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Movescapes and eco-evolutionary movement strategies in marine fish: Assessing a connectivity hotspot

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Abstract

Data from the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network, and sister networks, were used to evaluate fish movements in the Florida Keys—an extensive reef fish ecosystem just north of Cuba connecting the Atlantic Ocean and Gulf of Mexico. We analysed ~2 million detections for 23 species, ranging from reef fish such as Nassau grouper (*Epinephelus striatus*, Serranidae) to migratory apex predators such as white sharks (*Carcharodon carcharias*, Lamnidae). To facilitate comparisons across species, we used an eco-evolutionary movement strategy framework that identified measurable movement traits and their proximate and ultimate drivers. Detectability was species-specific and quantified with a detection potential index. Life stages detected in the study area varied by species and residency varied with life stage. Four annual movement types were identified as follows: high site-fidelity residents, range residents, seasonal migrants and general migrants. The endangered smalltooth sawfish (*Pristis pectinata*, Pristidae), a seasonal migrant, exhibited the greatest within-ecosystem connectivity. Site attachment, stopover and deep-water migration behaviours differed between individuals, species and annual movement types. All apex predators were migratory. General migrants were significantly larger than fish in the other movement types, a life-history and movement trait combination that is common but not exclusive, as many small pelagics also migrate. Most teleosts exhibited movements associated with spawning. As concerns grow over habitat and biodiversity loss, multispecies movescapes, such as presented here, are expected to play an increasingly important role in informing ecosystem-based and non-extractive fisheries management strategies.

KEYWORDS

acoustic telemetry, Florida Keys, migration, movement ecology, network analysis, space use

1 | INTRODUCTION

Species' movement patterns differ, affecting how they adapt to change. The movement ecology paradigm (Nathan et al., 2008) links lifetime movement to fitness, setting the foundation for movement to be understood as part of a species' life history. However, to facilitate application of this paradigm to inform management and conservation, a framework is needed to identify measurable traits at the species, stock, or population scale (Allen & Singh, 2016) and their ecological and evolutionary drivers. Ecological drivers include conspecific density and environmental conditions (e.g. temperature, habitat, currents, water quality, depth), spatially explicit stressors and habitat degradation (Tamario et al., 2019). At the evolutionary scale, movement patterns are selected for when they increase an animal's growth, survival or reproduction (Shaw, 2016). Ecological theory integrating these drivers focuses on growth and survival through optimal foraging theory (Gallagher et al., 2017; Wittemyer et al., 2019), the ideal free distribution (Fretwell & Lucas, 1969) and the pre-emptive distribution, linking breeding site selection with reproductive success (Pulliam & Danielson, 1991). For fish with the common small egg reproductive strategy (Andersen et al.,

2016)—breeding and birth sites are the same and birth site selection affects offspring survival (Ciannelli et al., 2015; Lowerre-Barbieri et al., 2017; Secor, 2002). Animals also move due to physiological constraints defining favourable environmental conditions. In some species, this results in seasonal movements to overwintering grounds, or to specific spawning grounds, and in all species, this affects their distribution, with important implications for management (McGowan et al., 2017).

Research on animal movement has grown rapidly and is shifting from traditional site- and species-specific approaches (Crossin et al., 2017; Holyoak et al., 2008) to movescapes—the synthesis of many movement signatures (i.e. locations over time) from animals with differing demographics and/or ecological organization (Lowerre-Barbieri et al., 2019). Evaluating movement at this larger scale has numerous applications to conservation and management (Fraser et al., 2018; Hays et al., 2019). Even though acoustic telemetry is more commonly used in aquatic systems (Hussey et al., 2015), marine movescapes have been primarily assessed using tracks from pop-up satellite archival tags (PSATs) (Block et al., 2011; Harrison et al., 2018; Rooker et al., 2019; Sequeira et al., 2018). This is because passive AT (hereafter referred to as AT) is range limited; that is,

it depends on the detection of a unique signal by a fixed underwater receiver when an acoustically tagged animal is in range, limiting early studies to small spatial scales with species-specific objectives and receiver array designs (Heupel et al., 2006). However, AT networks—organized associations of researchers at regional to global scales—are facilitating the exchange of detection data across receiver arrays (Donaldson et al., 2014; Hussey et al., 2015). These integrated tracking data are increasingly used to assess single species (DeGroot et al., 2021; Graham et al., 2021; Griffin et al., 2018; Pratt et al., 2018; Rider et al., 2021) and multispecies movements (Brodie et al., 2018; Friess et al., 2021; Udyawer et al., 2018).

Integrated tracking data change the spatial scale and sample size of tracked animals, critical to effective spatial management and to improving our ability to predict how species' movements will adapt to a changing ocean. This is particularly true of high-connectivity ecosystems, such as the Florida Keys. These ecosystems may act as spatial bottlenecks, where changes in animal movement negatively affect not only the given ecosystem but a range of connected ecosystems. The Florida Keys ecosystem includes the world's third largest barrier reef (580 km extent), expansive seagrass meadows, mangrove forests and >1,000 shipwrecks/artificial reef habitats, which are co-managed by the Florida Fish and Wildlife Conservation Commission and the Florida Keys National Marine Sanctuary (FKNMS; Montenero et al., 2020). Such reef ecosystems are critical to supporting marine diversity, but are increasingly affected by climate change (Graham et al., 2020), habitat degradation and high fishing pressure (Cinner et al., 2020). The Florida Keys region connects the Gulf of Mexico (GOM) and Atlantic Ocean and is just north of Cuba and the Caribbean (Figure 1). Multiple species such as king mackerel (*Scomberomorus cavalla*, Scombridae) and Spanish mackerel (*Scomberomorus maculatus*, Scombridae) migrate to this ecosystem to overwinter, providing seasonal prey pulses, which may attract larger predators (Clardy et al., 2008; Johnson et al., 1994). Due to these attributes, the Florida Keys was identified as a high priority site for collecting AT data for multiple species by the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network in collaboration with the Ocean Tracking Network (OTN)—a global aquatic tracking platform.

The Florida Keys ecosystem is also a high priority for biodiversity conservation through the 30% marine-protected areas (MPAs) by 2030 initiative by the International Union for Conservation of Nature (Zhao et al., 2020). However, the ability for spatial management to protect biodiversity and ecosystem function is dependent on better understanding space use and connectivity of species within the ecosystem—data currently lacking for the Florida Keys. To address this knowledge gap, we used integrated tracking data to assess multispecies movescapes and test hypotheses relevant to effective spatial management. We contextualize these hypotheses within an eco-evolutionary movement strategy framework with intra-annual, annual and lifetime traits. Data from three arrays for 23 species were collected over four years (Table 1) and used to assess how (a) maturation affects immigration and emigration in the study area; (b) annual movement type affects multi-ecosystem and

within-ecosystem connectivity; (c) species differ in site attachment, stopover behaviour and use of a deep-water migratory corridor; and (d) relationships vary between annual movement types, body size, trophic niche and spatial reproductive behaviour (i.e. spawning migrations and aggregations).

2 | METHODS

2.1 | Movement strategy framework

Eco-evolutionary movement strategies include measurable movement traits and their proximate and ultimate drivers (Riotte-Lampert & Matthiopoulos, 2020). These strategies can be evaluated at
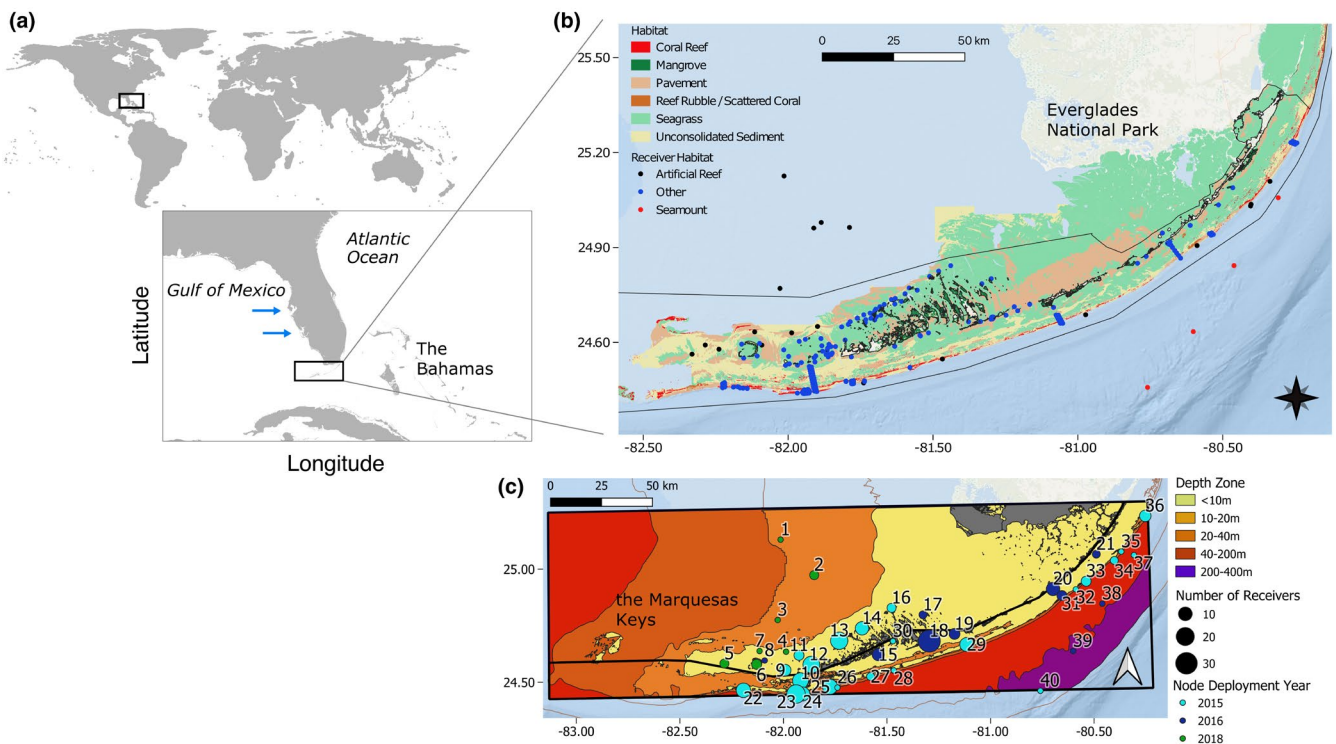
FIGURE 1 Geographic location of the study area (black rectangle), arrows indicate Tampa Bay (to the north) and Charlotte Harbor (a); boundaries of the Florida Keys National Marine Sanctuary (black lines), underlying habitat and deployed receiver sites, with red circles denoting seamount sites and black circles denoting artificial reef sites (b). Habitat types were obtained from Florida Unified Reef Tract data; nodes plotted by depth zone, coloured by deployment year and scaled by number of receivers in each node (c). The black line along the islands and just south of the Marquesas Keys denotes the boundary used to separate depth on the Atlantic versus Gulf side. The deep-water migratory corridor occurs from the reef track (nodes 22 to 36) to the seamounts (nodes 37 to 40, node 38 = Islamorada and 40 = Marathon)

different scales of ecological organization, applied here to species. This framework (Figure 2) facilitates the application of the movement ecology paradigm (Nathan et al., 2008) to address movements important to management and conservation. The movement ecology paradigm defines an individual's lifetime movement path as a function of external factors, internal state, and motion and navigation capacity. External drivers are the same in both frameworks. Movement strategies are shaped over multi-generational scales with fitness and density-dependent feedback loops which then determine an individual's genotype, that in turn affects its internal state, including personality (Hertel et al., 2020), motion and navigation capacity. Tracking data used to evaluate lifetime paths are affected by observation error, sample size and the animal to tag longevity ratio. Integrated tracking data from multiple studies (either PSAT tracks or shared detections) provide increased sample sizes and spatio-temporal scale of tracking. Emerging analytical tools to assess movescapes and movement strategy traits include cluster and network analysis (Jacoby & Freeman, 2016; Brodie et al., 2018).

