

Title 1: Movescapes and eco-evolutionary movement strategies in marine fish: assessing a connectivity hotspot

By

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Running title: Fish movescapes

Abstract

We use data from the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network, and sister networks, 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 analyzed ~2 million detections for 23 species, ranging from site-attached reef fish such as Nassau grouper, *Epinephelus striatus*, to migrant predators such as white sharks, *Carcharodon carcharias*. An eco-evolutionary movement strategy framework was developed to identify movement traits and their drivers, at multiple temporal scales, important to management. Detectability was species-specific and quantified with a detection potential index. Life stage use of the study area varied by species and residency varied with life stage. Hierarchical clustering identified four annual movement types: high site-fidelity residents, residents, seasonal migrants, and migrants. The greatest within-ecosystem connectivity was observed in the endangered smalltooth sawfish, *Pristis pectinata* — a seasonal migrant with strong stopover behavior. Site-attachment, stopover, and deep-water migration behaviors differed between individuals, species, and annual movement types. All apex predators were either migrants or seasonal migrants. Migrants were significantly larger than fish in the other movement types, suggesting a relationship between lower predation risk and spatial scale of movement. Movement to spawning sites was a common pattern in teleosts, regardless of annual movement type. As concerns grow over habitat and biodiversity loss, multi-species movescapes, such as presented here, are expected to play an increasingly important role in informing ecosystem-based and non-extractive management strategies.

Keywords: Acoustic telemetry, movement ecology, migration, migratory corridor, space use, network analysis, Florida Keys

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1 **1. Introduction**

2 It is well-known that species' movement patterns differ, affecting how species adapt to change.
3 The movement ecology paradigm (Nathan, 2008) identifies mechanistic components affecting
4 individual movement: external factors, internal state, and motion and navigation capacity. By
5 linking lifetime movement to fitness, it sets the foundation for movement to be understood as
6 part of a species' life history. However, to apply this paradigm to inform management and
7 conservation, we need a movement framework that identifies measurable traits at the species,
8 stock or population scale (Allen and Singh, 2016), and their ecological and evolutionary drivers.
9 Ecological drivers include con-specific density and environmental conditions (temperature,
10 habitat, currents, water quality, depth etc), spatially explicit stressors and habitat degradation
11 (Tamario et al., 2019). At the evolutionary scale, movement patterns are selected for when they
12 increase an animal's growth, survival or reproduction (Shaw, 2016). Ecological theory
13 integrating these drivers focuses on growth and survival through optimal foraging theory
14 (Gallagher et al., 2017; Wittemyer et al., 2019), the ideal free distribution (Fretwell and Lucas
15 1970) and the preemptive distribution, linking breeding site selection with reproductive success
16 (Pulliam and Danielson 1991). For fish with the common small egg reproductive strategy
17 (Andersen et al., 2016) — breeding and birth sites are the same and birth site selection affects
18 offspring survival (Secor, 2002; Ciannelli et al., 2015; Lowerre-Barbieri et al., 2017). Animals
19 also move due to physiological constraints defining favorable environmental conditions. In some
20 species, this results in seasonal movements to overwintering grounds, or to specific spawning
21 grounds, and in all species, this affects their distribution, with important implications for
22 management (McGowan et al., 2017).

23 Research on animal movement has grown rapidly and is shifting from traditional site- and
24 species-specific approaches (Holyoak et al., 2008; Crossin et al., 2017) to movescapes — the
25 synthesis of many movement signatures (locations over time) from animals of various size, life
26 stage, sex, and/or species (Lowerre-Barbieri et al., 2019a). Evaluating movement at this larger
27 scale has numerous applications to conservation and management (Fraser et al., 2018; Hays et
28 al., 2019), but in the marine realm, it has been primarily applied to data from pop-off satellite
29 archival transmitting (PSAT) tags (Block et al., 2011; Harrison et al., 2018; Sequeira et al., 2018;
30 Rooker et al., 2019), even though acoustic tagging is more common in aquatic animals (Hussey
31 et al., 2015). This is because passive acoustic telemetry depends on the detection by fixed
32 underwater receivers of a uniquely identified signal from an animal with a transmitter when it is
33 in range. Detectability originally limited this approach to small spatial scale studies with species-
34 specific objectives and receiver array designs (Heupel et al., 2006). However, telemetry networks
35 — organized associations of researchers at regional to global scales — are facilitating sharing
36 and the exchange of detection data across receiver arrays (Donaldson et al., 2014; Hussey et al.,
37 2015). These integrated tracking data are increasingly used to assess large scale single-species
38 (Griffin et al., 2018; Pratt et al., 2018; DeGroot et al., 2021; Graham et al., 2021; Rider et al.,
39 2021) and multi-species (Brodie et al., 2018; Udyawer et al., 2018; Friess et al., 2021) movement
40 patterns.

41 Spatial management, and our ability to predict how fish movements change with a
42 changing ocean, are dependent on these larger scale tracking data. This is particularly true of
43 high-connectivity ecosystems, such as the Florida Keys. These ecosystems may act as spatial
44 bottlenecks, where changes in animal movement negatively affect not only the given ecosystem
45 but a range of connected ecosystems. The Florida Keys ecosystem includes the world’s third

46 largest barrier reef (580 km extent), expansive seagrass meadows, mangrove forests, and >1000
47 shipwrecks/artificial reef habitats, which are co-managed by the Florida Fish and Wildlife
48 Conservation Commission and the Florida Keys National Marine Sanctuary (FKNMS;
49 Montenero et al., 2020). These habitats are considered critical to supporting marine diversity in
50 this ecosystem, as well as globally, but are increasingly affected by climate change (Graham et
51 al., 2020), habitat degradation and high fishing pressure (Cinner et al., 2020). The Florida Keys
52 region connects the Gulf of Mexico (GOM) and Atlantic Ocean and is just north of Cuba and the
53 Caribbean (Figure 1). Multiple species such as king mackerel, *Scomberomorus cavalla*, and
54 Spanish mackerel, *Scomberomorus maculatus*, migrate to this ecosystem to overwinter,
55 providing seasonal prey pulses, which may attract larger predators (Johnson et al., 1994; Clardy
56 et al., 2008). Due to these attributes, the Florida Keys was identified as a high priority site for
57 collecting telemetry data for multiple species by the Integrated Tracking of Aquatic Animals in
58 the Gulf of Mexico (iTAG) network in collaboration with the Ocean Tracking Network (OTN) –
59 a global aquatic tracking platform.

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

69 1) was used to assess how: (1) maturation affects immigration and emigration in the study area;
70 (2) annual movement types affect multi-ecosystem and within-ecosystem connectivity; (3)
71 species differ in site-attachment, stopover behavior, and use of a deep-water migratory corridor;
72 and (4) relationships between annual movement type, body size, trophic niche, and spatial
73 reproductive behavior (i.e., spawning migrations and aggregations) vary.

74 **2. Methods**

75 **2.1 Movement strategy framework**

76 We developed a conceptual model of eco-evolutionary movement strategies: their proximate and
77 ultimate drivers (Riotte-Lampert & Matthiopoulos, 2020) and measurable movement traits
78 important to management, that can be evaluated at the stock, population, or species scale. This
79 framework (Figure 2) builds on the movement ecology paradigm, which addresses the true
80 movement path of an individual organism (Nathan et al., 2008). External drivers are the same for
81 the movement ecology and movement strategy frameworks. However, the movement ecology
82 framework (Nathan et al., 2008) focuses on the individual lifetime scale, whereas the temporal
83 scale driving movement strategies is multi-generational with fitness and density-dependent
84 feedback loops. An individual's genotype is part of its internal state, as is personality (Hertel et
85 al., 2020) and these are shaped over multiple generations by ultimate drivers. Tracking data used
86 to study true lifetime paths are affected by observation error, sample size, and the ratio of animal
87 to tag longevity. Integrated tracking data from multiple studies (either PSAT tracks or shared
88 detections) can increase sample size and spatio-temporal scale to that needed for management.
89 Emerging analytical tools to assess this data include cluster and network analysis. Movescapes
90 synthesize multiple movement signatures over life stage, sex, size, behavior type and/or species.

91 Movement strategy traits are categorized at the lifetime, annual, and intra-annual
92 temporal scales (Figure 2). At the lifetime scale, important traits include natal dispersal —
93 although difficult to study with electronic tracking (Allen & Singh, 2016), and ontogenetic
94 habitat shifts (Gillanders et al., 2003; Grubbs, 2010), which are often associated with maturity
95 (Hazen et al., 2012). Annual scale movement traits are the most commonly studied, with annual
96 movement types often classified as resident, migrant, or nomad — although terms vary and there
97 are sub-divisions (Mueller & Fagan, 2008; Bastille-Rousseau et al., 2016; Abrahms et al., 2017;
98 Allen & Singh, 2016; Brodie et al., 2018, Berg et al., 2019). Resident typically refers to a range-
99 resident movement type, i.e., living year-round in a home range (Fagan & Gurarie, 2020). In
100 contrast, migrants make recurrent movements between non-overlapping activity spaces,
101 exhibiting cross-ecosystem connectivity. Their impact on an ecosystem differs depending on
102 whether they are seasonally resident in that ecosystem (seasonal migrants) or the ecosystem is
103 simply part of their migratory route (migrant). Nomads occupy different activity spaces with low
104 recurrence in annual movement paths (Mueller & Fagan, 2008). Connectivity within and across
105 ecosystems impacts ecosystem functioning. Behaviors affecting within-ecosystem space use
106 relevant to spatial management include site attachment, stopover behavior, and the use of
107 migratory corridors. Tracking data are also used at finer temporal scales to understand diel
108 activity, core areas, water column and functional habitat use (Wittemyer et al., 2019). Individual
109 variability in movement is an important trait — at all temporal scales (Hertel et al., 2020; Shaw
110 2020), as it affects the impact of habitat loss/degradation, availability to capture, and population
111 resilience.

112 Movement strategies are shaped by multiple ultimate drivers including predation,
113 resource acquisition, birth-site-specific survivorship, and physiological functionality. For species

114 to persist, reproductive success rates must be adequate to keep abundance levels above those
115 where depensation or the Allele effect occurs (Perälä & Kuparinen, 2017). Reproductive success
116 occurs when an individual produces offspring that survive to reproductive age, i.e., it survived
117 long enough to develop the energy reserves and physiological capacity to reproduce offspring
118 that can survive to maturity. Movement plays a critical role in this process, resulting in
119 movement strategies that overcome predation risk, meet energetic needs, and support
120 physiological functioning and offspring survival. Strategies can optimize one of these selection
121 axes, but more commonly include tradeoffs between them. Here we use this framework to assess
122 lifetime and annual movement traits and how they relate to ultimate drivers and life history
123 components (e.g., size, trophic niche). Because we did not have data on activity spaces outside of
124 the study area, we used as a proxy the number of basins (Atlantic, study area, Bahamas, GOM) a
125 fish was detected in annually.

126 **2.2. Application of the movement strategy framework**

127 We implemented our movement strategy framework to explicitly test a series of hypotheses
128 about movement traits important to spatial management: (1) within the study area, immature fish
129 of multiple species exhibit greater residency than adults, and movement to the study area from
130 outside nurseries is size-dependent; (2) annual movement type can be effectively assigned based
131 on the number of basins used and temporal residence indices; (3) within-ecosystem space use
132 and connectivity differ with annual movement type; (4) fine-scale behaviors — site attachment
133 in residents, and stopover behavior and use of a deep-water migratory corridor in migrants
134 (hereafter referred to as the migratory corridor) — vary across and within species; (5) size,
135 trophic niche, and birth site selection are related to annual movement types.

136 **2.2.1 Study area and receiver arrays**

137 The study area encompassed most of the FKNMS as well as several seamounts to the
138 south and artificial reefs to the north (Figure 1). Study area boundaries were 24.425° to 25.250°
139 latitude and -83.130° to -80.210° longitude. Receivers (VR2W, VR2-Tx Innovasea, Halifax,
140 Nova Scotia) were initially deployed to track reef fish (n = 39; Keller et al., 2020), permit (n =
141 123; Brownscombe et al., 2019), and multi-species migrations and stopover sites (n = 69; iTAG).
142 Substrate types where receivers were deployed included: seamount, coral reef, reef
143 rubble/scattered coral, seagrass, pavement, mangrove, and unconsolidated sediment (primarily
144 sand). Receivers were grouped into nodes (n = 40) based on proximity and habitat type,
145 irrespective of original study array. Although receiver numbers increased over the study period
146 from 176 in 2016 to 231 in 2018, Hurricane Irma in 2017 negatively affected receiver coverage,
147 resulting in data gaps in 10 nodes. In 2018, lost receivers were replaced, and new nodes were
148 established at the southernmost flats on the Gulf-side of the Florida Keys and at the northern
149 wrecks (nodes 1 through 7; Figure 1C).

150 **2.2.2 Tagging data**

151 Transmitter codes (n = 449) were assigned to tag owners and species based on iTAG, FACT (the
152 Florida Atlantic Coast Telemetry network), and ACT (Atlantic Cooperative Tracking network)
153 databases. Innovasea (formerly Vemco) contacted owners of unidentified tags (see Table 1 for
154 list of species and scientific names). Research groups (n = 22) with \geq five detected fish of a
155 given species were invited co-authors and provided the following tag metadata: species, tagging
156 date, location (Figure 3), number of fish tagged, tag expiration date, fish size and life stage at
157 tagging, and annual detection basins by fish. The GOM and Atlantic basins were considered
158 northwest and northeast of our study area, respectively, and The Bahamas refers to detections on
159 Bimini Biological Field Station receivers deployed in and near Bimini, The Bahamas. Co-authors

160 reviewed the literature for their species' annual movement type and trophic niche (**Supp., Table**
161 **1**). Trophic niche was used to integrate predation risk into detection period calculation (section
162 2.3.1) and to assess potential relationships with annual movement type.

163 **2.3 Data analysis**

164 **2.3.1 Detection potential**

165 Detection potential drives the capacity of telemetry data to accurately reflect true movement
166 paths. In single species studies, telemetry arrays are deployed to monitor habitat use of the target
167 species, and detection potential is assumed to be driven by detection range. In this study, we used
168 200 m, a conservative estimate of known range for this area (<100 m to more than 500 m;
169 Brownscombe et al., 2019; Keller et al., 2020). However, in multi-species studies, detection
170 potential is more complex, affected by species-specific monitoring and tracking power, where
171 monitoring power (MP) is defined as characteristics of the observation system (e.g., receiver
172 spatial coverage and density) and tracking power (TP) as species-specific sample size and
173 potential detection periods (i.e., time within the study when a tagged fish is assumed to be alive
174 and could be detected; hereafter referred to as detection period (DP). We calculated a detection
175 potential index (DPI) for each species i as the product of median MP and TP, scaled by median
176 space use (based on standard deviation ellipses, SDEs; see section 2.3.5). Each factor was scaled
177 by the maximum value observed across species:

$$178 \quad DP_i = \frac{MP_i}{\max(MP_i)} * \frac{TP_i}{\max(TP_i)} * \frac{\max(\sqrt{SDE_i})}{\sqrt{SDE_i}} \quad (1)$$

179 Tracking power was calculated as the sum of individual detection periods (dp):

$$180 \quad TP_i = \sum_{j=1}^{n_i} dp_{j,i} \quad (2)$$

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

$$185 \quad MP_{j,i} = \sum_{d=1} \sum_{g=1} phm_{d,g} * phu_{d,g,j,i} \quad (3)$$

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

$$194 \quad phm_{d,g} = \frac{\pi 200^2 nrec_{d,g}}{A_{d,g}} \quad (4)$$

195 where total area A by depth and region was calculated in QGIS 3 (QGIS Development Team,
 196 2021), 200 m is the detection radius for an individual receiver, and $nrec$ is the number of
 197 receivers in a region and depth zone. Since phu was unknown, we had to estimate it from the
 198 data. We did this by scaling the total number of depth-and-region-specific detections per
 199 individual by the number of receivers in that depth zone and region:

$$200 \quad rdet_{d,g,j,i} = \frac{ndet_{d,g,j,i}}{nrec_{d,g}} \quad (5)$$

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

$$204 \quad phu_{d,g,j,i} = \frac{rdet_{d,g,j,i}}{\sum_{d=1} \sum_{r=1} rdet_{d,g,j,i}} \quad (6)$$

205 Scaling MP and TP by space use was done to acknowledge that, all else being equal, greater
206 space use increases the amount of time spent in unmonitored habitat and thereby reduces the
207 DPI. The flipside of this is seen in reef fish with small activity spaces that were all tagged in the
208 study area and had receivers deployed at tagging sites, dramatically increasing their DPI.

