

1 **Title:** Space use patterns of sharks in relation to boat activity in an urbanized coastal waterway

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24 **Abstract**

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

37

38 **Keywords:** urbanization, movement ecology, global change, acoustic telemetry, elasmobranch,
39 coastal waters, vessel traffic

40

41 **1. Introduction**

42 Coastal areas are urbanizing rapidly (Creel, 2003; McGranahan et al., 2007), posing
43 increased anthropogenic stressors to the ecology and sustainability of nearshore ecosystems
44 (Todd et al., 2019). Marine systems adjacent to urban centers are subjected to increased resource
45 exploitation, habitat degradation, ocean sprawl and pollution (Todd et al., 2019). Among the
46 most ubiquitous threats of coastal urbanization to aquatic systems is increased boat activity,
47 which can damage habitats (Zieman, 1976), collide with wildlife (Lester et al., 2020; Speed et

48 al., 2008; Wells and Scott, 1997), and create noise pollution (Popper et al., 2003). A growing
49 number of studies have demonstrated that the presence, volume, and frequency of boat engine
50 noise can negatively impact the physiology (Wysocki et al., 2006) communication (Codarin et
51 al., 2009), and behavior of teleost fishes (Ferrari et al., 2018). Some studies have found that
52 teleosts will avoid areas of high boat activity (De Robertis and Wilson, 2011; Filous et al., 2017;
53 Sarà et al., 2007), while other studies have demonstrated minimal effects of boat activity on both
54 freshwater (MacLean et al., 2020; Maxwell et al., 2018) and marine fishes (Staaterman et al.,
55 2020), suggesting possible habituation. Comparative studies have yet to be performed examining
56 the potential effects of boat activity on elasmobranchs, which often rely on coastal subtropical
57 ecosystems for critical life history phases. Given that changes to the distribution or abundance of
58 top predators, such as sharks, can impact ecosystem structure and function, an identified key
59 research priority is to understand the direct and indirect effects of urbanization on the ecological
60 function and services of aquatic predators (Hammerschlag et al., 2019).

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

70 Although boat activity could theoretically trigger avoidance behavior in elasmobranchs, no
71 studies to date have specifically investigated this possible relationship (Casper et al., 2012).

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

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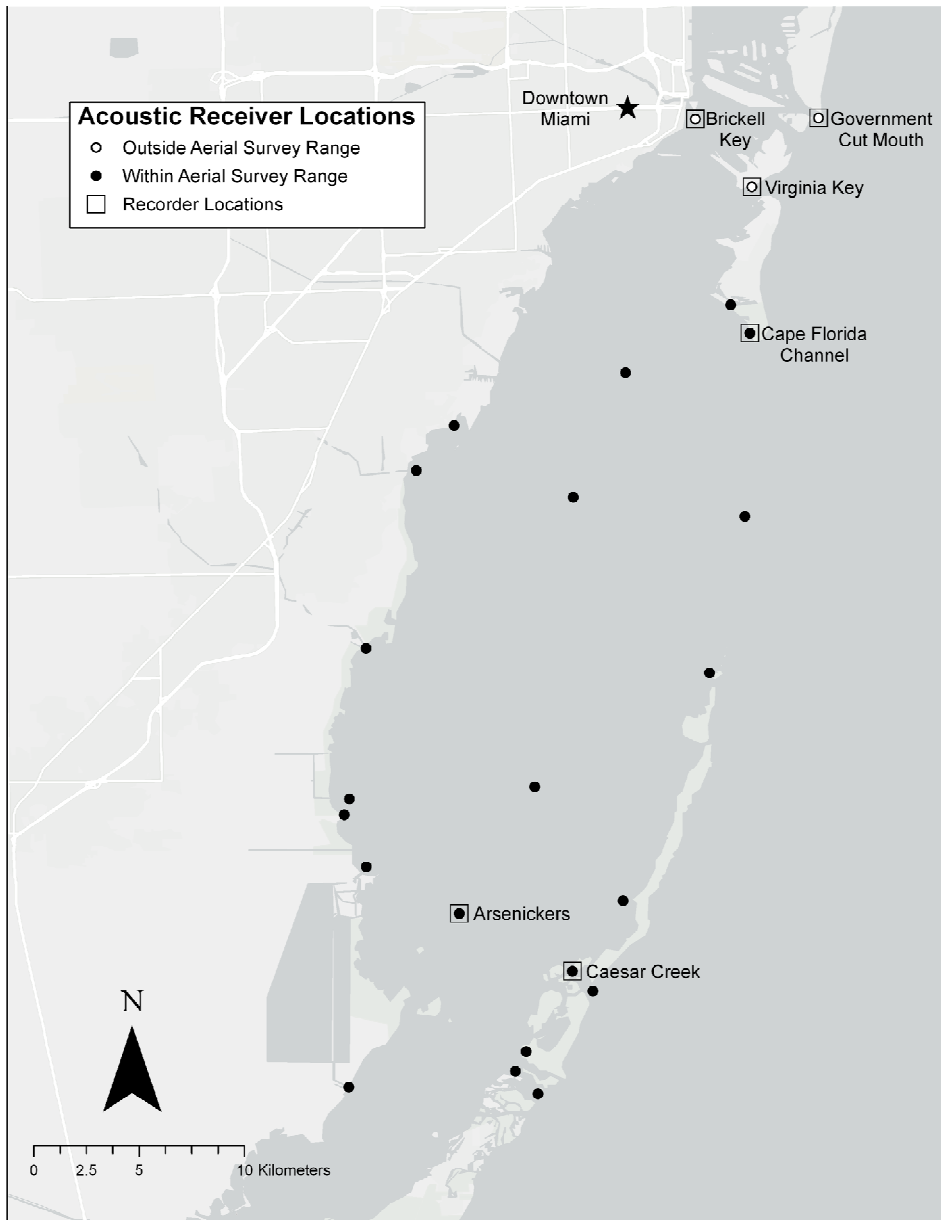
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89 **2. Materials and Methods**

90 *2.1. Study Site*

91 Miami is a metropolis situated proximal to Biscayne Bay, a shallow subtropical lagoon (56
92 by 13 km) that stretches from Haulover, past downtown Miami, to north Key Largo (Fig. 1). The

93 Bay's production is primarily benthic, as it contains communities of seagrasses, hard corals,
94 gorgonians, and sponges; however, it also contains some remnant estuarine habitats (Browder et
95 al. 2005). Biscayne Bay is by a gradient of urbanization, from intense development around
96 Miami to far less impacted areas in the south.