Movement strategy traits are categorized at the lifetime, annual and intra-annual temporal scales (Figure 2). At the lifetime scale, important traits include natal dispersal, although often difficult to study with electronic tracking (Allen & Singh, 2016), and ontogenetic habitat shifts (Gillanders et al., 2003; Grubbs, 2010) often associated with sexual maturity (Hazen et al., 2012). Annual scale movement is the most studied, with annual movement types often classified as

resident, migrant or nomad—although terms vary and there are often sub-divisions (Abrahms et al., 2017; Allen & Singh, 2016; Bastille-Rousseau et al., 2016; Berg et al., 2019; Brodie et al., 2018; Mueller & Fagan, 2008). Resident typically refers to a range resident movement type, that is living year-round in a home range (Fagan & Gurarie, 2020). In contrast, migrants make recurrent movements between non-overlapping activity spaces, exhibiting cross-ecosystem connectivity but the impact of these movements on an ecosystem differs depending on whether they are seasonally resident in that ecosystem (seasonal migrants) or the ecosystem is simply part of their migratory route (general migrants). Nomads occupy different activity spaces with low recurrence in annual movement paths (Mueller & Fagan, 2008). Connectivity within and across ecosystems impacts ecosystem functioning. Behaviours affecting within-ecosystem space use relevant to spatial management include site attachment, stopover behaviour and the use of migratory corridors. Tracking data are assessed at fine temporal scales to understand diel activity, core areas, water column and functional habitat use (Wittemyer et al., 2019). Individual variability in movement is also an important trait at all temporal scales (Hertel et al., 2020; Shaw, 2020), as it affects catchability and a population's resilience to disturbance.

Movement strategies are shaped by multiple ultimate drivers, including predation, resource acquisition, birth site-specific survivorship and physiological functionality. For species to persist, reproductive success must be adequate to keep abundance levels above those

TABLE 1 List of tracked species with their annual movement type reported in the literature and final movement type assignment considering literature and hierarchical cluster analysis conducted in this study

Common name	Scientific name	Family name	Movement (literature)	Movement (cluster)
1. Spotted Eagle Ray	*Aetobatus narinari*	Myliobatidae	Seasonal	Seasonal migrant
2. Bull Shark	*Carcharhinus leucas*	Carcharhinidae	Migratory	General migrant
3. Blacktip Shark	*Carcharhinus limbatus*	Carcharhinidae	Seasonal	Seasonal migrant
4. White Shark	*Carcharodon carcharias*	Lamnidae	Migratory	General migrant
5. Tiger Shark	*Galeocerdo cuvier*	Carcharhinidae	Migratory	General migrant
6. Nurse Shark	*Ginglymostoma cirratum*	Ginglymostomatidae	Migratory	Seasonal migrant
7. Lemon Shark	*Negaprion brevirostris*	Carcharhinidae	Migratory	General migrant
8. Smalltooth Sawfish	*Pristis pectinata*	Pristidae	Migratory	Seasonal migrant
9. Great Hammerhead	*Sphyrna mokarran*	Sphyrnidae	Migratory	General migrant
10. Crevalle Jack	*Caranx hippos*	Carangidae	Seasonal	*Unassigned*
11. Rock Hind	*Epinephelus adscensionis*	Serranidae	Resident	Range resident
12. Nassau Grouper	*Epinephelus striatus*	Serranidae	Resident	High site-fidelity resident
13. Mutton Snapper	*Lutjanus analis*	Lutjanidae	Resident	Range resident
14. Grey Snapper	*Lutjanus griseus*	Lutjanidae	Resident	Range resident
15. Black Grouper	*Mycteroperca bonaci*	Serranidae	Resident	High site-fidelity resident
16. Atlantic Tarpon	*Megalops atlanticus*	Megalopidae	Migratory	Seasonal migrant
17. Gag	*Mycteroperca microlepis*	Serranidae	Resident males/ migrant females	Range resident
18. Scamp	*Mycteroperca phenax*	Serranidae	Resident	Range resident
19. Yellowfin Grouper	*Mycteroperca venenosa*	Serranidae	Resident	High site-fidelity resident
20. Cobia	*Rachycentron canadum*	Rachycentridae	Migratory	General migrant
21. Greater Amberjack	*Seriola dumerili*	Carangidae	Seasonal	Range resident
22. Atlantic Bluefin Tuna	*Thunnus thynnus*	Scombridae	Migratory	General migrant
23. Permit	*Trachinotus falcatus*	Carangidae	Resident	Range resident

Note: Elasmobranchs are listed first and then teleosts. Within these groups, species are in alphabetical order by scientific name.

where depensation or the Allele effect occurs (Perälä & Kuparinen, 2017). Reproductive success occurs when an individual produces offspring that survive to reproductive age; that is, it survived long enough to develop the energy reserves and physiological capacity to produce offspring that survive to maturity. Movement plays a critical role in this process, resulting in movement strategies that overcome predation risk, meet energetic needs and support physiological functioning and offspring survival. Strategies can optimize one of these selection axes but more commonly include trade-offs between them. We used this movement strategy framework to assess lifetime and annual movement traits and how they relate to ultimate drivers and life-history components (e.g. size, trophic niche). Detection basins (i.e. Atlantic Ocean, Florida Keys study area, The Bahamas, GOM) were used as a proxy for non-overlapping activity spaces.

2.2 | Application of the movement strategy framework

We implemented our movement strategy framework to explicitly test a series of hypotheses about movement traits important to

spatial management: (a) within the study area, immature fish of multiple species exhibit greater residency than adults and movement to the study area from outside nurseries is size-dependent; (b) species exhibit different annual movement types, ranging from residents to nomads; (c) within-ecosystem space use and connectivity differ with annual movement type; (d) fine-scale behaviours—site attachment in residents, and stopover behaviour and use of a deep-water migratory corridor (hereafter referred to as the migratory corridor or corridor)—vary across and within species; and (e) size, trophic niche and birth site selection differ with annual movement type.

2.2.1 | Study area and receiver arrays

The study area encompassed most of the FKNMS, as well as several seamounts to the south and artificial reefs to the north (Figure 1). Study area boundaries were 24.425° to 25.250° latitude and −83.130° to −80.210° longitude. Receivers (VR2W and VR2-Tx, Innovasea, Halifax, Nova Scotia) were initially deployed to track reef fish (*n* = 39; Keller et al., 2020), permit (*Trachinotus falcatus*, Carangidae; *n* = 123; Brownscombe et al., 2019) and multispecies
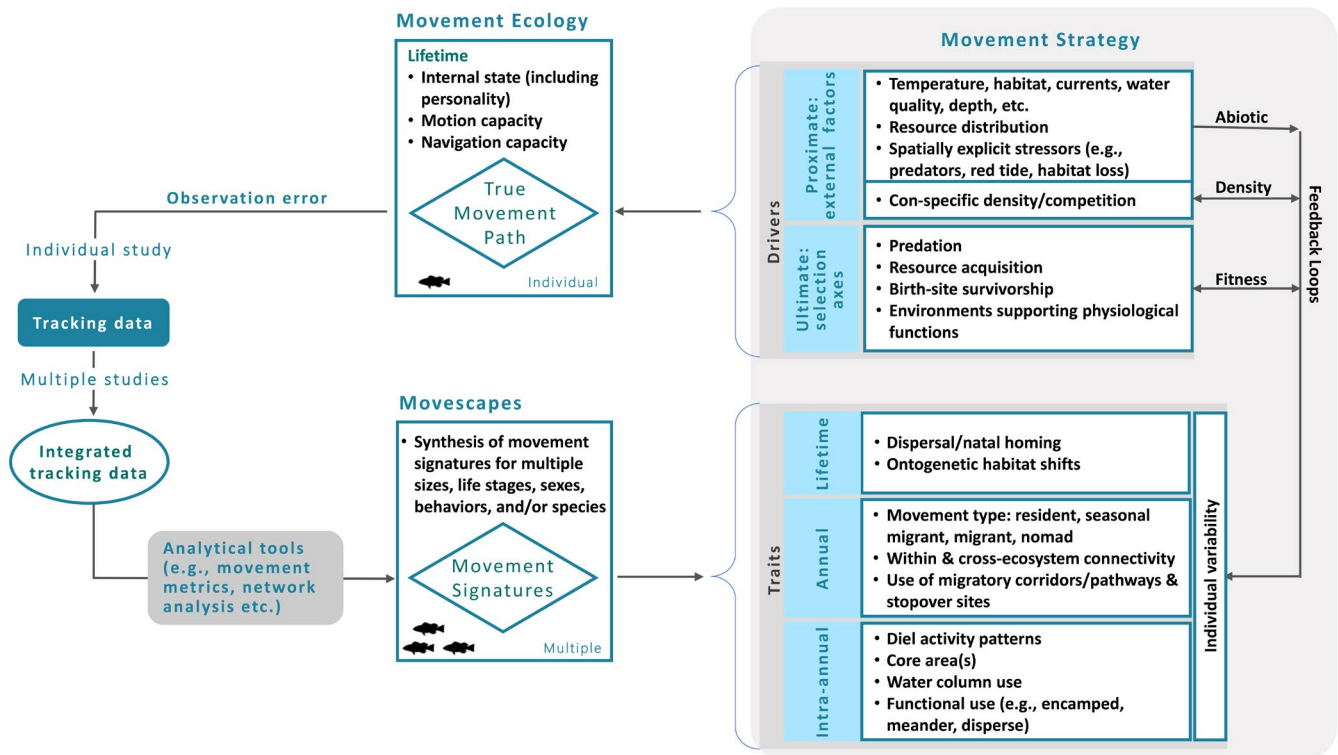
FIGURE 2 A conceptual model of eco-evolutionary movement strategies: proximate and ultimate drivers, feedback loops and measurable traits at lifetime, annual and intra-annual temporal scales. We present this model within the context of the movement ecology paradigm, and our ability to estimate traits using tracking data, integrated tracking data and movescapes

migrations and stopover sites ($n = 69$; iTAG) over the following substrates: seamounts, coral reef, reef rubble/scattered coral, seagrass, pavement, mangrove and unconsolidated sediment (primarily sand). Receivers were grouped into nodes ($n = 40$) based on proximity and substrate, irrespective of original study array. The study was from 15 June 2015 to 15 April 2019. The number of receivers increased over this time period from 176 in 2016 to 231 in 2018. However, Hurricane Irma in 2017 negatively affected receiver coverage, resulting in data gaps in 10 nodes. In 2018, lost receivers were replaced, and new nodes were established on the Gulf side of the study area (nodes 1–7; Figure 1c).

2.2.2 | Tagging data

Transmitter codes were assigned to tag owners and species based on iTAG, FACT (the Florida Atlantic Coast Telemetry network) and ACT (Atlantic Cooperative Tracking network) databases. Innovasea (formerly Vemco) contacted owners of unidentified tags (see Table 1 for list of species and scientific names). Research groups ($n = 22$) with ≥ five detected fish of a given species were invited to be co-authors, resulting in a total of 419 tracked fish in this study. Co-authors provided the following tag metadata: species, tagging date and location, number of fish tagged, tag expiration date, fish size and life stage at tagging, and annual detection basins. The GOM and Atlantic basins

were considered northwest and northeast of our study area, respectively, and The Bahamas refers to detections on Bimini Biological Field Station receivers deployed at and near Bimini, The Bahamas. Co-authors reviewed the literature for their species' annual movement type and trophic niche (Table S1). Trophic niche was used to integrate predation risk into detection period calculation (section 2.3.1) and to assess whether it varied with annual movement type.

