

REGULAR PAPER

Blacktip shark *Carcharhinus limbatus* presence at fishing piers in South Carolina: association and environmental drivers

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We tagged 12 *Carcharhinus limbatus* with acoustic transmitters and monitored their presence at five piers along the north-east coast of South Carolina, USA in 2016 and four piers in 2017 using acoustic receivers. Data were analysed with pier association indices (PAI), mixed models and fast Fourier transformation analyses to identify potential factors related to residence time and presence at piers and any cyclical patterns in visits to piers. While the majority of monitored *C. limbatus* were infrequently detected at piers, three (25.0%) were highly associated with piers (PAI \geq 0.50). Of the *C. limbatus* that were detected after initial capture, three (25.0%) recorded detection events only at the pier where they were tagged and two individuals (16.7%) recorded at least one detection event at all monitored piers. The best-fit model explaining *C. limbatus* residence time at piers included terms for pier location and diel cycle ($w_i = 0.88$), whereas the best fit model explaining presence-absence of *C. limbatus* at piers included terms for tidal height, diel cycle, barometric pressure and angler count ($w_i = 0.98$). *Carcharhinus limbatus* did not appear to display cyclical patterns in their visits to piers. Along the north-east coast of South Carolina, association of *C. limbatus* with piers is a phenomenon for a proportion of mature individuals, but continued research is necessary to understand if this behaviour is driven by attraction to and feeding on angler discards or increased foraging opportunities resulting from the attraction of potential prey to the physical structure provided by piers.

KEYWORDS

acoustic telemetry, blacktip shark, *Carcharhinus limbatus*, fishing piers, South Carolina

1 | INTRODUCTION

Coastal man-made structures, such as fishing piers, bridge pilings and docks, attract and support a wide variety of fishes (Barwick *et al.*, 2004; Burchmore *et al.*, 1985). Smaller fish congregate around these physically complex structures, which disrupt predator foraging efficiency (Glass, 1971; Savino & Stein, 1989) while providing cover for predatory fishes to ambush prey (Able *et al.*, 2013). The concentration of fishes around man-made structures provides coastal sharks, which are commonly observed around piers, with foraging opportunities (Ellis & Musick, 2007).

The blacktip shark *Carcharhinus limbatus* (Valenciennes 1839) is one of the most commonly observed shark species around fishing piers along the north-east coast of South Carolina, USA (K. Martin personal observation, June 2016). *Carcharhinus limbatus* migrates seasonally in the western north Atlantic Ocean (Castro, 1996; Kajiura &

Tellman, 2016) and from May until early November, they are one of the most commonly caught large coastal shark species in North Carolina (Thorpe *et al.*, 2004), South Carolina (Ulrich *et al.*, 2007) and the southern Georgia and north-east Florida waters (Trent *et al.*, 1997). Despite the seasonal abundance of *C. limbatus* and individuals commonly being observed near fishing piers, no scientific studies to date have specifically examined the association of *C. limbatus*, nor any other shark species, with coastal fishing piers.

Associative behaviour, 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 (Chapman *et al.*, 2015; Espinoza *et al.*, 2011; Heupel *et al.*, 2010; Heupel & Hueter, 2002; Kock *et al.*, 2013; Lowe *et al.*, 2006). In adult sharks, this behaviour is advantageous for feeding, mating, pupping, or resting (Speed *et al.*, 2010). In north-east South Carolina, sharks are commonly observed feeding on discarded fish and

entrails at piers and display conditioned responses to a splash in the water (K. Martin personal observation, June 2016), thus suggesting that sharks may in part congregate around fishing piers to feed. Although not intentional, provisioning sharks with food at fishing piers could influence their behaviour or where they aggregate. Moreover, association of *C. limbatus* with fishing piers could potentially make them vulnerable to exploitation from anglers (Kajiura & Tellman, 2016).

Carcharhinus limbatus are thought to respond to environmental cues that 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), water temperature (Castro, 1996; Kajiura & Tellman, 2016) and barometric pressure (Heupel *et al.*, 2003). Additionally, other factors, such as lunar cycle (West & Stevens, 2001) and number of anglers (*i.e.*, the amount of bait in the water or discards) could contribute to the presence of *C. limbatus* at fishing piers.

To address these knowledge gaps, we investigated factors that may potentially influence the association of *C. limbatus* with fishing piers along the north-east coast of South Carolina (pier location, diel cycle, tidal height, water temperature, lunar cycle, barometric pressure and the number of anglers fishing on the piers). Data were collected to address the following four questions: (a) does *C. limbatus* associate with fishing piers, (b) is there evidence of individual variation in association of sharks with specific fishing piers, (c) what environmental or physical factors, if any, influence shark residence time or presence at piers, and (d) does *C. limbatus* exhibit periodic or cyclical patterns in visits to fishing piers?

2 | MATERIALS AND METHODS

All animal handling complied with the institutional animal care and use committee policies and procedures.

2.1 | Site selection and positioning acoustic receivers

We studied the association of *C. limbatus* with fishing piers along the Grand Strand in north-east South Carolina during 2016 and 2017. The Grand Strand is a 93 km long region with a shallow, sloping coastal zone inundated by tidal inlets and swashes separated by predominantly wave-dominated and welded barrier islands and barrier spits (Baldwin *et al.*, 2004). Prior to hurricane Matthew in October 2016, ten fishing piers existed across the Grand Strand (Figure 1). Acoustic receivers (VR2W 69 kHz, Vemco; www.vemco.com) were placed at four of these piers: Pier 14, 2nd Avenue, Myrtle Beach State Park (MBSP) and Garden City piers (2017 only; Figure 1) to passively detect and record transmissions from implanted acoustic transmitters. Detections from receivers at two additional piers, Apache Pier and Springmaid Pier (Figure 1) were provided by the South Carolina Department of Natural Resources (SCDNR), until those piers were damaged by hurricane Matthew. Thus, five piers were monitored in 2016 (Apache, Pier 14, 2nd Avenue, Springmaid and MBSP) and four were monitored in 2017 (Pier 14, 2nd Avenue, MBSP and Garden City). Piers were selected based on proximity to one another