97

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

101

102 Miami-Dade County has the highest number of registered vessels in Florida (Florida
103 Department of Highway Safety and Motor Vehicles 2019)
104 ([https://www.flhsmv.gov/resources/driver-and-vehicle-reports/vehicle-and-vessel-reports-and-](https://www.flhsmv.gov/resources/driver-and-vehicle-reports/vehicle-and-vessel-reports-and-statistics/)
105 [statistics/](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 >
106 97% are recreational. Since Miami-Dade is directly adjacent to Biscayne Bay, a large portion of
107 those registered boats are likely used on the Bay. The highest amount of boat activity can be
108 observed in the northern portion of the Bay and on weekends and holidays (Ault et al., 2017;
109 Gorzelany, 2009). During peak hours of the day (12:00-15:00), boat activity in the Bay ranges
110 between 108-141 boats during weekdays and 349-723 boats on weekends/holidays (Ault et al.,
111 2017, 2005).

112

113 2.2. *Boat density via aerial surveys*

114 Spatiotemporal patterns of boat density were determined by analyzing aerial survey data
115 reported in Ault et al. (2017), which conducted monthly aerial surveys of boaters in the study
116 area during 2016-2017. Surveys were accomplished using a fixed-wing aircraft during three
117 seasons (spring, February-May 2016; summer, June-September 2016; and, fall-winter, October
118 2016-January 2017). To determine seasonal boating activity patterns at a broad scale, a sampling
119 ratio of 2:3 weekdays:weekends/holidays was selected based on a prior knowledge (Ault et al.
120 2008). Five flights were scheduled per month based on the sampling ratio depending on weather

121 and aircraft availability. Actual survey dates were randomly selected, but the weekends of
122 Memorial Day, Fourth of July, Columbus Day, and lobster mini-season (mid-July) were
123 preferentially chosen because of the known high volume of boat traffic in Biscayne Bay (Ault et
124 al., 2005; Eggleston et al., 2003). Aerial survey flights were conducted at altitudes ranging from
125 150 to 300 m, speeds of 165 to 185 km per hour, between 1200-1500 hours. During each flight,
126 three observers using binoculars spotted boats, noted the vessel type and activity, and recorded
127 positions on a tablet computer with an affixed external GPS. The Aerial Vis Survey algorithm
128 developed by Lance Garrison (Read et al., 2012) was used to calculate accurate boat coordinates
129 using real-time data on aircraft route, boat disposition, and angle of the boat from the aircraft
130 position.

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

141

142 *2.3. Boat traffic via acoustic recorders*

143 To quantify patterns of boat traffic, six underwater acoustic recorders (two DSG-ST and four
144 Snap; Loggerhead Instruments, Sarasota, FL, USA) were placed at different locations (squares in
145 Fig. 1). These sites were chosen because of their varying proximity to Miami and associated
146 varying levels of boat activity expected to occur at each. Recorders were paired with the acoustic
147 telemetry receivers (see section 2.4) to allow for simultaneous comparisons with shark residency
148 patterns.

149 The recorders at Cape Florida Channel and Brickell Key were initially deployed in March
150 2018. Arsenickers Key, Caesar Creek, and Government Cut were initially deployed in September
151 2018, and Virginia Key was initially deployed in March 2019 (see fig. 1).

152 These recorders were programmed to record 10 seconds every minute with a sample rate of
153 20 kHz and 32 kHz (decimated once), and sensitivity of -180.1 and -169.4 dBV/uPa for the
154 DSG-ST and Snap recorders, respectively. Selected sample rates allowed recorders to log
155 frequencies up to 10 kHz and 16 kHz, respectively. These sample rates were chosen because
156 both recreational and commercial boat engines produce sound frequencies within that range
157 (Barlett and Wilson, 2002; Fischer and Brown, 2005). Routine maintenance (i.e., swapping
158 batteries and memory cards) was performed on the recorders approximately every 20 to 55 days.

159 Boat traffic (i.e., passages per hour) were quantified from boat engine noise. To accomplish
160 this, we first determined the “normal” level of background noise at each recorder location, and
161 then examined the data for peaks in the noise which would be indicative of passing boats. To
162 calculate the median background noise, data were processed through a ‘filter analyzer’
163 developed by the Marine Environmental Research Infrastructure for Data Integration and
164 Application Network (MERIDIAN) of Dalhousie University (Nova Scotia, Canada). The filter
165 analyzer read each of the files and down sampled to a rate of 2000 Hz. The audio signal was

166 transformed using a Fast Fourier Transform (FFT) to create a spectrogram: Spectrogram = 20 x
167 $\log_{10}(\text{FFT}(\text{audio signal}))$. The spectrogram was split into frequency bands with central
168 frequencies of 31.2, 62.5, 125, 250, 500, and 1000 Hz. For each frequency band, the running
169 median of sound pressure level was computed using a window size of three seconds and a step
170 size of one second. This produced a time series of median sound pressure levels for each
171 frequency band. The median was computed using a window size of one minute and subtracted
172 from the median values for each frequency band. This produced a time series of background-
173 subtracted median values for each frequency band.

