Network analysis reveals multispecies spatial associations in the shark community of a Caribbean marine protected area

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ABSTRACT: Many shark species exhibit complex spatial ecology throughout their life histories, posing a challenge for conservation and management. Although most marine protected areas (MPAs) were originally established to protect less mobile organisms, protection of shark species from fishing and other impacts is possible if individuals exhibit high residency and site fidelity within the MPA boundaries. For this study, we used a fixed acoustic telemetry array to study the residency, habitat use, and interspecific space use among 4 shark species in Buck Island Reef National Monument (BIRNM), an MPA in St. Croix, US Virgin Islands. From June 2013 to May 2017, 11 nurse sharks *Ginglymostoma cirratum*, 6 lemon sharks *Negaprion brevirostris*, 13 Caribbean reef sharks *Carcharhinus perezi*, and 6 tiger sharks *Galeocerdo cuvier* were monitored in the array. Overall, residency was high for all species, with a mean residency index of 0.52 or higher for each species. Network analysis revealed complex inter- and intraspecific spatial associations among individuals. Community detection algorithms showed that *G. cirratum* and *N. brevirostris* frequently used the same areas in BIRNM, selecting for shallow sand and seagrass habitats near linear reefs, while *G. cuvier* and *C. perezi* had more individualized space use. *C. perezi* also exhibited ontogenetic shifts, developing individual territories and using deeper water with increasing body size. This work emphasizes the importance of MPA size, placement, and habitat composition when aiming to protect highly mobile species with potentially large home ranges and shifting space use throughout their life histories.

KEY WORDS: Elasmobranchs · Spatial ecology · Acoustic telemetry · Network analysis · Marine protected area

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1. INTRODUCTION

In ocean ecosystems, sharks occupy integral roles as highly mobile predators, connecting varied habitats and isolated regions through their movements (Papastamatiou et al. 2013, Ferreira et al. 2017). This is particularly true in coral reef ecosystems (Bond et al. 2018), where sharks exert predation pressure on populations at lower trophic levels (Bascompte et al. 2005) and act as important vectors of nutrient transport across reefs (Williams et al. 2018). Most shark species are *k*-selected, long-lived animals that mature late and produce relatively few offspring (Conrath & Musick 2012). In part because of their long

lifespans and changing biological needs, shark species can occupy several diverse habitats throughout their ontogeny (Grubbs 2010). In some cases, adults migrate between mating and pupping grounds, while juveniles can spend extensive periods in nursery areas (Chapman et al. 2015). Their long life spans, ontogenetic changes in habitat requirements, and the propensity to undergo long-distance movements render many shark populations particularly vulnerable to overfishing and habitat degradation (Dulvy et al. 2008, 2014). Therefore, understanding how these animals interact with their environment is critically important for improved conservation planning (Davidson & Dulvy 2017).

Over the last 2 decades, detailed information about the spatial ecology and migratory behavior of sharks has been collected using acoustic telemetry (Heupel et al. 2019). This technology facilitates the long-term tracking of individuals within a fixed array of receivers on a much finer scale than satellite telemetry and conventional tagging (Heupel et al. 2006). These data can then be used to quantify residency, site fidelity, and habitat selection (Kneebone et al. 2012, Espinoza et al. 2015), and to help define nursery areas (Heupel et al. 2004, Legare et al. 2015) and mating grounds (Whitney et al. 2010). To date, acoustic telemetry has been used to quantify residency and/or site fidelity in 31 shark species, including the 4 species in this study, during one or more stages of their ontogeny (Chapman et al. 2015). This information can be used for the conservation of these species through ecosystem-based management approaches (Heupel et al. 2019).

Acoustic telemetry is an effective tool for assessing the design, development, and efficacy of marine protected areas (MPAs; Knip et al. 2012, Lea et al. 2016). MPAs are a commonly used ecosystem-based management approach for conserving essential habitats (Rogers & Beets 2001) and protecting species aggregations (Carrier & Pratt 1998). However, for MPAs to be effective, a certain degree of residency or site fidelity must be exhibited by species within the MPA boundaries (Gruss et al. 2011, Chapman et al. 2015). MPAs fail when their boundaries are mismatched with species' spatial ecology and/or enforcement is lacking (Rouphael et al. 2015, Lea et al. 2016). Although MPAs in the Caribbean were traditionally established to protect sessile and more resident organisms, particularly corals and reef fish (Rogers & Beets 2001), they may also be effective for the conservation of sharks and other mobile species when the spatial ecology of those species overlaps with the boundaries of the MPA (Hyrenbach et al. 2000, Gruss et al. 2011, Ward-Paige 2017).

The development of statistical methods to analyze acoustic telemetry datasets has lagged behind the rapid rise in the use of this technology (Lédée et al. 2015, Becker et al. 2016). Traditional methods, including kernel utilization density and dynamic Brownian bridge movement models, have commonly been used to delineate core-use areas, but these methods can fail to identify ecologically important, yet less frequently used, movement corridors or feeding grounds, particularly in broad-scale arrays (Becker et al. 2016). It is essential to maintain these peripheral movements in analyses pertaining to MPAs because their loss through interpolation could result in missing boundary crossings. For instance, the use of a mating ground outside of an MPA may not fall within a 50 or 95 % density estimate because it is only visited for a small number of days over a long study period. The application of network analysis to spatial datasets can resolve this issue (Becker et al. 2016).

Network analysis is increasingly applied to acoustic telemetry data to quantify connections between tagged animals and acoustic receivers (reviewed by Jacoby & Freeman 2016). This methodology allows for the delineation of important movement corridors as well as core and general-use receivers within an array (Espinoza et al. 2015, Lédée et al. 2015, Becker et al. 2016). Network analysis can also be used to quantify spatiotemporal associations between individuals to better understand the social dynamics of populations and communities (Finn et al. 2014, Jacoby et al. 2016). Individuals can be grouped using community detection algorithms, and associations between these groups can be evaluated using node degree and Wilcoxon rank sum tests (Finn et al. 2014). These techniques make network analysis ideal for studying multiple species within an MPA, quantifying connectivity between regions, and identifying dynamic behaviors, such as territoriality, which may influence space use among conspecifics.

In this study, we applied network analysis to fixed-station acoustic telemetry data to examine the spatial relationships of 4 shark species: lemon *Negaprion brevirostris*, nurse *Ginglymostoma cirratum*, Caribbean reef *Carcharhinus perezi*, and tiger sharks *Galeocerdo cuvier*, within Buck Island Reef National Monument (BIRNM), an MPA in St. Croix, United States Virgin Islands (USVI), over a 4 yr period. Our goals were to quantify residency within the MPA, to explore spatial associations within and among species, and to identify important habitats for each species within the MPA. Ultimately, our objective was to better contextualize the role this MPA plays in the spatial ecology and conservation of regional shark

populations. Understanding the spatial extent to which each shark species uses this MPA is particularly important because the USVI appears to be one of the last strongholds for shark populations in the shark-depleted Caribbean (Ward-Paige et al. 2010). Despite this, information on shark spatial ecology, as well as population abundance, is severely lacking in this region (DeAngelis et al. 2008).

2. MATERIALS AND METHODS

2.1. Study area

BIRNM, located northeast of St. Croix in the USVI (17.7871° N, 64.6206° W), was established in 1961 to protect the extensive coral reef on the east end of the island (Pittman et al. 2008). BIRNM was one of the first MPAs designated in the USA, and originally encompassed 3.56 km^2 (Pittman et al. 2008, 2014a). In 2001, BIRNM was expanded to its current size of 77.0 km^2,

and it is currently a year-round no-take zone throughout its boundaries (Fig. 1; Pittman et al. 2014a). Immediately south and east of BIRNM lies the East End Marine Park (EEMP), a multi-use management zone whose goal is to promote sustainable use of the marine environment (The Nature Conservancy 2002). Portions of EEMP are no-take areas, while others are open to fishing or are restricted to recreational use (The Nature Conservancy 2002). Lang Bank, a coral reef system along St. Croix's continental shelf, extends east of BIRNM and EEMP. At its easternmost end, Lang Bank is closed seasonally to fishing for a red hind spawning aggregation (García-Sais et al. 2014).

BIRNM's marine environment is diverse, covering depths from 0–1800 m, with a range of benthic habitats including coral reefs, uncolonized hardbottoms, unconsolidated sediments, and seagrass beds (Pittman et al. 2014a). Buck Island, a small island 2 km across, lies at the center of BIRNM. Benthic habitats south and west of the island are largely dominated by sand and seagrass, while north and east is more complex habitat,
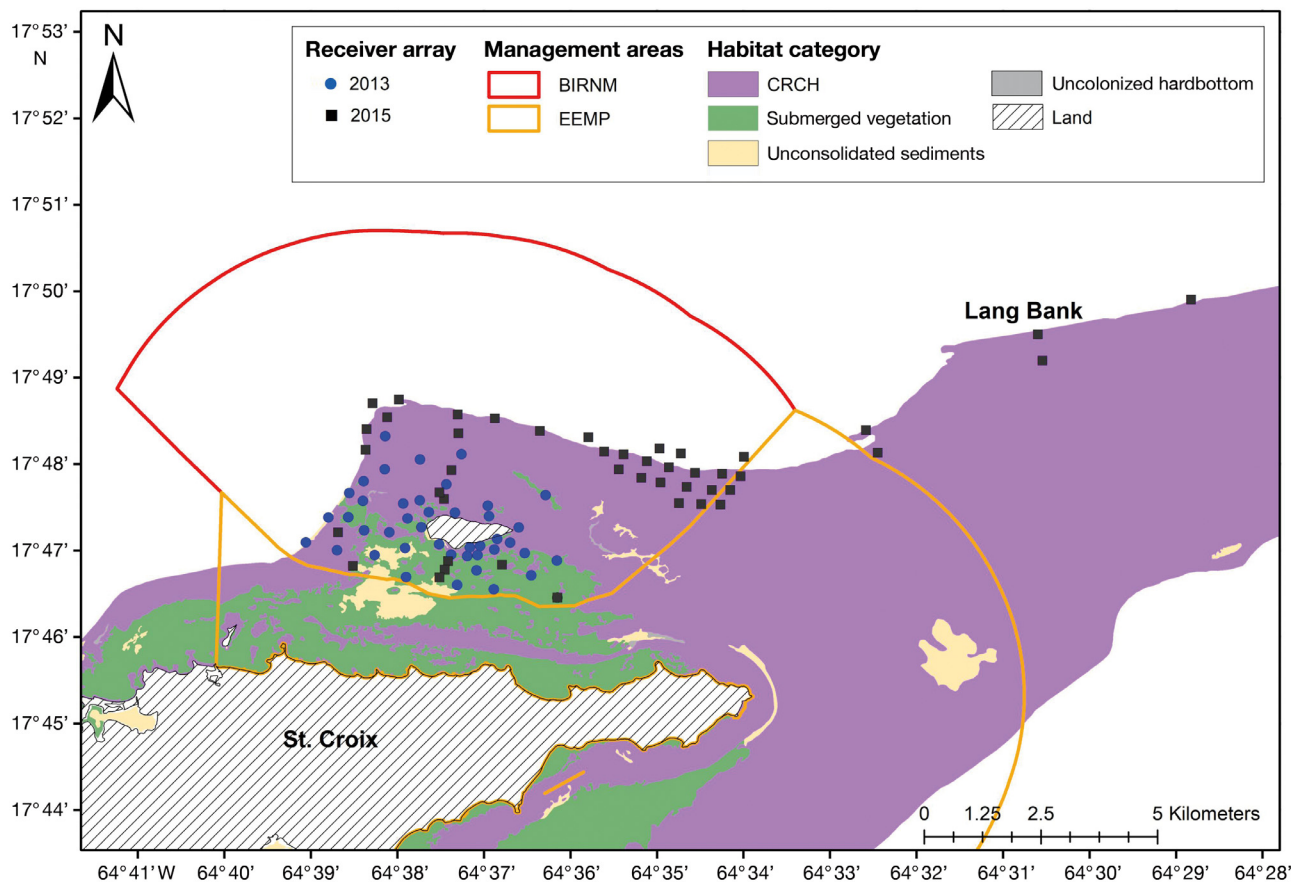

