted in 3,073 total individuals from 52 species (Table S1). Prey CPUE was 0.71 for 2016 and 0.53 for 2017. The Atlantic croaker (*Micropogonias undulatus*) was the most common species observed. Over the 2016 study period, water temperature ranged from 20.36 – 31.91°C ($\overline{x}$ = 27.07 ± 0.06°C).

In 2017, water temperature ranged from 22.97 – 30.64°C ($\bar{x}$ = 27.35 ± 0.01°C). The highest monthly mean temperature occurred in August for both study periods; 29.43°C for 2016 and 28.55°C for 2017. Tidal height by MSL ranged from -1.35 to 1.34 m.

Acoustic monitoring

I tagged 12 blacktip sharks from 14 July 2016 through 16 August 2017 at 2nd Avenue Pier and MBSP Pier (Table 4). Eight of the 12 individuals tagged were detected post-release resulting in 15,214 detections recorded from 25 July 2016 to 1 September 2017. Four sharks (33.3%) were not detected post-release; three in 2016 and one in 2017. The average number of days monitored (release date to date of last detection) was 55 and the average number of days detected was 26. Detection events ranged from 0.01 – 30 h ($\bar{x}$ ± SE; 1.68 ± 0.17 h, median = 0.44 h) with a total of 45,879 h recorded. The majority of detection events occurred during the day (71.1%; n = 324). Detection events during the full (n = 140) and 1st quarter (n = 142) outnumbered events during the new (n = 83) and 3rd quarter (n = 71) lunar phases. The last detection recorded in the Grand Strand in 2016 occurred on November 5. None of the sharks tagged in 2016 were subsequently detected in the study area in 2017 (as of September 1).

The eight individuals that were detected displayed varying degrees of fidelity at piers with pier association indices (PAIs) ranging from 0.119 to 0.702 (Table 4). The four individuals that displayed high PAIs were all adults (according to Branstetter 1987 and Killam & Parsons 1989) with total lengths (TL) ≥ 158 cm. Only one of the four individuals that displayed lower association index values was mature (Table 4). Similarly, only one of the individuals that was not detected post-release was mature. All detected sharks appeared to exhibit high use at a single pier location and five sharks exhibited high use at the specific pier location where they were tagged (Fig. 4). Additionally, two sharks spent 100% of their detectable time at the location where they were tagged, whereas two individuals were detected at all four monitored piers in 2017. One individual was solely detected at MBSP Pier and spent more than 24 h at that location on multiple occasions. This individual was initially thought to be deceased based on multiple periods with continuous detections, but was then visually observed at MBSP Pier on 1 September 2017.

The GLM model that best explained shark residence time at piers included terms for pier and diel cycle (w_i = 0.52; Table 5). The model selected had a 52% probability of being the true model and was 2.4 times more likely than the next most likely model (w_1/ w_2; Table 5). The coefficient estimate (95% CI) for diel cycle (night) was -0.504 (-0.806 - – -0.173), indicating that on average, residence time was 3 min greater during the day than at night for each individual (Table 6). Similarly, there was about a 4-minute difference in median residence time between day (26.9 min) and night (23.1 min). The coefficient estimate (95% CI) for MBSP Pier compared to 2nd Avenue Pier was 0.952 (0.417 – 1.461), indicating that on average, residence time was about 9 min greater at MBSP Pier than 2nd Avenue Pier. Conversely, residence time was on average, about 9 min greater at 2nd Avenue Pier than Pier 14 with a coefficient estimate (95% CI) for Pier 14 of -0.965 (-1.601 – -0.304; Table 6). Residence time at Garden City Pier did not differ from 2nd Avenue Pier with a coefficient estimate of -1.460 (-2.933 – 0.005). The most likely GLMM included terms for tidal height and diel cycle (w_i = 0.95; Table 7). The model selected had a 95% probability of being the true model and was 34 times more likely than the next most likely model (w_1/ w_2; Table 7). The odds ratio (95% CI) for tidal height was 1.315 (1.187 – 1.458), while the odds ratio (95% CI) for diel cycle (night) was 0.434 (0.382 – 0.493; Table 6). The odds ratios corresponded to a 32% increase in odds of presence with a 1 m increase in tidal height, when diel cycle was held constant and a 57% decrease in odds of presence at night when tidal height was held constant (Table 6). Spectral density plots generated from the fast Fourier transformation analyses did not reveal cyclical patterns in behavior (Fig. 5). Only sporadic peaks occurred in the graphs for each individual analyzed (Fig. 5), demonstrating non-periodic visits.

Discussion

To my knowledge, this is the first study to specifically examine the habitat use patterns of sharks at fishing piers and infer potential associations. I observed a high degree of fidelity at piers in four individuals, with four others displaying lower fidelity at piers. Fidelity to anthropogenic structures has also been observed in sandbar sharks (*Carcharhinus plumbeus*) to ocean-farming cages in Hawaii (Papastamatiou *et al.* 2010) and silky sharks (*Carcharhinus falciformis*) to fish aggregating devices in the Indian Ocean (Filmalter *et al.* 2011). Previous studies involving juvenile blacktip sharks have found high site fidelity (Heupel & Hueter 2002), here I found evidence of relatively high site fidelity at piers in adult individuals, but not juveniles.

Blacktip sharks in the western North Atlantic are known to migrate south to warmer waters during the winter months (Castro 1996). Ulrich *et al.* (2007) found blacktip sharks were present from May until early November off the coast of South Carolina. Although only one (44578) of the four blacktips tagged in 2016 was subsequently detected that year, it was observed throughout the summer months and then recorded its last detection in the area on 7 November 2016, when the average hourly water temperature was 19.8°C. My results support Castro (1996), who suggested that blacktip sharks migrate to warmer waters when sea surface temperatures drop below 21°C. Kajiura and Tellman (2016) observed peak blacktip shark abundance from January to March along the east coast of Florida. Consistent with previous observations, shark #44578 from my study was detected near Cape Canaveral, Florida in late December 2016 and early January 2017. The presence of this individual in Florida indicated that its seasonal migration was likely not prevented by a potential assocation to piers in the Grand Strand. Papastamatiou *et al*. (2010) also found that sandbar shark seasonal migration patterns were not disrupted by site fidelity to ocean-farming cages.

The lack of detections for some sharks tagged during this study could potentially be due to tag failure, death, or the individuals tagged were not pier-associated sharks. In 2016, only the smaller, immature sharks, with total lengths ≤141 cm, were not detected post-release. Results were similar for 2017, where the most frequently detected individuals at piers were all adults (TL >155 cm), with minimal degrees of fidelity recorded for the two smaller blacktip sharks (TL ≤140 cm; Table 4). One plausible explanation could be that larger individuals outcompete and drive out smaller individuals (Myrberg & Gruber 1974). Size is often the driver of dominance in social groups (Allee & Dickinson 1954). Limbaugh (1963) observed interspecific dominance between blacktip, silvertip (*Carcharhinus albimarginatus*), and Galapagos (*Carcharhinus galapagensis*) sharks. Although blacktip sharks were the most common species observed at piers during creel surveys, additional shark species were caught at or near piers, including tiger (*Galeocerdo cuvier*), sandtiger (*Carcharias taurus*), scalloped hammerhead (*Sphyrna lewini*), sandbar (*Carcharhinus plumbeus*), finetooth

(*Carcharhinus isodon*), blacknose (*Carcharhinus acronotus*), and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks. Additional tagging of blacktip sharks across all size ranges would need to be conducted to further evaluate size classes of sharks around fishing piers.