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

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

197

198 2.4. *Shark space use via acoustic telemetry*

199 Sharks were captured using a series of baited drumlines, as described in Gallagher et al.
200 (2014). Captured sharks were either secured alongside a boat in the water or on top of a floatable
201 platform, in preparation for electronic tagging. All sharks were tagged with the Innovasea V16-
202 4X internal acoustic transmitters (Amirix Inc., Bedford, NS, Canada), programmed with a
203 nominal delay of 60 to 90 seconds, however we used two different types of tag attachment
204 methods. *C. leucas* and *G. cirratum* were tagged via surgical implantation into the shark's body
205 cavity following the approach of Hammerschlag et al. (2017), whereas *S. mokarran* were tagged
206 via an externally tethered tag package, which used a dart anchor that was embedded in the
207 shark's dorsal musculature. The external tag approach was used for great hammerheads because
208 it allowed for faster tag attachment, considering this species' inherent sensitivity to capture and
209 handling stress (Gallagher et al., 2014; Jerome et al., 2018). While tag shedding is more likely
210 with external transmitters, this risk was minimized by looping the tag tether through the dorsal
211 fin prior to insertion in the dorsal musculature. Shark capture and tagging were conducted under

212 permits from Florida Fish and Wildlife Conservation Commission, the Florida Keys National
213 Marine Sanctuary, the US National Marine Fisheries Service, and the University of Miami
214 Animal Welfare and Care Committee (Protocol 18–154).

215 Reliable estimates of residency patterns from June 2015 to October 2019 were obtained using
216 an acoustic receiver array capable of detecting tagged sharks as described in Gutowsky et al.
217 (2021). This passive acoustic array consisted of 24 Innovasea VR2W – 69 kHz receivers (Amirix
218 Inc., Bedford, NS, Canada) deployed in Biscayne Bay, FL (Fig.1). Receivers were anchored to
219 the substrate at depths ranging from 1.5 to 12 m using a concrete stand. Detection data were
220 retrieved from receivers every six months (March and September).

221 Detection range testing was performed on three representative acoustic receivers at different
222 location that differed in exposure to environmental and acoustic conditions using methods
223 similar to those described by Kessel et al. (2014b) and Selby et al. (2016). For each receiver, we
224 estimated the range in which the probability of transmitter detection was 50% (median range)
225 and 5% (maximum range). Receiver range testing indicated a relatively small 50% detection
226 range of about 250 m, with 5% detectability (i.e., maximum range) of about 900 m. The radius
227 of receiver detection regions used for determining average boat densities was set equal to the
228 50% detection range.

