Marine Environmental Research 172 (2021) 105489

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Space use patterns of sharks in relation to boat activity in an urbanized coastal waterway

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ARTICLE INFO

Keywords:
Urbanization
Movement ecology
Global change
Acoustic telemetry
Elasmobranch
Coastal waters
Vessel traffic

ABSTRACT

Aquatic ecosystems face numerous anthropogenic threats associated with coastal urbanization, with boat activity being among the most prevalent. The present study aimed to evaluate a potential relationship between boat activity and shark space use in Biscayne Bay, Florida (USA), a coastal waterway exposed to high levels of boating. Spatiotemporal patterns in boat density and traffic were determined from aerial surveys and underwater acoustic recorders, respectively. These data were then compared with residency patterns of bull (*Carcharhinus leucas*), nurse (*Ginglymostoma cirratum*) and great hammerhead (*Sphyrna mokarran*) sharks quantified through passive acoustic telemetry. Results were mixed, with no detectable relationship between boat density and shark residency for any of the species. Hourly presence of *G. cirratum* decreased with increasing boat traffic, a relationship not seen in the other two species. Explanations for these results include habituation of sharks to the high levels of chronic boat activity in the study area and interspecific differences in hearing sensitivity.

1. Introduction

Coastal areas are urbanizing rapidly (Creel, 2003; McGranahan et al., 2007), posing increased anthropogenic stressors to the ecology and sustainability of nearshore ecosystems (Todd et al., 2019). Marine systems adjacent to urban centers are subjected to increased resource exploitation, habitat degradation, ocean sprawl and pollution (Todd et al., 2019). Among the most ubiquitous threats of coastal urbanization to aquatic systems is increased boat activity, which can damage habitats (Zieman, 1976), collide with wildlife (Lester et al., 2020; Speed et al., 2008; Wells and Scott, 1997), and create noise pollution (Popper et al., 2003). A growing number of studies have demonstrated that the presence, volume, and frequency of boat engine noise can negatively impact the physiology (Wysocki et al., 2006) communication (Codarin et al., 2009), and behavior of teleost fishes (Ferrari et al., 2018). Some studies have found that teleosts will avoid areas of high boat activity (De Robertis and Wilson, 2011; Filous et al., 2017; Sarà et al., 2007), while other studies have demonstrated minimal effects of boat activity on both freshwater (MacLean et al., 2020; Maxwell et al., 2018) and marine fishes (Staaterman et al., 2020), suggesting possible habituation. Comparative studies have yet to be performed examining the potential effects of boat activity on elasmobranchs, which often rely on coastal subtropical ecosystems for critical life history phases. Given that changes to the distribution or abundance of top predators, such as sharks, can impact ecosystem structure and function, an identified key research priority is to understand the direct and indirect effects of urbanization on the ecological function and services of aquatic predators (Hammerschlag et al., 2019).

Elasmobranchs are sensitive to low frequency sounds (Casper and Mann, 2006, 2009), such as those produced by boat engines, particularly those of large ships. Accordingly, elasmobranchs should be able to detect the presence of boat engine noise. The sensitivity to low sound frequencies exhibited by sharks has been hypothesized as an adaptation to aid in detection of prey, which, when injured or struggling, produce sounds at similar frequencies (Myrberg, 2001). Boat engine noise may therefore attract sharks to boats, particularly in cases where depredation on fishing lines has caused sharks to associate boat engine noise with the availability of hooked fish to consume (Mitchell et al., 2018a).

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https://doi.org/10.1016/j.marenvres.2021.105489
Received 8 May 2021; Received in revised form 24 September 2021; Accepted 26 September 2021
Available online 30 September 2021

Alternatively, boat noise could negatively impact elasmobranch foraging by masking the sounds produced by vulnerable prey (Hildebrand, 2009). Although boat activity could theoretically trigger avoidance behavior in elasmobranchs, no studies to date have specifically investigated this possible relationship (Casper et al., 2012).

The purpose of this study was to explore the potential relationship between boat activity and residency patterns of coastal sharks in an urbanized coastal waterway exposed to high boating. Research was conducted in waters off Miami, Florida, one of the most populous cities in the United States, with a coastal waterway exposed to high levels of recreational and commercial boating (Ault et al., 2017; Gorzelany, 2009). Here, spatiotemporal patterns in boat density were determined from published aerial survey data, whereas patterns of boat traffic (i.e., number of boat passages per hour) were quantified from underwater acoustic recordings using fixed hydrophones. These data were then compared with space use patterns of three coastal shark species, bull (*Carcharhinus leucas*), great hammerhead (*Sphyrna mokarran*), and nurse (*Ginglymostoma cirratum*) sharks quantified through passive acoustic telemetry. These data were used to test the central hypothesis that sharks, regardless of species, would exhibit boat avoidance behaviors, reducing their space use in places and times of higher boat activity given the growing number of studies that have found negative impacts of boat engine noise on fish physiology (Wysocki et al., 2006), communication (Codarin et al., 2009), and behavior (Ferrari et al., 2018).

2. Materials and methods

2.1. Study site

Miami is a metropolis situated proximal to Biscayne Bay, a shallow subtropical lagoon (56 by 13 km) that stretches from Haulover, past downtown Miami, to north Key Largo (Fig. 1). The Bay's production is primarily benthic, as it contains communities of seagrasses, hard corals, gorgonians, and sponges; however, it also contains some remnant estuarine habitats (Browder et al., 2005). Biscayne Bay is by a gradient of urbanization, from intense development around Miami to far less impacted areas in the south.