209 Tracking of multiple species that vary widely in size (Figure 4A) also necessitates
210 addressing size effects on DP. This is due to the relationship between size and natural mortality
211 (Lorenzen, 1996), trophic niche (Werner & Gilliam, 1984), and often migratory scale (Putman,
212 2018), making it more likely that a terminal lack of detections in small fish is due to mortality
213 while in large fish it is due to migration. To address this, we graphically identified 180 cm as a
214 size threshold which did not overlap with the species' core 25%–75% size quantiles (Figure 4).
215 Fish below or equal to this size were categorized as “small”, with the remaining fish categorized
216 as “large”. According to the literature, all species categorized as “large” were migrants and either
217 large meso- or apex predators. We then calculated size group-specific DP, where DP start date
218 for all fish was tagging date or the first date of the study period, whichever came later. For
219 “small” fish, subject to higher mortality, we followed the traditional method of using the date of
220 last detection to determine the DP end date, and for “large” fish, we used end of study period or
221 tag expiration date, whichever came first (with occasional extensions for tags detected after their
222 expiration date).

223 **2.3.2 Movement metrics**

224 We calculated movement metrics to evaluate annual movement type and for subsequent
225 hypothesis testing. To minimize the risk of false detections, we first removed duplicate
226 detections of transmitter codes at a receiver in < 30 s, and single detections that occurred in the
227 study area within a 24-hour period (Simpfendorfer et al., 2015). Only fish tagged a year or more
228 before the study's end date (15 April 2019; $n = 295$) were used. We calculated two residence
229 indices (RI) at differing temporal scales: (1) yearly RI (number of unique detection years/number
230 of potential detection years); and (2) monthly RI (number of unique detection months/number of
231 potential detection months). Because some species had low DPI, monthly RI was considered the
232 best measure of time spent in the study area. We also calculated the mean maximum consecutive
233 months each species was detected in the study period. Since none of the species-specific
234 movement metrics were distributed normally based on the Shapiro-Wilk test, the nonparametric
235 Kruskal-Wallis test was used to test for significant differences in metrics between annual
236 movement types (section 2.3.4) and species. A Dwass, Steel, Critchlow-Fligner (DSCF) post hoc
237 test was used to identify pairwise differences. To assess cross-ecosystem movements and
238 identify migrants, we estimated the mean and maximum number of basins individuals were
239 detected in annually, ranging from one (any basin) to four (a fish detected in the Atlantic, study
240 area, Bahamas, and the GOM). All mean results are presented plus and minus one standard
241 deviation (sd).

242 **2.3.3 Ontogenetic habitat shifts**

243 To evaluate how maturity affected immigration to and emigration from the study area, we tested
244 whether residency differed with life stage within the study area. For immigration analysis, we
245 analyzed species with \geq five immature fish tagged outside and later detected within the study
246 area. As maturation is size dependent, we tested if there was a significant linear relationship

247 between size at tagging and time elapsed (days) from tagging date to first detection in the study
248 area. For emigration analysis, we selected species with both immature and mature fish detected
249 within the Florida Keys with detection periods \geq six months, then tested for significant
250 differences in residency (as measured by monthly RI) with life stage using the Wilcoxon Mann-
251 Whitney test.

252 **2.3.4 Annual movement type**

253 We hypothesized that annual detection basins and temporal detection patterns within the study
254 area would be sufficient to identify the following annual movement types: residents, seasonal
255 migrants, migrants, and nomads. Residents were defined as species that used only the study area
256 year-round and thus would have been detected in only one basin and have a high monthly RI.
257 Migrants and seasonal migrants were expected to use more than one basin, with seasonal
258 migrants exhibiting greater residency in the study area than migrants. Both were expected to
259 have multi-year detections. Nomads were expected to have both low monthly and annual RI due
260 to low recurrence of movement paths.

261 Agglomerative hierarchical clustering was used to assign species to annual movement
262 types based on the mean and maximum number of detection basins, maximum consecutive
263 months detected, and monthly and annual RI. If not normally distributed, variables were log-
264 transformed and standardized by scaling to a mean of zero and sd of 1. Clustering was performed
265 on the dissimilarity matrix computed using Euclidian distances, and the clustering method that
266 resulted in the highest agglomerative coefficient was used. The resulting dendrogram was plotted
267 and species were assigned to one of four annual movement types that were compared to
268 movement types reported in the literature. Species-specific radar graphs were generated to
269 visualize cluster analysis input data, with each movement metric standardized to one.

270 **2.3.5 Within-ecosystem movement**

271 Differences in connectivity and space use between annual movement types were tested to
272 evaluate if within-ecosystem behavior differed. Connectivity was evaluated using network
273 analysis (NA) metrics, and space use was estimated by calculating SDEs. To conduct NA, we
274 calculated individual unipartite graphs (i.e., a movement graph constructed with a singular type
275 of node [Jacoby et al., 2012], in this case representing the 40 receiver nodes) and estimated
276 network metrics in the R package ‘igraph’ (Csardi & Nepusz, 2006). Individuals’ path numbers
277 were calculated as the sum of edges at each node. These were averaged by species to compare
278 species connectivity. SDEs for each individual were calculated using the R package ‘aspace’
279 (Bui, 2012) that estimates the standard deviation of x and y coordinates from the mean center
280 using the equations outlined in the Crimestat IV Manual (Levine, 2010). Centers of activity
281 (based on receivers rather than nodes) were first calculated by estimating average locations
282 during one-hour windows, and these served as input for SDE analysis. Only tracks with three or
283 more unique location points were used. Individuals with \geq five detection days detected at only
284 one or two receivers were assigned the expected area based on receiver range (0.13 or 0.25 km²).
285 Individual space use was averaged by species. Neither mean path number nor SDE were
286 normally distributed by species or group based on the Shapiro-Wilk test, resulting in the use of
287 the nonparametric Kruskal-Wallis test to test for differences in space use between annual
288 movement types and species and the DSCF post hoc test to identify movement groups and
289 species that differed significantly.

290 Within-ecosystem movements were evaluated for individual variability at the receiver
291 scale and three hypotheses were tested: (1) the prevalence of site-attachment varies between
292 resident species; (2) all migrants primarily use the migratory corridor (from the reef tract to the

293 seamounts, nodes 22-40); and (3) stopover behavior varies in location and prevalence in migrant
294 species. To assess individual site-attachment, we selected residents with ≥ 30 detection days and
295 a minimum DP of one year to ensure an appropriate temporal scale, as space use can increase
296 with time (Carlisle et al., 2019). The selected residents had a mean of 219 ± 170 detection days.
297 Individuals meeting these criteria were assigned as site attached if their space use was < 0.25
298 km^2 . To test if resident species differed in the proportion of individuals exhibiting site
299 attachment we tested this against the null hypothesis of no difference with the Chi-square test.
300 The same approach was applied to test for differences in stopover behavior in migrants (defined
301 as fish with ≥ 3 consecutive months of detection), and migratory corridor use by migrants.
302 Corridor use was quantified based on the proportion of detections from receivers within the
303 corridor versus outside of it.

304 **2.3.6 Movement strategies and life history traits**

305 We hypothesized that the annual movement type with the largest space use (based on detection
306 basins) would also be the lowest predation risk indicated by larger body size and their trophic niche.
307 Size was distributed normally; however, variances were not homogenous across movement
308 types. Thus, to test if size differed with annual movement type, we used Welch's ANOVA and a
309 Games-Howell post hoc test. We then evaluated the proportion of apex predators by movement
310 type. We further hypothesized that birth site selection (i.e., spawning aggregations or spawning
311 migrations based on the literature) would not differ significantly with annual movement type,
312 given that it has been selected for to increase offspring survival. To better understand habitat
313 associations with site-attachment behavior we assessed if all locations with this behavior had
314 structure (i.e., artificial or natural reefs).

315 **3. Results**

316 **3.1 Detections**

317 Approximately two million detections were recorded from 15 June 2015 to 15 April 2019 for 23
318 fish species. Based on the literature, these species were mostly migrants (44%) or year-long
319 residents (39%; Suppl Table 1; Table 1). Four species were considered seasonal migrants, either
320 over-wintering in the study area (i.e., blacktip shark, crevalle jack, spotted eagle ray, hereafter
321 eagle ray) or moving to the area to spawn during March through May (i.e., greater amberjack).
322 Slightly more than half of the detected fish were tagged outside the study area, with some tagged
323 as far away as Canada, the west coast of Florida, and The Bahamas (Table 2, Figure 3A & B).
324 All sharks — except four great hammerheads — were tagged outside the study area, as were
325 cobia and eagle rays. Mean size of tagged fish (Figure 4) ranged from 38.3 cm total length (TL;
326 grey snapper) to 367.6 cm TL (white sharks). Eight species had both immature and adult fish
327 tagged within the study period (Table 2).

328 **3.1.1. Detection potential**

329 Species had uneven TP, with the number of tagged fish per species ranging from 1 to 189 and
330 mean DP ranging from 39 d to over 1,000 d (Figure 5, Table 2). This resulted in TP of < 1,000
331 days for crevalle jack and most reef fish (excluding black and Nassau groupers); > 20,000 days
332 for Atlantic tarpon (hereafter tarpon), smalltooth sawfish (hereafter sawfish), great
333 hammerheads, white sharks and permit; and > 40,000 days for bull sharks. The study area was
334 ~21,153 km², with a receiver density of 0.011 receivers/km². Receiver coverage was not
335 homogenous across region or depth zones (Table 3). The greatest receiver density (0.05
336 receivers/km²) occurred in the 20 to 40 m depth zone in the Atlantic (Table 3), which also
337 detected the highest number of unique fish. However, the highest number of fish detected per
338 receiver (12.4) was in the deepest Atlantic depth zone (with receivers at an artificial reef and the

339 seamounts). Species-specific DPI was lowest in eagle rays and greatest in black grouper (Table
340 2; Figure 3C).

341 **3.2 Ontogenetic habitat shifts**

342 Multiple species moved to the study area after leaving nursery habitat, but size-dependence was
343 not uniform, nor was within-study area residency with life stage. Sawfish, blacktip sharks, and
344 white sharks had immature fish tagged outside the study area. Immature sawfish (156 to 364 cm
345 TL) were tagged in the Charlotte Harbor estuarine system (~200 km away, n=11, elapsed time:
346 25-275 d; Figure 3A) and Everglades National Park (~53 km away, n=12, elapsed time: 6 to 587
347 d; Figure 3B). Time elapsed between tag date and first detection of sawfish in the study area
348 decreased significantly (F-test, n = 23, p < 0.0001) with size. No significant relationship between
349 elapsed time and size was found for blacktip sharks (F-test, n = 7, p = 0.19) or white sharks (F-
350 test, n = 19, p = 0.59). Immature blacktip sharks (59 to 87 cm TL) were tagged ~322 km away
351 and elapsed time varied from 82 to 984 d. Similarly, immature white sharks tagged ~2,200 km
352 away (250 to 450 cm TL) exhibited a wide range of elapsed times (141 d to 803 d). DPIs for
353 blacktip sharks (0.15) and white sharks (0.54) were lower than in sawfish (0.68) and may have
354 affected results. Permit (resident) and tarpon (seasonal migrant) had immatures and adults tagged
355 in the study area. Each species exhibited changes in residency with life stage, but in permit adults
356 showed greater residency. Immature permit had a lower mean monthly RI of 0.49 ± 0.20 (n = 5)
357 than adults (0.71 ± 0.25 , n = 64), and these differences were significant (Mann Whitney
358 Wilcoxon, n = 69; p = 0.05). In contrast, immature tarpon had significantly higher (Mann
359 Whitney Wilcoxon, n = 26; p = 0.006) mean monthly RI (0.94 ± 0.82 , n=3) than adults ($0.36 \pm$
360 0.28 , n = 23).

361 **3.3 Annual movement type**

362 Although common annual movement types include residents, seasonal migrants, migrants, and
363 nomads, hierarchical clustering resulted in the following four annual movement types: high site
364 fidelity residents, residents, seasonal migrants, and migrants (Figure 6). These movement types
365 agreed well with the literature for all but two species (Table 1). Both migrant movement types
366 exhibited between ecosystem connectivity but differed in their mean number of detection basins
367 and residency. Seasonal migrants included three species detected in two basins: blacktip shark,
368 nurse shark, and eagle ray; and both blacktips and eagle rays were identified *a priori* as seasonal
369 migrants, while nurse sharks were assigned as migratory. However, tarpon and sawfish — also in
370 this group — were often detected in three basins, while also exhibiting high seasonal use of the
371 study area. Tarpon and sawfish had significantly greater (Mann Whitney Wilcoxon, $n = 217$; p
372 < 0.0001) monthly RIs (0.40 ± 0.30) than other migrants of both types (0.13 ± 0.12). All migrant
373 species were identified *a priori* as migratory. These species had low residence patterns and a
374 maximum detection basin of \geq three, except for bluefin tuna. Bluefin tuna were only detected in
375 two basins and never in the GOM, although they are known to migrate there. No individual
376 bluefin tuna were detected in more than one year, suggestive of nomads, but small sample size
377 ($n=9$) and low DPI (0.20) precludes assigning this.

378 Resident species (both movement types) were tagged in the study area and had low
379 sample sizes ($n=1-12$), with the exception of permit ($n = 102$). They also had low to no between-
380 ecosystem connectivity, again with the exception of permit. Six permit were detected outside the
381 study area. Most (83%) were detected < 50 km from study borders but one travelled > 200 km
382 along the east coast of Florida. Although overall measures of residency were greater in high site
383 fidelity residents than residents, monthly RIs overlapped between these movement types ranging
384 from 0.60 (scamp) to 0.83 (yellowfin grouper), except for gag and greater amberjack which had

385 much lower monthly RIs (0.38 and 0.27 ± 0.41 , respectively). The literature indicates female gag
386 are migratory and male gag are resident and greater amberjack are seasonal migrants (Table 1).