Throughout their residency in the Grand Strand, tagged sharks appeared to exhibit relatively higher use at particular piers over others, specifically Pier 14, 2nd Avenue Pier, or MBSP Pier (Fig. 4). The highest concentration of piers per km in the Grand Strand encompasses those three piers (Fig. 1). Certain piers could represent more favorable environment for individual sharks to exploit resources. However, Apache Pier, a pier where large numbers of sharks are commonly observed, did not record any detections in 2016, demonstrating that where each shark was tagged may be a better indicator for explaining the association of sharks to specific piers.

Diel cycle influenced the duration sharks spent at piers and their presence/absence at piers. The residence time of blacktip sharks at piers decreased, on average, by about 3 minutes for each individual from day to night and odds of presence at piers decreased by 57% from day to night (Table 6). While a 3-minute decrease in residence time is not substantial, approximately 71% of both residency events and detections were recorded during the day. Sandbar sharks also increased site fidelity to ocean-farming cages during the day (Papastamatiou *et al*. 2010). Papastamatiou *et al*. (2010) suggested that an increase in prey availability during the day influenced sandbar shark fidelity to ocean-farming cages. Increased activity at piers during the day could indicate that sharks are utilizing piers to feed, even though prey CPUE was not included in the most likely models. For example, the increase in activity at piers during the day is consistent with pier hours of operation. Many shark species are considered opportunistic foragers (Heithaus 2001, Melillo-Sweeting *et al*. 2014). Multiple observations were made during pier surveys of sharks feeding on discarded fish and even circling cleaning stations while a fisher was cleaning their fish and discarding scraps. Conversely, Barry *et al*. (2008) concluded that neonate and young of year blacktip sharks spent more time feeding as light level decreased. Nocturnal feeding patterns have been found in some diel feeding studies on sharks (Nelson 1974, Randall 1977, Tricas 1979, Klimley *et al*. 1988, Bush 2003); however, a review by Hammerschlag *et al*. (2017b) concluded that an increase in elasmobranch activity at night was largely not supported. Lowe *et al*. (1996) observed adult tiger sharks feeding both during the day and at night, but altering their foraging strategies with the diel cycle. Blacktip sharks could also be exhibiting diel shifts in feeding behavior; foraging with minimal energetic cost at piers during the day when piers are open and more active foraging strategies, or perhaps fasting, at night. A supplementary nearshore receiver (n = 1), approximately 3 km from the closest pier structure and equidistant with the pier from shore, indicated that 66% of detections (n = 534) and 61% of detection events (n = 128) were recorded during the day. Therefore, diel shark activity may not correspond with pier activity and sharks could simply be feeding close to shore during the day and then making their way offshore at night. Because all sharks were caught during the day, this study could have selected for sharks more likely to display nearshore activity during the day, while conspecifics could exhibit different behavior. The inclusion of an offshore receiver array and the tagging of sharks at night could elucidate shark diel cycle movements. Additionally, stomach content analysis from sharks caught throughout the diel cycle could clarify changes in foraging behavior.

The presence of sharks at piers was also influenced by an increase in tidal height (Table 6). Tidally influenced movements have been observed in juvenile blacktip (Steiner *et al*. 2007) and juvenile lemon sharks (*Negaprion brevirostris*; Wetherbee *et al*. 2007). Steiner *et al*. 2007 observed blacktip sharks travelling into open water with an outgoing tide and into backwater bays with an incoming tide. Although, Steiner *et al*. (2007) conducted their study in an estuary, blacktips sharks in the Grand Strand could be displaying similar behavior at piers. Economakis and Lobel (1998) also observed that grey reef shark (*Carcharhinus amblyrhynchos*) aggregation behavior was significantly correlated with water temperature, tidal height, and diel cycle. Interestingly, both tidal and diel cycle influenced shark presence at piers, but sharks did not visit piers at periodic stages in either cycle (Fig. 5; Papastamatiou *et al*. 2009, Papastamatiou *et al*. 2010). The lack of periodicity indicates that, while tidal and diel cycle were influencing factors, they were not the sole factors affecting their presence at piers. Other, unexplored factors such as barometric pressure (Heupel *et al*. 2003), dissolved oxygen (Carlson & Parsons 2001), or chlorophyll (Hearn *et al*. 2010, Meyer *et al*. 2010) could also be influencing their behavior at piers.

This study provides evidence of a potential association of some sharks to fishing piers, but more data are needed in order to validate and quantify this association and determine all the factors influencing such behavior. The majority of blacktip sharks displayed varying degrees of fidelity at piers. Tagging and monitoring of additional individuals could provide insight on the occurrence of blacktip shark fidelity to fishing piers. Papastamatiou *et al*. (2010) speculated that shifts in behavioral and density-mediated interactions could potentially result in sharks being displaced from other locations. Unfortunately, data are lacking on blacktip shark density and demographics in the Grand Strand prior to construction of the fishing piers. Future studies should also address the foraging ecology of blacktip sharks at fishing piers and how this may affect local prey communities. Supplementary monitoring sites including those like Pawley's Pier, which sees little, irregular fishing pressure, could potentially answer questions regarding the attraction of sharks to pier structure versus the effects of fishing effort and/or provisioning. A comprehensive array of receivers that includes a large network of nearshore receivers could answer questions regarding the attraction of sharks to piers compared to natural environments. Although this study was limited by the number of animals tagged and sites monitored, it has highlighted the varying habitat use behaviors of one species of shark at fishing piers and some factors that may influence this behavior.

Common name	Scientific name	Trent *et al.*1997	Thorpe *et al.* 2004	Ulrich *et al.* 2007
Small Coastal				
Atlantic sharpnose shark	*Rhizoprionodon terraenovae*	52.20	81.76	57.56
Finetooth shark	*Carcharhinus isodon*	3.90	0.91	9.01
Bonnethead	*Sphyrna tiburo*	6.80	8.60	8.57
Blacknose shark	*Carcharhinus acronotus*	20.31	1.93	4.88
Large Coastal				
Sandbar shark	*Carcharhinus plumbeus*	0.04	0.11	4.55
Blacktip shark	*Carcharhinus limbatus*	14.00	0.89	2.64
Scalloped hammerhead	*Sphyrna lewini*	3.00	0.29	2.39
Tiger shark	*Galeocerdo cuvier*	0.01	0.02	0.37
Spinner shark	*Carcharhinus brevipinna*	0.80	2.27	0.33
Nurse shark	*Ginglymostoma cirratum*			0.27
Dusky shark	*Carcharhinus obscurus*		0.10	0.09
Lemon shark	*Negaprion brevirostris*	0.01		0.06
Sand tiger	*Carcharias taurus*		0.08	0.03
Bull shark	*Carcharhinus leucus*	0.02		0.03
Silky shark	*Carcharhinus falciformis*			0.01
Great hammerhead	*Sphyrna mokarran*	0.20		
Pelagic				
Thresher shark	*Alopias vulpinus*			0.01
Dogfishes				
Smooth dogfish	*Mustelus canis*		2.88	7.93
Spiny dogfish	*Squalus acanthias*		0.02	1.27

Table 1. Proportional catches (%) of shark species from three different studies conducted along southern Georgia and northeastern Florida (Trent *et al*. 1997), southeastern North Carolina (Thorpe *et al*. 2004), and South Carolina (Ulrich *et al*. 2007).

Pier	2016	2017
Apache Pier	19	16
Pier 14	19	17
2nd Ave. Pier	11	13
Springmaid Pier	9	
MBSP Pier	12	10
Garden City Pier		7

Table 2. Number of creel surveys conducted at each pier for each sampling year. *MBSP* refers to Myrtle Beach State Park.