Miami-Dade County has the highest number of registered vessels in Florida (Florida Department of Highway Safety and Motor Vehicles, 2019) (https://www.flhsmv.gov/resources/driver-and-vehicle-reports/vehicle-and-vessel-reports-and-statistics/), 67,327 recreational and commercial vessels (including boats and jet skis), of which >97% are recreational. Since Miami-Dade is directly adjacent to Biscayne Bay, a large portion of those registered boats are likely used on the Bay. The highest amount of boat activity can be observed in the northern portion of the Bay and on weekends and holidays (Ault et al., 2017; Gorzelany, 2009). During peak hours of the day (12:00–15:00), boat activity in the Bay ranges between 108 and 141 boats during weekdays and 349–723 boats on weekends/holidays (Ault et al, 2005, 2017).

2.2. Boat density via aerial surveys

Spatiotemporal patterns of boat density were determined by analyzing aerial survey data reported in Ault et al. (2017), which conducted monthly aerial surveys of boaters in the study area during 2016–2017. Surveys were accomplished using a fixed-wing aircraft during three seasons (spring, February–May 2016; summer, June–September 2016; and, fall-winter, October 2016–January 2017). To determine seasonal boating activity patterns at a broad scale, a sampling ratio of 2:3 weekdays:weekends/holidays was selected based on a prior knowledge (Ault et al., 2008). Five flights were scheduled per month based on the sampling ratio depending on weather and aircraft availability. Actual survey dates were randomly selected, but the weekends of Memorial Day, Fourth of July, Columbus Day, and lobster mini-season (mid-July) were preferentially chosen because of the known high volume of boat traffic in Biscayne Bay (Ault et al., 2005; Eggleston et al., 2003). Aerial survey flights were conducted at altitudes ranging from 150 to 300 m, speeds of 165–185 km per hour, between 1200 and 1500 h. During each flight, three observers using binoculars spotted boats, noted the vessel type and activity, and recorded positions on a tablet computer with an affixed external GPS. The Aerial Vis Survey algorithm developed by Lance Garrison (Read et al., 2012) was used to calculate accurate boat coordinates using real-time data on aircraft route, boat disposition, and angle of the boat from the aircraft position.

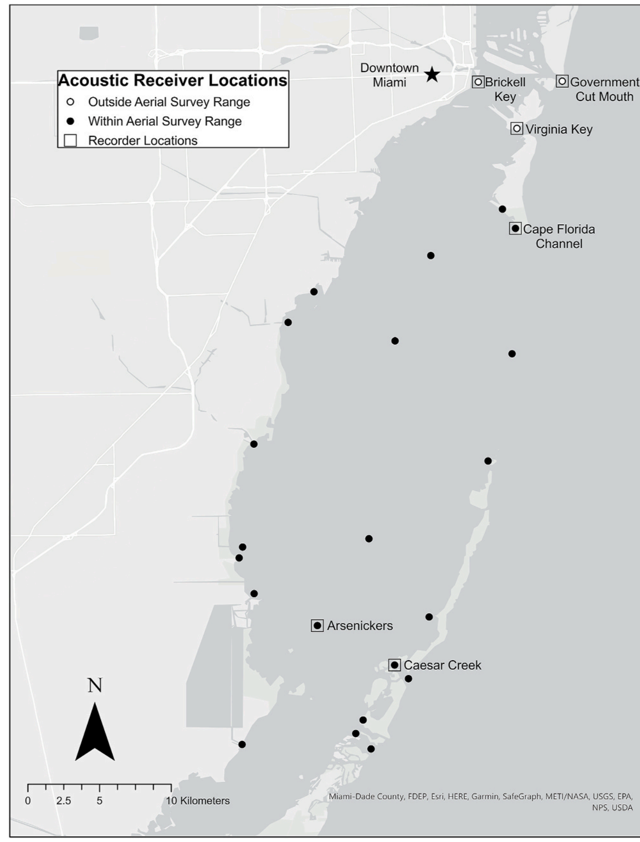

Fig. 1. Locations of acoustic receiver stations (dark circles) around Biscayne Bay, Florida. Black and white points represent stations within and outside of the aerial survey spatial range, respectively. Stations with underwater acoustic recorders are shown by squares and labeled.

To derive average boat densities, boat positions sighted in the aerial survey were plotted in ArcGIS 10.3 (Environmental Systems Research Institute, Inc., Redlands, California) using the NAD 1983 UTM Zone 17N projected coordinate system. A kernel density estimation was used to establish a boat density index within the survey's spatial range. Since boat activity was found to be higher on weekends and holidays as well as seasonally (Ault et al., 2017; Gorzelany, 2009), kernel density computations were carried out for each combination of day category (i.e., "weekday" vs. "weekend/holiday") and season (wet season: May 1 to October 31; dry season: November 1 to April 30). Those expected densities were then scaled by the number of surveys conducted per day category within each season: weekday dry season (n = 10), weekday wet season (n = 8), weekend/holiday dry season (n = 10), weekend/holiday wet season (n = 16).