Fig. 1. Locations of receivers anchored within Buck Island Reef National Monument (BIRNM) at the start of the study in 2013 (circles) and at its largest extent (2015–2017; squares), including receivers in the East End Marine Park (EEMP) and along Lang Bank. Once a station was established, it was present throughout the duration of the study. CRCH: coral, rock, and colonized hardbottom

largely coral reef and colonized hardbottom. A linear reef wraps from south to north around the eastern point of Buck Island, creating a sheltered shallow lagoon of largely sand and seagrass habitats (Pittman et al. 2008). North and east of the island and linear reef, the benthos is dominated largely by patch reef and colonized pavement (Pittman et al. 2014a). Extending away from the island, depths remain relatively shallow (<10 m), but increase quickly toward the continental shelf, to the west and north. Depths drop dramatically along the continental shelf break to approximately 300 m before gradually extending out to the 1800 m maximum along BIRNM's northern boundary.

2.2. Shark tagging

Ginglymostoma cirratum, *Negaprion brevirostris*, *Carcharhinus perezi*, and *Galeocerdo cuvier* were caught using longlines as described by DeAngelis et al. (2008). Shark tagging was conducted in BIRNM from 2013–2016 in May or June of each year. Sharks were caught using drop, pelagic, or bottom longline sets, based on water depth and target species (DeAngelis 2006). Drop sets consisted of a main line set vertically in the water, anchored by a Danforth anchor and suspended by a float. This set would fish the entire water column. Bottom longline sets consisted of a float and anchor system that allowed the mainline to fish the benthos horizontally, while pelagic longline sets consisted of a float and anchor system that allowed the mainline to fish horizontally along the water's surface. Sets were distributed randomly throughout the MPA and its habitats. Hook sizes were varied (12/0, 14/0, and 16/0 circle hooks) in an attempt to capture animals from multiple size and age classes, and were baited mainly with barracuda *Sphyraena barracuda* or bally- hoo *Hemiramphus brasiliensis*. Hook counts ranged from 10–32 hooks for bottom longline sets, 4–8 hooks for pelagic longline sets, and 1–5 hooks for drop line sets. Soak times varied, but lines were checked approximately hourly or immediately after witnessing a captured animal. Upon capture, sharks were identified to species, sexed, and measured (fork length [FL]). For males, maturity was determined based on clasper calcification (Clark & von Schmidt 1965). For females, maturity stage was determined based on published size-at-maturity estimates for each species (*N. brevirostris*, males: 225 cm total length [TL], females: 240 cm TL, Brown & Gruber 1988; *G. cirratum*, males: 223 cm TL, females 214 cm TL, Carrier & Luer 1990, Castro 2000; *G. cuvier*, males: 258 cm FL, females 265 cm FL, Branstetter et al. 1987, Kneebone et al. 2008;

C. perezi, males: 148.34 cm FL, females: 149.84 cm FL, Tavares 2009). *N. brevirostris* TLs were converted to FLs based on the regression formula published by Freitas et al. (2006). *G. cirratum* TLs were converted to FLs based on a conversion regression developed from previous catch data (T. Wiley unpubl. data).

Upon retrieval, sharks were secured with a tail rope and put in the supine position to induce tonic immobility. Once restrained, an acoustic tag was inserted into the abdominal cavity through an incision on the ventral side of the shark along the midline. Only sharks assessed to be in good condition (i.e. hooked in jaw, normal coloration, not lethargic) at the time of capture were acoustically tagged. If the shark was small enough to remove from the water during surgery (generally <100 cm FL), a pump was used to maintain saltwater flow over the gills (Legare et al. 2015). A pump was not necessary for large sharks that remained in the water for tagging because the current and the boat idling forward maintained water flow over the gills. Each shark was tagged with a coded acoustic transmitter (model V13 or V16, delay 60–180 s, battery life 360–3217 d, Vemco Division, AMIRIX Systems) depending on the size of the individual (Chapman et al. 2005, Legare et al. 2015). Smaller sharks received the smaller tag model (V13) when available. Tagging incisions were closed with 2 interrupted sutures (2–0 PDS II, Ethicon). Promptly following surgery, sharks were returned to an upright position, and their condition, based on energy level, was assessed before release. If necessary, sharks were resuscitated with assisted forward swimming before release. One small *N. brevirostris* was tagged opportunistically by National Park Service staff after being captured in shallow water using a dip net (model V9, 120 s delay, battery life 685 d, Vemco Division, AMIRIX Systems).

2.3. Acoustic telemetry

Presence/absence data from sharks were collected in an array of fixed acoustic receivers (Model VR2W, Vemco Division, AMIRIX Systems) deployed continuously from June 2013 to May 2017. Array size, both geographic area covered and receiver count, expanded from 43 receivers in 2013 to a maximum of 86 receivers in 2015 as additional collaborators joined the project and more funding became available (Fig. 1). Once a receiver station was established, that station was present throughout the duration of the study (i.e. all receivers deployed in 2013 remained as part of the array configuration through 2017). Sta-

tions were anchored to the bottom substrate with sandscrews or cinderblock and cement moorings. Most receivers were then suspended in the water column, on average 2.5 m above the bottom, by attaching the receiver to a polypropylene line buoyed by a subsurface float. The majority of receivers were located within the boundaries of BIRNM, with 8 receivers anchored in adjacent management areas: 3 in EEMP and 5 along Lang Bank (Fig. 1). Receivers were anchored in all habitat types within BIRNM: seagrass (n = 23), sand (n = 6), linear reef (n = 1), patch reef (n = 8), colonized pavement (n = 27), colonized pavement with sand channels (n = 10), and scattered coral and rock in unconsolidated sediments (SCRUS; n = 11). The western- and northern-most extent of the array bordered the continental shelf break. Receivers were anchored in water ranging from 2 to 40 m deep, and were downloaded approximately every 6 mo. Due to available equipment for receiver maintenance and retrieval, receiver deployments were limited by depth, and did not extend beyond the continental shelf break, which runs through the northern end of BIRNM. Receivers were also not deployed in the southeastern portion of the MPA, to avoid damaging the extensive coral reef in this area.

Of the 86 receivers deployed in the array, 19 array-representative receiver stations were range tested by Selby et al. (2016). Range testing used 4 acoustic transmitters, 2 Vemco V16-4Ls with a 10 s delay, 1 Vemco V16-4L with a 20 s delay, and 1 Vemco V13-1L with a 20 s delay. Tags were anchored to the bottom between 25 and 150 m from the receiver station, 1 at each cardinal direction, and remained deployed for a minimum of 1 h (see Selby et al. 2016 for more detailed methodology). A total of 323 hour-long deployments were conducted across 4 habitat classifications: homogeneous sand, mixed hardbottom with sand channels, high-rugosity reef, and low-rugosity hardbottom. The effective detection range, where ≥50% of detections were recorded, was 213.4 m for homogeneous sand, 123.9 m for low-rugosity hardbottom, 83.7 m in mixed hardbottom with sand channels, and 30.7 m in high-rugosity reef (Selby et al. 2016). There were no significant differences between tag type detection efficiency in the range testing (Selby et al. 2016). Based on these data, receiver detection range overlap is unlikely throughout most of the array (Selby et al. 2016).

2.4. Data analysis

All analyses were conducted in R version 3.3.2 (R Core Team 2016). To assure data quality, detec-

tions were filtered to remove those that occurred simultaneously due to overlapping receiver coverage and echoes caused by the physical structure of the environment based on tag delay and time elapsed between consecutive detections (Becker et al. 2016). To avoid bias, the detection that was removed was selected randomly from the two each time a simultaneous detection or echo occurred. To ensure our statistical analyses drew robust ecological conclusions about space use within the MPA, only individuals with >1000 valid detections were included in network and habitat use analyses (Finn et al. 2014, Becker et al. 2016). Sharks whose first and last valid detection were >1 mo apart but had <1000 valid detections were included in the residency index calculation but were excluded from network and habitat use analysis. Details on the sharks removed from analyses can be found in the Supplement at www.int-res.com/articles/suppl/m633p105_supp.pdf.

2.4.1 Residency

To quantify the temporal extent to which each species used the BIRNM MPA, a residency index (RI) was generated using only receivers anchored within the boundaries of the protected area. For each individual shark, a day of residency was defined as a day with 2 or more valid detections on 1 or more receivers within 1 h (Espinoza et al. 2015). The number of resident days was then divided by the number of days at liberty throughout the monitoring period to calculate the RI for each individual (Legare et al. 2015); RI ranged from 0, indicating no residency, to 1, indicating total residency. The number of days at liberty was defined as follows: the number of days between the tagging date and the date of the last receiver download for tags with a long enough battery life, the number of days between the tagging date and last detection for tags with a battery life shorter than the study duration but whose life exceeded the expected battery life, or the expected battery life for tags that were scheduled to die before the last download and did not exceed the expected battery life. Mean RI and standard deviation (SD) were then calculated for each species. A generalized linear model with binomial error distribution was used to determine if residency differed significantly among species (p < 0.05; Zuur et al. 2015).

In addition to daily residency, the maximum amount of time that sharks could have been outside of BIRNM was calculated. Sharks were deemed outside of the

MPA if the amount of time elapsed between detections was >1 h. The amount of time absent was then summed to determine the maximum amount of time that sharks were undetected, and a percentage of time absent was calculated based on the total amount of time the shark could have been detected, which was calculated from the number of days at liberty (Table S1).