Blacktip Shark Potential Prey Species

Common Name	Scientific Name	Total catch	CPUE
Bony Fishes			
Atlantic croaker	*Micropogonias undulatus*	707	0.149
Atlantic cutlassfish	*Trichiurus lepturus*	475	0.100
Southern whiting	*Menticirrhus americanus*	411	0.087
Pinfish	*Lagodon rhomboides*	391	0.083
Common sea robin	*Prionotus carolinus*	107	0.023
Florida pompano	*Trachinotus carolinus*	101	0.021
Spanish mackerel	*Scomberomorus maculatus*	88	0.019
Bluefish	*Pomatomus saltatrix*	85	0.018
Black sea bass	*Centropristis striata*	74	0.016
Spot croaker	*Leiostomus xanthurus*	65	0.014
Oyster toadfish	*Opsanus tau*	52	0.011
Pigfish	*Orthopristis chrysoptera*	24	0.005
Atlantic spadefish	*Chaetodipterus faber*	22	0.005
Red drum	*Sciaenops ocellatus*	21	0.004
Southern flounder	*Paralichthys lethostigma*	19	0.004
Atlantic menhaden	*Brevoortia tyrannus*	16	0.003
Spotted seatrout	*Cynoscion nebulosus*	14	0.003
Weakfish	*Cynoscion regalis*	14	0.003
Black drum	*Pogonias cromis*	13	0.003
Northern whiting	*Menticirrhus saxatilis*	13	0.003
Southern sheepshead	*Archosargus probatocephalus*	11	0.002
Atlantic bumper	*Chloroscombrus chrysurus*	5	0.001
Sciaenidae unid.	Sciaenidae	5	0.001
Spottail pinfish	*Diplodus holbrookii*	4	0.001
Inshore lizardfish	*Synodus foetens*	2	<0.001
Jack crevalle	*Caranx hippos*	2	<0.001
Rock sea bass	*Centropristis philadelphica*	1	<0.001
Gulf whiting	*Menticirrhus littoralis*	0	<0.001
Cartilaginous Fishes			
Atlantic sharpnose shark	*Rhizoprionodon terraenovae*	126	0.027
Atlantic stingray	*Hypanus sabina*	10	0.002
Bluntnose stingray	*Hypanus say*	7	0.001
Bonnethead	*Sphyrna tiburo*	6	0.001
Southern stingray	*Hypanus americana*	6	0.001
Smooth butterfly ray	*Gymnura micrura*	5	0.001
Blacknose shark	*Carcharhinus acronotus*	3	0.001
Blacktip shark	*Carcharhinus limbatus*	2	<0.001
Dasyatidae unid.	Dasyatidae	2	<0.001
Scalloped hammerhead	*Sphyrna lewini*	2	<0.001
Common guitarfish	*Rhinobatos rhinobatos*	1	<0.001
Sandbar shark	*Carcharhinus plumbeus*	1	<0.001
Crustaceans			
Blue crab	*Callinectes sapidus*	3	0.001
Florida stone crab	*Menippe mercenaria*	1	<0.001
Mottled purse crab	*Persephona mediterranea*	1	<0.001
Ocellate lady crab	*Ovalipes ocellatus*	0	<0.001

Table 3. List of species classified as potential prey for blacktip sharks (Walls *et al*. 2002, Bethea *et al*. 2004, Compagno *et al*. 2005) and recorded in pier creel surveys. *CPUE* refers to catch per unit effort and is defined as the total catch for both sampling seasons divided by the total number of rods (n = 4734).

Tag number	Total length (cm)	Sex	Area tagged	Release date	Date of last detection	Monitoring period	Number of days detected	Pier association index
48575	159	F	MBSP	20-May-17	31-Aug-17	104	73	0.702
48576	158	F	MBSP	20-May-17	31-Aug-17	104	71	0.682
97	162	F	MBSP	26-Jun-17	31-Aug-17	67	39	0.582
44578	168	M	2nd Ave.	21-Jul-16	5-Nov-16	108	50	0.463
48573	152	F	MBSP	9-Jun-17	29-Aug-17	82	19	0.232
48577	140	F	MBSP	20-May-17	1-Sep-17	105	17	0.162
96	133	F	MBSP	6-Aug-17	30-Aug-17	25	3	0.120
48574	170	M	MBSP	21-May-17	18-Jul-17	59	7	0.119
45355	113	F	2nd Ave.	22-Jul-16	21-Jul-16	0	0	0
44570	112	M	MBSP	25-Jul-16	24-Jul-16	0	0	0
44571	141	F	MBSP	25-Jul-16	24-Jul-16	0	0	0
98	170	F	MBSP	16-Aug-17	15-Aug-17	0	0	0

Table 4. Capture and detection information for the 12 sharks tagged between 21 July 2016 and 17 August 2017. The number of days monitored refers to the total number of days from release date to date of last detection. Pier association index is the total number of days detected at piers divided by the number of days monitored.

