



FEATURE ARTICLE

Urban sharks: residency patterns of marine top predators in relation to a coastal metropolis

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ABSTRACT: Understanding and ultimately predicting how marine organisms will respond to urbanization is central for effective wildlife conservation and management in the Anthropocene. Sharks are upper trophic level predators in virtually all marine environments, but if and how their behaviors are influenced by coastal urbanization remains understudied. Here, we examined space use and residency patterns of 14 great hammerheads *Sphyrna mokarran*, 13 bull sharks *Carcharhinus leucas*, and 25 nurse sharks *Ginglymostoma cirratum* in proximity to the coastal metropolis of Miami, Florida, using passive acoustic telemetry. Based on the terrestrial urban carnivore literature, we predicted sharks would exhibit avoidance behaviors of areas close to Miami, with residency patterns in these urban areas increasing during periods of lower human activity, such as during nocturnal hours and weekdays, and that dietary specialists (great hammerhead) would exhibit comparatively lower affinity towards highly urbanized areas relative to dietary generalists (bull and nurse shark). However, we did not find empirical support for these predictions. Space use patterns of tracked sharks were consistent with that of 'urban adapters' (species that exhibit partial use of urban areas). Modeling also revealed that an unmeasured spatial variable was driving considerable shark residency in areas exposed to high urbanization. We propose several hypotheses that could explain our findings, including food provisioning from shore-based activities that could be attracting sharks to urban areas. Ultimately, the lack of avoidance of urban areas by sharks documented here, as compared to terrestrial carnivores, should motivate future research in the growing field of urban ecology.



Researchers release an acoustically tagged nurse shark into waters off Miami, Florida, to investigate shark residency patterns in relation to coastal urbanization.

Photo: R. Roemer

KEY WORDS: Urban ecology · Elasmobranch · Acoustic telemetry · Movement ecology · Coastal development · Predator ecology · Anthropocene · Urban adapters

1. INTRODUCTION

One of the most pervasive impacts of humans on the natural world is urbanization. By 2050, it is predicted that 66% of the world's human population will live in urban areas (United Nations 2017), the majority of which will be centered at or near the coasts

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(Creel 2003, McGranahan et al. 2007, Bloom 2011, Seto et al. 2011, United Nations 2017). Currently, population density within 100 m of the ocean is approximately 3 times higher than the global average and is increasing (Small & Nicholls 2003, Baird 2009). Therefore, understanding and ultimately predicting how marine organisms will respond to current and growing levels of urbanization is informative for effective wildlife conservation and management (Magle et al. 2012). While there is a growing body of literature on terrestrial urban ecology, urban marine ecology remains a nascent field (Todd et al. 2019).

While definitions of 'urban' vary, it has been defined by Gehrt (2010) as an area of increased human residence, activity, and associated land area developed for those purposes, usually based on a threshold level of human density. However, this and other published definitions are only applicable to terrestrial systems. There exists no parallel definition of marine urbanization, but Todd et al. (2019) characterized marine urbanization as a combination of 3 major drivers: ocean sprawl, resource exploitation, and pollution.

Documented responses of terrestrial animals to urbanization vary greatly across species. As outlined by McKinney (2006), some species exhibit high sensitivity to urbanization and disappear from such environments ('urban avoiders'), others may thrive as urban commensals and can even become dependent on urban resources ('urban exploiters'), while some species may show some use of urban habitats but still largely rely on natural resources ('urban adapters'). How urbanization impacts the behavior of carnivores has emerged as a key research focus in the urban ecology literature, in part due to their relatively high vulnerability to exploitation and habitat fragmentation (Stark et al. 2020) as well as increases in the number of 'nuisance' carnivores using urban areas that result in human-wildlife conflict (Bateman & Fleming 2012, Lennox et al. 2018). Although some carnivores (e.g. raccoons *Procyon lotor*) exploit urban areas for food and shelter (i.e. 'urban exploiters' sensu McKinney 2006), most large-bodied mammalian carnivores tend to actively avoid urban areas (i.e. 'urban avoiders' sensu McKinney 2006). Ecological specialization has been shown to influence how large consumers respond to human-induced changes in the environment (e.g. Gallagher et al. 2015). Movements of terrestrial carnivores in response to urbanization also appear to be influenced by predator diet. As reviewed in Bateman & Fleming (2012), nearly all carnivore urban exploiters are generalists, able to make use of carrion and human waste food

(e.g. *P. lotor*). In contrast, urban avoiders are hypercarnivore hunters of live prey or specialists, such as pumas *Puma concolor*, grey wolves *Canis lupus*, and bobcats *Lynx rufus* (Bateman & Fleming 2012).

Previous studies have found a range of behavioral responses of terrestrial carnivores to urbanization, including spatial avoidance (e.g. *L. rufus* avoiding areas with roads; Young et al. 2019), reduced home range sizes (e.g. red fox *Vulpes vulpes*, grey fox *Urocyon cinereoargenteus*, coyote *Canis latrans*; Šálek et al. 2015), and changes in the timing of their activity periods (e.g. *L. rufus* and *C. latrans* exhibit higher night activity in developed areas; Riley et al. 2003). In fact, during the recent COVID-19 pandemic lockdown, many terrestrial predators increased their time in urban centers in the absence of human activity (Bates et al. 2021, Wilmers et al. 2021).

While a limited number of published studies have specifically examined the occurrence (Werry et al. 2012, Curtis et al. 2013, McDonnell et al. 2020) and nutrition (Rangel et al. 2021a,b) of marine predators in coastal urban areas, no studies have explicitly investigated space use and movement patterns of marine predators in relation to spatial variation in urbanization. While previous studies found regional population abundances to be lower in proximity to areas of high human activity, these observations were largely attributed to the exploitation of fisheries (Valdivia et al. 2017, MacNeil et al. 2020, Clementi et al. 2021), with no examination of how movement patterns relate to proximity to urban centers.

The present study aimed to examine space use patterns of 3 marine predators, the bull shark *Carcharhinus leucas*, nurse shark *Ginglymostoma cirratum*, and great hammerhead *Sphyrna mokarran*, in proximity to a coastal metropolis (Miami, Florida, USA). To accomplish this goal, we tracked sharks using an array of underwater acoustic receivers that differed in proximity to the ocean-based metropolis of Miami. Comparable to most large terrestrial carnivores, we hypothesized that our study species would be urban avoiders. Accordingly, we specifically evaluated the following predictions developed from the terrestrial urban carnivore literature: (P1) sharks will exhibit comparatively lower residency in areas of highest urbanization; (P2) sharks will show relatively greater use of highly urbanized areas during periods of lower human activity, such as during weekdays compared to weekends and holidays as well as at night compared to daylight hours; and (P3) strength of behavioral patterns will differ by species, with dietary specialists (great hammerhead) exhibiting comparatively lower affinity towards

highly urbanized areas relative to generalists (bull and nurse sharks).

2. MATERIALS AND METHODS

2.1. Study species

The bull shark *Carcharhinus leucas* is a large-bodied coastal species (Rider et al. 2021a) that undergoes long-distance seasonal migrations (Calich et al. 2021). Due to physiological specializations, this species is capable of using inshore estuarine and freshwater environments (Ebert et al. 2021). As a generalist apex predator, bull sharks primarily prey on a variety of large teleosts and elasmobranchs (Tuma 1973, Cortes 1997). The nurse shark *Ginglymostoma cirratum* is a medium-sized coastal species (Ebert et al. 2021), exhibiting relatively high residency and site fidelity to coastal areas (Garla et al. 2017, Friess et al. 2021). This species is a generalist mesopredator, feeding on a variety of small teleosts, crustaceans, and mollusks (Castro 2000). The great hammerhead *Sphyrna mokarran* is a large-bodied species that utilizes a variety of habitats, spanning inshore flats (Roemer et al. 2016), coral reefs (Guttridge et al. 2017), and pelagic environments (Hammerschlag et al. 2011). This species is a specialized apex predator (Gallagher et al. 2014a) that may selectively feed on elasmobranchs such as rays (Raoult et al. 2019).