2.3. Boat traffic via acoustic recorders

To quantify patterns of boat traffic, six underwater acoustic recorders (two DSG-ST and four Snap; Loggerhead Instruments, Sarasota, FL, USA) were placed at different locations (squares in Fig. 1). These sites were chosen because of their varying proximity to Miami and associated varying levels of boat activity expected to occur at each.

Recorders were paired with the acoustic telemetry receivers (see section 2.4) to allow for simultaneous comparisons with shark residency patterns.

The recorders at Cape Florida Channel and Brickell Key were initially deployed in March 2018. Arsenickers Key, Caesar Creek, and Government Cut were initially deployed in September 2018, and Virginia Key was initially deployed in March 2019 (see Fig. 1).

These recorders were programmed to record 10 s every minute with a sample rate of 20 kHz and 32 kHz (decimated once), and sensitivity of −180.1 and −169.4 dBV/uPa for the DSG-ST and Snap recorders, respectively. Selected sample rates allowed recorders to log frequencies up to 10 kHz and 16 kHz, respectively. These sample rates were chosen because both recreational and commercial boat engines produce sound frequencies within that range (Barlett and Wilson, 2002; Fischer and Brown, 2005). Routine maintenance (i.e., swapping batteries and memory cards) was performed on the recorders approximately every 20–55 days.

Boat traffic (i.e., passages per hour) were quantified from boat engine noise. To accomplish this, we first determined the "normal" level of background noise at each recorder location, and then examined the data for peaks in the noise which would be indicative of passing boats. To calculate the median background noise, data were processed through a 'filter analyzer' developed by the Marine Environmental Research Infrastructure for Data Integration and Application Network (MERIDIAN) of Dalhousie University (Nova Scotia, Canada). The filter analyzer read each of the files and down sampled to a rate of 2000 Hz. The audio signal was transformed using a Fast Fourier Transform (FFT) to create a spectrogram: Spectrogram $= 20 \text{ x} \log_{10}$(FFT(audio signal)). The spectrogram was split into frequency bands with central frequencies of 31.2, 62.5, 125, 250, 500, and 1000 Hz. For each frequency band, the running median of sound pressure level was computed using a window size of 3 s and a step size of 1 s. This produced a time series of median sound pressure levels for each frequency band. The median was computed using a window size of 1 min and subtracted from the median values for each frequency band. This produced a time series of background-subtracted median values for each frequency band.

Using those median values, an 'anomaly detector' (MERIDIAN) was used to identify any boat engine noise on the sound clip. The anomaly detector searched for peaks (i.e., instances with abnormally high sound levels) in the time series of x' for the frequency bands of 125, 250, and 500 Hz. These frequency bands were chosen because the dominant energy from boat engine noise tends to fall in this range. A peak was counted as a "positive" boat detection if it: 1) was separated by 2 min from the nearest neighboring peak, 2) occurred in a minimum of two of the three frequency bands, 3) exhibited a minimum height above the background fluctuations (i.e., prominence), and 4) did not exceed a certain threshold level (to account for miscellaneous high-amplitude sounds such as those produced by snapping shrimp). The minimum height was computed as $h_{\min} = p * M(|x - M(x)|)$, where p was the specified prominence, and $M(x)$ was the median operator. Specified prominence was manually adjusted for each station to account for differences in background noise. The boat detections were then verified by analyzing spectrograms produced from a random sample of sound clips for each recorder using the sound analysis software Raven Pro 1.4 (Cornell Lab of Ornithology). The outputs of this program were date-time stamps of boat detections.

To understand the maximum distance at which recorders could detect and positively log a boat passage, range testing took place at a subset of locations. The recorders were set to log continuously while a boat would begin driving along a transect away from the recorder. At distances of 100, 200, 400, 600, 800, and 1000 m, a 4.5 m boat with a 150 Mercury engine sped up to cruising speed, completed two tight circles (taking approximated 15–20 s), immediately returned to idle speed, and moved to the next distance. The sound files from range testing were then run through the boat detection software to determine the maximum detection range.

2.4. Shark space use via acoustic telemetry

Sharks were captured using a series of baited drumlines, as described in Gallagher et al. (2014). Captured sharks were either secured alongside a boat in the water or on top of a floatable platform, in preparation for electronic tagging. All sharks were tagged with the Innovasea V16–4X internal acoustic transmitters (Amirix Inc., Bedford, NS, Canada), programmed with a nominal delay of 60–90 s, however we used two different types of tag attachment methods. *C. leucas* and *G. cirratum* were tagged via surgical implantation into the shark's body cavity following the approach of Hammerschlag et al. (2017), whereas *S. mokarran* were tagged via an externally tethered tag package, which used a dart anchor that was embedded in the shark's dorsal musculature. The external tag approach was used for great hammerheads because it allowed for faster tag attachment, considering this species' inherent sensitivity to capture and handling stress (Gallagher et al., 2014; Jerome et al., 2018). While tag shedding is more likely with external transmitters, this risk was minimized by looping the tag tether through the dorsal fin prior to insertion in the dorsal musculature. Shark capture and tagging were conducted under permits from Florida Fish and Wildlife Conservation Commission, the Florida Keys National Marine Sanctuary, the US National Marine Fisheries Service, and the University of Miami Animal Welfare and Care Committee (Protocol 18–154).