Model	BIC	ΔBIC	w_i
Pier + Diel Cycle + (1|Transmitter)	1640.70	0.00	0.52
Pier + (1|Transmitter)	1642.48	1.77	0.22
Pier + CPUE + Diel Cycle + (1|Transmitter)	1642.92	2.21	0.17
Pier + CPUE + (1|Transmitter)	1646.69	5.98	0.03
Pier + Diel Cycle + Tidal Cycle + (1|Transmitter)	1647.61	6.90	0.02
Diel Cycle + (1|Transmitter)	1648.46	7.76	0.01
Pier + Tidal Cycle + (1|Transmitter)	1648.89	8.19	0.01
Pier + CPUE + Diel Cycle + Tidal Cycle + (1|Transmitter)	1649.94	9.23	0.01
Pier + Water Temp. + Diel Cycle + (1|Transmitter)	1650.17	9.47	<0.01
(1|Transmitter)	1650.27	9.56	<0.01
Diel Cycle + CPUE + (1|Transmitter)	1651.53	10.82	<0.01
Pier + Water Temp. + (1|Transmitter)	1652.16	11.46	<0.01
Pier + Water Temp. + CPUE + Diel Cycle + (1|Transmitter)	1652.99	12.29	<0.01
Pier + CPUE + Tidal Cycle + (1|Transmitter)	1653.16	12.45	<0.01
Pier + Diel Cycle + Lunar Cycle + (1|Transmitter)	1654.24	13.54	<0.01
CPUE + (1|Transmitter)	1655.17	14.46	<0.01
Diel Cycle + Tidal Cycle + (1|Transmitter)	1655.59	14.89	<0.01
Pier + Water Temp. + CPUE + (1|Transmitter)	1656.78	16.08	<0.01
Tidal Cycle+ (1|Transmitter)	1656.90	16.19	<0.01
Pier + Water Temp. + Diel Cycle + Tidal Cycle + (1|Transmitter)	1657.05	16.35	<0.01
Pier + CPUE + Diel Cycle + Lunar Cycle + (1|Transmitter)	1657.84	17.14	<0.01
Diel Cycle + Lunar Cycle + (1|Transmitter)	1658.37	17.67	<0.01
Pier + Lunar Cycle + (1|Transmitter)	1658.38	17.67	<0.01
Water Temp. + Diel Cycle + (1|Transmitter)	1658.45	17.75	<0.01
Pier + Water Temp. + Tidal Cycle + (1|Transmitter)	1658.55	17.84	<0.01
Diel Cycle + CPUE + Tidal Cycle + (1|Transmitter)	1658.83	18.12	<0.01
Pier + Water Temp. + CPUE + Diel Cycle + Tidal Cycle + (1|Transmitter)	1660.00	19.29	<0.01
Water Temp. + (1|Transmitter)	1660.36	19.66	<0.01
Pier + Diel Cycle + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1661.12	20.42	<0.01
Water Temp. + CPUE + Diel Cycle + (1|Transmitter)	1661.77	21.07	<0.01
CPUE + Tidal Cycle + (1|Transmitter)	1661.90	21.20	<0.01
Lunar Cycle + (1|Transmitter)	1662.42	21.72	<0.01
Pier + Water Temp. + Diel Cycle + Lunar Cycle + (1|Transmitter)	1662.73	22.02	0.00
Diel Cycle + CPUE + Lunar Cycle + (1|Transmitter)	1662.84	22.14	0.00
Pier + Water Temp. + CPUE + Tidal Cycle + (1|Transmitter)	1663.23	22.53	0.00
Pier + CPUE + Lunar Cycle + (1|Transmitter)	1663.60	22.89	0.00
Pier + Tidal Height + Lunar Cycle + (1|Transmitter)	1664.69	23.99	0.00
Pier + CPUE + Diel Cycle + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1664.84	24.13	0.00
Water Temp. + CPUE + (1|Transmitter)	1665.40	24.70	0.00
Diel Cycle + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1665.43	24.72	0.00
Water Temp. + Tidal Cycle + Diel Cycle + (1|Transmitter)	1665.57	24.86	0.00
Water Temp. + Tidal Cycle + (1|Transmitter)	1666.97	26.27	0.00
Pier + Water Temp. + CPUE + Diel Cycle + Lunar Cycle + (1|Transmitter)	1667.84	27.14	0.00
Pier + Water Temp. + Lunar Cycle + (1|Transmitter)	1668.07	27.36	0.00
CPUE + Lunar Cycle + (1|Transmitter)	1668.30	27.59	0.00
Water Temp. + Diel Cycle + Lunar Cycle + (1|Transmitter)	1668.40	27.70	0.00
Tidal Height + Lunar Cycle + (1|Transmitter)	1668.88	28.18	0.00
Water Temp. + Tidal Cycle + Diel Cycle + CPUE + (1|Transmitter)	1669.06	28.36	0.00
Pier + CPUE + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1669.97	29.27	0.00
Diel Cycle + CPUE + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1670.03	29.33	0.00
Pier + Water Temp. + Diel Cycle + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1670.58	29.88	0.00
Water Temp. + CPUE + Tidal Cycle + (1|Transmitter)	1672.13	31.42	0.00
Water Temp. + Lunar Cycle + (1|Transmitter)	1672.55	31.84	0.00
Water Temp. + Diel Cycle + Lunar Cycle + CPUE + (1|Transmitter)	1673.05	32.35	0.00
Pier + Water Temp. + CPUE + Lunar Cycle + (1|Transmitter)	1673.62	32.91	0.00
Pier + Water Temp. + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1674.34	33.64	0.00
Pier + Water Temp. + CPUE + Diel Cycle + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1674.82	34.11	0.00
CPUE + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1674.84	34.14	0.00
Water Temp. + Tidal Cycle + Diel Cycle + Lunar Cycle + (1|Transmitter)	1675.44	34.73	0.00
Water Temp. + CPUE + Lunar Cycle + (1|Transmitter)	1678.51	37.80	0.00
Water Temp. + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1678.98	38.28	0.00
Pier + Water Temp. + CPUE + Tidal Cycle + Lunar Cycle + (1|Transmitter)	1679.96	39.26	0.00
Water Temp. + Tidal Cycle+ Diel Cycle + Lunar Cycle + CPUE + (1|Transmitter)	1680.23	39.53	0.00
Water Temp. + Tidal Height + Lunar Cycle + CPUE + (1|Transmitter)	1685.04	44.33	0.00

Table 5. General linear mixed model results from all sharks tested for all possible subsets (lowest BIC first). *ΔBIC* indicates the lowest BIC value subtracted from the resulting model BIC value, and w_i is the Schwarz weight associated with each model for the duration sharks spent at piers.

	Independent Variable	Coefficient estimate (95% CI)	Odds ratio (95% CI)
GLM	Diel cycle (Day)	NA	NA
	Diel cycle (Night)	-0.504 (-0.806 – -0.173)	NA
	Pier (2nd Avenue)	NA	NA
	Pier (Garden City)	-1.460 (-2.933 – 0.005)	NA
	Pier (MBSP)	0.952 (0.417 – 1.461)	NA
	Pier (Pier 14)	-0.965 (-1.601 – -0.304)	NA
GLMM	Tidal Height	0.274 (0.171 – 0.377)	1.315 (1.187 – 1.458)
	Diel cycle (Day)	NA	NA
	Diel cycle (Night)	-0.835 (-0.963 – -0.708)	0.434 (0.382 – 0.493)

Table 6. Coefficient estimates and odds ratios for variables termed in the most likely model for GLM and GLMM. The abbreviation *NA* refers to not applicable.

Model	BIC	ΔBIC	w_i
Diel Cycle + Tidal Cycle + (1|Transmitter)	7538.87	0.00	0.95
Diel Cycle + Tidal Cycle + Lunar Cycle + (1|Transmitter)	7545.91	7.04	0.03
Diel Cycle + CPUE + Tidal Cycle + (1|Transmitter)	7546.97	8.10	0.02
Water Temp. + Tidal Cycle + Diel Cycle + (1|Transmitter)	7548.36	9.48	0.01
Diel Cycle + CPUE + Tidal Cycle + Lunar Cycle + (1|Transmitter)	7553.39	14.52	<0.01
Water Temp. + Tidal Cycle + Diel Cycle + Lunar Cycle + (1|Transmitter)	7555.16	16.29	<0.01
Water Temp. + Tidal Cycle + Diel Cycle + CPUE + (1|Transmitter)	7556.45	17.58	<0.01
Diel Cycle + (1|Transmitter)	7556.94	18.06	<0.01
Water Temp. + Tidal Cycle+ Diel Cycle + Lunar Cycle + CPUE + (1|Transmitter)	7562.91	24.04	<0.01
Diel Cycle + CPUE + (1|Transmitter)	7563.65	24.77	<0.01
Diel Cycle + Lunar Cycle + (1|Transmitter)	7564.56	25.68	<0.01
Water Temp. + Diel Cycle + (1|Transmitter)	7566.34	27.46	<0.01
Diel Cycle + CPUE + Lunar Cycle + (1|Transmitter)	7570.49	31.61	<0.01
Water Temp. + CPUE + Diel Cycle + (1|Transmitter)	7573.12	34.24	<0.01
Water Temp. + Diel Cycle + Lunar Cycle + (1|Transmitter)	7573.68	34.81	<0.01
Water Temp. + Diel Cycle + Lunar Cycle + CPUE + (1|Transmitter)	7580.02	41.14	<0.01
Tidal Cycle+ (1|Transmitter)	7706.57	167.70	<0.01
Tidal Height + Lunar Cycle + (1|Transmitter)	7713.47	174.60	<0.01
CPUE + Tidal Cycle + (1|Transmitter)	7715.17	176.30	<0.01
Water Temp. + Tidal Cycle + (1|Transmitter)	7715.61	176.74	<0.01
(1|Transmitter)	7721.43	182.56	<0.01
CPUE + Tidal Cycle + Lunar Cycle + (1|Transmitter)	7721.55	182.68	<0.01
Water Temp. + Tidal Cycle + Lunar Cycle + (1|Transmitter)	7721.92	183.05	<0.01
Water Temp. + CPUE + Tidal Cycle + (1|Transmitter)	7724.55	185.68	<0.01
Lunar Cycle + (1|Transmitter)	7728.90	190.03	<0.01
CPUE + (1|Transmitter)	7729.01	190.14	<0.01
Water Temp. + (1|Transmitter)	7730.25	191.37	<0.01
Water Temp. + Tidal Height + Lunar Cycle + CPUE + (1|Transmitter)	7730.61	191.74	<0.01
CPUE + Lunar Cycle + (1|Transmitter)	7735.81	196.94	<0.01
Water Temp. + Lunar Cycle + (1|Transmitter)	7737.12	198.25	<0.01
Water Temp. + CPUE + (1|Transmitter)	7738.40	199.52	<0.01
Water Temp. + CPUE + Lunar Cycle + (1|Transmitter)	7744.91	206.04	<0.01

Table 7. Generalized linear mixed models representing all possible subsets (lowest BIC first). *ΔBIC* indicates the lowest BIC value subtracted from the resulting model BIC value and w_i is the Schwarz weight associated with each model for presence versus absence.