2.2. Study area and urban gradient

Biscayne Bay is a shallow subtropical lagoon (56 × 13 km) that stretches from Haulover, past downtown Miami, to north Key Largo (Fig. 1A). 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). The natural mainland shoreline of Biscayne Bay is lined mostly with red mangrove *Rhizophora mangle*, the central portions of the bay are mostly tidal flats dominated by seagrasses and sand habitats, and the bay is enclosed by mangrove-lined leeward keys (Serafy et al. 2003). Beyond the ocean side of the leeward keys is a stretch of coral reef patches (reef track) that runs approximately north–south in varying water depths (Fig. 1A).

Marine urbanization is characterized by a combination of ocean sprawl, resource exploitation, and pollution (Todd et al. 2019). Given its proximity to the

metropolis of Miami, the Bay endures a wide array of these anthropogenic stressors, including recreational fishing, boat traffic, nutrient runoff, powerplant effluent, canal discharges, light pollution, and the conversion of natural mangrove shorelines and adjacent seagrass beds to seawalls, docks, marinas, and navigation channels (SFWMD 1995, Browder et al. 2005, Caccia & Boyer 2005, Ault et al. 2017, Millette et al. 2019). These anthropogenic stressors are highest in the northwest portion of the Bay, closest to Miami and the Miami Beaches, and decrease southward into Biscayne National Park and eastward away from the mainland. Indeed, while much of the mainland shoreline has been developed into seawalls and marinas in the northern portions of the Bay as well as innervated with several major canals, much of the natural mangrove shoreline and seagrass beds remain in southern portions of the Bay, which are protected within Biscayne National Park. Therefore, Biscayne Bay is subject to a northwest to southeast urban–natural gradient (SFWMD 1995, Browder et al. 2005, Caccia & Boyer 2005). Accordingly, we evaluated space use of sharks in response to this urban gradient, measured in terms of both distance to Miami and 8 spatial zones that differed in location and habitat type (mainland shoreline, flats in central of the bay, leeward key, coral reef) as well as the associated influence of anthropogenic stressors, generally decreasing from the northwest to southeast: (1) North Bay Urban, (2) Middle Bay Mainland, (3) Middle Bay Central, (4) Middle Bay Leeward Keys, (5) South Bay Mainland, (6) South Bay Central, (7) South Bay Leeward Keys, and (8) the Reef Track (Fig. 1A).

2.3. Acoustic telemetry array

To determine shark residency patterns across Biscayne Bay, we established an array of Innovasea VR2W receivers (Amirix) beginning in July 2015 as outlined in Rider et al. (2021a,b). The array initially comprised 12 receiver stations but ultimately grew to 40 between 2015 and 2019 (Fig. 1A, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m691p001_supp.pdf). Most of the receivers ($n = 34$) were placed 1–4 m deep within the Bay's boundaries, both adjacent to the mainland and leeward keys shores as well in the central part of the Bay along the intra-coastal waterway. The remaining 6 receivers were placed approximately 10 m deep along the reef track to the east of the Bay. Each receiver was anchored to the substrate via an earth anchor set within a concrete block. Routine receiver maintenance and data

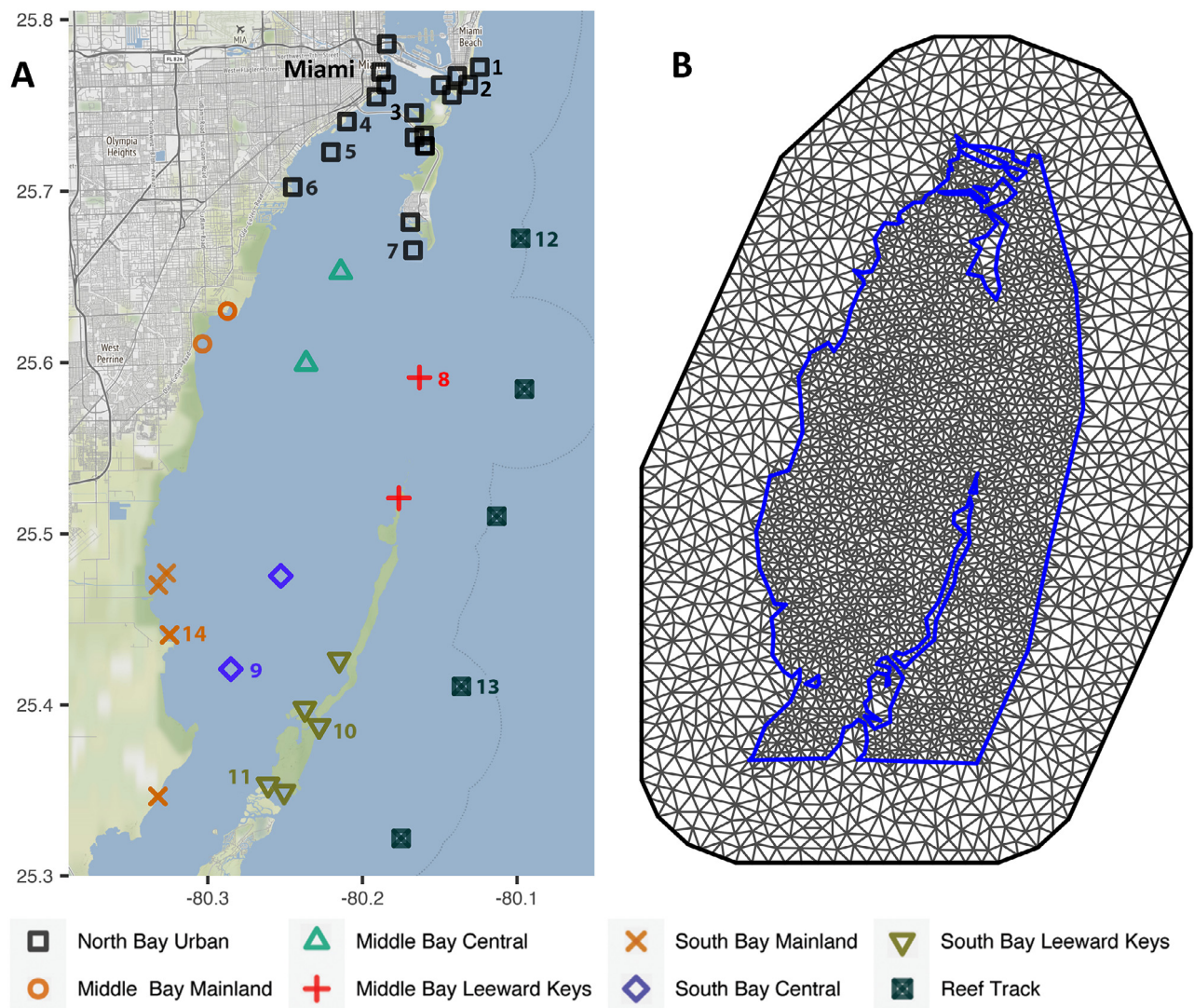


Fig. 1. Biscayne Bay and adjacent reef with (a) receiver station location and zone and (b) mesh of 3417 vertices created using constrained refined Delaunay triangulation. Key reference sites and/or those noted in the text are numerically labeled. 1: South Beach; 2: Government Cut; 3: Seagarium; 4: Mercy Hospital; 5: Dinner Key; 6: Gables Waterway; 7: Cape Florida Channel; 8: Solider Key; 9: Arsnickers; 10: Caesar's Creek; 11: Broad Key Channel (two stations represent the Broad Key Gate); 12: Key Biscayne Reef; 13: Ajax Reef; 14: Turkey Point Power Plant

downloads were performed every 6–12 mo. Receivers were assigned to one of the 8 spatial zones defined above.