Reliable estimates of residency patterns from June 2015 to October 2019 were obtained using an acoustic receiver array capable of detecting tagged sharks as described in Gutowsky et al. (2021). This passive acoustic array consisted of 24 Innovasea VR2W – 69 kHz receivers (Amirix Inc., Bedford, NS, Canada) deployed in Biscayne Bay, FL (Fig. 1). Receivers were anchored to the substrate at depths ranging from 1.5 to 12 m using a concrete stand. Detection data were retrieved from receivers every six months (March and September).

Detection range testing was performed on three representative acoustic receivers at different location that differed in exposure to environmental and acoustic conditions using methods similar to those described by Kessel et al. (2014b) and Selby et al. (2016). For each reviewer, we estimated the range in which the probability of transmitter detection was 50% (median range) and 5% (maximum range). Receiver range testing indicated a relatively small 50% detection range of about 250 m, with 5% detectability (i.e., maximum range) of about 900 m. The radius of receiver detection regions used for determining average boat densities was set equal to the 50% detection range.

2.5. Shark daily residency in response to boat density

Spatial boat densities were joined to specific acoustic receiver stations by averaging boat density indices within a specified buffer region around each receiver where the radius of the buffer region was equal to the 50% acoustic receiver detection range (i.e., 250 m) as measured by range testing (described above).

To prepare the shark residency data (response variable) from the raw acoustic detection data, false detections (i.e., detections occurring from either environmental noise or overlap between two or more acoustic transmitter signals) were removed if the time between transmissions for a given individual was greater than 60 min (Kessel et al., 2014a; McDougall et al., 2013). This amount of time was chosen because the probability of false detections occurring from the same transmitter within a short amount of time was extremely low.

Since aerial surveys were conducted during daylight hours, only diurnal shark detection data were used for this analysis. Shark daily residency indices were calculated as the number of days a shark was detected at a receiver station and scaled by number of possible days it could have been detected (i.e., days at liberty). Even though the aerial surveys were conducted between 2016 and 2017, we joined derived boat density values to shark detection data from 2016 to 2020 given the sparse amount of detection data from each of the three species. Thus, the daily residency indices were computed for each day category (i.e., weekday versus weekend/holiday) during each season (wet versus dry) from 2016 to 2020. If a shark was not detected during either day category at a station during a particular season, or if the total number of days it could have been detected within a season was less than 10, those observations were excluded from the analysis.

The relationship between shark daily residencies and boat density indices was assessed using a negative binomial generalized linear model (GLM). Since the negative binomial GLM requires count data, the residency index was split up where the number of days detected was left as the response variable and the log-transformed number of detectable days was set as the offset term. In addition to boat densities, season and day category were also included as explanatory variables. Best fit model selection was based on model diagnostics, specifically residual distribution, and error variance.

2.6. Shark hourly presence in response to boat traffic

To examine for a potential relationship between boat traffic and shark presence, we evaluated shark detections dependent on boat passages on an hourly basis at six stations with paired Snap recorders and VR2W receivers. A boat passage was defined as any vessel passage that produced noise in at least two of three frequency bands (i.e., 125, 250, and 500 Hz), characteristic of small recreational boat engine signatures (Barlett and Wilson, 2002), which comprise the majority of boat traffic in Biscayne Bay (Ault et al., 2017).

Due to a limited temporal overlap when recorders and receivers were both operational, insufficient data were available for analysis at the station level. Consequently, we grouped species data from all six stations. We considered an observation to be a 1-h period in which at least one shark was detected at a station. The relationship between shark detections dependent on boat passages was evaluated in a generalized linear model (GLM) using the R 'stats' package (R Core Team, 2019). Three different approaches were used to determine the best fit. First, a GLM with binomial error where the response variable was the proportion of recorded detections out of the total possible detections in a 1-h observational period (i.e., the number of recorded detections out of 48 possible detections within a 1-h observational period given a transmitter nominal delay of 60–90 s). Second, GLMs with both Gamma and Poisson errors where the response variable was the number of detections within a 1-h observation period. Third, a GLM with Gaussian error with detections recorded in an observation period as the response variable. Box-Cox transformations were applied to either the response variable, explanatory variable, or both. Best fit model selection was based on model diagnostics, specifically residual distribution, and error variance.

3. Results

3.1. Shark tagging

Between February 2015 and July 2019, a total of 82 individual sharks (*C. leucas*: n = 22; *S. mokarran*; n = 33; *G. cirratum:* n = 27) were acoustically tagged in Biscayne Bay. Only 42 individuals were detected on our array and therefore used in the following analyses (Table 1).

3.2. Shark daily residency vs boat density

From February 2016 to January 2017 (44 sampling days), aerial surveys observed 16,767 boats in Biscayne National Park (mean = 381 boats per day). The survey only designated coordinates for 15,629 boats due to equipment failure; therefore, only boat observations with designated coordinates were used for analyses. Overall, the dataset contained a higher mean number of boat observations per day during weekends/holidays (mean = 528) as opposed to weekdays (mean = 106). Differences in expected boat observations across the survey area were also evident for expected boat densities determined from the kernel density computations (Fig. 2). Boat densities across the survey domain were generally lower during weekdays (Fig. 2A and C) than weekends/holidays, especially along the eastern and northern boundaries of the survey domain (Fig. 2B and D). There was also a general increase in the boat density from dry season to wet season for both day categories with a higher incidence of boating occurring along the eastern boundary of the Bay. This increase in boat density was more evident during the weekends/holidays as opposed to the weekdays (Fig. 2).