2.4.2. Community detection

A bipartite network graph was created from a matrix of the number of detections for each tagged shark on each receiver, standardized by the shared time in the water for each tag and receiver pair to account for array expansion over time. For the standardization, we calculated the shared time in water for each tag-receiver pair based on tagging date and receiver deployment date and formed a normalization matrix by taking the reciprocal of the shared days in water for each pair. The resulting matrix was then multiplied by a matrix of the number of detections registered from each tag on each receiver. The nodes of the graph represent both individual sharks and receivers, while edges represent the connections between sharks and the receivers used by specific individuals. Edge thickness was scaled based on the number of times the connection between an individual shark and a receiver was observed. Nodes were scaled by degree distribution, with frequently detected sharks and frequently used receivers having larger nodes than those for sharks detected rarely and receivers logging fewer detections (Finn et al. 2014). Bipartite graphs were created using the 'igraph' package (Csardi & Nepusz 2006) in preparation for coupling with community detection algorithms.

Before proceeding with further analyses, our bipartite network was tested against 1000 randomly generated networks to determine if the network structure, and therefore fish movements, were significantly different from random observation (Dormann et al. 2009, Opsahl 2009). Random networks were generated using the bipartite package (Dormann et al. 2008) with the link reshuffling method, which maintains the observed network's degree distribution but changes the structure of the network by randomly generating edges (Opsahl 2009). A modified clustering coefficient for bipartite network graphs was calculated for both the observed network and the 1000 random networks (Opsahl 2013). The frequency distribution of clustering coefficient values was then compared to the observed value. The clus-

tering coefficient was significantly lower than the normal distribution of clustering values generated by the random networks, so we proceeded with network analysis (Fig. S1).

To determine similarity of array use among individuals, community detection algorithms were run on the bipartite network graph (Finn et al. 2014, Griffin et al. 2018). These algorithms identify groups of nodes that are more closely associated with each other than with the rest of the graph (Fortunato 2010, Finn et al. 2014). In graph theory, these groupings are called communities, but should not to be interpreted as ecological communities in the context of this study. Because of the relatively small spatial scale of our array and the mobility of our study species, the graph theory communities formed by the algorithms denote spatial groupings of sharks, regardless of species, with the receivers that they use most frequently. A number of algorithms have been developed to establish these groupings based on the interests of various fields, including statistical physics, biology, sociology, and applied mathematics (Yang et al. 2016). Six different community detection algorithms available in the 'igraph' package were run: Leading-Eigenvector (Newman 2006), Fast-Greedy (Clauset et al. 2004, Newman & Girvan 2004), Spin-Glass (Reichardt & Bornholdt 2006), Label-Propagation (Raghavan et al. 2007), Walktrap (Pons & Latapy 2006), and Multilevel (Blondel et al. 2008).

All of the algorithms look to maximize the modularity of the graph. Briefly, the Leading-Eigenvector algorithm creates groupings based on eigenvectors from the modularity matrix of the graph (Newman 2006). Fast-Greedy is a bottom up approach where each node starts in its own community and communities are merged together in an attempt to maximize the modularity score of the graph (Newman & Girvan 2004). Spin-Glass relies on the statistical mechanics of networks and physical Spin-Glass models to maximize modularity (Reichardt & Bornholdt 2006). Label-Propagation begins by assigning each node a unique label and iteratively relabels the nodes based on the labels of their neighbor until no further label changes can be made (Raghavan et al. 2007). Walktrap simulates short random walks in the graph and defines communities of nodes where the walk gets trapped (Pons & Latapy 2006). Multilevel assigns each node to a community and then nodes are shuffled among communities to maximize each node's individual contribution to the modularity score (Blondel et al. 2008). Modularity scores, which quantify the quality of the resulting

divisions (communities; Newman & Girvan 2004), were used to determine the best performing algorithm for the dataset. A modularity score is the proportion of edges within each network division minus the proportion of edges if the edges had a random distribution given the node degree; higher performing algorithms have higher modularity scores (Newman & Girvan 2004).

Once the highest performing algorithm was selected, communities designated by the algorithm were assessed as in-communities or out-communities. An in-community has significantly more in-strength, directed edges, coming from within the community, rather than outside, while an out-community has nodes that direct significantly more out-strength, directed edges, to nodes within their community (Landi & Piccardi 2014). For each community, indegree for nodes was defined as the number of edges connecting that node to other nodes within the same community. A node's out-degree was defined as the number of edges connecting that node to nodes outside of its community (Finn et al. 2014). Wilcoxon rank-sum tests determined if each community was a significant in-community or significant out-community ($p < 0.05$; Song & Singh 2013). Essentially, this testing is necessary to determine how strongly each community is connected to the rest of the directed network, with significant in-communities being more isolated than significant out-communities (Landi & Piccardi 2014).

Since bipartite graphs are not spatially oriented, spatial plots were created for each tagged shark. This allowed for visualization of receiver use in 2-dimensional (x, y) space. These networks are a visual representation of the connections between receivers (nodes) but the edges are not representative of the actual exact path traveled by the shark (i.e. edges are forced to be straight lines and the shark likely took a more circuitous path). For visualization purposes and a cleaner presentation, self-loops were removed from the edges displayed. However, these detections were not removed from the network, allowing nodes to remain scaled to the relative number of detections observed for each individual. Nodes were scaled by the relative number of detections on each receiver, and generally the number of detections for each receiver was divided by a given number to allow for reasonable visualization. Edges were scaled by the log transformation of edge weight, meaning the log of the frequency a path was traversed. These maps were created using the 'ggmap' (Kahle & Wickham 2013), 'GGally' (Schloerke et al. 2016), and 'geosphere' (Hijmans 2016) packages.

2.4.3. Habitat use

To explore relative habitat use for each species, circle plots of habitat connectivity were created using the 'circlize' package (Gu et al. 2014). Specific benthic habitat types were assigned to each receiver based on the substrate where the receiver was anchored. Habitat categories were based on benthic habitat mapping conducted by Kendall et al. (2001) in BIRNM. Habitat types were seagrass, sand, linear reef, patch reef, colonized pavement, colonized pavement and sand, and SCRUS. Movement matrices for each species were created based on origin and destination habitats for each detection, including sequential detections on the same receiver, also called self-loops, and without temporal constraints. These matrices were then standardized using matrix multiplication to account for uneven receiver distribution among habitats. To standardize, we constructed diagonal matrices of habitat type with the reciprocal of receiver count in each habitat type as the diagonal value. All remaining values in the matrix were 0. We then multiplied this matrix by the movement matrix and by the standardized matrix again to account for receiver distribution in the origin habitat and destination habitat. The circle plots allowed for visualization of relative habitat use for each species as well as movements within and among habitat types (Espinoza et al. 2015).

Binomial generalized linear mixed models (GLMMs) were developed for each species to predict the presence of a shark on a receiver, using monthly presence/absence data for each receiver, in relation to receiver depth, receiver habitat, and their interaction with individual shark as a random effect (Zuur et al. 2015). Using monthly presence/absence on a receiver allowed us to account for array expansion in our data set. This also allowed sharks to be dropped from the analysis if their tag battery life expired before the end of data collection, meaning sharks were not counted as absent on receivers that they could not access during any given month. Because of the uneven distribution of receivers throughout habitats, habitat types were aggregated into more general habitat categories based on benthic habitat mapping from Kendall et al. (2001). Sand receivers were reclassified as unconsolidated sediments, seagrass receivers as submerged vegetation, and linear reef, patch reef, colonized pavement, colonized pavement and sand, and scatter coral and rock in unconsolidated sediments as coral, rock, and colonized hardbottom (CRCH; Pittman et al. 2008). Models were checked for spatial and temporal autocorrelation

using methods outlined by Zuur et al. (2010). To minimize temporal autocorrelation, year and months since tagging were included as candidate explanatory variables in the global model. Akaike's information criterion corrected for small sample size (AICc) was used to select the best model from a candidate set of all possible variable combinations. Tukey's honestly significant difference (HSD) post hoc tests were run for each best model to verify significance using the 'multcomp' package (Hothorn et al. 2008; p < 0.05). Predictor plots for significant variables from each species' best model were constructed in base R following methods in Zuur et al. (2015).

3. RESULTS

3.1. Tagging

Sharks (n = 48) were tagged between June 2013 and June 2016: 11 *Ginglymostoma cirratum*, 12 *Negaprion brevirostris*, 18 *Carcharhinus perezi*, and 7 *Galeocerdo cuvier*. Of these, 10 *G. cirratum* (mean ± SD: 130.6 ± 31.6 cm FL), 5 *N. brevirostris* (109.6 ± 30.3 cm FL), 12 *C. perezi* (93.3 ± 26.6 cm FL), and 6 *G. cuvier* (223.0 ± 23.7 cm FL) registered >1000 valid detections within the array after filtering for simultaneous detections and echoes, and were included in all further analyses. Additionally, 1 *G. cirratum*, 1 *N. brevirostris*, and 1 *C. perezi* were detected for over 1 mo but with <1000 detections, and were included only in the RI calculations. All sharks were deemed immature when tagged, except for 1 female *G. cuvier* and 2 female *G. cirratum*. Three *C. perezi* had reached sexual maturity at the time of their last detection based on the projected growth rate from Tavares (2009).

3.2. Residency

Overall, individual residency was high, regardless of species. The number of resident days ranged from 5–1437 for *N. brevirostris*, 42–723 for *G. cirratum*, 17–1419 for *C. perezi*, and 70–478 for *G. cuvier* (Table 1). Mean RI for all species was ≥0.52, which is indicative of high site fidelity within the MPA (Kneebone et al. 2012). Mean residency was highest for *G. cuvier* (mean ± SD: 0.67 ± 0.28), followed by *C. perezi* (0.60 ± 0.44), *N. brevirostris* (0.54 ± 0.50), and *G. cirratum* (0.52 ± 0.39). A generalized linear model with binomial error distribution followed by Tukey's HSD post hoc tests revealed no significant differences in

RI between species (p = 1.0). The maximum amount of time outside of BIRNM for each individual ranged from 2.92–99.76% (Table S1). *G. cuvier* had the highest percent of time absent (86.55 ± 10.20%), followed by *N. brevirostris* (83.19 ± 29.36%), *G. cirratum* (81.68 ± 16.68%), and *C. perezi* (78.22 ± 29.25%).