229

230 2.5. *Shark daily residency in response to boat density*

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

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

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

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

258

259 2.6. *Shark hourly presence in response to boat traffic*

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

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

281

282 **3. Results**

283 *3.1. Shark tagging*

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

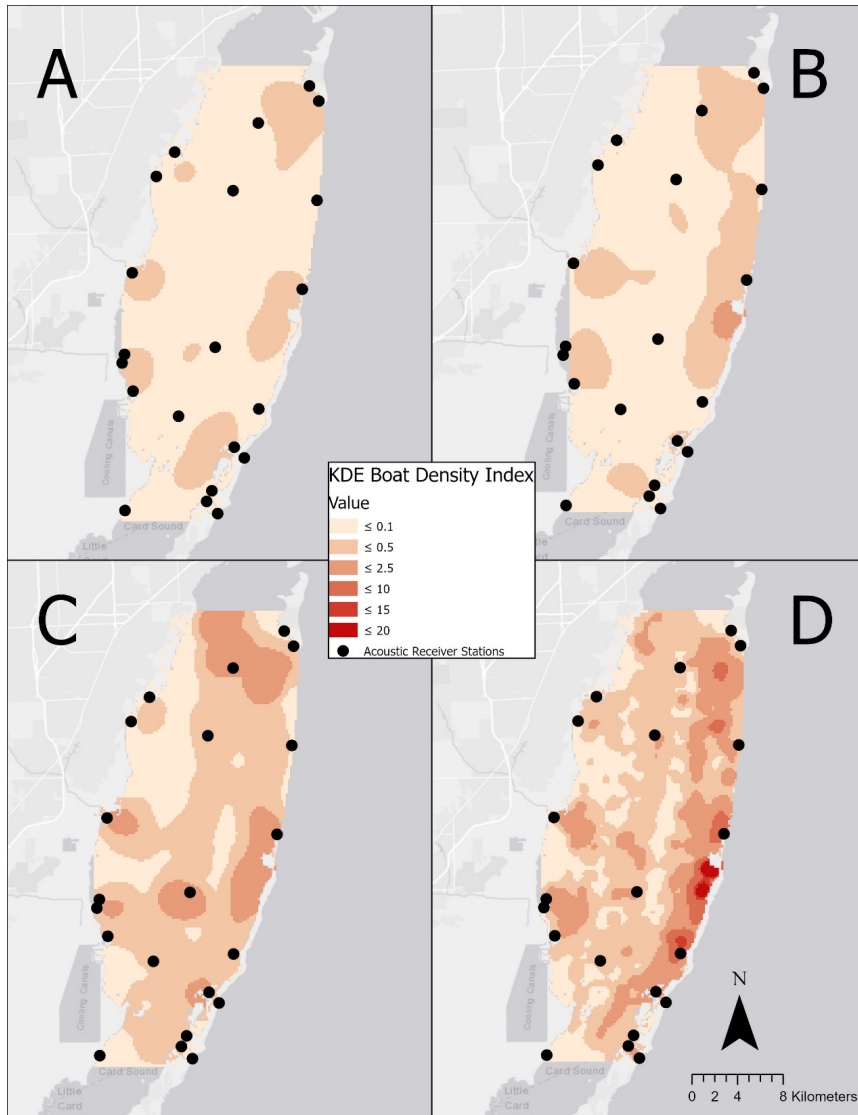
287

288 *3.2. Shark daily residency vs boat density*

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

302

303



304

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

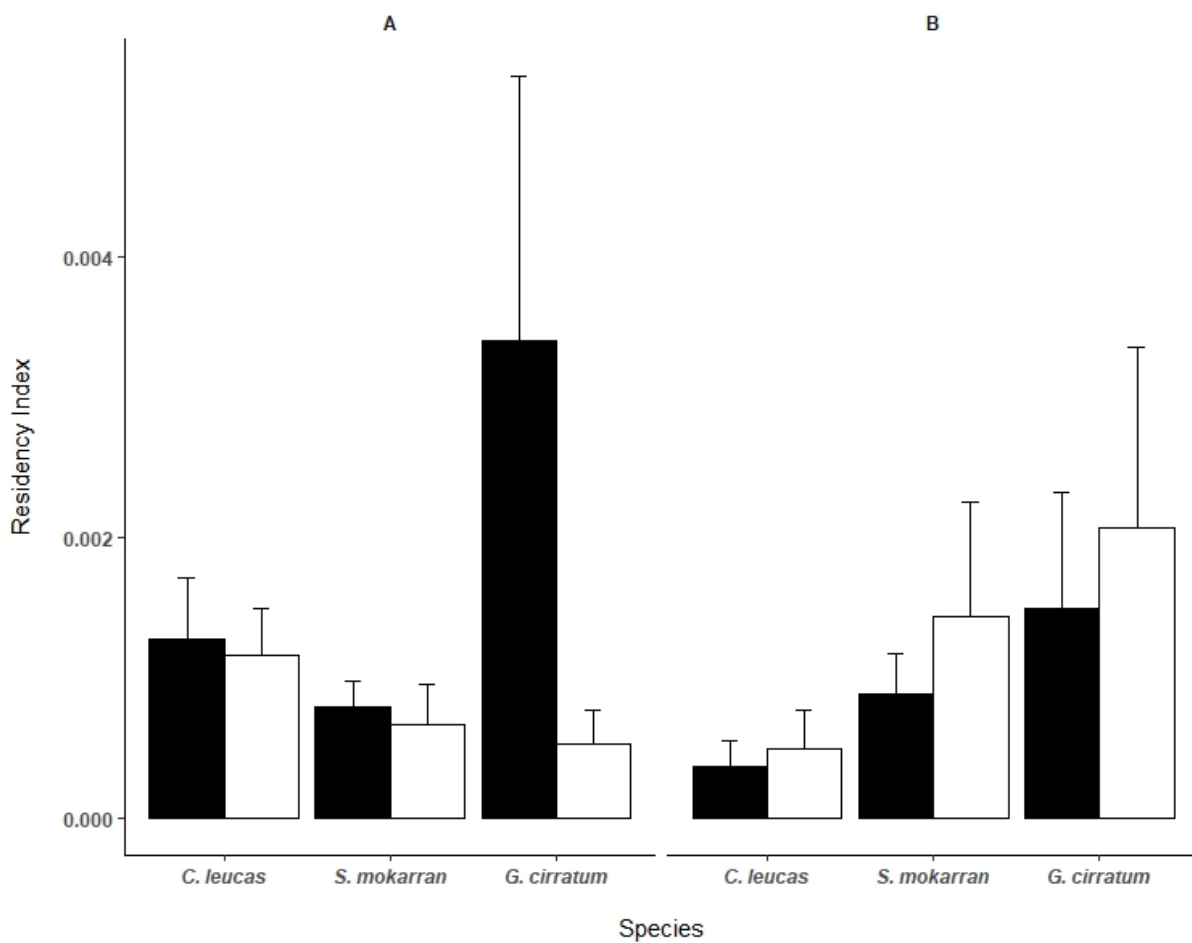
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310 Between February 2015 and June 2020, 33 individual sharks (*C. leucas*, n = 11; *S. mokarran*,
 311 n= 10; *G. cirratum*, n = 12) were detected. Of those 33 individuals, 30 (*C. leucas* = 11; *S.*

312 *mokarran* = 8; *G. cirratum* = 11) met the criteria (described above) to be included in the analyses
313 (Table 1).

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

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



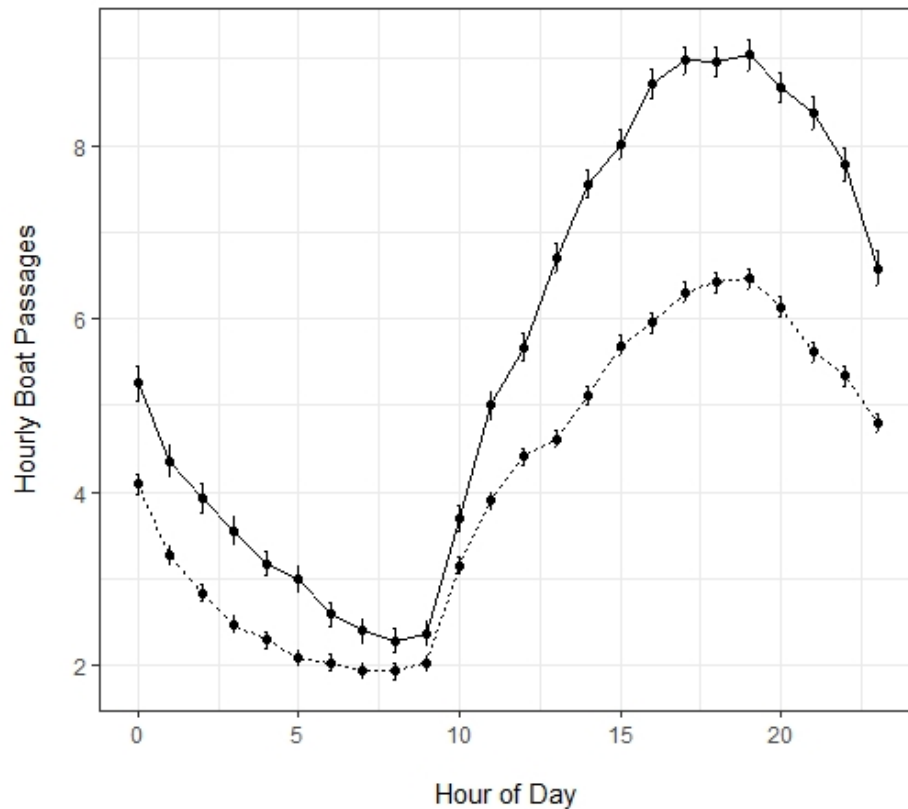
322 **Figure 3:** Bar graph depicting the mean residency indices (\pm standard error of mean) of each
323 species for each day category during the dry (A) and wet (B) seasons. Black and white bars
324 represent residency indices on weekdays and weekend/holidays, respectively.

325

326 3.3. Shark hourly presence and boat traffic

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

329 Overall, there was generally greater boat passages during the weekends/holidays (Fig. 4).



330 **Figure 4:** Mean hourly boat passages (\pm standard error of mean) for weekend/holidays (solid)
331 and weekdays (dashed) across all six stations with an underwater recorder.