Between February 2015 and June 2020, 33 individual sharks (*C. leucas,* n = 11; *S. mokarran,* n = 10; *G. cirratum,* n = 12) were detected. Of those 33 individuals, 30 (*C. leucas* = 11; *S. mokarran* = 8; *G. cirratum* = 11) met the criteria (described above) to be included in the analyses (Table 1).

The best for fit GLM for *C. leucas* consisted of a negative binomial distribution with only boat density index as the explanatory variable. The GLM for *C. leucas* indicated no dependence of shark residency on boat density (Table 2).

The best GLM fit for the relationship between the boat density index and daily residency of both *S. mokarran* and *G. cirratum* included season as an additional predictor variable. While there was a significant influence of season, as *S. mokarran* and *G. cirratum* exhibited higher mean residency during the dry and wet seasons, respectively (Fig. 3), there was no significant influence of boat density on residency of *G. cirratum* (Table 2).

3.3. Shark hourly presence and boat traffic

Across all stations with an underwater recorder, there was a general peak and trough in hourly boat passages in the middle of the day around 17:00 and 5:00, respectively (Fig. 4). Overall, there was generally

Table 1
Description of acoustically tagged sharks used within this study.

Transmitter	Species	Total Length (cm)	Sex	Date Tagged
13487[a]	*C. leucas*	196	F	1/12/2017
16325	*C. leucas*	244	F	10/3/2017
16328	*C. leucas*	196	M	7/2/2017
18415	*C. leucas*	191	F	10/22/2016
18419	*C. leucas*	236	F	1/20/2017
18421	*C. leucas*	242	F	4/2/2017
20563	*C. leucas*	256	F	4/12/2015
24655[a]	*C. leucas*	263	F	2/24/2015
24660	*C. leucas*	219	F	2/27/2015
58396	*C. leucas*	211	F	11/8/2015
58403	*C. leucas*	202	F	1/21/2016
14294	*S. mokarran*	293	F	6/5/2017
16171	*S. mokarran*	203	M	4/30/2017
16322[b]	*S. mokarran*	163	M	6/30/2017
16329	*S. mokarran*	267	F	7/2/2017
20770[a]	*S. mokarran*	293	F	4/16/2016
28083	*S. mokarran*	265	M	10/19/2018
28085	*S. mokarran*	263	F	5/10/2018
28089[a]	*S. mokarran*	275	F	4/26/2019
28093[a]	*S. mokarran*	263	M	4/29/2019
16326[b]	*G. cirratum*	154	F	8/2/2017
16327[b]	*G. cirratum*	173	M	8/2/2017
18405[a]	*G. cirratum*	173	F	6/28/2016
18416[b]	*G. cirratum*	165	F	5/11/2016
18420[b]	*G. cirratum*	194	F	1/30/2017
18422[a]	*G. cirratum*	239	F	8/2/2017
18425[b]	*G. cirratum*	174	F	1/30/2017
20772[b]	*G. cirratum*	200	F	4/26/2016
28095	*G. cirratum*	222	M	1/3/2019
28096[a]	*G. cirratum*	218	M	4/29/2019
28097	*G. cirratum*	226	M	5/2/2019
28098	*G. cirratum*	210	M	6/28/2019
28099[a]	*G. cirratum*	250	M	6/28/2019
28101	*G. cirratum*	198	F	6/28/2019
28102	*G. cirratum*	204	F	7/18/2019
28103	*G. cirratum*	232	F	10/31/2018

[a] Sharks included in both analysis of boat density and traffic.
[b] Sharks only included in boat traffic analysis.

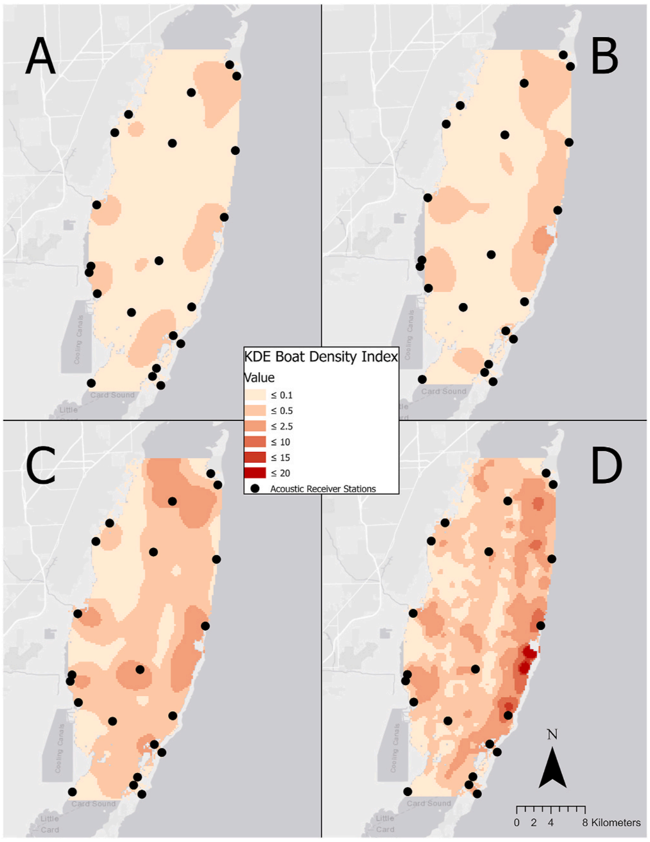

Fig. 2. Map showing average boat density indices calculated for: (A) weekdays during the dry season (B) weekdays during the wet season, (C) weekends/holidays during the dry season, and (D) weekend/holidays during the wet season. Black dots represent acoustic receiver stations within the range of the aerial surveys. Indices were scaled for easier interpretation.

