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High residency of a Critically Endangered hammerhead shark to a small area: implications for marine protected area management and design

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ABSTRACT: Hammerhead sharks are among the most iconic and threatened shark species. Research has focused on the large hammerhead species, with relatively little work conducted on their smaller-bodied relatives, which face many of the same threats. One such species, the scalloped bonnethead *Sphyrna corona*, is assessed as Critically Endangered by the IUCN Red List; however, there is no knowledge about its movements, which can compromise management and conservation efforts. Here, we used acoustic telemetry to describe the spatiotemporal movements of scalloped bonnetheads inside a national park's marine protected area along the Colombian Pacific coast, where this species still occurs in high numbers. The movements of 25 adult sharks were monitored over a 1.4 km^2 area for up to ~10 mo between 2022 and 2023. Scalloped bonnetheads exhibited high residency to the area (RI_{max} = 0.78 ± 0.18, RI_{min} = 0.59 ± 0.32, ±SD), with most sharks present during the majority of their monitoring period. Shark movements were influenced by tides and diel period, and the space sharks used was generally small (mean 50% utilization distribution: 0.3 ± 0.2 km^2), with most of their movements detected by 2 (out of 5) receivers separated by less than 2 km. These results indicate that scalloped bonnetheads spend a large amount of time in a small area, suggesting that even a spatially limited no-take zone in the National Natural Park is likely to benefit the conservation of this species. This study provides the first insights into the movement behavior of the scalloped bonnethead, with important information for its protection and management.

KEY WORDS: Spatial ecology · Acoustic telemetry · Residency · Movement ecology

1. INTRODUCTION

Chondrichthyans (i.e. sharks, rays, and chimeras) are the second-most threatened vertebrate class as assessed by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Dulvy et al. 2021). Mitigating anthropogenic threats, such as overfishing and habitat loss, is necessary for the protection and restoration of shark populations (MacNeil et al. 2020). One common conservation tool is the creation of marine protected areas (MPAs); however, their effectiveness is directly dependent on their size, location, enforcement, buy-in from local communities, and management based on the use of biological data of the species targeted for protection (Roberts 2000, Gill et al. 2017, Handley et al. 2020). Studying movement patterns can provide valuable information about home range size, habitat use, and

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seasonal changes in movement that can be used to determine management plans for species vulnerable to fishing (Espinoza et al. 2015a, Allen & Singh 2016, Lea et al. 2016, Speed et al. 2016). Species that have restricted movements or that spend a significant amount of their life cycle in a restricted area can benefit greatly from even spatially limited protection (Kramer & Chapman 1999). Wide-ranging species, however, may spend minimal amounts of time within a spatially restricted MPA and therefore receive limited protection (Dwyer et al. 2020). Information about the spatial ecology of a target species thus allows planners to determine the minimum MPA size that maximizes its protection (Dwyer et al. 2020, van Zinnicq Bergmann et al. 2022), or whether time–area closures are a better management strategy than permanent, limited-boundary MPAs (van Zinnicq Bergmann et al. 2022). However, habitat use and residency within an MPA (and hence risk to fishing) will also vary temporally (e.g. on seasonal, diel, or tidal scales). Therefore, effective MPA design and management requires knowledge of species movements over multiple time scales.

The biological and ecological traits of hammerhead sharks, combined with their high vulnerability to overexploitation by targeted fisheries and incidental capture from industrial and artisanal fisheries, has led to sharp population declines across their entire lineage (Gallagher et al. 2014, Dulvy et al. 2021). The species at the greatest risk, and therefore in most need of conservation and management plans, are those found in shallow tropical and subtropical coastal waters because of the high levels of anthropogenic stressors in these environments and the generally low capacity and ability to enforce and create management policies in tropical underdeveloped countries (Halpern et al. 2008, Momigliano & Harcourt 2014, Booth et al. 2019, Dulvy et al. 2021).

In an effort to protect these sharks, large-bodied hammerhead species have been the subject of multiple movement studies (e.g. Wells et al. 2018, Logan et al. 2020, Guttridge et al. 2022). In contrast, the spatial ecology of their smaller-bodied counterparts (i.e. winghead shark *Eusphyra blochii*, scalloped bonnethead *Sphyrna corona*, scoophead *S. media*, and smalleye hammerhead *S. tudes*) are less studied, even though their vulnerability is as high as most of the large-bodied hammerheads (Brennan 2020). One of the least studied hammerheads is the scalloped bonnethead *S. corona*, a gold-colored species endemic to the Eastern Tropical Pacific from the Gulf of California to Perú (Ebert et al. 2021). This species is the smallest of the 9 recognized hammerhead species (maximum total length [TL] of 92 cm), with both sexes reaching sexual maturity at ~57 cm TL (Orozco Guarín 2014). Scalloped bonnetheads are thought to use mangrove forests as nurseries, a habitat that covers more than 1000 km^2 of their distribution, although almost 1 km^2 of mangrove habitat is lost each year in some areas to agriculture, aquaculture, or coastal development (Lacerda et al. 2002, López-Angarita et al. 2018). In addition, there is intense fishing pressure throughout the scalloped bonnethead's range, resulting in bycatch in commercial and artisanal longline, gillnet, and trawl fisheries (Mejía-Falla & Navia 2017). As a result, there have been sharp declines in scalloped bonnethead populations over the last 2 decades, including their possible extirpation in Mexico and the Gulf of California (Pérez-Jiménez 2014, Saldaña-Ruiz et al. 2017). These population declines and range contractions of the scalloped bonnethead have led to their current assessment on the IUCN Red List as Critically Endangered (Pollom et al. 2020). To date, the only known area where this species is still captured frequently by artisanal fishers is the southern region of the Colombian Pacific coast (Orozco Guarín 2014, Pollom et al. 2020).

The Colombian Pacific coast is heavily fished by small-scale fisheries (Castellanos-Galindo & Zapata Padilla 2019), and about 7% of the coast is protected, with only 3 national parks in the region. One of these, Uramba Bahía Málaga National Natural Park, is an area where scalloped bonnetheads are still frequently caught by fishers (Galindo et al. 2021). However, artisanal longline and gillnet fisheries are still allowed in the park due to cultural and socioeconomic reasons, management plans are not implemented, and park enforcement is lacking. This park was created by the local communities in conjunction with the national government, with Resolution 1501 of the Colombian Ministry of Environment (2010) stating that local communities have the right to decide about the use, administration, and conservation of areas of traditional and subsistence activities. However, disagreements exist around the sustainable use of land and natural resources between local stakeholders.

Given the high fishing pressure on the scalloped bonnethead and its current conservation status, our goal was to study their movement patterns in the Uramba Bahía Málaga National Natural Park, Colombia, in order to assess (1) the level of scalloped bonnethead residency to this coastal area of the Colombian Pacific coast, (2) the influence of tides and time of day on their movements, and (3) the degree of protection that a no-take zone could provide in this location by estimating the space used by individual sharks.

2. MATERIALS AND METHODS

2.1. Study site

The study was carried out in the Uramba Bahía Málaga National Natural Park (Fig. 1), a 470 km^2 area established on the Colombian Pacific coast in 2010. The park is a biodiversity hotspot (Myers et al. 2000), featuring the highest above-ground mangrove forest biomass of any region outside the Coral Triangle (Hutchinson et al. 2014, Castellanos-Galindo & Krumme 2015). The park encompasses Malaga Bay, which receives relatively low freshwater input, and is bordered to the north by the San Juan River, the most extensive delta system on the Pacific coast of South America (800 km^2). This river has the largest water volume discharge (81.86 km^3 yr^{-1}) and sediment load (1.6 × 10^7 t yr^{-1}) of all the rivers on the western coast of South America (Restrepo et al. 2002), with peak discharge in October. Water salinity (1–30 ppt) and water temperature (26–29.7°C) vary throughout the day and year, with overall lowest salinities and temperatures occurring during the rainy season (April–November; Betancourt Portela et al. 2011). Due to sediments deposited by the San Juan River, the bottom substrate along the coast consists mainly of muddy sand, with some rocky areas further from the river mouth (Restrepo & Kjerfve 2002). The area is characterized by a semidiurnal tidal cycle with a tidal range of up to ~3.7 m (Restrepo et al. 2002).

