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Large sharks exhibit varying behavioral responses to major hurricanes

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ABSTRACT

Under global climate change, storm events are predicted to increase in strength and frequency. Although aquatic animals can be affected by acute natural disturbances, information on the immediate consequences of these weather systems on the behavioral ecology of highly mobile aquatic predators remains limited. Here we examine the spatial distributions, activity spaces, and ecological change-points of four large shark species (mean: 193 cm fork length ± 70 SD) via passive acoustic telemetry in two different locations in the subtropical Atlantic (Little Bahama Bank, Bahamas, and Biscayne Bay, Florida, USA) in relation to two separate major hurricane events (category 4 and 5). We tested whether sharks would evacuate shallow coastal habitats (and thus exit the acoustic arrays) during the hurricanes and exhibit comparable size of activity spaces pre- and post-storms, as has been previously found for smaller (50–150 cm fork length) sharks elsewhere. Located on the northwest edge of the Little Bahama Bank, Bahamas, an acoustic array consisting of 32 acoustic telemetry receivers tracking tiger sharks Galeocerdo cuvier sustained a direct hit from Hurricane Matthew in 2016. Daily detections of tagged tiger sharks within the array were consistent before and during the hurricane. Immediately following the storm, daily tiger shark detections approximately doubled. Size and extent of tiger shark activity space within the array were consistent pre- and post-storm. Located off Miami, within Biscayne Bay, an array of 32 acoustic receivers tracking bull Carcharhinus leucas, nurse Ginglymostoma cirratum, and great hammerhead sharks Sphyrna mokarran was exposed to tropical-storm-force winds from Hurricane Irma in 2017. As the eye of the storm passed 140 km to the west, most sharks previously present in the array were no longer detected, while two nurse sharks remained at receivers near Miami. Numbers of tagged bull sharks declined following Hurricane Irma, whereas other species did not. Ecological change point analyses indicated that seasonal changes - rather than storm conditions - cannot be ruled out as the primary driver of post-storm shark behavior. Unlike smaller shark species which have previously been found to evacuate shallow water habitats during storms, we found variable responses of large sharks to storm events.

1. Introduction

Human-driven climate change is predicted to increase the intensity of major tropical storm events (Kossin et al., 2020). Major storms can lead to short-term ecological regime shifts that affect a number of biological processes such as the transfer of energy via involuntary displacement of sessile animals and escape responses in mobile animals (Andersen et al., 2009; Jury et al., 1995; Lajtha, 1985; Pickett and White, 2013). While difficult to continuously monitor the behaviors of animals prior to, during, and following a tropical storm, any available tracking data will provide novel insights into how animal ecology and energy transfer operates in the marine environment (Kossin et al., 2014; Walsh et al., 2016; Bacheler et al., 2019).

Aquatic animals can be exposed to rapid fluctuations in water temperature, water depth, water movements (currents and waves), and barometric pressure associated with tropical storms (Fitzsimons and

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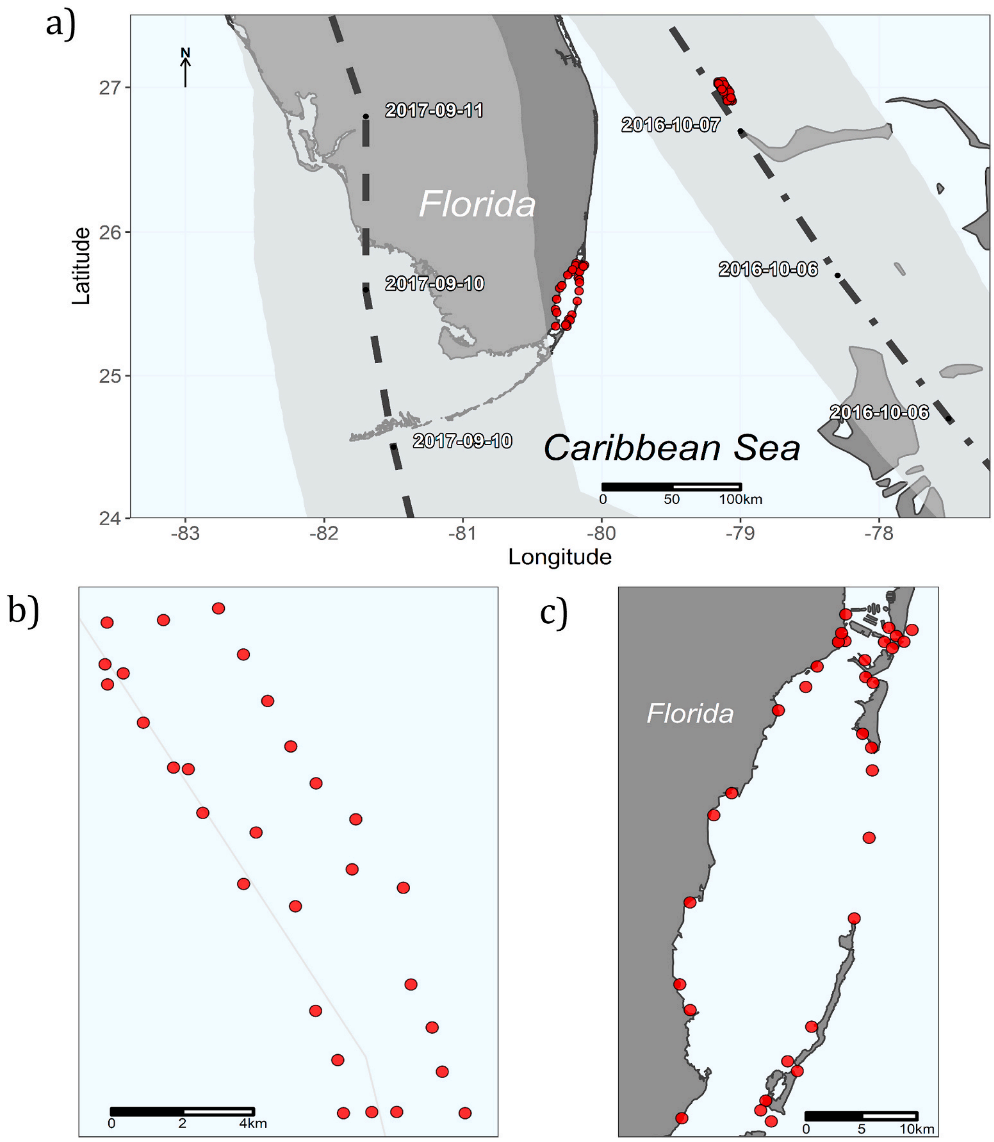

Fig. 1. Locations of the Bahamas and Miami Arrays in relation to the paths of Hurricane Matthew (a, path of eye as dot-dash line) and Hurricane Irma (a, path of eye as dashed line). The 64 knot (minimum sustained wind speed to categorize a hurricane) radii are indicated by grey shaded regions along each hurricane path. The Bahamas Array covered the northwestern portion of the Little Bahama Bank directly over Tiger Beach (b). The contour line (light grey) along the western side of the Tiger Beach Array indicates a drop-off to deep water. The Miami Array covered the perimeter of Biscayne Bay extending north to Miami Beach (c). The eye of Hurricane Matthew followed directly over Tiger Beach whereas the eye of Hurricane Irma passed approximately 140 km west of Biscayne Bay.