332

333 Between March 2018 and October 2019, 16 individual sharks (*C. leucas*, n = 2; *S. mokarran*,
334 n = 4; *G. cirratum*, n = 10) were detected on the six stations that had both acoustic receivers and
335 recorders. All 16 sharks were used in the following analyses (Superscripts in Table 1). There was
336 a small amount of data for *C. leucas* and *S. mokarran* as individuals were detected during ten and
337 21 one-hour observation periods, respectively, while *G. cirratum* individuals accounted for 217
338 observations (Table 3).

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

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

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

352

353 **4. Discussion**

354 This study used a combination of aerial surveys of boat density, acoustic estimates of boat
355 traffic, and passive acoustic tracking of sharks to evaluate the potential influence of boat activity
356 on shark space use. To date, no published studies have evaluated the relationship between boat

357 activity and shark behavior, but based on a growing number of studies which have found that the
358 presence, volume, and frequency of boat engine noise can negatively impact the physiology
359 (Wysocki et al., 2006), communication (Codarin et al., 2009), and behavior of teleost fishes
360 (Ferrari et al., 2018), we hypothesized that sharks would decrease their space use in places and
361 times of higher boat activity. However, our investigations revealed no evidence of boat
362 avoidance behavior in either *C. leucas* or *S. mokarran*. For both species, neither their daily
363 residency patterns, nor their hourly presence, was related to boat density or traffic. In contrast,
364 we found evidence of boat avoidance behaviors in *G. cirratum*. Specifically, their hourly
365 presence decreased with increasing boat traffic, although daily residency patterns of *G. cirratum*
366 were not related to boat density.

367 The boat engine noise recorded in this study is well within the frequency range detectable by
368 sharks, and it is well known that sharks can become attracted to the revving of boat engines
369 characteristic of fishing boats backing down when trying to land a fish on a line (Mitchell et al.,
370 2018b). However, our data do not suggest either avoidance or attraction to high boat activity,
371 except for the hourly presence of *G. cirratum* suggestive of avoidance. Therefore, our results are
372 somewhat unexpected, however we offer several testable hypotheses to explain these results.

373 The differences in species responses to boat activity found here could be related to
374 differences in their hearing abilities. Using auditory evoked potentials, the hearing sensitivity of
375 the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) was observed to be greatest at 20 Hz
376 (Casper and Mann, 2009). Since *R. terraenovae* and *C. leucas* stem from the same family
377 (*Carcharhinidae*), they may have similar hearing thresholds – meaning, *C. leucas* could be most
378 sensitive at very low frequencies (i.e., 20 Hz). A small boat engine operating at cruising speed
379 (i.e., 3100 - 4800 RPM) has the most acoustic energy between 300 and 600 Hz (Barlett and

380 Wilson, 2002). This may explain why *C. leucas* did not display boat attraction or avoidance
381 behavior in this study. In contrast, *G. cirratum* appears to have relatively greater hearing
382 sensitivity between 300 and 600 Hz (Casper and Mann, 2006), suggesting that this species is
383 capable of recognizing boat engine noise, which could explain why this species appeared to
384 decrease their space use in response to boat traffic. The hearing ability of hammerheads (family
385 *Sphyrnidae*) remains untested.

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

392 While there was a detectable relationship between hourly boat traffic and presence of *G.*
393 *cirratum*, it should be noted that there may be other confounding environmental variables that
394 could impact the pattern observed. The most notable of which would be diel period. This species
395 may increase their habitat use at night for foraging purposes which would inherently reduce their
396 chances of crossing paths with a boat as most recreational boat activity occurs during the day.
397 We unfortunately did not have enough data to include diel period in our analyses to control for
398 this potential effect.

399 It is also possible a shark could have indeed reacted to, or even been displaced by, boat
400 activity, but if that shark did not move beyond the detection range of the acoustic receiver (250 m
401 50% detection range), the shark would not have registered as an absence. Indeed, the onset of a
402 sudden loud sound has previously been shown to cause a rapid withdrawal in other shark species

403 (Myrberg et al., 1978), resulting in only a short displacement distance within the receiver
404 detection range. It is also possible that sharks could be altering their activity levels, or their depth
405 use in response to boat activity, both of which were not assessed here. Accordingly, to further
406 investigate the relationship between shark presence and boat passages at a finer spatial scale,
407 future research could utilize acoustic telemetry positioning systems, combined with sharks
408 tagged with transmitters equipped with accelerometers and depth sensors, to gauge the exact
409 location of an individual, as well as their activity levels and depth use, in response to a trackable
410 boat.

411 The lack of responses of sharks to boat activity investigated here could also be the result of
412 shark habituation given the extremely high levels of boating that occur off Miami (Ault et al.,
413 2017; Gorzelany, 2009). Indeed, sharks have previously been found to habituate to acoustic
414 stimuli. For example, silky sharks (*Carcharhinus falciformis*) habituated to low frequency pulsed
415 sounds (Nelson et al., 1969), while sharpnose sharks (*Rhizoprionodon* spp.) have been reported
416 to habituate to more prolonged sounds (Myrberg et al., 1969). While no study to date has directly
417 evaluated habituation of sharks to boat activity, teleost species have been documented to become
418 desensitized to prolonged exposure to boat engine noise (Holmes et al., 2017). Given the study
419 area is an urbanized coastal waterway exposed to high boat activity, it seems plausible that
420 sharks here could be habituated to boat engine noise. Despite studies from more ‘pristine areas’
421 reporting boat avoidance behaviors in dolphins (*Tursiops* species; Lusseau, 2005), bottlenose
422 dolphins (*Tursiops truncatus*) in this study area suggest they have become habituated to boat
423 activity (Rice, 2014). Here, *T. truncatus* have been consistently observed around the mouth of
424 the Miami River and Port Miami where boat activity is usually high (Rice, 2014). It is thus
425 possible that in more pristine areas, away from urban centers, boat activity may elicit avoidance

426 behavior in sharks. Future research could explore this by comparing shark responses to boat
427 activity as done here, in areas of high versus low boat activity.