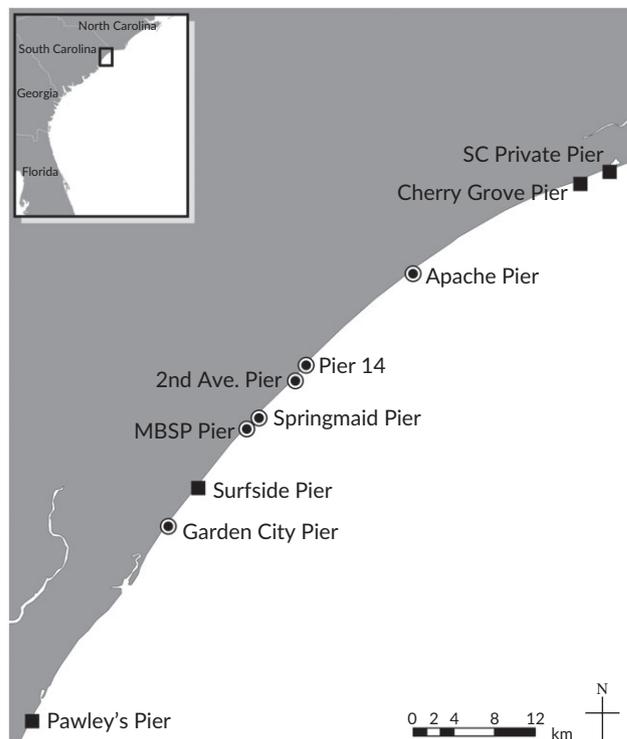


FIGURE 1 All piers in the Grand Strand, South Carolina in 2016 prior to Hurricane Matthew. Black circles indicate sites that were monitored with a receiver either in 2016, 2017, or both. Black squares indicate piers that were not monitored with an acoustic receiver. SC Private Pier, Sea Cabin Private Pier; MBSP Pier, Myrtle Beach State Park Pier; Ave., Avenue

(Figure 1). 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 were deployed c. 2–3 m from the bottom on rope secured to one of the horizontal supporting (collar) beams of the piers. Individual receiver deployment varied throughout the monitoring period, with some gaps in deployment due to equipment malfunction and the removal of equipment prior to hurricanes Matthew and Irma (Figure 2).

Detection efficiency and maximum detectable distance from the receiver were determined by conducting range testing at different distances from the MBSP Pier receiver. Limited detection range was desired to ensure that detected sharks could be assumed to be associated with piers. Starting 50 m east of the pier, we anchored a transmitter (Vemco V9-2 | 69 kHz, 15 s repeat rate, power output = 145 dB re 1 μ Pa at 1 m) in the water approximately 2–3 m from the bottom for 25 min to allow for 78 signal transmissions (Welsh & Bellwood, 2012). We then 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 & Bellwood, 2012).

2.2 | Tagging and environmental data collection

Carcharhinus limbatus were captured and tagged at two different locations within the Grand Strand: 2nd Avenue Pier and MBSP Pier.

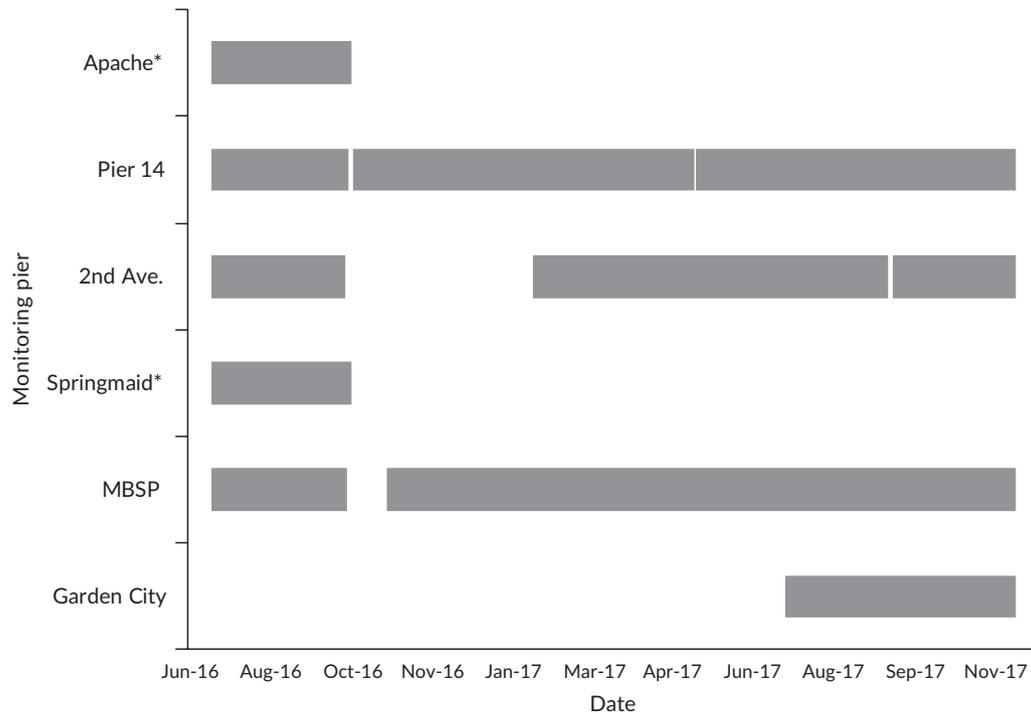


FIGURE 2 Receiver coverage by date 2016–2017 at piers monitoring *Carcharhinus limbatus* activity. Gaps represent absences in coverage for that location. MBSP, Myrtle Beach State Park Pier; 2nd Ave., 2nd Avenue Pier; *, piers monitored by the South Carolina Department of Natural Resources

Second Avenue Pier was the middle of monitored piers in 2016, whereas MBSP Pier became the middle pier in 2017 due to the inclusion of Garden City Pier (Figure 1). The middle pier was selected based on the assumption that tagged *C. limbatus* travelling to other piers might have a greater chance of being detected if the piers on either side of their release location were being monitored with acoustic receivers. Sharks were captured on baited longlines (as described in Abel *et al.*, 2007) and drum-lines set from a small boat near 2nd Avenue Pier and MBSP Pier and by hook-and-line directly from MBSP Pier. Nine *C. limbatus* were captured *via* the boat-based method and three were captured directly from the pier. *Carcharhinus limbatus* caught from the pier were brought alongside the pier, maneuvered into a net and lifted onto the pier. They were then placed in a 1.2 m diameter holding pool half filled with sea water at ambient temperature and salinity.

Once captured and secured, sharks were identified to species, sexed, and measured. Precaudal length (L_{PC}), fork length (L_F) and stretched total length (L_T) were recorded for each individual. Coded acoustic transmitters (V9-2 | 69 kHz, Vemco), with a battery life up to 1.5 years, were then implanted in the sharks. To implant transmitters, animals were first inverted and placed in tonic immobility. A 2 cm incision was made in the abdominal wall 2 cm off-centre and midway between the pelvic and pectoral fins (Holland *et al.*, 1999). Coated transmitters (9 × 29 mm, 2.9 g in air) 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 varied 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 righted and tagged with a unique colour-coded roto tag, or combination of tags (e.g., blue–blue), that were easily recognizable from fishing piers.