Nishimoto 1995; Jury et al., 1995; Patterson et al., 2001; Liu et al., 2010). Tropical storms can also physically displace individuals and alter the environment through wind, waves, and storm surge (Fong and Lirman, 1995; Jordán-Dahlgren and Rodríguez-Martínez, 1998; Posey et al., 1996; Walker, 2001). However, information on the behavioral ecology of many species in relation to such storm events remains limited. A key ecological question in the Anthropocene is understanding how imminent climate-driven changes, including increasing extreme weather events, might affect the ecosystem functions and services of aquatic predators (Hammerschlag et al., 2019a).

The basic function of stationary acoustic telemetry systems is to identify the behavior of tagged, freely-swimming animals. Relatively short-term changes in weather and longer-term changes in phenology (e.g., temperate seasons) can result in behavioral modifications (e.g., Udyawer et al., 2013); however, the effects of acute large-scale disturbances such as tropical storms are less commonly observed simply because of their rarity and chance of intercepting telemetry arrays. In the cases where storm events have converged with telemetry arrays monitoring sharks, barometric pressure is thought to drive the movement of juveniles or small species (50–150 cm in fork length) into and out of nearshore habitats (Heupel et al., 2003; Udyawer et al., 2013; Strickland et al., 2020). While some species appeared to remain inactive during a major storm event (e.g., blacktip reef sharks, C. melanopterus, Udyawer et al., 2013), generally these studies have indicated that small or juvenile sharks evacuate nearshore areas prior to major storms, presumably to take shelter in deeper waters. Unlike for small sharks, the movement of large, more transient apex predatory species found in both inshore and offshore telemetry arrays has not been characterized under the conditions associated with tropical storms. Given the seemingly increasing occurrence of tropical storms in coastal regions (e.g., Murakami et al., 2018), it is important to evaluate how ecologically important species may be affected (Hammerschlag et al., 2019a).

Here, we examined the habitat use of four large (mean: 193 cm fork length ± 70 SD) shark species in response to two major hurricanes within shallow water habitats of the subtropical Atlantic. Specifically, we examined acoustic telemetry data from tiger sharks Galeocerdo cuvier, bull sharks Carcharhinus leucas, nurse sharks Ginglymostoma cirratum, and great hammerhead sharks Sphyrna mokarran before, during, and after Hurricane Matthew (October 7, 2016) and Hurricane Irma (September 10, 2017). Tagged sharks were monitored in acoustic telemetry arrays on Little Bahama Bank in the Bahamas (Hurricane Matthew) and within Biscayne Bay, Florida (Hurricane Irma). The Little Bahama Bank acoustic array took a direct hit from the eye of Hurricane Matthew, while the eye of Hurricane Irma passed 140 km west of

Biscayne Bay, which experienced heavy rains and sustained winds of 50–64 knots. We explored behavior using a combination of descriptive methods and a change-point analysis (Andersen et al., 2009) to identify species-specific responses associated with the presence of hurricane conditions. Similar studies that monitored smaller species suggest that sharks will evacuate shallow habitats (and thus exiting the acoustic arrays) and return following the disturbance (Heupel et al., 2003; Udyawer et al., 2013, Strickland et al., 2019). Accordingly, we checked whether sharks would evacuate the shallow waters of the study areas in relation to the storm events and exhibit comparable size of activity spaces pre- and post-hurricanes.

2. Materials & methods

2.1. Study areas

The Little Bahama Bank extends off Grand Bahama Island and is mostly composed of underwater carbonate platforms. The habitat is dominated by shallow (average 5 m depth) sand flats with irregular seagrass patches and infrequent small patches of coral. Within the northwest edge of the Little Bahama Bank is an area dominated by female tiger sharks, nicknamed "Tiger Beach" (Fig. 1a). Here an acoustic array of 32 acoustic receivers (described below) was constructed in June 2014 as part of a larger study to investigate the behavioral ecology of tiger sharks at the site (Hammerschlag et al., 2017).

Biscayne Bay is a clear-water barrier island lagoon that spans the length of Miami-Dade County, Florida, USA and is approximately 56 km long and 13 km at its widest point. The coastal environment ranges from highly urbanized areas of downtown Miami to more natural mangrove shorelines in Biscayne Bay National Park. The bay contains several habitat types including mangrove forests, seagrass beds (e.g., turtle grass, Thalasia testudimum), hard bottom and coral reefs. It is a mangrove-fringed bay, bordered on the east by barrier islands primarily made of sand. The average depth of Biscayne Bay is 2.0 m (Lee and Rooth, 1975) and contains marine and estuarine habitats (Browder et al., 2005; Roessler and Beardsley, 1974). Here, an acoustic array of 32 acoustic receivers (Fig. 1a; described below) was established in September 2016 as part of larger study to investigate the activity and habitat-use of coastal sharks in relation to urbanization (McDonnell et al., 2020; Rider et al., 2021).

2.2. Acoustic arrays

2.2.1. Bahamas array

In both study areas, shark presence was recorded on acoustic telemetry receivers (i.e., VR2W receivers, Innovasea). An array of 32 single channel, omnidirectional receivers was deployed in and around the northwester edge of Little Bahama Bank, off Grand Bahama Island (hereafter, referred to as the Bahamas Array; Fig. 1b). The 32 receivers were spaced at approximately 750 m intervals, and were deployed in a ca. 12 × 3.2 km rectangle covering the northwestern area of Little Bahama Bank, with the western line of receivers bordering the inshore edge of the Bank (mean depth = 6.3 m ± 0.9 SD). A detailed description of the receiver anchoring system is described in Hammerschlag et al. (2017).