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

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

445 In summary, while *C. leucas* and *S. mokarran* may respond behaviorally to the presence of
446 boats in ways we did not measure here, this study only found a relationship between boat activity
447 and the presence of *G. cirratum* on a finer spatiotemporal scale. Though we propose several
448 hypotheses that may explain these results, it is certainly possible that the high levels of near

449 constant boat activity in the study area have led to habituation in *C. leucas* and *S. mokarran*, or
450 they simply are not responsive to them. Regardless of a shark's direct behavioral response to
451 boat activity, the frequencies produced by boat engines may still mask sounds produced by prey,
452 which could ultimately hinder their foraging success. We believe our results are applicable to
453 coastal waterways adjacent to urban centers exposed to high levels of boat activity. There may be
454 differences among species not studied here, which would be worthy of future research. Overall,
455 these data provide novel insights into the potential consequences from the various sources of
456 coastal urbanization on the life history of mobile marine predators.

457

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465

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475

476 **References**

- 477 Ault, J.S., Smith, S.G., Manges, J.M., Bryan, D., Luo, J., 2017. Aerial park and field marina
478 surveys to estimate boater use within Biscayne National Park, 2016-2017. Miami, FL, USA.
- 479 Ault, J.S., Smith, S.G., McClellan, D.B., Zurcher, N., Franklin, E.C., Bohnsack, J.A., 2008. An
480 aerial survey method for estimation of boater use in Biscayne National Park during 2003-
481 2004. NOAA Technical Memorandum SEFSC-577. Miami, FL, USA.
- 482 Barlett, M.L., Wilson, G.R., 2002. Characteristics of small boat signatures. *J. Acoust. Soc. Am.*
483 112, 2221.
- 484 Calich HJ, Rodríguez JP, Eguíluz VM, Hammerschlag N, Pattiaratchi C, Duarte CM, Sequeira
485 AM, 2021. Comprehensive analytical approaches reveal species-specific search strategies in
486 sympatric apex predatory sharks. *Ecography* <https://doi.org/10.1111/ecog.05953>
- 487 Casper, B.M., Halvorsen, M.B., Popper, A.N., 2012. Are sharks even bothered by a noisy
488 environment?, in: *The Effects of Noise on Aquatic Life*. Springer, New York, NY, pp. 93–
489 97. https://doi.org/10.1007/978-1-4419-7311-5_20
- 490 Casper, B.M., Mann, D.A., 2009. Field hearing measurements of the Atlantic sharpnose shark
491 *Rhizoprionodon terraenovae*. *J. Fish Biol.* 75, 2768–2776. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2009.02477.x)
492 8649.2009.02477.x
- 493 Casper, B.M., Mann, D.A., 2006. Evoked potential audiograms of the nurse shark
494 (*Ginglymostoma cirratum*) and the yellow stingray (*Urobatis jamaicensis*). *Environ. Biol.*

495 Fishes 76, 101–108. <https://doi.org/10.1007/s10641-006-9012-9>

496 Codarin, A., Wysocki, L.E., Ladich, F., Picciulin, M., 2009. Effects of ambient and boat noise on
497 hearing and communication in three fish species living in a marine protected area
498 (Miramare, Italy). *Mar. Pollut. Bull.* 58, 1880–1887.
499 <https://doi.org/10.1016/j.marpolbul.2009.07.011>

500 Creel, L., 2003. Ripple effects: population and coastal regions. Population Reference Bureau,
501 Washington, DC.

502 De Robertis, A., Wilson, C.D., 2011. Silent ships do not always encounter more fish (revisited):
503 comparison of acoustic backscatter from walleye pollock recorded by a noise-reduced and a
504 conventional research vessel in the eastern Bering Sea. *ICES J. Mar. Sci.* 68, 2229–2239.
505 <https://doi.org/10.1093/icesjms/fsr146>

506 Eggleston, D., Johnson, E., Kellison, G., Nadeau, D., 2003. Intense removal and non-saturating
507 functional responses by recreational divers on spiny lobster *Panulirus argus*. *Mar. Ecol.*
508 *Prog. Ser.* 257, 197–207. <https://doi.org/10.3354/meps257197>

509 Ferrari, M.C.O., McCormick, M.I., Meekan, M.G., Simpson, S.D., Nedelec, S.L., Chivers, D.P.,
510 2018. School is out on noisy reefs: The effect of boat noise on predator learning and
511 survival of juvenile coral reef fishes. *Proc. R. Soc. B Biol. Sci.* 285.
512 <https://doi.org/10.1098/rspb.2018.0033>

513 Filous, A., Friedlander, A.M., Koike, H., Lammers, M., Wong, A., Stone, K., Sparks, R.T., 2017.
514 Displacement effects of heavy human use on coral reef predators within the Molokini
515 Marine Life Conservation District. *Mar. Pollut. Bull.* 121, 274–281.
516 <https://doi.org/10.1016/j.marpolbul.2017.06.032>

517 Fischer, R.W., Brown, N.A., 2005. Factors affecting the underwater noise of commercial vessels

518 operating in environmentally sensitive areas, in: Proceedings of MTS/IEEE OCEANS,
519 2005. IEEE Computer Society, pp. 1982–1988.
520 <https://doi.org/10.1109/OCEANS.2005.1640049>

521 Gallagher, A., Serafy, J., Cooke, S., Hammerschlag, N., 2014. Physiological stress response,
522 reflex impairment, and survival of five sympatric shark species following experimental
523 capture and release. *Mar. Ecol. Prog. Ser.* 496, 207–218. <https://doi.org/10.3354/meps10490>

524 Garla, R.C., Gadig, O.B.F., Garrone-Neto, D., 2017. Movement and activity patterns of the nurse
525 shark, *Ginglymostoma cirratum*, in an oceanic Marine Protected Area of the South-western
526 Atlantic. *J. Mar. Biol. Assoc. United Kingdom* 97, 1565–1572.
527 <https://doi.org/10.1017/S0025315416001028>