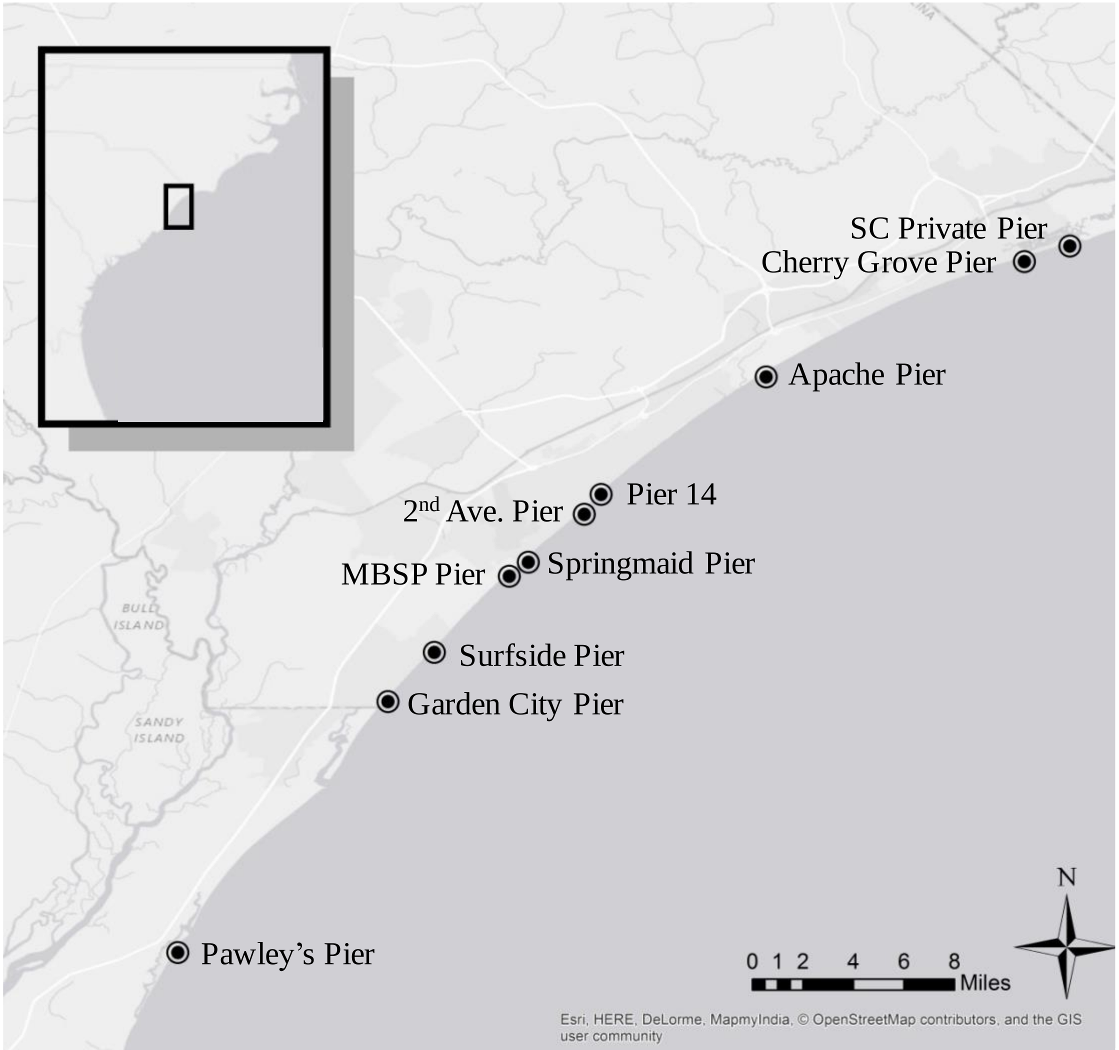

Fig. 1. All piers in the Grand Strand in 2016 prior to Hurricane Matthew. *SC Private Pier* refers to Sea Cabin Private Pier and *MBSP Pier* refers to Myrtle Beach State Park Pier. Basemap ESRI, Inc.

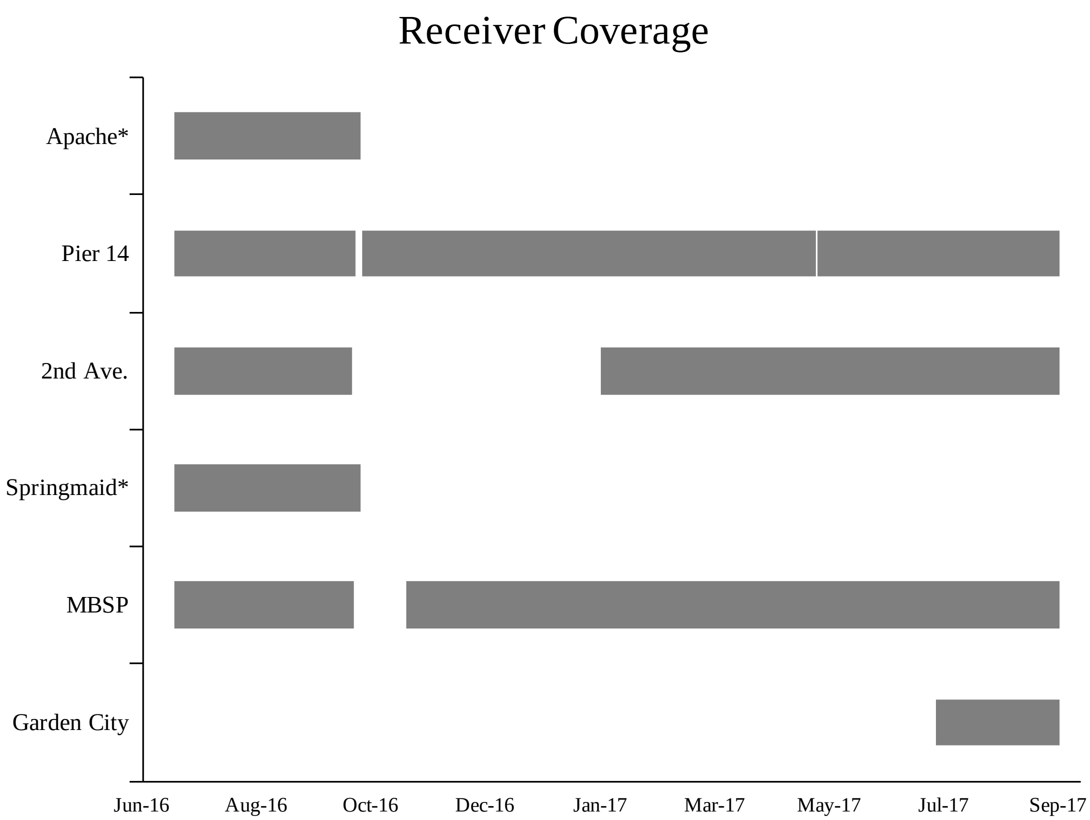

Fig. 2. Piers monitored with receivers and their corresponding coverages by date. Gaps represent absences in coverage for that location. Asterisks indicate piers monitored by the South Carolina Department of Natural Resources. *MBSP* refers to Myrtle Beach State Park Pier and the abbreviation *2nd Ave.* refers to 2nd Avenue Pier.