All 32 receivers were in place by June 25, 2014; however, three receivers failed to collect data, possibly due to malfunction. No receivers in this array were lost due to Hurricane Mathew. Receivers were range tested with V16-4X transmitter (Innovasea), the same type of transmitter used to track sharks. These tags have a low and high-power output (i.e., 1 db re 1 microPa @ 1 m) of 152 and 158, respectively. Diurnal range testing revealed a detection efficiency of 50% at 200 m, which is comparable to other passive acoustic telemetry studies in the region (e.g. Brownscombe et al., 2020).

2.2.2. Miami Array

An array of 32 VR2W receivers was deployed off Miami, Florida, within Biscayne Bay, spanning from Miami Beach southward to Turkey Point Nuclear Generating Station (Hereafter referred to as the Miami Array; Fig. 1c). Emphasis was placed on the periphery of Biscayne Bay, avoiding the central region of the bay, comprised of relatively homogeneous shallow (approximately 0.3 m–1.2 m) sand and rock flats environments with intermittent seagrass. Miami Array receivers were situated along the benthic substrate and followed a similar protocol to methods described by Murchie et al. (2012) and later modified by Ramsden et al. (2017). A segment of steel rebar (1.9 cm diam.) was inserted and mounted into either a singular cinder block or a 28 cm diameter piling cap, both of which were filled with concrete and allowed to cure. Acoustic receivers were covered with nylon stockings before deployment to prevent biofouling and loss of transmission range. Receivers were mounted to the unit and lowered to the benthic substrate by divers.

All 32 receivers were in place by September 8, 2016. Of these, one receiver fell victim to theft or vandalism as evidenced by cut cable ties, and one was lost to Hurricane Irma. Like the Bahamas array, receivers in the Miami array were range tested with V16-4X transmitters (Innovasea). Comparable to the Bahamas Array, diurnal range testing showed a detection efficiency of 50% at 250 m.

2.3. Tagging

Sharks were captured using standardized circle-hook drumlines (see Gallagher et al., 2017). The fishing gear consisted of a submerged 20-kg weight tied to a line running to the surface by means of an attached inflatable buoy. A 23-m monofilament ganglion line (~400 kg test) was attached to the submerged weight by a swivel, which terminated at a baited 16/0 5°-offset circle hook. This method permitted sharks to swim in a 23-m radius circle around the base when captured. Two sets of five baited drumlines were deployed simultaneously and allowed to soak for an hour before retrieval to check for shark presence. Captured sharks were brought to the boat and restrained on a dive platform or secured alongside the boat in water. To facilitate respiration, water was actively pumped through a hose inserted into the shark's mouth. Sex was recorded, and we measured pre-caudal length [PCL], fork length [FL], and stretched total length [TL] (Supplement A, Table S1).

Following Gallagher et al. (2021), acoustic transmitters (Innovasea V16, 69 kHz, 68 × 16 mm, 12 g) were inserted into the coelom of the shark via an approximate 2–4 cm paramedian incision along the left ventral body wall. The transmitter was positioned anterior to the incision to avoid strain on the incision site. The incision was closed with one to two simple interrupted absorbable nylon sutures. Sharks were released at the location of capture. The only exception was for great hammerhead sharks, which were tagged externally using a dart anchor system to a tethered transmitter. This approach was used on great hammerheads to reduce handling time given evidence of pronounced capture stress found in this species (Gallagher et al., 2014; Jerome et al., 2017). These transmitters had a high-power output (i.e., 1 db re 1 microPa @ 1 m) of 158 db and a nominal delay of 60–90 s.

On the Little Bahama Bank, Bahamas, 42 tiger sharks were tagged between October 2013 and November 2014 (Supplement A, Table S1). During a 60-day window around Hurricane Matthew, nine tiger sharks (mean 262.0 cm FL ± 66.5 SD), one of which was tagged in Biscayne Bay, were detected at Tiger Beach. Of these nine sharks, six had been tagged and released one year prior to the hurricane.

In Biscayne Bay, Florida, a total of 20 bull sharks, 20 great hammerheads, 16 nurse sharks, and 1 tiger shark was tagged between February 2015 and June 2017 (Table S1). At the time of Hurricane Irma, three bull sharks (mean 178 cm FL ± 47.2 SD), seven great hammerhead sharks (mean 198 cm FL ± 47.2), and nine nurse sharks (mean 133 cm FL ± 26.5 SD) had acoustic tags that were actively transmitting. Of these 19 animals, five were tagged and released one-year prior to the storm.