We performed range testing on a subset of 3 receiver stations in July 2020 using similar methods outlined by Kessel et al. (2014). At 6 different distances (100, 200, 400, 600, 800, and 1000 m) from the receiver station, an Innovasea V16-4X sentinel range testing tag with a nominal delay of 60 s was deployed for approximately 24 h. Each tag was deployed at 10 s intervals to reduce collisions of detection transmissions. Once the detection data

were downloaded, the number of detections received at each distance per hour was divided by the number of theoretical detections (i.e. 60). The detection probabilities, or detectability, at each distance were then plotted and fitted with a logistic regression curve to estimate the 50 and 5% detectability range of each receiver station. The resulting range at 50 and 5% detection efficiency was approximately 200–250 and 900–1000 m, respectively, which is comparable to passive acoustic telemetry studies in the region (Brownscombe et al. 2020, Gutowsky et al. 2021).

2.4. Shark capture and acoustic tagging

Sharks were captured using a series of baited drumlines, as described in Tinari & Hammerschlag (2021). Upon capture, sharks were either secured alongside a boat in the water or on top of a floatable platform and tagged with the Innovasea V16-4X internal acoustic transmitters (Amirix) as outlined in Rider et al. (2021a). Tags were programmed with a nominal delay of 60–90 s and had an estimated battery life between 4.4 and 6.6 yr; however, methods of tag attachment were species-specific. Bull and nurse sharks were tagged via surgical implantation into the body cavity following the approach of Hammerschlag et al. (2017). Great hammerheads were tagged via an externally tethered tag package, which used a dart anchor that was embedded in the shark's dorsal musculature. External tags were attached to great hammerheads because it allowed for faster attachment, considering this species' inherent sensitivity to capture and handling stress (Gallagher et al. 2014b, Jerome et al. 2018). While tag shedding is more likely with external transmitters (N. Hammerschlag & A. J. Gallagher pers. obs.), this risk was minimized by first looping the tag tether through the dorsal fin prior to insertion in the dorsal musculature.

2.5. Data analysis

Residency duration, defined as largely uninterrupted occupancy of a limited area over time, is a common metric for quantifying distributions, fidelity, or home range activity in sharks (Chapman et al. 2015). In the current study, space use was calculated as residency at receiver stations during time periods specifically relating to our predictions. Firstly, data were filtered to remove false detections or incomplete codes that may occur when transmissions are recorded simultaneously. Data were truncated to include the same sampling period across years, which spanned the warm wet (1 May–31 October) and cool dry seasons (1 November–30 April). We generated residency duration for each animal by receiver station with the R package 'VTrack' and its associated animal tracking toolbox (Campbell et al. 2012, Udyawer et al. 2018).

To evaluate shark residency patterns in relation to proximity to urbanization, the distance from urban area (DUA) to receiver station was measured via ArcGIS Pro (ESRI) as the shortest Euclidean distance between a receiver station and a terrestrial urban-

ized area within the boundary of the city of Miami or Key Biscayne. Based on our predictions, we paired shark detection history with several explanatory variables, including diel period (based on sunset and sunrise times) and day of the week (related to weekdays vs. weekends/holidays).

Prior to analysis, residency data were inspected to identify and remove outliers (>3 SD from mean) where residency was >60 h ($n = 4$ residency events). Next, we examined data using mapping packages (e.g. 'mapview'; Appelhans et al. 2021) and various plotting methods in the R statistical environment. Proportions of total residency for each categorical explanatory variable (i.e. season, diel period, weekday type weighted by number of days in weekday versus weekend categories) were calculated first by individual ID and then averaged across zone and species.

Mapping and evaluating residency as relative numbers and proportions led us to use the integrated nested Laplace approximation (INLA; Rue et al. 2009). Executed through the R-INLA package (www.r-inla.org), INLA is a fast and accurate approximation for Bayesian inference in latent Gaussian models. INLA consists of a univariate likelihood model to capture the marginal distribution of the data and a vector of hyperparameters that can appear in the likelihood as dispersion parameters, shape parameters, or represent otherwise unstructured variability in the data (e.g. random intercepts; Martino & Riebler 2020). In addition, a latent Gaussian field links the response variable, through its assumed distributional family, with a structured additive predictor. In most applications, the latent Gaussian fields have conditional independence properties of a sparse precision matrix, known as a Gaussian Markov random field (GMRF; Rue & Held 2005, Martins et al. 2013). The sparse precision matrix simplifies numerical calculations of spatial correlation, which are obtained via a stochastic partial differential equation (SPDE; Lindgren et al. 2011) estimated on a 2D grid called a mesh (Bivand et al. 2015). The mesh consists of a series of non-overlapping triangles (edges and vertices) across the entire domain with additional coverage to avoid boundary effects (Blangiardo et al. 2013). The ability to express models as GMRFs is highly applicable to ecological studies where correlation among sampling sites is likely, i.e. underwater acoustic telemetry systems (Whoriskey et al. 2019). For example, the bounds of a telemetry array can be considered the domain comprised of individual sampling units (i.e. receivers) and their coordinates. Repeating the

study under the same conditions would theoretically result in different realizations from the same underlying stochastic process. Assuming the samples are normally distributed, the domain is a continuous Gaussian field on which a mean and covariance matrix can be estimated by the SPDE approach (Lindgren et al. 2011, Zuur & Ieno 2018). R-INLA includes functions to further allow for non-exchangeable, exchangeable, and replicated temporal correlation (Zuur & Ieno 2018) that applies to systems where temporal effects are expected.

To begin the modeling procedure, residency was ln-transformed and assumed to follow a Gaussian distribution. Continuous variables were standardized (subtracting from the mean and dividing by the variance) for numerical stabilization during model runs. Then, a single spatiotemporal model was parameterized with main effects, 2-way interactions, and 3-way interactions formally defined as:

$$\begin{aligned} \text{Residency}_{tji} &\sim N(\mu_{tji}, \sigma^2) \\ E(\text{Residency}_{tji}) &= \mu_{tji} \quad \text{and} \quad \text{var}(\text{Residency}_{tji}) = \sigma^2 \\ \mu_{tji} &= \mathbf{X}_{tji} \times \boldsymbol{\beta} + a_{ti} + v_{tji} \\ a_{ti} &\sim N(0, \sigma^2_{\text{ID}}) \\ v_{tji} &= \phi \times v_{t-1,j} + u_{tji} \\ u_{tji} &\sim \text{GMRF}(0, \Omega) \end{aligned}$$

where \log_e residency at the j^{th} observation, t^{th} year, and i^{th} shark is normally distributed with an expected value μ_{tji} and variance σ^2 . \mathbf{X}_{tji} is a matrix of covariates with posterior mean values $\boldsymbol{\beta}$. The covariates of \mathbf{X}_{tji} testing our predictions include the main effect for DUA (P1), the 2-way interactions of DUA \times day of the week and DUA \times diel period (P2), and the 3-way interactions of DUA \times day of the week \times species and DUA \times diel period \times species (P3). The random intercept for shark ID, a_{ti} , is normally distributed with a mean 0 and variance σ^2_{ID} . The autoregressive expression v_{tji} varies according to the correlation ϕ . The normally distributed spatially dependent random intercept u_{tji} has a mean of zero and covariance

matrix Ω that is estimated by a Matérn correlation function using the SPDE approach (Lindgren et al. 2011).

The sampling domain was specified by a mesh (3417 vertices) across Biscayne Bay and extended inland and offshore to avoid boundary effects (Blangiardo et al. 2013, our Fig. 1B). The mesh is a discrete index of non-overlapping triangles created by a constrained refined Delaunay triangulation. Estimates of u_{tji} generated at the sampling domain vertices results in residency being explained by spatially correlated random effects (referred to throughout as spatial correlation) rather than by fixed effects or other hyperparameters. Posterior mean estimates (i.e. mean and variance) are then mapped with the coordinates used to calculate the Matérn correlation (e.g. UTM meters). Year was used as a grouping factor ($n = 5$) to incorporate non-exchangeable temporal correlation into the model. An autoregressive correlation structure was specified such that high values of ϕ (e.g. $\phi = 0.9$) indicate the response changes little from one year to the next (Zuur et al. 2017). The model was validated following procedures outlined by Zuur et al. (2010). All analyses were performed in the R statistical environment (R Core Team 2020).