387 **3.4 Within-ecosystem movement**

388 Within-ecosystem connectivity, measured by NA path number, differed significantly
389 between annual movement types (Kruskal-Wallis, $\chi^2 = 25.1591$, $p < 0.0001$). Mean path numbers
390 fell along a continuum from seasonal migrants (11.57 ± 13.15), migrants (8.63 ± 11.46), residents
391 (5.6 ± 6.57) to high site fidelity residents (1.17 ± 1.20). Connectivity between the Atlantic and
392 GOM sides of the study area also differed (Figure 7). With the exception of permit, no resident
393 species (both types) were detected in the GOM. Two seasonal migrants had the majority of their
394 detections in the GOM: blacktip sharks and eagle rays (97% and 95%, respectively). Tarpon and
395 bull sharks had ~20% of their detections in the GOM and sawfish had ~10%. Detections in the
396 GOM were low to none in the rest of the migrant species: 2-3% (great hammerhead, lemon
397 shark, nurse shark, and tiger shark), 0.13% (white shark), 0% (bluefin tuna, cobia).

398 Path numbers, SDEs, and contiguous use of the study area varied by species and were
399 affected by DPI (Figure 8). Although mean path number did not differ significantly between
400 migrant types (Mann Whitney Wilcoxon, $n = 217$; $p = 0.2258$), it did between species within
401 these types (both groups; Kruskal-Wallis, $\chi^2 = 60.5938$, $p < 0.0001$). Significant within-group
402 differences also occurred for residents (Kruskal-Wallis, $\chi^2 = 25.6568$, $p = 0.0023$). Permit had a
403 mean path number of 7.0 ± 6.8 , while all other residents had ≤ 2 (Figure 8A). Similarly, SDEs
404 differed significantly by annual movement type (Kruskal-Wallis, $\chi^2 = 95.9491$, $p < 0.0001$),
405 although not between seasonal migrants and migrants (post hoc DSCF test, $p=0.0057$). For
406 migrant species (both types) there was not a significant correlation between path number and
407 SDE (Pearson's correlation coefficient = 0.14351, $p = 0.0553$, $n = 179$) due to individual

408 variability in space use and MP of those spaces. Path number correlated highly with space use
409 only in species with high site fidelity. Nassau and black grouper exhibited small activity spaces
410 and the highest maximum consecutive months of detections. Seasonal migrants exhibiting strong
411 contiguous use of the study area included nurse shark, tarpon, and sawfish.

412 Use of the migratory corridor, based on detections at receivers deployed in the corridor,
413 varied among migrant species (both types) and these differences were significant ($\chi^2 = 36311$, n
414 $= 80,317$, $p < 0.0001$). Blacktip sharks and eagle rays, although commonly detected in the GOM,
415 were rarely detected in the corridor (0% and 2% of detections, respectively). Corridor detections
416 were highly variable for the other seasonal migrants: 95% in nurse sharks, 58% in sawfish and
417 only 4% in tarpon. Bull sharks were similar to sawfish with 55% of detections in the corridor.
418 The remaining migrant species had GOM detections ranging from 85% (great hammerheads), >
419 90% (cobia, lemon shark, tiger shark) to ~100% (bluefin tuna and white sharks).

420 Individual variability in movement occurred in most species and across movement types
421 (Figure 9). Species with relatively consistent movement signatures included: bluefin tuna, which
422 exhibited vertical lines representing rapid longitudinal movements; cobia, which exhibited a
423 zigzag pattern, indicative of rapid longitudinal movements from east to west, a gap in detections
424 of ~ one year and then the same rapid longitudinal movements from east to west again; and reef
425 fish species exhibiting horizontal, almost-daily detections at either the same station or stations in
426 close proximity. Some individual black grouper, gag, Nassau grouper, permit, rock hind, scamp,
427 and yellowfin grouper exhibited site-attached behavior (detection period \geq one year, detection
428 days ≥ 30 , and space use ≤ 0.25 km²). The sites supporting this behavior were all near or on
429 natural or artificial reefs. However, the proportion of fish showing this behavior differed
430 significantly by species ($\chi^2 = 16.48$, $n = 50$, $p = 0.0114$). Discounting species with only one

431 tagged fish, permit had the lowest proportion of site-attached individuals (6 out of 32), Nassau
432 grouper were intermediate (1 out of 3), and black grouper had the highest (8 out of 11).

433 Stopover behavior and location also varied, with the proportion of fish exhibiting
434 stopover behavior varying significantly among migrant species ($\chi^2 = 65.52$, $n = 217$, $p < 0.0001$).
435 No stopover behavior (defined as \geq three consecutive detection months) was observed in bluefin
436 tuna, white sharks, or cobia. Those fish detected in more than two basins but assigned as
437 seasonal migrant species had the greatest stopover behavior: sawfish (67%, $n = 27$), tarpon (52%,
438 $n = 29$), and nurse sharks (40%, $n = 5$). Nurse sharks and three additional migrant species
439 exhibited stopover behavior within the corridor (Figure 10): tiger sharks (25%, $n = 12$), great
440 hammerheads (17%, $n = 23$), and lemon sharks (13%, $n = 8$). Eagle rays (20%, $n = 10$), and bull
441 sharks (12%, $n = 41$) exhibited stopover behavior outside the corridor.

442 **3.5 Movement strategies and life history traits**

443 We hypothesized that size, trophic niche, and birth site selection were related to annual
444 movement type and our results supported this. Size differed significantly with annual movement
445 type (Welch's ANOVA, $n = 294$, $p < 0.0001$). Migrants were significantly larger ($260 \text{ cm} \pm 92$
446 cm TL ; $p < 0.0001$) than seasonal migrants ($202 \pm 111 \text{ cm TL}$), residents ($71 \pm 20 \text{ cm TL}$), and
447 high site fidelity residents ($61 \pm 15 \text{ cm TL}$). Trophic level also varied significantly with annual
448 movement type ($\chi^2 = 20.1$, $n = 22$, $p = 0.0026$). No residents (both groups) were apex predators.
449 Most migrant species (86%) and some seasonal migrants (20%) were apex predators. These
450 relationships with migratory scale suggest a link between decreased predation risk and increased
451 migratory scale and, presumably, consumption to support the larger body mass. These findings
452 highlight how size plays a role in the evolution of movement strategies to address tradeoffs
453 between predation and resource acquisition. Teleost species tracked in this study were all

454 reported to exhibit movements associated with birth site selection (Suppl, Table 1), regardless of
455 annual movement type or size.

456 **4. Discussion**

457 **4.1 Movement strategy framework**

458 Multiple frameworks have been proposed to help understand drivers of individual movements
459 (Nathan et al., 2008), scaling those drivers to population dynamics (Doherty & Driscoll, 2018),
460 and applying the concepts of movement ecology to understanding biodiversity (Jeltsch et al.,
461 2013) and wildlife management (Allen & Singh, 2016; Fraser et al., 2018). How movements
462 affect fisheries management from single species to ecosystem based has also been outlined
463 (Lowerre-Barbieri et al., 2019a). However, we could find no literature that provided a movement
464 strategy framework integrating a species' movement traits and drivers over temporal scales — a
465 framework needed to compare species' movement ecology and how it affects resilience to
466 stressors such as fishing, habitat degradation and climate change. The movement strategy
467 framework presented here is intended to fill this gap and begin the process of standardizing terms
468 that often vary across studies, species, and realms (Allen and Singh 2016; Bastille-Rousseau et
469 al., 2016; Brodie et al., 2018; Berg et al., 2019). The intent is to be universally applicable,
470 although water column use would need to be changed to altitude in terrestrial and avian species
471 and depth for burrowing species. To fully evaluate this framework will necessitate asking
472 scientists studying movement in other realms and species to test it and provide feedback.

473 The advantage of framing movement strategies in a fashion similar to life history
474 strategies is two-fold: (1) it integrates the concept of movement strategies evolving over
475 evolutionary time under conditions potentially quite different from those they currently exist in;
476 and (2) identifies measurable traits, providing a foundation for future trait-based analyses

477 (Beukhof et al., 2019). Fisheries science-to-date has focused mainly on changes in
478 movements/distributions due to ecological context (Morley et al., 2018; Pinsky et al., 2020) or
479 density dependence (MacCall, 1990; Thorson et al., 2016). However, inherited components of
480 species-specific movement strategies will mediate how these strategies respond to changing
481 conditions. Drawing from the fast-slow continuum of life history strategies (Promislow and
482 Harvey, 1990), we hope this framework will provide a similar foundation to assess species-
483 specific movement strategies, although an understanding of how movement strategies relate to
484 population resilience is still emerging. Adult movement strategies fall along a continuum from
485 site attached to highly migratory (although they both often move to specific birth sites). Long-
486 term site attachment is only possible in environments where energetic and survival needs can be
487 met in one location. Advantages of site attachment include the “resident advantage” against
488 competitors for prime habitat, increased efficiency in extracting resources from “well-known”
489 habitats, and effective predator avoidance (Gerber et al., 2019). In migration and nomadism,
490 animals move to optimal locations for feeding, offspring survival, and physiological functioning
491 (Shaw 2016), but in consequence giving up the advantages of site attachment.

492 Birth site selection is a common driver of movement in marine ecosystems, occurring in
493 marine mammals, teleosts and elasmobranchs (Shaw 2016). Most teleosts in this study exhibited
494 birth site selection and it occurred across a wide range of sizes, trophic niches and in all annual
495 movement types. Resident species in this study all formed spawning aggregations, with the
496 possible exception of gag (Lowerre-Barbieri et al., 2020). Given that many of them also were
497 highly site-attached, this suggests tradeoffs in movement choices to meet adult and offspring
498 survival needs. The only seasonal migrant which was a teleost was tarpon. They form pre-
499 spawning aggregations prior to migrating to presumed deep-water spawning sites (Luo et al.,

500 2019). Cobia and bluefin tuna are migrants and both undertake movements associated with birth
501 site selection. Cobia migrate from south Florida to the northern GOM, where they spawn in
502 aggregations (Perkinson et al., 2019). Bluefin tuna are known to migrate between northern
503 foraging grounds to spawning grounds in the Caribbean and GOM, although they do not form
504 spawning aggregations (Block et al., 2005; Hazen et al., 2016). Although spawning site selection
505 remains poorly understood in marine fish, it will affect how a species adapts to a changing ocean,
506 with concern for phenological disconnects negatively affecting productivity. This has been
507 observed in multiple bird species for which cues to initiate migration no longer result in arriving
508 at fixed breeding grounds at the optimal time (Møller et al., 2008).

509 **4.2 Detection potential**

510 Large scale and long-term movement data is needed to better understand movement strategies.
511 Current solutions to collecting this data marine fish are: (1) synthesizing tracks of many animals
512 from archival tags (including satellite); or (2) sharing detection data through acoustic telemetry
513 networks (Hussey et al., 2015; Lennox et al., 2019; Lowerre-Barbieri et al., 2019a; Bangle et
514 al., 2020). Integrated tracking data has greatly improved the scale of inferences we can make
515 from acoustic telemetry but also presents new challenges in terms of separating process from
516 observation effects (Friess et al., 2021) and a need to develop new methods to address issues
517 such as varying detection periods and the varying efficacy of receiver coverage to detect
518 different species. To begin to address this, we quantified TP and MP, and developed the DPI to
519 quantify disparate observation capacity by species. However, in an ideal world DPI would be
520 determined from independent space use data or prior information about species habitat
521 preferences and integrate variability in range with habitat and over time. The opportunistic nature
522 of the networked data requires a temporal threshold considered representative of annual

523 movements. Here we used a year. Crevalle jack exemplify this need. Within the study period
524 they had a mean detection period of 39 days and were detected only within the study area.
525 However, consequent detections (after the study ended) of Crevalle jack were made in the Gulf
526 of Mexico and in the Atlantic basin (Gervasi pers. comm.). Tagging location and numbers tagged
527 also affects accurate representation of within-species variability at the contingent and individual
528 scales. For example, resident and migrant contingents of blacktip shark use the study area
529 (Grubbs, pers. comm.), but because the fish tracked in this study were all tagged in the GOM
530 only the migratory contingent is represented in these data.

531 **4.3 Life cycle space use**

532 Although we can rarely track an animal over its lifetime, using tracking to help inform
533 life cycle space use has important implications for management. Spatial population structure,
534 natal homing, and biocomplexity affect a species' resilience to environmental and
535 anthropogenic perturbations (Goethel et al., 2020) and ontogenetic habitat shifts are common,
536 affecting availability to capture and harvest control rules (Carruthers et al., 2015). Components
537 of space use at this scale typically differ between teleosts and elasmobranchs due to different
538 reproductive strategies. In teleosts, mating and birthing grounds are usually the same, with
539 models needed to predict birth site and nursery ground connectivity (Swearer et al., 2019). In
540 contrast, most elasmobranchs have separate mating and birthing sites and the overlap between
541 birth and nursery grounds is species-specific, with some species not using nursery grounds
542 (Heupel et al., 2007). Immature blacktip sharks, sawfish, and white sharks tagged outside the
543 study area were detected, but only sawfish showed the hypothesized size dependence in arrival
544 time. This appears to be due to varying life cycle space use and DPIs (Table 2). In west-central
545 Florida, blacktip sharks use estuarine nursery grounds and exhibit homing to these grounds after

546 seasonal migrations to the Florida Keys (Hueter et al., 2004), tropical storm-induced movements
547 (Heupel et al., 2003), and experimental displacement (Gardiner et al., 2015). Sawfish nursery
548 grounds are also estuarine and documented in the Charlotte Harbor system and Everglades
549 National Park (Norton et al., 2012). Large juvenile sawfish tagged in Charlotte Harbor
550 commonly move to the study area, later returning to the tagging area (Graham et al., 2021).
551 However, it is not yet known if this is due to seasonal changes in temperature, changing foraging
552 opportunities, or mating site selection. The white shark migratory scale is much larger, including
553 transoceanic, as well as long distance coastal migrations (Bonfil et al., 2005; Skomal et al.,
554 2017). White sharks tracked in this study were primarily tagged off Massachusetts, a known
555 foraging ground, south of the New York Bight, which acts as a nursery area (Curtis et al., 2018).
556 The birth site of these white sharks remains unknown.

557 Shifts in habitat use and annual movement type with maturity are common in fish
558 (Lowerre-Barbieri et al., 2016) as well as many other species — especially those with major
559 changes in body size or morphology with life stage, such as amphibians and insects (Werner &
560 Gilliam, 1984). These shifts have been traditionally thought to be driven by the size to predation
561 risk relationship, with animals leaving their nursery grounds when the benefits of increased
562 growth outweigh those of increased mortality. However, shifts in habitat use and/or annual
563 movement type can be driven by any trait that takes time to develop and affects foraging,
564 survival, or reproduction, including the development in birds of salt glands or muscular gizzards
565 (Fokkema et al., 2020), or in some fish, the ability to successfully defend a territory (Gruss et al.,
566 2011). Given the need to reach an energetics threshold both to mature and to migrate,
567 reproductive development and ontogenetic habitat shifts are linked to an animal's condition
568 (Goossens et al., 2020), potentially driving the individual variability observed in the timing of

569 emigration from nursery grounds (Walters Burnsed et al., 2020). We hypothesized adults would
570 exhibit lower residency than immature fish, a common pattern, which was observed in tarpon but
571 not permit. However, most permit appear to spend their full life cycle within the study area,
572 whereas adult tarpon are seasonal migrants that undertake long migrations (Griffin et al., 2018;
573 Luo et al., 2019).

574 **4.4 Annual movement type**

575 We hypothesized that basin use and temporal detection patterns could effectively
576 categorize species' annual movement types and our results supported this and agreed well with
577 the literature (Table 1). However, sample size, number of clusters, and variable DPI affected
578 results. Five species had only one tagged fish, and cannot be considered representative of the
579 species, but were retained because their movement type agreed with the literature. In our cluster
580 analysis, we chose four clusters *a priori* to represent the four major types of annual movement
581 (residents, seasonal migrants, migrants, and nomads). However, results grouped species into two
582 resident types (high site fidelity versus range resident), seasonal migrants, and migrants.