2.3 | Data analysis

2.3.1 | Detection potential

Detection potential drives the capacity of telemetry data to accurately reflect true movement paths. In single-species studies, telemetry arrays are deployed to monitor space used by the target species, and detection potential is assumed to be driven by detection range. We used 200 m as a conservative estimate of range for this area (<100 m to more than 500 m; Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020; Keller et al., 2020). However, in multispecies studies, detection potential is more complex, affected by species-specific monitoring and tracking power. Monitoring power (MP) is defined as a characteristic of the observation system (e.g. receiver spatial coverage and density) and tracking power (TP) as species-specific sample size times mean

potential detection period (i.e. time within the study when a tagged fish is assumed to be alive and could be detected; hereafter referred to as detection period, DP). A detection potential index (DPI) was calculated for each species (*i*) as the product of median MP and TP, scaled by median space use based on standard deviation ellipses, SDEs (see section 2.3.5). Each factor was scaled by the maximum value observed across species:

$$DPI_i = \frac{MP_i}{max\left(MP_i\right)} \times \frac{TP_i}{max\left(TP_i\right)} \times \frac{max\left(\sqrt{SDE_i}\right)}{\sqrt{SDE_i}} \quad (1)$$

Tracking power was calculated as the sum of individual DPs:

$$TP_i = \sum_{j=1}^{n_i} DP_{j,i} \quad (2)$$

where n_i is the number of tagged individuals *j* within species *i*. Theoretically, species-specific monitoring power is the sum of the proportion of habitats used (*phu*) multiplied by the proportion of those habitats monitored (*phm*) in the study area, with a maximum of one, if 100% of the habitats used by a species are monitored. Thus, we calculated individual MP as:

$$MP_{j,i} = \sum_{d=1} \sum_{g=1} phm_{d,g} \times phu_{d,g,j,i} \quad (3)$$

where *d* is depth zone and *g* is region. Species monitoring power MP_i was obtained by calculating median MP across individuals within species. We used depth as a proxy for habitat, due to a lack of habitat information outside shallow-water zones. The spatial distribution of depth differs significantly on the GOM versus Atlantic side of the Florida Keys, so those regions were treated separately. We used a border along the islands and just south of the Marquesas Key to ensure no nodes were split between regions (Figure 1c). Four depth zones were categorized in each region: 0–10 m, 10.1–20 m, 20.1–40 m and 40.1–200 m, resulting in eight cells. The proportion of habitat monitored was calculated as:

$$phm_{d,g} = \frac{\pi 200^2 nrec_{d,g}}{A_{d,g}} \quad (4)$$

where total area *A* by depth and region was calculated in QGIS 3 (QGIS Development Team, 2021), 200 m is the detection radius for an individual receiver, and *nrec* is the number of receivers in a region and depth zone. Since *phu* was unknown, we had to estimate it from the data. We did this by scaling the total number of depth-and-region-specific detections per individual by the number of receivers in that depth zone and region:

$$rdet_{d,g,j,i} = \frac{ndet_{d,g,j,i}}{nrec_{d,g}} \quad (5)$$

This gave us relative detections (*rdet*) in which cells with fewer receivers were upweighted relative to those with more receivers. From *rdet*, we obtained the proportions of relative detections within each zone and region, which we used as a proxy for *phu*:

$$phu_{d,g,j,i} = \frac{rdet_{d,g,j,i}}{\sum_{d=1} \sum_{r=1} rdet_{d,g,j,i}} \quad (6)$$

Scaling MP and TP by space use was done to acknowledge that resident species, with predominantly small space use, were tagged in the study area and had receivers deployed at tagging sites, dramatically increasing their DPI.

Tracking multiple species that vary widely in size (Figure 3a) also necessitates addressing size effects on DP. This is due to the relationship between size and natural mortality (Lorenzen, 1996), trophic niche (Werner & Gilliam, 1984) and often migratory scale (Putman, 2018), making it more likely that a terminal lack of detections in small fish is due to mortality while in large fish it is due to migration. To address this, we graphically identified 180 cm as a size threshold which did not overlap with any species' core 25%–75% size quantiles (Figure 3). Fish below or equal to this size were categorized as "small", with the remaining fish categorized as "large". According to the literature, all species categorized as "large" were migratory and either large meso- or apex predators. We then calculated size group-specific DP, where DP start date for all fish was tagging date or the first date of the study period, whichever came later. For "small" fish subject to higher mortality, we followed the traditional method of using the last date of detection as the DP end date. For "large" fish, we used end of study period or tag expiration date, whichever came first (with occasional extensions for tags detected after their manufacturer-predicted expiration date).

2.3.2 | Movement metrics

We calculated movement metrics to help evaluate annual movement type and for subsequent hypothesis testing. To minimize the risk of false detections, we first removed duplicate detections of transmitter codes at a receiver in <30 s and single detections that occurred in the study area within a 24-hour period (Simpfendorfer et al., 2015). Only fish tagged a year or more before the study's end date (15 April 2019; n = 295) were used. We calculated two residence indices (RI) at differing temporal scales: (a) yearly RI (number of unique detection years per number of potential detection years); and (b) monthly RI (number of unique detection months per number of potential detection months). Because some species had low DPI, monthly RI was considered the best measure of time spent in the study area. We also calculated the mean for each species of maximum consecutive months fish were detected in the study period. Since none of the species-specific movement metrics were distributed normally based on the Shapiro–Wilk test, the nonparametric Kruskal–Wallis test was used to test for significant differences in metrics between
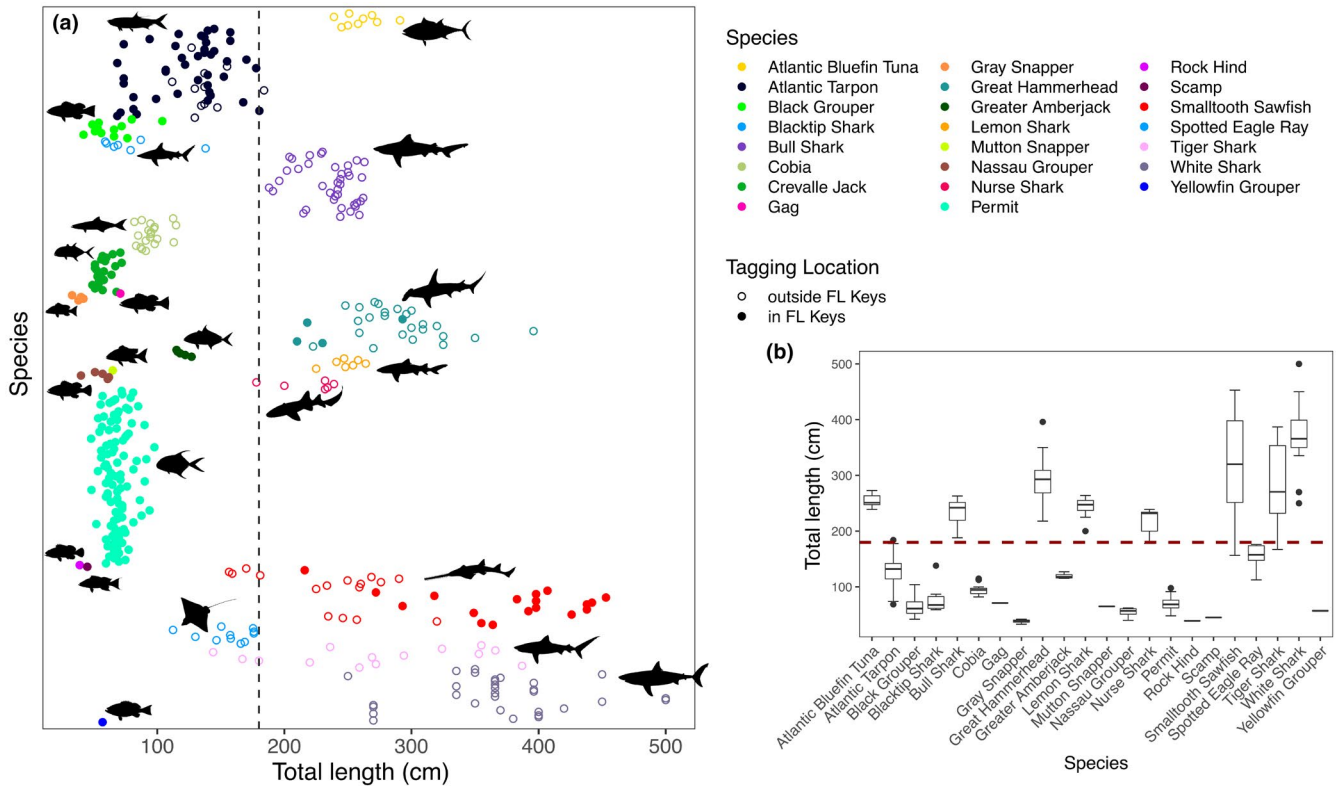
FIGURE 3 Individual (a) and summary statistics (b) for size in cm (disc width for eagle rays; total length for others) for species tracked in this study. Dashed lines indicate the 180 cm size threshold. In (a) fish tagged within the study area are indicated by filled circles

annual movement types (section 2.3.4) and species. A Dwass, Steel, Critchlow-Fligner (DSCF) post hoc test was used to identify pairwise differences. To assess cross-ecosystem movements, we estimated the mean and maximum number of basins in which individuals were detected in annually, ranging from one (the study area) to four (a fish detected in the Atlantic Ocean, Florida Keys study area, The Bahamas, and the GOM). All means are presented plus and minus one standard deviation (SD).

2.3.3 | Ontogenetic habitat shifts

To evaluate how maturity affected immigration to and emigration from the study area, we tested if time to arrival from outside nursery habitat was size-dependent and if residency differed with life stage. For both analyses, we chose species with a sample size of ≥ five and only fish tagged within the study period. Because sexual maturity and emigration from nursery habitat are size-dependent, we tested whether fish immigrating to the study area from outside nursery habitats showed a significant linear relationship between size at tagging and time elapsed (days) from tagging date to first detection in the study area. Only fish tagged a year before the study ended were included in this analysis. For emigration analysis, we selected species which had both immature and mature fish tagged within the study area and a DP ≥ six months and tested for significant differences

in residency (as measured by monthly RI) with life stage using the Wilcoxon–Mann–Whitney test.

2.3.4 | Annual movement type

We hypothesized that species would exhibit different annual movement types and were interested in identifying residents, seasonal migrants, general migrants and nomads. To assess this, we first conceptualized the relationship between the biological definition of these movement types and the following movement metrics: the mean and maximum number of detection basins, maximum consecutive months detected, and monthly and annual RI. To visualize species-specific patterns in these metrics, we used radar graphs, with each metric standardized to one. Residents were defined as species that used only the study area year-round, expected to have most, if not all, individuals detected in only one basin and a high monthly RI. Seasonal and general migrants were expected to use more than one basin, with seasonal migrants exhibiting greater residency in the study area than general migrants. All residents and migrants were expected to have multi-year detections. Low monthly and yearly RIs were expected in nomads due to low recurrence of movement paths. The above movement metrics were then used to calculate a dissimilarity matrix using Euclidian distances for agglomerative hierarchical clustering to assist with movement type classification. We used

Ward's method (Murtagh et al., 2014) and log-transformed variables if transformation improved normality, assessed with the Shapiro–Wilk test. The resulting dendrogram and clusters were compared to movement types reported in the literature.