2.2. Sampling and tagging

Scalloped bonnetheads were captured using handlines with 4/0 circle hooks baited with anchovy *Anchovia macrolepidota*. Hooked sharks were brought on board the vessel and placed in a large plastic container containing seawater. Individuals were measured to the nearest centimeter (TL), sexed, and tagged with

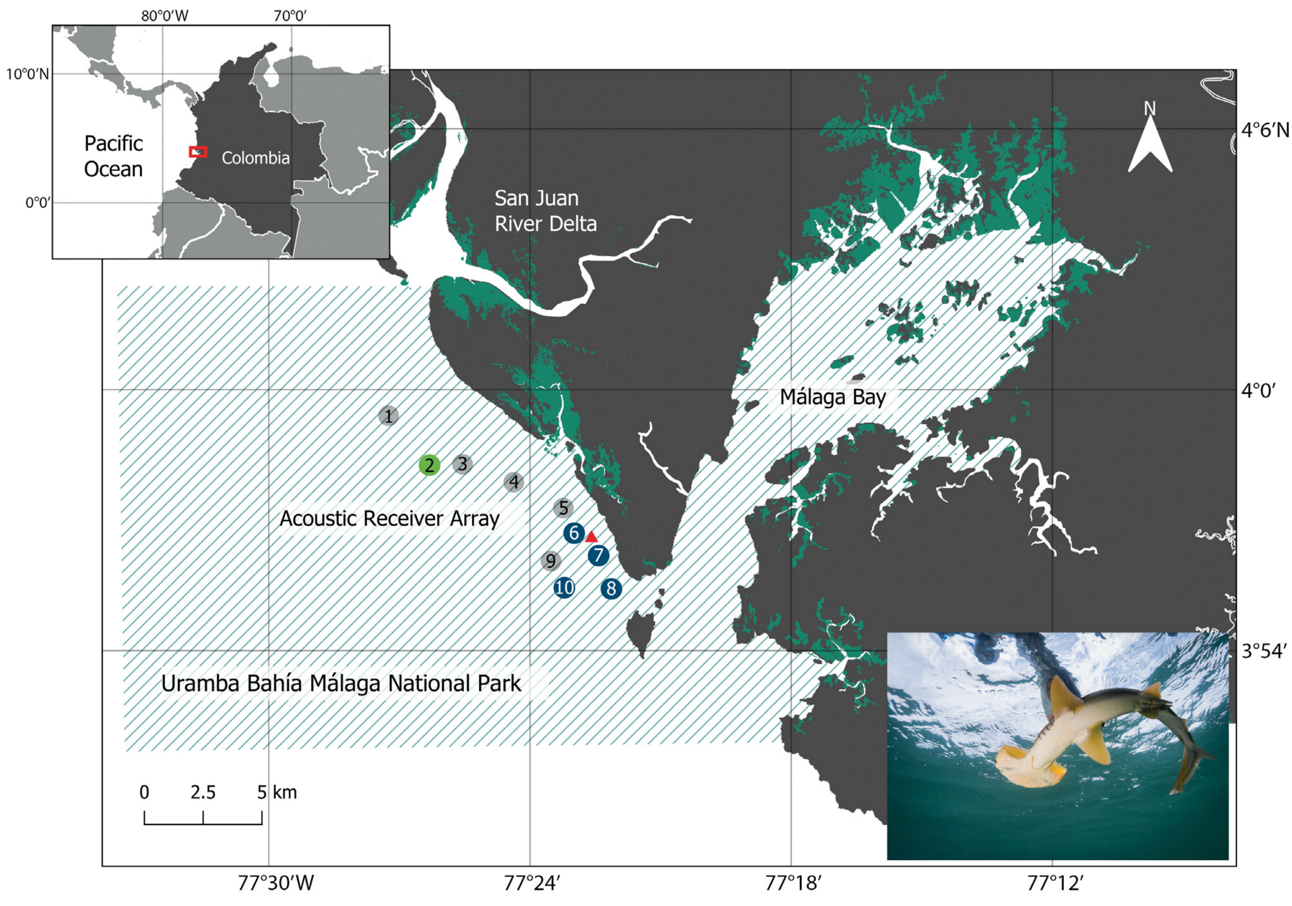

Fig. 1. Study area in Uramba Bahía Málaga National Natural Park (hatched area), Colombia, and its location on the Colombian Pacific Coast (inset map). Mangrove forests are shown in green. All receivers were deployed from 29–30 August 2023. Gray circles: initial receiver array, with numbers indicating receiver number; blue circles: final receivers; green circle: the receiver that was only deployed for ~3 mo. Red triangle: approximate location where sharks were captured

a conventional spaghetti tag in the musculature at the base of the first dorsal fin for external identification. To track their movements, acoustic transmitters (Innovasea V13-1H; 13 × 36 mm, 69 kHz, 120 s nominal delay, battery life: ~1 yr) were surgically implanted into 27 sharks. Sharks were placed in tonic immobility and the acoustic transmitters were inserted into the body cavity via a 3–4 cm incision on the ventral surface of the sharks (Heupel & Hueter 2001). The wound was closed using 2 separate dissolvable surgical sutures and sharks were released. The total handling time was approximately 5 min. All sharks were tagged in an area identified by local fishermen as having high scalloped bonnethead abundance (see Fig. 1).

2.3. Acoustic monitoring array

Shark movements were measured using a fixed array of 10 single-channel (69 kHz) acoustic receivers (Innovasea VR2W) deployed in the study area (Fig. 1). To maximize coverage of the coastal area, receivers were placed in a linear arrangement along the coast. To increase coverage in the vicinity of our capture sites, the 5 southernmost receivers (6, 7, 8, 9, and 10) were deployed in 2 lines parallel to shore. This area mainly consists of muddy flats with a depth range of 6–8 m during low tide. Receivers were attached using rope to a cinder block pre-filled with cement and an 8.2 kg anchor. A sub-surface buoy was used to keep the receiver off the bottom. Range testing within the array indicated that receivers had a detection radius of 200–400 m (mean: 300 m), for a total of 1.4 km^2 covered per receiver. Data from the receivers was downloaded every 4 mo during the study period (August 2022 to July 2023). Early in the study, 5 receivers (1, 3, 4, 5, and 9; Fig. 1) were lost before data could be downloaded, and one (Receiver 2) was taken by a fisherman and returned after being deployed for ~3 mo. To gather information about shark presence within the area where receivers were lost, we conducted 10 boat acoustic transects throughout the study area, including the area where receivers were recovered. The transects were conducted by drifting with the current/wind for 1 km or for 1 h, whichever occurred first. The transects included 8 additional sharks tagged in July 2023. To detect the tagged sharks, an acoustic receiver was suspended off the boat at a depth of 3 m with a weight to keep it vertical in the water column. Two transects per day were conducted over 1 wk in July 2023. The transects were not included in the analysis and were used for discussion purposes only.

2.4. Data analysis

Detection data were filtered to remove possible false detections based on the short interval criteria (Pincock 2012); detections from an individual that were separated in time by more than 1 h were omitted (as suggested for tags with 120 s nominal delay). Additionally, individuals detected for less than 10 d total (n = 2) were removed from further analysis. All statistical and movement analyses were carried out using R software v.4.1.2 (R Core Team 2021).

2.4.1. Temporal analysis

For overall residency, maximum and minimum residency indices were calculated for each shark. The maximum residency index (RI_{max}) is the total number of days a shark was present divided by the number of days from tag deployment to the last day detected. The minimum residency index (RI_{min}) is the total number of days a shark was detected divided by the total number of days monitored (i.e. from tag deployment to the end of the study: 8 July 2023; Appert et al. 2023). Residency values for both indices range from 0–1, with values closer to 1 indicating high residency, and values close to 0 indicating low residency. Sharks were considered to be present on a day when at least 2 detections were recorded on any receiver. Using the R package 'mgcv' v.1.8-34 (Wood 2011), the effect of size, sex, and the interaction of sex and size on residency were examined using a generalized linear model with a quasi-binomial distribution and a logit link to fit the over-dispersed proportional data.