528 Gorzelany, J.F., 2009. Recreational boating activity in Miami-Dade County. Sarasota, FL, USA.

529 Gutowsky LF, Rider M, Roemer RP, Gallagher AJ, Heithaus MR, Cooke SJ, Hammerschlag N.,
530 2021. Large sharks exhibit varying behavioral responses to major hurricanes. *Estuarine,
531 Coastal and Shelf Science*, 256,107373. <https://doi.org/10.1016/j.ecss.2021.107373>

532 Guttridge, T.L., Van Zinnicq Bergmann, M.P.M., Bolte, C., Howey, L.A., Finger, J.S., Kessel,
533 S.T., Brooks, J.L., Winram, W., Bond, M.E., Jordan, L.K.B., Cashman, R.C., Tolentino,
534 E.R., Grubbs, R.D., Gruber, S.H., 2017. Philopatry and regional connectivity of the great
535 hammerhead shark, *Sphyrna mokarran* in the U.S. and Bahamas. *Front. Mar. Sci.* 4.
536 <https://doi.org/10.3389/fmars.2017.00003>

537 Hammerschlag, N., Gutowsky, L.F.G., Gallagher, A.J., Matich, P., Cooke, S.J., 2017. Diel
538 habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high use
539 area exposed to dive tourism. *J. Exp. Mar. Bio. Ecol.* 495, 24–34.
540 <https://doi.org/10.1016/j.jembe.2017.05.010>

541 Hammerschlag, N., Schmitz, O.J., Flecker, A.S., Lafferty, K.D., Sih, A., Atwood, T.B.,
542 Gallagher, A.J., Irschick, D.J., Skubel, R., Cooke, S.J., 2019. Ecosystem function and
543 services of aquatic predators in the anthropocene. *Trends Ecol. Evol.*
544 <https://doi.org/10.1016/j.tree.2019.01.005>

545 Hildebrand, J.A., 2009. Anthropogenic and natural sources of ambient noise in the ocean. *Mar.*
546 *Ecol. Prog. Ser.* 395, 5–20. <https://doi.org/10.3354/meps08353>

547 Holmes, L.J., McWilliam, J., Ferrari, M.C.O., McCormick, M.I., 2017. Juvenile damselfish are
548 affected but desensitize to small motor boat noise. *J. Exp. Mar. Bio. Ecol.* 494, 63–68.
549 <https://doi.org/10.1016/j.jembe.2017.05.009>

550 Jerome, J.M., Gallagher, A.J., Cooke, S.J., Hammerschlag, N., 2018. Integrating reflexes with
551 physiological measures to evaluate coastal shark stress response to capture. *ICES J. Mar.*
552 *Sci.* 75, 796–804. <https://doi.org/10.1093/icesjms/fsx191>

553 Kessel, S., Chapman, D., Franks, B., Gedamke, T., Gruber, S., Newman, J., White, E., Perkins,
554 R., 2014. Predictable temperature-regulated residency, movement and migration in a large,
555 highly mobile marine predator (*Negaprion brevirostris*). *Mar. Ecol. Prog. Ser.* 514, 175–
556 190. <https://doi.org/10.3354/meps10966>

557 Kessel, S.T., Cooke, S.J., Heupel, M.R., Hussey, N.E., Simpfendorfer, C.A., Vagle, S., Fisk,
558 A.T., 2014. A review of detection range testing in aquatic passive acoustic telemetry
559 studies. *Rev. Fish Biol. Fish.* <https://doi.org/10.1007/s11160-013-9328-4>

560 Lester, E., Meekan, M., Barnes, P., Raudino, H., Rob, D., Waples, K., Speed, C., 2020. Multi-
561 year patterns in scarring, survival and residency of whale sharks in Ningaloo Marine Park,
562 Western Australia. *Mar. Ecol. Prog. Ser.* 634, 115–125. <https://doi.org/10.3354/meps13173>

563 Lusseau, D., 2005. Residency pattern of bottlenose dolphins *Tursiops* spp. in Milford Sound,

564 New Zealand, is related to boat traffic. *Mar. Ecol. Prog. Ser.* 295, 265–272.
565 <https://doi.org/10.3354/meps295265>

566 MacLean, K., Prystay, T.S., Lawrence, M.J., Zolderdo, A.J., Gutowsky, L.F.G., Staaterman, E.,
567 Gallagher, A.J., Cooke, S.J., 2020. Going the distance: influence of distance between boat
568 noise and nest site on the behavior of paternal smallmouth bass. *Water. Air. Soil Pollut.*
569 231, 1–11. <https://doi.org/10.1007/s11270-020-04470-9>

570 Maxwell, R.J., Zolderdo, A.J., de Bruijn, R., Brownscombe, J.W., Staaterman, E., Gallagher,
571 A.J., Cooke, S.J., 2018. Does motor noise from recreational boats alter parental care
572 behaviour of a nesting freshwater fish? *Aquat. Conserv. Mar. Freshw. Ecosyst.* 28, 969–
573 978. <https://doi.org/10.1002/aqc.2915>

574 McDougall, C.A., Blanchfield, P.J., Peake, S.J., Anderson, W.G., 2013. Movement patterns and
575 size-class influence entrainment susceptibility of lake sturgeon in a small hydroelectric
576 reservoir. *Trans. Am. Fish. Soc.* 142, 1508–1521.
577 <https://doi.org/10.1080/00028487.2013.815659>

578 McGranahan, G., Balk, D., Anderson, B., 2007. The rising tide: assessing the risks of climate
579 change and human settlements in low elevation coastal zones. *Environ. Urban.* 19, 17–37.
580 <https://doi.org/10.1177/0956247807076960>

581 Millette, N. C., Kelble, C., Linhoss, A., Ashby, S., Visser, L., 2019. Using spatial variability in
582 the rate of change of chlorophyll a to improve water quality management in a subtropical
583 oligotrophic estuary. *Estuaries and Coasts.* 427, 1792-1803.

584 Mitchell, J.D., McLean, D.L., Collin, S.P., Taylor, S., Jackson, G., Fisher, R., Langlois, T.J.,
585 2018a. Quantifying shark depredation in a recreational fishery in the Ningaloo Marine Park
586 and Exmouth Gulf, Western Australia. *Marine Ecology Progress Series*, 587, 141-157.