2.3.5 | Within-ecosystem movement

Differences in connectivity and space use between annual movement types were tested to evaluate whether within-ecosystem behaviour differed. Connectivity was evaluated using network analysis (NA) metrics, and space use was estimated by calculating SDEs. To conduct NA, we calculated individual unipartite graphs (i.e. a movement graph constructed with a single type of node [Jacoby et al., 2012], in this case representing the 40 receiver nodes) and estimated network metrics in the R package "igraph" (Csárdi & Nepusz, 2006). Individuals' path numbers were calculated as the sum of edges at each node. These were averaged by species to compare species connectivity. Individual SDEs were calculated using the R package "aspace" (Bui et al., 2012) that estimates the SD of x and y coordinates from the mean centre using the equations outlined in the CrimeStat Manual (Levine, 2010). Centres of activity (based on receivers rather than nodes) were first calculated by estimating average locations during one-hour windows, and these served as input for SDE analysis. Only fish detected on three or more receivers were used. Individuals with ≥ five detection days detected at only one or two receivers were assigned the expected area based on receiver detection range (0.13 or 0.25 km^2). Individual space use was averaged by species. Neither mean path number nor SDE were normally distributed by species or annual movement type based on the Shapiro–Wilk test, resulting in the use of the nonparametric Kruskal–Wallis test to test for differences in space use within annual movement types and species, and the DSCF post hoc test to identify movement types and species that differed.

Within-ecosystem movements were evaluated for individual variability at the receiver scale and three hypotheses were tested: (a) the prevalence of site attachment varies between resident species; (b) all migrants primarily use the migratory corridor (from the reef tract to the seamounts, nodes 22–40; Figure 1c); and (c) stopover behaviour varies in location and prevalence in migrant species. To assess individual site attachment, we selected residents with ≥ 30 detection days and a minimum DP of one year to ensure an appropriate temporal scale, as space use can increase with time (Carlisle et al., 2019). The selected residents had a mean of 219 ± 170 detection days. Individuals meeting these criteria were assigned as site attached if their space use was <0.25 km^2. To better understand habitat associations with site attachment behaviour, we assessed whether all locations with this behaviour had structure (i.e. artificial or natural reefs). To test whether resident species differed in the proportion of individuals exhibiting site attachment, we tested this against the null hypothesis of no difference with the chi-square test. The same approach was applied to test for differences in individual stopover behaviour in migrants (defined as fish with

≥three consecutive months of detection) and use of the migratory corridor by migrants. Migratory corridor use was quantified based on the proportion of detections from receivers within the corridor versus outside.

2.3.6 | Movement strategies and life-history traits

We hypothesized that size, trophic niche and birth site selection would differ with annual movement type. Size was distributed normally; however, variances were not homogenous across movement types. Thus, to test whether size differed with annual movement type, we used Welsh's ANOVA and a Games–Howell post hoc test. We then evaluated the proportion of apex predators by movement type. Birth site selection behaviour was based on reports in the literature of a species forming spawning aggregations or making spawning migrations.

3 | RESULTS

3.1 | Detections

Approximately two million detections were recorded. Slightly more than half of the detected fish tagged outside the study area, some as far away as Canada. Others were tagged on the west coast of Florida or in The Bahamas (Table 2, Figure 4a,b). All sharks—except four great hammerheads (*Sphyrna mokarran*, Sphyrnidae)—were tagged outside the study area, as were cobia (*Rachycentron canadum*, Rachycentridae) and spotted eagle rays (*Aetobatus narinari*, Myliobatidae, hereafter eagle rays). Mean size of tagged fish (Figure 3) ranged from 38.3 cm total length (TL; grey snapper, *Lutjanus griseus*, Lutjanidae) to 367.6 cm TL (white sharks, *Carcharodon carcharias*, Lamnidae). Eight species had both immature and adult fish tagged (Table 2).

3.1.1 | Detection potential

Species had uneven tracking power (TP), with the number of tagged fish per species ranging from 1 to 189 and mean detection period (DP) ranging from 39 days to over 1,000 days (Figure 5, Table 2). TP was <1,000 days for crevalle jack (*Caranx hippos*, Carangidae) and most reef fish (excluding black grouper *Mycteroperca bonaci*, Serranidae and Nassau grouper *Epinephelus adscensionis*, Serranidae). TP was >20,000 days for Atlantic tarpon (*Megalops atlanticus*, Megalopidae, hereafter tarpon), smalltooth sawfish (*Pristis pectinata*, Pristidae, hereafter sawfish), great hammerheads, white sharks and permit; and >40,000 days for bull sharks (*Carcharhinus leucas* Carcharhinidae). The study area was ~21,153 km^2, with a receiver density of 0.011 receivers/km^2. Receiver coverage was not homogenous across regions or depth zones (Table 3). The greatest receiver density (0.05 receivers/km^2) occurred in the 20 to 40 m depth zone in the Atlantic (Table 3), which also detected the highest number of unique fish.

TABLE 2 Species detected, trophic niche, maximum distance travelled from tagging site in either the Atlantic (A), Gulf of Mexico (G) or Bahamas (B), mean detection period, number of tagged fish by life stage (I = immature; A = adult; U = unknown), maximum detection basins (Atlantic, Keys, Bahamas and Gulf), tags detected, proportion tagged in the Keys and detection potential index (DPI)

Common name	Trophic niche	Max. distance from tag site	Mean detection period (d)	Life stage	Max # basins	Tags	Keys tag ratio	DPI
1. Atlantic bluefin tuna	Apex	2,976 (A)	699	A	2	9	0	0.20
2. Atlantic tarpon	Meso	953 (A); 631 (G)	433	11 I, 42 A	3	53	0.79	0.60
3. Black grouper	Meso		449	7 I, 5 A	1	12	1	14.40
4. Blacktip shark	Meso	322 (G)	343	I	2	7	0	0.15
5. Bull shark	Apex	310 (B)	1082	3 I, 38 A	4	41	0	0.69
6. Cobia	Apex	434 (A)	396	A	3	20	0	0.17
7. Crevalle jack	Meso		39	A	1	24	1	
8. Gag	Meso		448	A	1	1	1	1.15
9. Grey snapper	Meso		84	A	1	4	1	0.23
10. Great hammerhead	Apex	214 (A) 310 (B)	935	1 I, 27 A	3	28	0.14	0.50
11. Greater amberjack	Meso		472	A	1	5	1	0.02
12. Lemon shark	Meso	310 (B)	1268	A	3	8	0	0.21
13. Mutton snapper	Meso		348	A	1	1	1	0.30
14. Nassau grouper	Meso		375	A	1	5	1	3.07
15. Nurse shark	Meso	208 (A), 278 (B)	1090	A	2	6	0	0.47
16. Permit	Meso		284	9 I, 93 A	2	102	1	2.78
17. Rock hind	Meso		163	A	1	1	1	0.42
18. Scamp	Meso		110	A	1	1	1	0.40
19. Smalltooth sawfish	Apex	190 (G)	733	23 I, 11 A	3	34	0.29	0.68
20. Spotted eagle ray	Meso	322 (G)	715	A	2	11	0	0.01
21. Tiger shark	Apex	831 (A), 310 (B)	1004	6 I, 8 A	4	14	0	0.30
22. White shark	Apex	2,201 (A)	909	19 I, 11 A, 1 U	3	31	0	0.54
23. Yellowfin grouper	Meso		324	A	1	1	1	0.52

However, the highest number of fish detected per receiver (12.4) was in the deepest Atlantic depth zone (with receivers at an artificial reef and the seamounts). Species-specific DPI was lowest in eagle rays and greatest in black grouper (Table 2; Figure 4c).

3.2 | Ontogenetic habitat shifts

Multiple species moved to the study area after leaving their nursery habitat, but size dependence was not uniform, nor was within-study area residency with life stage. Sawfish, blacktip sharks (*Carcharhinus limbatus*, Carcharhinidae) and white sharks had ≥ four immature fish tagged outside the study area. Immature sawfish (156 to 364 cm TL) were tagged in the Charlotte Harbor estuarine system (~200 km away, $n = 6$, elapsed time: 32–275 days; Figure 4a) and Everglades National Park (~53 km away, $n = 10$, elapsed time: 6–587 days; Figure 4b). Time elapsed between tag date and first detection of sawfish in the study area decreased significantly (F test, $n = 16$, $p < 0.0003$) with size. No significant relationship between elapsed time and size was found for blacktip sharks (F test, $n = 5$, $p = 0.21$) or white sharks (F test, $n = 18$, $p = 0.37$). Immature blacktip sharks (59–87 cm TL) were

tagged ~322 km away and elapsed time varied from 82 to 984 days. Similarly, immature white sharks tagged ~2,200 km away (250–450 cm TL) exhibited a wide range of elapsed times (141–803 days). DPIs for blacktip sharks (0.15) and white sharks (0.54) were less than sawfish (0.68) and may have affected results.

Permit and tarpon had immature and adult fish tagged in the study area and both exhibited changes in residency with life stage. However, in permit, adults showed greater residency. Immature permit had a lower mean monthly RI of 0.49 ± 0.20 ($n = 5$) than adults (0.71 ± 0.25, $n = 65$), and these differences were significant (Wilcoxon-Mann–Whitney, $n = 70$; $p = 0.05$). In contrast, immature tarpon had significantly higher (Wilcoxon-Mann–Whitney, $n = 26$; $p = 0.006$) mean monthly RI (0.94 ± 0.82, $n = 3$) than adults (0.36 ± 0.28, $n = 23$).

3.3 | Annual movement type

Agglomerative clustering differentiated between residents and migrants, with several sub-groups within each (Figure 6), but not nomads. All resident species were tagged in the study area and had
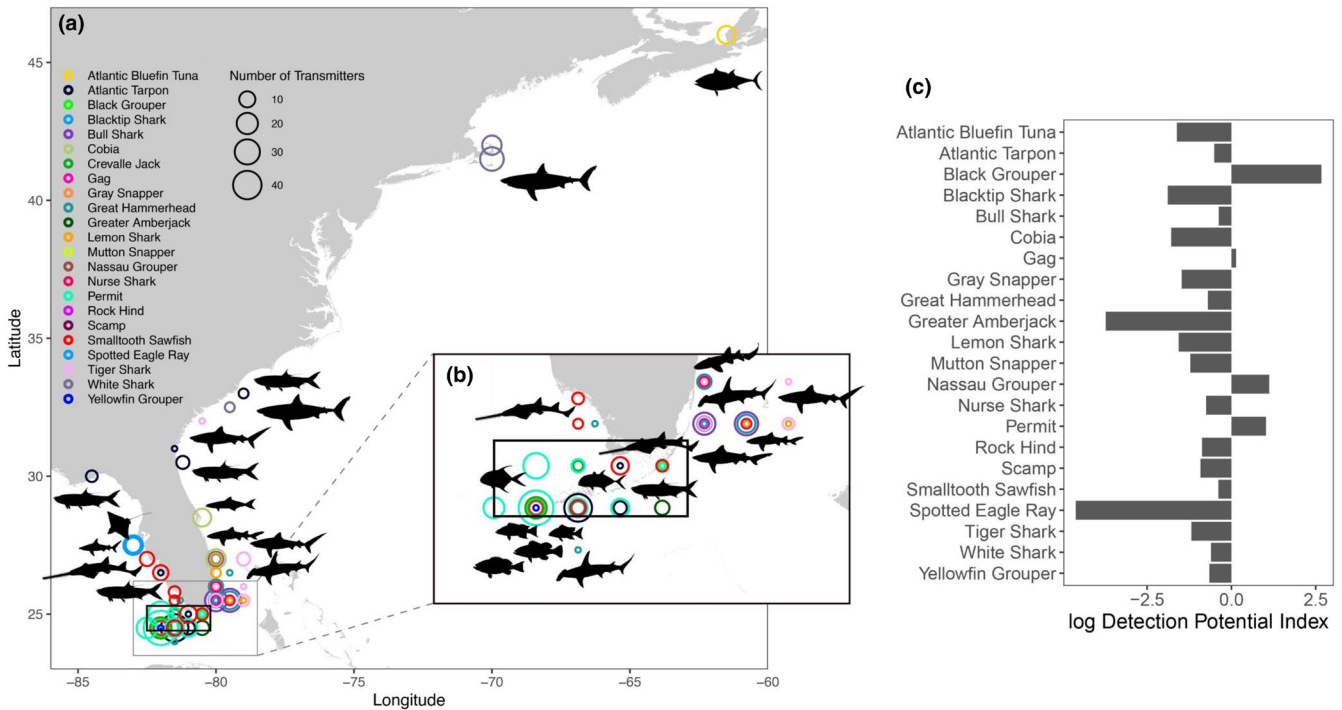
FIGURE 4 The spatial distribution of tagging sites for species detected in the study area (a & b), with the relative number of fish detected in this study from each tagging site represented by circle diameter. Fish tagged within or near the study area (b); log-scaled species-specific detection potential index (c)