To investigate temporal patterns in residency, we calculated a residency index for each month by adding the number of days a shark was detected and dividing it by the number of days monitored per month. Only complete months for each shark were used in the analysis, e.g. months where each shark was at liberty for its whole duration. In order to investigate if residency changed monthly, with size, or with sex, we used a 1-inflated beta regression mixed model from the 'GAMLSS' package v.5.4-22 (Stasinopoulos & Rigby 2007, Douma & Weedon 2019). Beta regression was used due to the proportional nature of the response (monthly residency for each shark that ranged from 0–1; Schmid et al. 2013). To account for the repeated measures nature of the data, shark ID was treated as a random factor in the model. Additionally, the data were 1-inflated, so a beta 1-inflated distribution with a logit link was used.

To study the sharks' temporal patterns in more detail, we used hourly data obtained from the receivers. However, receiver detection ranges are strongly influenced by external factors such as current speeds, wind speed, and biological noise (Heupel et al. 2006a, Simpfendorfer et al. 2008); therefore, the use of the number of detections to detect rhythmic patterns may be biased (Payne et al. 2010, Goossens et al. 2022). Thus, detection data were transformed into presence data expressed as the proportion of time per hour individuals spent within the detection radius of a receiver. Presence was calculated by summing together the time between detections that were <10 min apart. The 10 min cutoff was selected based on the assumption that if a shark has not been detected within 10 min, it is likely outside the detection area of the receiver. To assess the proportion of time the sharks spent in the area, and how much of that time sharks would be protected if a small no-take zone around the most used receiver areas were in place, the total amount of time spent within the array's detectable area was calculated by dividing the total number of minutes present by the time at liberty (i.e. from first to last detection of each shark) for each day per shark. The percentage of detection gaps lasting <10 min across the array was also calculated for each individual.

We identified cyclic patterns in shark presence data using fast Fourier transformations (FFTs) with Hamming window smoothing using the 'signal' R package v.1.8-0 (Signal Developers 2023). The FFT decomposes time-series data from the receivers into frequencies to identify dominant patterns. For each individual, the receiver with the most detections was selected. FFT analysis was performed for each shark individually and for all animals combined (Meyer et al. 2010).

To examine whether shark presence within the array was affected by environmental variables, we used generalized additive mixed models. For this analysis, only the data from Receivers 6 and 7 were used, as they comprised 98.5% of the data. Hourly proportion of time spent around each receiver was modeled as a function of time of day, tidal height, tidal coefficient, lunar illumination, month, sex, and size, with individual included as a random effect. To account for temporal autocorrelation, we added a first-order correlation structure with time bins as a covariate (corAR1 function). The tidal coefficient ranged from 20 to 120 and is a measure of the gravitational influence of the moon and the sun on tides, with higher values indicating stronger tidal forces and more pronounced tidal variations; tidal coefficients were obtained from local tidal charts and can be used as a proxy of tidal current strength (i.e. spring tides lead to greater tidal current velocities than neap tides; Lessa 2000). Lunar illumination was defined in terms of illumination percentages, with 0% corresponding to a new moon and 100% to a full moon. Hourly tidal height for the study area was obtained from an OTT RLS® tidal gauge at geographic position 3° 54' 54.5" N and 77° 21' 32.4" W, belonging to the Colombian General Maritime Directorate (DIMAR). The models were fitted using the beta distribution inflated at 0 and 1 with a logit link in the 'GAMLSS' package in R (Stasinopoulos & Rigby 2007). For model selection, we used forward and backward stepwise elimination using the 'stepGAIC' function in the 'GAMLSS' package (Stasinopoulos et al. 2017). Correlations between variables were assessed using Kendall's rank correlation coefficient prior to their inclusion in the model. Covariates with correlations of >0.5 were not included in the same model.

2.4.2. Spatial analysis

To assess the benefits of a small no-take zone, we calculated the space use of each shark. Using the 'VTrack' package in R (Campbell et al. 2012), the center of activity location of each shark was calculated every 60 min with a mean position algorithm (Simpfendorfer et al. 2002). Space use (50 and 95% utilization distributions [UDs]) was calculated using a Brownian bridge movement model based on the centers of activity (Horne et al. 2007).

3. RESULTS

In total, 22 female and 5 male scalloped bonnetheads (60–96 cm TL) were tagged with acoustic transmitters between 31 August 2022 and 5 April 2023 (Table 1). All captured males were considered sexually mature as determined by the presence of calcified claspers. Although all females were larger than the generally considered size at first maturity (i.e. 57 cm; Orozco Guarín 2014), 3 of the females were <62 cm, a size at which some females have been shown to still be immature (Orozco Guarín 2014). Two of the tagged sharks (ID 2 [male] and ID 14 [female]), were only detected for 6 and 7 consecutive days after tagging, respectively, and then never detected again, so they were not included in any further analyses. One individual (ID 4) was recaptured 303 d later in the same location at which it was originally tagged.

The 5 recovered receivers recorded 419 723 detections from the tagged sharks, although deployment duration and the number of sharks detected varied

Table 1. Overview of the data for tagged scalloped bonnetheads in the Uramba Bahía Málaga National Park, Colombia. Sex, total length (TL, cm), tag deployment, last detection dates, total number of detections, percentage of detection gaps that lasted less than 10 min, and maximum and minimum residency indices per shark are shown. Fast Fourier transformation (FFT) peaks are shown in days for sharks with more than 2000 detections. RI_{max}: total number of days present / total number of days at liberty; RI_{min}: total number of days present / total number of days monitored. —: analysis not carried out due to short period of time present

Shark ID	Sex	TL	Deployment	Last detection	Total detections	% Detection gap >10 min	Days present	RI_{max}	RI_{min}	FFT peaks (d)
1	F	69.0	31-Aug-22	08-Jul-23	50987	93.2	294	0.94	0.94	13, 25
2	M	61	31-Aug-22	06-Sep-22	1141	—	7	—	—	—
3	F	96.5	01-Sep-22	30-Jan-23	13041	95.2	72	0.47	0.23	6
4	F	60.0	02-Sep-22	08-Jul-23	46735	93.6	269	0.87	0.87	13, 25
5	F	66.0	02-Sep-22	08-Jul-23	19176	91.4	201	0.65	0.65	13
6	F	83.5	02-Sep-22	24-Oct-22	5994	95.1	43	0.81	0.14	4
7	F	69.0	03-Sep-22	10-Jan-23	22145	96.5	113	0.87	0.37	5, 10
8	F	61.0	09-Jan-23	08-Jul-23	6724	89.6	80	0.44	0.44	7.5
9	F	71	10-Jan-23	08-Jul-23	19834	91.7	135	0.75	0.75	7, 15
10	F	73	10-Jan-23	26-Jan-23	2152	93.1	15	0.88	0.08	No peaks
11	F	83	10-Jan-23	26-Jan-23	1607	92.4	14	0.82	0.08	No peaks
12	F	78.5	12-Jan-23	31-May-23	19088	90.7	112	0.80	0.63	6, 11, 17, 29
13	F	68	13-Jan-23	07-Jul-23	11539	92.4	103	0.59	0.58	7, 15
14	F	62	14-Jan-23	19-Jan-23	641	—	6	—	—	—
15	F	61	15-Jan-23	08-Jul-23	25044	93.7	127	0.73	0.73	7
16	M	65	15-Jan-23	09-Jul-23	28443	91.5	175	0.99	0.99	7, 14
17	M	72	17-Jan-23	09-Jul-23	24696	90.7	170	0.98	0.98	7, 14, 29
18	M	65	17-Jan-23	07-Jul-23	18013	89.8	163	0.95	0.94	No peaks
19	M	61	17-Jan-23	08-Jul-23	34499	92.3	161	0.93	0.93	7, 14, 21
20	F	89	02-Apr-23	26-Jun-23	7259	92.9	41	0.48	0.42	13
21	F	81	02-Apr-23	08-Jul-23	5926	91.9	43	0.44	0.44	No peaks
22	F	87	03-Apr-23	08-Jul-23	7410	92.6	71	0.73	0.73	7, 14
23	F	96	04-Apr-23	07-Jul-23	7050	92.3	65	0.68	0.68	7, 14
24	F	75	05-Apr-23	08-Jul-23	4246	90.7	69	0.73	0.73	7, 14
25	F	65	05-Apr-23	07-Jul-23	14584	92.7	82	0.87	0.86	7
26	F	73	05-Apr-23	08-Jul-23	14607	92.1	93	0.98	0.98	7, 14
27	F	66	05-Apr-23	07-Jul-23	8905	91.5	75	0.80	0.79	No peaks

