REGULAR ARTICLE

Migratory patterns and seasonal habitat use of great hammerhead sharks (*Sphyrna mokarran*) in the southeastern United States

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Abstract

The great hammerhead shark (*Sphyrna mokarran*) is a highly mobile shark species whose population in the United States declined dramatically through the early 2000s. Their spatial ecology is poorly understood, creating challenges for effective conservation of this enigmatic marine predator. Using acoustic telemetry and network analyses, we describe the movement patterns of 15 mature great hammerhead sharks (207–331.5 cm fork length) primarily within the waters of the southeastern United States from April 2019 to December 2022, including identifying movement corridors, core use areas and seasonal shifts in habitat use. Great hammerheads exhibited partial migration; some sharks undertook consistent, repeatable, round-trip migrations between the tagging site in the Florida Keys and northern points in the Gulf of Mexico and Atlantic coast. Conversely, others remained in the Florida Keys year-round. Network analysis coupled with community detection algorithms revealed that individual great hammerheads displayed oceanic basin affinity, favouring migration to either the Atlantic Ocean or Gulf of Mexico. Great hammerheads that remained in the Florida Keys shifted their habitat use seasonally from inshore channels (spring and summer) to offshore artificial reefs and the natural reef tract (summer

through winter). These shifts may be driven by prey availability, as core use areas often corresponded to known locations of seasonal spawning aggregations for reef fish. These data fill an important knowledge gap for great hammerhead migratory patterns that can improve spatial management strategies for this historically over-exploited species. We discuss the importance of drawing upon data from multiple tagging locations for highly mobile species management, particularly in the designation of essential fish habitat.

1 | INTRODUCTION

Animal movements are driven by a variety of interacting biotic and abiotic factors across space and time that ultimately influence individual biological fitness and ecosystem dynamics (Lubitz et al., 2022; Nathan et al., 2008; Riotte-Lambert & Matthiopoulous, 2020). Fluctuations in prey availability, seasonal temperature regimes and reproduction can all drive annual migratory patterns (Chapman et al., 2015; Lubitz et al., 2023; Shaw, 2016; Yates et al., 2015). For highly mobile species, long-distance movements to fulfil life-history requirements can be energetically costly but have evolved to maximize an individual's lifetime fitness (Alerstam et al., 2003; Blem, 1980). As such, mobile organisms employ various movement strategies to meet their life-history needs, such as reproduction, while maximizing the potential for energetic gains (Lowerre-Barbieri et al., 2021). In some species, this results in high variability in individual migratory behaviour, ranging from nomadism to partial migration, where only a fraction of the population migrates (Chapman et al., 2012; Chapman et al., 2015; Teitelbaum & Mueller, 2019).

Quantifying movement patterns, their drivers and the degree of individual variability for highly mobile species is essential for informing policy and management regulations (Carlson et al., 2021; Mannocci et al., 2017). Understanding individual variability in space use from year to year and across individuals in a population is particularly important for these species, as they often cross state or federal jurisdictional boundaries (Heupel et al., 2015; Song et al., 2017). However, when exploring spatially explicit data, variation in movement patterns among individuals is often overlooked in favour of determining overall population trends (Lowerre-Barbieri, Kays, et al., 2019; Lubitz et al., 2022). Although population-level data are essential, individual variation in movement patterns can significantly affect the success of spatially based management (Lea et al., 2018). For example, by documenting individual variation in tiger shark *Galeocerdo cuvier* (Péron & Lesueur 1822) migrations, Daly et al. (2018) demonstrated a spatial mismatch between existing protected areas and individual high-use areas. As resource managers move from single species' stock management towards more ecosystem-based approaches (Crowder & Norse, 2008; Massol et al., 2011), the need for improved spatial data has increased, particularly as it pertains to boundary crossing and defining essential fish habitat (Moore et al., 2016; Taylor et al., 2017).

The rise of biologging and biotelemetry has allowed for significant advances in our ability to quantify the spatial ecology of highly mobile species (Hussey et al., 2015). In aquatic systems, acoustic telemetry presents a relatively affordable method for tracking animal movement at finer scales than satellite telemetry (Hussey et al., 2015; Matley et al., 2022). The widespread use of acoustic telemetry has allowed for the formation of regional data-sharing networks to facilitate broader-scale studies than single, individually managed acoustic receiver array (Bangley et al., 2020; Friess et al., 2021; Young et al., 2020). Inter-agency and inter-institutional acoustic telemetry collaborations have been established throughout the coastal United States, including the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG), FACT in the southeastern United States and Mid-Atlantic acoustic telemetry observation system in the northeastern United States, whereas the Ocean Tracking Network (OTN) facilitates acoustic telemetry data sharing on a global scale. For highly migratory coastal shark species, the use of acoustic telemetry networks has helped revolutionize our understanding of shark habitat use and migratory behaviour (Heupel et al., 2019; Lédée et al., 2021).

The great hammerhead shark *Sphyrna mokarran* (Rüppell 1837) is a large coastal species that occupies a range of habitats from relatively shallow sand and seagrass flats (Lubitz et al., 2023; Roemer et al., 2016) to oceanic waters adjacent to the continental shelf (Calich et al., 2018; Calich et al., 2021; Graham et al., 2016). They are circumtropical and globally assessed as critically endangered by the International Union for the Conservation of Nature Red List (Rigby et al., 2019). In the United States, recent assessments of relative abundance indicate that the population is showing modest signs of recovery (Pacoureau et al., 2023; SEDAR, 2022) after dramatic declines during 1990s and early 2000s (Jiao et al., 2009).

Little is known about the life history and ecology of great hammerheads (Gallagher & Klimley, 2018). In particular, the need for more spatial ecology data to inform management has been noted, especially related to fine-scale habitat use, specific migration corridors and female philopatry (Gallagher & Klimley, 2018; Miller et al., 2014). These data can be used to inform the designation of essential fish habitat, which is required in the United States by the Consolidated Highly Migratory Species Fishery Management Plan to fulfil the requirements of the Magnuson-Stevens Fishery Conservation and

Management Act (NMFS, 2006). Essential fish habitats are defined as habitats that are necessary for the survival of a species at each life stage, including spawning, breeding, feeding or growth to maturity. The National Marine Fisheries Service is required to minimize the effect of fishing and other actions on essential fish habitat and promote its conservation and enhancement. These habitats are defined for all highly migratory species in federal waters, including great hammerheads, and are reviewed regularly to include the most up-to-date scientific information (NOAA Fisheries, 2017).

Much of what is known about great hammerhead distribution and spatial ecology in the United States comes from limited mark-recapture tagging studies (Kohler & Turner, 2019), fisheries-dependent landings data (Miller et al., 2014; SEDAR, 2022) and broad-scale telemetry studies that have largely used satellite transmitters (Calich et al., 2018; Graham et al., 2016; Guttridge et al., 2017; Hammerschalg et al., 2011). Collectively, spatial ecology studies have shown that great hammerhead sharks tagged in the greater Miami, Florida, area can range as far north as New Jersey in the Atlantic (Hammerschalg et al., 2011), spend over 90% of their time within the U.S.-exclusive economic zone (Graham et al., 2016) and use habitats along the south-central Atlantic coast of Florida year-round (Calich et al., 2018). Given the ever-expanding infrastructure of coastal acoustic telemetry networks (Young et al., 2020) and the smaller spatial error generally associated with acoustic telemetry (Kessel et al., 2014), that can then be better connected to benthic habitat characteristics (Novak et al., 2020), acoustic telemetry can be a valuable tool for filling the remaining spatial knowledge gaps. For instance, in Bimini, The Bahamas, integrating acoustic telemetry, satellite telemetry and photo identification of great hammerhead sharks allowed for the documentation of annual site fidelity from October to April, as well as connectivity between The Bahamas and Atlantic coast of the southeastern United States (Guttridge et al., 2017).

In this study, we examined the spatial ecology of great hammerhead sharks tagged in the Lower Florida Keys, including quantifying migratory connectivity between the Florida Keys and other regions and characterizing seasonal shifts in space use within the Florida Keys. To achieve these goals, we used an extensive dataset generated from an acoustic telemetry array spanning the length of the Florida Keys, from Key Largo to the Marquesas (Brownscombe et al., 2020), as well as data sharing from multiple acoustic telemetry networks. Collectively, these detection data allowed us to examine individual-level movement patterns of great hammerhead sharks across a vast spatial scale and across multiple years, thus filling important knowledge gaps about this critically endangered species.

2 | METHODS

2.1 | Shark capture and tagging

Fishing for great hammerhead sharks was conducted near an Atlantic tarpon *Megalops atlanticus* (Valenciennes 1847) pre-spawning aggregation in Bahia Honda Channel (24.658° N, −81.287° W), a high-flow channel in the Lower Florida Keys, from March to May of 2019–2022. Great hammerhead sharks were targeted using handlines or a small longline baited with crevalle jack *Caranx hippos* (Linnaeus 1766) or barracuda *Sphyraena barracuda* (Edwards 1771) on 18/0 or 20/0 circle hooks (Casselberry et al., 2024). A coded acoustic transmitter (Model V16, 69 kHz, tag delay 90–180 s, estimated battery life 2685 days, Innovasea, Halifax, Nova Scotia, Canada) tethered to a titanium dart (Large Ti Anchor, Wildlife Computers, Redmond, Washington, USA) was inserted at the base of the dorsal fin. External tag attachment was selected to shorten workup times, reducing the physiological stress response (Gallagher et al., 2014; Gulak et al., 2015) to help ensure survival. Prior to release, sharks were measured (fork length) to the nearest 0.5 cm, and sex was determined based on the external characteristics, namely presence of claspers for males.
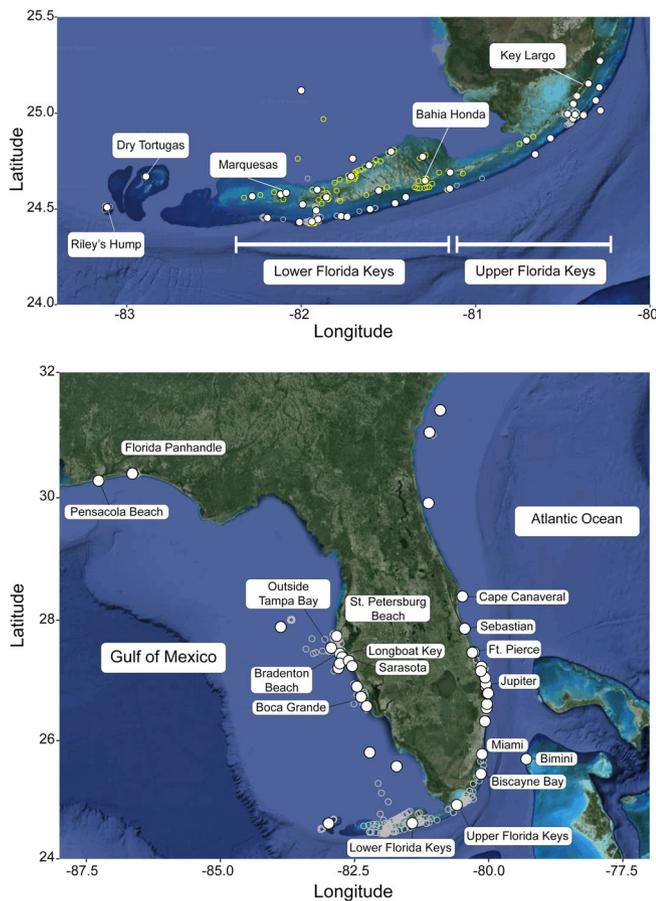
2.2 | Acoustic telemetry data collection

The Florida Keys are an approximately 350-km-long archipelago extending from the southern tip of Florida, bordered by the Gulf of Mexico to the north and west and the Atlantic Ocean to the south and east (Lapointe & Matzie, 1996). The Florida Keys host the third-largest coral barrier reef in the world, as well as a diversity of other nearshore channel and seagrass flat habitats (Lapointe et al., 2004; Maliao et al., 2008). Sharks were tracked throughout the Florida Keys in an array of 143 acoustic receivers (model VR2W and model VR2Tx, Innovasea, Halifax, Nova Scotia, Canada), ranging from Key Largo to the Marquesas at depths between 0.1 and 18.8 m (Figure 1; Table S1). The array was originally designed to track the movements and habitat use of two gamefish, Atlantic tarpon and permit *Trachinotus falcatus* (Linnaeus 1758), with receivers distributed across different habitat types, including natural reef, artificial reef, seagrass flats and high-flow channels (Brownscombe et al., 2020; Brownscombe et al., 2023; Griffin, Brownscombe, et al., 2022; Griffin, Casselberry, et al., 2022). Detailed range testing using V13 transmitters showed variable detection efficiency based on habitat but was generally between 75 and 300 m (Brownscombe et al., 2019). The V16 transmitters used in this study have a higher power output than V13 transmitters, and thus 50% detection efficiency is likely a greater distance for these tags. Additional detections from receiver arrays in the Florida Keys and throughout the Gulf of Mexico and Atlantic coast were added to the dataset through data sharing with acoustic telemetry networks, namely iTAG, FACT and OTN (Figure 1). Detections for this study were compiled from 10 April 2019 to 31 December 2022, and all further analyses were conducted using R version 4.1.2 (R Core Team, 2021).

2.3 | Data analysis

2.3.1 | Regional connectivity

To assess regional connectivity throughout the southeastern United States, as well as individual variation in migratory behaviour,

FIGURE 1 Map of acoustic receivers that detected great hammerhead sharks in the Florida Keys (upper) and the full distribution of receivers that detected great hammerhead sharks in coastal Florida, Georgia, and The Bahamas (lower). In the upper panel, open circles are receiver locations maintained by the UMass research team (yellow) and members of telemetry networks (grey). White circles are mean coordinates used to define receiver nodes. In the lower panel, open circles (grey) represent all receiver locations, and white circles are mean coordinates used to define receiver notes. Locations mentioned specifically in the text are labelled.

we coupled bipartite network graphs with community detection algorithms (Finn et al., 2014). Prior to generating networks, acoustic receiver stations were grouped into regional clusters based on their proximity to coastal features (e.g., Tampa Bay) or cities (e.g., Miami Beach), which also often coincided with individual array owners. For this analysis, the Florida Keys receivers were grouped into two regional nodes, with the Lower Keys defined as all receivers from the Seven Mile Bridge west to the Marquesas, and the Upper Keys from Marathon Key east to Key Largo. Bipartite network graphs consist of two types of nodes, in this instance, individual sharks and regional receiver clusters. Shark nodes are connected to the regional nodes where they were detected via directed edges. The bipartite network was constructed using the *igraph* package (Csardi & Nepusz, 2006). To account for uneven receiver distribution across regions (e.g., 187 receivers in the Lower Keys and 4 receivers in Pensacola Beach), we multiplied our matrix of observed connections between sharks and

regions with the inverse of receiver count for each region before the edge list was created. To ensure that inferences were valid, and sharks were moving non-randomly within the network, we created a list of 10,000 random bipartite networks using the nullmodel command in the *bipartite* package to reshuffle the links in our observed network (Dormann et al., 2008). Nestedness was calculated for the observed and random networks using the *vegan* package (Oksanen et al., 2020), with the observed network value falling outside of the distribution of random networks.