3.3. Community detection

The bipartite graph coupled with community detection algorithms shows strong inter- and intraspecific clustering of individuals (Fig. 2). Of the 7 community detection algorithms run, the Fast-Greedy and Multilevel algorithms performed the best, with modularity scores of 0.590 and 0.587, respectively (Table 2). Because there was strong agreement in the community composition between both algorithms, results from the former (which had a slightly better modularity score) were used for further analyses. The Fast-Greedy algorithm separated sharks and receivers into 9 different spatial communities (Fig. 2), with significant overlap in array use across communities as indicated by the large number of significant out-communities (Table 3). Six of the 9 communities consisted of individuals from a single species, and only 2 communities contained individuals from 3 species. *G. cuvier* and *N. brevirostris* were never determined to use space similarly (Table 3).

The 9 communities correspond to unique spatial groupings of receivers and the sharks that used them most frequently. Community 1 contained 2 *G. cuvier* and 20 receivers, mainly deepwater receivers along BIRNM's northeastern shelf break, as well as the 3 EEMP receivers and 4 Lang Bank receivers. Mean ± SD receiver depth was 26.90 ± 6.67 m. Community 1 mainly had receivers in colonized pavement (n = 11), followed by SCRUS (n = 4), colonized pavement and sand (n = 4), and patch reef (n = 1). Community 2 held 2 *N. brevirostris*, 2 *G. cirratum*, and 2 *C. perezi* with 20 receivers at a mean depth of 15.54 ± 8.96 m. These receivers were mainly north of Buck Island and along the western shelf break and occupied varied habitat: colonized pavement (n = 5), colonized pavement and sand (n = 5), patch reef (n = 3), SCRUS (n = 3), seagrass (n = 3), and sand (n = 1). Community 3 held 5 *C. perezi* and 4 receivers at mean depths of 13.76 ± 4.93 m. These receivers were equally spread between colonized pavement, patch reef, seagrass, and sand east of Buck Island. There were 3 *N. brevirostris* and 6 *G. cirratum* with 15 receivers in Community 4. Seagrass (n = 6) and colonized pavement (n = 6) were the dominant habitat types, followed by SCRUS (n = 2)

Table 1. Life history data collected for sharks at tagging, including sex, size (fork length), estimated age, and maturity state, number of days in Buck Island Reef National Monument (BIRNM) and days at liberty for residency index calculation, estimated life history data at the time of last detection, and community assigned by the Fast-Greedy community detection algorithm. LEM: lemon shark *Negaprion brevirostris*; N: nurse shark *Ginglymostoma cirratum*; R: Caribbean reef shark *Carcharhinus perezi*; T: tiger shark *Galeocerdo cuvier*; M: male; F: female; U: unidentified; NA: community not assigned for sharks included only in residency index calculation

| Tag	Sex	Size at tagging (cm)	Estimated age at tagging (yr)	Maturity state at tagging	Date tagged (mo/d/yr)	Resident days in BIRNM	Days at liberty	Residency index	Estimated size at last detection	Estimated age at last detection	Maturity state at last detection	Assigned community
LEM1	F	126	5.5	Immature	6/11/13	1435	1435	1.00	170.85	9.44	Immature	4
LEM10	F	148	7	Immature	6/2/16	349	350	1.00	154.46	7.96	Immature	4
LEM2	M	116	5	Immature	6/11/13	1437	1437	1.00	165.57	8.94	Immature	4
LEM5	U	80	2.5	Immature	6/1/16	5	351	0.01	82.57	2.52	Immature	2
LEM4	M	78	2	Immature	1/27/16	96	476	0.20	92.86	3.21	Immature	2
LEM12	M	53	0	Immature	6/1/16	15	349	0.04	53.82	0.04	Immature	NA
N10	F	179	14.7	Mature	5/7/15	709	742	0.96	205.56	16.73	Mature	5
N11	F	122	9	Immature	6/1/16	345	351	0.98	134.56	9.96	Immature	4
N2	M	104	7.5	Immature	5/13/14	474	1100	0.43	121.51	8.84	Immature	4
N3	M	102	7	Immature	5/13/14	63	1101	0.06	104.26	7.17	Immature	4
N4	M	99	7	Immature	6/12/13	258	360	0.72	108.80	7.75	Immature	4
N5	M	162	13	Immature	5/14/14	104	1098	0.09	166.67	13.36	Immature	2
N6	F	131	10	Immature	5/6/15	118	743	0.16	135.41	10.34	Immature	2
N7	F	111	8	Immature	5/6/15	723	761	0.95	137.67	10.04	Immature	4
N8	F	116	8.7	Immature	5/6/15	252	743	0.34	125.08	9.39	Immature	4
N9	F	180	14.9	Mature	5/7/15	665	742	0.90	206.56	16.93	Mature	5
N1	F	99	1	Immature	6/11/13	42	360	0.12	100.51	1.12	Immature	NA
R1	F	87.5	1	Immature	6/11/13	82	1437	0.06	91.61	1.23	Immature	9
R10	M	65	0	Immature	5/15/14	1092	1099	0.99	130.14	3.01	Immature	3
R11	F	69.5	0	Immature	5/15/14	17	1099	0.02	67.05	0.06	Immature	5
R13	F	138	3	Immature	5/6/15	729	737	0.99	155.24	5.01	Mature	8
R14	M	115	2	Immature	5/7/15	734	742	0.99	146.59	4.03	Immature	6
R15	M	103	1	Immature	5/7/15	698	742	0.94	130.09	3.00	Immature	3
R16	F	99	1	Immature	5/8/15	227	741	0.31	107.17	1.69	Immature	3
R3	M	113	2	Immature	6/11/13	1419	1435	0.99	170.61	5.92	Mature	2
R4	F	111	2	Immature	6/12/13	380	381	1.00	126.57	3.04	Immature	7
R5	F	64	0	Immature	5/13/14	1056	1101	0.96	133.37	3.02	Immature	3
R7	F	83	0	Immature	5/14/14	157	1100	0.14	107.39	1.70	Immature	3
R9	M	144	4	Immature	5/14/14	359	1100	0.33	180.49	6.90	Mature	2
R12	F	83	0	Immature	5/15/14	19	360	0.05	84.64	0.05	Immature	NA
T2	F	211	6	Immature	5/6/15	478	695	0.69	236.87	8.03	Immature	1
T3	F	219	6.7	Immature	6/1/16	335	351	0.95	231.88	7.66	Immature	5
T4	F	270	10.9	Mature	6/2/16	274	350	0.78	278.91	11.86	Mature	5
T6	F	212	6.3	Immature	6/3/16	313	349	0.90	226.01	7.24	Immature	5
T7	F	205.5	5.9	Immature	6/3/16	180	348	0.52	216.10	6.57	Immature	5
T5	M	220.5	7	Immature	6/2/16	70	350	0.20	231.86	7.95	Immature	1
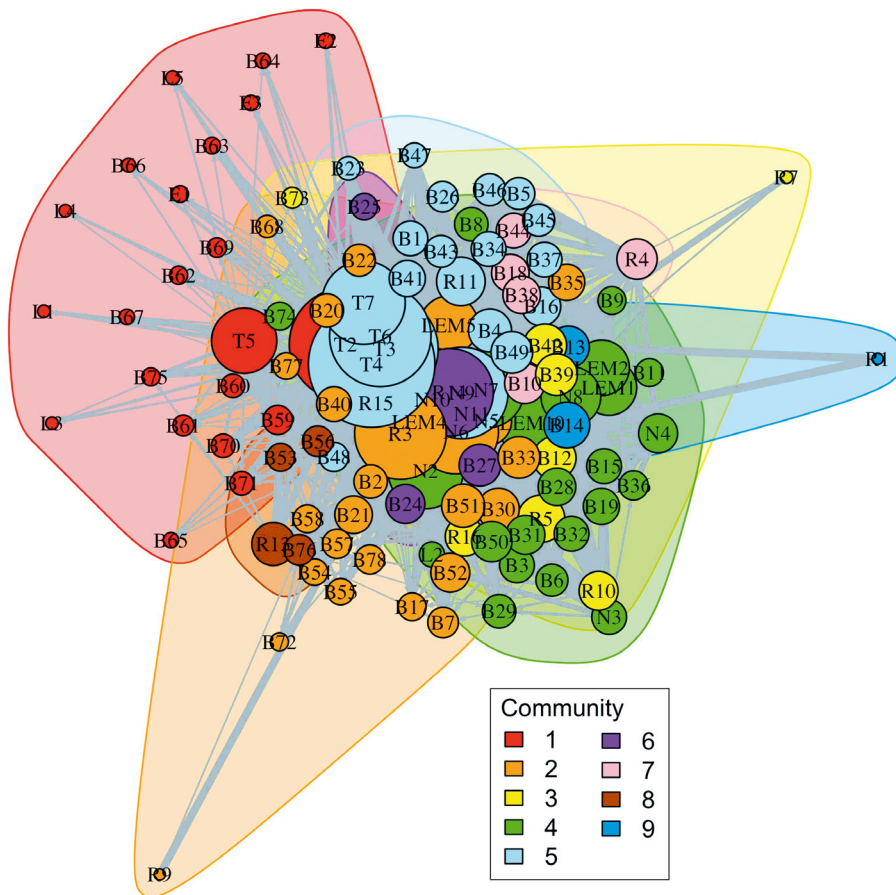
Fig. 2. Bipartite graph connecting sharks with frequently used receivers based on the Fast-Greedy community detection algorithm. Sharks are grouped with frequently used receivers in color-coded communities. Sharks are represented by nodes starting with T (tiger shark), N (nurse shark), R (Caribbean reef shark), or LEM (lemon shark), while receivers are labeled B (Buck Island Reef National Monument), L (Lang Bank), and E (East End Marine Park). Sharks and receivers are numbered. Nodes are scaled by the relative number of detections, i.e. sharks that were detected more frequently have larger nodes. Receivers that registered more detections are larger than receivers that registered fewer detections. Edge thickness is also scaled according to the strength of the connection: the thicker the edge, the more frequently a shark was detected on a receiver. Note: this graph is not spatially oriented

and linear reef (n = 1). These receivers were mainly those closest to Buck Island, but also included 1 receiver on Lang Bank (7.01 ± 6.99 m). Community 5 was the last large community with 2 *G. cirratum*, 1 *C. perezi*, 3 *G. cuvier*, and 15 receivers south of Buck Island in the seagrass beds. Ten receivers were anchored in seagrass, followed by sand (n = 4) and colonized pavement (n = 1) in average depths of 13.47 ± 3.18 m. Community 6 contained a single *C. perezi* and 3 receivers, 1 each in seagrass, colonized pavement, and SCRUS. The receivers were at mean depths of 7.82 ± 1.96 m east of Buck Island. Community 7 contained 1 *C. perezi* and 4 receivers. These receivers were in deeper waters south of Buck Island, 12.65 ± 3.00 m, in seagrass (n = 3) and patch reef (n = 1). Community 8 held 1 *C. perezi* and 3 receivers in colonized pavement, colonized pavement and sand, and SCRUS. These receivers were in deep water, 29.06 ± 4.52 m, along the northern continental shelf break. Finally, community 9 held 1 *C.*

perezi and 2 receivers in patch reef southeast of Buck Island in 12.95 ± 1.51 m depths.