FIGURE 5 Dates of detection by individual and species, exhibiting variable detection periods, sample sizes and temporal patterns

low sample sizes (*n* = 1–12), except for permit (*n* = 102). Residents also had low to no between-ecosystem connectivity, again except for permit—a few of which (*n* = 6) were detected outside the study

area. Five of these non-resident permit were detected <50 km away, but one moved up Florida's east coast ~200 km. Three clusters were identified within residents, corresponding to high site fidelity, range

TABLE 3 Measures of monitoring power within categories defined by region and depth zone: nodes, number of receivers, total area, number of unique fish detected in that area, number of unique fish detected per receiver, total monitored area, receiver density and mean receiver depth

| Region	Depth zone	Nodes	Total # receivers	Total area (km²)	# Fish detected	# Fish/receiver	Monitored area (km²)	Receiver density (#/km²)	Receiver depth +/- SD (m)
Gulf	0–10	4,5,6,7,8,9,12,11,13,14,16,17,20,	76	7048	126	1.7	9.55	0.011	3.1 ± 1.17
Gulf	10–20	1,2,3	5	3749	25	5	0.63	0.001	18.2 ± 1.60
Gulf	20–40	–	0	5583	0	0	0	0	
Gulf	40–200	–	0	2581	0	0	0	0	
Atlantic	0–10	10,15,21,22,24,29,31,36	65	1975	153	2.4	8.17	0.033	6.1 ± 2.15
Atlantic	10–20	10,22,23,24,25,27,29,33,36	31	1060	185	6	3.9	0.029	14.3 ± 2.89
Atlantic	20–40	22,23,24,25,27,28,29,30,31,32,33, 34,35,36	49	979	213	4.4	6.16	0.05	31.9 ± 5.57
Atlantic	40–200	26,37,38,39,40	5	3524	62	12.4	0.63	0.001	105 ± 44.49

Note: Receivers in nodes often were distributed across multiple depth zones.

residence, and uncertain residence. Two species with uncertain residency had lower monthly RIs (<0.60) than other residents. These were gag (*Mycteroperca microlepis*, Serranidae) and greater amberjack (*Seriola dumerili*, Carangidae), with monthly RIs of 0.38 ($n = 1$) and 0.27 ± 0.41, respectively. The literature indicates female gag are migratory and male gag are resident. Greater amberjack, in the literature, are considered to be seasonal migrants based on traditional tag-recapture data (Table 1). However, our tracking data suggest there could be a deep-water resident contingent. Grey snapper had a mean monthly RI > 0.60 but clustered in the uncertain residency group due to low consecutive months of detection. They are reported as resident in the literature. Taking the cluster results and literature into consideration, we assigned these species with uncertain residence to the range resident movement type, with the caveat that further research is needed to confirm their movement type.

Migrants clustered into two movement types: seasonal and general migrants (Figure 6). All migrants exhibited between-ecosystem connectivity but differed in their mean number of detection basins and residency. Seasonal migrants included three species detected in two basins: nurse sharks (*Ginglymostoma cirratum*, Ginglymostomatidae), blacktip sharks and eagle rays, with the latter two also identified in the literature as seasonal migrants. Tarpon and sawfish were reported in the literature to be migratory and multiple fish were detected in three basins. However, they grouped with seasonal migrants and had significantly greater (Wilcoxon-Mann–Whitney, $n = 217$; $p < 0.0001$) monthly RIs (0.41 ± 0.30) than all other migrants (0.13 ± 0.12). General migrants were all reported as migratory in the literature. These species had low residence patterns and a maximum detection basin of ≥ three, except for Atlantic bluefin tuna (*Thunnus thynnus*, Scombridae, hereafter bluefin tuna). Bluefin tuna were only detected in two basins and never in the GOM, although they are known to migrate there. No individual bluefin tuna were detected in more than one year, suggestive of nomads, but detectability was too low to confirm this.

3.4 | Within-ecosystem movement

Within-ecosystem connectivity (Figure 7), measured by NA path number between nodes, differed significantly between annual movement types (Kruskal–Wallis, $\chi^2 = 25.1591$, $p < 0.0001$). The highest mean path numbers occurred in seasonal migrants (11.57 ± 13.15), with general migrants slightly lower (8.63 ± 11.46). Mean path numbers decreased in resident species: 5.6 ± 6.57 in range residents and 1.17 ± 1.20 in high site-fidelity residents. Species-specific within-ecosystem connectivity between the Atlantic and GOM sections of the study area also differed. Except for permit, no residents were detected in the GOM section. Seasonal migrants had the greatest proportion of GOM section detections: blacktip sharks and eagle rays had 97% and 95%, respectively, while tarpon had 22% and sawfish had 11%. Nurse sharks only had 2% GOM detections, similar to general migrants. Except for bull sharks (23% GOM detections), general migrants had ≤ 3% GOM section detections (great hammerhead,
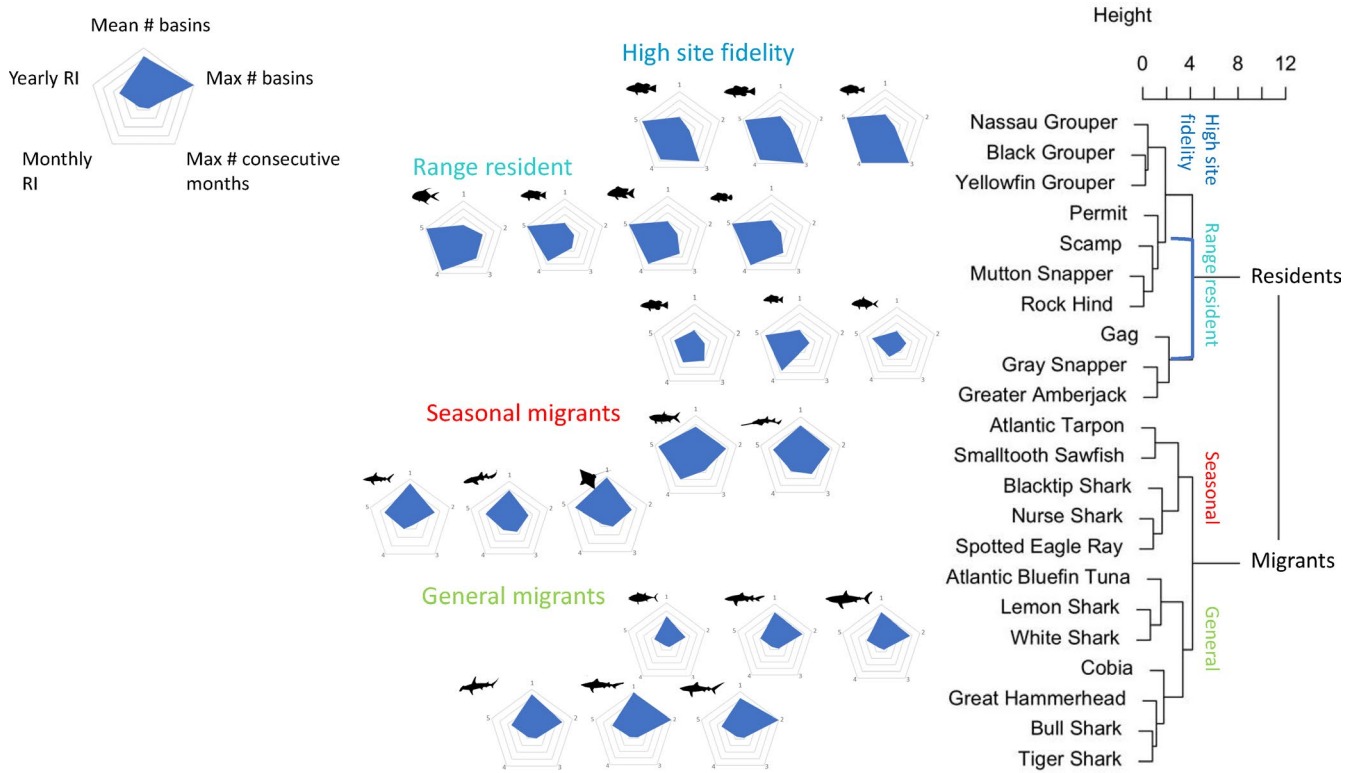
FIGURE 6 Results of the agglomerative hierarchical clustering based on maximum and mean number of basins of detection, maximum consecutive detection months and yearly and monthly residence indices. Height represents the total within-cluster variance. Species-specific radar graphs depict the relative value of the variables used for the cluster analysis (i.e. each variable was standardized by its maximum for the radar plots)

lemon shark (*Negaprion brevirostris*, Carcharhinidae), nurse shark and tiger shark, (*Galeocerdo cuvier*, Carcharhinidae)). Three species were either never detected in the GOM section (bluefin tuna and cobia), or extremely rarely (white sharks, 0.13%).

Path numbers, space use (SDEs), contiguous use of the study area (maximum consecutive months) and DPI varied by species (Figure 8). Mean path number did not differ significantly between migrant movement types (Wilcoxon-Mann–Whitney, $n = 217$; $p = 0.2258$), but did between species within these types (Kruskal–Wallis, $\chi^2 = 60.5938$, $p < 0.0001$). Species with the highest mean path numbers (>10) were nurse sharks, lemon sharks, bull sharks, great hammerhead and sawfish. Sawfish had the greatest within-ecosystem connectivity (mean paths: 19 ± 16). Significant within-group differences also occurred for residents (Kruskal–Wallis, $\chi^2 = 25.6568$, $p = 0.0023$). Permit had a mean path number of 7.0 ± 6.8, while all other residents had ≤2 (Figure 8a). Similarly, SDEs differed by annual movement type (Kruskal–Wallis, $\chi^2 = 127.8636$, $p < 0.0001$), with the greatest mean SDE in general migrants ($2,526 \text{ km}^2 \pm 1,991$) and the least in high site-fidelity residents ($1.8 \text{ km}^2 \pm 5.9$). Migrants did not show a significant correlation between individual path number and SDE (Pearson's correlation coefficient $= 0.14351$, $p = 0.0553$, $n = 179$) due to individual variability and species-specific differences in monitoring power. Contiguous use of the study area was greatest in high site-fidelity residents (9.4 ± 7.3 months) .

Use of the migratory corridor, based on detections at receivers deployed in the corridor, varied among migrant species and these differences were significant (chi-square test, $\chi^2 = 36311$, $n = 80,317$, $p < 0.0001$). Although blacktip sharks and eagle rays were rarely detected in the migratory corridor (0% and 2% of detections, respectively), corridor detections in other seasonal migrants varied: 4% in tarpon, 58% in sawfish and 95% in nurse sharks. General migrants had higher proportions of detections in the corridor, except bull sharks (55%), ranging from great hammerheads (85%), to >90% for the remaining species, cobia, lemon sharks and tiger sharks. Bluefin tuna and white sharks had ~100% of their detections in the migratory corridor.