A suite of six community detection algorithms from the *igraph* package were applied to our observed network: Leading-Eigenvector (Newman, 2006), Fast-Greedy (Clauset et al., 2004; Newman & Girvan, 2004), Spin-Glass (Reichardt and Bornholdt 2006), Label-Propagation (Raghavan et al., 2007), Walktrap (Pons & Latapy, 2006) and Multilevel (Blondel et al., 2008). These algorithms seek to maximize the modularity of the graph (Newman & Girvan, 2004) by identifying groups of nodes that are more closely associated with each other than the rest of the graph (Finn et al., 2014; Fortunato, 2010). In this study, graph theory communities (not to be confused with ecological communities) are composed of regional nodes and sharks. Modularity score was used to assess algorithm performance and the quality of community divisions. More details on these algorithms, as well as the application of community detection algorithms to acoustic telemetry data, can be found in Finn et al. (2014) and Casselberry et al. (2020).

The delineated communities from the best-performing community detection algorithm were then assessed as in-communities or out-communities. An in-community has nodes that receive significantly more of their in-strength (in degree) from nodes within the community. An out-community consists of nodes that direct significantly more of the out-strength (out degree) towards nodes within their community (Landi & Piccardi, 2014). A community without significant differences is considered an in-/out-community (Landi & Piccardi, 2014). In- and out degrees were calculated for each node, and Wilcoxon rank-sum tests were used to determine significant differences in strength for each community ($p < 0.05$, Finn et al., 2014).

To better highlight movement corridors and broad regional connectivity, a unipartite network graph, including all tagged individuals, was constructed using *igraph*. Unipartite networks consist of one node type, in this case, regional aggregations of receivers, with movements between nodes represented by directed edges. Edges, or movement corridors between nodes, were weighted based on the number of times they were traversed by individuals. These networks were then visualized using *ggmap* (Kahle & Wickham, 2013) and *ggplot2* (Wickham, 2016). This was also done for movements exclusively within the Florida Keys. To allow for better visualization of movement corridors within the Florida Keys, individual receivers were aggregated into local nodes as described in Lowerre-Barbieri et al. (2021) and Griffin, Casselberry, et al. (2022) based on receiver proximity and shared habitat characteristics. Unipartite networks for Florida Keys detections alone were also visualized using *ggmap* (Kahle & Wickham, 2013) and *ggplot2* (Wickham, 2016).

2.3.2 | Seasonal migratory patterns

To determine if there were seasonal shifts in space use, unipartite network graphs were constructed from detections for each shark for each season-year combination. Seasons were defined as follows: winter from December to February, spring from March to May, summer from June to August and autumn from September to November. Networks were constructed using the *igraph* package (Csardi & Nepusz, 2006). As with the unipartite graphs described above, acoustic receiver stations were grouped into regional clusters, including smaller habitat-based groupings within the Florida Keys. Prior to further analyses, individual sharks were determined to be moving non-randomly by generating 10,000 random networks maintaining degree distribution using the *tnet* package (Opsahl, 2009). T-tests were then used to determine if the observed network's clustering coefficient and network reciprocity were significantly different from the distribution of each network metric in the 10,000 randomly generated networks (Opsahl & Panzarasa, 2009).

Individual core use areas were identified based on node-level network metrics of centrality using a principal component analysis (PCA) approach developed by Lédée et al. (2015). For each node in each network, in degree, out degree, eigenvector centrality and closeness were calculated using *igraph* commands. Nodes with high eigenvector centrality had a strong influence on the structure of the network with high node strength and strong connections to other receiver groups with high node strength (Lédée et al., 2015). Nodes with high closeness are strongly connected to the other nodes in the network. Closeness is calculated by the reciprocal of the sum of the shortest paths between the node of interest and other nodes in the network. Metrics were checked for collinearity using Spearman's rank correlation coefficient, and metrics with a correlation coefficient greater than 0.75 were removed. Preference for retaining metrics was as follows: (1) eigenvector centrality, (2) in degree, (3) out degree and (4) closeness. PCA using the *prcomp* command in the *stats* package (R Core Team, 2021) was used on the remaining metrics to determine those that were most influential in the network. The metric or metrics that had the highest absolute loading value within each component were used to select core use areas, retaining components with up to 80% of the variation explained. Receivers with the highest values for the selected metrics were designated as core use areas. Structural equivalence graphs were created using the equiv.clust command in the *sna* package (Butts, 2022) to identify nodes that had similar characteristics in the network to PCA-identified core use nodes, and these nodes were added to the core use group. Core use nodes were then compiled across all sharks for each season to visualize seasonal shifts and overlapping core space use.

To assess seasonal changes in residency throughout the study area, we calculated monthly residency indices for each shark in each general location. Receivers were deemed to be in the Florida Keys if they were located between the Marquesas and Key Largo. As with the bipartite and unipartite network graphs, the Dry Tortugas were treated as their own receiver group. Residency events were calculated using the *glatos* package (Holbrook et al., 2021). Sharks with two or more detections within one hour were deemed present in an area for that day, creating a residency event. If more than an hour passed between detections, a new event was started. A monthly residency index for each individual was then calculated by dividing the number of days an individual was present in an area by the number of days in that month (Appert et al., 2023). This was then averaged across individuals for a mean monthly residency index for events within the Florida Keys and outside of the Florida Keys. Fluctuations in monthly residency were assessed relative to mean monthly sea surface temperature (SST) in the Florida Keys, obtained using the *rerddapXtracto* package (Mendelssohn, 2021; dataset ID: jplMURSST41, bounding box longitude: −81.096, −81.496 latitude: 24.445, 24.846).

Generalized linear mixed models with individual shark as the random effect were used to determine the factors that most influence great hammerhead shark detection. Binary monthly presence (1 = present, 0 = absent) data were generated for each individual within and outside of the Florida Keys based on the previously calculated monthly residency index for each individual in both locations. The global model included location (Florida Keys or outside of the Florida Keys), season and mean monthly SST with individual shark as a random effect:

$$\text{Monthly presence} \sim \text{location} + \text{season} + \text{mean SST} + (1|\text{individual shark})$$

Independent variables were checked for correlation using Spearman's rank correlation coefficients with a threshold of 0.6. A candidate model set was constructed using *lme4* (Bates et al., 2015), and the best model was selected using corrected Akaike information criterion (AICc) with *AICcmodavg* (Mazerolle, 2020). Subsequent model fit was evaluated using the *MuMIn* package (Bartoń, 2020), and Tukey's post hoc pair-wise comparisons of categorical variables for significance were calculated using the *multcomp* package (Hothorn et al., 2008). Finally, variations in the probability of presence were visualized by computing estimated marginal means for significant covariates from the best model using *emmeans* (Lenth, 2021).

2.3.3 | Habitat use

To determine if there were seasonal shifts in habitat use within the Florida Keys, relative habitat use was visualized using a chord diagram. Each receiver was assigned a habitat designation based on coastal features and water flow related to receiver location as detailed in Brownscombe et al. (2019). This resulted in six habitat levels: channels, flats, reef tract, artificial reef, banks and basins. For each season, movement matrices were created based on habitat origin and destination for each detection. To account for uneven receiver distribution throughout habitat types, movement matrices were multiplied by a diagonal matrix of the inverse of receiver count for each habitat (Casselberry et al., 2020). Seasonal chord diagrams for both habitat descriptions were created using the mig_chord command in the *migest* package (Abel, 2022). To visualize if these habitat shifts were reflected in shifts in core use areas within the Florida Keys, maps of core use areas

colour coded by habitat type were generated for each season using *ggmap* (Kahle & Wickham, 2013) and *ggplot2* (Wickham, 2016).

To examine how habitat use and depth may shift seasonally within the Florida Keys, generalized linear mixed models were developed from binary monthly presence/absence data. The global models were:

$$Monthly\ presence \sim habitat + season + mean\ SST + (1|individual\ shark)$$

and

$$Monthly\ presence \sim depth + season + mean\ SST + (1|individual\ shark)$$

Similar to the methods detailed above, AICc was used to select the best-performing model, fit was assessed using corrected R^2 and post-hoc comparisons for categorical variables were done using Tukey contrasts. Finally, model predictions were constructed using estimated marginal means in *emmeans* (Lenth, 2021).

3 | RESULTS

From April 2019 to December 2022, 18 great hammerhead sharks were captured and tagged in Bahia Honda Channel. The female-to-male sex ratio was 5:1. Female sharks (mean: 281.82 cm fork length, range: 207–331.5 cm fork length) were generally larger than males (mean 257.7 cm fork length, range: 221–283.2 cm fork length), with only two female sharks smaller than 221 cm fork length. All sharks were mature at the time of capture based on clasper calcification for males and estimated size at maturity for females in the Gulf of Mexico and northwestern Atlantic (176.0 cm fork length, Piercy et al., 2010). Of the 18 tagged sharks, three registered fewer than 10 detections (2 females and 1 male) and were excluded from further analysis. These sharks with limited detection histories may have shed their external acoustic tags, which was documented for the recaptured individuals discussed below, emigrated outside of the array or experienced mortality either from harvest or the tagging event itself. One of these individuals, GHH5, was double tagged with an acoustic and pop-up satellite archival tag (PSAT). The PSAT report indicated that the tag detached and reported early due to a pin-break, indicative of the shark shedding the tag. The acoustic tag may have been shed at the same time. The cause of the limited detection history is unknown for the other two individuals. The remaining 15 sharks registered 18,338 detections over the 45-month study period (Table 1) throughout the Florida Keys, Gulf of Mexico and Atlantic Ocean (Figure 2). Three individuals were recaptured in Bahia Honda, once each in subsequent years. Recaptured sharks grew on average 6.2 cm (± 2.4 cm standard deviation) with 1–2 years at liberty (see Table 1 for details). All recaptured sharks had shed their external acoustic tags by snapping the tether external to the body and retaining the tag anchor. Individuals were identified based on cattle tags on the dorsal fin (see Casselberry et al., 2024) or retained satellite tags applied for

other studies and were retagged with an acoustic transmitter prior to release.

3.1 | Regional connectivity

Community detection analyses to determine regional connectivity for great hammerhead sharks found four communities using the Walktrap algorithm (Figure 3a). This algorithm had a slightly lower modularity score than the best-performing algorithm (difference of 0.003) but identified more significant communities (Table 2). Two communities were broad regional groupings of receivers encompassing the Gulf and Atlantic coasts of Florida, respectively, whereas the remaining communities encompassed smaller, more distinct regions (Figure 3b). Community 1 consisted of four sharks, the Upper Florida Keys and the majority of the Atlantic coast receiver groups. Eight sharks that primarily used the Lower Keys, the region with the highest-degree strength within the network, were placed in Community 2. Other notable locations for Community 2 sharks included Bimini, The Bahamas and the Dry Tortugas. Community 3 contained two sharks and all locations in the Gulf of Mexico. Community 4 consisted of one shark and a small group of receivers between Ft. Pierce and Sebastian, Florida, along the Atlantic coast. Communities 1 and 3 were both significant in-communities ($p = 0.005$ and 0.002, respectively). The remaining two communities were in-/out-communities, meaning sharks in these communities are highly connected to areas both within and outside of their community. This was largely driven by the regular use and return to the Lower Keys by most sharks in the study (Figure 2).

Unipartite graphs of regional connectivity showed that sharks took varying routes to reach points outside of the Florida Keys, but strong regional connectivity exists between the Lower and Upper Keys, as well as within the Tampa Bay area (Figure 4). Edges were traversed between 1 and 65 times throughout the study. The corridor between the Lower and Upper Keys had the highest edge weight in the network, followed by connections in the Tampa Bay area, including outside of Tampa Bay to St. Petersburg Beach, Longboat Key to Bradenton Beach and Bradenton Beach to outside of Tampa Bay. There was also a moderate degree of connectivity between the Upper Keys and Biscayne Bay, as well as Sarasota and Longboat Key. On the west coast of Florida, most routes to the Florida panhandle went through Tampa Bay, but there were tracks directly connecting the Florida Keys to the panhandle, showing the potential for offshore movements traversing the Gulf of Mexico.

Given the high degree of connectivity within the Florida Keys, an additional unipartite graph was made on a finer scale to examine movement corridors within the Florida Keys. Movements between local nodes were widespread (Figure S1), with edges traversed up to 47 times throughout the study period. The highest edge weights were given to the connections between Bahia Honda Channel and the Middle Keys Flats, Lower Keys Atlantic Flats, Centermass bridge rubble and Adolphus Busch wreck (Figure 5). The Centermass and Adolphus Busch artificial reef sites were entry points for highly traversed edges

TABLE 1 Tagging details for the great hammerhead sharks presented in this study, including number of detections in each basin (Atlantic, Gulf of Mexico and Florida Keys).

	Individual characteristics			Tagging and detections				Oceanic basin use		
Shark ID	Date tagged	Sex	Fork length (cm)	Date last detected	Total detections	# Days detected	# Days at liberty	Atlantic	Gulf of Mexico	Florida keys
GHH1	4/9/19	F	267	4/8/20	411	52	366	0	29	382
GHH2	4/9/19	F	271	12/11/22	2117	165	1343	0	1986	131
GHH3	4/10/19	F	260	9/20/21	673	75	895	0	3	670
GHH4	4/10/19	F	247	8/30/19	567	64	143	25	0	542
GHH5	4/11/19	F	277	10/24/22	3118	387	1293	90	4	3024
GHH6	4/12/19	F	280	7/30/19	471	57	110	178	50	243
GHH7	4/13/19	F	207	12/26/22	2541	347	1354	54	0	2487
GHH8	4/13/19	F	331	4/21/19	2	1	9	0	0	2
GHH9[a]	4/30/19	F	277	6/11/20	661	75	409	30	0	631
GHH10	5/23/19	F	212	5/25/19	8	2	3	0	0	8
GHH11	3/22/20	F	254	3/15/22	1175	108	724	0	1	1174
GHH12	3/23/20	M	269	10/13/20	277	56	205	0	0	277
GHH13	3/24/20	F	284	5/25/20	276	26	62	0	0	276
GHH14[a]	3/22/20	F	322.5	1/5/21	1478	78	290	3	59	1416
GHH15	4/6/21	M	283	NA	0	0	NA	0	0	0
GHH16	4/8/21	M	221	12/30/22	1479	154	632	116	0	1363
GHH17	4/19/22	F	320	09/09/22	488	47	144	0	0	448
GHH18[a]	3/24/20	F	322.5	12/08/22	2646	235	990	188	0	2458