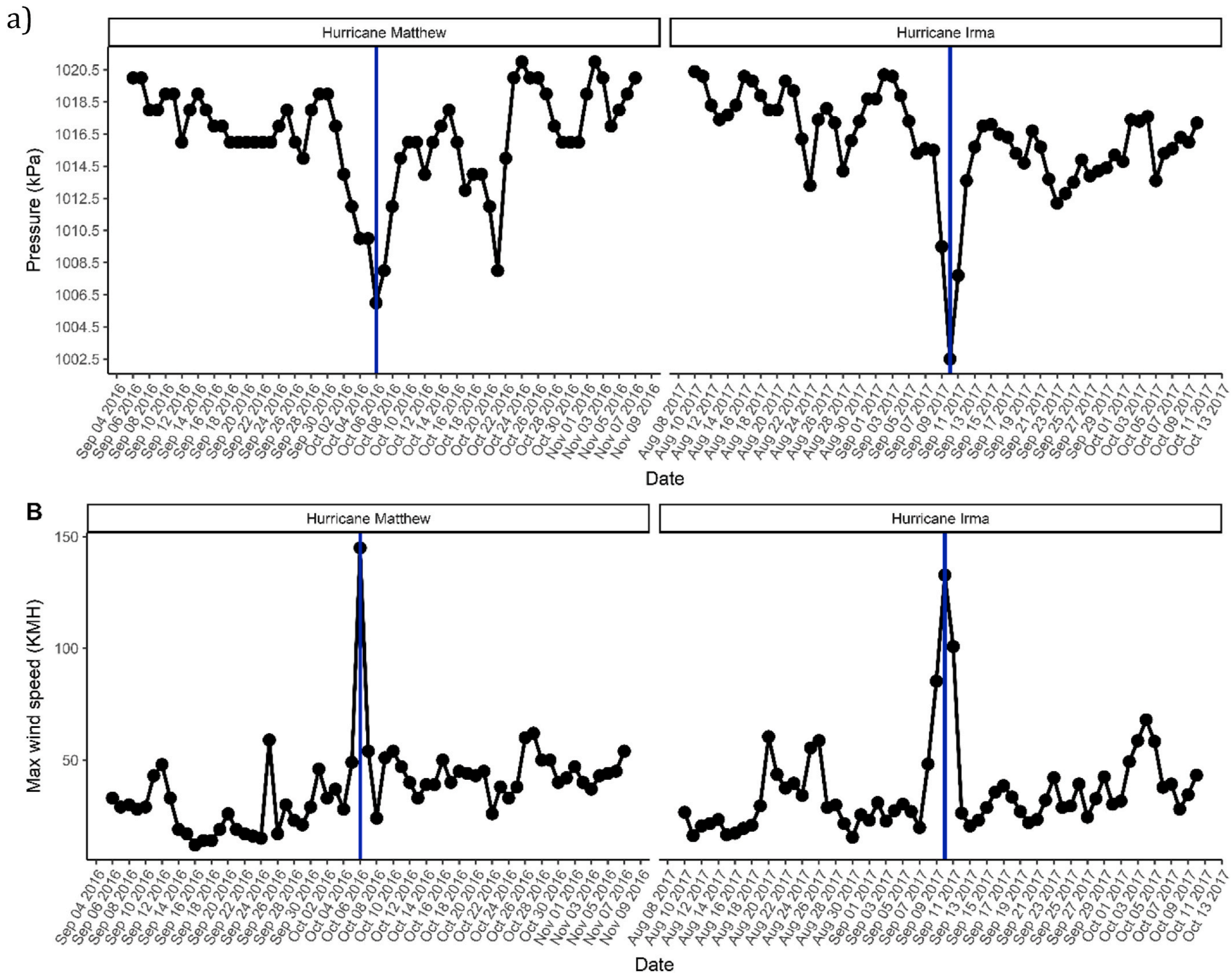

Fig. 2. (a) Maximum barometric pressure (kPa) recorded at the Berry Islands weather station (Hurricane Matthew, Lat 25.82, Lon −77.94) and the Fowey Rock weather buoy (Hurricane Irma, NOAA station FWYF1, Lat 25.591, Lon −80.097). Data for the Berry Islands were collected from weatherunderground.com. Data for the NOAA weather buoy were collected from ndbc.noaa.gov. The vertical blue line indicates the approximate dates when the Hurricanes were nearest to their respective weather stations. (b) Maximum wind speed (KMH) recorded at the Berry Island weather station (Hurricane Matthew, Lat 25.82, Lon −77.94) and the Fowey Rock weather buoy (Hurricane Irma, NOAA station FWYF1, Lat 25.591, Lon −80.097). Data for the Berry Islands were collected from weatherunderground.com. Data for the NOAA weather buoy were collected from ndbc.noaa.gov. The vertical blue line indicates the approximate dates when the Hurricanes were nearest to their respective weather stations. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.4. Environmental data

To determine the approximate daily weather conditions during each storm event, wind and barometric pressure was collected from the closest available weather station to each array. For Hurricane Matthew, weather conditions were collected from the Berry Islands weather station (25.82 N, −77.94 W) located approximately 160 km south of the Bahamas Array. Data for the Berry Islands were collected via a personal weather station and are available publicly at weatherunderground.com. For the Miami Array, the Fowey Rock weather buoy located outside of Biscayne Bay was used to source data for Hurricane Irma (National Oceanic and Atmospheric Administration station FWYF1, 25.59 N, −80.10 W). Data for the Fowey Rock weather buoy are available from ndbc.noaa.gov. These stations were chosen because of their proximity to the telemetry arrays and the completeness of barometric pressure and wind data during both storms. Neither weather station recorded wave height or storm surge, however further details on the weather conditions during Hurricane Matthew and Hurricane Irma can be found in Stewart (2017) and Cangialosi et al. (2018).

2.5. Analyses

Data were first filtered to remove false detections resulting from code collisions and environmental noise (Heupel et al., 2006). In addition, unrecognized codes from concurrent research programs were excluded from the database. A coded transmission was considered valid only if accompanied by an identical code number within a 20-min window. Receiver clock drift was corrected using the software program VUE (VEMCO Division, AMIRIX Systems). Data recorded simultaneously on two or more receivers were considered a single detection, whereby the first recorded detection was retained, and the others discarded. Following quality assurance measures, data were imported to the R Statistical Environment (Version 4.0.0; R Core Team, 2020).

To examine whether sharks exhibited a behavioral change in relation to the storms, daily shark presence was first explored by plotting abundance (sharks per day) and the number of detections by transmitter