3. RESULTS

Between 2015 and 2019, a total of 24 bull sharks *Carcharhinus leucas*, 27 nurse sharks *Ginglymostoma cirratum*, and 36 great hammerheads *Sphyrna mokarran* were tagged either within or just offshore of Biscayne Bay, Florida (Fig. S1). Of these tagged individuals, 13 bull sharks (228 ± 26.4 cm TL), 25 nurse sharks (187 ± 41.3 cm TL), and 14 great hammerheads (253 ± 39.3 cm TL) were subsequently detected in our array (Table 1). The raw data contained 197 351 detections (Fig. S2) that were filtered and processed to generate 3535 residency events across individuals, and all species were detected at least once at each station (Table 1). Residency was

Table 1. Mean (\pm SD) total length (TL), residency, distance to urban area (DUA), and sample size by sex for tagged shark species (bull shark *Carcharhinus leucas*, nurse shark *Ginglymostoma cirratum*, great hammerhead *Sphyrna mokarran*) used in the analysis of residency time

Species	TL (cm)	Residency (h)	Residency range (h)	DUA (km)	DUA range (km)	2016		2017		2018		2019		2020	
						M	F	M	F	M	F	M	F	M	F
Bull shark	228 \pm 26.4	1.70 \pm 3.4	0.01–53	6.49 \pm 11.5	0.02–43.5	0	6	1	11	0	9	0	10	0	6
Nurse shark	187 \pm 41.3	1.66 \pm 4.8	0.02–57	3.75 \pm 9.62	0.01–43.5	2	3	6	7	3	9	9	11	6	11
Great hammerhead	253 \pm 39.3	0.32 \pm 0.49	0.02–4.5	12.2 \pm 15.8	0.01–43.5	0	2	3	6	3	3	2	3	0	2

greater than 60 h in 4 events recorded by nurse sharks. These residency values exceeded our threshold of >3 SD from the mean, accounting for 0.1% of the data, and therefore were considered outliers and excluded from further analyses.

The North Bay Urban receiver stations tended to detect the greatest number of unique IDs annually compared to stations in any other zone (Fig. 2). Specifically, receiver stations located off South Beach, Government Cut, Dinner Key, Seaquarium, and Cape Florida Channel (as indicated in Fig. 1) detected the most individuals by species each year. While bull sharks frequented stations in the North

Bay Urban zone, between Dinner Key and Seaquarium, there appeared to be an expansion in the number of individuals detected in the middle of the bay, especially around Solider Key in 2019 (Fig. 2); however, this also coincided with expanding the array to these sites (Fig. S1). In 2020, there was an increase in the number of bull sharks detected along the Reef Track from Key Biscayne Reef to Ajax Reef (Fig. 2), but again this coincided with the expansion of the array to these areas (Fig. S1). Great hammerheads concentrated in high numbers within the North Bay Urban zone during 2017, specifically off South Beach, Seaquarium, Dinner Key, and Cape Florida

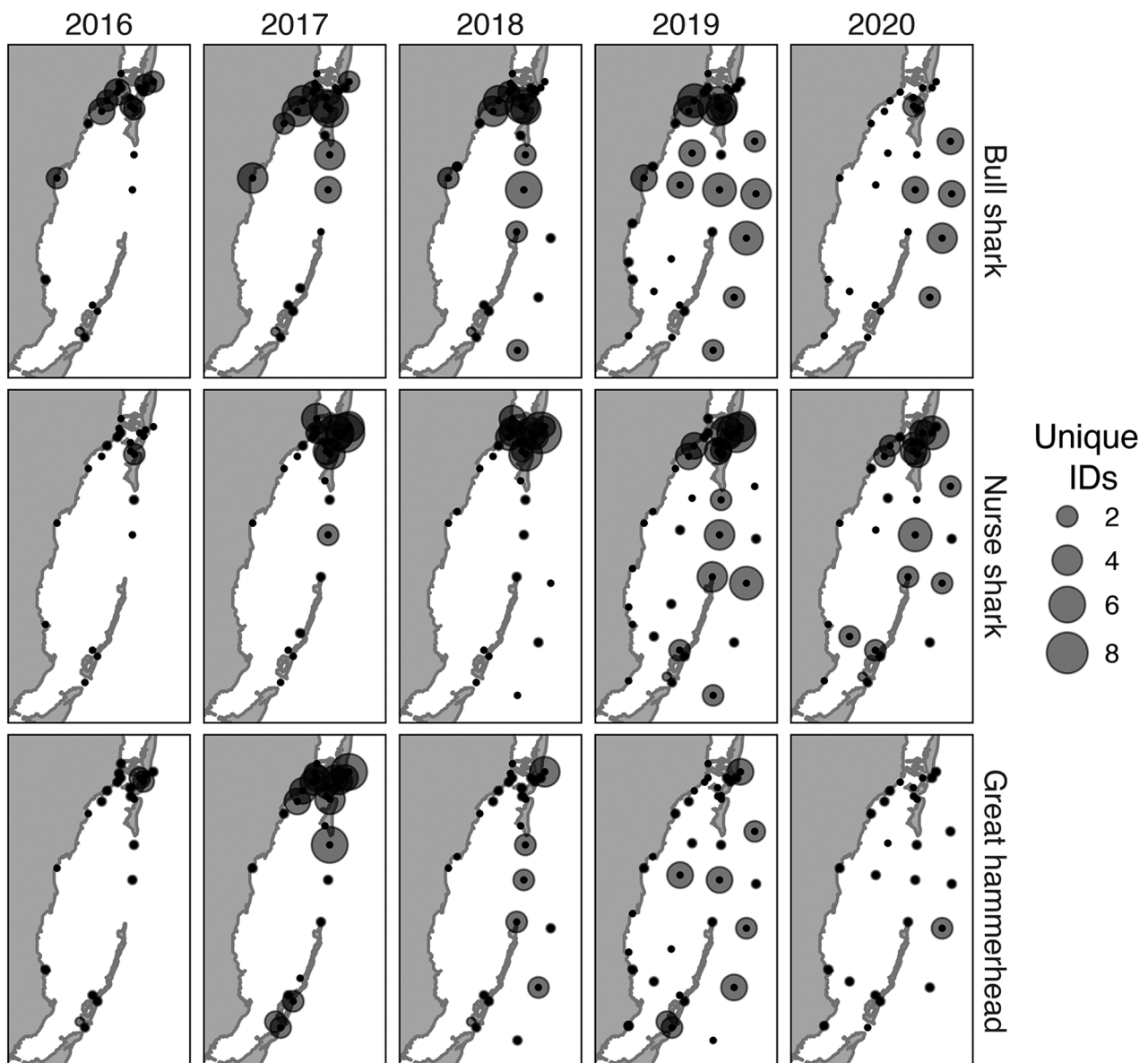


Fig. 2. Distribution and number of unique IDs of tagged shark species at telemetry stations across Biscayne Bay and adjacent reef, spanning 2016–2020

Channel, but distributed more broadly in 2018 and 2019 along the Middle Bay/Leeward Keys and Reef Track (Fig. 2). In 2020, there was a sharp decrease in the number individuals detected across all stations, with only one receiver station along the reef track detecting more than one individual; however, this could be also a result of tag battery life exhaustion. Nurse sharks were abundant in the North Bay Urban zone from 2017–2020, especially at the Government Cut and Seaquarium receiver stations, which recorded between 6 and 8 different individuals (Fig. 2). In 2019 and 2020, there were more individuals detected farther south along the Middle Bay/Leeward keys and the Reef Track (Fig. 2), but this expansion also coincided with the expansion of the array to these sites (Fig. S1).