Note: Due to tag shedding, days at liberty was defined as the number of days between the tagging date and the date of last detection. Because it is impossible to know when exactly a recaptured shark, tagged with only an acoustic transmitter, shed its tag, days at liberty for these sharks likely include time periods when they did not have an acoustic transmitter attached. Although GHH15 was never detected in an acoustic array, this shark was double tagged with an acoustic tag and pop-up satellite archival transmitter (PSAT). The PSAT was shed on 4 December 2021 via a pin break, indicative of the shark actively breaking the tag off its attachment point to the dorsal fin, and not a mortality. It is likely that the acoustic tag was shed on the same date.
[a]Represents sharks that were recaptured: GHH9 recaptured on 22 March 2020, GHH14 recaptured on 3 April 2022 and GHH18 recaptured on 12 April 2021.
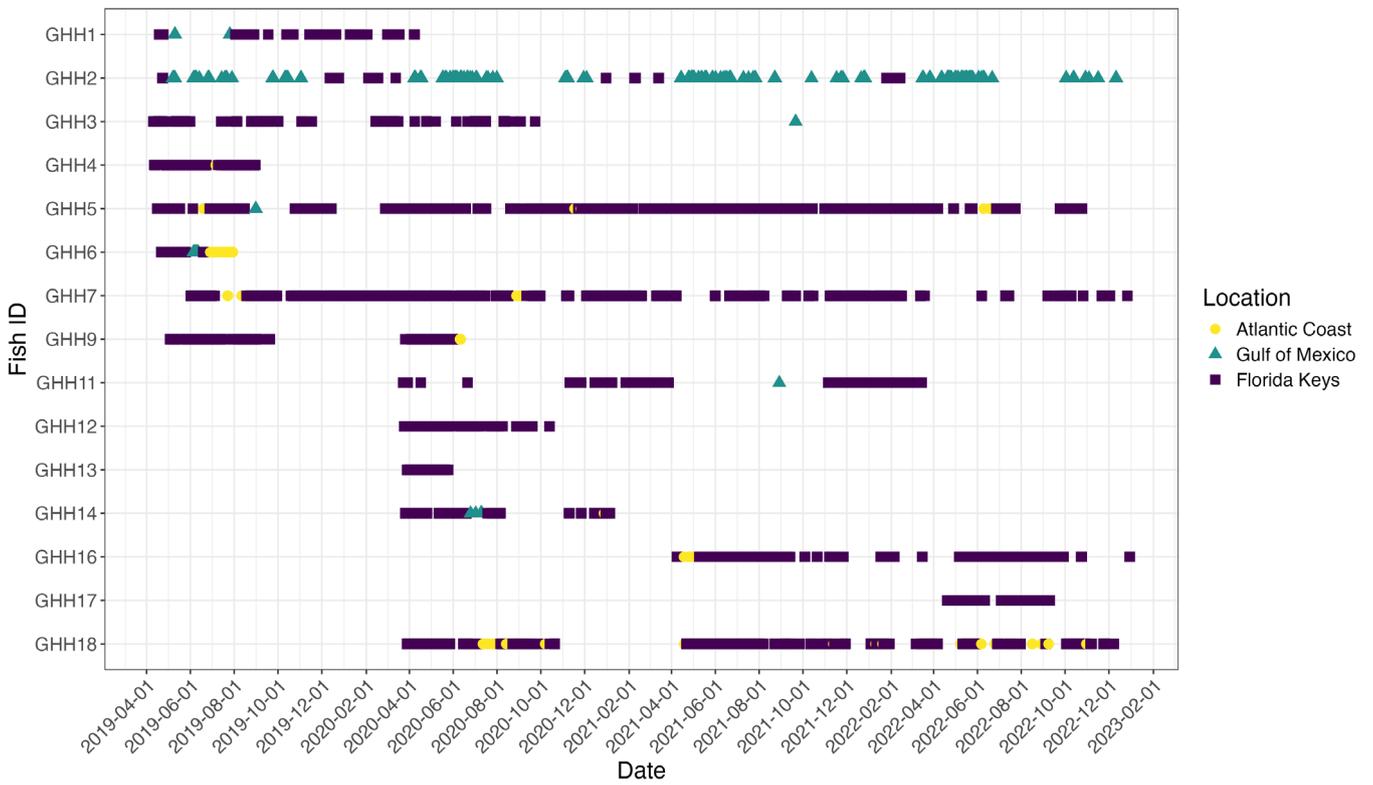
along the reef tract in the Lower Keys, which included both natural and artificial reef sites, such as Eyeglass Bar, Western Dry Rocks and the Vandenberg wreck (Figure 5). A high degree of connectivity was also present among the back country flats on the Gulf of Mexico side of the Lower Keys and between the Aquarius Research Base, a submerged research station in Florida Keys National Marine Sanctuary, and Pickles Reef in the Upper Keys. The strongest connection between the Lower and Upper Keys came from movements between Bahia Honda and the Aquarius Research Base (Figure 5).
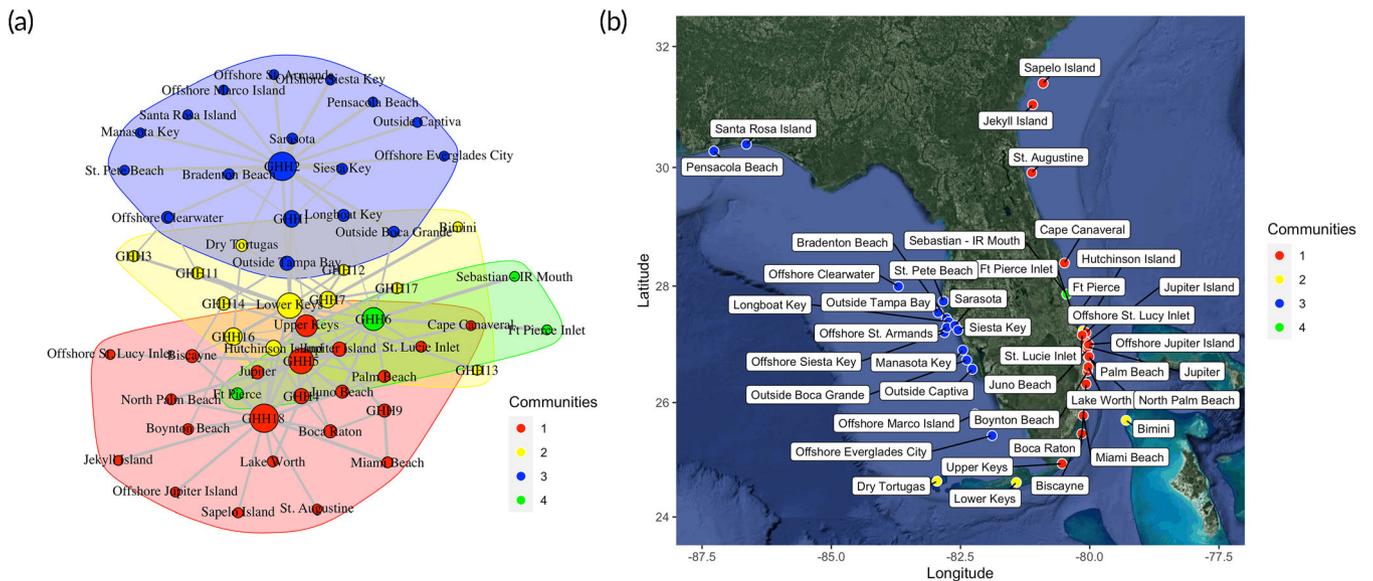
3.2 | Migratory patterns

Although great hammerhead sharks in our study were present in the Florida Keys year-round, detections in both the Gulf of Mexico and Atlantic occurred in pulses, largely from May to November (Supplemental Figure 2). Notably, for all years of the study, the Florida Keys was the only location where great hammerheads were detected in February. Residency index was low both within and outside of the Florida Keys (below 20% of all possible detection days), but residency

outside of the Florida Keys tended to coincide with seasonal increases in SST in the Florida Keys (Supplemental Figure 3). The generalized linear mixed model predicting the regional probability of presence performed best with the additive predictor variables of location and season with individual shark as a random effect (conditional $R^2 = 0.49$). The probability of presence was significantly higher within the Florida Keys than outside (Table S2), and great hammerhead sharks were significantly more likely to be detected in the spring and summer than winter (Table S3). Though probability of presence was highest in the Florida Keys, 95% confidence intervals surrounding predicted means were never above a 50% probability (Figure 6).

Seasonal unipartite network graphs revealed varying migratory and resident behaviours across individuals. Some sharks were remarkably consistent in their patterns (Figure S4). For instance, GHH2 completed four round-trip migrations from April 2019 to December 2022, moving from the Florida Keys to the Tampa Bay area on Florida's west coast each spring, continuing north in the Gulf of Mexico to the Florida panhandle through autumn, and then returning to Tampa and subsequently the Florida Keys in winter. This was the only shark that left the Florida Keys that showed a consistent annual migratory pattern

FIGURE 2 Great hammerhead shark detections registered on acoustic receivers over the course of the study coded by broad oceanic basin detection location. The absence of data points indicates times when sharks were not detected by acoustic receivers.
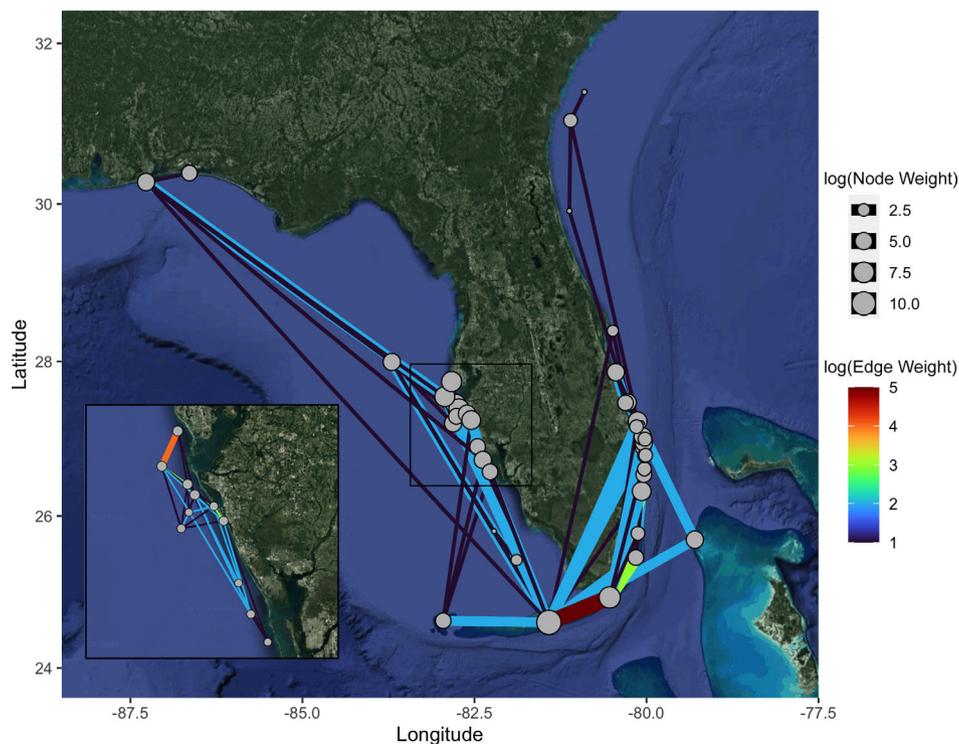

FIGURE 3 (a) Four distinct communities of sharks and regional receiver groups identified by the Walktrap algorithm within the bipartite network graph, presented in network space. Sharks and receivers are colour coded by community. Sharks are represented by nodes starting with GHH. All other nodes are named by general receiver location. All nodes are scaled by the relative number of detections, with sharks that are detected more frequently having larger node size. Edge thickness is scaled relative to the strength of the connection. Sharks that visit a regional node more frequently have thicker edges. (b) Geographic distribution of network communities identified by the Walktrap algorithm.

(Figure S5). Other sharks exhibited migratory patterns that varied annually. GHH7 made regular migrations from the Florida Keys to Bimini, The Bahamas, in the summer of 2019 and 2020 before moving

to the east coast of Florida and migrating south back to the Florida Keys but was not detected outside of the Florida Keys in 2021 and 2022 (Figure S5). Other sharks showed an alternate-year pattern.

TABLE 2   Modularity scores and community designations from the suite of six community detection algorithms run on the bipartite network graph of great hammerhead sharks and regional receiver clusters.

Algorithm	Modularity	Communities detected	Significant in-communities	Significant out-communities	In-/out-communities
Leading-Eigenvector	0.552	5	1	0	4
Fast-Greedy	0.566	4	1	0	3
Spin-Glass	0.557	6	2	1	3
Label-Propagation	0.555	5	1	0	4
Walktrap	0.563	4	2	0	2
Multilevel	0.566	4	1	0	3

FIGURE 4   Unipartite network map of regional connectivity throughout coastal Florida, Georgia, and The Bahamas. The inset highlights movement corridors between nodes in the greater Tampa Bay area, between Boca Grande and St. Petersburg. Node size is scaled based on the log of the number of detections in each location. Edges are scaled and colour coded based on the log of the number of times each path was traversed. Edges are representations of connections between two locations, not the true path followed by individual sharks.

GHH18 was tracked from the Florida Keys in summer 2020 north along the east coast of Florida to coastal Georgia before returning to the Florida Keys (Figure S5). This shark then remained in the Florida Keys throughout 2021 before resuming movements between the Florida Keys and east coast of Florida in spring 2022. Unlike in 2020, in 2022, GHH18 was not detected north of Ft. Pierce, Florida.

Only three sharks detected outside of the Florida Keys were detected in both the Gulf of Mexico and Atlantic Ocean basins. In summer 2019, both GHH5 and GHH6 were tracked from the Florida Keys to the east coast of Florida, back through the Florida Keys, and then north to the Tampa Bay area, before returning to the Florida Keys. These sharks traversed ∼1000 km straight-line distance in 2–3 months. Although GHH6 had only a brief detection history, GHH5 was detected through October 2022. This shark was detected exclusively in the Florida Keys until summer 2022 when it moved north to receivers near Cape Canaveral, Florida, before migrating south along Florida's east coast and returning to the Lower Keys. In summer 2020,
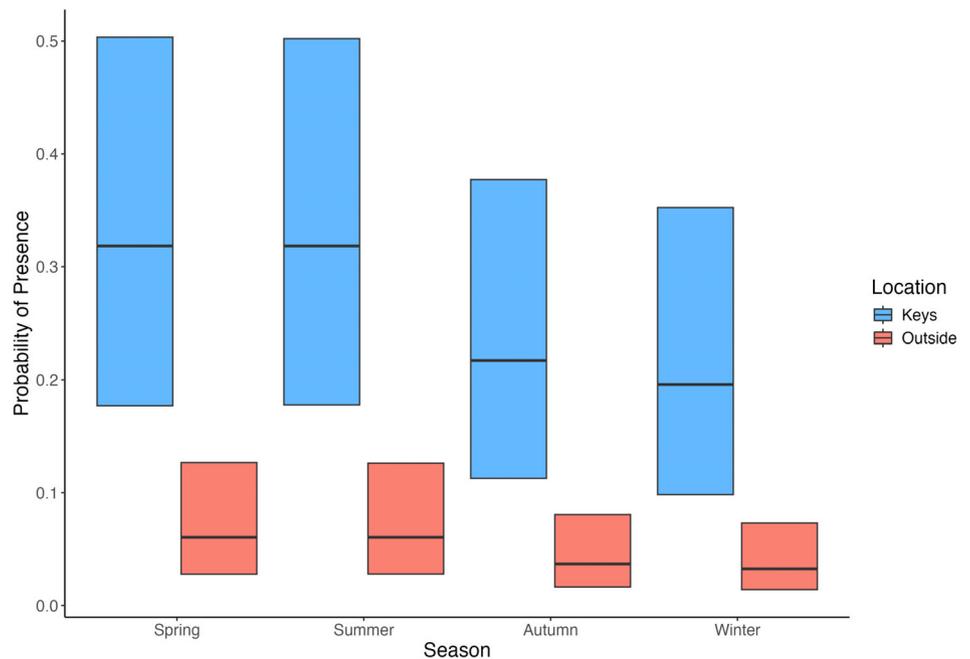
GHH14 left the Florida Keys and was subsequently detected on receivers outside of Tampa Bay, Florida, before returning to the Lower Florida Keys. This shark was also briefly detected outside of Biscayne Bay along the Atlantic coast. None of the tagged sharks registered more detections in the Atlantic than they did in the Florida Keys, whereas one shark, GHH2, was detected more frequently in the Gulf of Mexico than in the Florida Keys (Table 1; Figure S5).