Table 2. Information on receiver array used to detect tagged scalloped bonnetheads

Receiver	Depth at low tide (m)	Deployment date	Retrieval date	Duration (d)	No. of detections (% of total)	Detections per day (±SD)	Individual sharks detected
2	13.7	30-Aug-22	05-Dec-22	98	126 (0.03%)	14 (7)	2
6	7.1	29-Aug-22	08-Jul-23	310	255275 (60.8%)	818 (592)	25
7	5.3	29-Aug-22	08-Jul-23	310	158141 (37.7%)	517 (487)	25
8	13.1	29-Aug-22	05-Apr-23	220	892 (0.2%)	22 (26)	10
10	9.5	29-Aug-22	08-Jul-23	310	5289 (1.3%)	60 (52)	12

among receivers (Table 2). Receivers 6 and 7 recorded the greatest number of detections (~260 000 and ~160 000, respectively) and the highest number of detections per day (~820 and ~520, respectively). These 2 receivers accounted for 99% of the total number of detections in the array and were the only 2 receivers that detected all tagged sharks. Receiver 2, which was entangled in a fisherman's net and returned, provided 98 d of data, had the lowest total number of detections, and recorded the presence of 2 sharks. By the time Receiver 2 was removed from the array, Receivers 6 and 7 each had twice as many detections as Receiver 2 and had detected all sharks tagged. Receivers 8 and 10 accounted for ~1% of the detections combined and recorded the presence of 10 and 12 sharks, respectively.

The drifting receiver transects showed a pattern similar to the acoustic array data. Sharks were detected on 5 of the transects, all of them in the area around Receivers 4, 5, 6, and 7, with the highest number of detected individuals (15) and the highest number of detections (48) in the area around Receivers 5 and 6. Only one shark was detected on the transects north of Receiver 4, and no sharks were detected in the northernmost area (Fig. 2).

Tagged sharks were detected on 14–294 d (mean ± SD: 111 ± 70 d) and total days at liberty (to last detection) ranged from 17 to 310 d (mean: 144 ± 80 d; Table 1, Fig. 3). During early 2023, 11 of the 12 sharks present in the array left within 8 d of each other (27 February–6 March). However, all sharks returned after a few weeks or a month, with most of the sharks returning no later than 24 March, and one returning in April. One of the sharks did not leave the array for long periods and was present almost every day of the monitoring period (Fig. 3).

Scalloped bonnetheads showed a high degree of residency to the small array area. RI_{max} ranged from 0.44 to 0.99, with a mean of 0.78 ± 0.18 and a median of 0.81, while RI_{min} ranged from 0.08 to 0.99, with a mean of 0.59 ± 0.32 and a median of 0.68 (Table 1). Size influenced both residency indices (p_{RImax} = 0.03, p_{RImin} = 0.0002), with residency values decreasing with increasing size (Fig. 4a,b). Sex also influenced both residency indices (p_{RImax} = 0.0008, p_{RImin} = 0.006), with males showing higher residency values than females (mean female RI_{max} = 0.74 ± 0.2; mean male RI_{max} = 0.97 ± 0.03; mean female RI_{min} = 0.58 ± 0.3, mean male RI_{min} = 0.96 ± 0.03; Fig. 4a,b). The interaction between sex and size did not affect residency. Even though residency varied across months, these changes were not significant (Fig. 4c). Sex and size also had no effect on monthly residency.

A total of 25 of the 27 tagged sharks had sufficient data (i.e. >2000 detections) for FFT analysis. Of these, 14 individuals showed peaks at ~7 and ~14 d, with peaks at 14 d having a higher spectral density (Table 1, Fig. 5). The FFT for all sharks combined showed one dominant peak at 13 d and a weak peak at 25 d (Fig. 5). The ~14 d period coincides with lunar illumination and tidal coefficient changes, with a full moon or new moon occurring every 14 d, and tidal coefficient increasing every 14 d.

Lunar illumination was correlated with both tidal coefficient and tidal height ($p < 0.001$); however, in both cases, the strength of the correlation was less than 0.5 (τ_b = 0.007 and 0.01, respectively). Therefore, all variables were kept in candidate models. Time spent

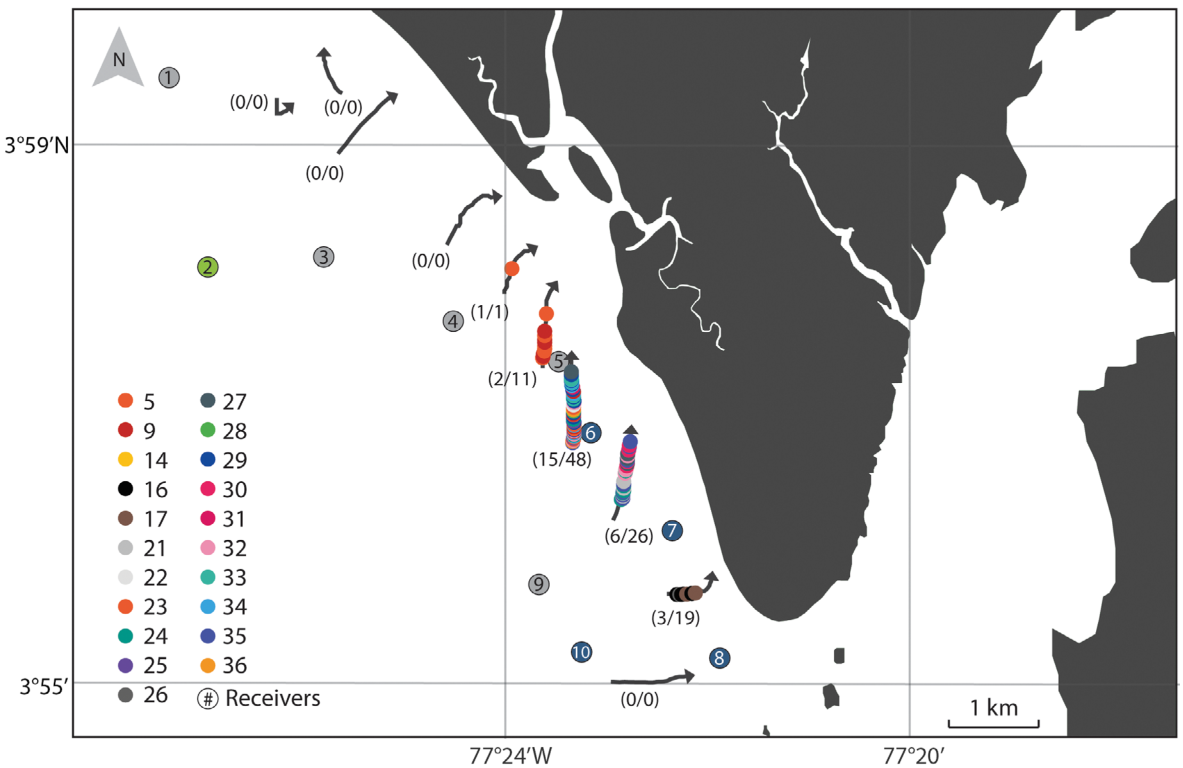

Fig. 2. Drifting acoustic receiver transects performed during 1 wk of July 2023. Arrows: length and direction of the surveys; numbers in parenthesis: number of scalloped bonnetheads detected / number of detections. Color-coded circles: detections of individual sharks; numbered circles: stationary receivers (dark blue: active receivers; green: receiver taken out by a fisherman; gray: receivers that were lost)