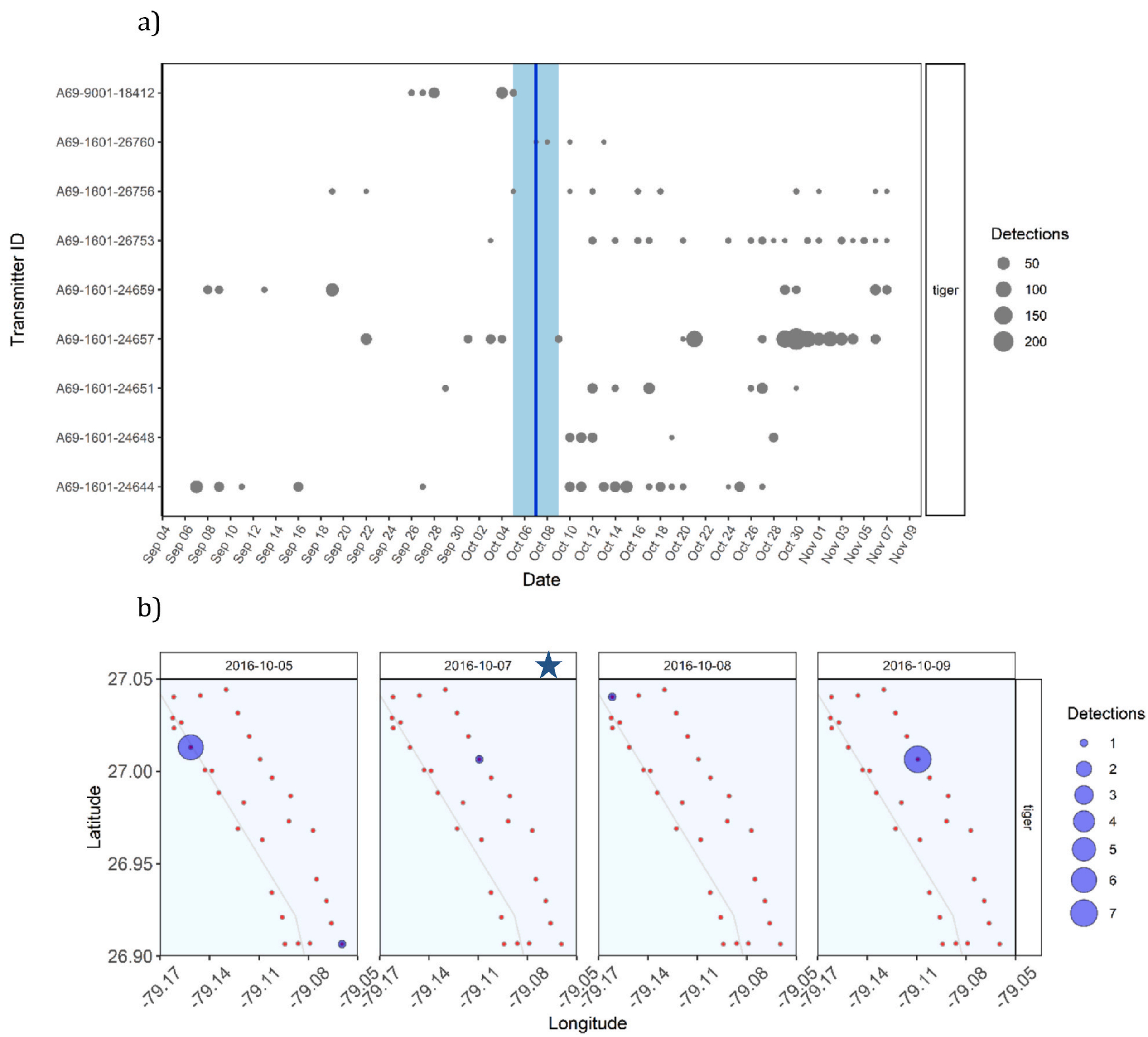

Fig. 3. (a) Daily detections for all tagged animals recorded within the Bahamas Array from September 6 to November 7, 2016. The vertical blue line indicates the approximate date when Hurricane Matthew passed over the Bahamas Array. (b) Number of detections by shark species within the Bahamas Array from 2016 to 10-05 to 2016-10-09 (the day of the hurricane is denoted by a star, B). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

ID in scatterplots and in a geographic information system (ArcGIS, Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA). For analyses, we focused on a period of one month pre and post storm. Paired t-tests were used to assess differences in the number of days each shark was detected at least once pre- and post-storm. The same analysis was conducted for years when the telemetry arrays were not impacted by major storms: September 6, 2015–November 7, 2015 at the Bahamas Array and August 9, 2019–October 10, 2019 at the Miami Array. A change-point analysis was used to determine when any changes in daily shark abundance occurred in years with and without majour hurricanes. Change-point or structural breaks analysis is typically used in econometrics to identify break points in stock markets (Perron, 2006), however the method has been used to identify ecological regime shifts, change points and thresholds (Andersen et al., 2009; Hammerschlag et al., 2019b). Breakpoints analysis uses an algorithm to estimate deviations in stability from a classical linear equation model. Breakpoints occur where the coefficients shift between stable regression relationships (Zeileis et al., 2002). The theory, algorithm and practical use of structural breaks analysis can be found in Bai and Perron (1998), Bai and Perron (2003), Zeileis et al. (2003), and references therein. We used the R package "strucchange" to identify breakpoints in shark abundance (Zeileis et al. 2002, 2003).

To identify how shark activity was potentially affected by major hurricanes, we calculated activity space (km^2) with minimum convex polygons (MCPs) at the core (50%) and extent (95%) of space use (Calenge 2006) for tiger sharks in the Bahamas Array. MCP was not conducted for the Miami array given the arrangement and density of receivers there did not lend themselves to such analysis. In addition to being a simple and universally accepted method for calculating activity space, MCP has previously been used to quantify tiger shark activity in the Bahamas Array (Hammerschlag et al., 2017). We calculated the median position of sharks in the Bahamas array based on 30 min intervals of detections (Simpfendorfer et al., 2002; Udyawer et al., 2013). MCPs were calculated for each animal detected at least five times over the one-month period pre or post Hurricane Matthew in 2016. Activity space was also estimated over the same two-month time period in 2015, when no major storm events impacted the Bahamas Array. Activity space (core and extent) was estimated as a function of time period (one