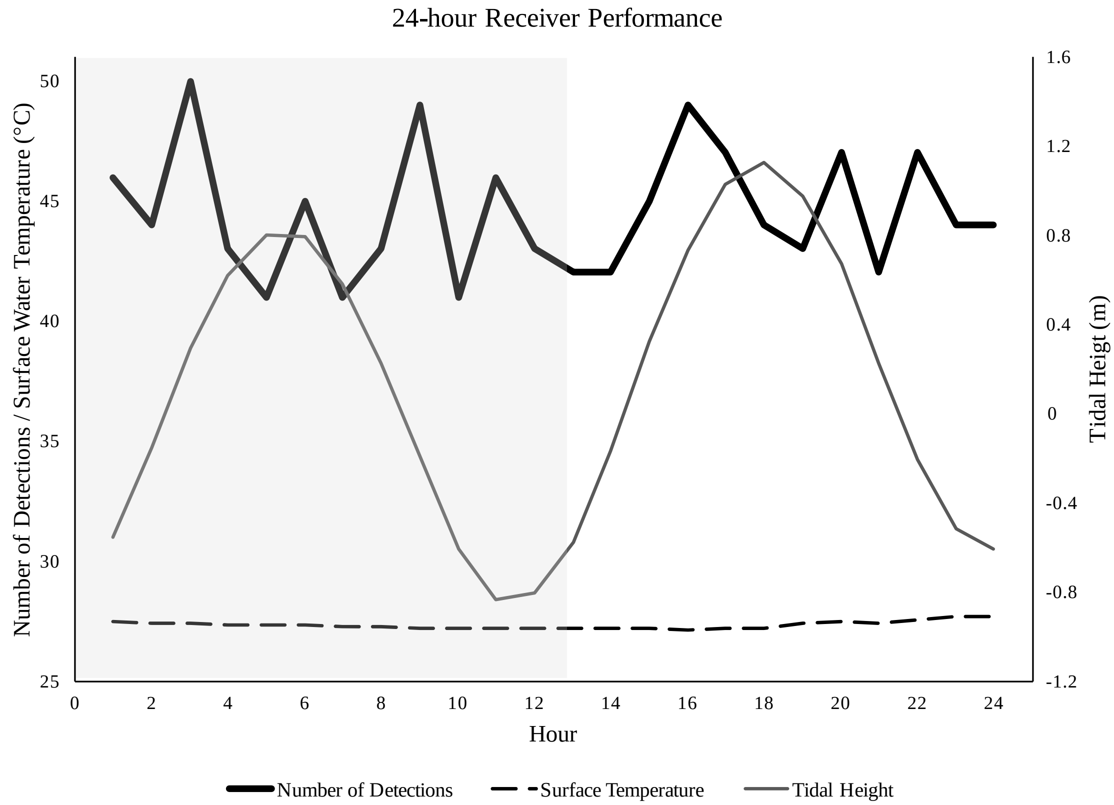

Fig. 3. Number of detections per hour from a deceased shark plotted against tidal height and surface water temperature. Shaded region indicates night; unshaded region indicates day.

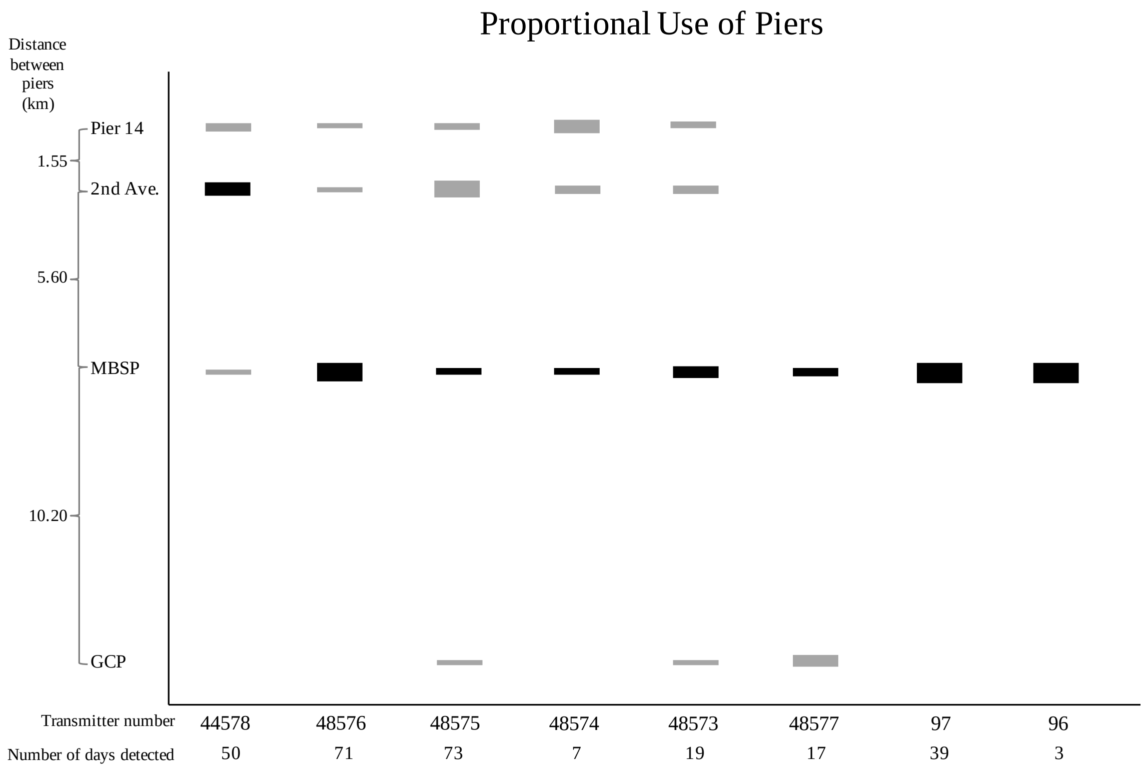

Fig. 4. Proportional use of piers for each shark (x-axis) detected post-release. Bar thickness is proportional to the fraction of days spent at that location over the number of days detected. Black bars indicate that the shark was tagged at the corresponding pier on the y-axis. Pier locations along the y-axis are in order from the most northerly pier at the top to the most southerly at the bottom. The total number of days detected at piers is indicated below each tag number.