Individual variability in movement occurred in most species and across movement types (Figure 9). Species with relatively consistent movement signatures included the following: bluefin tuna, which exhibited vertical lines representing rapid longitudinal movements; cobia, which exhibited a zigzag pattern, indicative of rapid longitudinal movements from east to west, a gap in detections of ~ one year and then the same rapid longitudinal movements from east to west again; and reef fish species exhibiting horizontal, almost-daily detections at either the same station or stations in close proximity. Some individual black grouper, gag, Nassau grouper, permit, rock hind (*Epinephelus adscensionis*, Serranidae), scamp (*Mycteroperca phenax*, Serranidae) and yellowfin grouper (*Mycteroperca venenosa*, Serranidae) exhibited site-attached behaviour (detection period ≥ 1 year, detection days ≥ 30 and space use ≤ 0.25 km²). The sites supporting this behaviour were all near or on natural or artificial reefs. However, the proportion of fish showing this behaviour differed by species (chi-square test,
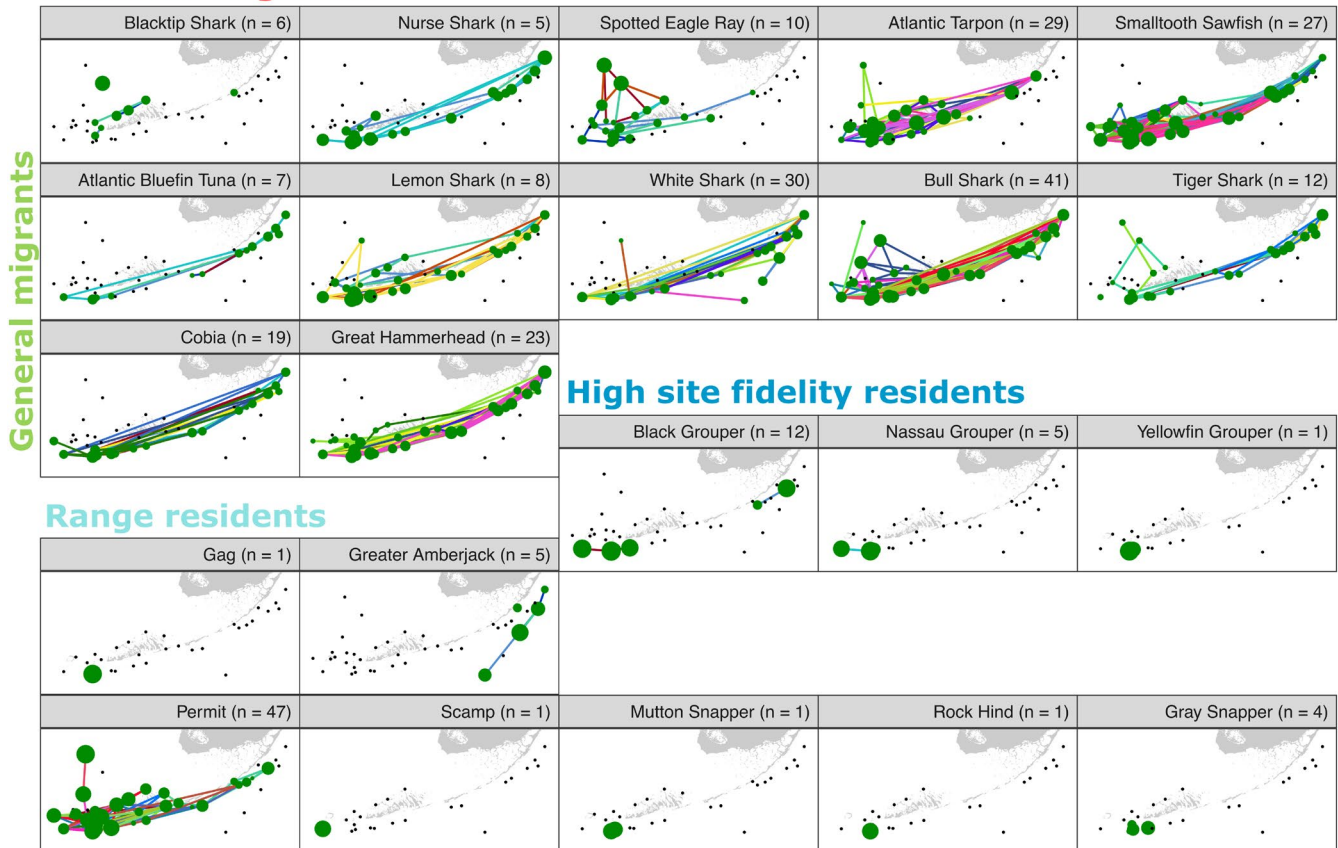
FIGURE 7 Species-specific network analysis graphs, which are grouped by annual movement type. Sample sizes for fish with detection periods of a year or greater are indicated above each network. Colours indicate individuals' paths. Circle size is scaled to indicate nodes with the greatest paths for each species. Crevalle jack were excluded from this analysis due to their short detection periods

$\chi^2 = 16.48$, $n = 50$, $p = 0.0114$). Of the species with more than one tagged fish, permit had the lowest proportion of site-attached individuals (6 of 32), Nassau grouper were intermediate (1 of 3), and black grouper had the highest (8 of 11).

Stopover behaviour and location also varied, with the proportion of fish exhibiting stopover behaviour differing significantly among migrant species (chi-square test, $\chi^2 = 65.52$, $n = 217$, $p < 0.0001$). No stopover behaviour (defined as ≥ three consecutive detection months) was observed in bluefin tuna, white sharks or cobia. Species with the most individuals exhibiting stopover behaviour were sawfish (67%, $n = 27$), tarpon (52%, $n = 29$) and nurse sharks (40%, $n = 5$). Nurse sharks demonstrated stopover behaviour within the migratory corridor, as did tiger sharks (25%, $n = 12$), great hammerheads (17%, $n = 23$) and lemon sharks (13%, $n = 8$; Figure 10). Eagle rays (20%, $n = 10$) and bull sharks (12%, $n = 41$) exhibited stopover behaviour outside the migratory corridor.

3.5 | Movement strategies and life-history traits

Size differed with annual movement type (Welch's ANOVA, $n = 295$, $p < 0.0001$). General migrants were larger (260 cm ± 92 cm TL; $p < 0.0001$) than seasonal migrants (202 ± 111 cm TL), range residents (71 ± 20 cm TL) and high site-fidelity residents (61 ± 15 cm TL). Trophic level also varied with annual movement type (chi-square test, $\chi^2 = 20.1$, $n = 22$, $p = 0.0026$). No resident species were apex predators, while apex predators made up the majority (86%) of general migrants and 20% of seasonal migrants. These relationships with movement type suggest that for many species, a highly migratory movement strategy is associated with large body size, decreased predation risk and, presumably, the need to cover greater space to support the larger body mass. All teleost species tracked in this study were reported to exhibit movements associated with birth site selection (Table S1), except crevalle jack (*Caranx hippos*, Carangidae) for which this behaviour is currently unknown.

4 | DISCUSSION

4.1 | Movement strategy framework

Frameworks have been proposed to help understand drivers of individual movements (Nathan et al., 2008), scaling those drivers to population dynamics (Doherty & Driscoll, 2018) and applying the concepts of movement ecology to understanding biodiversity (Jeltsch et al., 2013) and wildlife management (Allen & Singh, 2016;
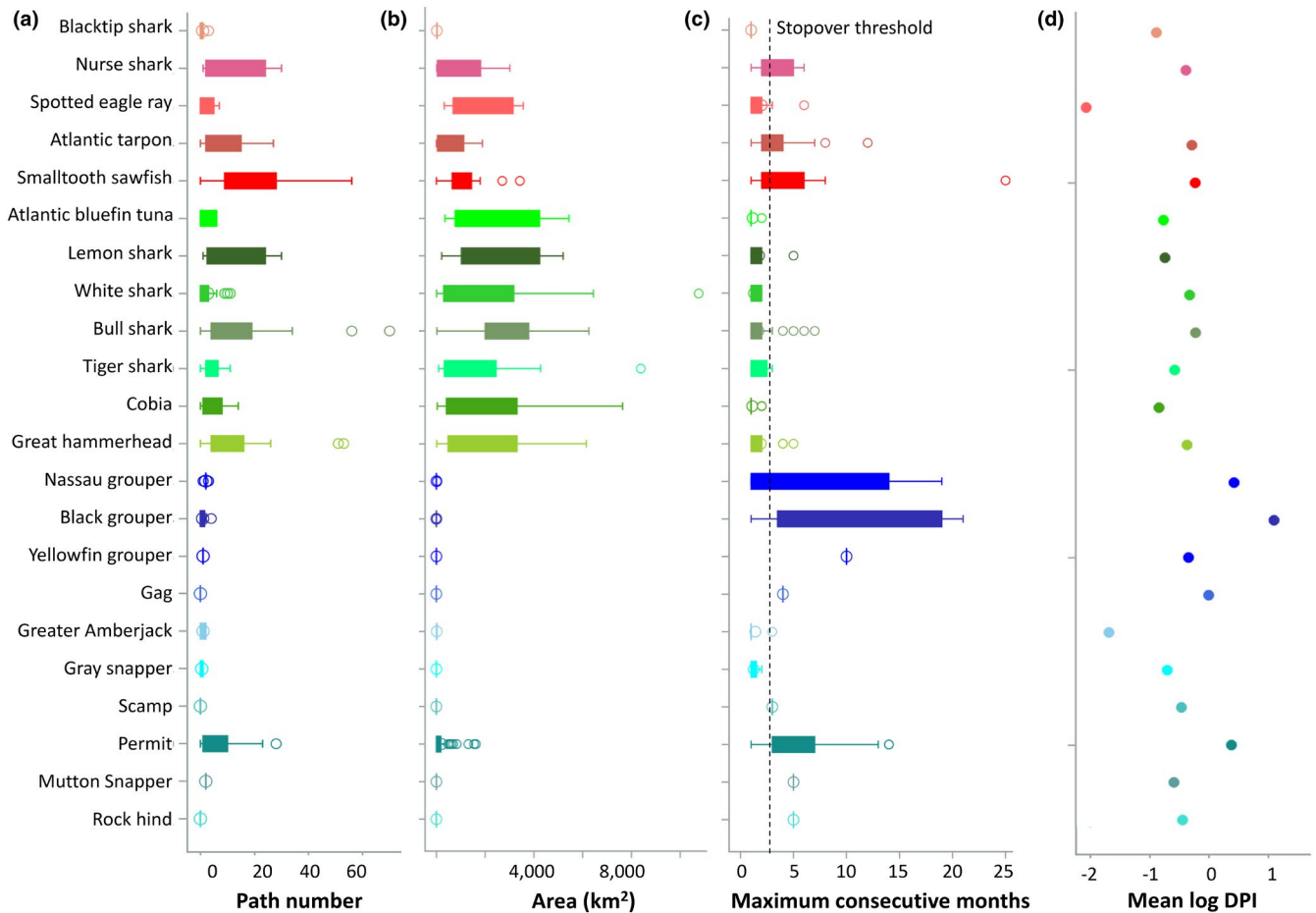
FIGURE 8 Species-specific path numbers (a), space use, based on standard deviation ellipses (b), maximum consecutive detection months with a reference line at the threshold for stopover behavior (three months) (c) and log-scaled species-specific detection potential index (d). Boxes represent 25th and 75th percentiles, whiskers are the minimum and maximum and circles are outliers. Annual movement types are coloured similarly (reds/pinks = seasonal migrants; greens = general migrants; blues = high site-fidelity residents, aquas = range resident). Crevalle jack were excluded from these analyses due to their short detection periods

Fraser et al., 2018). How movements affect single species to ecosystem-based fisheries management has also been outlined (Lowerre-Barbieri, Kays, et al., 2019). However, we could not find a movement strategy framework that integrated multiple traits over varying temporal scales and their drivers—which is needed to facilitate the comparison of movement ecology across species and better understand relationships between movement and management. The framework presented here is envisioned as a way to fill this gap and begin the process of standardizing terms that often vary across studies, species, stocks and realms (Allen & Singh, 2016; Bastille-Rousseau et al., 2016; Berg et al., 2019; Brodie et al., 2018). The intent is to be universally applicable. To test this will necessitate asking scientists studying movement in other realms and species to evaluate it and provide feedback.