G. cuvier and *N. brevirostris* showed the highest similarity of within-species array use, with each species separated into 2 spatially distinct communities containing conspecifics (Table 3). *C. perezi* showed the highest within-species individuality, and were separated into 7 communities. In addition, 4 of the 9 communities consisted of only 1 *C. perezi* paired with its most frequently used receivers (Table 3). *C. perezi* and *G. cuvier* were most frequently found in com-

Table 2. Modularity score, number of communities detected, and number of significant in- and out-communities found for each community detection algorithm run. See Section 2.4.2 for details on community detection algorithm selection

Algorithm	Modularity	Communities detected	Significant in-communities	Significant out-communities
Leading-Eigenvector	0.542	7	0	4
Fast-Greedy	0.590	9	0	8
Spin-Glass	0.002	14	0	11
Label-Propagation	0.562	14	0	9
Walktrap	0.219	9	0	7
Multilevel	0.587	8	0	7

Table 3. Community composition and significance as determined by the Fast-Greedy algorithm. Each community represents a grouping of sharks with their most frequently used receivers, allowing for the determination of overlapping space use across species. See Section 2.4.2 for more details on community detection

Community	*Negaprion brevirostris*	*Ginglymostoma cirratum*	*Carcharhinus perezi*	*Galeocerdo cuvier*	Receivers	Community significance
1	0	0	0	2	20	Out
2	2	2	2	0	20	Out
3	0	0	5	0	4	Out
4	3	6	0	0	15	Out
5	0	2	1	4	15	Out
6	0	0	1	0	3	Out
7	0	0	1	0	4	Out
8	0	0	1	0	3	Out
9	0	0	1	0	2	Not significant

munities with conspecifics, while *N. brevirostris* and *G. cirratum* were more frequently found together in mixed communities of the 2 species.

When community divisions from the Fast-Greedy algorithm were coupled with spatially oriented networks, distinct spatial associations emerged in relation to the life-history stage of the tagged individuals. The 3 communities of *G. cirratum* showed expanding array use with size. The smallest *G. cirratum*, which ranged from 99–122 cm FL when tagged, were placed in Community 4 (n = 6), which was characterized by heavy use of the shallow-water coral, sand, and seagrass habitats (<10 m deep) immediately surrounding Buck Island (Fig. 3a). Based on their size at tagging, these sharks were juveniles ranging in age from 7–9 yr (Table 1). The *G. cirratum* in Community 2 (n = 2), larger and older juveniles (131–162 cm FL; 10–13 yr), used a larger portion of the array when compared to the smaller *G. cirratum*, being detected in both shallow water, patch reef habitats north of the island, and deep water north and east of the island along the shelf break (2.4–34.5 m deep, median depth = 13.7 m; Fig. 3b). Community 5 included 2 mature *G. cirratum*, both approximately 180 cm FL at tagging (14+ yr old). These sharks frequently used the sand and seagrass habitats south of Buck Island, but were also regularly detected in deeper water east and north of the island along the shelf break (8.8–19.5 m deep, median depth 14.3 m; Fig. 3c).

The smallest tagged *N. brevirostris*, placed in Community 2 (n = 2), were 78–80 cm FL and approximately 2 yr old. These sharks were detected extensively on shallow-water receivers immediately around Buck Island, and frequently used the shelf break northeast of the island (Fig. 4a). In contrast, the larger *N. brevirostris* (116–148 cm FL, 5–7 yr) in Community 4 (n = 3) concentrated their movements on the receivers closest to Buck Island (<10 m deep),

but also frequently moved between receivers immediately east of Buck Island and the shallowest Lang Bank receiver (13.7 m deep; Fig. 4b). Because of the lack of detections on several receivers between the eastern shore of Buck Island (mean depth 13.3 m) and this Lang Bank receiver, it is likely that these *N. brevirostris* were exiting the receiver array, and BIRNM's protected boundaries, to access this receiver. This movement pattern was seen consistently across all *N. brevirostris* in Community 4.

Although there was little variation in size for tagged *G. cuvier*, 2 distinct patterns of space use emerged. *G. cuvier* in Community 1 (n = 2) were detected exclusively in habitats northeast of Buck Island, largely colonized pavement, as well as in the East End Marine Park and Lang Bank at depths of 26.05 ± 7.223 m (Fig. 5a), while *G. cuvier* in Community 5 (n = 4) also regularly used waters south of Buck Island at depths of 13.48 ± 3.146 m (Fig. 5b).

Five of the 12 tagged *C. perezi* were placed in Community 3, characterized by frequent use of shallow coral reef habitat north and east of Buck Island (Fig. 6a). All of the sharks in this community were young of the year (YOY) or age-1 juveniles (65–103 cm FL). The remaining 7 *C. perezi* were placed into 6 communities, 5 consisting of only 1 shark. All but 2 of these sharks were over 2 yr old (69.5–144 cm FL; Table 1). These larger, older sharks exhibited fidelity to unique areas within the receiver array when compared to each other as well as to the large community of YOY and age-1 sharks (Fig. 6).

3.4. Habitat use

For *G. cirratum*, *N. brevirostris*, and *C. perezi*, the best performing GLMM to predict presence on a receiver included depth, habitat category, year, and
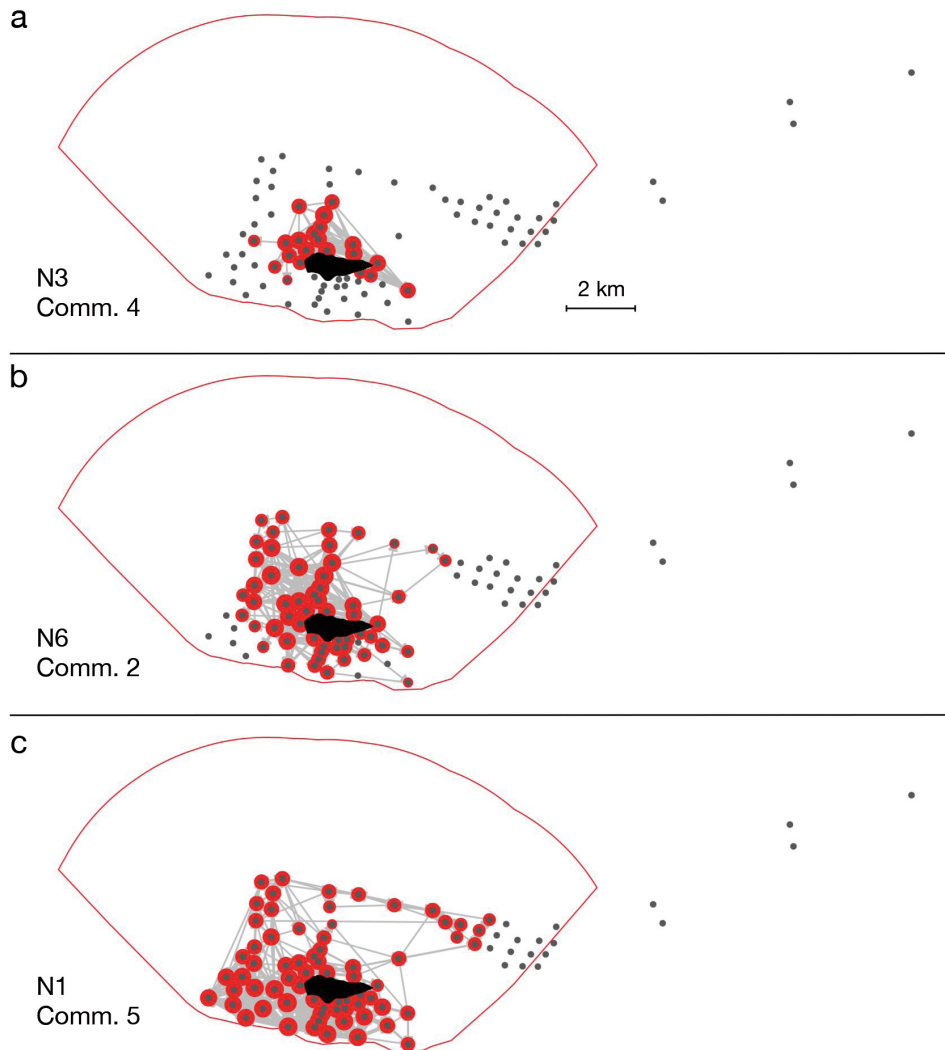
Fig. 3. Spatial networks for individual nurse sharks *Ginglymostoma cirratum* representative of movement patterns seen in each of the 3 communities containing *G. cirratum*. The size and age of *G. cirratum* at tagging increases from top to bottom, as does the area covered by individuals in each community. Grey dots represent anchored receivers. Receivers that detected the tagged shark are surrounded by a colored halo, or node. The relative size of the node represents the frequency of detections. The red outline represents the boundary of the BIRNM MPA. Movements of (a) a male (102 cm fork length [FL] ~7 yr old) placed in Community 4 with *G. cirratum* ranging from 99–122 cm FL; (b) a female (131 cm FL, ~10 yr old) placed in Community 2 with *G. cirratum* ranging from 131–162 cm FL; (c) a female (179 cm FL, ~14.7 yr old) placed in Community 5 with *G. cirratum* ranging from 179–180 cm FL

the interaction between habitat category and depth. For *G. cirratum*, all explanatory variables were significant terms in the model ($p < 0.05$), excluding the interaction between unconsolidated sediments and bottom depth ($p = 0.062$) and the years 2015 ($p = 0.125$) and 2016 ($p = 0.060$). After running Tukey's HSD tests, all habitat categories were significantly different from each other ($p < 0.05$), and the probability of presence on a receiver was significantly lower in 2014 than in 2013 ($p = 0.031$). For *N. brevirostris*, all explanatory variables were significant ($p < 0.05$), excluding year at all levels. Tukey's HSD post hoc tests confirmed significant differences among all habitat types ($p < 0.05$) and found that the probability of presence on a receiver was significantly lower in 2015 than in 2014 ($p = 0.007$). Both *G. cirratum* and *N. brevirostris* were more likely to be detected in waters <15 m deep in all 3 habitats: submerged vegetation, unconsolidated sediments, and CRCH. *G.*

cirratum were most likely to be detected on receivers in unconsolidated sediments (Fig. 7a), while *N. brevirostris* were more likely to be detected in areas with seagrass and unconsolidated sediments than in CRCH (Fig. 7b). Predictive plots revealed very little variation in these relative trends across years for both species.