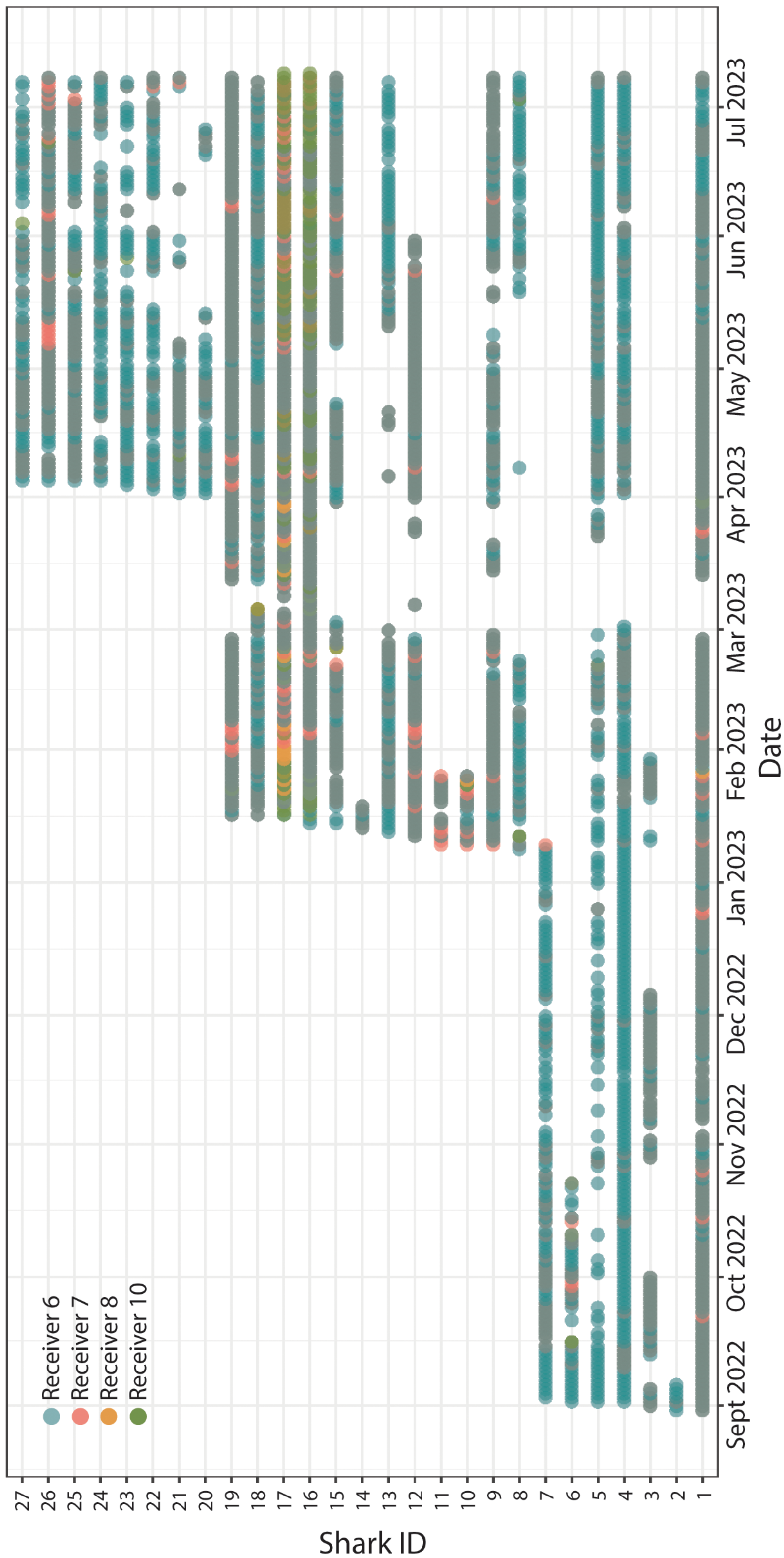

Fig. 3. Time-series plot of tagged scalloped bonnetheads monitored in Uramba Bahía Málaga National Park between September 2022 and July 2023. Three tagging trips were conducted. Overlap of Receiver 6 and Receiver 7 appears gray

around receivers was best predicted by month, tidal coefficient, and time of day with global smoothers, and time of day, tidal height, and lunar illumination with level-specific smoothers (e.g. a different pattern for each receiver) (Table S1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m743p047_supp.pdf). Sharks spent more time around Receiver 7 during the nighttime hours, but time spent around Receiver 6 did not change throughout the day (Fig. 6a). The time sharks spent in the area also changed by month, with a lower presence in March. During July–August, due to the small sample size at that time, the time spent in the area varied greatly by shark. Overall, the effect of month was generally not strong (Fig. 6b). Sharks showed a dramatic decline in the time spent in the area when the tidal coefficient was highest (Fig. 6c). The effect size of tidal height on the sharks' movements was small and the differences between receivers were minimal (Fig. 6d). For the whole area (e.g. Receivers 6 and 7), time of day had an effect on shark presence, with less time spent in the area in the morning hours and more time spent in the area at night (Fig. 6e). Similarly, lunar illumination was related to the time spent in the area (Fig. 6f); however, the difference in time spent between receivers was not large and the effect was weak.

The total amount of time each shark spent in the detectable area ranged from 6 to 35% of the time at liberty, with a mean of 19 ± 3%. Absence intervals between detections were generally short, with 92.4 ± 1.6% of all detection gaps lasting less than 10 min (Table 1, Fig. S2). Overall, 50% UDs ranged from 0.07 to 1.1 km^2 (mean: 0.3 ± 0.2 km^2), and 95% UDs ranged from 0.5 to 27 km^2 (mean: 3.7 ± 5.5 km^2), with most sharks using the same small area. Only 2 sharks (both females; 66 and 96 cm TLs) used Receiver 2, the northernmost recovered receiver, during the 3 mo it was deployed. Nine sharks occasionally used the southernmost areas; 8 females (61–

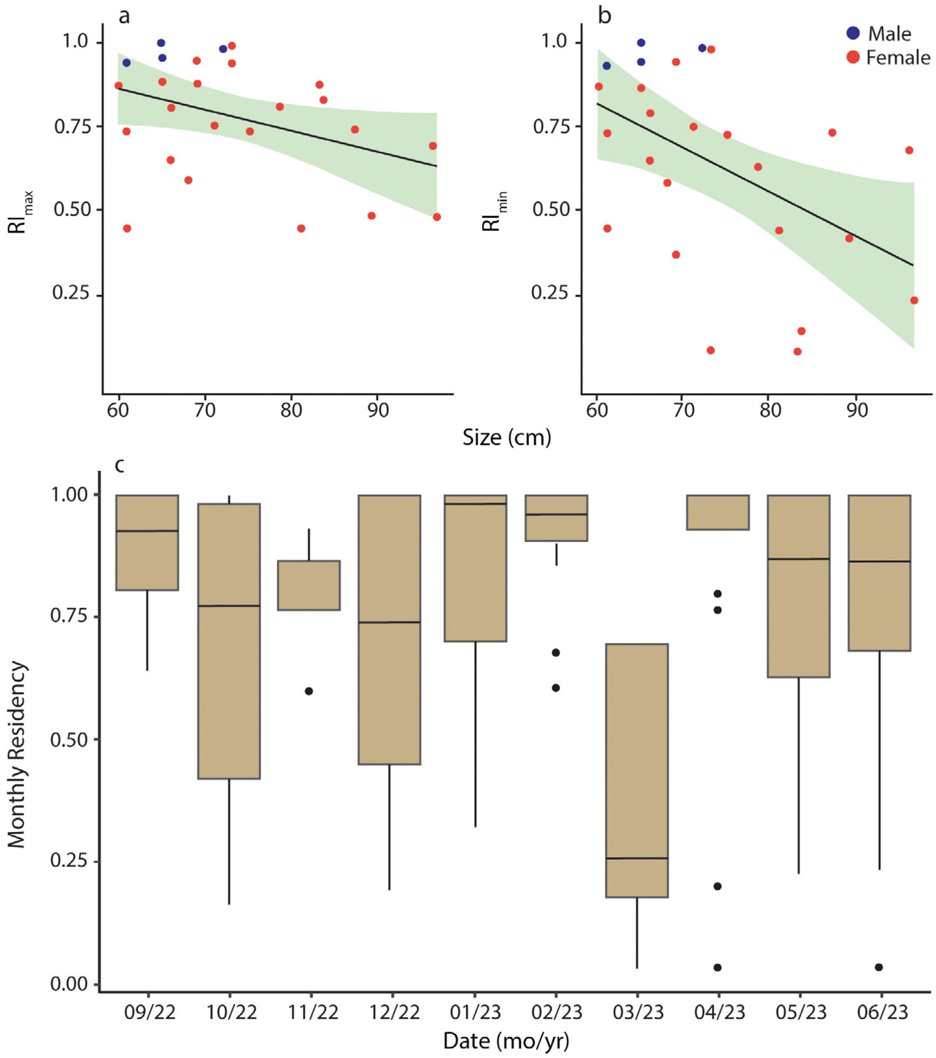

Fig. 4. Scalloped bonnethead residency indices and their relation to size, sex, and month. (a) Maximum residency index (RI_{max}) and (b) minimum residency index (RI_{min}) by size. Shaded areas: 95% CI. (c) Monthly residency, which did not differ between months. Horizontal line within each box: median value; box limits: inter-quartile range (i.e. 25 and 75% quantiles); whiskers (vertical lines): 1.5 times the inter-quartile range; dots: outliers

96 cm TL size range) and 2 males (65 and 72 cm TL). The remaining 14 sharks were only detected at 2 of the receivers during the whole monitored period (Fig. 7).