583 Our results support those of Brodie et al. (2018) and Friess et al. (2021) that acoustic
584 telemetry, with appropriate monitoring power, can determine annual movement types. For gag
585 and greater amberjack, our movement type results differed from the literature, in large part due
586 to the range of species in the study and the constraint of four movement types. Greater amberjack
587 demonstrate both the importance of adequate monitoring power and within-species annual
588 movement type analysis to identify partial migration. Greater amberjack form large spawning
589 aggregations at the Islamorada and Marathon seamounts (Figure 1C, nodes 38 and 40; Hargrove
590 et al., 2018) and, based on conventional tag recaptures, are believed to make long, coastal
591 migrations to these sites (Harris et al., 2011). None of our fish were detected outside the study

592 area and virtually all detections occurred at the seamounts, suggesting there could be partial
593 migration. However, greater amberjack has low MP and DPI and this was underscored by the
594 recapture of one fish ~600 km north of the study area.

595 **4.5 Within-ecosystem behavior**

596 Our results are a first step towards providing the movement data needed for future spatial
597 management and multi-species dynamic ocean management (Hazen et al., 2018) in the study
598 area. MPAs are often created to protect spawning aggregations for resident species. In the study
599 area, spawning aggregation sites have been documented for mutton snapper, grey snapper (Keller
600 et al., 2020), permit (Brownscombe et al. 2020) and greater amberjack (Harris et al., 2011).
601 However, it is also important to design MPAs to protect key areas for migrating species such as
602 foraging and reproductive habitats (Runge et al., 2014; Hays et al., 2019), migratory corridors,
603 and stopover sites. For ecosystem-based management (EBM), it is especially important to protect
604 these habitats for migratory meso- and apex predators, given their importance to ecosystem
605 health (Heithaus et al., 2010; Speed et al., 2010; Hammerschlag et al., 2019). The UN's target to
606 increase MPAs by 2030 provides an opportunity to support additional studies like this to identify
607 and protect these habitats (Sequeira et al., 2019).

608 Species' movement strategies evolved in habitats unaltered by humans but now have to
609 adapt to the available habitat mosaic — habitat contiguity and quality (e.g., Section 2.1.2.1 in
610 Adams, 2017). Connectivity will be affected by these factors and our ability to accurately
611 measure it depends on the overlap between movement routes and receiver coverage (i.e., MP).
612 Low connectivity occurred in residents of both movement types (other than permit), blacktip
613 sharks, eagle rays, bluefin tuna and white sharks – but not for the same reasons. Residents
614 exhibited little horizontal movement and were well-tracked at their tagging sites. However, it is

615 often assumed that site attached species leave the array primarily due to predation, recently
616 documented by Bohaboy et al. (2020). But fish also leave due to natural triggers, such as tropical
617 storms (Secor et al., 2019), but their probability of being detected at other arrays is often low.
618 This was the case for red snapper off the west coast of Florida (Friess et al., 2021), presumably
619 due to high site fidelity at the new location.

620 Blacktip sharks and eagle rays migrated to the GOM to over-winter. They had low DPIs,
621 due to lower receiver coverage along migratory routes from the GOM compared to the Atlantic.
622 In contrast, bluefin tuna and white sharks appear to exhibit rapid migrations through the study
623 area within the migratory corridor, although much remains unknown about use of the corridor,
624 seamounts, and deeper waters. Only two receivers were deployed in waters 50 m to 400 m.
625 Given these conditions, the detection of approximately a third of the white sharks tagged off
626 Massachusetts suggests this is a common migratory route for this population. However, to
627 understand movements within the corridor, the range of species using it, and whether species will
628 change movements due to climate change and anthropogenic stressors requires additional
629 tracking studies and synthesis of PSAT tracks from prior studies with catch-based data.

630 Stopover (or staging) sites are commonly studied in birds, but less so in fish. The term
631 refers to intermediary sites used during migration that provide resources and environmental
632 conditions supporting effective migration (Warnock 2010). Here we defined stopover behavior
633 based on three or more consecutive months of detection but is certainly possible at shorter
634 durations. Again, our ability to assess it will be affected by species-specific DPIs. Seasonal
635 migrants, not surprisingly, had the most individuals exhibiting stopover behavior: sawfish (67%,
636 $n = 27$), tarpon (52%, $n = 29$), and nurse sharks (40%, $n = 5$). Stopover sites for these species
637 ranged from within the corridor (nurse sharks), only in shallower waters (tarpon) or in both

638 (sawfish). The mechanistic driver of this behavior is unknown, with the exception of tarpon
639 which form pre-spawning aggregations, an increasingly acknowledged form of stopover
640 behavior, where fish feed and increase their energy reserves prior to undertaking spawning
641 migrations. In terms of spatial protection, stopover sites in shallow water are expected to be the
642 most impacted by anthropogenic stressors and thus should be prioritized.

643 **5 Conclusions**

644 Given that movement links habitat with life history processes important to population
645 dynamics, conservation, and management (Hays et al., 2019; Wittemyer et al., 2019), there is a
646 clear need to integrate spatial processes into fisheries management (Berger et al., 2017;
647 Cumming et al., 2017; Lowerre-Barbieri et al., 2019b; Link et al., 2020). Roadblocks to doing so
648 (for tracking data) are both methodological and conceptual. Acoustic telemetry networks have
649 greatly increased the biological and spatial scale over which marine fish can be tracked, but also
650 present new challenges including data standardization (Sequeira et al., 2021) and the need to
651 move from opportunistic data to designed network studies to monitor multi-species movements.
652 This, of course, necessitates funding. Such an approach would address the issues we encountered
653 in terms of varying TP, MP, and DPI. However, there is also a need to invest in long-term arrays
654 that can track changes in movements over time.

655 While, conceptually, the linkage between movement strategies and management is clear,
656 how to incorporate movement strategies into management is less so, given the current
657 management paradigm. Within a traditional stock assessment framework, there is increased
658 integration of tracking results into stock identification (Cadrin 2020) and interest in developing
659 spatially explicit stock assessment models (Goethel et al., 2020). We would like to also
660 encourage the integration of movement into management strategy evaluations to assess how

661 movement affects catchability. Specifically, we suggest simulations which address: (1) spatio-
662 temporal patterns of effort and life cycle space use to identify vulnerability bottlenecks; (2) how
663 movement affects availability to capture and thus catch-based estimates of abundance; and (3) at
664 the multi-species scale, how movement affects by-catch. We also suggest that water depths and
665 annual movement types be used to refine definitions of stock complexes, recognizing their
666 importance to more than just highly migratory and coastal migratory species.

667 Within- and cross-ecosystem movements (space use, connectivity, migratory routes,
668 stopover sites, and functional use of habitats) are also important to productivity and ecosystem
669 functioning. However, traditional management is extraction-based, using life history parameters
670 and catch data (fisheries-dependent and fisheries-independent) to manage stocks in terms of the
671 optimal catches they can sustain. However, management is shifting from optimizing single
672 species yield to managing ocean use and ecosystem health (Halpern et al., 2015), with the
673 following management approaches not predicated on single species biomass optimization: spatial
674 management, dynamic ocean management (DOM; Lewison et al., 2015), and EBM (Dolan et al.,
675 2016). These new management paradigms will necessitate new data streams and the funding to
676 provide them. Similar to the investment in surveys to estimate relative abundance for the current
677 management paradigm, spatial management, DOM, and EBM will need data on movements and
678 how they change with climate and habitat degradation (Lotze et al., 2006). To effectively collect
679 these data, we need to identify globally important connectivity hot spots under stress from the
680 Anthropocene, like the Florida Keys, and provide long-term funding for infrastructure,
681 technological innovation, and personnel who can bridge the gap between traditional and
682 emerging ocean management.

683

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698

699 **DATA AVAILABILITY STATEMENT:** The data that support the results in this study were
700 shared through iTAG and are archived through the Ocean Tracking Network (OTN), whose data
701 system is an Associate Data Unit of the Intergovernmental Oceanographic Commission’s
702 International Oceanographic Data and Information Exchange. Access to the data on the OTN
703 system is guided by the public data policies of OTN and the member nodes who participate in
704 the system. There is no fee to access the data from the system, and OTN staff are available to
705 assist with data requests. A citation format crediting the owners of the data is available from the
706 OTN publication data repository [https://members.oceantrack.org/data/pblctn_data/publication-](https://members.oceantrack.org/data/pblctn_data/publication-data-repository#10%3Cucode%3E%3Cucodep%3E&middledot;%3C/)
707 [data-repository#10%3Cucode%3E%3Cucodep%3E&middledot;%3C/](https://members.oceantrack.org/data/pblctn_data/publication-data-repository#10%3Cucode%3E%3Cucodep%3E&middledot;%3C/)

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711 REFERENCES

- 712 Abrahms, B., Seidel, D. P., Dougherty, E., Hazen, E. L., Bograd, S. J., Wilson, A. M., . . . Getz,
713 W. M. (2017). Suite of simple metrics reveals common movement syndromes across
714 vertebrate taxa. *Movement Ecology*, 5, 12. <https://doi.org/10.1186/s40462-017-0104-2>
- 715 Adams, A. (2017). Guidelines for evaluating the suitability of catch and release fisheries:
716 Lessons learned from Caribbean flats fisheries. *Fisheries Research*, 186, 672–680.
- 717 Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and
718 conservation. *Frontiers in Ecology and Evolution*, 3.
719 <https://doi.org/10.3389/fevo.2015.00155>
- 720 Andersen, K. H., Berge, T., Goncalves, R. J., Hartvig, M., Heuschele, J., Hylander, S., . . .
721 Kiorboe, T. (2016). Characteristic Sizes of Life in the Oceans, from Bacteria to Whales.
722 *Annual review of marine science*, 8, 217-241. doi:10.1146/annurev-marine-122414-
723 034144.
- 724 Bangley, C. W., Whoriskey, F. G., Young, J. M., & Ogburn, M. B. (2020). Networked animal
725 telemetry in the northwest Atlantic and Caribbean waters. *Marine and Coastal Fisheries*,
726 12, 339–347. <https://doi.org/10.1002/mcf2.10128>
- 727 Bastille-Rousseau, G., Potts, J. R., Yackulic, C. B. Frair, J. L., Ellington, E. H., & Blake, S.
728 (2016). Flexible characterization of animal movement pattern using net squared
729 displacement and a latent state model. *Movement Ecology*, 4, 15.
730 <https://doi.org/10.1186/s40462-016-0080-y>
- 731 Berg, J. E., Hebblewhite, M., St. Clair, C. C., & Merrill, E. H. (2019). Prevalence and
732 mechanisms of partial migration in ungulates. *Frontiers in Ecology and Evolution*, 7.
733 <https://doi.org/10.3389/fevo.2019.00325>

734 Berger, A. M., Goethel, D. R., Lynch, P. D., Quinn, T., Mormede, S., McKenzie, J., & Dunn, A.
735 (2017). Space oddity: The mission for spatial integration. *Canadian Journal of Fisheries*
736 *and Aquatic Sciences*, 74(11), 1698-1716. doi:10.1139/cjfas-2017-0150

737 Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A., Dencker, T. S., Solmundsson, J., . . .
738 Lindegren, M. (2019). Marine fish traits follow fast-slow continuum across oceans. *Sci*
739 *Rep*, 9(1), 17878. doi:10.1038/s41598-019-53998-2

740 Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J., . . .
741 Williams, T. D. (2005). Electronic tagging and population structure of Atlantic bluefin
742 tuna. *Science*, 293, 2077-2079. doi:10.1029/2002pa000862

743 Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., . . .
744 Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean.
745 *Nature*, 475, 86–90

746 Bohaboy, E. C., Guttridge, T. L., Hammerschlag, N., Van Zinnicq Bergmann, M. P., Patterson,
747 W. F. III (2020) Application of three-dimensional acoustic telemetry to assess the effects of
748 rapid recompression on reef fish discard mortality. *ICES Journal of Marine Science*, 77,
749 83–96. <https://doi.org/10.1093/icesjms/fsz202>

750 Bonfil, R., Meyer, M., Scholl, M. C., Johnson, R., O'Brien, S., Oosthuizen, H., . . . Paterson, M.
751 (2005). Transoceanic migration, spatial dynamics, and population linkages of white
752 sharks. *Science*, 310, 100–103

753 Brodie, S., Lédée, E. J. I., Heupel, M. R., Babcock, R. C., Campbell, H. A., Gledhill, D. C., . . .
754 Harcourt, R. G. (2018). Continental-scale animal tracking reveals functional movement
755 classes across marine taxa. *Scientific Reports*, 8. [https://doi.org/10.1038/s41598-018-](https://doi.org/10.1038/s41598-018-21988-5)
756 21988-5

757 Brownscombe, J. W., Griffin, L. P., Morley, D., Acosta, A., Hunt, J., Lowerre-Barbieri, S. K., . .
758 . Cooke, S. J. (2020). Application of machine learning algorithms to identify cryptic
759 reproductive habitats using diverse information sources. *Oecologia*. doi:10.1007/s00442-
760 020-04753-2

761 Brownscombe, J. W., Griffin, L. P., Morley, D., Acosta, A., Hunt, J., Lowerre-Barbieri, S. K., ...
762 & Cooke, S. J. (2019). Seasonal occupancy and connectivity amongst nearshore flats and
763 reef habitats by permit *Trachinotus falcatus*: considerations for fisheries management.
764 *Journal of Fish Biology*, 96, 469–479.

765 Bui, R., Buliung, R. N. and Rimmel, T. K. (2012). aspace: A collection of functions for
766 estimating centrographic statistics and computational geometries for spatial point
767 patterns. R package version 3.2. <https://CRAN.R-project.org/package=aspace>.

768 Cadrin, S. X. (2020). Defining spatial structure for fishery stock assessment. *Fisheries Research*,
769 221, 105397. doi:10.1016/j.fishres.2019.105397

770 Carlisle, A. B., Tickler, D., Dale, J. J., Ferretti, F., Curnick, D. J., Chapple, T. K., Schallert, R. J.,
771 Castleton, M., & Block, B. A. (2019). Estimating space use of mobile fishes in a large
772 marine protected area with methodological considerations in acoustic array design.
773 *Frontiers in Marine Science*, 6.

774 Carruthers, T. R., Walter, J. F., McAllister, M. K., Bryan, M. D. (2015) Modelling age-
775 dependent movement: an application to red and gag groupers in the Gulf of Mexico.
776 *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1159–1176.
777 <https://doi.org/10.1139/cjfas-2014-0471>

778 Ciannelli, L., Bailey, K., & Olsen, E. M. (2015). Evolutionary and ecological constraints of fish
779 spawning habitats. *ICES Journal of Marine Science*, 72, 285–296.
780 <https://doi.org/10.1093/icesjms/fsu145>

781 Cinner, J. E., Zamborain-Mason, J., Gurney, G. G., Graham, N. A. J., MacNeil, M. A., Hoey, A.
782 S., . . . Mouillot, D. (2020). Meeting fisheries, ecosystem function, and biodiversity goals
783 in a human-dominated world. *Science*, 368, 307–311.

784 Clardy, T. R., III, W. F. P., DeVries, D. A., & Palmer, C. (2008). Spatial and temporal variability
785 in the relative contribution of king mackerel (*Scomberomorus cavalla*) stocks to winter
786 mixed fisheries. *Fisheries Bulletin*, 106, 152-160.