The location of core use areas varied by season, but several locations were important to great hammerheads year-round. Bahia Honda, the tagging site, was a year-round core use area and the only area identified as core use for all 15 sharks (Figure 7). All other year-round core use areas fell along the reef tract in the Lower Florida Keys, with the exception of the receiver node off of Longboat Key, just south of Tampa Bay on Florida's west coast. In spring and summer, core use areas were concentrated in the Florida Keys but extended north to the Tampa Bay area on the west coast and Ft. Pierce on the east coast of Florida (Figure 7a,b). Autumn brought an increased use of offshore

FIGURE 5   Unipartite network map of highly traversed paths within the Florida Keys. Node size is scaled based on the log of the number of detections in each location. Edges colour coded based on the log of the number of times each path was traversed. Edge weights 1 and 2 have been removed to highlight movement corridors. High connectivity locations mentioned in the text are labelled. A full network of movements can be found in the supplemental information.
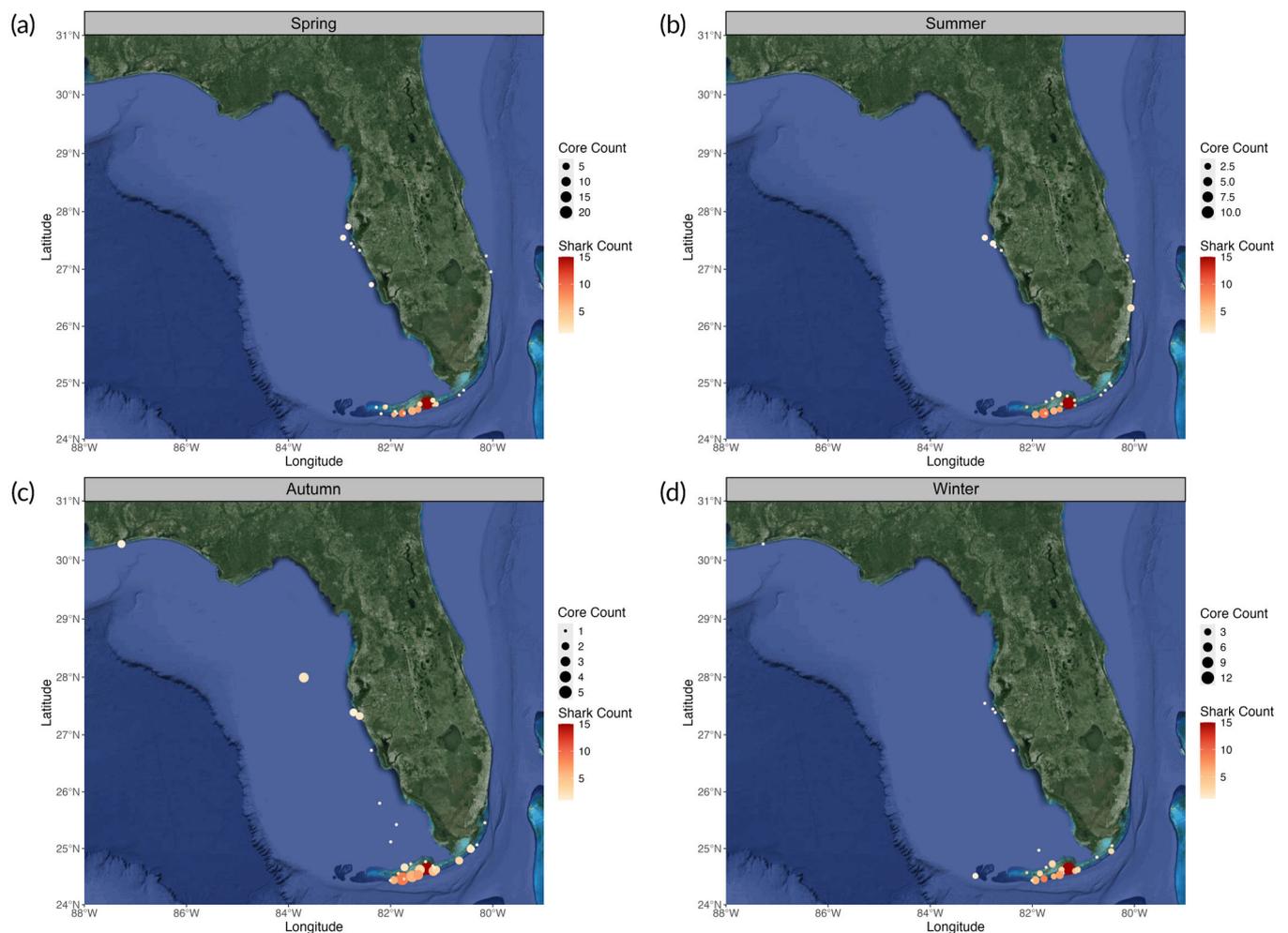
FIGURE 6   Predictive plot generated from the binomial generalized linear mixed models (GLMM) showing the effect of season on great hammerhead shark location. Means are bounded by 95% confidence intervals.

areas and northern extension of core use areas to Pensacola Beach in the Florida panhandle (Figure 7c). Core use areas also shifted away from points along the east coast in favour of the Upper Florida Keys. Pensacola Beach remained a core use area in the winter, but core use areas also shifted back towards nearshore points between Tampa Bay and Boca Grande in the Gulf of Mexico, as well as the Lower Florida Keys and Riley's Hump, west of the Dry Tortugas (Figure 7d).

3.3 | Habitat use

Within the Florida Keys, collective association with benthic habitat shifted seasonally, but channels and artificial reef habitats were used substantially year-round (Figure 8). Use of channels was most frequent during the spring, which was also the only season that saw regular use of flats habitats. The use of deeper water basins was more

FIGURE 7 Core use regions for great hammerhead sharks in (a) spring, (b) summer, (c) autumn and (d) winter. Points are scaled in size by the number of times that location was identified as a core use location (Core Count) and coloured based on the number of individuals for which the location was core use (Shark Count).

frequent in summer through winter, peaking in autumn, whereas artificial reefs were used most often in winter. These shifts are also reflected in the core use receiver habitats, which show the frequent use of channels, particularly in the spring, along with regular presence on the reef tract in the Lower Keys (Figure S6).
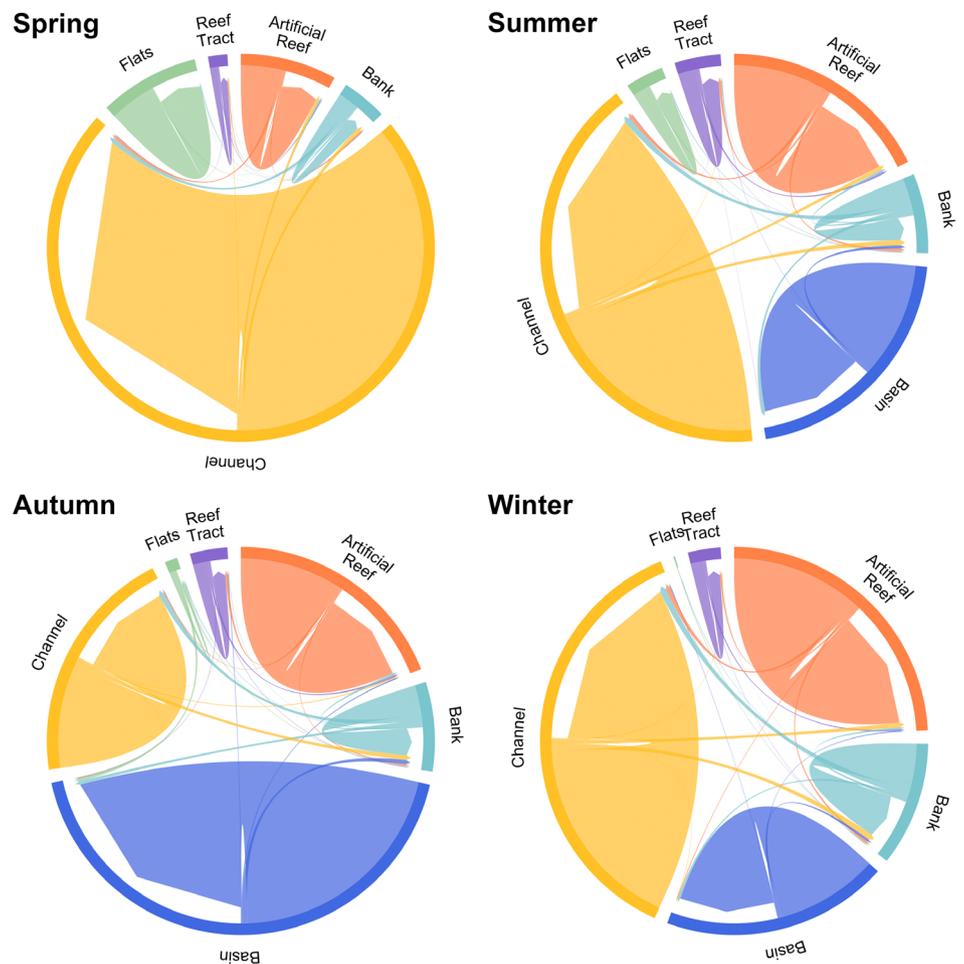
The best-performing binomial generalized linear mixed models for drivers of presence in the Florida Keys were the global additive models. For the habitat model, monthly presence varied significantly with season and habitat type but not mean SST (conditional $R^2 = 0.42$; Figure 9a; Table S4). Tukey's post hoc comparisons showed that monthly presence was significantly higher in spring and summer than in autumn (Supplemental Table 5). Tukey's post hoc comparisons showed that the probability of presence was significantly higher in channels than all other habitat types (Table S6). Use of the reef tract was significantly higher than artificial reefs, banks, basins and flats, whereas artificial reef use was significantly higher than banks and flats (Table S6). In the depth model, monthly presence varied significantly with depth and season, but not mean SST (conditional

$R^2 = 0.37$, Figure 9b; Table S7). The probability of detecting great hammerheads increased significantly with increasing depth and was significantly higher in spring and summer than autumn based on Tuckey's post hoc comparisons (Table S8).

4 | DISCUSSION

Great hammerheads are generally described as a solitary species (Miller et al., 2014), and our study showed high individual variation in space use for those tagged in the Lower Florida Keys. Sharks were tagged in close proximity to an Atlantic tarpon pre-spawning aggregation in Bahia Honda Channel. After tagging, individuals exhibited partial migration, with some regularly leaving the Florida Keys, whereas others remained in the area year-round. Bahia Honda was the only location to emerge as a core use area for all sharks tagged in the study. Further, all of the sharks tracked for over 1 year ($n = 9$) returned to the tagging site in subsequent years, highlighting the

FIGURE 8 Chord diagrams highlight the shifts in relative habitat use through the seasons for great hammerhead sharks within the Florida Keys. Each colour represents a unique habitat type, with directional arrows representing movement between or within habitats.
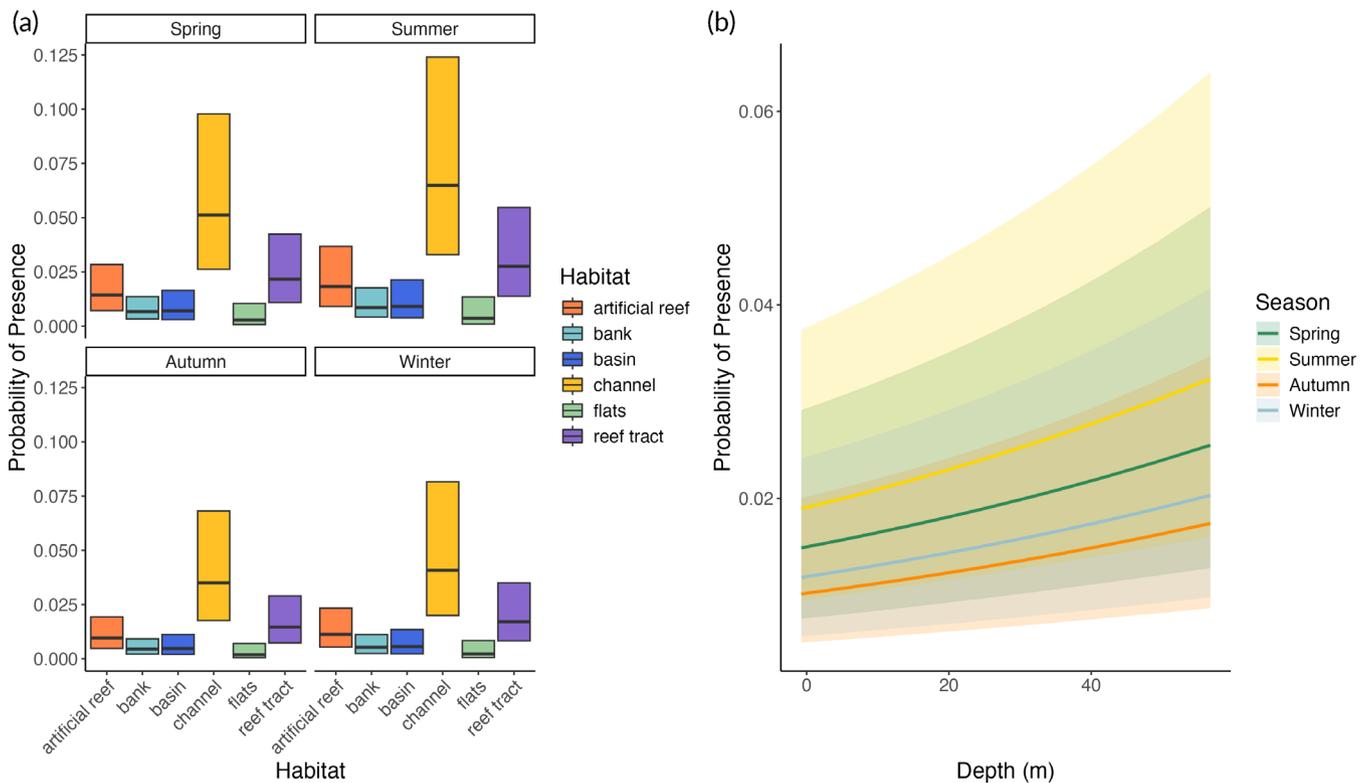

importance of Bahia Honda to these individuals. Notably, all of these sharks left the Florida Keys at some point during the study but consistently returned to Bahia Honda in the spring, coinciding with the seasonal aggregation of Atlantic tarpon in this location (Casselberry et al., 2024). Atlantic tarpon are a known prey item for great hammerhead sharks, particularly within the Florida Keys (Casselberry et al., 2024; Compagno, 1984). The results presented here add to the growing body of evidence that great hammerhead sharks can exhibit seasonal site fidelity to regions with abundant food sources (Guttridge et al., 2017; Heim et al., 2021), despite previously being described as a nomadic species (Compagno, 1984; Gallagher & Klimley, 2018). This is similar to other true apex predator shark species, including tiger sharks (Papastamatiou et al., 2013; Wirsing et al., 2007), bull sharks *Carcharhinus leucas* (Valenciennes 1839) (Griffin, Casselberry, et al., 2022) and white sharks *Carcharodon carcharias* (Linnaeus 1758) (Skomal et al., 2017; Winton et al., 2023). Instead of nomadic migrants, that infrequently repeat movement patterns and lack spatial and/or temporal regularity (Teitelbaum & Mueller, 2019), great hammerhead sharks in the Lower Florida Keys are partial migrants, with some individuals completing highly repeatable round-trips to and from the Florida Keys while others make seasonal shifts among habitats within the Florida Keys.