Table 2
Generalized linear model (GLM) parameter estimates of shark residencies dependent on boat density indices and season where dry season is the reference level.

Species	Parameter	Estimate	Std. Error	z value	p value
C. leucas	Intercept	−3.862	0.153	−25.264	<0.001*
	Boat Density	5.666	8.680	0.653	0.514
S. mokarran	Intercept	−4.498	0.154	−29.176	<0.001*
	Boat Density	−1.501	2.372	−0.633	0.527
	Season: Wet	0.456	0.231	1.970	0.049*
G. cirratum	Intercept	−4.200	0.242	−17.297	<0.001*
	Boat Density	−1.326	1.969	−0.674	0.500
	Season: Wet	1.126	0.365	3.087	0.002*

greater boat passages during the weekends/holidays (Fig. 4).

Between March 2018 and October 2019, 16 individual sharks (*C. leucas*, n = 2; *S. mokarran*, n = 4; *G. cirratum*, n = 10) were detected on the six stations that had both acoustic receivers and recorders. All 16 sharks were used in the following analyses (Superscripts in Table 1). There was a small amount of data for *C. leucas* and *S. mokarran* as individuals were detected during ten and 21 1-h observation periods, respectively, while *G. cirratum* individuals accounted for 217 observations (Table 3).

For *C. leucas* and *S. mokarran*, the best models included an inverse and square-root transformations of detections, respectively. The models for these two species indicated no dependence of shark detections on boat passages (Table 4).

The best model fit to the data for the relationship between boat passages and detections of *G. cirratum* was a GLM using a Box-Cox transformation (λ = 0.3) of the dependent variable and a square-root transformation of the independent variable (Table 4). Shark detections dependent on boat passages were significantly negative (Table 4).

The interaction of day category and hourly boat passages did not end up in any of the three models described above as their addition to the models did not satisfy model fit or convergence. However, while there was a general increase in boat traffic on the weekends/holidays, mean hourly detections did not differ between day categories for either *C. leucas* or *S. mokarran* (Table 3). Mean hourly detections was greater during weekdays for *G. cirratum*, but the standard deviation was considerably high (Table 3).

4. Discussion

This study used a combination of aerial surveys of boat density, acoustic estimates of boat traffic, and passive acoustic tracking of sharks to evaluate the potential influence of boat activity on shark space use. To date, no published studies have evaluated the relationship between boat activity and shark behavior, but based on a growing number of studies which have found that the presence, volume, and frequency of boat engine noise can negatively impact the physiology (Wysocki et al., 2006), communication (Codarin et al., 2009), and behavior of teleost fishes (Ferrari et al., 2018), we hypothesized that sharks would decrease their space use in places and times of higher boat activity. However, our investigations revealed no evidence of boat avoidance behavior in either *C. leucas* or *S. mokarran*. For both species, neither their daily residency patterns, nor their hourly presence, was related to boat density or traffic. In contrast, we found evidence of boat avoidance behaviors in *G. cirratum*. Specifically, their hourly presence decreased with increasing boat traffic, although daily residency patterns of *G. cirratum* were not related to boat density.

The boat engine noise recorded in this study is well within the frequency range detectable by sharks, and it is well known that sharks can become attracted to the revving of boat engines characteristic of fishing boats backing down when trying to land a fish on a line (Mitchell et al., 2018b). However, our data do not suggest either avoidance or attraction to high boat activity, except for the hourly presence of *G. cirrutum* suggestive of avoidance. Therefore, our results are somewhat unexpected, however we offer several testable hypotheses to explain these results.

The differences in species responses to boat activity found here could be related to differences in their hearing abilities. Using auditory evoked potentials, the hearing sensitivity of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) was observed to be greatest at 20 Hz (Casper and Mann, 2009). Since *R. terraenovae* and *C. leucas* stem from the same family (*Carcharhinidae*), they may have similar hearing thresholds – meaning, *C. leucas* could be most sensitive at very low frequencies (i.e., 20 Hz). A small boat engine operating at cruising speed (i.e., 3100–4800 RPM) has the most acoustic energy between 300 and 600 Hz (Barlett and Wilson, 2002). This may explain why *C. leucas* did not display boat attraction or avoidance behavior in this study. In contrast, *G. cirratum* appears to have relatively greater hearing sensitivity between 300 and 600 Hz (Casper and Mann, 2006), suggesting that this species is capable of recognizing boat engine noise, which could explain why this species appeared to decrease their space use in response to boat traffic. The hearing ability of hammerheads (family *Sphyrnidae*) remains untested.