787 Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen,
788 V. M., . . . Cooke, S. J. (2017). Acoustic telemetry and fisheries management. *Ecological*
789 *Applications*, 27, 1031–1049. <https://doi.org/10.1002/eap.1533>. Epub 2017 May 2

790 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research.
791 *InterJournal, Complex Systems*, 1695, 1–9.

792 Cumming, G. S., Morrison, T. H., & Hughes, T. P. (2017). New directions for understanding the
793 spatial resilience of social-ecological systems. *Ecosystems*, 20(4), 649-664.
794 [doi:doi:http://dx.doi.org.lp.hscl.ufl.edu/10.1007/s10021-016-0089-5](https://doi.org/10.1007/s10021-016-0089-5)

795 Curtis, T. H., Metzger, G., Fischer, C., McBride, B., McCallister, M., Winn, L. J., . . . Ajemian,
796 M. J. (2018). First insights into the movements of young-of-the-year white sharks
797 (*Carcharodon carcharias*) in the western North Atlantic Ocean. *Scientific Reports*, 8,
798 10794. <https://doi.org/10.1038/s41598-018-29180-5>

799 DeGroot, B. C., Bassos-Hull, K., Wilkinson, K. A., Lowerre-Barbieri, S., Poulakis, G. R., &
800 Ajemian, M. J. (2021). Variable migration patterns of whitespotted eagle rays *Aetobatus*

801 *narinari* along Florida's coastlines. *Marine Biology*, 168, 18.
802 <https://doi.org/10.1007/s00227-021-03821-2>

803 Doherty, T. S., & Driscoll, D. A. (2018). Coupling movement and landscape ecology for animal
804 conservation in production landscapes. *Proceedings Biological Sciences*, 285.
805 <https://doi.org/10.1098/rspb.2017.2272>

806 Dolan, T. E., Patrick, W. S., and Link, J. S. (2016). Delineating the continuum of marine
807 ecosystem-based management: a US fisheries reference point perspective. *ICES Journal*
808 *of Marine Science*, 73, 1042–1050.

809 Donaldson, M. R., Hinch, S.G., Suski, C.D., Fisk, A.T., Heupel, M.R. and Cooke, S.J. (2014).
810 Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Frontiers*
811 *in Ecology and Environment*, 12, 565–573

812 Fagan, W. F., & Gurarie, E. (2020). Spatial Ecology: Herbivores and Green Waves - To Surf or
813 Hang Loose? *Curr Biol*, 30(17), R991-R993. doi:10.1016/j.cub.2020.06.088

814 Fokkema, W., van der Jeugd, H. P., Lameris, T. K., Dokter, A. M., Ebbinge, B. S., de Roos, A.
815 M., . . . Olf, H. (2020). Ontogenetic niche shifts as a driver of seasonal migration.
816 *Oecologia*, 193(2), 285-297. doi:10.1007/s00442-020-04682-0

817 Fraser, K. C., Davies, K. T., Davy, C. M., Ford, A. T., Flockhart, D. T., & Martins, E. G. (2018).
818 Tracking the conservation promise of movement ecology. *Frontiers in Ecology and*
819 *Evolution*, 6, 150

820 Fretwell, S. D., and H. L. Lucas. 1970. On territorial behaviour and other factors influencing
821 habitat distribution in birds. *Acta Biotheoretica* 19:16-36

822 Friess, C. co*, Lowerre-Barbieri, S.K. co*, Poulakis, G.R., Hammerschlag, N., Gardiner, J.M.,
823 Kroetz, A.M., ... Griffin, L.P. *In press*. Regional-scale variability in the movement

824 ecology of marine fishes revealed by an integrative acoustic tracking network. *Marine*
825 *Ecology Progress Series*.

826 Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy landscapes and the
827 landscape of fear. *Trends in Ecology & Evolution*, 32, 88-96.
828 <http://dx.doi.org/10.1016/j.tree.2016.10.010>

829 Gardiner, J. M., Whitney, N. M., & Hueter, R. E. (2015). Smells like home: The role of olfactory
830 cues in the homing behavior of blacktip sharks, *Carcharhinus limbatus*. *Integrative and*
831 *Comparative Biology*, 55, 495-506. <https://doi.org/10.1093/icb/icv087>

832 Gerber, B. D., Hooten, M. B., Peck, C. P., Rice, M. B., Gammonley, J. H., Apa, A. D., . . .
833 Lemaître, J. F. (2019). Extreme site fidelity as an optimal strategy in an unpredictable and
834 homogeneous environment. *Functional Ecology*, 33(9), 1695-1707. doi:10.1111/1365-
835 2435.13390

836 Gillanders, B. M., Able, K. W., Brown, J. A., Eggleston, D. B., & Sheridan, P. F. (2003).
837 Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an
838 important component of nurseries. *Marine Ecology Progress Series*, 247, 281-295.

839 Goethel, D. R., Bosley, K. M., Langseth, B. J., Deroba, J. J., Berger, A. M., Hanselman, D. H., &
840 Schueller, A. M. (2020). Where do you think you're going? Accounting for ontogenetic
841 and climate-induced movement in spatially stratified integrated population assessment
842 models. *Fish and Fisheries*. doi:10.1111/faf.12510

843 Goossens, S., Wybouw, N., Van Leeuwen, T., & Bonte, D. (2020). The physiology of
844 movement. *Movement Ecology*, 8, 5. <https://doi.org/10.1186/s40462-020-0192-2>

845 Graham, N. A. J., Robinson, J. P. W., Smith, S. E., Govinden, R., Gendron, G., & Wilson, S. K.
846 (2020). Changing role of coral reef marine reserves in a warming climate. *Nature*
847 *Communications*, 11, 2000. <https://doi.org/10.1038/s41467-020-15863-z>

848 Graham, J., Kroetz, A. M., Poulakis, G. R., Scharer, R. M., Carlson, J. K., Lowerre-Barbieri, S., .
849 . . Grubbs, R. D. (2021). Large-scale space use of large juvenile and adult smalltooth
850 sawfish *Pristis pectinata*: implications for management. *Endangered Species Research*,
851 *44*, 45–59. <https://doi.org/10.3354/esr01088>

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

856 Grubbs, R.D. (2010) Ontogenetic Shifts in Movements and Habitat Use. In Carrier JF, Musick
857 JA, Heithaus MR (eds.). *Sharks and Their Relatives II: Biodiversity, Adaptive*
858 *Physiology, and Conservation*, CRC Press, New York, New York, USA. pp. 319-350.

859 Gruss, A., Kaplan, D. M., & Hart, D. R. (2011). Relative impacts of adult movement, larval
860 dispersal and harvester movement on the effectiveness of reserve networks. *PLoS ONE*,
861 *6*, e19960. <https://doi.org/10.1371/journal.pone.0019960>

862 Halpern, B. S., Longo, C., Lowndes, J. S., Best, B. D., Frazier, M., Katona, S. K., . . . Selig, E. R.
863 (2015). Patterns and emerging trends in global ocean health. *PLoS ONE*, *10*, e0117863.
864 <https://doi.org/10.1371/journal.pone.0117863>

865 Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., . . .
866 Cooke, S. J. (2019). Ecosystem function and services of aquatic predators in the

867 Anthropocene. *Trends in Ecology and Evolution*, 34, 369-383.
868 <https://doi.org/10.1016/j.tree.2019.01.005>.

869 Hargrove, J. S., Murie, D. J., Parkyn, D. C., Saarinen, E. V., & Austin, J. D. (2018). Mixing rates
870 in weakly differentiated stocks of greater amberjack (*Seriola dumerili*) in the Gulf of
871 Mexico. *Genetica*, 146, 393-402. <https://doi.org/10.1007/s10709-018-0031-1>

872 Harris, P. J., Wyanski, D. M., White, D. B., Mikell, P. P., & Eyo, P. B. (2011). Age, growth, and
873 reproduction of greater amberjack off the southeastern U.S. Atlantic coast. *Transactions*
874 *of the American Fisheries Society*, 136, 1534-1545. <https://doi.org/10.1577/t06-113.1>

875 Harrison, A.-L., Costa, D. P., Winship, A. J., Benson, S. R., Bograd, S. J., Antolos, M., . . .
876 Block, B. A. (2018). The political biogeography of migratory marine predators. *Nature*
877 *Ecology & Evolution*, 2(10), 1571-1578. doi:10.1038/s41559-018-0646-8

878 Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., ... & de
879 Bruyn, P. N. (2019). Translating marine animal tracking data into conservation policy
880 and management. *Trends in Ecology & Evolution*, 34, 459-473.

881 Hazen, E. L., Maxwell, S. M., Bailey, H., Bograd, S. J., Hamann, M., Gaspar, P., . . . Shillinger,
882 G. L. (2012). Ontogeny in marine tagging and tracking science: technologies and data
883 gaps. *Marine Ecology Progress Series*, 457, 221-240. <https://doi.org/10.3354/meps09857>

884 Hazen, E. L., Carlisle, A. B., Wilson, S. G., Ganong, J. E., Castleton, M. R., Schallert, R. J., . . .
885 Block, B. A. (2016). Quantifying overlap between the Deepwater Horizon oil spill and
886 predicted bluefin tuna spawning habitat in the Gulf of Mexico. *Scientific Reports*, 6,
887 33824. doi:10.1038/srep33824

888 Hazen, E. L., Scales, K. L., Maxwell, S. M., Briscoe, D. K., Welch, H., Bograd, S. J., . . .
889 Lewison, R. L. (2018). A dynamic ocean management tool to reduce bycatch and support
890 sustainable fisheries. *Science Advances*, 4, eaar3001.

891 Heithaus, M., Frid, A., Vaudo, J., Worm, B., & Wirsing, A. (2010). Unraveling the Ecological
892 Importance of Elasmobranchs. In Carrier JF, Musick JA, Heithaus MR (eds.). *Sharks and
893 Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*, CRC Press,
894 New York, New York, USA. pp. 611-637.

895 Hertel, A. G., Niemela, P. T., Dingemanse, N. J., & Mueller, T. (2020). A guide for studying
896 among-individual behavioral variation from movement data in the wild. *Movement
897 Ecology*, 8, 30. <https://doi.org/10.1186/s40462-020-00216-8>

898 Heupel, M. R., Simpfendorfer, C. A., & Hueter, R. E. (2003). Running before the storm: blacktip
899 sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle.
900 *Journal of Fish Biology*, 63, 1357-1363. [https://doi.org/10.1046/j.1095-
901 8649.2003.00250.x](https://doi.org/10.1046/j.1095-8649.2003.00250.x)

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

905 Heupel, M. R., Carlson, J. K., & Simpfendorfer, C. A. (2007). Shark nursery areas: concepts,
906 definition, characterization and assumptions. *Marine Ecology Progress Series*, 337, 287-
907 297.

908 Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. (2008). Trends and missing
909 parts in the study of movement ecology. *Proceedings of the National Academies of
910 Science*, 105, 19060–5.

911 Hueter, R. E., M. R. Heupel, E. J. Heist, and D. B. Keeney (2004) Evidence of philopatry in
912 sharks and implications for the management of shark fisheries, *Journal of Northwest*
913 *Atlantic Fishery Science*, 35, 239-247.

914 Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., . . .
915 Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the
916 underwater world. *Science*, 348, 1255642. <https://doi.org/10.1126/science.1255642>

917 Jacoby, D. M. P., Brooks, E. J., Croft, D. P., & Sims, D. W. (2012). Developing a deeper
918 understanding of animal movements and spatial dynamics through novel application of
919 network analyses. *Methods in Ecology and Evolution*, 3, 574-583.
920 <https://doi.org/10.1111/j.2041-210X.2012.00187.x>

921 Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., . . . Bauer, S.
922 (2013). Integrating movement ecology with biodiversity research - exploring new
923 avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1, 6.
924 <https://doi.org/10.1186/2051-3933-1-6>

925 Johnson, A. G., Jr., W. A. Fable, Jr., Grimes, C. B., Trent, L., & Perez, J. V. (1994). Evidence
926 for distinct stocks of king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico.
927 *Fishery Bulletin*, 92, 91-101.

928 Keller, J. A., Herbig, J. L., Morley, D., Wile, A., Barbera, P., & Acosta, A. (2020). Grouper
929 tales: Use of acoustic telemetry to evaluate grouper movements at western Dry Rocks in
930 the Florida Keys. *Marine and Coastal Fisheries*, 12, 290-307.
931 <https://doi.org/10.1002/mcf2.10109>

932 Lennox R.J., Paukert C.P., Aarestrup K., Auger-Méthé M., Baumgartner L., Birnie-Gauvin,
933 K...Cooke, S.J. (2019). One Hundred Pressing Questions on the Future of Global Fish

934 Migration Science, Conservation, and Policy. *Frontiers in Ecology and Evolution*,
935 7(286). doi:10.3389/fevo.2019.00286

936 Levine, N. (2010). CrimeStat: A Spatial Statistics Program for the Analysis of Crime Incident
937 Locations (v 3.3). Ned Levine & Associates, Houston, TX, and the National Institute of
938 Justice, Washington, DC. July.

939 Lewison, R., Hobday, A. J., Maxwell, S., Hazen, E., Hartog, J. R., Dunn, D. C., . . . Crowder, L.
940 B. (2015). Dynamic Ocean Management: Identifying the Critical Ingredients of Dynamic
941 Approaches to Ocean Resource Management. *BioScience*, 65(5), 486-498.
942 doi:10.1093/biosci/biv018

943 Link, J. S., Huse, G., Gaichas, S., & Marshak, A. R. (2020). Changing how we approach
944 fisheries: A first attempt at an operational framework for ecosystem approaches to
945 fisheries management. *Fish and Fisheries*. 21: 393-434. <https://doi.org/10.1111/faf.12438>

946 Lorenzen, K. (1996). The relationship between body weight and natural mortality in juvenile and
947 adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology*,
948 49, 627-642. <https://doi.org/10.1111/j.1095-8649.1996.tb00060.x>

949 Lotze, H. K., Lenihan, H.S., Bourque, B.J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell,
950 S. M, Kirby, M. X., Peterson, C. H., and Jackson, J. B. C. (2006). Depletion, degradation,
951 and recovery potential of estuaries and coastal seas. *Science*, 312, 1806–1809.