For *C. perezi*, all explanatory variables were significant ($p < 0.05$), excluding the interaction between unconsolidated sediments and depth ($p = 0.713$). Additionally, 2015 was the only significant year ($p = 0.014$). Tukey's HSD confirmed this and found that there was no significant difference between the probability of presence in seagrass and unconsolidated sediments ($p = 0.143$). The only significant annual difference was that the probability of presence on a receiver was significantly lower in 2015 than in 2014 ($p < 0.001$). Overall, *C. perezi* had the lowest probability of presence on a receiver in any habitat
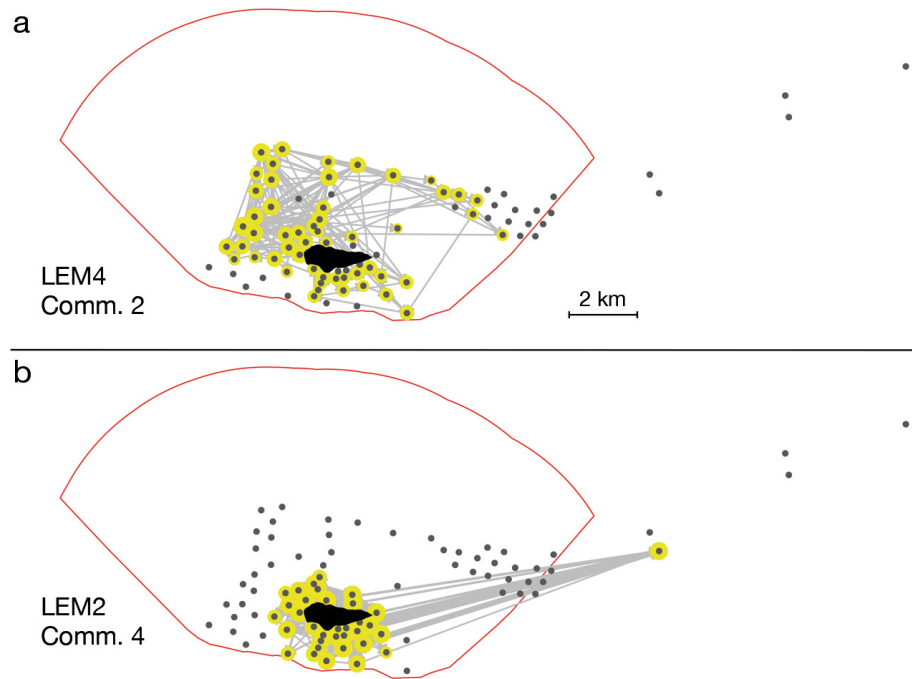
Fig. 4. Spatial networks for individual lemon sharks *Negaprion brevirostris* representative of movement patterns seen in the 2 communities containing lemon sharks. Details as in Fig. 3. (a) Smaller *N. brevirostris* were more wide ranging within BIRNM's boundaries, with 2 individuals (78–80 cm FL) placed in Community 2. The movements of a 78 cm FL male are shown here. (b) Larger *N. brevirostris* (116–126 cm FL in Community 4) regularly appeared outside of BIRNM on Lang Bank receiver L2. The movements of a 116 cm FL male are shown here

Fig. 5. Spatial networks for individual tiger sharks *Galeocerdo cuvier* representative of movement patterns seen in the 2 communities containing *G. cuvier*. *G. cuvier* were wide ranging and had little variation in size, and were split into 2 communities: (a) sharks that preferred deeper waters north of Buck Island along the continental shelf break, up to 39 m deep, and (b) sharks that also used waters south of Buck Island, north of coastal St. Croix, as shallow as 5 m deep
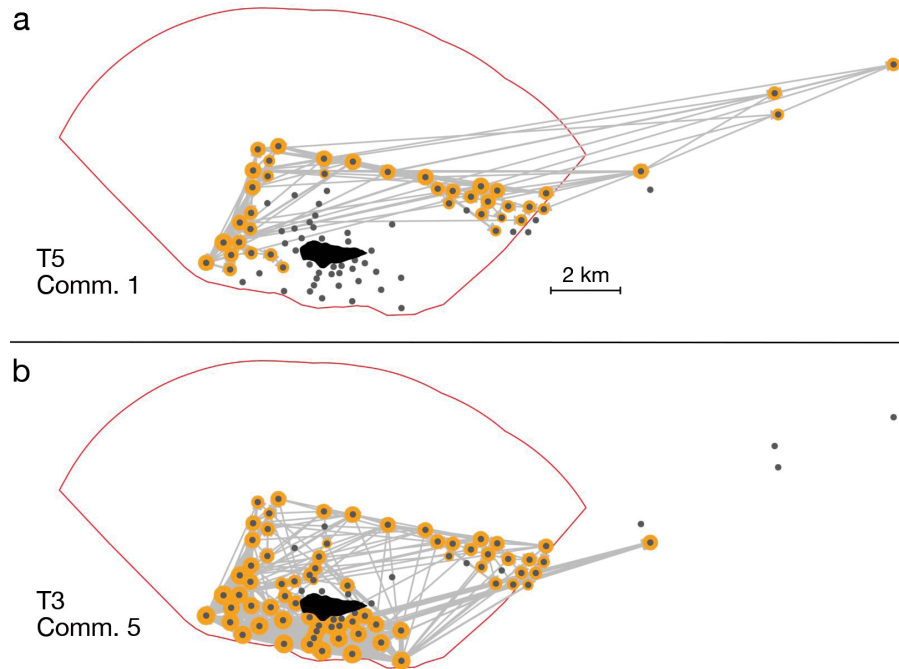
out of all species, with a mean probability of presence below 0.4 regardless of depth. Generally, *C. perezi* use shallow CRCH habitats most frequently (≤10 m deep; Fig. 7c).

The best model for *G. cuvier* included depth, habitat category, months since tagging, and the interaction between habitat category and depth. All variables were significant ($p < 0.05$) excluding the interaction between unconsolidated sediments and bottom depth. Tukey's HSD post hoc tests confirmed significant differences among all habitat types ($p < 0.05$). Across all habitats, the probability of detection on a receiver decreased over time. *G. cuvier* were more likely to inhabit deep (depths >10 m) water
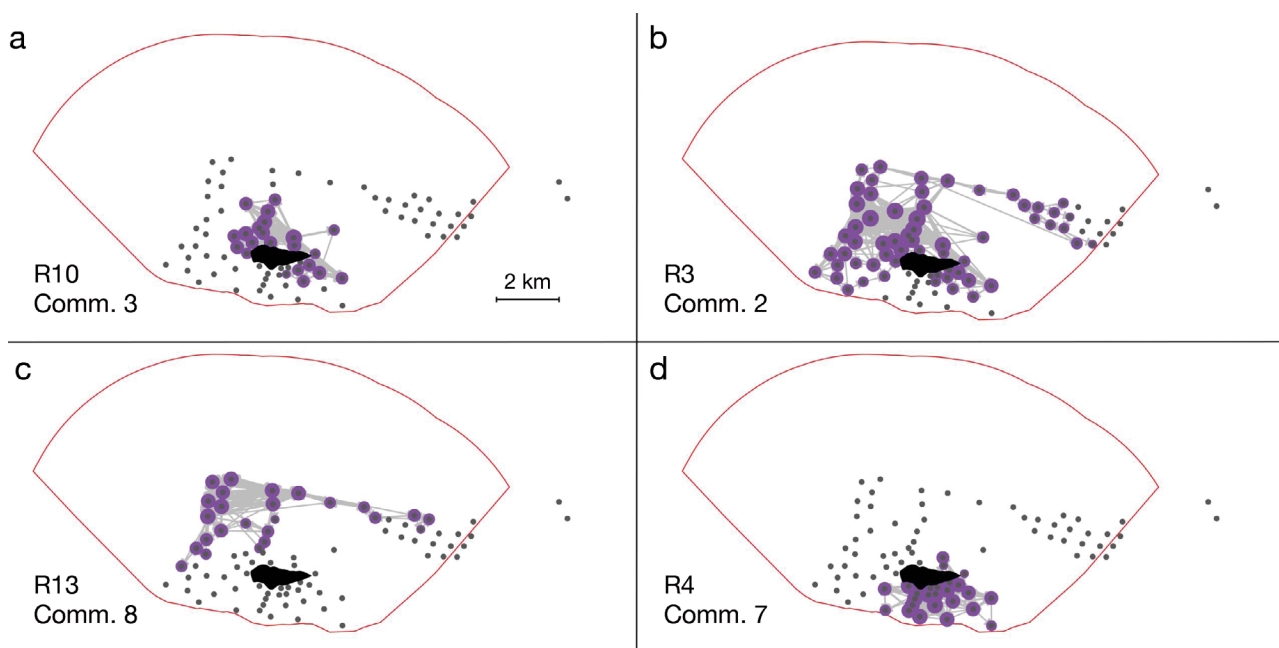
Fig. 6. Spatial networks for individual Caribbean reef sharks *Carcharhinus perezi* representative of movement patterns seen in communities containing *C. perezi*. Each panel shows the distinct spatial use exhibited by individuals throughout their life history: (a) representative of the largest community of young-of-the-year and age-1 juveniles. (b–d) age 2+ juveniles (3 of 5), placed in their own communities with no other shark species

areas across all habitat types. Overall, the probability of presence on a receiver was highest in unconsolidated sediments, regardless of depth. They also displayed a strong association with submerged vegetation deeper than 10 m, while use of CRCH habitats steadily increased with depth (Fig. 7d).

Circle plots of relative habitat use revealed varying levels of movement between habitats for each species, with *G. cirratum*, *C. perezi*, and *G. cuvier* moving frequently within sand habitats, while *N. brevirostris* most often moved within linear reef habitat (Fig. 8). *G. cirratum* also had a high number of relative movements within linear reef habitats, with very little use of colonized pavement and colonized pavement with sand channels. In addition to linear reef, *N. brevirostris* also used seagrass, patch reef, and SCRUS, with very few detections on receivers anchored in sand or colonized pavement. *C. perezi* and *G. cuvier* largely used CRCH habitats in addition to sand with fewer detections occurring in seagrass. Movements across habitat types were relatively low for *G. cirratum* and *N. brevirostris*, with the most occurring between sand and seagrass, and seagrass and linear reef, respectively. Of the 4 species, *C. perezi* exhibited the highest movement between habitats, regularly connecting all CRCH habitats to sand and seagrass (Fig. 8). *G. cuvier* also moved reg-

ularly across habitats and used the colonized pavement with sand channels, commonly found in water deeper than 15 m, more often than any other species.