We collected environmental data to analyse the possible effects of physical variations in the environment on *C. limbatus* association with fishing piers. The factors explored in this study were chosen based on previously documented relationships with *C. limbatus* movements or anecdotal observations suggesting an influence on *C. limbatus* 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 6-h 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 categorisation ensured that all of high tide (1 h on either side of the time for high tide) and all of low tide (1 h 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; www.tidesandcurrents.noaa.gov) predictions at each pier. Hourly tidal height data by mean sea level (MSL) for Springmaid Pier were downloaded directly from NOAA's website and used for quantitative tidal cycle data. Following the destruction of Springmaid Pier by hurricane Matthew, we used NOAA's predicted tidal height data until measured data were again available (3.3% of observations). We deemed predicted tidal height data to be suitable for our analyses because on average, predicted high water heights were within 0.128 m of measured heights; predicted low water heights were within 0.144 m; and hourly heights were within 0.138 m (www.tidesandcurrents.noaa.gov).

We categorised lunar cycle using per cent illumination, gathered by the United States Naval Observatory (USNO; www.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. Per cent 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 (www.aa.usno.navy.mil). Sea surface temperature, barometric pressure and turbidity (to test detection efficiency) 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 monitoring equipment on 2nd Avenue Pier could not be reinstalled until early 2017. As a result, water temperature and barometric pressure data (2.8%) were used from a similar monitoring station at Cherry Grove Pier (Figure 1) when data at 2nd Avenue Pier were no longer available. Finally, count data for the total number of anglers fishing on all piers throughout the study area were obtained from the SCDNR. Although individual pier data were not available, count data across piers hypothetically reflects seasonal trends in angling effort or variation in effort as the result of weather conditions (e.g., lower effort on rainy days) that can be generalized across piers.

2.3 | Data analysis

Because there were no individuals that were detected in both 2016 and 2017, detection data were combined from 2016 and 2017 study periods for all analyses. The 2016 study period spanned from 14 July to 6 November and from 20 May to 27 November for 2017. The beginning dates correspond to the release date of the first individual tagged that year and the end dates correspond to the date of last detection for all tagged *C. limbatus* for that year.

To investigate the association of sharks with piers, we evaluated receiver data for each shark based on (a) number of days monitored, (b) detection events, (c) total number of days with a detection event, and (d) number of days with a detection event at each individual pier. Data gathered in the first 12 h were not included in analyses to allow a reasonable time for 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. We defined detection events as a minimum of two detections within a 30 min period from a single individual (Topping & Szedlmayer, 2011; Hammerschlag *et al.*, 2017a). A pier association index (PAI) value was generated for each *C. limbatus* by dividing the number of days with a detection event by the monitoring period. Individuals with PAIs greater than 0.50 were considered to be highly associated with fishing piers. The proportion of days detected at each pier was also calculated for each shark by dividing the number of days with a detection event at a particular pier by the total number of days with a detection event. We considered a shark exhibiting high use of a pier if an individual spent greater than 50% of their days with a detection event at a specific pier.

We used a linear mixed model (LMM) to assess if pier location, lunar cycle, tidal cycle, diel cycle, water temperature, barometric pressure and the number of anglers influenced the duration of detection

events at piers (Papastamatiou *et al.*, 2011). Prior to analysis, a natural log transformation of residence time plus one was calculated to normalize residuals and homogenize variances. Tidal and lunar cycle data were included as categorical variables because some detections spanned considerable periods of time. For example, detection events spanned 24 h 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 and barometric pressure were based on the beginning of detection events in order to evaluate the effect of those variables on the presence, or arrival, of *C. limbatus* at piers. Transmitter number was assigned as a random intercept variable to account for the disproportionate number of detection events across all individuals.

We used a binomial generalized linear mixed model (GLMM) to assess the potential influence of water temperature, tidal height, diel cycle, lunar cycle (per cent illumination), barometric pressure and the number of anglers on presence of individual *C. limbatus* at piers. Environmental data 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. Pier location was not included in this model because absences could not be assigned to a specific pier. Quantitative tidal and lunar cycle were used for the GLMM. Transmitter number was again assigned as a random variable. All possible model sub-sets were examined for the LMM and GLMM to identify relationships between independent variables and the response variables. Because the objective of these analyses was exploratory and not predictive, it was not necessary to break data into training and testing data sets to test model performance. We used Bayesian information criterion (BIC; Schwarz, 1978), information loss (Δ BIC; Raftery, 1995) and Schwarz weights (w_i ; Burnham & Anderson, 2004) to select the most likely model for each analysis. Finally, we calculated coefficient estimates (95% CI) for variables contained in the most likely LMM and coefficient estimates and odds ratios (95% CI) for variables contained in the most likely GLMM. About 9% of data points from the LMM ($n = 69$) and the GLMM ($n = 1864$) had to be removed due to missing water temperature or barometric pressure data as a result of sensor failure or removal of equipment prior to hurricanes Matthew and Irma. Statistical analyses for the mixed models were performed using the *lme4* package (Bates *et al.*, 2013) within RStudio (www.r-project.org).

Time series analyses were used to identify possible cyclical patterns in *C. limbatus* detections. Detections for individuals with greater than 200 observations were first summed into hourly bins (Papastamatiou *et al.*, 2009). We then conducted a fast Fourier transformation (FFT) with hamming window smoothing (Papastamatiou *et al.*, 2009), which converts detections into component frequencies and then searches the data set for cyclical patterns (Papastamatiou *et al.*, 2009). Periodicity of detections would be represented as peaks in a power spectrum. If power spectrum graphs had major and finite peaks, which would indicate that an individual had a high frequency of detections at a recurring interval (see Papastamatiou *et al.*, 2011), then sharks were determined to have displayed periodicity in their visits to piers. Multiple minor peaks were considered noise and sharks were determined to not have displayed periodicity (Papastamatiou *et al.*, 2009). Spectral analyses were performed using the interactive data language 4 (IDL; Harris Geospatial Solutions; www.harrisgeospatial.com).

3 | RESULTS

3.1 | Receiver performance and environmental data

Range testing confirmed that only detections 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 data on tag performance over a 24 h period were provided by the opportunistic use of a dead *C. limbatus* estimated to be less than 50 m from the receiver based on detection efficiency. Of 1152 transmissions from this animal, 1069 were recorded, resulting in a detection efficiency of 0.93. Potential relationships between detection efficiency and environmental variables such as turbidity, wind speed (indicative of wave height) and tidal height were assessed to determine if environmental conditions affected receiver performance. Neither turbidity, wind speed, nor tidal height appeared to influence the number of detections per hour throughout the 24 h period.

In 2016, water temperature ranged from 20.4–31.9°C ($\bar{x} = 27.1 \pm 0.06^\circ\text{C}$ SE) and in 2017, water temperature ranged from 18.8–30.6°C ($\bar{x} = 26.7 \pm 0.02^\circ\text{C}$). The highest monthly mean temperature occurred in August in both years; 29.4°C in 2016 and 28.6°C in 2017. Tidal height by msl ranged from –1.03 – +1.34 m in 2016 and from –1.36 – +1.37 m in 2017. Barometric pressure ranged from 750.8–770.9 mmHg in 2016 ($\bar{x} = 762.8 \pm 0.06$ mmHg) and from 746.2–772.3 mmHg ($\bar{x} = 761.7 \pm 0.02$ mmHg) in 2017. Total angler count per day for all piers included in the study site ranged from 169–1328 in 2016 and from 167–1494 in 2017. Angler count throughout the study period reached peak abundance in July for both

2016 and 2017 and then steadily declined until reaching minimum abundance in October for 2016 and November for 2017.