952 Lowerre-Barbieri, S. K., Walters Burns, S. L., & Bickford, J. W. (2016). Assessing
953 reproductive behavior important to fisheries management: a case study with red drum,
954 *Sciaenops ocellatus*. *Ecological Applications*, 26, 979-995. [https://doi.org/10.1890/15-](https://doi.org/10.1890/15-0497)
955 0497

956 Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I. A., Muhling, B., Erisman, B., . . . Paris,
957 C. B. (2017). Reproductive resilience: a paradigm shift in understanding spawner-recruit
958 systems in exploited marine fish. *Fish and Fisheries*, 18, 285–312.
959 <https://doi.org/10.1111/faf.12180>

960 Lowerre-Barbieri, S. K., Kays, R., Thorson, J. T., & Wikelski, M. (2019a). The ocean’s
961 movescape: fisheries management in the bio-logging decade (2018–2028). *ICES Journal*
962 *of Marine Science*, 76, 477-488. <https://doi.org/10.1093/icesjms/fsy211>

963 Lowerre-Barbieri, S. K., Catalán, I. A., Frugård Opdal, A., & Jørgensen, C. (2019b). Preparing
964 for the future: integrating spatial ecology into ecosystem-based management. *ICES*
965 *Journal of Marine Science*, 76, 467-476. <https://doi.org/10.1093/icesjms/fsy209>

966 Lowerre-Barbieri, S., Menendez, H., Bickford, J., Switzer, T. S., Barbieri, L., & Koenig, C.
967 (2020). Testing assumptions about sex change and spatial management in the
968 protogynous gag grouper, *Mycteroperca microlepis*. *Marine Ecology Progress Series*,
969 639, 199-214. doi:10.3354/meps13273

970 Luo, J., Ault, J. S., Ungar, B. T., Smith, S. G., Larkin, M. F., Davidson, T. N., . . . Robertson, J.
971 (2019). Migrations and movements of Atlantic tarpon revealed by two decades of satellite
972 tagging. *Fish and Fisheries*. doi:10.1111/faf.12430

973 McCall, A. 1990. Dynamic geography of marine fish populations. University of Washington
974 Press, Seattle, 153p.

975 McGowan, J., Beger, M., Lewison, R., Harcourt, R., Campbell, H., Priest, M., Dwyer, R. G., et
976 al. 2017. Integrating research using animal-borne telemetry with the needs of
977 conservation management. *Journal of Applied Ecology*, 54: 423–429

978 Møller, A. P., Rubolini, D., and Lehikoinen, E. (2008). Populations of migratory bird species that
979 did not show a phenological response to climate change are declining. *Proceedings of the*
980 *National Academies of Science. USA*, 105, 16195–16200.
981 <https://doi.org/10.1073/pnas.0803825105>

982 Montenero, K.A., C.R. Kelble, and E. Spooner, 2020: Florida Keys integrated ecosystem
983 assessment ecosystem status report. NOAA Technical Report, OAR-AOML-52
984 (<https://doi.org/10.25923/f7ce-st38>), 64 pp.

985 Morley, J. W., Selden, R. L., Latour, R. J., Froëlicher, T. L., Seagraves, R. J., & Pinsky, M. L.
986 (2018). Projecting shifts in thermal habitat for 686 species on the North American
987 continental shelf. *PLoS ONE* 13(5): e0196127.
988 <https://doi.org/10.1371/journal.pone.0196127>. <https://doi.org/10.1371/journal>

989 Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments - from
990 individual behaviours to population distributions. *Oikos*, 117, 654–664.
991 <https://doi.org/10.1111/j.0030-1299.2008.16291.x>

992 Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E.
993 (2008). A movement ecology paradigm for unifying organismal movement research.
994 *Proceedings of the National Academies of Science USA*, 105, 19052-19059.
995 <https://doi.org/10.1073/pnas.0800375105>

996 Norton, S. L., Wiley, T. R., Carlson, J. K., Frick, A. L., Poulakis, G. R., & Simpfendorfer, C. A.
997 (2012). Designating critical habitat for juvenile endangered smalltooth sawfish in the
998 United States. *Marine and Coastal Fisheries*, 4, 473–480.
999 <https://doi.org/10.1080/19425120.2012.676606>

1000 Perälä, T., & Kuparinen, A. (2017). Detection of Allee effects in marine fishes: analytical biases
1001 generated by data availability and model selection. *Proceedings of the Royal Society B:*
1002 *Biological Sciences*, 284(1861), 20171284. doi:doi:10.1098/rspb.2017.1284

1003 Perkinson, M., Darden, T., Jamison, M., Walker, M. J., Denson, M. R., Franks, J., . . . Orbesen,
1004 E. S. (2019). Evaluation of the stock structure of cobia (*Rachycentron canadum*) in the
1005 southeastern United States by using dart-tag and genetics data. *Fishery Bulletin*, 117(3),
1006 220-233. doi:10.7755/fb.117.3.9

1007 Pinsky, M. L., Selden, R. L., & Kitchel, Z. J. (2020). Climate-Driven Shifts in Marine Species
1008 Ranges: Scaling from Organisms to Communities. *Annual Reviews in Marine Science*,
1009 12, 153-179. doi:10.1146/annurev-marine-010419-010916

1010 Pratt, H. L. J., Pratt, T. C., Morley, D., Lowerre-Barbieri, S., Collins, A., Carrier, J. C., . . .
1011 Whitney, N. M. (2018). Partial migration of the nurse shark, *Ginglymostoma cirratum*
1012 (Bonnaterre), from the Dry Tortugas Islands. *Environmental Biology of Fishes*, 101, 515-
1013 530.

1014 Promislow, D.E.L. & Harvey, P.H. (1990) Living fast and dying young: a comparative analysis
1015 of life-history variation among mammals. *Journal of Zoology*, 220, 417–437.

1016 Pulliam, H. R., & Danielson, B. J. (1991). Sources, Sinks, and Habitat Selection: A Landscape
1017 Perspective on Population Dynamics. *The American Naturalist*, 137, S50-S66.

1018 Putman, N. (2018). Marine migrations. *Current Biology*, 28, R972-R976.
1019 <https://doi.org/10.1016/j.cub.2018.07.036>

1020 QGIS Development Team, 2021. QGIS Geographic Information System. Open Source
1021 Geospatial Foundation. URL <http://qgis.org>

1022 Rider, M. J., McDonnell, L. H., & Hammerschlag, N. (2021). Multi-year movements of adult
1023 and subadult bull sharks (*Carcharhinus leucas*): philopatry, connectivity, and
1024 environmental influences. *Aquatic Ecology*. doi:10.1007/s10452-021-09845-6

1025 Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and
1026 consequence of animal movement. *Trends in Ecology & Evolution*, 35, 163-174.
1027 <https://doi.org/10.1016/j.tree.2019.09.009>.

1028 Rooker, J. R., Dance, M. A., Wells, R. J. D., Ajemian, M. J., Block, B. A., Castleton, M. R., . . .
1029 Walter, J. F. (2019). Population connectivity of pelagic megafauna in the Cuba-Mexico-
1030 United States triangle. *Scientific Reports*, 9, 1663. [https://doi.org/10.1038/s41598-018-](https://doi.org/10.1038/s41598-018-38144-8)
1031 [38144-8](https://doi.org/10.1038/s41598-018-38144-8)

1032 Rothermel, E. R., Balazik, M. T., Best, J. E., Breece, M. W., Fox, D. A., Gahagan, B. I., . . .
1033 Secor, D. H. (2020). Comparative migration ecology of striped bass and Atlantic sturgeon
1034 in the US Southern mid-Atlantic bight flyway. *PLoS ONE*, 15(6), e0234442.
1035 doi:10.1371/journal.pone.0234442

1036 Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving
1037 mobile species. *Frontiers in Ecology and the Environment*, 12, 395-402.

1038 Secor, D. H. (2002). Historical roots of the migration triangle. *ICES Marine Science Symposia*,
1039 215, 323-329.

1040 Secor, D. H., Zhang, F., O'Brien, M. H. P., & Li, M. (2019). Ocean destratification and fish
1041 evacuation caused by a Mid-Atlantic tropical storm. *ICES Journal of Marine Science*, 76,
1042 573–584. doi:10.1093/icesjms/fsx241. doi:10.1093/icesjms/fsx241

1043 Sequeira, A. M. M., Rodríguez, J. P., Eguíluz, V. M., Harcourt, R., Hindell, M., Sims, D. W., . . .
1044 Thums, M. (2018). Convergence of marine megafauna movement patterns in coastal and

1045 open oceans. *Proceedings of the National Academy of Sciences*, 115(12) 3072-3077;
1046 <https://doi.org/10.1073/pnas.1716137115>

1047 Sequeira, A. M., Hays, G. C., Sims, D. W., Eguíluz, V. M., Rodríguez, J. P., Heupel, M. R., . . .
1048 Duarte, C. M. (2019). Overhauling ocean spatial planning to improve marine megafauna
1049 conservation. *Frontiers in Marine Science*, 6. <https://doi.org/10.3389/fmars.2019.00639>

1050 Sequeira, A. M. M., O'Toole, M., Keates, T. R., McDonnell, L. H., Braun, C. D., Hoenner, X., . .
1051 . Codling, E. (2021). A standardisation framework for bio-logging data to advance
1052 ecological research and conservation. *Methods in Ecology and Evolution*.
1053 doi:10.1111/2041-210x.13593

1054 Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments.
1055 *Evolutionary Ecology*, 30(6), 991-1007. doi:10.1007/s10682-016-9860-5

1056 Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement.
1057 *Movement Ecology* 8, 12. <https://doi.org/10.1186/s40462-020-0197-x>

1058 Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt,
1059 R., & Heupel, M. R. (2015). Ghosts in the data: false detections in VEMCO pulse
1060 position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry*, 3.
1061 <https://doi.org/10.1186/s40317-015-0094-z>

1062 Skomal, G. B., Braun, C. D., Chisholm, J. H., & Thorrold, S. R. (2017). Movements of the white
1063 shark *Carcharodon carcharias* in the North Atlantic Ocean. *Marine Ecology Progress*
1064 *Series*, 580, 1-16. doi:10.3354/meps12306

1065 Speed, C. W., Field, I. C., Meekan, M. G., & Bradshaw, C. J. A. (2010). Complexities of coastal
1066 shark movements and their implications for management. *Marine Ecology Progress*
1067 *Series*, 408, 275-293. <https://doi.org/10.3354/meps08581>

1068 Swearer, S. E., Trembl, E. A., & Shima, J. S. (2019). A Review of Biophysical Models of Marine
1069 Larval Dispersal. *Oceanography and Marine Biology An Annual Review*, 57, 325-356.
1070 doi:10.1201/9780429026379-7

1071 Tamario, C., Sunde, J., Petersson, E., Tibblin, P., & Forsman, A. (2019). Ecological and
1072 Evolutionary Consequences of Environmental Change and Management Actions for
1073 Migrating Fish. *Frontiers in Ecology and Evolution*, 7. doi:10.3389/fevo.2019.00271

1074 Thorson, J. T., Rindorf, A., Gao, J., Hanselman, D. H., & Winker, H. (2016). Density-dependent
1075 changes in effective area occupied for sea-bottom-associated marine fishes. *Proc Biol*
1076 *Sci*, 283(1840). doi:10.1098/rspb.2016.1853wallac

1077 Udyawer, V., Dwyer, R. G., Hoenner, X., Babcock, R. C., Brodie, S., Campbell, H. A., . . .
1078 Heupel, M. R. (2018). A standardised framework for analysing animal detections from
1079 automated tracking arrays. *Animal Biotelemetry*, 6(1). [https://doi.org/10.1186/s40317-](https://doi.org/10.1186/s40317-018-0162-2)
1080 [018-0162-2](https://doi.org/10.1186/s40317-018-0162-2)

1081 Walters Burnsed, S., Lowerre-Barbieri, S., Bickford, J., & Hoerl Leone, E. (2020). Recruitment
1082 and movement ecology of red drum *Sciaenops ocellatus* differs by natal estuary. *Marine*
1083 *Ecology Progress Series*, 633, 181-196. <https://doi.org/10.3354/meps13183>

1084 Warnock, N. (2010). Stopping vs. staging: the difference between a hop and a jump. *Journal of*
1085 *Avian Biology*, 41(6), 621-626. doi:10.1111/j.1600-048X.2010.05155.x

1086 Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-
1087 structured populations. *Annual Review of Ecology and Systematics*, 15, 393-425.

1088 Wittemyer, G., Northrup, J. M., & Bastille-Rousseau, G. (2019). Behavioural valuation of
1089 landscapes using movement data. *Philosophical Transactions of the Royal Society*

1090 *London B Biological Sciences*, 374(1781), 20180046.
1091 <https://doi.org/10.1098/rstb.2018.0046>
1092 Zhao, Q., Stephenson, F., Lundquist, C., Kaschner, K., Jayathilake, D., & Costello, M. J. (2020).
1093 Where marine protected areas would best represent 30% of ocean biodiversity. *Biological*
1094 *Conservation*, 244, 108536. <https://doi.org/10.1016/j.biocon.2020.108536>

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1111 Tables

1112 TABLE 1 List of tracked species with their annual movement type reported in the literature

1113 versus movement type assigned with hierarchical cluster analysis in this study. Elasmobranchs

1114 are listed first and then teleosts. Within these groups, species are in alphabetical order by

1115 scientific name.

Common name	Scientific name	Movement (literature)	Movement (cluster)
Spotted Eagle Ray	<i>Aetobatus narinari</i>	Seasonal	Seasonal migrant
Bull Shark	<i>Carcharhinus leucas</i>	Migratory	Migrant
Blacktip Shark	<i>Carcharhinus limbatus</i>	Seasonal	Seasonal migrant
White Shark	<i>Carcharodon carcharias</i>	Migratory	Migrant
Tiger Shark	<i>Galeocerdo cuvier</i>	Migratory	Migrant
Nurse Shark	<i>Ginglymostoma cirratum</i>	Migratory	Seasonal migrant
Lemon Shark	<i>Negaprion brevirostris</i>	Migratory	Migrant
Smalltooth Sawfish	<i>Pristis pectinata</i>	Migratory	Seasonal migrant
Great Hammerhead	<i>Sphyrna mokarran</i>	Migratory	Migrant
Rock Hind	<i>Epinephelus adscensionis</i>	Resident	Resident
Nassau Grouper	<i>Epinephelus striatus</i>	Resident	High site fidelity resident
Mutton Snapper	<i>Lutjanus analis</i>	Resident	Resident
Gray Snapper	<i>Lutjanus griseus</i>	Resident	Resident
Black Grouper	<i>Mycteroperca bonaci</i>	Resident	High site fidelity resident
Gag grouper	<i>Mycteroperca microlepis</i>	Resident males/ migrant females	Resident
Scamp	<i>Mycteroperca phenax</i>	Resident	Resident
Yellowfin Grouper	<i>Mycteroperca venenosa</i>	Resident	High site fidelity resident
Cobia	<i>Rachycentron canadum</i>	Migratory	Migrant
Greater Amberjack	<i>Seriola dumerili</i>	Seasonal	Resident
Crevalle Jack	<i>Caranx hippos</i>	Seasonal	<i>Unassigned</i>
Atlantic Bluefin Tuna	<i>Thunnus thynnus</i>	Migratory	Migrant
Atlantic Tarpon	<i>Megalops atlanticus</i>	Migratory	Seasonal migrant
Permit	<i>Trachinotus falcatus</i>	Resident	Resident

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1117 TABLE 2 Species detected, trophic niche, maximum distance travelled from tagging site in
 1118 either the Atlantic (A), Gulf of Mexico (G) or Bahamas (B), mean detection period, number of
 1119 tagged fish by life stage (I = immature; A = adult; U=unknown), maximum detection basins
 1120 (Atlantic, Keys, Bahamas, and Gulf), tags detected, proportion tagged in the Keys, and detection
 1121 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
Atlantic bluefin tuna	Apex	2,976 (A)	699	A	2	9	0	0.20
Atlantic tarpon	Meso	953 (A); 631 (G)	433	11 I, 42 A	3	53	0.79	0.60
Black grouper	Meso		449	7 I, 5 A	1	12	1	14.40
Blacktip shark	Meso	322 (G)	343	I	2	7	0	0.15
Bull shark	Apex	310 (B)	1082	3 I, 38 A	4	41	0	0.69
Cobia	Apex	434 (A)	396	A	3	20	0	0.17
Creville jack	Meso		39	A	1	24	1	
Gag grouper	Meso		448	A	1	1	1	1.15
Gray snapper	Meso		84	A	1	4	1	0.23
Great hammerhead	Apex	214 (A) 310 (B)	935	1 I, 27 A	3	28	0.14	0.50
Greater amberjack	Meso		472	A	1	5	1	0.02
Lemon shark	Meso	310 (B)	1268	A	3	8	0	0.21
Mutton snapper	Meso		348	A	1	1	1	0.30
Nassau grouper	Meso		375	A	1	5	1	3.07
Nurse shark	Meso	208 (A), 278 (B)	1090	A	2	6	0	0.47
Permit	Meso		284	9 I, 93 A	2	102	1	2.78
Rock hind	Meso		163	A	1	1	1	0.42
Scamp	Meso		110	A	1	1	1	0.40
Smalltooth sawfish	Apex	190 (G)	733	23 I, 11 A	3	34	0.29	0.68

Spotted eagle ray	Meso	322 (G) 831 (A),	715	A	2	11	0	0.01
Tiger shark	Apex	310 (B)	1004	6 I, 8 A 19 I, 11 A,	4	14	0	0.30
White shark	Apex	2,201 (A)	909	1 U	3	31	0	0.54
Yellowfin grouper	Meso		324	A	1	1	1	0.52

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1129 TABLE 3. Measures of monitoring power within categories defined by region and depth zone:
 1130 nodes, number of receivers, total area, number of unique fish detected in that area, number of
 1131 unique fish detected per receiver, total monitored area, receiver density, and mean receiver
 1132 depth. Receivers in nodes often were distributed across multiple depth zones.