4. DISCUSSION

Using multiple analytical methods, we were able to demonstrate the high daily use, and likely importance, of the varied habitats found within BIRNM to the local shark community. The variety of sand, seagrass, coral reef, and hardbottom habitats and wide depth range within the boundaries of BIRNM provided sufficient habitats for all 4 species studied, as evidenced by the high mean residency for each species. On average, all species spent ≥1 h within BIRNM for at least 52% of their tagged days at liberty. Further, the areas that tagged sharks frequented in the MPA varied significantly among species and individuals, emphasizing the value of BIRNM's expanded size. Without the 2001 expansion, most tagged individuals would occupy space beyond the initially protected reefs east of the island. This study demonstrates the utility of community detection algorithms to compare inter- and intraspecific space use within an acoustic telemetry array when coupled with traditional acoustic telemetry metrics, like RI and GLMMs.
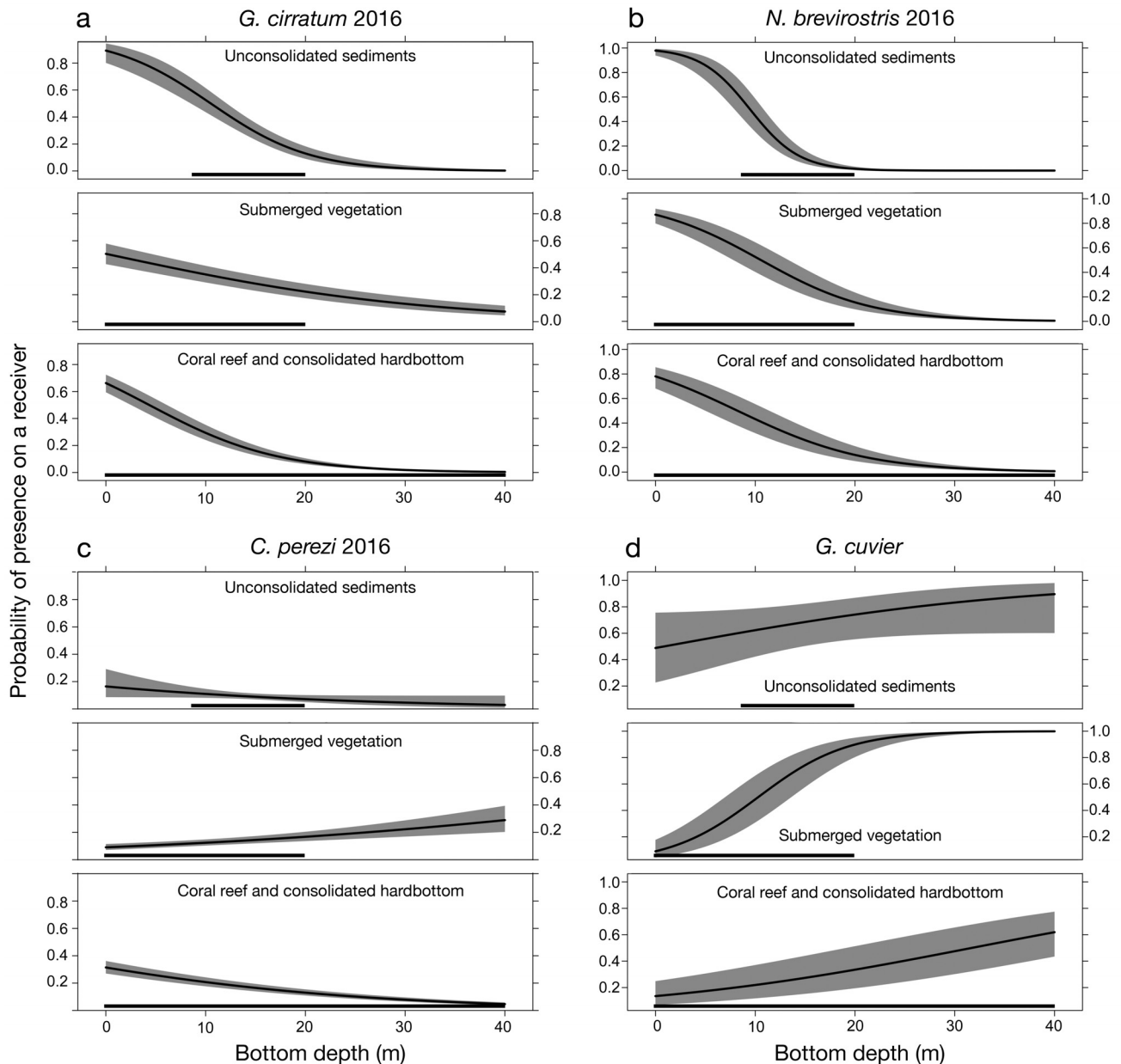
Fig. 7. Predictions based on the best fitting generalized linear mixed model for each species with standard error (grey shading). The depth range covered by receivers anchored in each habitat is indicated by the thick black line along the x-axis. (a) Nurse sharks *Ginglymostoma cirratum* show an affinity for shallow water and a strong use of sandy habitats. (b) Lemon sharks *Negaprion brevirostris* show an affinity for shallow water and a slightly higher use of sand and seagrass habitats over coral reef habitats. (c) Caribbean reef sharks *Carcharhinus perezi* show relatively low probabilities of presence on any receivers regardless of habitat type and depth. Shallow coral reef habitats are used most frequently. (d) Tiger sharks *Galeocerdo cuvier* show relatively strong use of deep water over shallow as well as sandy habitats

It is important to emphasize that the calculations for maximum time spent outside of BIRNM are very likely an overestimate of time in unprotected waters, due to the species tagged and the configuration of our array. The assumption that sharks that were undetected for >1 h were outside of BIRNM is highly conservative, and there are many scenarios in which sharks could be within BIRNM's boundaries but undetected by the array. Because of the nature of acoustic telemetry, our detection range was limited in high-rugosity reef habitats. This combined with the limited number of receivers
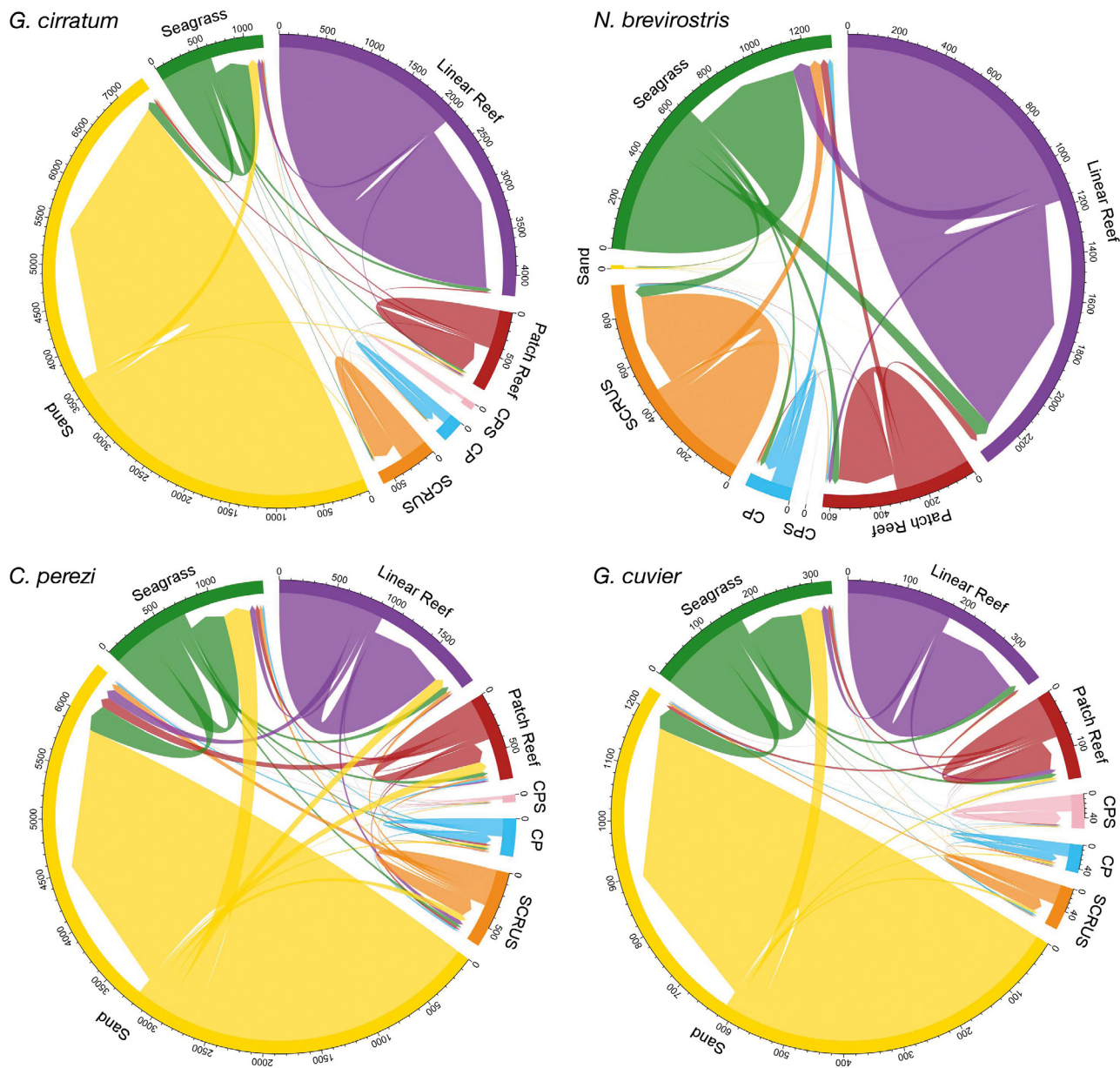
Fig. 8. Relative number of shark detections in each habitat as well as movements within and across habitats for each species. CP: colonized pavement; CPS: colonized pavement with sand channels; SCRUS: scattered coral and rock in unconsolidated sediments

available for the study meant that parts of BIRNM were not within the listening range of an acoustic receiver. It is possible for sharks to still be within BIRNM and outside of the range of an acoustic receiver, particularly north of the continental shelf and in the southeastern patch reefs. *Negaprion brevirostris* and *Ginglymostoma cirratum* are also able to buccal pump, meaning they could easily spend an extended period of time resting on benthic habitat within BIRNM's boundaries but outside of the range of a receiver. These limitations have

been acknowledged in previous acoustic telemetry studies focused on MPA use, particularly Pittman et al. (2014b).

Of the 4 species studied, *Galeocerdo cuvier* were the widest ranging, and were likely the driver behind the high number of significant out-communities found in our community detection analyses. Out-communities are indicative of overlapping space use among tagged individuals. Although sharks are placed in communities with the receivers they use most frequently, sharks from other communities also

visit those receivers. Considering the size range and species composition of our tagged sharks, it is reasonable to expect spatial overlap among tagged individuals over the expanse of our array. *G. cuvier* have large home ranges of hundreds to thousands of square kilometers (Heithaus et al. 2007, Meyer et al. 2009), much larger than the spatial scale of our array. The *G. cuvier* in this study were observed using nearly all of the receivers in our array, across depths and habitats, inside and outside of the BIRNM boundary.