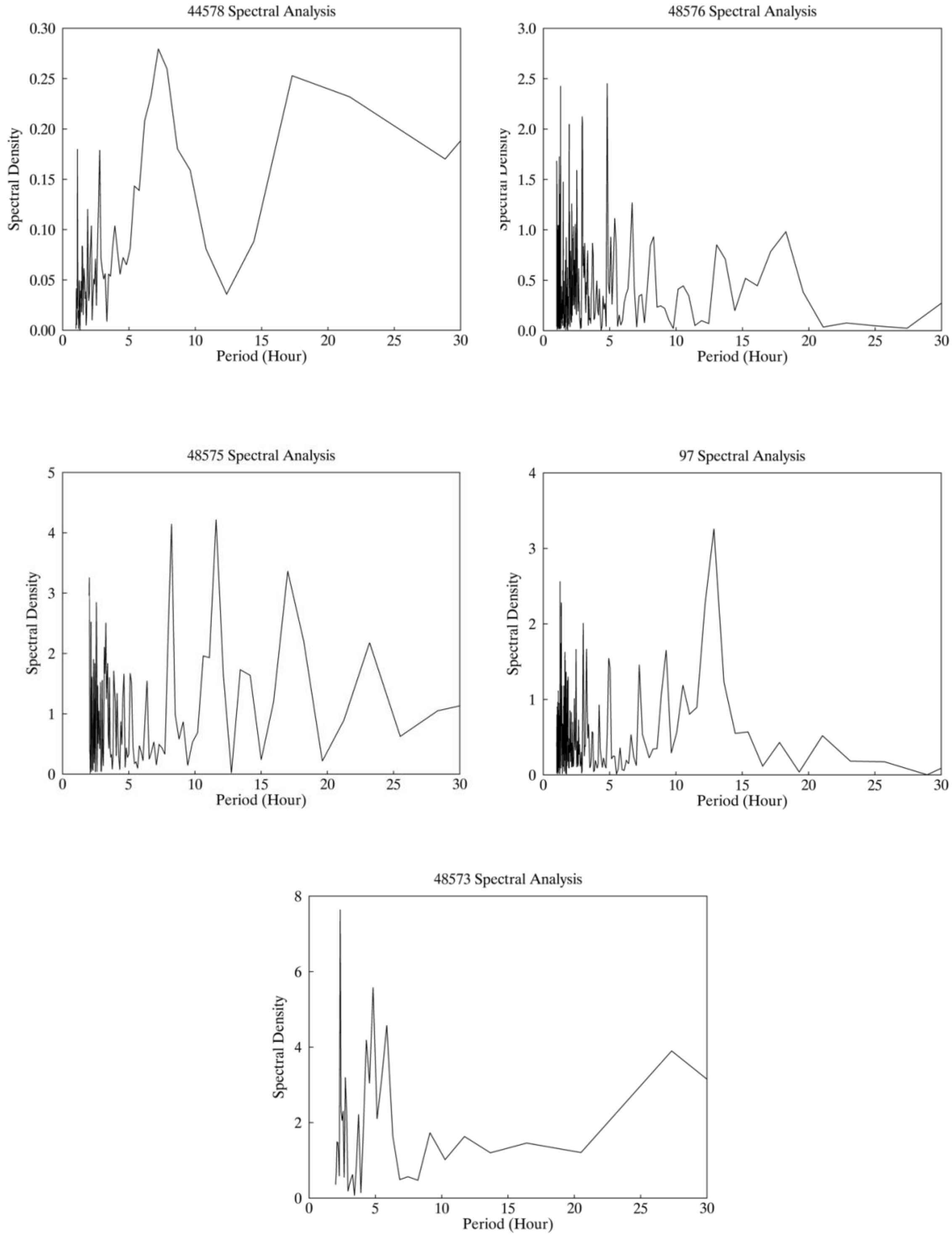

Fig. 5. Spectral density graphs generated from the fast Fourier transformation analyses for individuals with greater than 200 detections.

References

Abel DC, Young RF, Garwood JA, Travaline MJ, Yednock BK (2007) Survey of the shark fauna in two South Carolina estuaries and the impact of salinity structure. Am Fish Soc Symp 50:109

Able KW, Grothues TM, Kemp IM (2013) Fine-scale distribution of pelagic fishes relative to a large urban pier. Mar Ecol Prog Ser 476:185-198

Allee WC, Dickinson Jr JC (1954) Dominance and subordination in the smooth dogfish *Mustelus canis* (Mitchill). Physiol Zool 27:356-364

Baldwin WE, Morton RA, Denny JF, Dadisman SV, Schwab WC, Gayes PT, Driscoll NW (2004) Maps showing the stratigraphic framework of South Carolina's Long Bay from Little River to Winyah Bay. Open-file Rep (US Geol Surv) 1013:28

Barry KP, Condrey RE, Driggers WB, Jones CM (2008) Feeding ecology and growth of neonate and juvenile blacktip sharks *Carcharhinus limbatus* in the Timbalier–Terrebone Bay complex, LA, USA. J Fish Biol 73:650-662

Barwick RD, Kwak TJ, Noble RL, Barwick DH (2004) Fish populations associated with habitat-modified piers and natural woody debris in Piedmont Carolina reservoirs. N Am J Fish Manage 24:1120-1133

Bates D, Maechler M, Bolker B, Walker S (2017) Linear Mixed-Effects Models using 'Eigen' and S4. R package version 1.1-14. Available at https://CRAN.R-project.org/web/packages/lme4 (accessed February 2017)

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser 268:245-264

Branstetter S (1987) Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. Copeia 964-974

Burchmore JJ, Pollard DA, Bell JD, Middleton MJ, Pease BC, Matthews J (1985) An ecological comparison of artificial and natural rocky reef fish communities in Botany Bay, New South Wales, Australia. Bull Mar Sci 37:70-85

Burgess GH (1998) Diving with elasmobranchs: a call for restraint. Shark News 11:1-3

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261-304

Bush A (2003) Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kāne'ohe Bay, Ō'ahu, Hawai'i. Environ Biol Fishes 67:1-11

Carlson JK, Parsons GR (2001) The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. Environ Biol Fishes 61:427-433

Castro JI (1996) Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. Bull Mar Sci 59:508-522

Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Annu Rev Mar Sci 7:547-570

Compagno LJV, Dando M, Fowler S (2005) Princeton Field guides: sharks of the world. Princeton University Press, Princeton, NJ, p 300

Economakis AE, Lobel PS (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environ Biol Fishes 51:129-139

Ellis JK, Musick JA (2007) Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. Environ Biol Fishes 80:51-67

Espinoza M, Farrugia TJ, Lowe CG (2011) Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. J Exp Mar Biol Ecol 401:63-74

Filmalter JD, Dagorn L, Cowley PD, Taquet M (2011) First descriptions of the behavior of silky sharks, *Carcharhinus falciformis*, around drifting fish aggregating devices in the Indian Ocean. Bull Mar Sci 87:325-337

Fréon P, Dagorn L (2000) Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. Rev Fish Biol Fish 10:183-207

Glass NR (1971) Computer analysis of predation energetics in the largemouth bass. Syst Anal Sim Ecol 1:325-363

Hammerschlag N, Gutowsky LFG, Gallagher AJ, Matich P, Cooke SJ (2017a) Diel habitat use patterns of a marine apex predator (tiger shark, Galeocerdo cuvier) at a high use area exposed to dive tourism. J Exp Mar Biol Ecol 495:24-34

Hammerschlag N, Skubel RA, Calich H, Nelson ER, Shiffman DS, Wester J, and others (2017b) Nocturnal and crepuscular behavior in elasmobranchs: a review of movement, habitat use, foraging, and reproduction in the dark. Bull Mar Sci 93:355-374

Hearn A, Ketchum J, Klimley AP, Espinoza E, Penaherrera C (2010) Hotspots within hotspots? hammerhead shark movements around wolf island, galapagos marine reserve. Mar Biol 157:1899-1915

Heithaus MR (2001) Predator–prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. J Zool 253:53-68

Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Aust J Mar Freshwater Res 53:543-550

Heupel MR, Simpfendorfer CA (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239-1249

Heupel MR, Simpfendorfer CA, Fitzpatrick R (2010) Large-scale movement and reef fidelity of grey reef sharks. PLOS ONE 5:e9650

Heupel MR, Simpfendorfer CA, Hueter RE (2003) Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. J Fish Biol 63:1357-1363