4.1 | Broad-scale migratory patterns

Our study provides documentation of partial migration in great hammerhead sharks in coastal Florida. Partial migration occurs when a population contains both resident and migratory individuals (Chapman et al., 2012). An emerging body of literature has documented partial migration in sharks, particularly for tropical and subtropical species where seasonal changes in water temperature are less likely to necessitate cyclical migrations (Espinoza et al., 2016; Papastamatiou et al., 2013; Pratt Jr. et al., 2018). These patterns of partial migration are largely attributed to reproductive patterns (Bass et al., 2016; Espinoza et al., 2016; McMilan et al., 2019; Papastamatiou et al., 2013; Pratt Jr. et al., 2018; Shaw & Levin, 2011), though ontogenetic variation (Lea et al., 2018) and shifting prey distribution (Espinoza et al., 2016; McMilan et al., 2019) also influence these movements.

Much of our understanding of great hammerhead shark spatial ecology in the coastal waters of the United States comes from satellite telemetry data coupled with analyses that aggregate individual data (e.g., kernel density estimates, habitat suitability models) to generate population-level trends across seasons (Calich et al., 2018; Calich et al., 2021; Graham et al., 2016; Queiroz et al., 2016). Such an

FIGURE 9 Predictive plots for the best-performing binomial generalized linear mixed models (GLMMs) of monthly presence within the Florida Keys with individual shark as a random effect. Probability of presence varied significantly with (a) habitat and season and (b) depth and season.

approach may not capture individual-level variation in movement patterns that could have significant ramifications for successful species management when coupled with small sample sizes (Hertel et al., 2020; Muff et al., 2018). Great hammerhead sharks tagged in northwestern Australia showed high individuality in their movement networks (Lubitz et al., 2023). In our study, by applying network analyses to the movements of individual sharks, we demonstrate that individual great hammerhead sharks have an affinity for specific oceanic basins with individuals either moving into the Atlantic Ocean or Gulf of Mexico but rarely visiting both. Of the nine great hammerheads tracked for over a year, only one was detected in both the Gulf of Mexico and Atlantic Ocean.

Previous modelling of habitat suitability for great hammerhead sharks based on satellite telemetry data showed a relatively low probability of presence in the Gulf of Mexico when compared to the Atlantic coast of the United States (Calich et al., 2018, Calich et al., 2021). To our knowledge, the vast majority of great hammerhead shark spatial ecology data in the Western Hemisphere has been generated from sharks tagged in the Atlantic Ocean, specifically between Miami and Jupiter, Florida, as well as Bimini, The Bahamas (Calich et al., 2018; Calich et al., 2021; Graham et al., 2016; Guttridge et al., 2017). In contrast, the great hammerheads tagged in Bahia Honda (~230 km west of Bimini and ~165 km west of Miami) showed strong connectivity between the Florida Keys and the Tampa Bay area in the Gulf of Mexico. Multiple individuals regularly moved into the Gulf of Mexico,

with one individual demonstrating remarkably consistent annual migrations along Florida's Gulf Coast. Collectively, this suggests that the results of tagging studies could be greatly influenced by the tagging location, even for highly migratory species, as this small shift to the west revealed more frequent use of the Gulf of Mexico. If individual hammerheads do indeed have oceanic basin affinity, then sharks tagged in previous studies in the Atlantic would be less likely to occupy habitats in the Gulf of Mexico.

The Florida Straits, where Gulf and Atlantic meet south of the Florida Keys, are a well-documented vicariance zone for some coastal shark species, including scalloped hammerhead *Sphyrna lewini* (Griffith and Smith 1834), bonnethead *Sphyrna tiburo* (Linnaeus 1758), finetooth *Carcharhinus isodon* (Valenciennes 1839) and blacknose sharks *Carcharhinus acronotus* (Poey 1860) (Daly-Engel et al., 2012; Dimens et al., 2019; Portnoy et al., 2015; Portnoy et al., 2016). The genetic population structure of great hammerheads in the southeastern United States is still largely undocumented. If the Gulf of Mexico and Atlantic basins do not have genetically distinct stock structures, the Florida Keys could potentially represent an area where sharks from each basin come together to mate, allowing for gene flow between the two basins, though mating scars were not observed on the females captured in Bahia Honda.

Documenting oceanic basin affinity highlights the ecological importance of the Florida Keys as an area of mixing for the great hammerhead shark population in the coastal United States. Although

reproductive state is often a driver of partial migration in female sharks, more information on reproductive state connected to movement patterns would be necessary to determine if this drives partial migration for great hammerheads in the Florida Keys. Currently, limited data are available regarding reproductive behaviour, including mating and pupping timing and location for great hammerheads (Miller et al., 2014). It is thought that females pup every 2 years in late spring or early summer after an 11-month gestation period, with mating occurring at a similar time of the year (Ebert & Stehmann, 2013; Stevens & Lyle, 1989). Recently, neonate and young-of-the-year great hammerheads have been documented in coastal South Carolina, the Florida panhandle and Biscayne Bay (Barker et al., 2017; Macdonald et al., 2021).

During this study, we completed an ultrasound on one mature female. Originally tagged in 2020, GHH18 was recaptured on 6 April 2021, and confirmed to be pregnant using ultrasonography (Sulikowski & Hammerschlag, 2023). After recapture, GHH18 was first detected 12 days later outside of Biscayne Bay. The shark then returned to the Lower Keys where it was detected almost daily until 16 June. It is possible that GHH18 moved from its capture location in Bahia Honda to the Biscayne Bay area to pup. Although not detected within the boundaries of the bay, it is hypothesized that mature females may give birth outside of estuaries, and neonates then travel the short distance inshore (Barker et al., 2017). In the Florida panhandle, another tagged hammerhead (GHH2) was detected in July 2019 and 2020, as well as in August 2021 (but not in 2022), in the Pensacola Beach area, ~190 km from where a neonate was captured in St. Joseph Bay in August 2014 (Barker et al., 2017). Though we were not able to ultrasound this shark to determine its reproductive status, GHH2 was large enough to be mature at tagging and was likely to be pregnant at least one of these years, given the species' 2-year reproductive cycle (Ebert & Stehmann, 2013, Stevens & Lyle, 1989).

In Bahia Honda, we observed sexual segregation with predominantly mature females captured, in contrast to broader longline studies in the Lower Florida Keys, which had a slightly male-skewed sex ratio (4:3 M:F, Heithaus et al., 2007). Sexual segregation across habitats is not uncommon in elasmobranchs and has been observed in multiple species (Jacoby et al., 2012; Wearmouth & Sims, 2008). Among sphyrnids, this behaviour is well documented for scalloped hammerheads (Klimley, 1987). Although less pronounced in great hammerheads, mature females may be more commonly encountered in inshore tropical areas (Harry, Macbeth, et al. 2011; Harry, Tobin, et al. 2011), as was observed in this study. Inshore regions of the Lower Florida Keys may serve as a feeding ground (Casselberry et al., 2024; Griffin, Casselberry, et al., 2022) for pregnant female sharks, who then migrate up both the east and west coasts of Florida to pup. However, additional ultrasonography work is needed to confirm pregnancy in more individuals and confirm this hypothesis.

4.2 | High-use areas within the Florida Keys

Overall residency for great hammerhead sharks was low throughout the study area, but it was significantly higher within the Florida Keys

than points outside, particularly in the spring and summer. A multi-species study of fish space use within the Florida Keys characterized great hammerhead sharks as general migrants, because they displayed higher residency to basins outside of the Florida Keys than within the Florida Keys (Lowerre-Barbieri et al., 2021); however, only 14% of the individuals included in the study were tagged in the Florida Keys. In contrast, the individuals tagged in our study exhibited the highest residency within the Florida Keys, suggesting that this region is not simply a migratory corridor for these individuals. These contrasting results further highlight the need for data sourced from multiple tagging locations and larger sample sizes when drawing conclusions about highly mobile species' spatial ecology.

Within the Florida Keys, we documented high connectivity between Bahia Honda Channel and the reef tract in the Lower Florida Keys. High-use movement corridors, as well as core use areas, were more frequently identified in the Lower Florida Keys than in the Upper Keys, suggesting a degree of site fidelity to the local tagging region when individuals were present within the Florida Keys. Although all sharks moved throughout the Florida Keys, the core use areas identified most frequently were located exclusively within the Lower Florida Keys. Outside of Bahia Honda, this included natural reef sites, like Eyeglass Bar and Western Dry Rocks, adjacent artificial reef sites and nearshore flats on the Atlantic side between the keys and the reef tract. In the Lower Florida Keys, numerous high-flow channels and seagrass flats are a relatively short distance from the reef tract. This may offer more foraging opportunities both inshore and offshore than in the Upper Florida Keys, where sharks were mainly detected along the reef tract. Stable isotope analyses of great hammerhead shark tissues from eastern Australia suggest that they occupy multiple food webs, relying on inshore, reef-associated and pelagic food sources (Raoult et al., 2019; Raoult et al., 2020). The frequent movements between seagrass flats habitats and the reef highlight the role that great hammerheads likely play as vectors of nutrients, promoting energetic connectivity between disparate habitats, as has been documented for other large shark species (Shipley et al., 2023; Williams et al., 2018).

4.3 | The role of prey distribution and temperature as movement drivers

Within the Florida Keys, great hammerhead sharks exhibited seasonal shifts in habitat use, which were likely driven by both prey availability and seasonal temperature changes. The Florida Keys experiences seasonal pulses of potential prey for great hammerheads and hosts a number of spawning aggregation sites for tropical and subtropical fish species (Brownscombe et al., 2023; Burton et al., 2005; Eklund et al., 2000; Keller et al., 2020). For example, annual Atlantic tarpon pre-spawning aggregations occur in the Florida Keys from April to early July (Crabtree et al., 1992; Crabtree et al., 1997; Griffin et al., 2018; Griffin, Brownscombe, et al., 2022), and great hammerheads seek out these aggregation sites non-randomly in response to tarpon presence, presumably as foraging opportunities (Griffin,

Casselberry, et al., 2022). Observations of foraging behaviour, gut content analyses and stable isotope analyses for mature great hammerheads support a reliance on a combination of smaller elasmobranchs, particularly batoids, as well as teleosts as prey (Stevens & Lyle, 1989, Strong et al., 1990, Cliff, 1995, Roemer et al., 2016, Raoult et al., 2019, Chumchuen & Sukramongkol, 2022, Lubitz et al., 2023). Thus, aggregations of these potential food sources may drive great hammerhead shark movement patterns (Guttridge et al., 2017; Lubitz et al., 2023).

In the spring, sharks exhibited the heavy use of channels, which often corresponded to Atlantic tarpon pre-spawning aggregation sites (e.g., Bahia Honda). These seasonal influxes of tarpon influence great hammerhead foraging behaviour (Griffin, Casselberry, et al., 2022), providing both natural foraging opportunities and the ability to opportunistically capitalize on distressed prey through depredating tarpon hooked in the recreational fisheries in these areas (Casselberry et al., 2024). Limited data are available for great hammerhead diet composition in Florida, but given the repeated annual return to tarpon pre-spawning aggregation sites, tarpon likely represent a significant and reliable prey source for great hammerheads during this time (Casselberry et al., 2024). The majority of adult Atlantic tarpon migrate away from the Florida Keys in late May or early June when water temperatures are between 27 and 29°C (Griffin, Brownscombe, et al., 2022). The departure of the tarpon corresponds with a shift in habitat use for great hammerheads in the Florida Keys, increasing use of the reef tract, artificial reefs and basins.

Although Atlantic tarpon aggregation sites play a significant role in great hammerhead shark spatial ecology in the Florida Keys (Casselberry et al., 2024, Griffin, Casselberry, et al., 2022), those that migrate away from the Florida Keys in the summer do not appear to frequent other inshore tarpon aggregation sites. Sharks that moved north along the west coast of Florida were not detected with regularity at other known aggregation sites, like Boca Grande Pass and the Sunshine Skyway Bridge in Tampa Bay, in the same way that they are in the Florida Keys (Casselberry et al., 2024; Griffin, Casselberry, et al., 2022) despite extensive receiver coverage in those areas. Instead of frequenting channels and bridges where tarpon are known to aggregate (Guindon, 2011), the great hammerheads that migrate to the Tampa Bay area were detected only on receivers at the mouth of the bay. Instead, these individuals may pursue tarpon outside of the barrier islands as they pass in and out of channels that are also subject to fishing pressure (L. Griffin personal communicaion) or farther offshore as they migrate to deep water to spawn (Crabtree et al., 1992).

Satellite tagging data of great hammerhead sharks in the western North Atlantic show that they prefer temperatures between 23 and 28°C (Guttridge et al., 2022). Through the duration of this study, mean monthly SST ranged between 22.5 and 30.9°C in the Florida Keys, with the highest temperatures occurring mainly between July and September of each year. Although these seasonal temperature increases corresponded with a number of individuals leaving the Florida Keys, those that remained shifted their habitat use towards deeper water habitats, which corresponded to increasing presence on artificial reefs and the natural reef tract. Studies of great hammerhead

seasonal vertical habitat use indicate that some individuals occupy significantly deeper depths in summer through winter than in the spring (Guttridge et al., 2022). In addition to temperature, prey availability may influence this summer shift, as cubera snapper *Lutjanus cyanopterus* (Cuvier 1828), grey snapper *L. griseus* (Linnaeus 1758) and permit spawn on reef and wreck sites (artificial reefs) throughout the summer months (Brownscombe et al., 2023; Domeier & Colin, 1997; Lindeman et al., 2000). These spawning aggregation sites correspond to great hammerhead summer core use areas, particularly Eyeglass Bar and Western Dry Rocks, supporting prey abundance as a driver of shifting space use.

Similarly, seasonal aggregations may be a draw to great hammerheads that migrate away from the Florida Keys. Along the west coast of Florida, the seasonal presence of batoids, particularly spotted eagle rays *Aetobatus narinari* (Euphrasen 1790), in the summer and autumn months (Bassos-Hull et al., 2014) may be a draw for migrants. Batoids are a well-documented prey source for great hammerheads (Roemer et al., 2016), and their abundance likely influences their home range size (Lubitz et al., 2023). Additionally, red drum *Sciaenops ocellatus* (Linnaeus 1766) spawning aggregations also form outside of Tampa Bay in late summer through autumn (Lowerre-Barbieri, Tringali, et al., 2019), which may serve as another abundant food source (Compagno, 1984; Friess et al., 2021).

Great hammerhead movements into the Atlantic were primarily during the late spring and summer. Core use locations overlapped with a substantial aggregation of blacktip shark *Carcharhinus limbatus* (Valenciennes 1839) between Boynton Inlet and Jupiter Inlet, where hammerheads have been documented foraging (Doan & Kajiura, 2020). Tagged individuals generally arrived after the aggregation dissipates in April/May, but blacktip sharks are present in the area year-round (Kajiura & Tellman, 2016). Thus, movements away from the Florida Keys may be driven by both individual temperature preferences and generalized prey availability.