3.2 | Acoustic monitoring

We tagged 12 *C. limbatus* from 21 July 2016 through 16 August 2017 at 2nd Avenue Pier and MBSP Pier. Nine of the 12 individuals tagged were detected post-release resulting in 24,260 detections recorded at piers from 25 July 2016 to 27 November 2017 (Figure 3). Three *C. limbatus* (33.3%) were not detected post-release; two tagged in 2016 and one tagged in 2017. On average, *C. limbatus* were detected 36 days and the monitoring period for individuals averaged 112 days (release date plus 12h to date of last detection). Detection events (two detections from an individual within a 30 min period) ranged from 0.01–29.60 h ($\bar{x} = 1.52 \pm 0.12$ h SE; median = 0.44 h) with a total of 63,236.6 h recorded. About 72.4% ($n = 502$) of detection events were recorded during the day. Detection events recorded during the full ($n = 140$) and 1st quarter ($n = 142$) outnumbered events during the new ($n = 83$) and 3rd quarter ($n = 71$) lunar phases. Only one of the *C. limbatus* tagged in 2016 (tag #45355) was detected in 2017 (Figure 3). This individual was tagged in July 2016 but was not detected until November 2017 (Figure 3) at the same pier as it was initially captured.

The nine individuals that were detected displayed varying degrees of association with piers with PAIs ranging from 0.01 to 0.64 (Table 1). All but one of the five individual *C. limbatus* that displayed moderate to high PAIs were all adults (according to Branstetter, 1987 and Killam & Parsons, 1989) with $L_T \geq 158$ cm (Table 1). The majority of detection events for any individual tended to occur at a single pier. Six *C. limbatus* exhibited high use at the pier where they were tagged (Figure 4). Of those six sharks, three had detection events solely at the location where they were tagged (Figure 4). Conversely, two individuals had detection

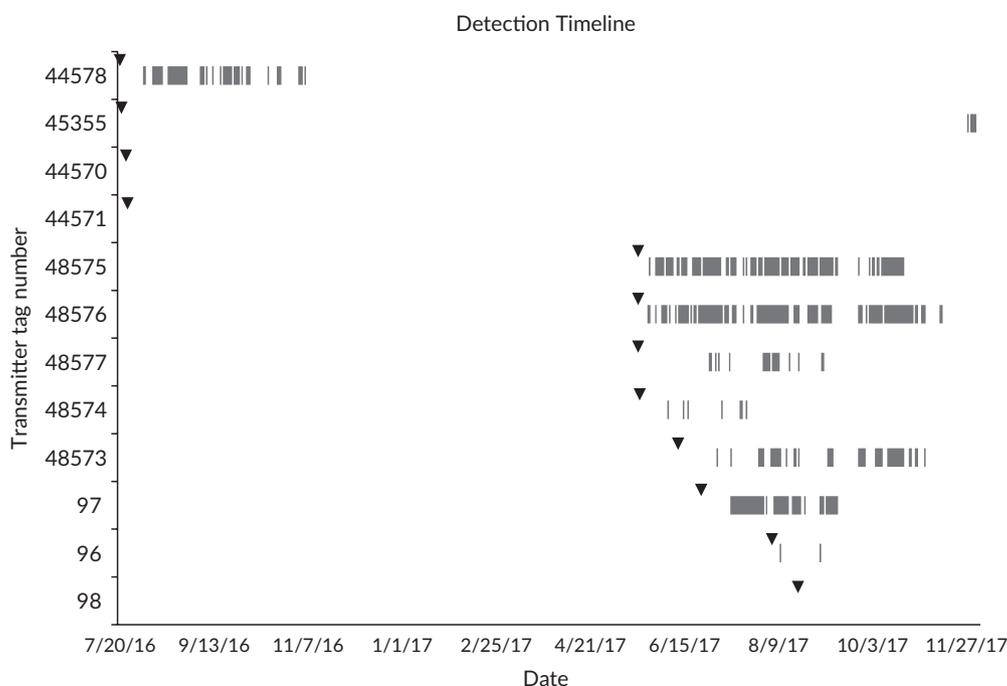


FIGURE 3 Timeline of detections for each *Carcharhinus limbatus* detected with an acoustic receiver in the Grand Strand, South Carolina. Black triangles indicate the release date for each individual

TABLE 1 Capture and detection information for the 12 *Carcharhinus limbatus* tagged between 21 July 2016 and 17 August 2017

Tag number	L_T (cm)	Sex	Area tagged	Release date	Date of last detection	MP (days)	Days with a detection event	PAI	Mean time spent at piers (min day ⁻¹)
48576	158	F	MBSP	20 May 17	8 Nov 17	173	108	0.64	175.27
97	162	F	MBSP	26 Jun 17	8 Sep 17	74	38	0.51	271.52
48575	159	F	MBSP	20 May 17	17 Oct 17	150	73	0.49	30.56
48573	152	F	MBSP	9 June 17	29 Oct 17	143	45	0.34	50.81
44578	168	M	2nd Ave.	21 July 16	7 Nov 16	110	38	0.31	5.33
96	133	F	MBSP	6 Aug 17	30 Aug 17	24	2	0.08	11.13
48574	170	M	MBSP	21 May 17	18 July 17	59	3	0.05	0.53
48577	140	F	MBSP	20 May 17	8 Sept 17	112	1	0.01	0.01
45355	113	F	2nd Ave.	22 July 16	27 Nov 17	299 ^a	2	0.01	0.18
44570	112	M	MBSP	25 July 16	25 July 16	0	0	0	0
44571	141	F	MBSP	25 July 16	25 July 16	0	0	0	0
98	170	F	MBSP	16 Aug 17	16 Aug 17	0	0	0	0

Note. The monitoring period refers to the number of days from release date (plus 12 h) to date of last detection. L_T , Total length; MP, monitoring period; PAI, pier association index (the total number of days with a detection event at piers divided by the monitoring period); MBSP, Myrtle Beach State Park; Ave., Avenue.

^a Because tag #45355 was tagged in 2016 and not detected until late November 2017, the monitoring period refers to the sum of the days from release date (or first release date for 2017) to date of last detection for each year.

events at all four monitored piers in 2017 (Figure 4). One individual was detected solely at MBSP Pier and spent more than 24 h at that location on multiple occasions. This individual was initially thought to be dead based on multiple periods with continuous detections (Figure 3), but was then visually observed by identification of colour-coded roto tags at MBSP Pier on 1 September 2017.