Average individual total residency, expressed as pair-wise proportions, was similar in both the wet and dry season across zones (Fig. 3). The only excep-

tions were bull sharks at North Bay Urban and Reef Track stations (Fig. 3). For instance, bull sharks spent considerably more time at stations during the dry season (0.83 ± 0.32) compared with the wet season (0.22 ± 0.35) in North Bay Urban, with this difference exaggerated at Reef Track (Fig. 3). Patterns in proportional residency by day and night indicated a potential diel effect for bull sharks at Reef Track stations, great hammerheads at Middle Bay Central stations, and nurse sharks at Middle Bay Leeward Keys stations (Fig. 3). There was no discernable difference in residency by diel period at North Bay Urban stations for any species, despite the relatively large number of individuals in the pairwise categories (Fig. 3). On the contrary, for bull sharks, the majority (0.79 ± 0.17) of residency events at Reef Track stations occurred at night. Great hammerheads showed relatively high residency during daylight at Middle Bay Central and South Bay Leeward Keys stations,

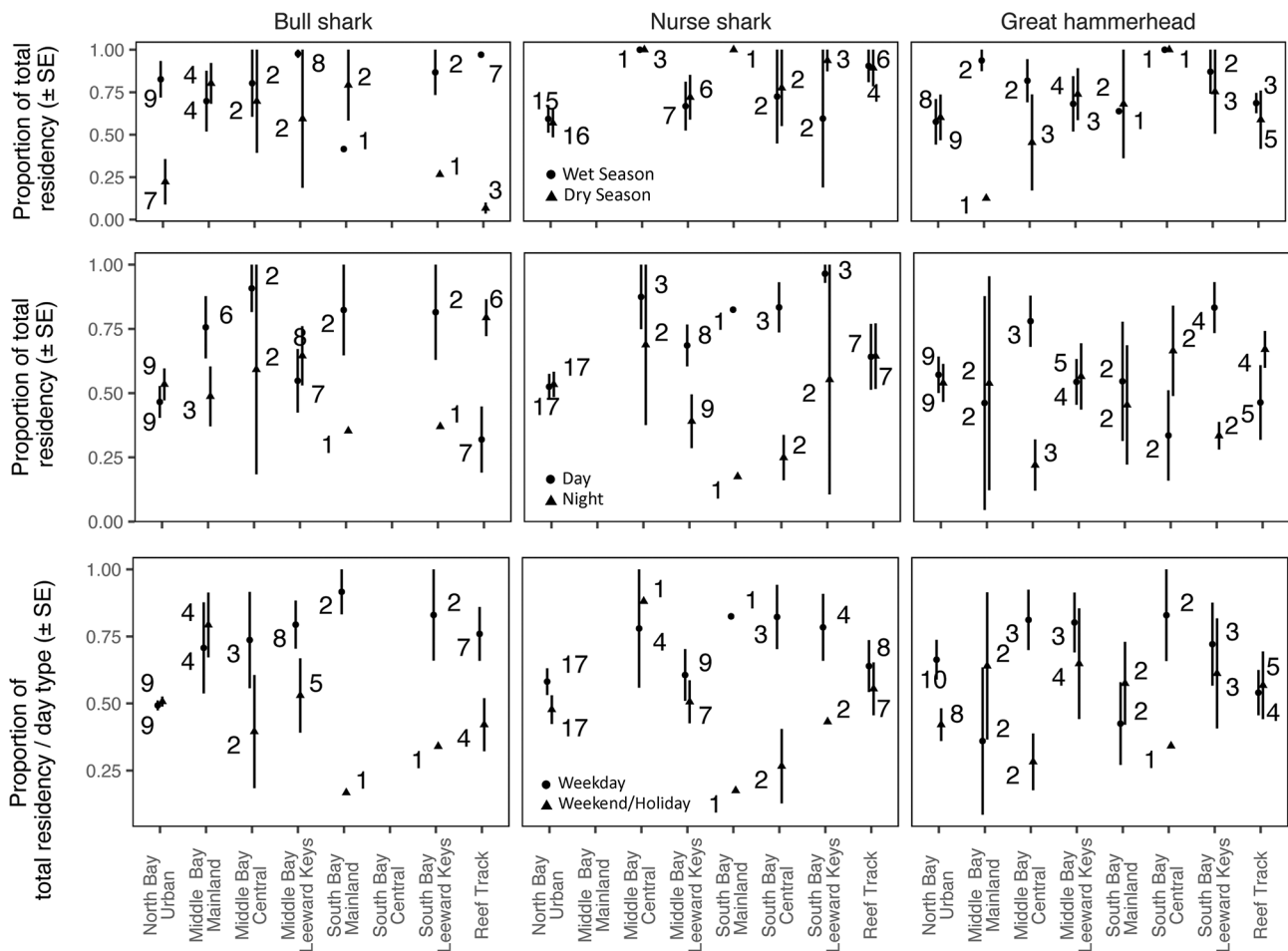


Fig. 3. Total proportion (\pm SE) of residency duration of sharks within each spatial zone by season (top row; circles: dry season; triangles: wet season), by diel period (middle row; circles: day; triangles: night), and by day of the week (bottom row; circles: weekday; triangles: weekend/holiday). Data from 2016–2020. The number of unique sharks is indicated at each data point

but sample size was small ($n = 2$) in the latter zone. The largest potential effect of diel period for nurse sharks was observed at Middle Bay Leeward Keys stations, where this species showed relatively high residency (0.68 ± 0.23) during the day. Interestingly, there was no apparent difference in proportional residency at Reef Track stations (Fig. 4). Weekdays tended to have the highest proportion of residency (weighted by number of weekday types detected) for each species (Fig. 3). Notably large differences occurred for bull sharks at Reef Track stations, great hammerheads at Urban North Bay Urban stations, and nurse sharks in the South Bay (Fig. 3).

The INLA model fit ln-residency with a correlation of $r = 0.64$ between the raw observed and estimated values. Important terms included the main effects for diel period and weekday type, such that residency duration decreased at night and during weekends (Fig. 4). Despite apparent effects among categories in the observed data (Figs. 3–5), no effects of the statistical interactions were different from zero (Table 2). Given that neither distance

to urban area (P1) nor any interactions (P2 & P3) were important, the statistical model of shark residency failed to support our predictions. Variance of the random intercept was $\sigma_{\text{shark}} = 0.462$, and intraclass correlation (ICC) indicated dissimilarity in residency dura-

Table 2. Fixed effects from the top model to estimate shark residency in Biscayne Bay, Florida. DUA.std: standardized distance to urban area. Upper and lower bounds of the 95% credible intervals are indicated as 2.5 and 97.5% CI, respectively. Intervals that do not overlap zero are shown in **bold** (i.e. important variables in the model)

Term	Estimate	2.5% CI	97.5% CI
Intercept	2.66	2.233	3.07
DUA.std	-0.161	-0.426	0.102
Weekend	-0.361	-0.512	-0.210
Great hammerhead	-0.152	-0.621	0.326
Nurse shark	0.1	-0.292	0.497
Night	-0.159	-0.254	-0.065
DUA.std × weekend	-0.018	-0.188	0.151
DUA.std × great hammerhead	0.094	-0.033	0.421
DUA.std × nurse shark	-0.016	-0.28	0.31
Weekend × great hammerhead	0.16	-0.108	0.428
Weekend × nurse shark	0.079	-0.137	0.295
DUA.std × night	0.068	-0.086	0.222
DUA.std × weekend × great hammerhead	0.012	-0.249	0.225
DUA.std × weekend × nurse shark	0.067	-0.185	0.333
DUA.std × night × great hammerhead	-0.202	-0.415	0.011
DUA.std × night × nurse shark	-0.059	-0.312	0.193