4.4 | Potential caveats

The data derived from this study were relatively sparse, even within the Florida Keys, which had extensive receiver coverage. Retention of acoustic tags for our study was variable. One-third of the sharks retained their tags into the final year of the study based on detection history, whereas all three recaptured individuals had shed their external acoustic tag. This makes it difficult to conclude whether sharks with short detection durations left the receiver array through migration, experienced mortality or simply shed their tags outside the detection range of receivers. Although external tagging can reduce handling time and related stress, it may be prudent to re-evaluate implanting tags as an option for longer-term data collection.

Collecting data using acoustic telemetry is limited by the extent of acoustic receiver coverage. Though a number of sharks were detected within the Florida Keys during all months of the year, detection gaps when sharks were not in proximity to acoustic receivers existed for all individuals (Figure 2). To our knowledge, there is little

to no acoustic receiver coverage in Cuban waters, and given the proximity, it is possible that sharks travel south when they leave the Florida Keys towards Cuba, where they are harvested in commercial fisheries (Aguilar et al., 2014). Acoustic receiver coverage is also often limited by depth, as the receivers must be recovered to be downloaded (Heupel et al., 2006), but the increasing availability of acoustic release receivers and drones now allow for deployments at deeper depths (Tarnecki & Patterson III, 2020). Our data indicate that great hammerheads likely spend time in deeper waters in the Gulf of Mexico while migrating between the Florida Keys, Tampa Bay and the Florida panhandle, considering the individuals were infrequently detected at inshore points between these regions where there is known receiver coverage (e.g., Cape Sable, Ft. Meyers). Integrating satellite telemetry, using real-time transmitting or pop-up archival tags, with acoustic telemetry data could increase our understanding of great hammerhead shark movements in areas without receiver coverage, though tag retention remains a challenge for pop-up tags (Guttridge et al., 2017, Casselberry unpublished data), and previous real-time transmitting tag deployments yielded sparse and variable detection data, as they rely on the dorsal fin surfacing to transmit (Drymon & Wells, 2017; Graham et al., 2016).

4.5 | Conservation and management implications

Though the exact percentage of population decline is debated (Baum et al., 2005; Burgess et al., 2005), the large hammerhead shark complex, which includes great, scalloped and smooth *Sphyrna zygaena* (Linnaeus 1758) hammerheads, experienced dramatic declines through the early 2000s (Baum et al., 2003; Baum & Blanchard, 2010). Although great hammerhead populations are showing signs of stabilization and slow recovery (Pacoureau et al., 2023), significant knowledge gaps related to fundamental ecology remain (Gallagher & Klimley, 2018). Much of our understanding of great hammerhead movements comes from tagging studies on Florida's east coast and Bimini, The Bahamas (Calich et al., 2018; Graham et al., 2016; Guttridge et al., 2017; Guttridge et al., 2022). Our study provides some of the first substantive telemetry data west of Key Largo in Florida and demonstrates that individuals that do migrate exhibit basin-specific affinity during their summer and autumn migrations. Sharks in the Gulf of Mexico will be exposed to different levels of commercial and recreational fishing pressure than those in the Atlantic (Calich et al., 2018; Graham et al., 2016; Graham et al., 2021). These results highlight the need to improve our understanding of great hammerhead shark spatial ecology outside of southeastern Florida. The high individual variability in these animals emphasizes the need to diversify tagging locations when drawing conclusions about spatial ecology at the population level.

Tagging location in relation to extensive barrier reefs has been shown to influence conclusions drawn from spatial ecology studies in highly migratory shark species outside of Florida. Nearly 50% of individual bull sharks tagged in New South Wales, Australia, moved to acoustic receiver arrays on the Great Barrier Reef, whereas only 3%

tagged on the barrier reef moved to receiver arrays in New South Wales (Heupel et al., 2015). As in our study, the authors postulate that pulsed prey aggregations on the reef influenced the disparity in movements. Using carbon stable isotope analyses, Raoult et al. (2020) demonstrated that great hammerheads sampled in New South Wales relied substantially on northern foraging sites, corresponding to latitudes encompassing the Great Barrier Reef, demonstrating that these latitudes were an area of mixing for individuals in the population. Pulsed prey sources, such as fish spawning aggregations, have been shown to substantially alter space use in smaller-bodied sharks (Mourier et al., 2016, Pickard et al., 2016, Rhodes et al., 2019), but direct connections between aggregate fish spawning behaviour and large, apex predator shark movements in coral reef systems remain underexplored (Graham & Castellanos, 2012; Griffin, Casselberry, et al., 2022). A deeper understanding of the influence these aggregations may have on the spatial ecology of highly migratory sharks tagged across a breadth of sites is warranted (Mourier et al., 2016), particularly as managers move towards multi-species, ecosystem-based approaches to fisheries management (Erisman et al., 2016).

Population-level inferences for highly mobile species can be inaccurate when they are based on a small number of individuals tagged in a restricted area (Cooke et al., 2022). This can be especially true for apex predators where individuals are capable of extensive migrations, and the anomalous movements from one individual may be reflective of an underrepresented behaviour type that is smoothed out of the model. In 2017, essential fish habitat for the great hammerhead shark in the southeastern United States was reduced by removing the region from the continental shelf beginning at Anclote Key and extending north and west through the Florida panhandle (NOAA Fisheries, 2017). Essential fish habitat now only encompasses the Florida continental shelf along the east-central coast surrounding Jupiter, Florida, as well as just north of Biscayne Bay through the Florida Straits to the Dry Tortugas, fully encompassing the Florida Keys, and ranging northwest to Anclote Key, north of the mouth of Tampa Bay (NOAA Fisheries, 2017). Based on the available data at the time, the Florida panhandle was believed to be an area that great hammerheads only used briefly as a movement corridor, which contributed to the removal of this region from the essential fish habitat designation (NOAA Fisheries, 2017). In contrast to previous data, here we documented repeated, annual use of the same sites in the Florida panhandle, identifying Pensacola Beach as a core use area for great hammerhead sharks in both autumn and winter. Additionally, network analysis indicates that a subset of sharks had a higher affinity for sites along the west coast of Florida than the tagging site. Given the high individual variation in movements, further studies are needed throughout the range of the great hammerhead sharks in the coastal United States to better identify areas of residency and regional connectivity.

The Florida Keys serves as an area where individuals from the Atlantic Ocean and Gulf of Mexico mix, as has been observed in other fish species, including Atlantic tarpon (Griffin et al., 2023). Similar to the aggregation sites in Bimini (Guttridge et al., 2017; Heim et al., 2021), the majority of sharks in our study displayed high

annual site fidelity to the tagging site. This is likely driven by prey availability, particularly in the spring when Atlantic tarpon pre-spawning aggregations form (Casselberry et al., 2024; Griffin, Casselberry, et al., 2022). Some sharks were present in the Florida Keys year-round, but mean monthly residency in the Florida Keys, or elsewhere, was low throughout the study period. Though individuals are clearly transient, residency within Florida Keys National Marine Sanctuary provides a unique opportunity to harness spatial management to further protect aggregation sites for this species amid increasing conflicts with recreational anglers (Casselberry et al., 2022; Casselberry et al., 2024). Specific research into the reproductive status of great hammerheads in the Florida Keys, as well as their genetic structure of the population in the western North Atlantic and Gulf of Mexico, should improve our understanding of the broader ecological role the Florida Keys play in the life history of great hammerhead sharks.

AUTHOR CONTRIBUTIONS

Grace A. Casselberry, Andy J. Danylchuk, Gregory B. Skomal, Lucas P. Griffin, Jacob W. Brownscombe and Steven J. Cooke contributed to study conception and design. Fieldwork and data collection, including receiver array downloads, were conducted by Grace A. Casselberry, Andy J. Danylchuk, Gregory B. Skomal, Lucas P. Griffin, Jacob W. Brownscombe, Joseph Dello Russo, Peter E. Holder, Jeff Kneebone, James Sulikowski, Brooke N. Anderson, Ben Daughtry, Danielle Morley and Susan K. Lowerre-Barbieri. Data analysis was performed by Grace A. Casselberry and John T. Finn. The first draft of the manuscript was written by Grace A. Casselberry, and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGEMENTS

FUNDING INFORMATION

DATA AVAILABILITY STATEMENT

The data that support the results of this study were shared through iTAG and are archived through the Ocean Tracking Network (OTN, https://urldefense.com/v3/__https://members.oceantrack.org/OTN/projects__;!!N11eV2iwtfs!tnVJIxl67PnOlW0MrAjeP-mSofbfN8WQHgzSjitwowrzEQ4sBxbONXXODmAEe9hsjdfrF7RIw3Dp$). OTN dictates data be released after 2 years following the expiration of any given tag. Additional support and access can be provided directly from the corresponding author.

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REFERENCES

Abel, G. J. (2022). migest: Methods for the indirection estimation of bilateral migration. R package version 2.0.3. https://CRAN.R-project.org/package=migest

Aguilar, C., González-Sansón, G., Hueter, R., Rojas, E., Cabrera, Y., Briones, A., Borroto, R., Hernández, A., & Baker, P. (2014). Shark catches in the northwest region of Cuba. *Latin American Journal of Aquatic Research*, 42, 477–487.

Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: Evolution and determinants. *Oikos*, 103, 247–260.

Appert, C., Udyawer, V., Simpfendorfer, C. A., Heupel, M. R., Scott, M., Currey-Randall, L. M., Harborne, A. R., Jaine, F., & Chin, A. (2023). Use, misuse, and ambiguity of indices of residence in acoustic telemetry studies. *Marine Ecology Progress Series*, *714*, 27–44.

Bangley, C. W., Whoriskey, F. G., Young, J. M., & Ogburn, M. B. (2020). Networked animal telemetry in the Northwest Atlantic and Caribbean waters. *Marine and Coastal Fisheries*, *12*, 339–347.

Barker, A. M., Frazier, B. S., Bethea, D. M., Gold, J. R., & Portnoy, D. S. (2017). Identification of young-of-the-year great hammerhead shark *Sphyrna mokarran* in northern Florida and South Carolina. *Journal of Fish Biology*, *91*, 664–668.

Bartoń, K. (2020). MuMIn: Multi-model inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bass, N. C., Mourier, J., Knott, N. A., Day, J., Brown, C., & Guttridge, T. (2016). Long-term migration patterns and bisexual philopatry in a benthic shark species. *Marine and Freshwater Research*, *68*, 1414–1421.

Bassos-Hull, K., Wilkinson, K. A., Hull, P. T., Dougherty, D. A., Omori, K. L., Ailloud, L. E., Morris, J. J., & Heuter, R. E. (2014). Life history and seasonal occurrence of the spotted eagle ray, *Aetobatus narinari*, in the eastern Gulf of Mexico. *Environmental Biology of Fishes*, *97*, 1039–1056.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Baum, J. K., & Blanchard, W. (2010). Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. *Fisheries Research*, *102*, 229–239.

Baum, J. K., Kehler, D., & Myers, R. A. (2005). Robust estimates of decline for pelagic shark populations in the northwest Atlantic and Gulf of Mexico. *Fisheries*, *30*, 27–29.

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., & Doherty, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, *299*, 389–392.

Blem, C. R. (1980). The energetics of migration. In S. A. Gauthreaux, Jr. (Ed.), *Animal migration, orientation, and navigation* (pp. 175–213). Academic Press, Inc..

Blondel, V. D., Guillaume, J. L., Lambiotte, R., & Lefebvre, E. (2008). Fast unfolding communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment*, P10008. https://doi.org/10.1088/1742-5468/2008/10/P10008

Brownscombe, J. W., Griffin, L. P., Chapman, J. M., Morley, D., Acosta, A., Crossin, G. T., Iverson, S. J., Adams, A. J., Cooke, S. J., & Danylchuk, A. J. (2019). A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. *Methods Ecol Evol*, *11*, 82–94.

Brownscombe, J. W., Griffin, L. P., Morely, D., Acosta, A., Hunt, J., Lowerre-Barbieri, S. K., Crossin, G. T., Iverson, S. J., Boucek, R., Adams, A. J., Cooke, S. J., & Danylchuk, A. J. (2020). Seasonal occupancy and connectivity amongst nearshore flats and reef habitats by permit *Trachinotus falcatus*: Considerations for fisheries management. *Journal of Fish Biology*, *96*, 469–479.

Brownscombe, J. W., Griffin, L. P., Morley, D., Acosta, A., Boucek, R., Adams, A. J., Danylchuk, A. J., & Cooke, S. J. (2023). Spatial-temporal patterns of permit (*Trachinotus falcatus*) habitat residency in the Florida keys, USA. *Environmental Biology of Fishes*, *106*, 419–431.

Burgess, G. H., Beerkircher, L. R., Cailliet, G. M., Carlson, J. K., Cortés, E., Goldman, K. J., Grubbs, R. D., Musick, J. A., Musyl, M. K., & Simpfendorfer, C. A. (2005). Is the collapse of shark populations in the Northwest Atlantic Ocean and gulf of Mexico real? *Fisheries*, *30*, 19–26.

Burton, M. L., Brennan, K. J., Muñoz, R. C., & Parker, R. O., Jr. (2005). Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's hump two years after establishment of the Tortugas south ecological reserve. *Fishery Bulletin*, *103*, 404–410.

Butts, C. T. (2022). sna: Tools for social network analysis. R package version 2.7. https://CRAN.R-project.org/package=sna

Calich, H., Estevanez, M., & Hammerschlag, N. (2018). Overlap between highly suitable habitats and longline gear management areas reveals vulnerable and protected regions for highly migratory sharks. *Marine Ecology Progress Series*, *602*, 183–195.

Calich, H. J., Rodríguez, J. P., Eguíluz, V. M., Hammerschlag, N., Pattiaratchi, C., Duarte, C. M., & Sequeira, A. M. M. (2021). Comprehensive analytical approaches reveal species-specific search strategies in sympatric apex predatory sharks. *Ecography*, *44*, 1544–1556.

Carlson, B. S., Rotics, S., Nathan, R., Wikelski, M., & Jetz, W. (2021). Individual environmental niches in mobile organisms. *Nature Communications*, *12*, 4572.

Casselberry, G. A., Danylchuk, A. J., Finn, J. T., DeAngelis, B. M., Jordaan, A., Pollock, C. G., Lundgren, I., Hillis-Starr, Z., & Skomal, G. B. (2020). Network analysis reveals multispecies associations in the shark community of a Caribbean marine protected area. *Marine Ecology Progress Series*, *633*, 105–126.

Casselberry, G. A., Markowitz, E. M., Alves, K., Dello Russo, J., Skomal, G. B., & Danylchuk, A. J. (2022). When fishing bites: Understanding angler responses to shark depredation. *Fisheries Research*, *246*, 106174.

Casselberry, G. A., Skomal, G. B., Griffin, L. P., Brownscombe, J. W., Filous, A., Holder, P. E., Dello Russo, J., Morgan, C., Kneebone, J., Adams, A. J., Cooke, S. J., & Danylchuk, A. J. (2024). Depredation rates and spatial overlap between great hammerheads and tarpon in a recreational fishing hot spot. *Marine and Coastal Fisheries*, *16*, e10277.

Chapman, B. B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A., & Brönmark, C. (2012). Partial migration in fishes: Definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, *81*, 479–499.

Chapman, D. D., Feldheim, K. A., Papsatmatiou, Y. P., & Hueter, R. E. (2015). There and back again: A review of residency and return migrations in sharks, with implications for population structure and management. *The Annual Review of Marine Science*, *7*, 547–570.