A supplementary nearshore receiver equidistant from shore as the receiver on 2nd Avenue Pier and located midway between 2nd Avenue Pier and Springmaid Pier (Figure 1) on muddy bottom, recorded 882 detections and 196 detection events from seven individuals. Detection events ranged from 0.01–0.43 h ($\bar{x} = 0.06 \pm < 0.01$ h SE; median = 0.05 h). About 66.4% of detections ($n = 586$) and 65.3% of

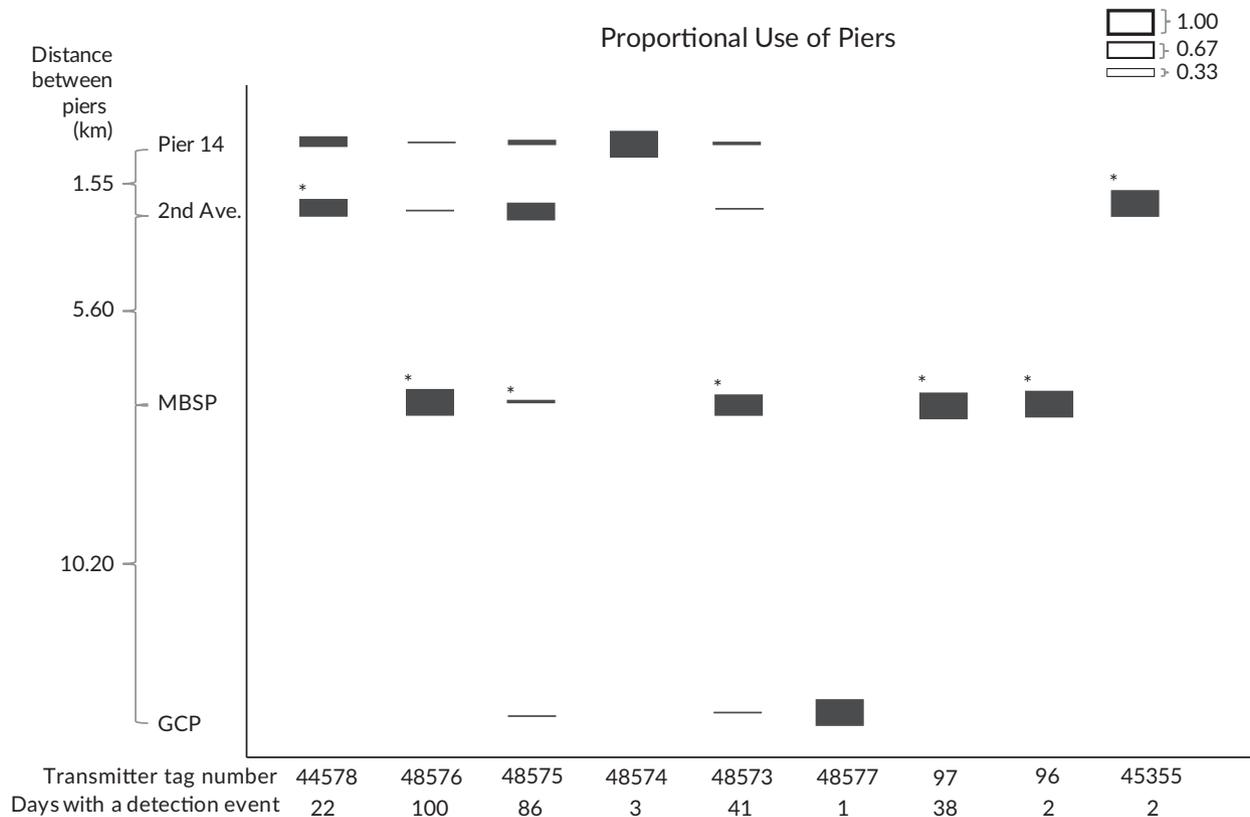


FIGURE 4 Proportional use of piers (Pier 14 in north, GCP in south) for each *Carcharhinus limbatus* (transmitter tag number) detected by acoustic receivers post-release. Bar thickness is equivalent to the proportion of days with a detection event at that location divided by the total number of days with a detection event for each individual. For each individual, an asterisk above the bar indicates that the shark was tagged at the corresponding pier on the y-axis. Ave., Avenue; MBSP, Myrtle Beach State Park; GCP, Garden City Pier

detection events ($n = 128$) were recorded during the day. Four individuals also recorded detections off the coast of Charleston, South Carolina and one individual recorded detections off of Hilton Head, South Carolina (Table S1; detections courtesy of M. Arendt and B. Frazier of the SCDNR). Additionally, five *C. limbatus* were detected on receivers off Cape Canaveral, Florida (detections courtesy of E. Reyier of the Kennedy Space Center Ecological Program). One individual (tag #44578) had 52 detections during the winter of 2016–17 (20 December 2016–2 January 2017) and four separate individuals (tag #48573, 48575, 48576 and 48577) had a total of 576 detections during the 2017–18 winter (18 November 2017 to 16 March 2018). One of those individuals (tag #48573) was also detected ($n = 3$) by a receiver off Fort Pierce, Florida on 14 January 2018 (detections courtesy of M. McCallister of Florida Atlantic University).

The LMM model that best explained *C. limbatus* residence time at piers included terms for pier location and diel cycle ($w_i = 0.88$; Table 2) and was 13 times more likely than the next best model ($w_1w_2^{-1}$; Table 2). The coefficient estimate (95% CI) for diel cycle (day) indicated that residence time was about 1 min greater during the day than at night for each individual (Table 3). Interestingly, there was about a 10 min difference in median residence time between day (28.2 min) and night (18.6 min). The coefficient estimate (95% CI) for MBSP Pier compared with 2nd Avenue Pier indicated that residence time was about 1 min greater at MBSP Pier than 2nd Avenue Pier (Table 3). Conversely, residence time was about 1 min greater at 2nd Avenue Pier than Pier 14 and about 4 min greater at 2nd Avenue Pier than Garden City Pier (Table 3).

The most likely GLMM included terms for tidal height, diel cycle, barometric pressure and angler count ($w_i = 0.98$) and was about 80 times more likely than the next most likely model ($w_1w_2^{-1}$; Table 4). Model results indicated that the probability of detecting a *C. limbatus* at a pier was greatest during the day and positively associated with tidal height, barometric pressure and angler count. With all other variables in the model held constant, the odds ratios corresponded to a 36% increase in odds of presence with a 1 m increase in tidal height, a 168% increase in odds of presence during the day, a 25% increase in odds of presence with a 2 mmHg increase in

TABLE 2 Results from the linear mixed model testing if pier location, diel cycle, tidal cycle, lunar cycle, water temperature, barometric pressure, and angler count influenced the length of time of *Carcharhinus limbatus* detection events using Bayesian information criterion (BIC)

Model	BIC	Δ BIC	w_i
Pier + diel cycle + (1 transmitter)	2558.48	0.00	0.88
Pier + BP + diel cycle + (1 transmitter)	2563.61	5.13	0.07
Diel cycle + (1 Transmitter)	2565.34	6.86	0.03
Pier + diel cycle + tidal cycle + (1 transmitter)	2566.97	8.49	0.01
Diel cycle + BP + (1 transmitter)	2569.94	11.45	< 0.01

Note. The table includes results from all *C. limbatus* tested for the top five models (lowest BIC first) with transmitter as a random variable. Δ BIC was calculated by subtracting the lowest BIC value from each corresponding BIC value.

w_i , Schwarz weight associated with each model for the duration sharks spent at piers. BP, Barometric pressure.