Region	Depth zone	Nodes	Total # receivers	Total area (km²)	# Fish	# Fish/receiver	Total area (km²)	Receiver density (#/km²)	Receiver depth ± SD (m)
Gulf	20-40	--	0	5583	0	0	0	0	
Gulf	40-200	--	0	2581	0	0	0	0	
Gulf	10-20	1,2,3	5	3749	25	5	0.63	0.001	18.2 ± 1.60
Atlantic	40-200	26,37,38,39,40	5	3524	62	12.4	0.63	0.001	105.0 ± 44.49
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
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	0-10	10,15,21,22,24,29,31,36	65	1975	153	2.4	8.17	0.033	6.1 ± 2.15
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

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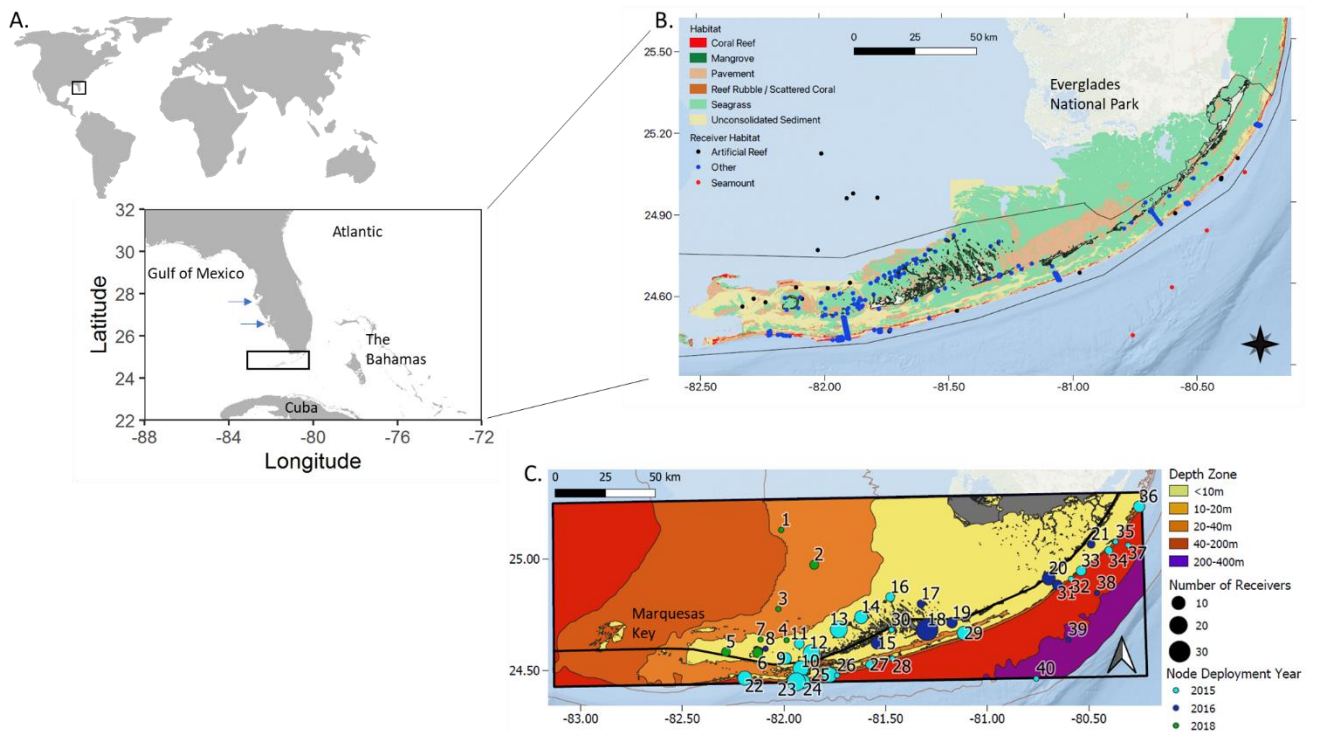
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1139 FIGURE 1 Geographic location of the study area, arrows indicate Tampa Bay (to the north) and
 1140 below that Charlotte Harbor (A); boundaries of the Florida Keys National Marine Sanctuary
 1141 (black lines), underlying habitat, and deployed receiver sites, with red markers denoting
 1142 seamount sites and black artificial reef sites (B). Habitat types were obtained from Florida
 1143 Unified Reef Tract data; (C) nodes plotted by depth zone, colored by deployment year and scaled
 1144 by number of receivers in each node. The black line along the islands and just south of
 1145 Marquesas Key denotes the boundary used to separate depth on the Atlantic versus Gulf side.
 1146 Nodes 37 through 40 are seamounts, 38=Islamorada and 40=Marathon.

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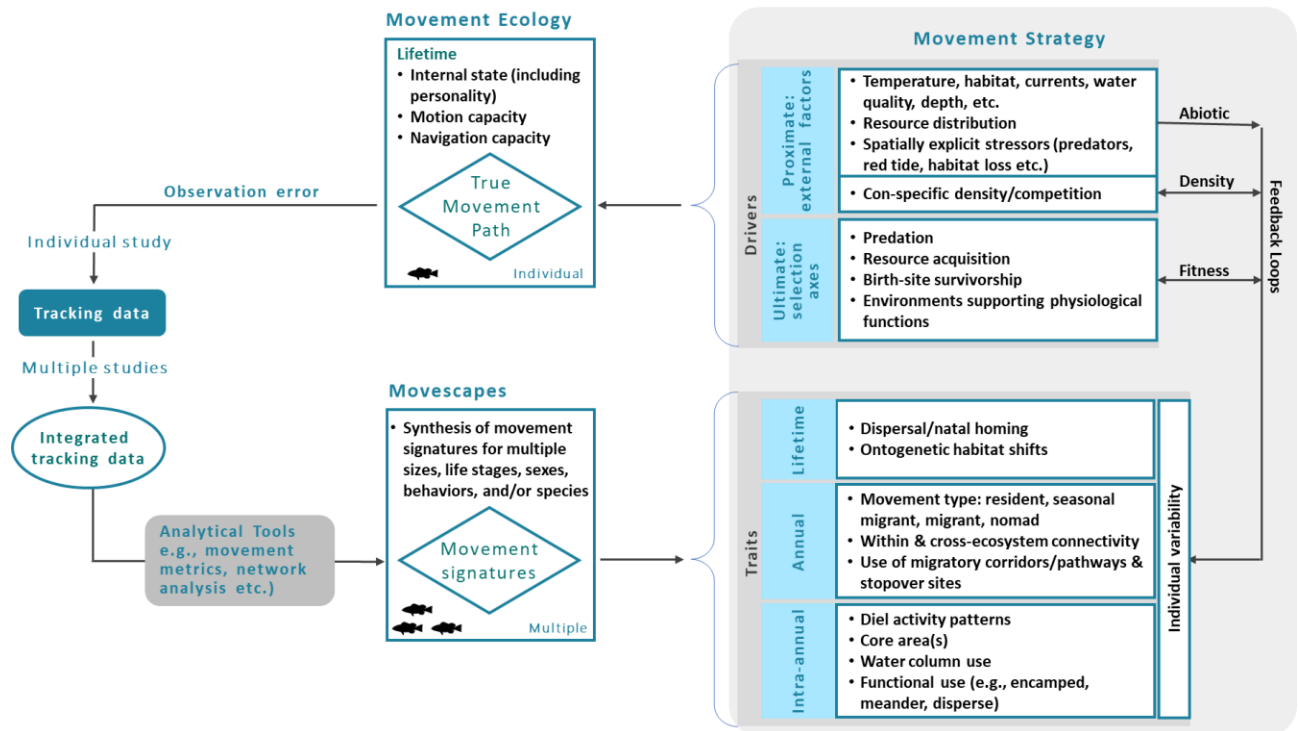
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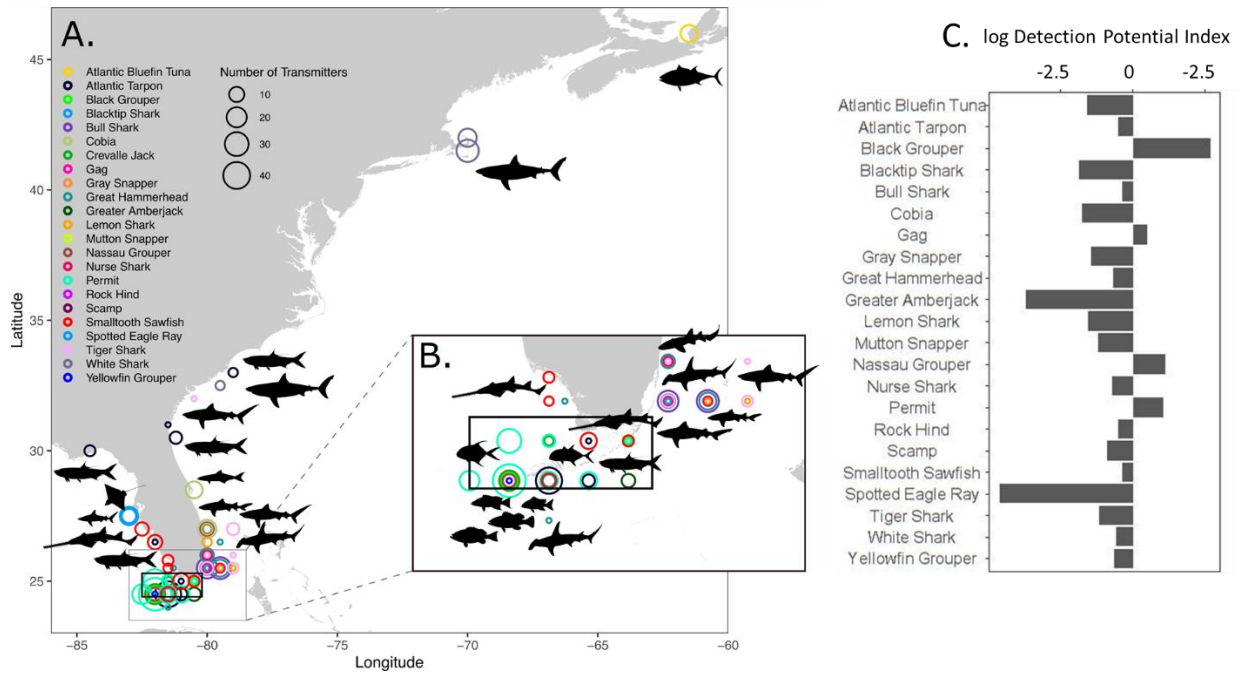
1152 FIGURE 2 A conceptual model of the proposed movement strategy framework addressing how
 1153 well tracking data reflect true movement paths, and thus the accuracy of our movement metrics
 1154 and analysis to inform species' eco-evolutionary movement strategies. These strategies are made
 1155 up of movement traits which occur at the lifetime, annual, and intra-annual time scales,
 1156 exhibiting varying levels of intra-specific variability. These characteristics are mediated by
 1157 inherited optimization end points and ecological context, with behavioral choices resulting in
 1158 both density-dependent and fitness feedback loops.



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1164 FIGURE 3 The spatial distribution of tagging sites for species detected in the study area (A) The
 1165 relative number of fish detected in this study from each tagging site is represented by marker
 1166 diameter. Fish tagged within or near the study area (B); log-scaled species-specific detection
 1167 potential (C).

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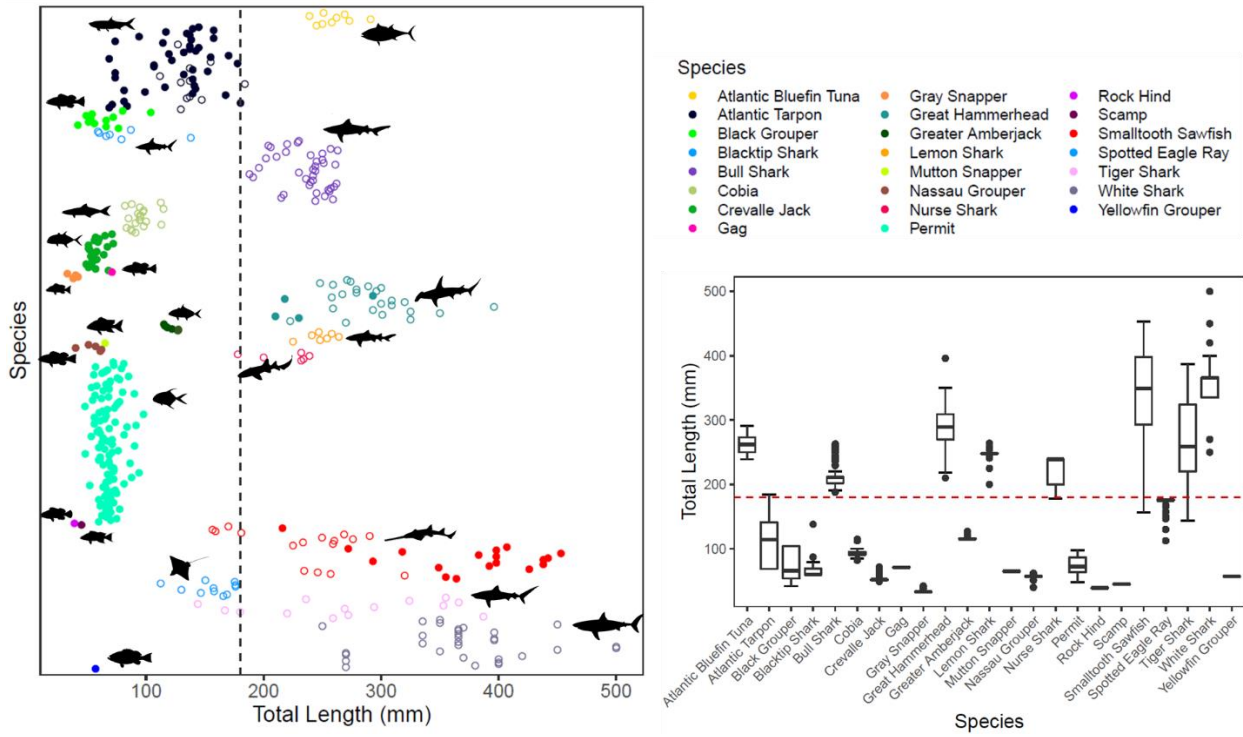
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1177 FIGURE 4 Individual (A) and summary statistics (B) for size in cm (disc width for rays; total
 1178 length for others) for species tracked in this study and dashed lines indicate the 180 cm size
 1179 threshold. In A. fish tagged within the study site are indicated by filled markers.