4. DISCUSSION

Tagged scalloped bonnetheads displayed high residency to a small area off the Colombian Pacific coast, moving along at least 3 km of coast. Most individuals were present for periods of weeks or months, with some present for most of their monitoring period (e.g. RI_{min} = 0.99). Residency indices of scalloped bonnetheads were higher than or comparable to values reported for other coastal shark species (Knip et al. 2012a, Munroe et al. 2014, Escalle et al. 2015). Although our estimates of residency and space use are underestimates due to our low acoustic receiver spatial coverage, we suggest that the actual residency times and space use of scalloped bonnetheads are likely small because of (1) the short periods of time when tagged sharks were absent from the detection range of our receivers, suggesting short-range movements, (2) the low duration between detections (>90% were less than 10 min), and (3) acoustic transect data indicating that no sharks were detected northward beyond the tagging location. These results suggest that even small MPAs or no-take zones may be sufficient to provide partial protection for this species.

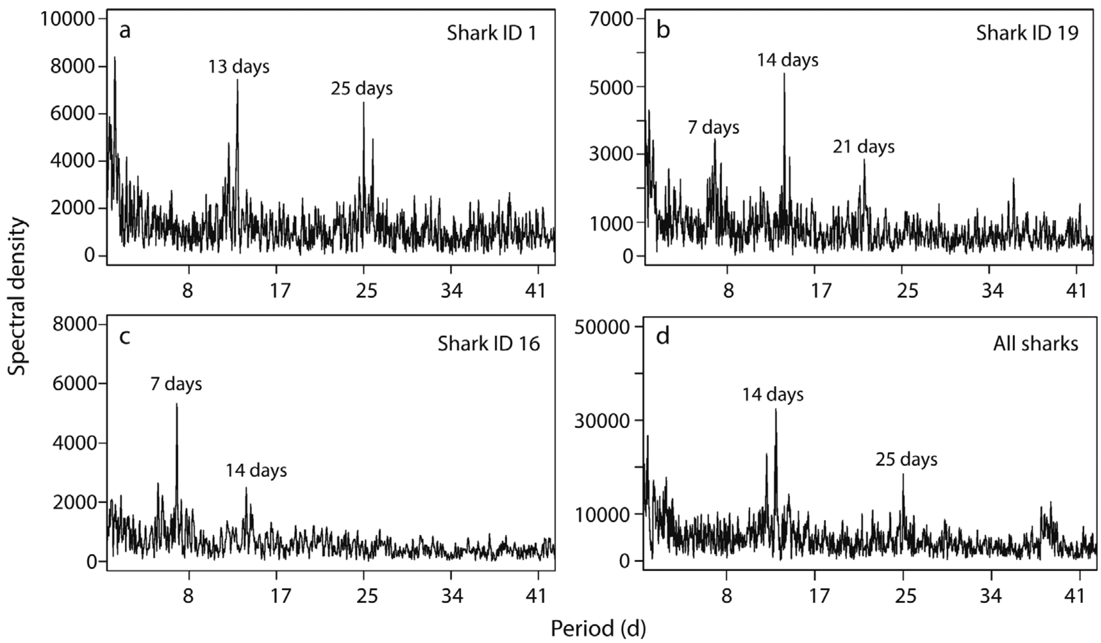

Fig. 5. Time-series spectral analysis for scalloped bonnetheads. Fast Fourier transformation of time detected per hour at acoustic receivers for (a,b,c) 3 sharks (IDs 1, 19, and 16) and (d) all sharks combined. Individual sharks were haphazardly chosen for illustration purposes, but all sharks showed similar patterns (see Table 2)

Sex and size influenced residency indices, with smaller females and all males displaying higher residency than larger females. Males have been shown to exhibit higher residency than females in Port Jackson sharks *Heterodontus portusjacksoni* (Bass et al. 2021), but this trend has not been found in other species (Espinoza et al. 2015b, Schlaff et al. 2020), including the scalloped bonnethead's sister species, the bonnethead shark *S. tiburo* (Heupel et al. 2006b). Interestingly, most of the sharks captured at our fishing spot were females, suggesting sexual segregation, a phenomenon well documented in coastal and reef-associated sharks (Klimley 1987, Knip et al. 2012b, Pillans et al. 2021). Differences between the sexes should be taken with caution however, due to our low sample size of males (n = 4).

The decrease in residency for larger individuals coupled with the small acoustic coverage suggests that these larger animals might move more and further than smaller individuals. The same pattern has been observed for bonnetheads, with hourly space use increasing with body size (Dawdy et al. 2022). This pattern can be driven by changes in metabolic requirements, diet preferences, or behavioral changes due to reduced predation risk or hunting capabilities, all of which vary when animals increase in size (Bethea et al. 2007, Lucifora et al. 2009, Newman et al. 2012).

During March, most tagged animals left the array for periods ranging from days to weeks, coinciding with a red tide event that occurred from late February to early April (authors' pers. obs.). The exact reasons why the sharks left the area at a time coinciding with the algal bloom remain unknown, but it may have been to avoid stressors such as toxins, lower dissolved oxygen, low habitat quality, or lack of prey due to mass mortalities (Landsberg 2002, Bornman et al. 2021, Vilas et al. 2023). Notably, after the red tide event passed, the sharks returned to the array and stayed in the area for the rest of the monitoring period, which suggests high site fidelity to this area, a likely key habitat for these sharks. This gap in shark presence is the reason March had an overall lower residency than other months and why this month had a significant effect on shark presence. Other than this event, shark presence did not strongly vary across different months.

Tidal coefficient is related to tidal amplitude, and higher values indicate stronger tidal currents (Krumme 2009). With increasing tidal coefficients, sharks may spend less time in the area, perhaps moving to regions where currents are weaker (McInturf et al. 2019). Time of day also affected the shark's movement, with sharks spending more time closer to shore during nighttime hours, and less time during morning hours. The fact that their presence remains the same throughout the day in the core area but time spent around the closer-to-shore area increases at night could suggest more movement and, thus, more activity at night.