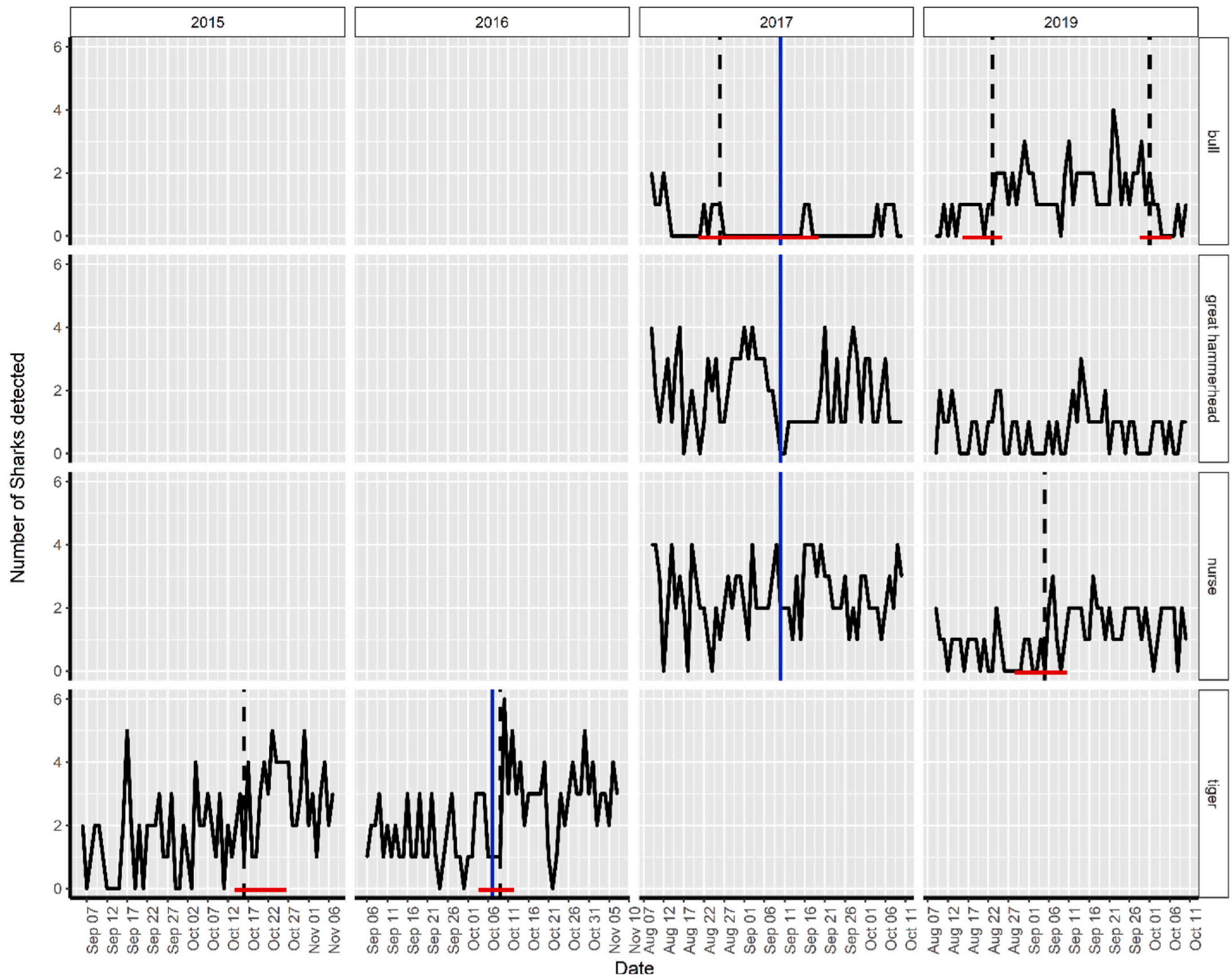

Fig. 4. The number of sharks detected per day across the Bahamas Array (September 6 and November 7, 2015 and 2016) and the number of nurse sharks, bull sharks, and great hammerhead sharks detected per day across the Miami Array (August 9 and October 10, 2017 and 2019). Vertical blue lines demarcate when a respective major storm was at approximately equal latitude to a telemetry array. Vertical hashed lines indicate a structural break in the data plus or minus 95% CI (horizontal red bar). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

month pre vs. one month post the date of Hurricane Matthew), year, fork length, and all possible statistical interactions by GLMMs. Fork length was included in the model to control for any influence of body size on activity space. Shark ID was included as a random effect to account for multiple observations from the same individual.

3.0. Results

3.1. Bahamas array

In the Bahamas array, one month prior to the eye of Hurricane Matthew passing through, the average number of tiger sharks detected per day was 1.0 (1.0 SD). One month following Matthew, we observed an average of 2.3 (0.51 SD) individuals per day (Supplement A, Table S1). The number of tiger sharks at Tiger Beach significantly increased one month following Hurricane Matthew (paired *t*-test: $t_8 = 2.56$; $p = 0.03$). There was no difference in the number of days that tiger sharks were detected at least once over a 30-day period pre versus post October 7, 2015 (paired *t*-test: $t_{13} = 1.78$; $p = 0.10$).

Twelve tiger sharks were detected at least once in the month preceding and following Hurricane Mathew (September 6, 2016 to October 7, 2016) striking the Bahamas array. At the Berry Islands, one day prior to Matthew passing over the Bahamas array, barometric pressure dropped to1006 kPa and wind speeds reached at least 145 km h^{-1} (Fig. 2). During the storm on 7 October, one tiger shark (ID 26760) was detected in the array for the first time in a month and subsequently remained in the array for approximately one week (Fig. 3). Five of the 12 detected tiger sharks (33%) were located in the Bahamas array within two days of Hurricane Matthew. Two of these animals appeared for the first time (i.e., ID 26760 & ID 24648) in the array since September 7, 2016 (Fig. 3). One shark (i.e., ID, 18412) did not return to the array following Matthew and before November 7, 2016 (Fig. 3). Following the storm, shark numbers increased within the Bahamas array (Figs. 3 and 4). In particular, a change-point in daily abundance was detected during a window of time in which the storm was over Tiger Beach (change point: October 9, 2016, 3 October – October 12, 2016 ± 95% CI, Fig. 4). The sudden drop and subsequent spike in abundance roughly corresponded to the rapid fall and rise in barometric pressure (Fig. 2). Of note, there was yet another synchronous event in tiger shark abundance and barometric pressure two weeks following Hurricane Matthew (October 21, 2016). Although the number of days in which tiger sharks were detected was not different pre and post October 7, 2015, there was a

Table 1
Parameter estimates from the linear mixed effects models of mcp area (km^2) for acoustically tagged Tiger sharks within the Bahamas Array.

Model	Term	Estimate	SE	DF	t-value	p-value
95% extent	Intercept	13.96	28.04	14	0.50	0.63
	Period:After	−37.28	54.03	5	−0.69	0.52
	Year:2016	53.42	41.76	5	1.28	0.26
	FL	0.041	0.113	14	0.36	0.72
	Period:After x Year:2016	−45.47	79.32	5	−0.57	0.59
	Period:After x FL	0.163	0.202	5	0.81	0.46
	Year:2016 x FL	−0.195	0.162	5	−1.20	0.28
	Period:After x Year:2016 x FL	0.206	0.291	5	0.71	0.51
50% core	Intercept	48.86	24.57	13	1.99	0.068
	Period:After	−45.11	24.59	2	−1.83	0.21
	Year:2016	−31.85	28.25	2	−1.13	0.38
	FL	−0.154	0.093	13	−1.67	0.12
	Period:After x Year:2016	49.61	35.74	2	1.39	0.30
	Period:After x FL	0.187	0.092	2	2.04	0.18
	Year:2016 x FL	0.096	0.106	2	0.91	0.46
	Period:After x Year:2016 x FL	−0.176	0.130	2	−1.35	0.31

change point in abundance on 16 October (13 October – October 27, 2015 ± 95% CI, Fig. 4).

Size of tiger shark extent (95%) and core (50%) activity space within the array did not differ pre or post October 7 in either 2015 or 2016. Further, no effects of body size nor the interactions among time period, year and body size were detected on either metric of activity space (Table 1). For an average size tagged tiger shark used in the analysis (262 cm FL), extent activity space within the Bahamas array was 24.8 (12.6–37.0, 95% CI) and 30.2 (19.5–40.9, 95% CI) km^2 pre and post October 7, 2015, respectively. Pre and post Hurricane Matthew, the same size shark was estimated to have an extent activity space of 27.2 km^2 (7.7–42.4, 95% CI) and 41.1 km^2 (6.2–53.2, 95% CI). Core activity space for the same size shark in 2015 was 8.4 km^2 (2.3–13.4, 95% CI) and 12.5 km^2 (19.5–40.9, 95% CI) pre and post October 7, respectively. Core activity space for an average size tiger shark during 2016 when Matthew crossed the Bahamas array was 1.7 km^2 (3.6–8.7, 95% CI) and 9.3 km^2 (2.8–14.7, 95% CI) pre and post hurricane, respectively.