The advantage of framing movement strategies similar to life-history strategies is twofold: it (a) integrates the concept of movement strategies evolving over evolutionary time under conditions potentially quite different from those they currently exist in; and (b) identifies measurable traits, providing a foundation for future trait-based analyses (Beukhof et al., 2019). To date, fisheries science has focused mainly on changes in movements and distributions due to proximate drivers—environmental conditions (Morley et al., 2018; Pinsky et al., 2020) or density dependence (MacCall, 1990; Thorson et al., 2016). However, inherited components of species-specific movement strategies will mediate how these strategies respond to changing conditions. Drawing from the fast–slow continuum of life-history strategies (Promislow & Harvey, 1990), we hope this framework will provide a similar foundation to assess species-specific movement strategies, although an understanding of how movement strategies relate to population resilience is still emerging. Adult movement strategies fall along a continuum from site attached to highly migratory. Potential advantages of site attachment include the "resident advantage" against newcomers competing for prime habitat, increased efficiency in extracting resources from "well-known" habitats and effective predator avoidance (Gerber et al., 2019). However, long-term site attachment is only possible in stable environments where energetic and survival needs can be met, with potential trade-offs in foraging and reproductive success.
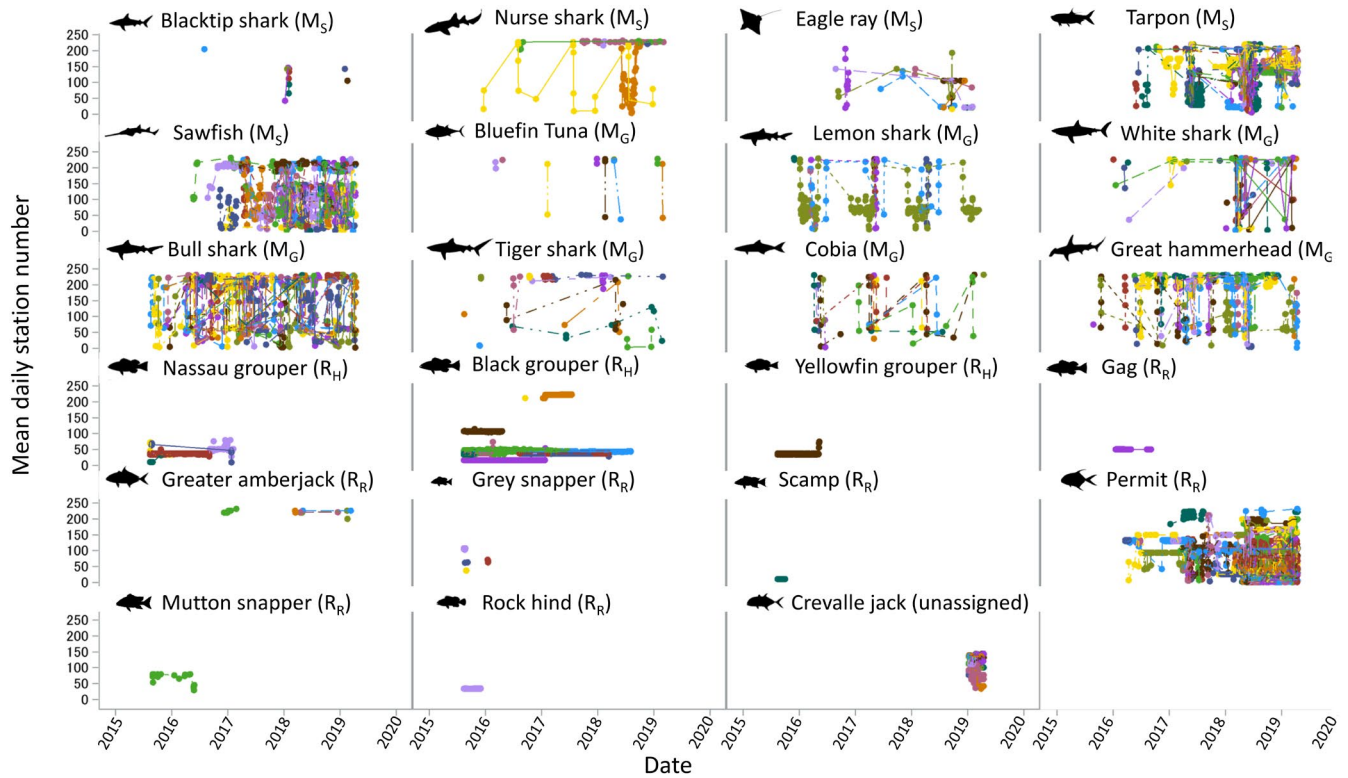
FIGURE 9 Individual movement signatures by species based on daily mean longitudinal position. Station numbers were assigned to receivers based on deployment longitude, with the lowest number representing the western-most station so that daily mean station (circles) of detection could be evaluated over the study period. Each year on the *x*-axis represents 1 January. Detection days of each individual are connected (dashed and coloured lines) to make it easier to see shifts in location, but do not necessarily indicate a direct movement from one location to another. Site fidelity results in horizontal lines, while rapid movement along a longitudinal gradient results in vertical lines. Different colour and line patterns were used to distinguish individual fish. Annual movement types are indicated in parenthesis after species names (M_G = general migrant, M_S = seasonal migrant, R_H = high site-fidelity resident, R_R = range resident)

In migration and nomadism, animals move to optimal locations for feeding, offspring survival and physiological functioning (Shaw, 2016) but expend energy to do so and give up the advantages of site attachment.

Birth site selection is a common driver of movement in marine ecosystems, occurring in marine mammals, teleosts and elasmobranchs (Shaw, 2016). The movement of high site-fidelity residents to spawning aggregation sites suggests trade-offs in movement choices to meet adult versus offspring survival needs. Seasonal migration is often associated with movement to specific spawning grounds outside foraging activity spaces used in the non-reproductive period. Tarpon, a seasonal migrant, form pre-spawning aggregations prior to migrating to presumed deep-water spawning sites (Luo et al., 2020). Cobia and bluefin tuna are general migrants and both undertake movements associated with birth site selection. Cobia migrate from south Florida to the northern GOM, where they spawn in aggregations (Perkinson et al., 2019). Bluefin tuna are known to migrate from northern Atlantic foraging grounds to spawning grounds in the Caribbean and GOM, although they do not form spawning aggregations (Block et al., 2005; Hazen et al., 2016). Although birth site selection remains poorly understood in marine fish, it will affect how a species adapts to a changing ocean, with concern for phenological disconnects negatively affecting productivity. This has been

observed in multiple bird species for which cues to initiate migration no longer result in arriving at fixed breeding grounds at the optimal time (Møller et al., 2008).

4.2 | Detection potential

Large-scale and long-term movement data are needed to better understand movement strategies. Current solutions to collecting these data for marine fish are (a) synthesizing tracks of many animals from archival tags; and/or (b) sharing detection data through AT networks (Bangley et al., 2020; Hussey et al., 2015; Lennox et al., 2019). Although integrated tracking data increase the research questions we can address with AT, these data also present new challenges in terms of separating process from observation effects (Friess et al., 2021), and a need to develop new methods to address issues such as varying DP and MP. Here, we quantified TP and MP and developed the DPI to address disparate observation capacity by species. However, in an ideal world, DPI would be determined from independent space use data or prior information about species habitat preferences. It would also integrate variability in range with tag type, habitat and over time. The opportunistic nature of the networked data requires identifying a temporal threshold representative of a
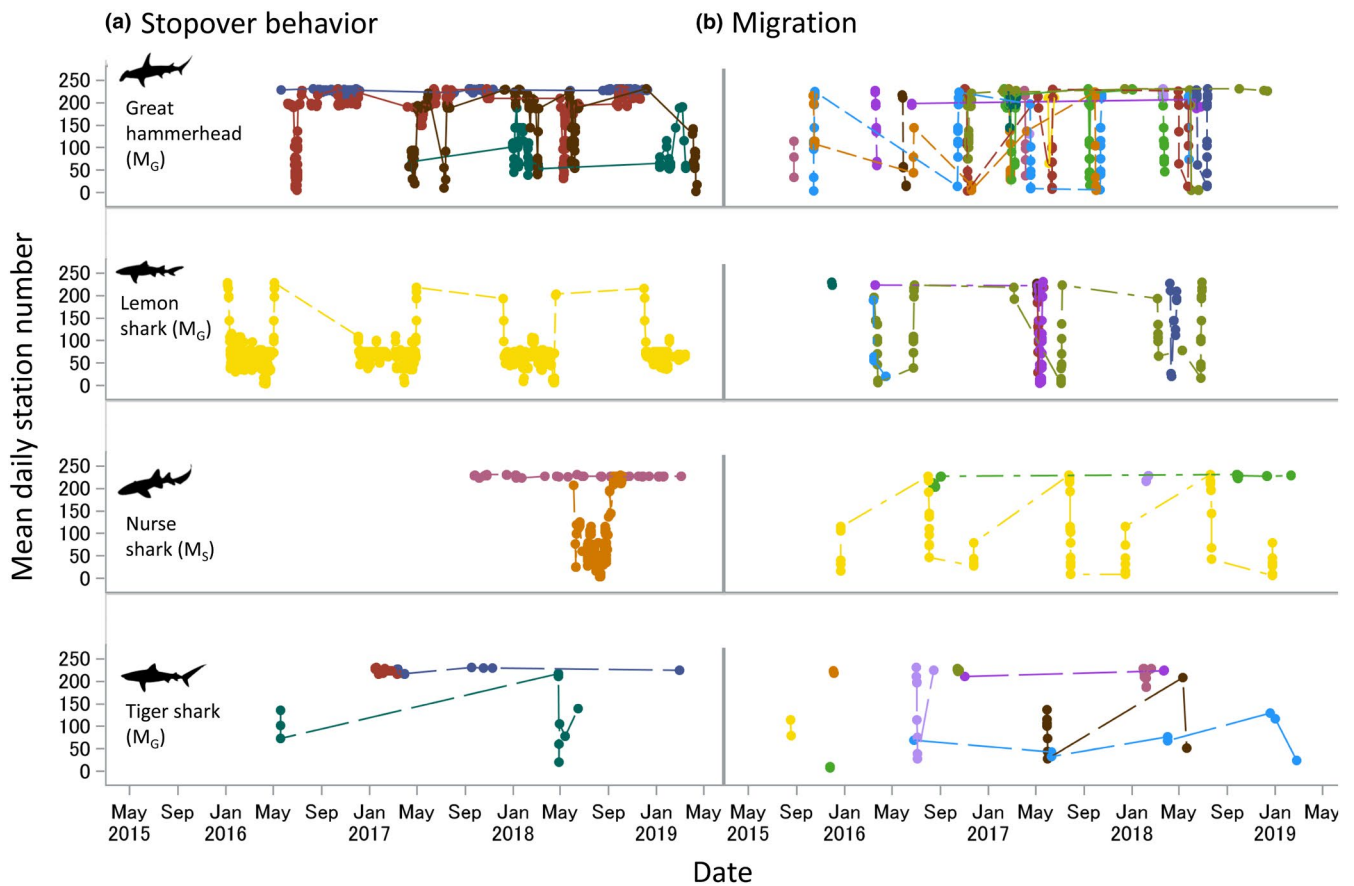
FIGURE 10 Movement signatures of individual migrants detected for three consecutive months or more, defined as stopover behaviour (a) versus migration through the study area (b). Station numbers were assigned to each receiver based on its longitudinal position, with the lowest station number representing the western-most station. Mean daily station is indicated with circles, which are connected (dashed and coloured lines) to make it easier to see shifts in location, but do not necessarily indicate a direct movement from one location to another. Cluster analysis movement types are indicated in parenthesis (M_G = general migrant, M_S = seasonal migrant)

species' movements. Here, we used a year and individuals with DPs shorter than this were excluded from annual movement type assignment. Crevalle jack exemplified this need. Within the study period, they had a mean detection period of 39 days and were not detected outside the study area. However, they have since been detected in the GOM and the Atlantic basin (C. Gervasi, unpublished data/personal communication). Tagging location and numbers tagged also affect accurate representation of within-species variability in annual movement type. For example, resident and migrant contingents of blacktip sharks occur in the study area (D. Grubbs, unpublished data/personal communication.) but all bakctip sharks in this study were assigned as seasonal migrants, given they were all tagged outside the study area.