Chumchuen, W., & Sukramongkol, N. (2022). Diet and feeding habits of predatory fishes around anchored fish aggregating devices in Thai waters, the Andaman Sea. *Phuket Marion Biological Center Research Bulletin*, *79*, 87–103.

Clauset, A., Newman, M. E. J., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E*, *70*, 066111.

Cliff, G. (1995). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The great hammerhead shark *Sphyrna mokarran* (Rüppell). *South African Journal of Marine Science*, *15*, 105–114.

Compagno, L. J. V. (1984). FAO Species Catalogue Vol. 4 Sharks of the world: An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniforms. Food and Agriculture Organization of the United Nations. Rome, Italy. ISBN 92-5-101383-7.

Cooke, S. J., Bergman, J. N., Twardek, W. M., Pivzak, M. L., Casselberry, G. A., Lutek, K., Dahlmo, L. S., Bimie-Gauvin, K., Griffin, L. P., Brownscombe, J. W., Raby, G. D., Standen, E. M., Horodysky, A. Z., Johnsen, S., Danylchuk, A. J., Furey, N. B., Gallagher, A. J., Lédée, E. J. I., Midwood, J. D., ... Lennox, R. J. (2022). The movement ecology of fishes. *Journal of Fish Biology*, *101*, 756–779.

Crabtree, R. E., Cyr, E. C., Bishop, R. E., Falkenstein, L. M., & Dean, J. M. (1992). Age and growth of tarpon, *Megalops atlanticus*, larvae in the eastern Gulf of Mexico, with notes on relative abundance and probable spawning areas. *Environmental Biology of Fishes*, *25*, 361–370.

Crabtree, R. E., Cyr, E. C., Chacón Chaverri, D., McLarney, W. O., & Dean, J. M. (1997). Reproduction of tarpon, *Megalops atlanticus*, from Florida and costa Rican waters and notes on their age and growth. *Bulletin of Marine Science*, *61*, 271–285.

Crowder, L., & Norse, E. (2008). Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Marine Policy*, *32*, 772–778.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695. https://cran.r-project.org/web/packages/igraph/citation.html

Daly, R., Smale, M. J., Singh, S., Anders, D., Shivji, M., Daly, C. A. K., Lea, J. S. E., Sousa, L. L., Wetherbee, B. M., Fitzpatrick, R., Clarke, C. R., Sheaves, M., & Barnett, A. (2018). Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators. *Diversity and Distributions*, *24*, 1217–1230.

Daly-Engel, T. S., Seraphin, K. D., Holland, K. N., Coffey, J. P., Nance, H. A., Toonen, R. J., & Bowen, B. W. (2012). Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the endangered scalloped hammerhead shark (*Sphyrna lewini*). *PLoS One*, *7*, e29986.

Dimens, P. V., Willis, S., Grubbs, R. D., & Portnoy, D. S. (2019). A genomic assessment of movement and gene flow around the South Florida vicariance zone in the migratory coastal blacknose shark, *Carcharhinus Acronotus*. *Marine Biology*, *166*, 86.

Doan, M. D., & Kajiura, S. M. (2020). Adult blacktip sharks (*Carcharhinus limbatus*) use shallow water as a refuge from great hammerheads (*Sphyrna mokarran*). *Journal of Fish Biology*, *2020*, 1–4.

Domeier, M. L., & Colin, P. L. (1997). Tropical reef fish spawning aggregations: Defined and reviewed. *Bulletin of Marine Science*, *60*, 698–726.

Dormann, C. R., Gruber, B., & Fruend, J. (2008). Introducing the bipartite package: Analysing ecological networks. *The Open Ecology Journal*, *2*, 7–24.

Drymon, J. M., & Wells, R. J. D. (2017). Double tagging clarifies post-release fate of great hammerheads (*Sphyrna mokarran*). *Animal Biotelemetry*, *5*, 28.

Ebert, D. A., & Stehmann, M. F. W. (2013). Sharks, batoids and chimaeras of the North Atlantic. In *FAO species catalogue for fishery purposes No. 7* (p. 523). Food and agriculture Organization of the United Nations.

Eklund, A.-M., McClellan, D. B., & Harper, D. E. (2000). Black grouper aggregations in relation to protected areas within the Florida keys National Marine Sanctuary. *Bulletin of Marine Science*, *66*, 721–728.

Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropenza, O., & Nemeth, R. S. (2016). Fish spawning aggregations: Where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries*, *18*, 128–144.

Espinoza, M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2016). Evidence of partial migration in a large coastal predator: Opportunistic foraging and reproduction as key drivers? *PLoS One*, *11*, e0147608.

Finn, J. T., Brownscombe, J. W., Haak, C. R., Cooke, S. J., Cormier, R., Gagne, T., & Danylchuk, A. J. (2014). Applying network methods to acoustic telemetry data: Modeling the movements of tropical marine fishes. *Ecological Modeling*, *293*, 139–149.

Fortunato, S. (2010). Community detection in graphs. *Physics Reports*, *486*, 75–174.

Friess, C., Lowerre-Barbieri, S. K., Poulakis, G. R., Hammerschlag, N., Gardiner, J. M., Kroetz, A. M., Bassos-Hull, K., Bickford, J., Bohaboy, E. C., Ellis, R. D., Menendez, H., Patterson, W. F., III, Price, M. E., Rehage, J. S., Shea, C. P., Smukall, M. J., Walters Burnsed, S., Wilkinson, K. A., Young, J., ... Griffin, L. P. (2021). Regional-scale variability in the movement ecology of marine fishes revealed by an integrative acoustic tracking network. *Marine Ecology Progress Series*, *663*, 157–177.

Gallagher, A. J., & Klimley, A. P. (2018). The biology and conservation status of the large hammerhead shark complex: The great, scalloped, and smooth hammerheads. *Reviews in Fish Biology and Fisheries*, *28*, 777–794.

Gallagher, A. J., Serafy, J. E., Cooke, S. J., & Hammerschlag, N. (2014). Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Marine Ecology Progress Series*, *496*, 207–218.

Graham, F., Rynne, P., Estevanez, M., Luo, J., Ault, J. S., & Hammerschlag, N. (2016). Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks. *Diversity and Distributions*, *2016*, 1–13.

Graham, J., Kroetz, A. M., Poulakis, G. R., Scharer, R. M., Carlson, J. K., Lowerre-Barbieri, S. K., Morey, D., Reyier, E. A., & Grubbs, R. D. (2021). Commercial fishery bycatch risk for large juvenile and adult smalltooth sawfish (*Pristis pectinata*) in Florida waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *32*, 401–416.

Graham, R. T., & Castellanos, D. (2012). Apex predators target mutton snapper spawning aggregation. *Coral Reefs*, *31*, 1017.

Griffin, L. P., Brownscombe, J. W., Adams, A. J., Boucek, R. E., Finn, J. T., Heithaus, M. R., Rehage, J. S., Cooke, S. J., & Danylchuk, A. J. (2018). Keeping up with the silver king: Using cooperative acoustic telemetry networks to quantify the movements of Atlantic tarpon (*Megalops atlanticus*) in the coastal waters of the southeastern United States. *Fisheries Research*, *205*, 65–76.

Griffin, L. P., Brownscombe, J. W., Adams, A. J., Holder, P. E., Filous, A., Casselberry, G. A., Wilson, J. K., Boucek, R. E., Lowerre-Barbieri, S. K., Acosta, A., Morley, D., Cooke, S. J., & Danylchuk, A. J. (2022). Seasonal variation in the phenology of Atlantic tarpon in the Florida keys: Migration, occupancy, repeatability, and management implications. *Marine Ecology Progress Series*, *684*, 133–155.

Griffin, L. P., Brownscombe, J. W., Adams, A. J., Wilson, J. K., Casselberry, G. A., Holder, P. E., Filous, A., Lowerre-Barbieri, S. K., Cooke, S. J., & Danylchuk, A. J. (2023). Individual variation and repeatability of Atlantic tarpon migrations in the southern United States: Implications for conservation and management. *Marine Biology*, *170*, 168.

Griffin, L. P., Casselberry, G. A., Lowerre-Barbieri, S. K., Acosta, A., Adams, A. J., Cooke, S. J., Filous, A., Friess, C., Guttridge, T. L., Hammerschlag, N., Heim, V., Morley, D., Rider, M. J., Skomal, G. B., Smukall, M. J., Danylchuk, A. J., & Brownscombe, J. W. (2022). Predator-prey landscapes of large sharks and game fishes in the Florida keys. *Ecological Applcations*, *32*, e2584.

Guindon, K. Y. (2011). Evaluating lethal and sub-lethal effects of catch-and-release angling in Florida's Central Gulf Coast recreational Atlantic tarpon (Megalops atlanticus) fishery. Dissertation submitted to the College of Marine Science University of South Florida. 163 pp.

Gulak, S. J. B., de Ron Santiago, A. J., & Carlson, J. K. (2015). Hooking mortality of scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* sharks caught on bottom longlines. *African Journal of Marine Sciences*, *37*, 267–273.

Guttridge, T. L., Müller, L., Keller, B. A., Bond, M. E., Grubbs, R. D., Winram, W., Howey, L. A., Frazier, B. S., & Gruber, S. H. (2022). Vertical space use and thermal range of the great hammerhead (*Sphyrna mokarran*), (Rüppell, 1837) in the western North Atlantic. *Journal of Fish Biology*, *101*, 797–810.

Guttridge, T. L., Van Zinnicq Bergmann, M. P. M., Bolte, C., Howey, L. A., Finter, J. S., Kessel, S. T., Brooks, J. L., Winram, W., Bond, M. E., Jordan, L. K. B., Cashman, R. C., Tolentino, E. R., Grubbs, R. D., & Gruber, S. H. (2017). Philopatry and regional connectivity of the great hammerhead shark *Sphyrna mokarran* in the U.S. and Bahamas. *Frontiers in Marine Science*, *4*(3), 15.

Hammerschalg, N., Gallagher, A. J., Lazarre, D. M., & Slonim, C. (2011). Range extension of the endangered great hammerhead shark *Sphyrna mokarran* in the Northwest Atlantic: Preliminary data and significance for conservation. *Endangered Species Research*, *13*, 111–116.

Harry, A. V., Macbeth, W. C., Gutteridge, A. N., & Simpfendorfer, C. A. (2011). The life histories of endangered hammerhead sharks

(Carcharhiniformes, Sphyrnidae) from the east coast of Australia. *Journal of Fish Biology*, 78, 2026–2051.

Harry, A. V., Tobin, A. J., Simpfendorfer, C. A., Welch, D. J., Mapleston, A., White, J., Williams, A. J., & Stapley, J. (2011). Evaluating catch and mitigating risk in a multispecies tropical, inshore shark fishery within the great barrier reef world heritage area. *Marine and Freshwater Research*, 62, 710–721.

Heim, V., Dhellemmes, F., Smukall, M. J., Gruber, S. H., & Guttridge, T. L. (2021). Effects of food provisioning on the daily ration and dive site use of great hammerhead sharks, *Sphyrna Mokarran*. *Frontiers in Marine Science*, 8, 628469.

Heithaus, M. R., Burkholder, D., Hueter, R. E., Heithaus, L. I., Pratt, H. L., Jr., & Carrier, J. C. (2007). Spatial and temporal variation in shark communities of the lower Florida keys and evidence for historical population declines. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 1302–1313.

Hertel, A. G., Niemelä, P. T., Dingemanse, N. J., & Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology*, 8, 30.

Heupel, M. R., Kessel, S. T., Matley, J. K., & Simpfendorfer, C. A. (2019). Acoustic telemetry. In J. C. Carrier, M. R. Heithaus, & C. A. Simfendorfer (Eds.), *Shark research: Emerging technologies and applications for the field and laboratory* (pp. 133–156). CRC Press.

Heupel, M. R., Semmens, J. M., & Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, 57, 1–13.

Heupel, M. R., Simpfendorfer, C. A., Espinoza, M., Smoothey, A. F., Tobin, A., & Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. *Frontiers in Marine Science*, 2, 12.

Holbrook, C., Hayden, T., Binder, T., & Pye, J. (2021). glatos: A package for the Great Lakes Acoustic Telemetry Observation System. R package version 0.5.1. https://gitlab.oceantrack.org/GreatLakes/glatos

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Mills Flemming, J. E., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, 348, 1255642.

Jacoby, D. M. P., Croft, D. P., & Sims, D. W. (2012). Social behaviour in sharks and rays: Analysis, patterns and implications for conservation. *Fish and Fisheries*, 13, 399–417.

Jiao, Y., Hayes, C., & Cortés, E. (2009). Hierarchical Bayesian approach for population dynamics modelling of fish complexes without species-specific data. *ICES Journal of Marine Science*, 66, 367–377.

Kahle, D., & Wickham, H. (2013). Ggmap: Spatial visualization with ggplot2. *The R Journal*, 5, 144–161.

Kajiura, S. M., & Tellman, S. L. (2016). Quantification of massive seasonal aggregations of blacktip sharks (*Carcharhinus limbatus*) in Southeast Florida. *PLoS One*, 11, e0150911.

Keller, J. A., Herbig, J. L., Morley, D., Wile, A., Barbera, P., & Acosta, A. (2020). Grouper Tales: Using acoustic telemetry to evaluate grouper movements at Western dry rocks in the Florida keys. *Marine and Coastal Fisheries*, 12, 290–307.

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Review in Fish Biology and Fisheries*, 24, 199–218.

Klimley, A. P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*, 18, 27–40.

Kohler, N. E., & Turner, P. A. (2019). Distributions and movements of Atlantic shark species: A 52-year retrospective atlas of mark and recapture data. *Marine Fisheries Review*, 81, 1–93.

Landi, P., & Piccardi, C. (2014). Community analysis in directed networks: In-, out-, and pseudocommunities. *Physical Review E: Statistical, Nonlinear, and Soft Matter Physics*, 89, 012814.

Lapointe, B. E., Barile, P. J., & Matzie, W. R. (2004). Anthropogenic nutrient enrichment of seagrass and coral reef communities in the lower Florida keys: Discrimination of local versus regional nitrogen sources. *Journal of Experimental Marine Biology and Ecology*, 308, 23–58.

Lapointe, B. E., & Matzie, W. R. (1996). Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida keys. *Estuaries*, 19, 422–435.

Lea, J. S., Wetherbee, B. M., Sousa, L. L., Aming, C., Burnie, N., Humphries, N. E., Queiroz, N., Harvey, G. M., Sims, D. W., & Shivji, M. S. (2018). Ontogenetic partial migration is associated with environmental drivers and influences fisheries interactions in a marine predator. *ICES Journal of Marine Science*, 75, 1383–1392.

Lédée, E. J. I., Heupel, M. R., Taylor, M. D., Harcourt, R. G., Jaine, F. R. A., Hueveneers, C., Udyawer, V., Campbell, H. A., Babckock, R. C., Hoenner, X., Barnett, A., Braccini, M., Brodie, S., Butcher, P. A., Cadiou, G., Dwyer, R. G., Espinoza, M., Ferreira, L. C., Fetterplace, L., … Simpfendorfer, C. A. (2021). Continental-scale acoustic telemetry and network analysis reveal new insights into stock structure. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22, 987–1005.

Lédée, E. J. I., Heupel, M. R., Tobin, A. J., Knip, D. M., & Simpfendorfer, C. A. (2015). A comparison between traditional kernel-based methods and network analysis: An example from two nearshore shark species. *Animal Behaviour*, 103, 17–28.