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fishes 71:135-142

Holland KN, Wetherbee BM, Lowe CG, Meyer CG (1999) Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Mar Biol 134:665-673

Kajiura SM, Tellman SL (2016) Quantification of massive seasonal aggregations of blacktip sharks (*Carcharhinus limbatus*) in Southeast Florida. PLOS ONE 11:e0150911

Killam KA, Parsons GR (1989) Age and growth of the blacktip shark, *Carcharhinus limbatus*, near Tampa Bay, Florida. Fish Bull 87:845-857

Klimley AP, Butler SB, Nelson DR, Stull AT (1988) Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. J Fish Biol 33:751-761

Kock A, O'Riain MJ, Mauff K, Meÿer M, Kotze D, Griffiths C (2013) Residency, habitat use and sexual segregation of white sharks, Carcharodon carcharias in False Bay, South Africa. PLOS ONE 8:e55048

Libes S, Kindelberger S (2010) Hypoxia in the nearshore coastal waters of South Carolina along the Grand Strand. Proc 2010 S C Environ Con

Limbaugh C (1963) Field notes on sharks. Sharks Surv 2:63-94

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fishes 47:203-211

Lowe CG, Wetherbee BM, Meyer CG (2006) Using acoustic telemetry monitoring techniques to quantify movement patterns and site fidelity of sharks and giant trevally around French Frigate Shoals and Midway Atoll. Atoll Res Bull 543:281-303

Melillo-Sweeting K, Turnbull SD, Guttridge TL (2014) Evidence of shark attacks on Atlantic spotted dolphins (Stenella frontalis) off Bimini, The Bahamas. Mar Mamm Sci 30:1158-1164

Meyer CG, Papastamatiou YP, Holland KN (2010) A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. Mar Biol 157:1857-1868

Myrberg Jr AA, Gruber SH (1974) The behavior of the bonnethead shark, *Sphyrna tiburo*. Copeia 358-374

Nelson DR (1974) Ultrasonic telemetry of shark behavior. Nav Rev 27:1-21

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996-1008

Papastamatiou YP, Itano DG, Dale JJ, Meyer CG, Holland KN (2010) Site fidelity and movements of sharks associated with ocean-farming cages in Hawaii. Mar Freshwater Res 61:1366-1375

Raftery AE (1995) Bayesian model selection in social research. Sociol Methodol 111-163

Randall JE (1977) Contribution to the biology of the whitetip reef shark (*Triaenodon obesus*). Pac Sci 31:143-164

RStudio Team (2015) RStudio: Integrated Development for R. RStudio, Inc., Boston, MA

Savino JF, Stein RA (1989) Behavioural interactions between fish predators and their prey: effects of plant density. Anim Behav 37:311-321

Schwarz G (1978) Estimating the dimension of a model. Ann Appl Stat 6:461-464

Speed CW, Field IC, Meekan MG, Bradshaw CJ (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408:275-293

Steiner PA, Michel MARCEL, O'Donnell PM (2007) Effects of tidal current on the movement patterns of juvenile bull sharks and blacktip sharks. Am Fish Soc Symp 50: 251.

Thorpe T, Jensen CF, Moser ML (2004) Relative abundance and reproductive characteristics of sharks in southeastern North Carolina coastal waters. Bull Mar Sci 74:3-20

Topping DT, Szedlmayer ST (2011) Site fidelity, residence time and movements of red snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring. Mar Ecol Prog Ser 437:183-200

Trent L, Parshley DE, Carlson JK (1997) Catch and bycatch in the shark drift gillnet fishery off Georgia and east Florida. Mar Fish Rev 59:19-28

Tricas TC (1979) Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fish Bull 77:175-182

Ulrich GF, Jones CM, Driggers WB, Drymon JM, Oakley D, Riley C (2007) Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. Am Fish Soc Symp 50:125

Voegeli F, Smale M, Webber D, Andrade Y, O'Dor R (2001) Ultrasonic Telemetry, Tracking and Automated Monitoring Technology for Sharks. Environ Biol Fishes 1:267-282

Walls EA, Berkson J, Smith SA (2002) The horseshoe crab, *Limulus polyphemus*: 200 million years of existence, 100 years of study. Rev Fish Sci 10:39-73

Watwood S (2015) Use of Acoustic Telemetry to Examine Habitat Preferences and Migration Patterns of Finetooth and Blacknose Sharks. Ann Meet Am Fish Soc

Welsh JQ, Bellwood DR (2012) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. Coral Reefs 31:55-65

West GJ, Stevens JD (2001) Archival tagging of school shark, *Galeorhinus galeus,* in Australia: initial results. In: The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson. Springer, Netherlands, p 283-298

Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. Mar Ecol Prog Ser 343:283-293

Appendix 1

Common Name	Scientific Name
Bony fishes	
Atlantic bumper	*Chloroscombrus chrysurus*
Atlantic croaker	*Micropogonias undulatus*
Atlantic cutlassfish	*Trichiurus lepturus*
Atlantic spadefish	*Chaetodipterus faber*
Black drum	*Pogonias cromis*
Black sea bass	*Centropristis striata*
Bluefish	*Pomatomus saltatrix*
Common sea robin	*Prionotus carolinus*
Conch	Melongenidae
Florida pompano	*Trachinotus carolinus*
Gulf whiting	*Menticirrhus littoralis*
Inshore lizardfish	*Synodus foetens*
Jack crevalle	*Caranx hippos*
Atlantic menhaden	*Brevoortia tyrannus*
Northern whiting	*Menticirrhus saxatilis*
Oyster toadfish	*Opsanus tau*
Pigfish	*Orthopristis chrysoptera*
Pinfish	*Lagodon rhomboides*
Red drum	*Sciaenops ocellatus*
Remora	*Remora remora*
Rock sea bass	*Centropristis philadelphica*
Sciaenidae unid.	Sciaenidae
Southern flounder	*Paralichthys lethostigma*
Southern puffer	*Sphoeroides nephelus*
Southern sheepshead	*Archosargus probatocephalus*
Southern whiting	*Menticirrhus americanus*
Spanish mackerel	*Scomberomorus maculatus*
Spot croaker	*Leiostomus xanthurus*
Spottail pinfish	*Diplodus holbrookii*
Spotted seatrout	*Cynoscion nebulosus*
Striped burrfish	*Chilomycterus schoepfi*
Weakfish	*Cynoscion regalis*
Cartilaginous Fishes	
Atlantic sharpnose	*Rhizoprionodon terraenovae*
Atlantic stingray	*Hypanus sabina*
Blacknose shark	*Carcharhinus acronotus*
Blacktip shark	*Carcharhinus limbatus*
Bluntnose stingray	*Hypanus say*
Bonnethead	*Sphyrna tiburo*
Common guitarfish	*Rhinobatos rhinobatos*
Dasyatidae unid.	Dasyatidae
Sandbar shark	*Carcharhinus plumbeus*
Scalloped hammerhead	*Sphyrna lewini*
Smooth butterfly ray	*Gymnura micrura*
Southern stingray	*Hypanus americana*
Crustaceans	
Atlantic horseshoe crab	*Limulus polyphemus*
Blue crab	*Callinectes sapidus*
Florida stone crab	*Menippe mercenaria*
Mottled purse crab	*Persephona mediterranea*
Ocellate lady crab	*Ovalipes ocellatus*
Other	
Purple sea urchin	*Arbacia punctulata*
Scotch bonnet sea snail	*Semicassis granulata*
Sea nettle	*Chrysaora fuscescens*
Sea turtle unid.	Cheloniidae
Whelk	Buccinidae

Table S1: Comprehensive list of species observed during pier surveys. The abbreviation *unid.* refers to unidentified.