3.2. Miami Array

In the Miami array, two nurse sharks were observed on the day (September 10, 2017) when Hurricane Irma was at approximately equal latitude with Biscayne Bay (Fig. 5a). Bull sharks were not detected during Hurricane Irma in the Miami array. Great hammerhead were most frequently detected in the month preceding Irma, with a single animal detected during the storm. Neither bull (paired *t*-test: $t_2 = 1.25$; $p = 0.34$), great hammerhead (paired *t*-test: $t_6 = -1.01$; $p = 0.35$), nor nurse (paired *t*-test: $t_9 = 0.28$; $p = 0.79$) sharks exhibited a difference in the number of days detected 30 days previous to versus 30 days following Hurricane Irma in 2017 or over the same time span in 2019 ($P > 0.05$ in all cases).

Within the Miami array, three bull sharks, seven great hammerhead sharks and 10 nurse sharks were detected at least once in the month preceding and following Hurricane Irma (August 9, 2017 to October 10, 2017). Although the eye of Hurricane Irma passed 140 km west of Miami on September 10, 2017, barometric pressure in Biscayne Bay reached a low of 1002.5 kPa, and wind speeds reached a high of 132.8 km h^{-1}. One bull (33%), two great hammerhead (28%) and two nurse sharks (20%) appear 3–26 days following the storm. Two great hammerhead sharks (28%) and six nurse sharks (60%) were detected in the Miami Array within a five-day window of Hurricane Irma. In the two days preceding the storm, two nurse sharks and one great hammerhead were detected in areas of Biscayne Bay (Fig. 5). As the storm passed immediately to the west, two nurse sharks were again detected in the more urbanized coastal areas near Miami. Two days following the storm, nurse sharks could be found in the shallow, leeward sides of Sands and Elliot Keys in Biscayne Bay National Park (Fig. 5). Bull sharks showed a change-point in daily abundance where it appears daily abundance decreased immediately following the storm (Fig. 4). No change-points were observed in daily abundance for either great hammerhead or nurse sharks in Biscayne Bay. Two change points were indicated for bull sharks, where abundance increased and decreased in 2019 (Fig. 4). A change point was indicated for nurse shark abundance in early September of 2019 (Fig. 4).

4.0. Discussion

We used acoustic telemetry to examine several aspects of habitat use for multiple large shark species preceding, during, and following two major hurricanes (category 4 and 5) in shallow-water habitats of the subtropical Atlantic. Sharks were predicted to evacuate shallow coastal habitats (and thus exit the acoustic arrays) during the hurricanes and exhibit comparable size of activity spaces pre- and post-storms, as has been found for smaller sharks elsewhere (Heupel et al., 2003; Udyawer et al., 2013; Strickland et al., 2020). However, we found variable responses by large sharks to storm events. Specifically, tiger sharks did not show evidence of fleeing the Bahamas Array during a direct hit from Hurricane Mathew, with daily detections of tagged tiger sharks consistent before and during the hurricane. Immediately following the storm, daily tiger shark detections approximately doubled, while size and extent of tiger shark activity space within the array were consistent pre- and post-hurricane. In contrast of Miami, the majority of sharks present in the array a month prior were no longer detected as the eye of the storm passed to the west. Numbers of tagged nurse and great hammerheads in the Miami array were similar a month prior to compared to a month following Hurricane Irma, whereas detections of bull sharks appeared to decline in the array a month following the storm.

Species-specific physiology is one tenable explanation for the variable responses to the storm events found here. Although there is no empirical research on the effects of such storm disturbances on shark physiology, presumably storm conditions have the potential to impact energy use and homeostasis of sharks through changes in environmental conditions. During the hurricanes, one tiger and two nurse sharks remained in the arrays while all other individuals evacuated the areas. Studies using stress biomarkers to understand resiliency to external challenges (e.g., capture) have consistently shown that both nurse and tiger sharks are species with robust physiologies and muted stress responses compared to bull and especially great hammerheads (Jerome et al., 2017; Gallagher et al., 2017). Moreover, nurse sharks possess low metabolic rates (Whitney et al., 2016; Pratt et al., 2018) and are often observed refuging under coral ledges. Individual nurse sharks detected in the Miami array during the hurricane may have taken refuge under such ledges. In contrast, the higher physiological sensitivity of bull and great hammerheads, at least as indicated through capture stress studies, could have in part be responsible for the lower detections of these species seen in the Miami array during the storm.

Numerous empirical studies have demonstrated that fish, birds, and invertebrates react to dropping barometric pressure (Heupel et al., 2003; Oh et al., 2017; Gibson et al., 2018; Nakayama et al., 2018). Juvenile blacktip shark Carcharhinus limbatus, Australian reef shark Carcharhinus tilstoni, spot-tail shark Carcharhinus sorrah and pigeye shark Carcharhinus amboinensisi, and juvenile bull sharks have been shown to evacuate nearshore habitat as barometric pressure drops with approaching tropical storms (Heupel et al., 2003; Udyawer et al., 2013; Strickland et al., 2020). Our study also suggests that sharks could be responding to barometric pressure. For example, we observed an overall synchronicity in tiger shark behavior that coincided with changes in