587 Mitchell, J.D., McLean, D.L., Collin, S.P., Langlois, T.J., 2018b. Shark depredation in
588 commercial and recreational fisheries. *Rev. Fish Biol. Fish.* [https://doi.org/10.1007/s11160-](https://doi.org/10.1007/s11160-018-9528-z)
589 [018-9528-z](https://doi.org/10.1007/s11160-018-9528-z)

590 Myrberg, A.A., 2001. The behavior and sensory biology of elasmobranch fishes: an anthology in
591 memory of Donald Richard Nelson, in: *The Behavior and Sensory Biology of*
592 *Elasmobranch Fishes: An Anthology in Memory of Donald Richard Nelson*. Springer, pp.
593 31–46.

594 Myrberg, A.A., Banner, A., Richard, J.D., 1969. Shark attraction using a video-acoustic system.
595 *Mar. Biol.* 2, 264–276. <https://doi.org/10.1007/BF00351149>

596 Myrberg, A.A., Gordon, C.R., Klimley, A.P., 1978. Rapid withdrawal from a sound source by
597 open-ocean sharks. *J. Acoust. Soc. Am.* 64, 1289–1297. <https://doi.org/10.1121/1.382114>

598 Nelson, D.R., Johnson, R.H., Waldrop, L.G., 1969. Responses in Bahamian sharks and
599 groupers, to low-frequency, pulsed sounds. *Bull. South. Calif. Acad. Sci.* 68, 131–137.

600 Popper, A.N., Fewtrell, J., Smith, M.E., McCauley, R.D., 2003. Anthropogenic sound: Effects on
601 the behavior and physiology of fishes. *Mar. Technol. Soc. J.* 37, 35–40.
602 <https://doi.org/10.4031/002533203787537050>

603 R Core Team., 2019. R: A language and environment for statistical computing. RFoundation for
604 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

605 Read, A.J., Urian, K.W., Roberts, B., Waples, D.M., Burt, M.L., Paxton, C.G.M., 2012.
606 Occurrence, distribution, and density of marine mammals in Camp Lejeune. Jacksonville,
607 NC.

608 Rice, B., 2014. A preliminary analysis of bottlenose dolphin distribution in the Port of Miami
609 and Biscayne Bay. University of Miami.

610 Rider, M.J., McDonnell, L.H., Hammerschlag, N., 2021. Multi-year movements of adult and
611 subadult bull sharks (*Carcharhinus leucas*): philopatry, connectivity, and environmental
612 influences. *Aquat. Ecol.* 1–19. <https://doi.org/10.1007/s10452-021-09845-6>

613 Sarà, G., Dean, J., D’Amato, D., Buscaino, G., Oliveri, A., Genovese, S., Ferro, S., Buffa, G.,
614 Martire, M., Mazzola, S., 2007. Effect of boat noise on the behaviour of bluefin tuna
615 *Thunnus thynnus* in the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 331, 243–253.
616 <https://doi.org/10.3354/meps331243>

617 Selby, T.H., Hart, K.M., Fujisaki, I., Smith, B.J., Pollock, C.J., Hillis-Starr, Z., Lundgren, I., Oli,
618 M.K., 2016. Can you hear me now? Range-testing a submerged passive acoustic receiver
619 array in a Caribbean coral reef habitat. *Ecol. Evol.* 6, 4823–4835.
620 <https://doi.org/10.1002/ece3.2228>

621 Speed, C.W., Meekan, M.G., Rowat, D., Pierce, S.J., Marshall, A.D., Bradshaw, C.J.A., 2008.
622 Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *J. Fish Biol.* 72,
623 1488–1503. <https://doi.org/10.1111/j.1095-8649.2008.01810.x>

624 Staaterman, E., Gallagher, A., Holder, P., Reid, C., Altieri, A., Ogburn, M., Rummer, J., Cooke,
625 S., 2020. Exposure to boat noise in the field yields minimal stress response in wild reef fish.
626 *Aquat. Biol.* 29, 93–103. <https://doi.org/10.3354/ab00728>

627 Todd, P.A., Heery, E.C., Loke, L.H.L., Thurstan, R.H., Kotze, D.J., Swan, C., 2019. Towards an
628 urban marine ecology: characterizing the drivers, patterns and processes of marine
629 ecosystems in coastal cities. *Oikos* 128, 1215–1242. <https://doi.org/10.1111/oik.05946>

630 Wells, R.S., Scott, M.D., 1997. Seasonal incidence of boat strikes on bottlenose dolphins near
631 Sarasota, Florida. *Mar. Mammal Sci.* 13, 475–480. [https://doi.org/10.1111/j.1748-](https://doi.org/10.1111/j.1748-7692.1997.tb00654.x)
632 [7692.1997.tb00654.x](https://doi.org/10.1111/j.1748-7692.1997.tb00654.x)

633 Wysocki, L.E., Dittami, J.P., Ladich, F., 2006. Ship noise and cortisol secretion in European
634 freshwater fishes. *Biol. Conserv.* 128, 501–508.

635 <https://doi.org/10.1016/j.biocon.2005.10.020>

636 Zieman, J.C., 1976. The ecological effects of physical damage from motor boats on turtle grass
637 beds in Southern Florida. *Aquat. Bot.* 2, 127–139. <https://doi.org/10.1016/0304->

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639

640 **Tables**

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

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

642 ^a Sharks included in both analysis of boat density and traffic

643 ^b Sharks only included in boat traffic analysis

644

645
 646 **Table 2:** Generalized linear model (GLM) parameter estimates of shark residencies dependent
 647 on boat density indices and season where dry season is the reference level.

Species	Parameter	Estimate	Std. Error	z value	p value
<i>C. leucas</i>	Intercept	-3.862	0.153	-25.264	<0.001*
	Boat Density	5.666	8.680	0.653	0.514
<i>S. mokarran</i>	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*
<i>G. cirratum</i>	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*

648
 649 **Table 3** Summary statistics of hourly detections across all six stations and hours of the day for
 650 each day category.

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

652 **Table 4:** Generalized linear model (GLM) parameter estimates of shark detections dependent on
 653 boat passages within a 1-hour period.

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

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