TABLE 3 Coefficient estimates and adjusted odds ratios for variables termed in the most likely linear mixed model testing factors affecting the length of time of *Carcharhinus limbatus* detection events at piers (top) and for the most likely generalized linear mixed model testing factors affecting shark presence at piers (bottom)

Model Term	Coefficient estimate (95% CI)	Odds ratio (95% CI)
Detection event at pier		
Diel cycle (Night)	NA	NA
Diel cycle (Day)	0.645 (0.384–0.890)	NA
Pier (2nd Avenue)	NA	NA
Pier (Garden City)	–1.391 (–2.701 to –0.062)	NA
Pier (MBSP)	0.823 (0.349–1.306)	NA
Pier (Pier 14)	–0.775 (–1.317 to –0.218)	NA
Shark presence at pier		
Tidal Height	0.309 (0.239–0.394)	1.362 (1.251–1.483)
Diel cycle (Night)	NA	NA
Diel cycle (Day)	0.966 (0.881–1.093)	2.682 (2.413–2.984)
Barometric Pressure	0.113 (0.096–0.130)	1.254 (1.211–1.298)
Anglers	0.0006 (0.0004–0.0007)	1.060 (1.038–1.077)

Note. The adjusted odds ratio for model term Anglers refers to an increase of 100 anglers and the adjusted odds ratio for model term Barometric Pressure refers to an increase of 2 mmHg. NA, Not applicable.

TABLE 4 Results from the generalized linear mixed model testing if water temperature, tidal cycle, diel cycle, lunar cycle, barometric pressure, and angler count influenced the presence of *Carcharhinus limbatus* at piers using Bayesian information criterion (BIC)

Model	BIC	Δ BIC	w_i
Anglers + BP + diel cycle + tidal cycle + (1 transmitter)	10,846.27	0.00	0.98
Anglers + WT + BP + diel cycle + tidal cycle + (1 transmitter)	10,855.05	8.78	0.01
Anglers + BP + diel cycle + tidal cycle + lunar cycle + (1 transmitter)	10,855.75	9.48	0.01
Anglers + WT + BP + diel cycle + tidal cycle + lunar cycle + (1 transmitter)	10,864.55	18.28	< 0.01
WT + BP + tidal cycle + diel cycle + (1 transmitter)	10,871.50	25.23	< 0.01

Note. The table includes results from the top five models (lowest BIC first) with transmitter as a random variable. Δ BIC was calculated by subtracting the lowest BIC value from each corresponding BIC value. w_i , Schwarz weight associated with each model for shark presence at piers. WT, Water temperature; BP, Barometric pressure.

barometric pressure and a 6% increase in odds of presence with an increase of 100 anglers (Table 3).

Spectral density plots generated from the fast Fourier transformation analyses did not reveal cyclical patterns in behaviour (Figure 5). Only minor and sporadic peaks occurred in the graphs for each individual analysed, indicating individuals did not display periodicity in their visits to fishing piers.

4 | DISCUSSION

Three *C. limbatus* were highly or very near highly associated with piers ($PAI \geq 0.50$), with four others displaying low association with piers ($PAI \leq 0.08$). Association with man-made structures has also been

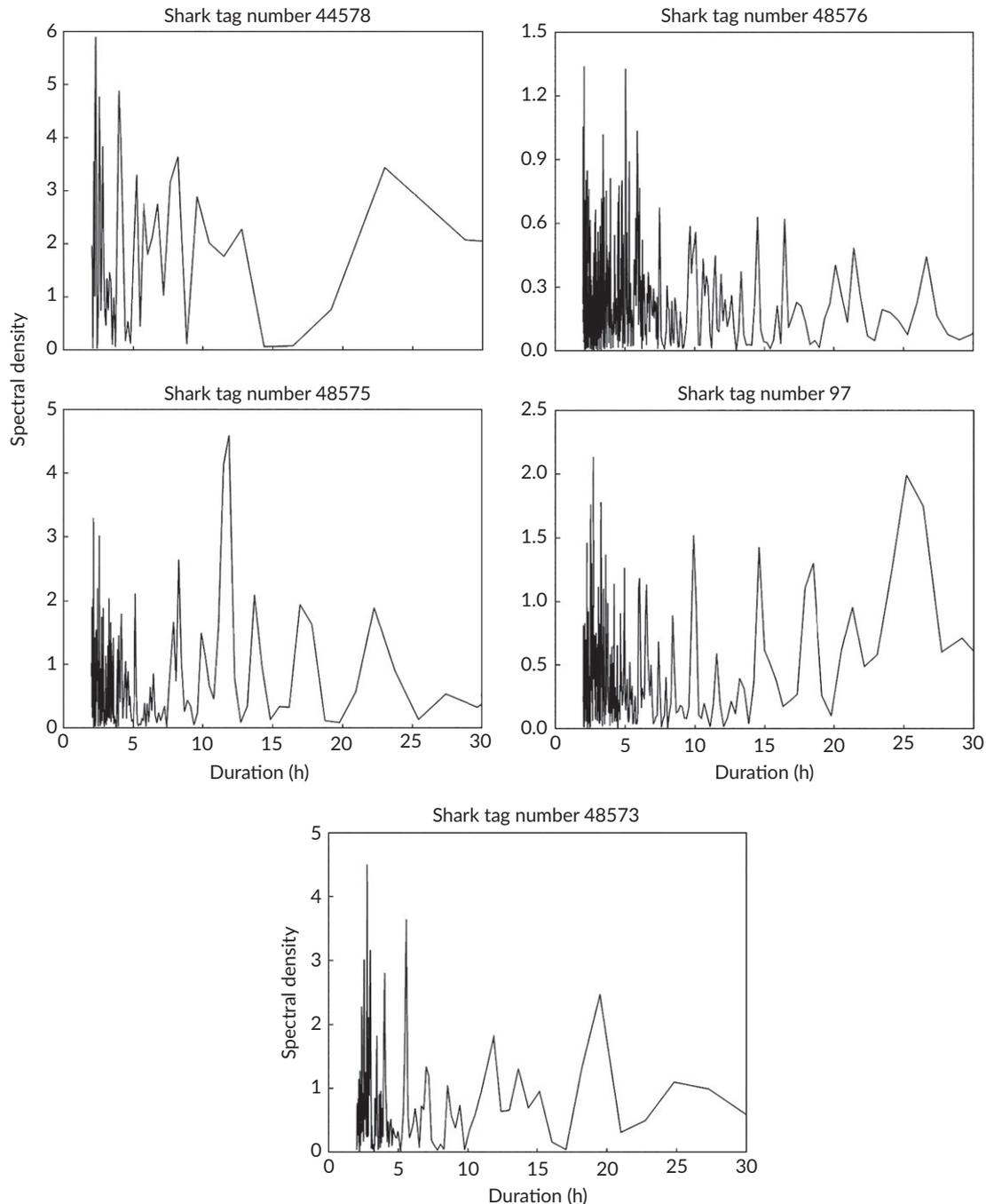


FIGURE 5 Spectral density graphs generated from the fast Fourier transformation analyses for each *Carcharhinus limbatus* with greater than 200 detections by acoustic receivers in the Grand Strand, South Carolina