4.1. *Ginglymostoma cirratum* and *Negaprion brevirostris*

Of all species pairings, our analyses placed *G. cirratum* and *N. brevirostris* into the same communities most frequently. This is perhaps unsurprising, given previous acoustic telemetry studies showing that both species prefer relatively shallow waters with sand and seagrass habitats (Morrissey & Gruber 1993, Chapman et al. 2005, DeAngelis et al. 2008, Murchie et al. 2010). However, the Fast-Greedy algorithm allows us to assign significance to this overlapping spatial use, which is likely driven by similar habitat preferences. The binomial GLMMs also support previous research suggesting juvenile *N. brevirostris* and *G. cirratum* frequent shallow-water habitats (Pikitch et al. 2005, Garla et al. 2017), with both species having the highest probability of detection on receivers in waters <10 m deep, regardless of benthic habitat. The circle plots of relative habitat use for both species showed regular movements within linear reef habitat. Only 1 receiver in our array is anchored in linear reef habitat, and it sits near a small break in the reef. The reef break provides an access point to the shallow sand and seagrass lagoon that lies between the reef and Buck Island's shores. The reef and protected lagoon run along the southeastern portion of Buck Island. The receiver is anchored on the open-water side of the reef structure, meaning sharks are most likely detected on this receiver as they traverse the outside of the reef to enter the lagoon through the reef break. Use of this receiver, especially for smaller *N. brevirostris*, likely emphasizes the importance of the shallow, reef-protected seagrass and sand habitats. Smaller *N. brevirostris* and *G. cirratum* also regularly used the complex CRCH habitats north of the island. This complex habitat likely provides refuge from predators, despite these sharks using much deeper

water than comparably sized *N. brevirostris* tracked elsewhere in the USVI (DeAngelis et al. 2008, Legare et al. 2015)

4.2. *Galeocerdo cuvier*

Compared to other acoustic telemetry studies of *G. cuvier* (Holland et al. 1999, Meyer et al. 2009), the individuals that we tagged in BIRNM exhibited high site fidelity to the area, with a mean RI of 0.67. Studies of *G. cuvier* in the Hawaiian Islands and French Frigate Shoals showed that residency in an area often varies by individual, with some exhibiting prolonged fidelity to the study area throughout the duration of observations and others traveling as far as 1460 km away from the tagging location in less than 1 yr (Meyer et al. 2010, 2018, Papastamatiou et al. 2013). Similar observations were made in Shark Bay, Australia, where some satellite-tagged individuals remained close to their tagging location while others traveled thousands of kilometers in just over 2 mo (Heithaus et al. 2007). All but 1 of the *G. cuvier* tagged in BIRNM were immature at the time of tagging. Previous studies of *G. cuvier* tracked throughout the Hawaiian Islands found juvenile *G. cuvier* to be wider ranging than adults and detected over shorter time frames (Meyer et al. 2009). Although we did not have the sample size to make comparisons across life history stages, *G. cuvier* was the widest-ranging species in this study, with 5 individuals using ≥50 receivers. Since BIRNM encompasses only 77 km^2, there is reason to believe that these sharks are also using large areas outside the boundaries of BIRNM and beyond the limited receiver coverage in Lang Bank and the EEMP. This is supported by our calculations of maximum time outside of BIRNM. On average, *G. cuvier* went undetected more than the other 3 species (Table S1), but due to the array configuration, they likely are also using areas of BIRNM that do not have acoustic receiver coverage, particularly deep-water areas in northern BIRNM along the continental slope, and southeastern coral and hard-bottom habitats bordering EEMP. This means that the mean RI of 0.67 for daily MPA use could be an underestimate.

G. cuvier in BIRNM extensively occupied deep waters across all habitat types, and were detected most frequently in areas characterized by unconsolidated sediments. Previous research on *G. cuvier* habitat use suggested that their distribution is driven more by prey abundance than benthic habitat type (Heithaus et al. 2002, 2006). *G. cuvier* in BIRNM were more likely to

inhabit waters deeper than 10 m over sand or seagrass habitats. This may be to take advantage of areas frequented by reef fish, particularly yellowtail snapper *Ocyurus chrysurus* and horse-eye jack *Caranx latus*, that regularly use these areas, close to the shelf break (Novak 2018). Although diet studies for *G. cuvier* in the Caribbean have not been conducted, *G. cuvier* have been documented to consume lutjanids (Simpfendorfer et al. 2001) and carangids (Lowe et al. 1996, Aines 2018) elsewhere. Moreover, teleost fish still comprise a significant portion of the *G. cuvier* diet for sharks 165–260 cm FL (Lowe et al. 1996, Simpfendorfer et al. 2001), making it reasonable to assume that aggregations of reef fish would be of interest for the tagged sharks in this study when foraging.

4.3. *Carcharhinus perezi*

Despite being one of the largest carcharhinids in the Caribbean, the spatial ecology of *C. perezi* is the least studied of the 4 species monitored in BIRNM. Longline surveys indicate that this species undergoes ontogenetic shifts in habitat use (Pikitch et al. 2005, Brooks et al. 2013), and acoustic telemetry data indicate that these sharks often occupy restricted home ranges (Garla et al. 2006) with high site fidelity (Bond et al. 2012). Based on our analyses, *C. perezi* had the highest inter-individual variability in space use, which increased with age. Four communities consisted of a single *C. perezi* and its frequently used receivers. The majority of tagged sharks younger than age 2 were grouped into a single community characterized by heavy use of patch reef and colonized pavement close to the eastern shore of Buck Island. The remaining 5 *C. perezi*, age 2 or older (111+ cm FL) at tagging, were placed into 4 communities. All of these sharks exhibited unique space use within the array, using a combination of shallow, near-island and deep, shelf break habitat.

Our analyses show that older *C. perezi* have a stronger affinity for deeper waters bordering the continental shelf break (13–40 m deep) than near-island reefs. The shelf in BIRNM drops off sharply to depths of 218 m (Battista 2005) before sloping to maximum depths of 1800 m (Pittman et al. 2014a). Use of the shelf break appears to increase with age and size, with age-3 and -4 sharks using almost exclusively shelf-associated habitats (Fig. 6c). This shift occurs before the sharks reach maturity at age 5, around 148 cm FL (Tavares 2009). Affinity for deeper waters was observed in previous studies of mature *C. perezi*, which indicate that deep dives over 100 m are not uncommon (Chapman et al. 2007, Shipley et al. 2017). Shipley et al. (2018) also found that large immature and mature *C. perezi* spent their time exclusively along the continental shelf drop off in South Eleuthera, The Bahamas.

Out of all 4 species, *C. perezi* had the lowest probability of presence across habitats and depths. This low predictive power may be driven by the individuality of spatial use demonstrated by the community detection algorithm. Previous studies of *C. perezi* habitat use have shown that juveniles prefer reef habitats at depths <40 m (Pikitch et al. 2005) and may avoid shallow seagrass flats (Chapman et al. 2005). The GLMM and circle plots support this, with the highest probability of presence on CRCH receivers <10 m and a relatively low use of seagrass habitats. Overall, large juvenile space use may not be driven by underlying habitat and may instead be a result of territoriality or resource partitioning.

The GLMM found that the probability of presence on a receiver for *C. perezi* was significantly lower in 2015 than it was in 2014. This is likely because of the dramatic array expansion that occurred in 2015 combined with the highly individualized movements displayed by *C. perezi* within in the study site (Fig. 6). Although 4 additional *C. perezi* were tagged during the 2015 season and standardization methods were used to account for the addition of receivers, this may not have been enough to compensate for the addition of 35 receivers, largely in deep water along the continental shelf. Most YOY and age-1 *C. perezi* occupy a specific, confined area along the reef system close to Buck Island, leaving much of the array unused (Fig. 6a). The receivers in this area were largely part of the original 2013 array, meaning the array expansion mainly decreased the probability of presence of these sharks on a receiver.

Although ontogenetic shifts in habitat and depth with spatiotemporal segregation between adult and juvenile *C. perezi* have been observed previously (Pikitch et al. 2005, Brooks et al. 2013), we found strong spatial segregation much earlier, starting with juveniles age 2 and older (111+ cm FL). Similar to our observations, Bond et al. (2012) noted that acoustically tagged *C. perezi*, including immature individuals, in Glover's Reef were rarely detected simultaneously on the same acoustic receiver. We hypothesize that this observed spatial segregation may be driven by intraspecific territoriality or resource partitioning necessitated by direct competition for food. Further research into prey availability in BIRNM and direct behavioral observations among conspecifics would be necessary to better determine the drivers behind these patterns.

5. CONCLUSIONS

This research adds to the growing support for network analysis as a tool to understand animal movements and interactions, particularly in aquatic environments. Although many studies have used network analysis to look at the movements of a single species with acoustic telemetry (see Jacoby et al. 2016 for review), fewer have applied network analyses to explore both intra- and interspecific spatial overlap of simultaneously tracked animals (Finn et al. 2014, Espinoza et al. 2015, Lédée et al. 2015, 2016, Heupel et al. 2018). As previously demonstrated by Finn et al. (2014), community detection algorithms can illustrate similarities and differences in spatial ecology between species. Our study expands upon that, demonstrating that community detection algorithms can also discern intra-specific changes in space use related to the life history stage of the tagged individual.

BIRNM is able to provide protection from fishing pressure to both wide-ranging species like *Galeocerdo cuvier* and spatially segregating species like *Carcharhinus perezi* because of its relatively large size, depth range, and habitat complexity. Our findings emphasize the importance of scale and including heterogeneous habitats when designing MPAs for large, mobile species. The diversity of habitats encompassed within BIRNM's expanded boundaries, as opposed to protecting a single focal reef, affords protection to more individual *C. perezi*, a number of highly mobile *G. cuvier*, as well as *Negaprion brevirostris* and *Ginglymostoma cirratum* that rely on shallower habitats and complex reef systems for protection from predators and foraging opportunities. Although we are unable to accurately quantify boundary crossing between BIRNM's protected waters and adjacent management areas due to limited receiver coverage beyond the MPA boundaries, it is clear that BIRNM plays a significant role in the daily movements of multiple shark species in St. Croix's waters. Future studies exploring connectivity between BIRNM and mixed-use areas like the EEMP, offshore seasonally protected areas like Lang Bank, and coastal St. Croix will be vital to further contextualize the role BIRNM plays in shark conservation and fisheries management in the USVI and the greater Caribbean.

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