Given we found little evidence of direct effects of boat activity on sharks, we suspect that any effects of boat noise are more likely to act indirectly as it has been proven to alter certain fish species, especially those that are physiologically capable of processing sound pressure. There's a possibility that boat activity is deterring certain prey species in the area and forcing sharks like *G. cirratum* to search for prey elsewhere. Future research should aim to study the effects of boat noise and activity on prominent prey species of *G. cirratum*.

While there was a detectable relationship between hourly boat traffic and presence of *G. cirratum*, it should be noted that there may be other

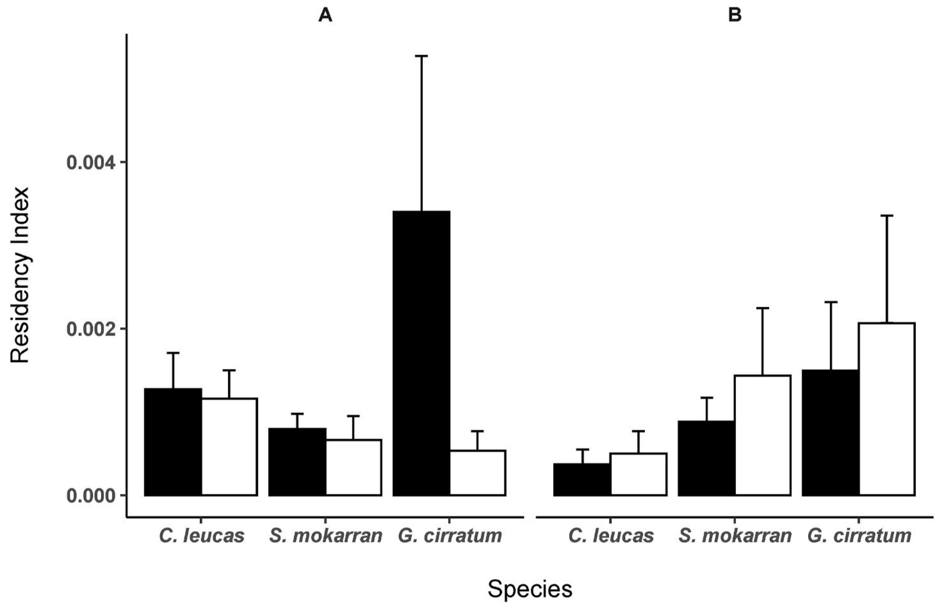

Fig. 3. Bar graph depicting the mean residency indices (+/− standard error of mean) of each species for each day category during the dry (A) and wet (B) seasons. Black and white bars represent residency indices on weekdays and weekend/holidays, respectively.

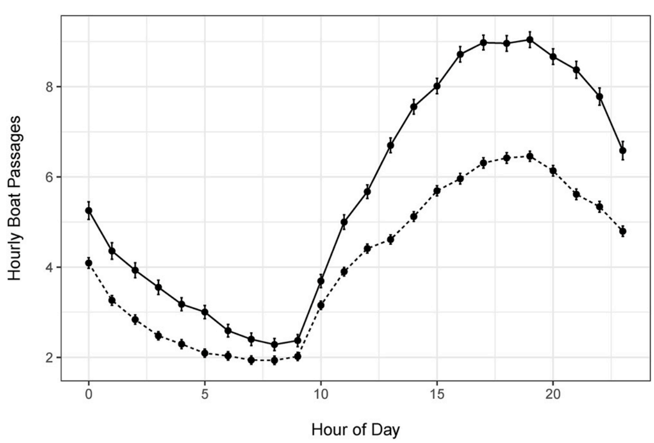

Fig. 4. Mean hourly boat passages (+/− standard error of mean) for weekend/holidays (solid) and weekdays (dashed) across all six stations with an underwater recorder.

confounding environmental variables that could impact the pattern observed. The most notable of which would be diel period. This species may increase their habitat use at night for foraging purposes which would inherently reduce their chances of crossing paths with a boat as most recreational boat activity occurs during the day. We unfortunately did not have enough data to include diel period in our analyses to control for this potential effect.

It is also possible a shark could have indeed reacted to, or even been displaced by, boat activity, but if that shark did not move beyond the detection rage of the acoustic receiver (250 m 50% detection range), the shark would not have registered as an absence. Indeed, the onset of a sudden loud sound has previously been shown to cause a rapid withdrawal in other shark species (Myrberg et al., 1978), resulting in only a short displacement distance within the receiver detection range. It is also possible that sharks could be altering their activity levels, or their depth use in response to boat activity, both of which were not assessed here. Accordingly, to further investigate the relationship between shark presence and boat passages at a finer spatial scale, future research could utilize acoustic telemetry positioning systems, combined with sharks tagged with transmitters equipped with accelerometers and depth sensors, to gauge the exact location of an individual, as well as their activity levels and depth use, in response to a trackable boat.

The lack of responses of sharks to boat activity investigated here could also be the result of shark habituation given the extremely high levels of boating that occur off Miami (Ault et al., 2017; Gorzelany, 2009). Indeed, sharks have previously been found to habituate to acoustic stimuli. For example, silky sharks (*Carcharhinus falciformis*)

Table 4
Generalized linear model (GLM) parameter estimates of shark detections dependent on boat passages within a 1-h period.