observed for sandbar sharks *Carcharhinus plumbeus* (Nardo 1827) to ocean-farming cages in Hawaii (Papastamatiou *et al.*, 2011) and for silky sharks *Carcharhinus falciformis* (Müller and Henle 1839) to fish aggregating devices in the Indian Ocean (Filmlater *et al.*, 2011). Juvenile *C. limbatus* have been observed displaying high site fidelity to a nursery ground in Florida (Heupel & Hueter, 2002); here we found evidence of seasonal association with piers in adult individuals, but not juveniles (Table 1). Despite the possibility that sharks were simply attracted to the nearshore area that coincidentally encompassed the pier structure, it is reasonable to assume that sharks repeatedly visiting fishing piers are displaying associative behaviour, which could be due to the availability of potential prey. Furthermore, we deliberately

used transmitters with a limited detection range (< 100 m) to maximize the probability that a detected *C. limbatus* was associating with the pier. A limited detection range and the use of detection events to define the association index, indicates that we have conservatively identified individuals that are highly associated with piers over relatively long monitoring periods (74–173 days) considering their seasonal residence in the Grand Strand.

Carcharhinus limbatus in the western North Atlantic Ocean are known to migrate south to warmer waters during the winter months (Castro, 1996). Off the coast of South Carolina, they are present from May until early November, when sea surface temperatures drop below 21°C (Ulrich *et al.*, 2007) and are then thought to migrate to

Florida (Castro, 1996). Although only one (tag #44578) of the four *C. limbatus* tagged in 2016 was subsequently detected that year, it was observed throughout the summer months and then was last detected in the area on 7 November 2016, when the average water temperature was 19.8°C. Conversely, the dates of last detection for sharks tagged in 2017 were more sporadic and less parsimonious with previous findings such as Castro (1996), who suggested that *C. limbatus* migrate from the area in early November. Only three of the eight *C. limbatus* tagged in 2017 were last detected in late October or early November (Table 1) when the average water temperature ranged 23.5–21.4°C. The other five sharks were either not detected post-release ($n = 1$) or recorded their last detections on July 18 ($n = 1$), August 30 ($n = 1$), or September 8 ($n = 2$), when the average water temperature ranged 25.7–27.2°C, which is inconsistent with previous findings (Castro, 1996). However, *C. limbatus* could have still been in the area but were not detected because they were simply no longer visiting monitored locations. Interestingly, one of the five *C. limbatus* that appeared to depart the Grand Strand earlier than expected (tag #48577) was subsequently detected on 30 November 2017 off the coast of Cape Canaveral, Florida. Kajjura & Tellman (2016) documented peak abundance of *C. limbatus* along the east coast of Florida from January to March. Five sharks (tag #44578, 48575, 48576, 48573, 48577) in our study were detected near Cape Canaveral, Florida during the late autumn and winter months of 2016 and 2017 (data provided by E. Reyier of the Kennedy Space Center Ecological Program). These detections indicate that *C. limbatus* migrating south from South Carolina to Florida may depart the area at different times based on different environmental cues.

The lack of detections for some *C. limbatus* tagged during this study could potentially be due to tag failure, death, or individuals tagged were not pier-associated. In 2016, only the smaller, immature *C. limbatus*, 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 ($L_T \geq 158$ cm), with minimal degrees of association recorded for the two smaller *C. limbatus* ($L_T \leq 140$ cm; Table 1). Because size is often the driver of dominance in social groups (Allee & Dickinson, 1954), larger individuals could potentially outcompete and drive out smaller individuals (Myrberg & Gruber, 1974). Limbaugh (1963) observed interspecific dominance between *C. limbatus*, silvertip *Carcharhinus albimarginatus* (Rüppell 1837) and Galapagos *Carcharhinus galapagensis* (Snodgrass & Heller 1905) sharks. Although *C. limbatus* was the most commonly observed species at piers, additional shark species were caught at or near piers including tiger *Galeocerdo cuvier* (Péron & LeSueur 1822), sandtiger *Carcharias taurus* (Rafinesque 1810), scalloped hammerhead *Sphyrna lewini* (Griffith and Smith 1834), *C. plumbeus*, finetooth *Carcharhinus isodon* (Valenciennes 1839), blacknose *Carcharhinus acronotus* (Poey 1860) and Atlantic sharpnose *Rhizoprionodon terraenovae* (Richardson 1837) sharks. Inter or intraspecific interactions may stunt associative behaviour of smaller, immature *C. limbatus* with piers. Additional tagging of *C. limbatus* across all size ranges would need to be conducted to further evaluate the relationship between size classes and association with piers.

Throughout their residency along the Grand Strand, tagged *C. limbatus* appeared to exhibit relatively higher use at particular piers

over others, specifically Pier 14, 2nd Avenue Pier and MBSP Pier (Figure 4). The highest concentration of pier structures per km in the Grand Strand encompasses those three piers (Figure 1). Certain piers could represent more favourable environment for individual sharks to exploit resources. However, Pier 14 is only about 89 m long and the water depth can be < 2 m at the offshore end during low tide resulting in very little fishing effort compared with other piers monitored in this study. Additionally, no detections were recorded in 2016 on Apache Pier, a pier where large numbers of sharks are commonly observed. Detections at Pier 14 and a lack of detections at Apache Pier potentially indicates that where each *C. limbatus* was tagged played an important role in determining the piers where they were subsequently detected. The tendency of individuals to remain at the location where they were tagged provides further evidence that some *C. limbatus* displayed associative behaviour with piers and, in some cases, site fidelity.