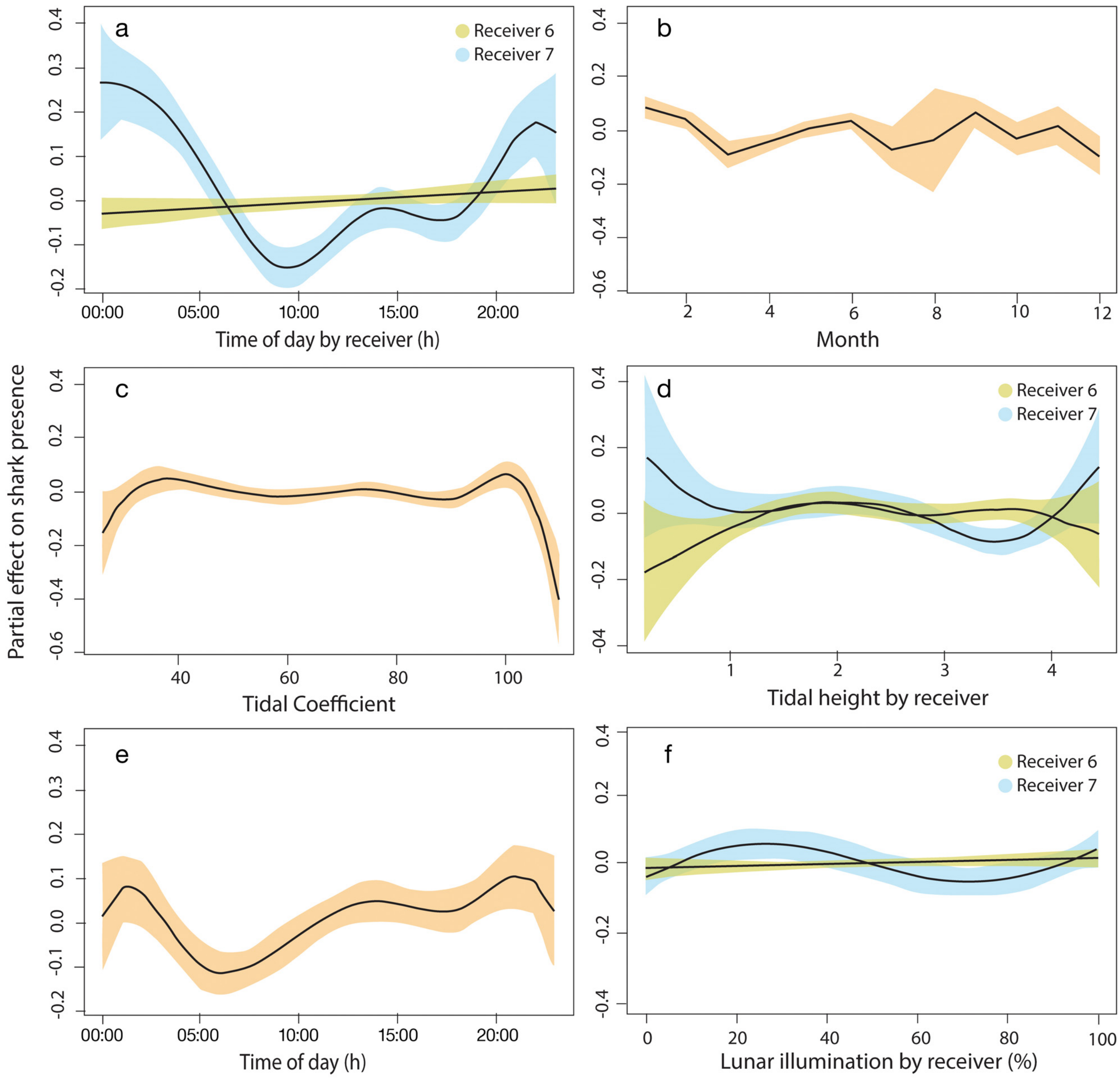

Fig. 6. Partial effect and non-linear relationships of (a) diel periods by receiver, (b) month, (c) tidal coefficient, (d) tidal height by receiver, (e) time of day, and (f) lunar illumination on scalloped bonnethead presence (time spent / hour) from the generalized additive mixed model. Shaded areas: 95% CI

Similarly, blacktip reef sharks *Carcharhinus melanopterus* move over a larger area at night but still include the same daytime areas (Papastamatiou et al. 2018a). These movements might be related to the nocturnal activity of crustaceans, scalloped bonnethead's main prey (Galindo et al. 2021), which inhabit the mud flats characteristic of our study site. Likewise, predator avoidance could also explain some of their movement closer to shore during nighttime hours (Meyer et al. 2009). The weak effects of tidal height contrast with observations of other species where tide plays a strong role in habitat use (Ackerman et al. 2000, Carlisle & Starr 2010, Lea et al. 2020). However, in those cases, movements were primarily driven by the opportunity to exploit newly available habitats at high tide, and in the case of our study area, tidal height does not dramatically change the available habitats. Moreover, bonnethead movements, the sister species of scalloped bonnetheads, are not affected by tides in Florida, although tidal currents there are much weaker than at our study site (Heupel et al. 2006b).

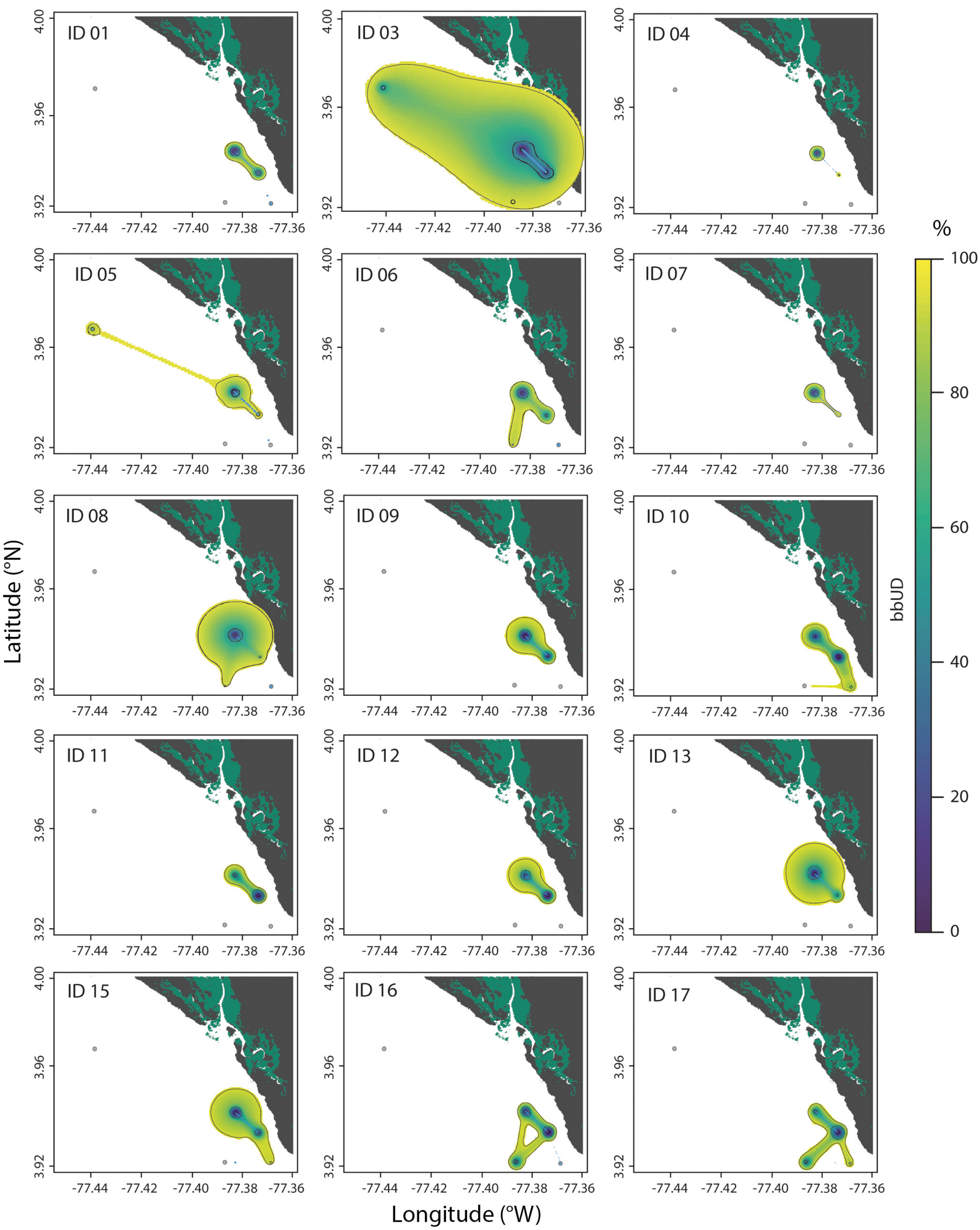

Fig. 7. (Above and following page.) Utilization distributions (UD) of scalloped bonnethead sharks from a Brownian bridge (bb) movement model. Gray dots: receiver locations