4.3 | Life cycle space use

Although we can rarely track an animal over its lifetime, tracking animals by life stage can improve our understanding of life cycles from a spatial perspective (i.e., life cycle space use). Spatial population structure, natal homing and biocomplexity affect a

species' resilience to environmental and anthropogenic perturbations (Goethel et al., 2021). Ontogenetic habitat shifts are common, affecting availability to capture and management refernece points (Carruthers et al., 2015). Components of space use at this scale typically differ between teleosts and elasmobranchs due to different reproductive strategies. In teleosts with the small eggs reproductive strategy, mating and birthing sites are the same, with models needed to predict birth site and nursery ground connectivity (Swearer et al., 2019). In contrast, many elasmobranchs are viviparous and have separate mating and birthing sites but birth and nursery ground overlap is species-specific, with some species not using nursery grounds (Heupel et al., 2007). Immature fish tagged outside the study area (blacktip sharks, sawfish and white sharks) moved to the study area, but only sawfish showed the hypothesized size dependence in arrival time, apparently due to varying life cycle space use and DPI (Table 2). In west-central Florida, blacktip sharks use estuarine nursery grounds and exhibit homing to these grounds after seasonal migrations to the Florida Keys (Hueter et al., 2005), tropical storm-induced movements (Heupel et al., 2003) and experimental displacement (Gardiner et al., 2015). Sawfish nursery grounds are also estuarine and documented in the Charlotte Harbor estuarine

system and Everglades National Park (Norton et al., 2012). Large juvenile sawfish tagged in Charlotte Harbor commonly move to the study area, with some returning to the tagging region afterwards (Graham et al., 2021). However, it is not yet known whether this is due to seasonal changes in temperature, changing foraging opportunities or mating site selection. White shark migrations include transoceanic, as well as long-distance coastal migrations (Bonfil et al., 2005; Skomal et al., 2017). Those tracked in this study were primarily tagged off Massachusetts, a known foraging ground, south of the New York Bight nursery area (Curtis et al., 2018). Birth sites for these fish remain unknown.

Shifts in habitat use and annual movement type with maturity are common in fish (Lowerre-Barbieri et al., 2016) as well as many other species—especially those with major changes in body size or morphology with life stage, such as amphibians and insects (Werner & Gilliam, 1984). These shifts have been traditionally thought to be driven by the size to predation risk relationship, with animals leaving their nursery grounds when the benefits of increased growth outweigh those of increased mortality. However, shifts in habitat use or annual movement type can be driven by any trait that takes time to develop and affects foraging, survival or reproduction, including the development of salt glands or muscular gizzards in birds (Fokkema et al., 2020), or the ability to successfully defend a territory in some fish (Grüss et al., 2011). Given the need to reach an energetics threshold both to mature and to migrate, reproductive development and ontogenetic habitat shifts are linked to an animal's condition (Goossens et al., 2020), potentially driving the individual variability observed in the timing of emigration from nursery grounds (Walters Burnsed et al., 2020). We hypothesized adults would exhibit lower residency than immature fish, a common pattern, which was observed in migratory tarpon but not in range resident permit.

4.4 | Annual movement type

Annual movement type affects space use and multiple management measures. However, our ability to accurately assign it is affected by sample size, variable detection potential and the sensitivity of cluster results to method and data transformations. Five resident species had only one tagged fish and cannot be considered representative of the species. They were retained because their movement type agreed with the literature. Detection potential also affected movement metrics. For example, blacktip sharks and eagle rays were identified in the literature as seasonal migrants, but their residence was lower than other seasonal migrants due to poor detectability. A nomad movement type was not identified nor reported in the literature for the species in this study. However, our understanding of this behaviour is evolving (Teitelbaum & Mueller, 2019) and future analyses should include a metric measuring recurrence of movement paths. In addition, the clustering method we used was sensitive to variable transformations. Some variable distributions could not be normalized, and log-transformations that resulted in small changes

to variable skewness produced slightly different clusters, mostly in the migrant groups.

Our results support those of Brodie et al. (2018) and Friess et al. (2021) that AT, with appropriate monitoring power, can determine annual movement types. However, not all species can be easily tracked with AT. This includes important seasonal migrants to this study area such as small pelagics and mackerel species. In addition, without an *a priori* sampling design in multispecies studies, species-specific MP will affect results. Greater amberjacks are a good example. They form large spawning aggregations at the Islamorada and Marathon seamounts (Figure 1c, nodes 38 and 40; Hargrove et al., 2018). Based on conventional tag recaptures, they are believed to make long, coastal migrations to these sites (Harris et al., 2011). However, none of our fish were detected outside the study area and virtually all detections occurred at the seamounts, suggesting a potential resident contingent. This could not be confirmed, however, as greater amberjacks had low MP and DPI. The observation error associated with this low MP was demonstrated by a fish recaptured ~600 km north of the study area.

4.5 | Within-ecosystem behaviour

Our results are a first step towards providing the movement data needed for future spatial management and multispecies dynamic ocean management (Hazen et al., 2018). MPAs are often created to protect range resident species' spawning aggregations. In the study area, spawning aggregation sites have been documented for mutton snapper (*Lutjanus analis*, Lutjanidae), grey snapper (Keller et al., 2020), permit (Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Adams, et al., 2020) and greater amberjack (Harris et al., 2011). However, it is also important to design MPAs to protect additional migrant habitats, including foraging areas (Hays et al., 2019; Runge et al., 2014), migratory corridors and stopover sites. For ecosystem-based management (EBM), it is especially important to protect these habitats for migratory meso- and apex predators, given their importance to ecosystem health (Hammerschlag et al., 2019; Heithaus et al., 2010; Speed et al., 2010). The UN's target to increase MPAs by 2030 provides an excellent opportunity to support additional studies like this to identify and protect these habitats (Sequeira et al., 2019).

Species' movement strategies evolved in habitats unaltered by humans but now must adapt to the available habitat mosaic—habitat contiguity and quality (e.g. Section 2.1.2.1 in Adams, 2017). Connectivity will be affected by these factors, and our ability to accurately measure it depends on the overlap between movement routes and receiver coverage (i.e. MP). Low connectivity occurred in all residents (except permit), as well as blacktip sharks, eagle rays, bluefin tuna and white sharks—but for different reasons. Bluefin tuna and white sharks used poorly monitored deep-water habitat, while residents, other than permit, exhibited little horizontal movement and were well detected. When site-attached species leave the array, it is often assumed to be due to predation, recently documented by

Bohaboy et al. (2020). However, we know they also leave due to natural triggers, such as tropical storms (Secor et al., 2019), but unlike migrants, they are rarely detected on other arrays (Friess et al., 2021), presumably due to high site fidelity at a new location.

Migratory routes from the GOM versus from the Atlantic appear to differ. Cobia movements highlight this, as they were commonly detected moving in the Atlantic section of the study to the GOM, but rarely detected returning. They, like most general migrants, used the deep-water migratory corridor. However, little monitoring in depths from 50 to 400 m (four receivers) means much remains unknown about what and how species use this habitat. Given these conditions, the detection of approximately a third of the white sharks tagged off Massachusetts suggests this is a common migratory route for this population and seamounts may act as attractants. However, to understand movements within the corridor, the range of species using it, and whether species will change movements due to climate change and anthropogenic stressors requires additional tracking studies, synthesis of PSAT tracks from prior studies and the integration of catch-based data.

Stopover (or staging) sites are commonly studied in birds, less so in fish (but see Rothermel et al., 2020). The term refers to intermediary sites used during migration that provide resources and environmental conditions supporting effective migration (Warnock, 2010). Here, we used three or more consecutive months of detection as an indicator of stopover behaviour, but this should be refined in studies with better detectability. Seasonal migrants, not surprisingly, had the most individuals exhibiting stopover behaviour: sawfish (67%, $n = 27$), tarpon (52%, $n = 29$) and nurse sharks (40%, $n = 5$). Stopover sites for these species included within the corridor (nurse sharks), only in shallower waters (tarpon) and in both (sawfish). The mechanistic driver of this behaviour is unknown, except for tarpon which form pre-spawning aggregations, an increasingly acknowledged form of stopover behaviour, where fish feed and increase their energy reserves prior to undertaking spawning migrations. In terms of spatial protection, stopover sites in shallow water are expected to be the most impacted by anthropogenic stressors and thus should be prioritized for conservation.

5 | CONCLUSIONS

Given that movement links habitat with life-history processes important to population dynamics, conservation and management (Hays et al., 2019; Wittemyer et al., 2019), there is a clear need to integrate spatial processes into fisheries management (Berger et al., 2017; Cumming et al., 2017; Link et al., 2020; Lowerre-Barbieri et al., 2019). Roadblocks to using tracking data to do so are both methodological and conceptual. AT networks have greatly increased the biological and spatial scale over which marine fish can be tracked, but also present new challenges including data standardization (Sequeira et al., 2021) and the need to move from opportunistic data to designed multispecies studies that address TP, MP and DPI for

species *a priori*. There is also the need to invest in long-term arrays that can track changes in movements over time.

While, conceptually, the linkage between movement strategies and management is clear, incorporating movement strategies into management is less so. Electronic tracking data are increasingly used for stock identification (Cadrin, 2020) and have been identified as important to spatially explicit stock assessment models (Goethel et al., 2021). However, we recommend increased integration of movement into management strategy evaluations. Specifically, we suggest simulations which address (a) spatio-temporal patterns of fishing effort and life cycle space use to identify vulnerability bottlenecks; (b) how movement, and changes in movement, affects availability to capture and thus catch-based estimates of relative abundance; and (c) how multispecies movements affect fisheries by-catch. We also suggest movement type be better integrated into how we define a stock, as well as to refine stock complexes beyond the current designations of highly migratory and coastal migratory species.

Within- and cross-ecosystem movements (space use, connectivity, migratory routes, stopover sites and functional use of habitats) affect productivity and ecosystem functioning but are not easily integrated into the traditional single-species management framework. Historically, this framework has been extraction-based and is used to develop harvest control rules for maximum sustainable yield. The inefficiencies of this framework are recognized (Karnauskas et al., 2021) and management frameworks are shifting from optimizing single-species yield to managing ocean use and ecosystem health (Halpern et al., 2015). Several more recent approaches, not predicated on single-species biomass optimization, include the following: spatial management, dynamic ocean management (Lewison et al., 2015) and EBM (Dolan et al., 2016). These management frameworks necessitate new data streams and the funding to provide them. Similar to the investment in surveys to estimate relative abundance for the traditional single-species management framework, spatial management, dynamic ocean management and EBM will need data on movements and how they change with climate and habitat degradation (Lotze et al., 2006). To effectively collect these data, we need to identify globally important connectivity hotspots under stress during the Anthropocene, like the Florida Keys, and provide long-term funding for infrastructure, technological innovation and personnel who can bridge the gap between traditional and emerging ocean management and conservation.

DATA AVAILABILITY STATEMENT

The data that support the results in this study were shared through iTAG and are archived through the Ocean Tracking Network (OTN), whose data system is an Associate Data Unit of the Intergovernmental Oceanographic Commission's International Oceanographic Data and Information Exchange. Access to the data on the OTN system is guided by the public data policies of OTN and the member nodes who participate in the system. There is no fee to access the data from the system, and OTN staff are available to assist with data requests. A citation format crediting the owners of the data is available from the OTN publication data repository https://members.ocean track.org/data/pblctn_data

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.