While the association of some individuals with piers has been illustrated thus far, results from the mixed models elucidate the ecological significance of this relationship. The inclusion of angler count and diel cycle in the best model for presence could indicate that *C. limbatus* are using the piers to feed. For example, Papastamatiou *et al.* (2011) suggested that an increase in prey availability during the day influenced *C. plumbeus* fidelity to ocean-farming cages. In our study, increased presence and residence time of *C. limbatus* were recorded during the day compared with at night. Similarly, angler activity at piers is greater during the day than at night, which results in more opportunities for sharks to feed on discarded fish. *Carcharhinus limbatus* can be considered opportunistic foragers (Heithaus, 2001; Melillo-Sweeting *et al.*, 2014). Multiple observations were made of *C. limbatus* feeding on discarded fish and even circling cleaning stations while anglers were cleaning their fish and discarding scraps. In contrast, Barry *et al.* (2008) concluded that neonate and young of year *C. limbatus* spent more time feeding as light level decreased. Nocturnal feeding patterns have been found in some diel feeding studies on sharks (Bush, 2003; Klimley *et al.*, 1988; Nelson, 1976; Randall, 1977; Tricas, 1979). However, a review by Hammerschlag *et al.* (2017b) concluded that an increase in elasmobranch activity at night was largely not supported. Adult *G. cuvier* have been observed feeding both during the day and at night but altered their foraging strategies with the diel cycle (Lowe *et al.*, 1996). *Carcharhinus limbatus* could be exhibiting similar diel shifts in feeding behaviour; potentially foraging with minimal energetic cost at piers during the day when piers are open to anglers, then resorting to more active foraging strategies, or perhaps fasting, at night. Interestingly, the supplementary nearshore receiver also recorded a greater percentage of detections (66.4%) and detection events (65.3%) during the day, indicating diel shark activity may not correspond with pier activity and *C. limbatus* could simply be feeding close to shore during the day and making their way offshore at night. Because all *C. limbatus* were caught during the day, this study could have selected for individuals more likely to display nearshore activity during the day, while conspecifics could exhibit different diel activity. It is also worth noting that while diel cycle was a statistically important factor in the LMM, residence time was similar between day and night. 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 behaviour.

Carcharhinus limbatus presence at piers was also influenced by an increase in tidal height (Table 3), which has been observed in juvenile *C. limbatus* (Steiner *et al.*, 2007) and juvenile lemon sharks *Negaprion brevirostris* (Poey 1868) (Wetherbee *et al.*, 2007). Steiner *et al.* (2007) observed *C. limbatus* 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, *C. limbatus* in the Grand Strand could be displaying similar behaviour at piers. Furthermore, the influence of barometric pressure on *C. limbatus* presence has also been documented for juvenile *C. limbatus* (Heupel *et al.*, 2003) along with other shark species (Hammerschlag *et al.*, 2006; Udyawer *et al.*, 2013). Juvenile *C. limbatus* appeared to leave their nursery after a large decrease in barometric pressure associated with a tropical storm event in Florida (Heupel *et al.*, 2003). Heupel *et al.* (2003) and Udyawer *et al.* (2013) have investigated the effects of large declines in barometric pressure associated with storm events with sharks in estuarine systems and discovered that responses to severe events were species specific. Additionally, Hammerschlag *et al.* (2006) suggested that barometric pressure influenced white shark *Carcharodon carcharias* (L. 1758) feeding patterns at Seal Island, South Africa. Hammerschlag *et al.* (2006) attributed this change in feeding pattern to an increase in seal activity prior to a severe storm event. Hurricane Matthew affected the study site in 2016; unfortunately, receivers were removed prior to landfall in order to prevent equipment loss. Despite the lack of data during tropical storm events, our study observed a 25% increase in odds of presence with a 2 mmHg increase in barometric pressure. In comparison, barometric pressure associated with a tropical storm event can decrease by more than 50 mmHg. Therefore, *C. limbatus* in this study may be responding to changes in barometric pressure that are less than changes associated with tropical systems. *Carcharhinus limbatus* appeared to show acute sensitivity to changes in barometric pressure, which could be a response to avoid increased wave height and current strength that usually accompany a drop in barometric pressure (Heupel *et al.*, 2003; Udyawer *et al.*, 2013). Alternatively, a drop in barometric pressure could lead to a disorientation of their pressure sensing mechanism, driving sharks to seek deeper waters (Heupel *et al.*, 2003). The behavioural responses of *C. limbatus* to changes in barometric pressure may also, in part, be an innate response to avoid stranding in shallow water environments (Heupel *et al.*, 2003). Decreasing barometric pressure associated with a rainfall or storm event could also influence the number of anglers fishing on the pier, which, as aforementioned, limits the number of opportunities for sharks to feed on discarded fish.

The influence of barometric pressure and angler count on *C. limbatus* presence at piers are further supported by the lack of periodicity in detections. If the behaviour of tagged individuals was solely influenced by the tidal or diel cycle, peaks at either the 6, 8, 12, or 24 h would have been observed in the associated power spectrums (Papastamatiou *et al.*, 2009; Figure 5). These results have been reported by Papastamatiou *et al.* (2011) for *C. plumbeus* in Hawaii, but spectral analyses in our study did not demonstrate peaks associated with either tidal or diel cycle indicating that other factors, such as barometric pressure and angler count, influenced visits to piers. It is

worth noting that unexplored factors, such as dissolved oxygen (Carlson & Parsons, 2001) or chlorophyll (Hearn *et al.*, 2010; Meyer *et al.*, 2010) could also be influencing *C. limbatus* behaviour at piers and could be evaluated in future studies of this kind. Furthermore, although turbidity, wind speed and tidal height did not appear to affect acoustic signal transmissions over a 24 h period, temperature, time of day, lunar cycle, wave height and period and episodic weather events have been shown to interfere with acoustic signal transmissions (How & de Lestang, 2012; Mathies *et al.*, 2014) and could have influenced our results. Future studies of this kind should include a sentinel tag, or a tag permanently placed near one of the receivers, to provide continuous data on the environmental factors that interfere with acoustic signal transmissions.

The majority of *C. limbatus* displayed varying degrees of association with piers, but the individuals that were highly associated may be using the piers to feed on fishes aggregated at piers or discarded from fishers. Including angler count data for each individual pier and tagging and monitoring of additional individuals paired with video surveillance cameras could provide insight on this hypothesis. Papastamatiou *et al.* (2011) speculated that shifts in behavioural and density-mediated interactions could potentially result in sharks being displaced from other locations. Unfortunately, data are lacking on *C. limbatus* density and demographics in the Grand Strand prior to construction of the fishing piers. Future studies should also address the foraging ecology of *C. limbatus* 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 *v.* the effects of fishing effort or provisioning. Finally, a comprehensive array of receivers that includes a large network of nearshore receivers could answer questions on the attraction of sharks to piers compared with natural environments. In summary, this study provides empirical evidence of association of adult *C. limbatus* with fishing piers, but more data are needed to better understand key factors influencing such behaviour.

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Authors contributions

Conceived and designed the experiment: K.L.M., D.C.A., D.P.C., N.H., E.J.B. Tagging and data collection: K.L.M., D.P.C. Analysis of the data: K.L.M., D.C.A., D.P.C. Wrote the paper: K.L.M. Major reviews: D.C.A., D.P.C., N.H., E.J.B.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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