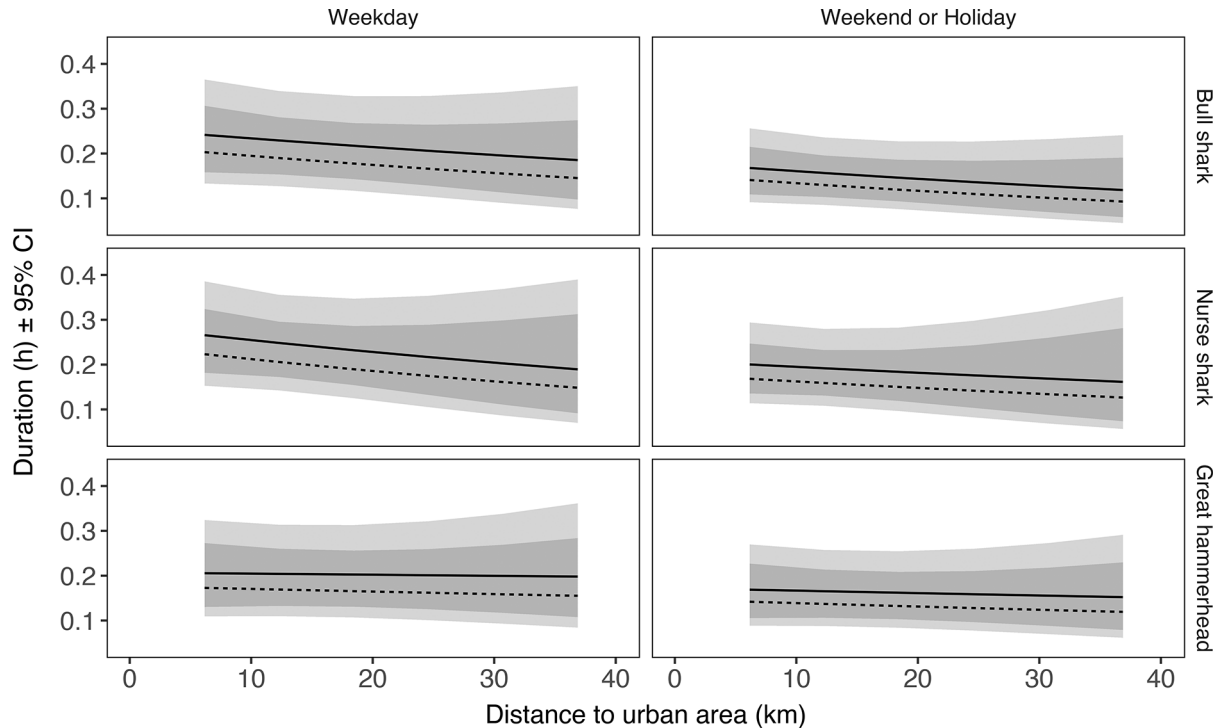


Fig. 4. Estimated residency of tagged sharks relative to covariates of the integrated nested Laplace approximation model

tion by individual ($ICC_{\text{shark}} = 0.11$; Table 3). Matérn correlation was $\leq 10\%$ where receivers were spaced at least 1.7 km apart (Table 3). The GMRF showed that latent effects varied little overall across years ($\varphi = 0.725$), but some annual differences were apparent (Fig. 5). Residency duration was greatly explained by the spatially correlated random effects, which manifested prominently at several North Bay Urban stations and to a lesser extent South Bay Leeward Keys stations (Fig. 5). In general, receiver location and distance between receiver locations were predictors of residency, whereas the hyperparameter for

sampling year and most fixed covariates had little to no effects (Tables 2 & 3). For example, residency duration within a 250 m buffer of Seaquarium piling station in North Bay Urban was extraordinary and overestimated on the GMRF (247 ± 500 h). The large variation resulted from an estimated mean residence duration of >1100 h in 2020 (Fig. 5). Relative to the remainder of the array, residency duration explained by spatial correlation was high (0.46 ± 0.42 h) at the Broad Creek Gates (South Bay Leeward Keys). Areas along the western shoreline of North Bay Urban, including Mercy Hospital, Dinner Key, and Gables

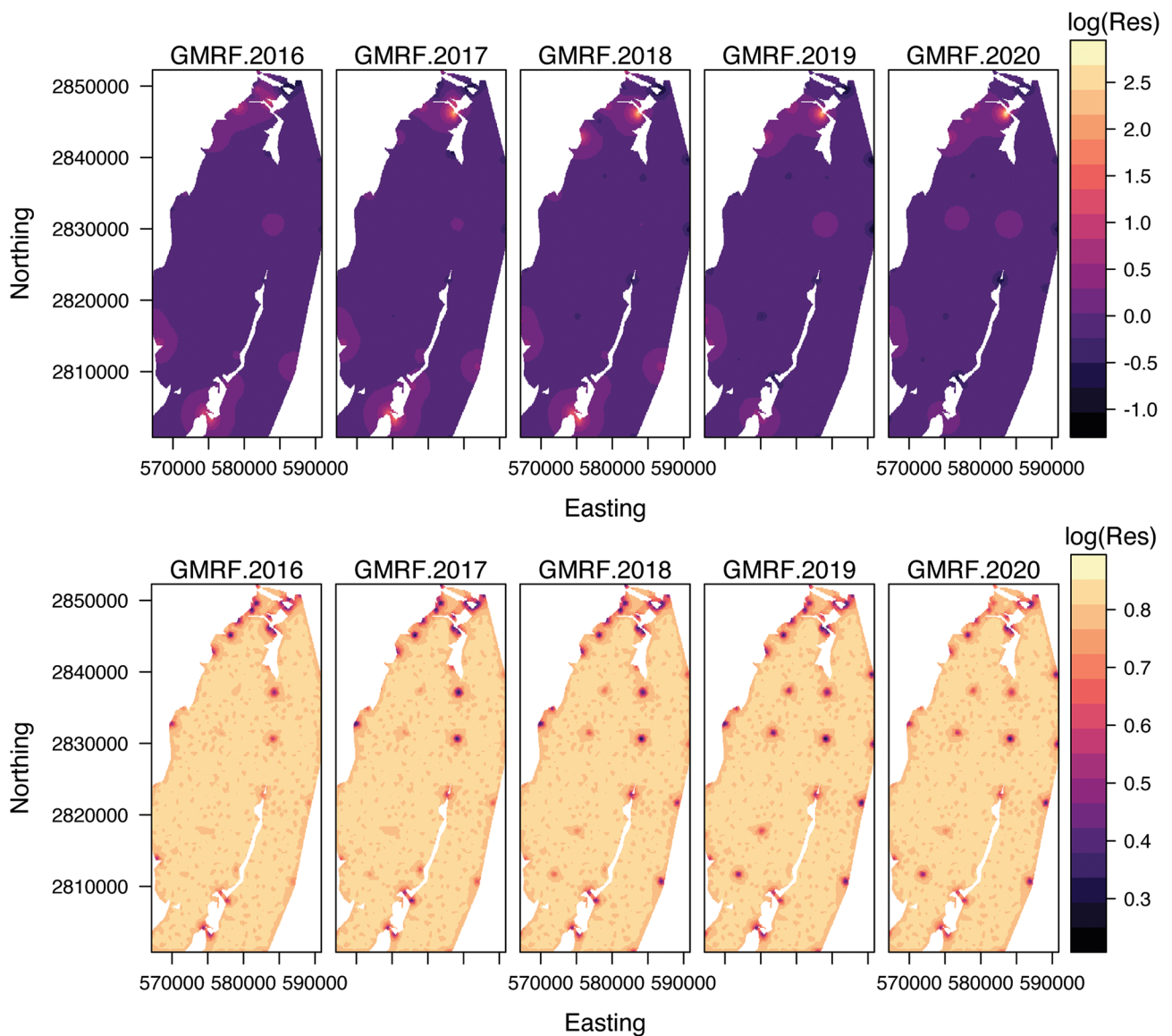


Fig. 5. Top: Posterior mean values (log scale) of the Gaussian Markov random field (GMRF) estimated for shark residency calculated annually. Darker color shades: areas of increased residency unexplained by the model. Bottom: Posterior mean values of the variation of the GMRF estimated for shark residency calculated annually. Darker colors: increased variation. Estimates were generated using non-exchangeable correlation and plotted by the coordinates (UTM meters) to calculate spatial correlation

Table 3. Hyperparameters and intraclass correlation (ICC) from the integrated nested Laplace approximation model to estimate shark residency in Biscayne Bay. Model hyperparameters are kappa (κ), variance of the spatial random effect (σ_u), the range of spatial correlation (Range), phi (φ), variance of the Gaussian observations ($\sim 1 / \tau$; σ), variance in the random intercept (σ_{shark}), and ICC of the random intercept ($\text{ICC}_{\text{shark}}$)

Parameter	Value
κ	0.002
σ_u	0.762
Range (km)	1.71
φ	0.725
σ	1.33
σ_{shark}	0.471
$\text{ICC}_{\text{shark}}$	0.111

Waterway stations, revealed moderately high annual shark residency (0.09 ± 0.06 h) according to the GMRF. Additional noteworthy stations of high mean annual residency include Soldier Key (0.05 ± 0.01 h, Middle Bay Leeward Keys), Ajax Reef (0.06 ± 0.03 h), and Turkey Point Power Plant (0.08 ± 0.2 h, South Bay Mainland; Fig. 5).