Lenth, R. V. (2021). emmeans: Estimated marginal means, aka least-squares means. R package version 1.7.1–1. https://CRAN.R-project.org/package=emmeans

Lindeman, K. C., Pugliese, R., Waugh, G. T., & Ault, J. S. (2000). Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. *Bulletin of Marine Science*, 66, 929–956.

Lowerre-Barbieri, S. K., Friess, C., Griffin, L. P., Morley, D., Skomal, G. B., Bickford, J. W., Hammerschlag, N., Rider, M. J., Smukall, M. J., van Zinnicq Bergmann, M. P. M., Guttridge, T. L., Kroetz, A. M., Grubbs, R. D., Gervasi, C. L., Rehage, J. S., Poulakis, G. R., Bassos-Hull, K., Gardiner, J. M., Casselberry, G. A., … Brownscombe, J. W. (2021). Movescapes and eco-evolutionary movement strategies in marine fish: Assessing a connectivity hotspot. *Fish and Fisheries*, 22, 1321–1344.

Lowerre-Barbieri, S. K., Kays, R., Thorson, J. T., & Wikelski, M. (2019). The ocean's movescape: Fisheries management in the bio-logging decade (2018-2028). *ICES Journal of Marine Science*, 76, 447–488.

Lowerre-Barbieri, S. K., Tringali, M. D., Shea, C. P., Walters Burnsed, S., Bickford, J., Murphy, M., & Porch, C. (2019). Assessing red drum spawning aggregations and abundance in the eastern Gulf of Mexico: A multidisciplinary approach. *ICES Journal of Marine Science*, 76, 516–529.

Lubitz, N., Abrantes, K., Crook, K., Currey-Randall, L. M., Chin, A., Sheaves, M., Fizpatrick, R., Barbosa Martins, A., Bierwagen, S., Miller, I. B., & Barnett, A. (2023). Trophic ecology shapes spatial ecology of two sympatric predators, the great hammerhead shark (*Sphyrna mokarran*) and bull shark (*Carcharhinuus leucas*). *Frontiers in Marine Science*, 10, 1274275.

Lubitz, N., Bradley, M., Sheaves, M., Hammerschlag, N., Daly, R., & Barnett, A. (2022). The role of context in elucidating drivers of animal movement. *Ecology and Evolution*, 12, e9128.

Macdonald, C., Jerome, J., Pankow, C., Perni, N., Black, K., Shiffman, D., & Wester, J. (2021). First identification of probable nursery habitat for critically endangered great hammerhead *Sphyrna mokarran* on the Atlantic Coast of the United States. *Conservation Science and Practice*, 3, e418.

Maliao, R. J., Turingan, R. G., & Lin, J. (2008). Phase-shift in coral reef communities ini the Florida keys National Marine Sanctuary (FKNMS), USA. *Marine Biology*, *154*, 841–853.

Mannocci, L. A. M., Boustany, J. J., Roberts, D. M., Palacios, D. C., Dunn, P. N., Halpin, S., Viehman, J., Moxley, J., Cleary, H., Bailey, S. J., Bograd, E. A., Becker, B., Gardner, J. R., Hartog, E. L., Hazen, M. C., Ferguson, K. A., Forney, B. P., Kinlan, M. J., Oliver, C. T., … Winship, A. J. (2017). Temporal resolutions in species distribution models of highly mobile marine animals: Recommendation for ecologists and managers. *Diversity and Distributions*, *23*, 1098–1109.

Massol, F., Gravel, D., Mouquet, N., Cadotte, M. W., Fukami, T., & Leibold, M. A. (2011). Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*, *14*, 313–323.

Matley, J. K., Klinard, N. V., Barbosa Martins, A. P., Aarestrup, K., Aspillaga, E., Cooke, S. J., Cowley, P. D., Heupel, M. R., Lowe, C. G., Lowerre-Barbieri, S. K., Mitamura, H., Moore, J., Simpfendorfer, C. A., Stokesbury, M. J. W., Taylor, M. D., Thorstad, E. B., Vandergoot, C. S., & Fisk, A. T. (2022). Global trends in aquatic animal tracking with acoustic telemetry. *Trends in Ecology and Evolution*, *37*, 79–94.

Mazerolle, M. J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3–1. https://cran.r-project.org/package=AICcmodavg

McMilan, M. N., Huveneers, C., Semmes, J. M., & Gillanders, B. M. (2019). Partial female migration and cool-water migration pathways in an overfished shark. *ICES Journal of Marine Science*, *76*, 1083–1093.

Mendelssohn, R. (2021). rerddapXtracto: Extracts environmental data from 'ERDDAP' web services. R package version 1.1.2. https://CRAN.R-project.org/package=rerddapXtracto

Miller, M. H., Carlson, J., Hogan, L., & Kobayashi, D. (2014). Status review report: Great hammerhead shark (*Sphyrna mokarran*). In *Final report to National Marine Fisheries Service, Office of Protected Resources* (p. 116). https://repository.library.noaa.gov/view/noaa/16286

Moore, C., Drazen, J. C., Radford, B. T., Kelley, C., & Newman, S. J. (2016). Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. *Marine Policy*, *69*, 32–41.

Mourier, J., Maynard, J., Parravinci, V., Ballesta, L., Clua, E., Domeier, M. L., & Planes, S. (2016). Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. *Current Biology*, *26*, 2011–2016.

Muff, S., Singer, J., & Fieberg, J. (2018). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, *89*, 80–92.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *PNAS*, *105*, 19052–19059.

Newman, M. E. J. (2006). Finding community structure using the eigenvectors of matrices. *Physical Review E*, *74*, 036104.

Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E: Statistical, Nonlinear, and Soft Matter Physics*, *69*, 026113.

NMFS. (2006). Final consolidated Atlantic highly migratory species fishery management plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, highly migratory species management division, Silver Spring, MD. Public Document. pp. 1600.

NOAA Fisheries. (2017). Final: Amendment 10 to the 2006 consolidated Atlantic Highly Migratory Species Fishery Management Plan: Essential Fish Habitat and Environmental Assessment. Office of Sustainable Fisheries, Atlantic Highly Migratory Species Management Division.

Novak, A. J., Becker, S. L., Finn, J. T., Pollock, C. G., Hillis-Starr, Z., & Jordaan, A. (2020). Scale of biotelemetry data influences ecological interpretations of space and habitat use in yellowtail snapper. *Marine and Coastal Fisheries*, *12*, 364–377.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H., Szoecs, E., & Wagner, H. (2020). vegan: community ecology package. R package version 2.5–7. https://CRAN.R-project.org/package=vegan

Opsahl, T. (2009). *Structure and evolution of weighted networks* (pp. 104–122). University of London (Queen Mary College).

Opsahl, T., & Panzarasa, P. (2009). Clustering in weighted networks. *Social Networks*, *31*, 155–163.

Pacoureau, N., Carlson, J. K., Kindsvater, H. K., Rigby, C. L., Winker, H., Simpfendorfer, C. A., Charvet, P., Pollom, R. A., Barreto, R., Sherman, C. S., Talwar, B. S., Skerritt, D. J., Sumaila, U. R., Matsushiba, J. H., VanderWright, W. J., Yan, H. F., & Dulvy, N. K. (2023). Conservation successes and challenges for wide-ranging sharks and rays. *PNAS*, *120*, e2216891120.

Papastamatiou, Y. P., Meyer, C. G., Carvalho, F., Dale, J. J., Hutchinson, M. R., & Holland, K. N. (2013). Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology*, *94*, 2595–2606.

Pickared, A. E., Vaudo, J. J., Wetherbee, B. M., Nemeth, R. S., Blondeau, J. B., Kadison, E. A., & Shivji, M. S. (2016). Comparative use of a Caribbean mesophotic coral ecosystem and association with fish spawning aggregations by three species of shark. *PLoS One*, *11*, e0151221.

Piercy, A. N., Carlson, J. K., & Passerotti, M. S. (2010). Age and growth of the great hammerhead shark, *Sphyrna mokarran*, in the north-western Atlantic Ocean and Gulf of Mexico. *Marine and Freshwater Research*, *61*, 992–998.

Pons, P., & Latapy, M. (2006). Computing communities in large networks using random walks. *Journal of Graph Algorithms and Applications*, *10*, 191–218.

Portnoy, D. S., Hollenbeck, C. M., Bethea, D. M., Frazier, B. S., Gelsleichter, J., & Gold, J. R. (2016). Population structure, gene flow, and historical demography of a small coastal shark (*Carcharhinus isodon*) in US waters of the Western Atlantic Ocean. *ICES Journal of Marine Science*, *73*, 2322–2332.

Portnoy, D. S., Puritz, J. B., Hollenbeck, C. M., Gelsleichter, J., Chapman, D., & Gold, J. R. (2015). Selection and sex-based dispersal in a coastal shark: The influence of philopatry on adaptive variation. *Molecular Ecology*, *24*, 5877–5885.

Pratt, H. L., Jr., Pratt, T. C., Morley, D., Lowerre-Barbieri, S., Collins, A., Carrier, J. C., Hart, K. M., & Whitney, N. M. (2018). Partial migration of the nurse shark, *Ginglymostoma cirratum* (Bonnaterre), from the Dry Tortugas Islands. *Environmental Biology of Fishes*, *101*, 515–530.

Queiroz, N., Humphries, N. E., Mucientes, G., Hammerschlag, N., Lima, F. P., Scales, K. L., Miller, P. I., Sousa, L. L., Seabra, R., & Sims, D. W. (2016). Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *PNAS*, *113*, 1582–1687.

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raghavan, U. N., Albert, R., & Kumara, S. (2007). Near linear time algorithm to detect community structures in large-scale networks. *Physical Review E*, *76*, 036106.

Raoult, V., Broadhurst, M. K., Peddemores, V. M., Williamson, J. E., & Gaston, T. F. (2019). Resource use of great hammerhead sharks (*Sphyrna mokarran*) off eastern Australia. *Journal of Fish Biology*, *95*, 1430–1440.

Raoult, V., Trueman, C. N., Kingsbury, K. M., Gillanders, B. M., Broadhurst, M. K., Williamson, J. E., Nagelkerken, I., Booth, D. J., Peddemors, V., Courtuier, L. I. E., & Gaston, T. F. (2020). Predicting geographic ranges of marine animal populations using stable isotopes: A case study of great hammerhead sharks in eastern Australia. *Frontiers in Marine Science*, *7*, 594636.

Rhodes, K. L., Baremore, I., & Graham, R. T. (2019). Grouper (Epinephelidae) spawning aggregations affect activity space of grey reef sharks, *Carcharhinus amblyrhynchos*, in Pohnpei, Micronesia. *PLoS ONE*, *14*, e0221589.

Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K., Jabado, R. W., Liu, K. M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R. B., & Winker, H. (2019). Sphyrna mokarran. The IUCN Red List of Threatened Species 2019: e.T39386A2920499.

Riotte-Lambert, L., & Matthiopoulous, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends Ecol Evol*, *35*, 163–174.

Roemer, R. P., Gallagher, A. J., & Hammerschlag, N. (2016). Shallow water tidal flat use and associated specialized foraging behavior of the great hammerhead shark (*Sphyrna mokarran*). *Marine and Freshwater Behavior and Physiology*, *4*, 235–249.

SEDAR. (2022). SEDAR 77 HMS hammerhead sharks: Data workshop final report. SEDAR southeast data, assessment, and review. North Charleston, SC, USA. 247 pp.

Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, *30*, 991–1007.

Shaw, A. K., & Levin, S. A. (2011). To breed or not to breed: A model of partial migration. *Oikos*, *120*, 1871–1879.

Shipley, O. N., Matich, P., Hussey, N. E., Brooks, A. M. L., Chapman, D., Frisk, M. G., Guttridge, A. E., Guttridge, T. L., Howey, L. A., Kattan, S., Madigan, D. J., O'Shea, O., Polunin, N. V., Power, M., Smukall, M. J., Schneider, E. V. C., Shea, B. D., Talwar, B. S., Winchester, M., … Gallagher, A. J. (2023). Energetic connectivity of diverse elasmobranch populations – Implications for ecological resilience. *Proceedings of the Royal Society B*, *290*, 20230262.

Skomal, G. B., Braun, C. D., Chisholm, J. H., & Therrold, S. R. (2017). Movements of the white shark *Carcharodon carcharias* in the North Atlantic Ocean. *Marine Ecology Progress Series*, *580*, 1–16.

Song, A. M., Scholtens, J., Stephen, J., Bavinck, M., & Chuenpagdee, R. (2017). Transboundary research in fisheries. *Marine Policy*, *76*, 8–18.

Stevens, J. D., & Lyle, J. M. (1989). Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. Lewini*) from northern Australia. *Australian Journal of Marine and Freshwater Research*, *40*, 129–146.

Strong, W. R., Jr., Snelson, F. F., Jr., & Gruber, S. H. (1990). Hammerhead shark predation on stingrays: An observation of prey handling by *Sphyrna mokarran*. *Copeia*, *3*, 836–840.

Sulikowski, J. A., & Hammerschlag, N. (2023). A novel intrauterine satellite transmitter to identify parturition in large sharks. *Science Advances*, *9*, eadd6340.

Tarnecki, J. H., & Patterson, W. F., III. (2020). A mini ROV-based method for recovering marine instruments at depth. *PLoS One*, *15*, e023521.

Taylor, M. D., Babcock, R. C., Simpfendorfer, C. A., & Crook, D. A. (2017). Where technology meets ecology: Acoustic telemetry in contemporary Australian aquatic research and management. *Marine and Freshwater Research*, *68*, 1397–1402.

Teitelbaum, C. S., & Mueller, T. (2019). Beyond migration: Causes and consequences of nomadic animal movements. *Trends Ecol Evol*, *34*, 569–581.

Wearmouth, V. J., & Sims, D. W. (2008). Sexual segregation in marine fish: Reptiles, birds and mammals: Behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, *54*, 107–170.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Williams, J. J., Papastamatiou, Y. P., Caselle, J. E., Bradley, D., & Jacoby, D. M. P. (2018). Mobile marine predators: An understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B*, *285*, 20172456.

Winton, M. V., Fay, G., & Skomal, G. B. (2023). An open spatial capture-recapture framework for estimating the abundance and seasonal dynamics of white sharks at aggregation sites. *Marine Ecology Progress Series*, *715*, 1–25.

Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007). Can measures of prey availability improve our ability to predict the abundance of large marine predators? *Oecologia*, *153*, 563–568.

Yates, P. M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2015). Ecological drivers of shark distributions along a tropical coastline. *PLoS One*, *10*, e0121346.

Young, J. M., Bowers, M. E., Reyier, E. A., Morley, D., Ault, E. R., Pye, J. D., Gallagher, R. M., & Ellis, R. D. (2020). The FACT network: Philosophy, evolution, and management of a collaborative coastal tracking network. *Marine and Coastal Fisheries*, *12*, 258–271.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Casselberry, G. A., Skomal, G. B., Griffin, L. P., Brownscombe, J. W., Finn, J. T., Dello Russo, J., Filous, A., Holder, P. E., Daughtry, B., Kneebone, J., Morley, D., Lowerre-Barbieri, S. K., Anderson, B. N., Sulikowski, J., Cooke, S. J., & Danylchuk, A. J. (2025). Migratory patterns and seasonal habitat use of great hammerhead sharks (*Sphyrna mokarran*) in the southeastern United States. *Journal of Fish Biology*, *107*(2), 350–371. https://doi.org/10.1111/jfb.70039