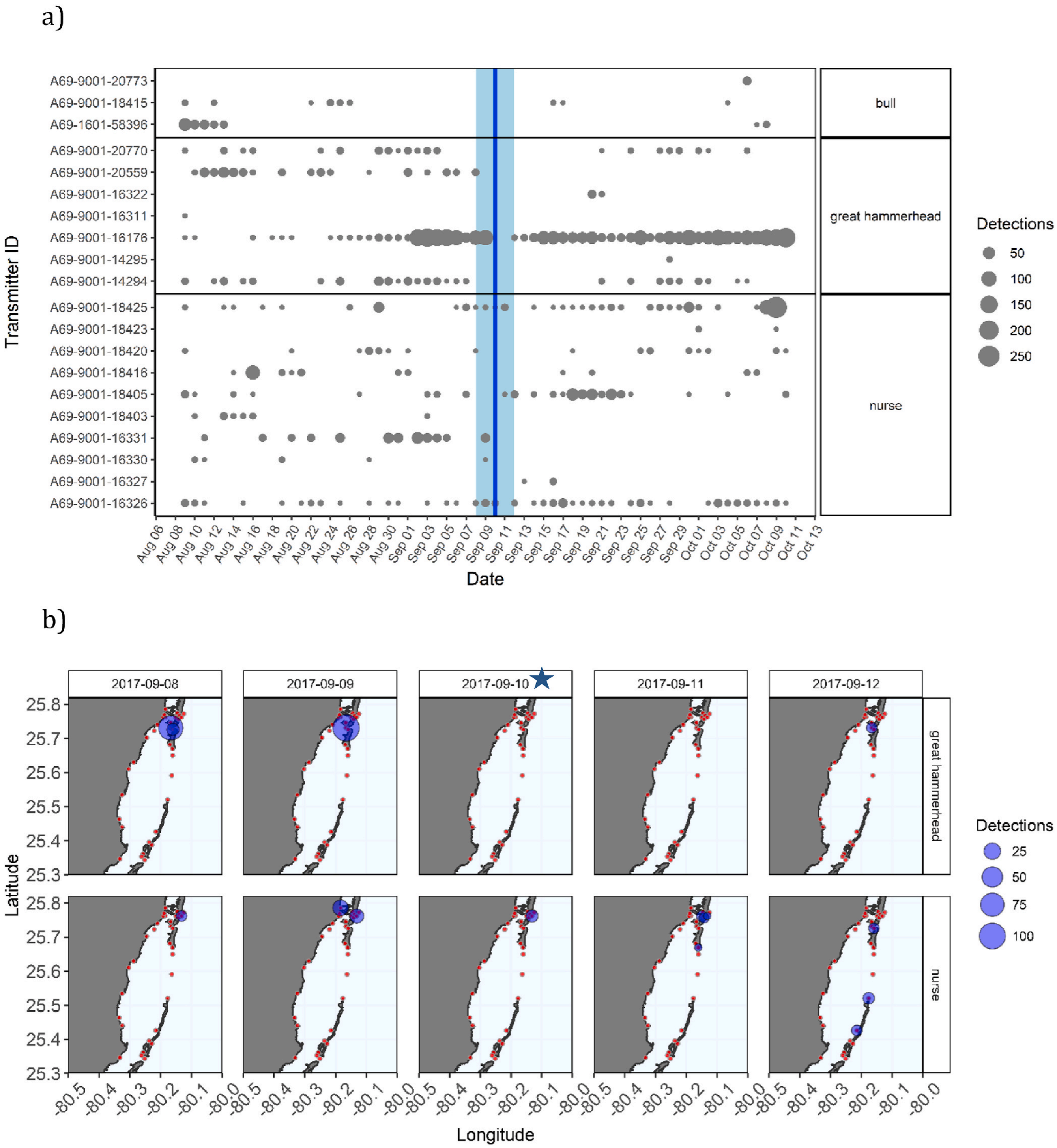

Fig. 5. (a) Daily detections for all tagged animals recorded within the Miami Array from August 9 to October 10, 2017. The vertical blue line indicates the approximate date when Hurricane Irma was at equal latitude to Biscayne Bay. (b) Number of detections by shark species within the Miami Array from 2017 to 09-08 to 2017-09-12 (the day of the hurricane is denoted by a star, B). Note that Hurricane Irma was at approximately equal latitude with Biscayne Bay 2017-09-10. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

barometric pressure during Hurricane Matthew and again on October 22, 2016.

Here, tiger sharks notably increased their activity immediately following Hurricane Matthew in 2016. It is possible that feeding opportunities could follow within the direct path of episodic events such as large tropical storm where small sedentary marine species are either displaced or killed (Posey et al., 1996; Wilson et al., 2006). Additionally, tiger sharks have been found to scavenge on dead birds, including those suffering mortality from unforeseen weather events (Gallagher et al., 2011; Drymon et al., 2019). That said, a similar change point in shark abundance detected around Hurricane Mathew occurred during 2015 at the same time of year (fall) when no major storm passed over the Bahamas array. Given the change point in 2015, it is plausible that tiger sharks were returning to the area in response to seasonal cues for refuging in warm waters that include supporting gestation as hypothesized by Sulikowski et al. (2016). Unlike in smaller shark species, tiger sharks in particular deviated little from their natural behavior in response to the disturbance caused by a major hurricane.

Although we provide the first evaluation of large (>190 cm fork length) or apex predatory shark species' behavior during storm events, there are several caveats to the results interpretation. Neither array contained the necessary sync tags to assess detection range efficiency (Kessel et al., 2014). Given normal tidal and marine traffic, we assume that transmission and detection efficiency was similar before and after the storms. It is possible that during the storms, detection ranges decreased from acoustic noise. This, however, would result in lower detection efficiency. The fact that sharks were detected during storm events strengthens the findings suggesting some species did not flee the arrays during the storms. In addition, acoustic telemetry only provides information about behavior when animals are detected. Animals that evacuate the detection range of a receiver array effectively only provide information regarding the time associated with their absence (Bacheler et al., 2019; Whoriskey et al., 2019). While the activity space increased for tiger sharks following Hurricane Matthew, these comparisons are relative to the detection range of the array and would constitute only a fraction of the realized home range for these animals (Holland et al., 1999; Heithaus et al., 2007). Finally, change-points in shark activity do not reveal the apparent mechanisms driving behavior. Small numbers of tagged animals, the widely spaced telemetry receivers that limited the number of daily detections per animal, and their mobility combined to make it impossible to directly associate environmental variables to shark behavior in these systems. Nevertheless, the observations here in coastal Florida and the Bahamas present an important and exciting opportunity for future research.

Regime shifts are abrupt changes between contrasting, persistent states of any complex system (DeYoung et al., 2008). In the marine realm, regime shifts are characterized by abiotic and biotic processes driven by natural and anthropogenic components (Lees et al., 2006; DeYoung et al., 2008). While some species appeared to exit shallow or coastal areas, others indicated little response to the immediate consequences of violent storms. Instead, these larger sharks appeared to transition quickly to predictable seasonal patterns in behavior. Should tropical storm intensity increase as most climatological models predict (Walsh et al., 2016; Kossin et al., 2020), shark species will likely differ in their response with currently unknown ecosystem consequences. We are only beginning to understand how these events may drive ecological regime shifts that affect top predators and their subsequent effects on marine ecosystems.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Authorship contributions

Conception and design of study: NH; Acquisition of data: NH, MR, RR, MH, SC, AG; Analysis and/or interpretation of data: NH, LG; Drafting the manuscript: NH, LG; Revising the manuscript critically for important intellectual content: NH, LG, SC, MR, MH, AG, RR; Approval of the version of the manuscript to be published (the names of all authors must be listed): Lee Gutowsky, Neil Hammerschlag, Steven Cooke, Mitchell Rider, Robert Roemer, Austin Gallagher, Michael Heithaus.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107373.

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