4. DISCUSSION

In the present study, we used passive acoustic telemetry to examine space use patterns of 3 shark species (great hammerhead *Sphyrna mokarran*, bull shark *Carcharhinus leucas*, and nurse shark *Ginglymostoma cirratum*) in relation to a spatial gradient of urbanization associated with the coastal metropolis of Miami. The majority of large-bodied terrestrial carnivores tend to be urban avoiders (McKinney 2006). Therefore, our first prediction was that sharks would exhibit comparatively lower residency in areas of highest urbanization, closest to Miami (i.e. the North Bay Urban zone). This was not the case across all 3 shark species and seasons (Figs. 2 & 3). While bull sharks were found in urban areas during both seasons, their proportional seasonal residency within the North Bay Urban zone was relatively lower during the wet season. Indeed, previous tracking of bull sharks tagged in Biscayne Bay found that adult females migrate away from the Bay during the wet season, likely linked to reproduction (Rider et al. 2021a). Thus, the decreased proportional residency observed for this species in the North Bay Urban zone during the wet season does not represent behavioral avoidance of an urban-impacted area.

Our second prediction was that sharks would show relatively higher use of urban areas during periods of lower human activity, such as during nighttime compared to during daylight hours. For example, black bears *Ursus americanus*, bobcats *Lynx rufus*, and coyotes *Canis latrans* tend to increase their activity in developed areas at night (Riley et al. 2003, Stark et al. 2020). Here, we failed to find evidence of these patterns. Overall shark residencies were lower throughout the entire array during night versus day. Since many sharks are generally nocturnal foragers (Hammerschlag et al. 2017), it is possible that they left the confines of the Bay during the night to forage in offshore reef habitats as has been seen in reef sharks elsewhere (e.g. Williams et al. 2018).

We also predicted that shark residencies within urban-impacted areas close to Miami would be higher during weekdays, when human boat-based activities would be lower compared to weekends and holidays. Again, we failed to find support for this prediction. While overall shark residencies across the array were lower during the weekend, this pattern did not differ with proximity to Miami. Boat traffic in Biscayne Bay, especially in the North Bay Urban zone, is significantly higher during weekends and holidays than during weekdays (Ault et al. 2017, Rider et al. 2021b). Some studies have demonstrated that the noise pollution, including that generated from boat engines, can negatively impact the physiology (Wysocki et al. 2006, Cartolano et al. 2020) communication (Codarin et al. 2009), and behavior of teleost fishes (Ferrari et al. 2018); however, these patterns are not consistent among species or regions (Staaterman et al. 2020). Recent research in the Bay by Rider et al. (2021b) found no detectable relationship between boat density and residencies of bull, nurse, and great hammerhead sharks; only the hourly presence of nurse sharks decreased with increasing boat traffic (albeit a weak pattern), a relationship not seen in the other 2 species. However, we cannot entirely rule out the potential for increased boat traffic during weekends and holidays to have caused acoustic disturbances which could have masked acoustic transmitter detections on the receivers (Reubens et al. 2019); this supposition will require further testing.

In a review of the urban ecology literature, Bateman & Fleming (2012) reported that terrestrial carnivores with more specialized diets (e.g. pumas *Puma concolor*) typically exhibited greater avoidance of urbanized areas compared to species with generalist diets (e.g. raccoons *Procyon lotor*). Therefore, our

third prediction was that strength of behavioral patterns would differ by species, with dietary specialists (great hammerheads) exhibiting comparatively lower affinity towards highly urbanized areas relative to dietary generalists (nurse and bull sharks). Our data did not support this prediction, with all 3 species exhibiting similar patterns of residency.

Interestingly, results of the GMRF analysis revealed that an important but otherwise unmeasured latent variable in our model was driving considerable spatial correlation in the northern part of the Bay, an area exposed to high levels of urbanization from Miami. While the reasons for these patterns are unknown, below we propose 3 non-mutually exclusive hypotheses that could explain our findings.

First, nutrient runoff into coastal waters is a syndrome associated with marine urbanization (Paerl et al. 2014, Todd et al. 2019). The location of Miami on the water's edge coupled with numerous canal outflows into Biscayne Bay creates a mechanism for land-based nutrient and sewage discharge into the north Bay. High concentrations of nutrient concentrations (Milletto et al. 2019) and associated cyanobacterial blooms (Brand et al. 2010) are well documented in the north Bay. It is plausible that this increased primary productivity could be supporting local food webs through bottom-up trophic processes, thus creating increased prey availability that attracts or aggregates sharks as has been observed in other studies (e.g. Queiroz et al. 2016). Recently, Rangel et al. (2021a) found that nurse sharks sampled in urban-impacted areas of Biscayne Bay had higher concentrations of plasma-saturated and bacterial fatty acids compared to conspecifics sampled in southern, less urban-impacted areas of the Bay. This result is indicative of a dietary pattern of feeding on a bacterial-based food web; for example, due to domestic sewage effluent that is highly correlated with urbanization (e.g. Boëchat et al. 2014, Jiménez Martínez et al. 2019). Moreover, the body condition of these nurse sharks was relatively high, suggesting possible increased foraging opportunities in urban sites of Biscayne Bay compared to the adjacent less-impacted area (Moorhead 2019).

Second, akin to terrestrial carnivores like black bears and raccoons, which are known to forage at trash sites in urban areas (Bateman & Fleming 2012), food subsidies associated with the numerous marinas situated along the shoreline of the north Bay (Ault et al. 2017) could be attracting sharks. At these marinas, anglers returning from a day of fishing com-

monly discard fish carcasses after removing the filets, even at marinas with no discard regulations in place. Sharks are regularly seen in marinas scavenging on these fish carcasses, which may be attracting or aggregating sharks to these locations. Indeed, a previous study in the Indian River Lagoon, Florida, revealed high use of boat marinas by tracked juvenile bull sharks (Curtis et al. 2013). This explanation is further supported by data from acoustically tracked short-tail stingrays *Bathytoshia brevicaudata* at a boat ramp in Jervis Bay, Australia, where anglers provision rays with discarded fish carcasses (Pini-Fitzsimmons et al. 2018). Results of that study revealed that stingrays visited the boat ramp more often during periods of fish-cleaning, and stingrays also exhibited anticipatory behavior, starting to arrive at the boat ramp in advance of the time when anglers usually clean their fish (Pini-Fitzsimmons et al. 2018). Comparable anticipatory behavior was also observed in experimentally provisioned juvenile lemon sharks *Negaprion brevirostris* in the Bahamas (Heinrich et al. 2021).