Species	Parameter	Estimate	Std. Error	z value	p value
C. leucas	Intercept	0.239	0.147	1.627	0.142
	Boat Passages	0.042	0.033	1.254	0.245
S. mokarran	Intercept	1.816	0.152	11.978	<0.001
	Boat Passages	0.00007	0.021	0.003	0.997
G. cirratum	Intercept	1.210	0.067	17.952	<0.001*
	Boat Passages	−0.156	0.037	−4.206	<0.001*

Table 3
Summary statistics of hourly detections across all six stations and hours of the day for each day category.

Species	Day Category	Individuals Detected	Hours Detected	Mean	Std. Deviation	Std. Error
C. leucas	Weekday	2	9	4.56	2.88	0.96
	Weekend/Holiday	1	1	5.00	N/A	N/A
S. mokarran	Weekday	3	10	3	1.19	0.77
	Weekend/Holiday	3	11	3.91	1.45	0.47
G. cirratum	Weekday	10	179	7.84	10.68	0.47
	Weekend/Holiday	6	38	3.29	2.88	0.44

habituated to low frequency pulsed sounds (Nelson et al., 1969), while sharpnose sharks (*Rhizoprionodon* spp.) have been reported to habituate to more prolonged sounds (Myrberg et al., 1969). While no study to date has directly evaluated habituation of sharks to boat activity, teleost species have been documented to become desensitized to prolonged exposure to boat engine noise (Holmes et al., 2017). Given the study area is an urbanized coastal waterway exposed to high boat activity, it seems plausible that sharks here could be habituated to boat engine noise. Despite studies from more 'pristine areas' reporting boat avoidance behaviors in dolphins (*Tursiops* species; Lusseau, 2005), bottlenose dolphins (*Tursiops truncates*) in this study area suggest they have become habituated to boat activity (Rice, 2014). Here, *T. truncatus* have been consistently observed around the mouth of the Miami River and Port Miami where boat activity is usually high (Rice, 2014). It is thus possible that in more pristine areas, away from urban centers, boat activity may elicit avoidance behavior in sharks. Future research could explore this by comparing shark responses to boat activity as done here, in areas of high versus low boat activity.

In addition to boat activity, other threats to sharks associated with urbanization in the study area include chemical and light pollution, changes in water quality, as well as habitat degradation. For example, the study area has been exposed to increased chlorophyll *a* and nutrient levels associated with runoff and canal discharges (Millette et al., 2019). This led to significant reductions in sea grass populations in the Bay resulting in fewer prey species, which may have ultimately impacted sharks as well. However, the behavioral effects of these factors on sharks are unknown. Questions regarding the impact of other anthropogenic stressors need to be answered to fully understand how urbanization impacts these predators.

It should be noted that a limitation of this study was relatively low detection data from *C. leucas* and *S. mokarran* especially for analyses regarding boat passages. This is most likely due to the migratory behavior of each species as both are more present in Biscayne Bay or similar latitudes during the dry season (Rider et al., 2021; Guttridge et al., 2017; Calich et al., 2021) when boat activity across the bay is less prominent (Fig. 2). This would also explain why there was a greater amount of data for *G. cirratum* as they tend to exhibit higher site fidelity (Garla et al., 2017). Thus, we believe that the methods used in this study would be especially useful for analyzing the influences of boat activity on species that exhibit site fidelity to areas that are heavily used.

In summary, while *C. leucas* and *S. mokarran* may respond behaviorally to the presence of boats in ways we did not measure here, this study only found a relationship between boat activity and the presence of *G. cirratum* on a finer spatiotemporal scale. Though we propose several hypotheses that may explain these results, it is certainly possible that the high levels of near constant boat activity in the study area have led to habituation in *C. leucas* and *S. mokarran*, or they simply are not responsive to them. Regardless of a shark's direct behavioral response to boat activity, the frequencies produced by boat engines may still mask sounds produced by prey, which could ultimately hinder their foraging success. We believe our results are applicable to coastal waterways adjacent to urban centers exposed to high levels of boat activity. There may be differences among species not studied here, which would be worthy of future research. Overall, these data provide novel insights into the potential consequences from the various sources of coastal urbanization on the life history of mobile marine predators.

Author contributions

Mitchell J. Rider: Conceptualization, Investigation, Methodology, Formal Analysis, Data Curation, Writing – Original Draft. **Oliver S. Kirsebom:** Software, Writing – Review & Editing. **Austin J. Gallagher:** Resources, Writing – Review & Editing. **Erica Staaterman:** Resources, Writing – Review & Editing. **Jerald S. Ault:** Resources, Methodology, Writing – Review & Editing. **Christopher R. Sasso:** Resources, Writing – Review & Editing. **Tom Jackson:** Methodology, Writing – Review & Editing. **Joan A. Browder:** Writing – Review & Editing. **Neil Hammerschlag:** Resources, Writing – Study design, Original Draft, Supervision, Validation, Funding Acquisition.

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.

Acknowledgements

This research was assisted by the University of Miami's Shark Research and Conservation Program team members, with special thanks to Stephen Cain and Robbie Roemer for their help with the acoustic receiver array. A special thanks to Maria Estevanez for her help with spatial analyses and interpretation. Funds for this research were provided by the Batchelor Foundation, Herbert W. Hoover Foundation, Ocean Tracking Network, Save Our Seas Foundation and Disney Conservation Fund.

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