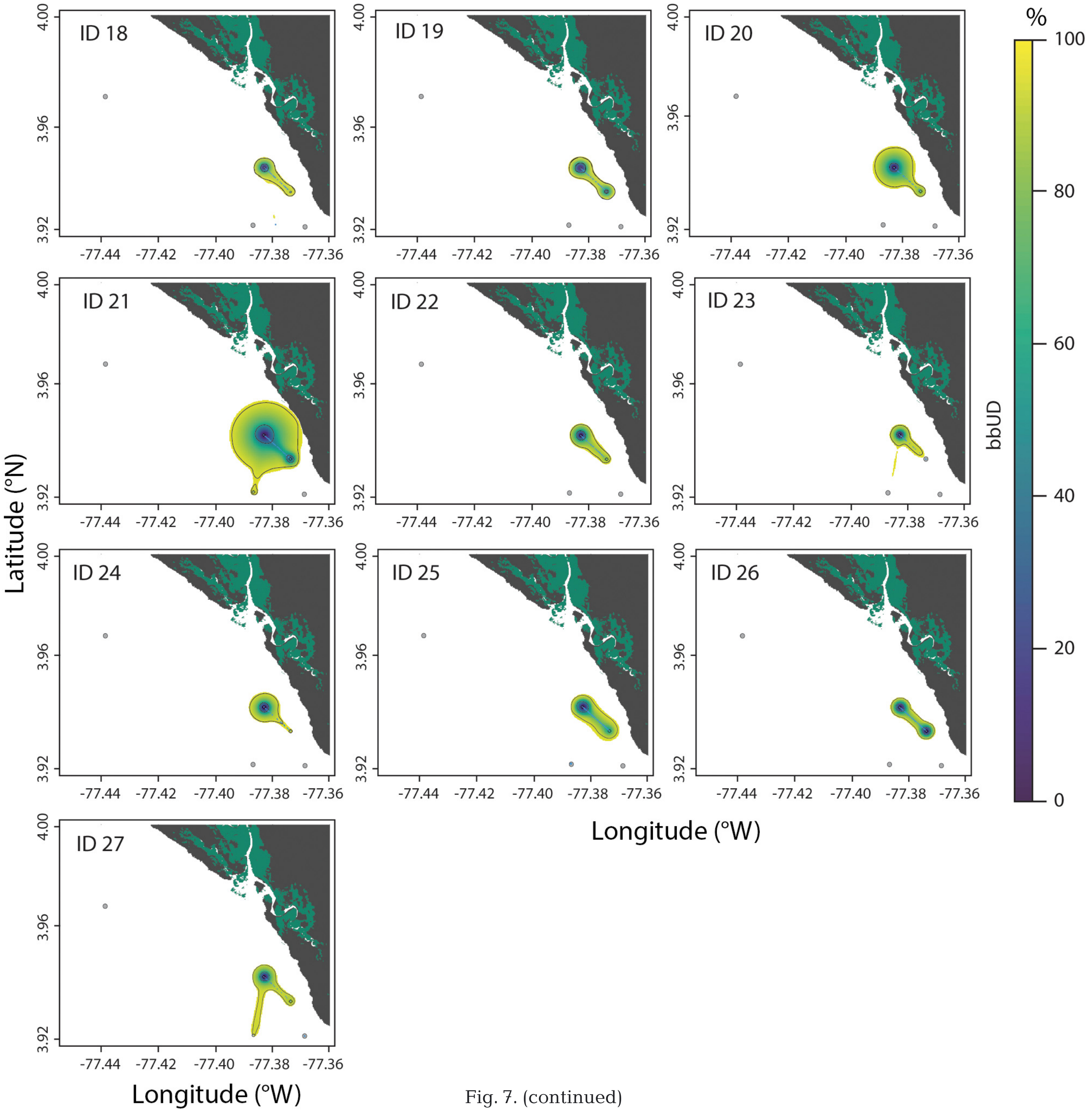

Fig. 7. (continued)

The spaces used were generally small and mostly limited to an area between 2 receivers, suggesting that sharks might obtain most of their resources from this small area. Our study site, known as a shrimp fishing ground for a trawling fishery, experiences concentrated fishing efforts predominantly in its northernmost region. The area surrounding the receivers, however, remains less frequented by local trawling and gillnet fisheries due to the perceived presence of a structure, thought to be a sunken boat, that could potentially damage their nets. Potential higher prey availability in this particular location due to lower fishing effort could also explain some of the scalloped bonnethead's preference to stay in the core area.

Given the limited movements observed here and that local fishers capture this shark species in other nearby coastal locations (M. A. Herrera & D. Cardeñosa pers. obs.) suggests that there are other subpopulations of scalloped bonnethead sharks along the coast. Scalloped bonnetheads may exhibit spatial partitioning, with different sub-groups using distinct small areas, as has been seen in other reef-associated shark species, and this separation may be driven by intraspecific competition and/or social associations (Barnett et al. 2012, Papastamatiou et al. 2018b).

The combination of small space use and high residency makes the scalloped bonnethead especially vulnerable and at high risk of local extirpation due to fishing pressure (Brook et al. 2008, Field et al. 2009). However, that same combination of traits makes a strong case for the establishment of an MPA surrounding their core use areas. MPA success strongly depends on the designation of no-take zones, enforcement, age, size, and isolation of the area (Edgar et al. 2014). In the case of our study site, the establishment of a small no-take zone inside the national park's MPA that is 3 km along the coastline and extending 2 km offshore could encompass a significant amount of the area used by this small coastal shark. Due to its vulnerability to localized fishing pressure, protecting the area from the occasional trawlers and periodical longline fishing could have great benefits for conservation (Yates et al. 2016, Rolim et al. 2019). We acknowledge that our estimates of space use are underestimates due to the small acoustic coverage, and we do not know the full extent of the scale of movements of our tagged sharks or their connectivity with adjacent sub-groups. However, our results suggest limited movements by tagged sharks beyond the detection range of our receivers, given that 92.4% of the detections occurred within 10 min of each other. This indicates that the proposed no-take zone could provide significant conservation benefits to this subgroup of sharks. Clearly, future research needs to be able to track individuals across a larger spatial area of the coastline and to tag individuals from other regions to investigate connectivity. Further research should also focus on (1) stock identification and potential male-mediated gene flow using molecular tools (Daly-Engel et al. 2012, Cardeñosa et al. 2014), (2) mark—recapture data within the boundaries of the proposed no-take zone to assess the number of individuals using this area (Petit & Valiere 2006), (3) fine-scale movements of tagged sharks in the proposed no-take zone to assess time spent within its boundaries (Shipley et al. 2018), and (4) application of environmental DNA tools to detect other possible core areas along the coastline of the Eastern Pacific (Takahara et al. 2012). The development of similar or larger no-take zones for this species within the boundaries of the national park and beyond requires identifying other core areas like the one presented here. Additionally, it requires the willingness of local communities to reach conservation agreements that consider the impact on fishing activities and livelihoods. The degree of effectiveness of the MPA will depend on how much time the sharks spend inside and outside of the no-take zone boundaries, the fishing practices management in other areas of the MPA, and compliance by local fishing communities. The compliance aspect is especially relevant throughout the distribution range of this Critically Endangered shark species. Despite being located within a national park, our study site is situated in one of the poorest regions in Colombia (Ortegón-León & León 2020), with many people depending on fishing for food and livelihood security. These aspects hamper policy-based strategies because compliance and enforcement are usually lacking or inefficient (Momigliano & Harcourt 2014, Booth et al. 2019). Therefore, the creation of an MPA or no-take zones in such areas must be accompanied by local-level bottom-up approaches that implement more feasible management actions and increase compliance within each community (Booth et al. 2019). Actions that could be taken in the area may include but are not limited to (1) promoting alternative economic opportunities for local communities around research and tourism, (2) offering incentives to encourage the adoption of more sustainable fishing practices and gear (e.g. hook and line; MacNeil et al. 2020), and (3) creating citizen-science-based programs to provide an alternative income source to communities and support scientific efforts.

The findings we present here have been shared with the local communities and, in a joint effort with them, the goal is to establish a no-take zone that safeguards the needs of the community and is under the management of local stakeholders. Fortunately, the core area used by sharks in this study, even though it is used by the locals occasionally, is not in the main fishing area, which has increased the support from the local community for establishing a no-take zone. However, the capture of scalloped bonnetheads in longline hauls in adjacent fishing areas suggests that other core areas might exist. The creation of potential no-take or strict management zones in these locations could be more challenging due to the higher frequency of fishing activities. Therefore, incorporating shark movement data with the interests of all local stakeholders is needed for an optimal MPA to be effective (van Zinnicq Bergmann et al. 2022).

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