Third, fish parts being regularly discarded into the water by the Miami Seaquarium, located on Virginia Key, could also be attracting sharks to the area. The Seaquarium staff regularly discard leftover fish not fed to their captive animals into the adjacent Bay waters of the North Bay Urban zone, which is well known to attract sharks. The aquarium staff report seeing sharks commonly feeding on the fish discards, including large bull sharks that appear to aggregate at the discard site. In fact, the location identified by the GMRF as possessing the highest spatial correlation is the water's edge of the Seaquarium. Moreover, receiver detections at the Seaquarium have approximately an order of magnitude more detections than any other receiver in the array. As mentioned above, anthropogenic food-subsidies have previously been shown to attract and aggregate elasmobranchs. In many cases, fish discarded can be a major contribution to the overall diets of elasmobranchs (Forman & Dunn 2012, Fondo et al. 2015).

The behaviors exhibited by the 3 shark species tracked here are most consistent with those considered to be 'urban adapters', exhibiting partial use of urbanized sites while largely relying on more natural areas (McKinney 2006). These space use patterns are consistent with relative abundance surveys of large coastal sharks in the region (Tinari & Hammerschlag 2021); although sharks are routinely captured in close proximity to Miami, catch rates tend to be lower here than in adjacent areas that are less urban-impacted. These space use patterns are in stark con-

trast to those generally exhibited by large terrestrial carnivores, which tend to be urban avoiders (Bateman & Fleming 2012). While the ecological reasons underlying the differences between terrestrial versus marine predators are unknown, it could be due to fundamental differences in how urbanization impacts land versus ocean landscapes, specifically with respect to habitat fragmentation. In terrestrial environments, fragmentation often involves physical barriers (e.g. fences, roads, walls, buildings) which likely impede and even often prevent movement of carnivores among habitat fragments. The same cannot be said for ocean environments, where comparable manmade barriers to movement that fragment habitats do not exist. While docks and jetties may create obstacles to movement (Cooke et al. 2020), they do not fragment the landscape in the same way as land-based structures which would otherwise restrict or prevent movement. Indeed, the ocean has no fences. One notable exception would be dams or flood gates, but these structures tend to occur within inshore estuarine or riverine environments, which were not assessed here. As a result, highly mobile ocean predators may be less sensitive to urbanization than land predators.

The relatively high use of urban areas by tracked sharks found in this study has consequences for both shark health and human safety. Notably, high use of urban-impacted sites exposes sharks to increased vulnerability from land- and boat-based angling in the region (Shiffman & Hammerschlag 2014, Shiffman et al. 2017). While sharks in Florida are often caught and released for sport, great hammerhead sharks exhibit a pronounced capture stress response and are vulnerable to post-release mortality (Gallagher et al. 2014b, Jerome et al. 2018). Sharks exposed to urbanization are also exposed to poor water quality and chemical pollution that could have health and immunological consequences. Indeed, various species of shark sampled in Biscayne Bay have shown high levels of mercury and cyanobacterial toxins (Hammerschlag et al. 2016). Sharks feeding in urban areas may be feeding on lower nutritional quality items. For example, dietary biomarkers from nurse sharks sampled in Biscayne Bay revealed urban nurse sharks had relatively lower percentages of essential fatty acids, higher saturated fatty acids, and increased bacterial markers compared to conspecifics sampled in less urbanized areas (Rangel et al. 2021a). Such poor nutritional quality prey could be the result of sharks feeding on fish carcasses that have been cleaned of meat and/or by sharks feeding on poor quality prey

found in urban areas resulting from nutrient runoff causing lower transfer rate of physiologically important essential fatty acids to higher trophic levels (Gladyshev et al. 2012, Gomes et al. 2016, Whorley et al. 2019, Rangel et al. 2021a). Nurse sharks sampled in urban areas also had fatty acid profiles indicative of relatively lower prey diversity (mainly piscivores), while non-urban nurse sharks had fatty acid profiles indicative of relatively higher prey diversity, including fishes, crustaceans, and mollusks, which could have also impacted their nutrition (Rangel et al. 2021a). Inadequate dietary intake of essential fatty acids can have negative consequences for immune function, brain development, reproductive success, and cardiac performance (Sargent et al. 1999, Tocher 2003, 2010, Birnie-Gauvin et al. 2017), ultimately affecting fitness. Indeed, sharks sampled near urban areas often exhibit non-normal patterning and/or coloration on their skin (N. Hammerschlag & A. J. Gallagher pers. obs.), suggesting that these non-essential somatic processes may be traded-off with more important functions resulting from lower quality diets. Finally, high use of nearshore urban areas by sharks may put bathers at risk of shark encounters, especially in areas where sharks may be attracted to scavenge on fish discards. While relatively rare, shark bites on humans have previously occurred in the North Bay Urban zone, identified here as a location of high shark residency (e.g. https://wsvn.com/news/local/man-rushed-to-hospital-after-shark-bite-near-key-biscayne/?utm_medium=social&utm_source=twitter_wsvn). Thus, to promote both human safety and shark conservation, our data pinpoint areas within our array that may drive human-wildlife conflict and should thus be avoided by human water users to reduce the probability of a negative shark encounter.

A limitation of this study was the lack of complete coverage by our receiver array of Biscayne Bay as well as the limited detection range of each receiver (i.e. the 200–250 m 50% detectability range). As such, we were unable to accurately measure patterns of shark absence, which is why the analysis was restricted to residency patterns. Another limitation of this study is that we only focused on shark space use without directly evaluating for potential influences of environmental parameters. It is likely that a range of factors not evaluated here, such as spatial and temporal variations in temperature, salinity, depth, habitat type, nutrients, and dissolved oxygen concentrations, directly or indirectly influence shark residency patterns. Such factors have previously been shown to

affect relative abundance rates of great hammerheads as well as bull and nurse sharks in Biscayne Bay (Phenix et al. 2019, Tinari & Hammerschlag 2021, Rider et al. 2021a). Therefore, we recommend that future research seek to incorporate such environmental and water quality factors into assessments of shark space use and residency patterns in Biscayne Bay and how these parameters interact with proximity to the North Bay Urban zone.

In summary, we found that bull, nurse, and great hammerhead sharks tagged within Biscayne Bay did not avoid urbanized areas, nor did they increase their use of urban sites during periods of lower human activity, nor did they differ with respect to their relative dietary specialization, as predicted *a priori* based on studies of terrestrial urban carnivores. We also detected increased residency not explained by our model, which mostly occurred in urban areas. We speculate that this increased presence of sharks may be driven by shore-based inputs that increase foraging opportunities. Taken together, the sharks tracked here exhibited behaviors consistent with urban adapters, which differ from typical urban avoidance behaviors exhibited by terrestrial carnivores. The reason behind the differing behavioral responses towards urbanization exhibited by marine versus terrestrial carnivores remains unknown, but we hypothesize it could relate to fundamental differences in how urbanization impacts land versus ocean landscapes, specifically with respect to habitat fragmentation. We suggest that this difference be considered in future urban ecology research as wildlife becomes increasingly challenged by a rapidly changing world in the Anthropocene.

Acknowledgements. We are thankful to the University of Miami's Shark Research and Conservation Program team members who assisted in data collection. We are also thankful for the Reviewer and Editorial comments that helped strengthen the manuscript. This research was made possible through support from the Ocean Tracking Network, the Disney Conservation Fund, the Save Our Seas Foundation, the National Oceanic and Atmospheric Administration (NOAA) Southeast Fisheries Science Center, the Batchelor Foundation, the Herbert W. Hoover Foundation, Ruta Maya Coffee, the International Seakeepers Society, and through a grant 'Implementing a Marine Biodiversity Observation Network (MBON) in South Florida to Advance Ecosystem-Based Management' funded under the National Oceanographic Partnership Program (NOPP, RFP ONR BAA #N00014-18-S-B007, in partnership with NOAA, BOEM, and NASA) and the US Integrated Ocean Observing System (IOOS) Program Office. Research was conducted under permits from the National Marine Fisheries Service Highly Migratory Species Division, Florida Fish and Wildlife, Biscayne National Park, and the University of Miami Institutional Animal Care and Use Committee.

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*Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA*

Reviewed by: B. de Sousa Rangel and 1 anonymous referee

Submitted: February 4, 2022

Accepted: May 19, 2022

Proofs received from author(s): June 12, 2022