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1189 FIGURE 5 Dates of detection by individual and species, exhibiting variable detection periods,
1190 sample sizes, and temporal patterns.



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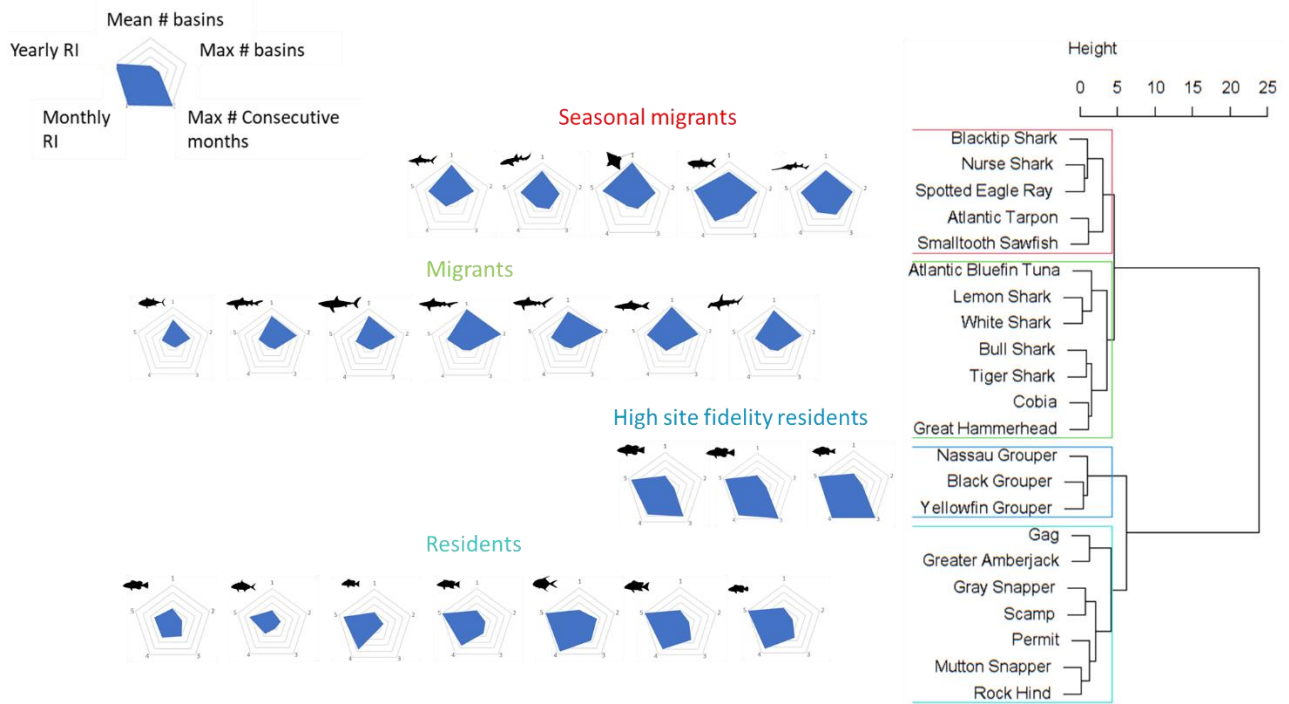
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1201 FIGURE 6 Results of the agglomerative hierarchical clustering based on maximum and mean
 1202 number of basins of detection, maximum consecutive detection months and yearly and monthly
 1203 residence indices. Also shown are species-specific radar graphs depicting the relative value of
 1204 the variables used for the cluster analysis (i.e., each variable was standardized by its maximum
 1205 for the radar plots).

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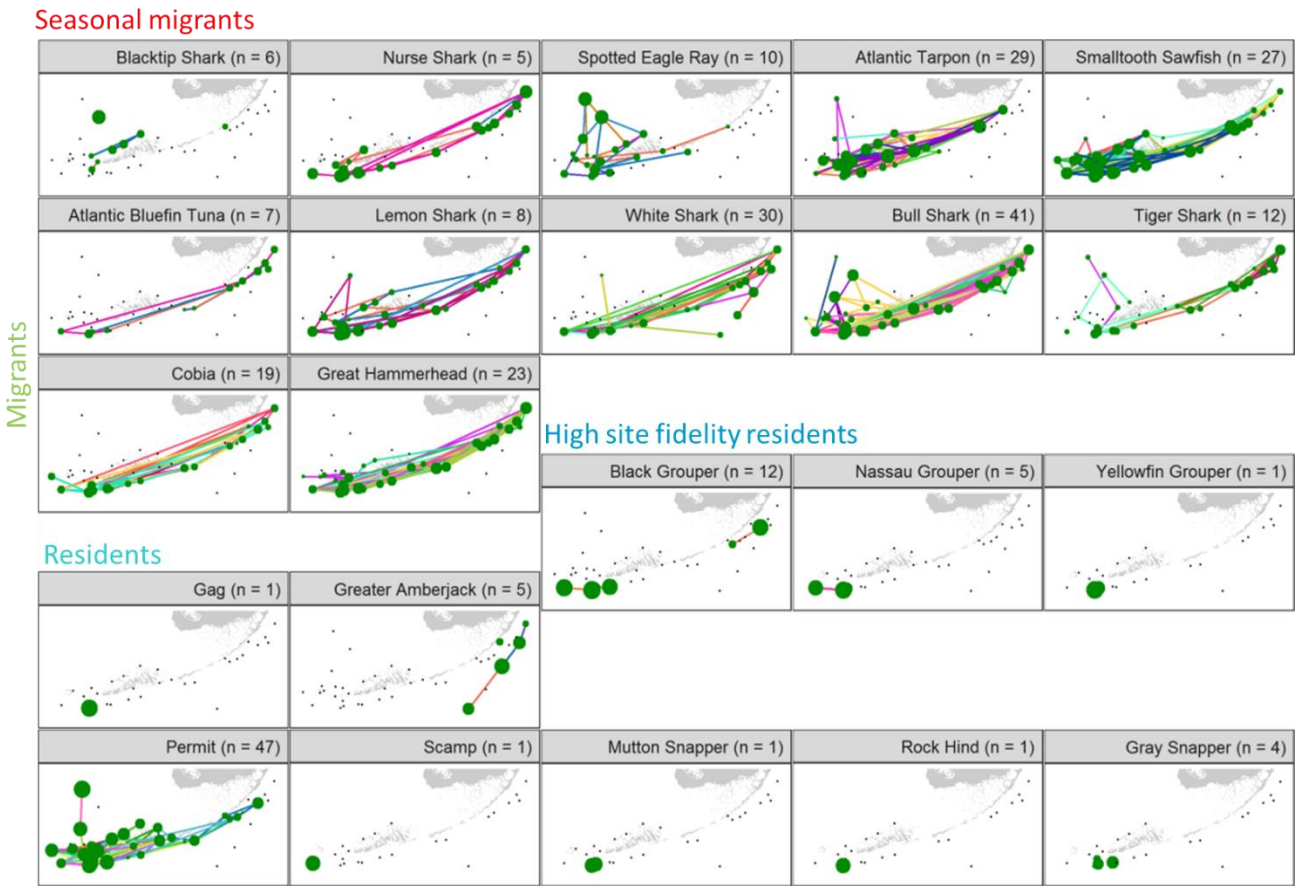
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1214 FIGURE 7 Species-specific network analysis graphs, which are grouped by annual movement
 1215 type. Sample sizes for fish with detection periods of a year or greater are indicated above each
 1216 network. Colors indicate individuals' paths. Marker size is scaled to indicate nodes with the
 1217 greatest paths for each species.

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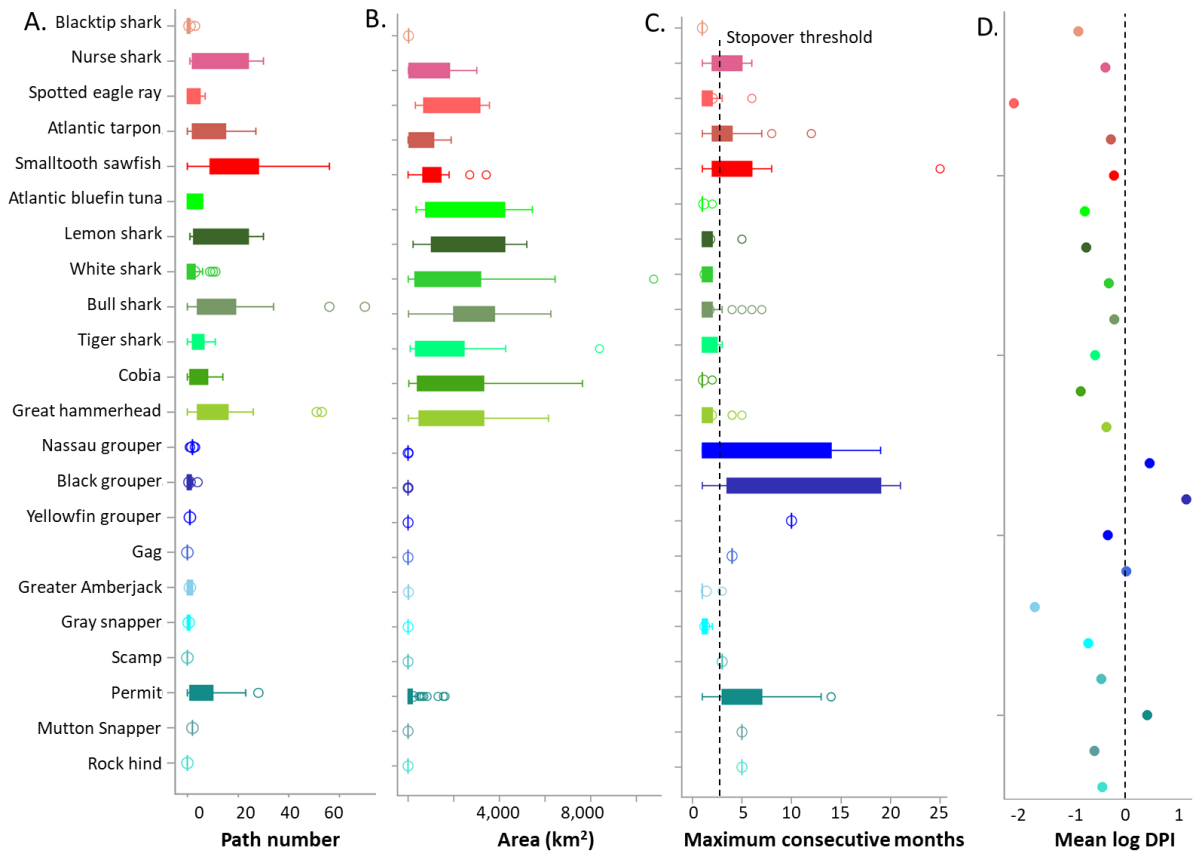
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1225 FIGURE 8 Species space use based on standard deviation ellipses (A); maximum consecutive
 1226 detection months (B); and dates of detection (C). Annual movement types are colored similarly
 1227 (reds/pinks=seasonal migrants; greens=migrants; blues=high-site fidelity residents,
 1228 aquas=resident). Crevalle jack are not represented due to their short detection periods.

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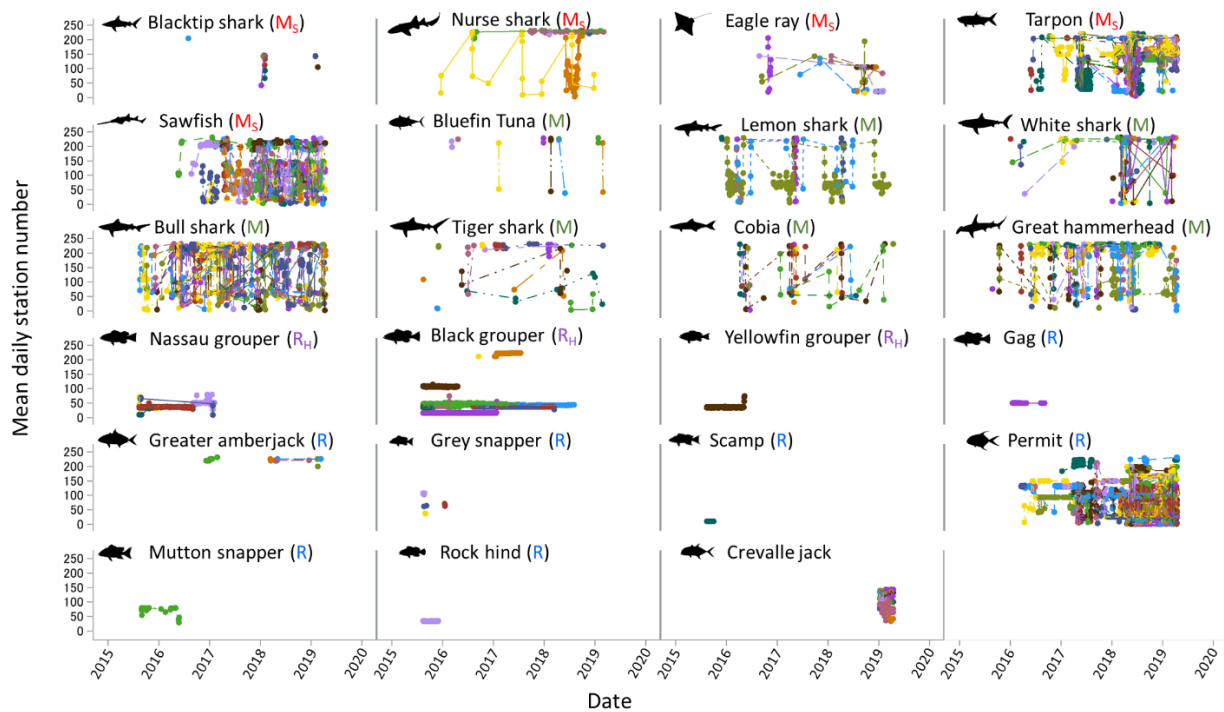
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1236 FIGURE 9 Station numbers were assigned to each receiver based on longitude, with the lowest
 1237 number representing the western-most station. This allowed us to calculate and plot mean daily
 1238 station (circles) of detection over the study period. January 1 of each year is noted on the x axis.
 1239 All detection days are connected (dashed and colored lines) to make it easier to see shifts in
 1240 location, but do not necessarily indicate a direct movement from one location to another. Site
 1241 fidelity results in horizontal lines, while rapid movement along a longitudinal gradient results in
 1242 vertical lines. Different color and line patterns were used to distinguish individual fish. Cluster
 1243 analysis movement types are indicated in parenthesis after species names (M = migrant, M_S =
 1244 seasonal migrant, R_H = high site fidelity resident, R = resident) and colored-coded.



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1249 FIGURE 10 Movement signatures of individual migrants exhibiting stopover behavior (left)

1250 versus those rapidly migrating through the study area (right). Station numbers were assigned to

1251 each receiver based on longitude, with the lowest number representing the western-most station.

1252 Mean daily station is indicated with markers, which are connected (dashed and colored lines) to

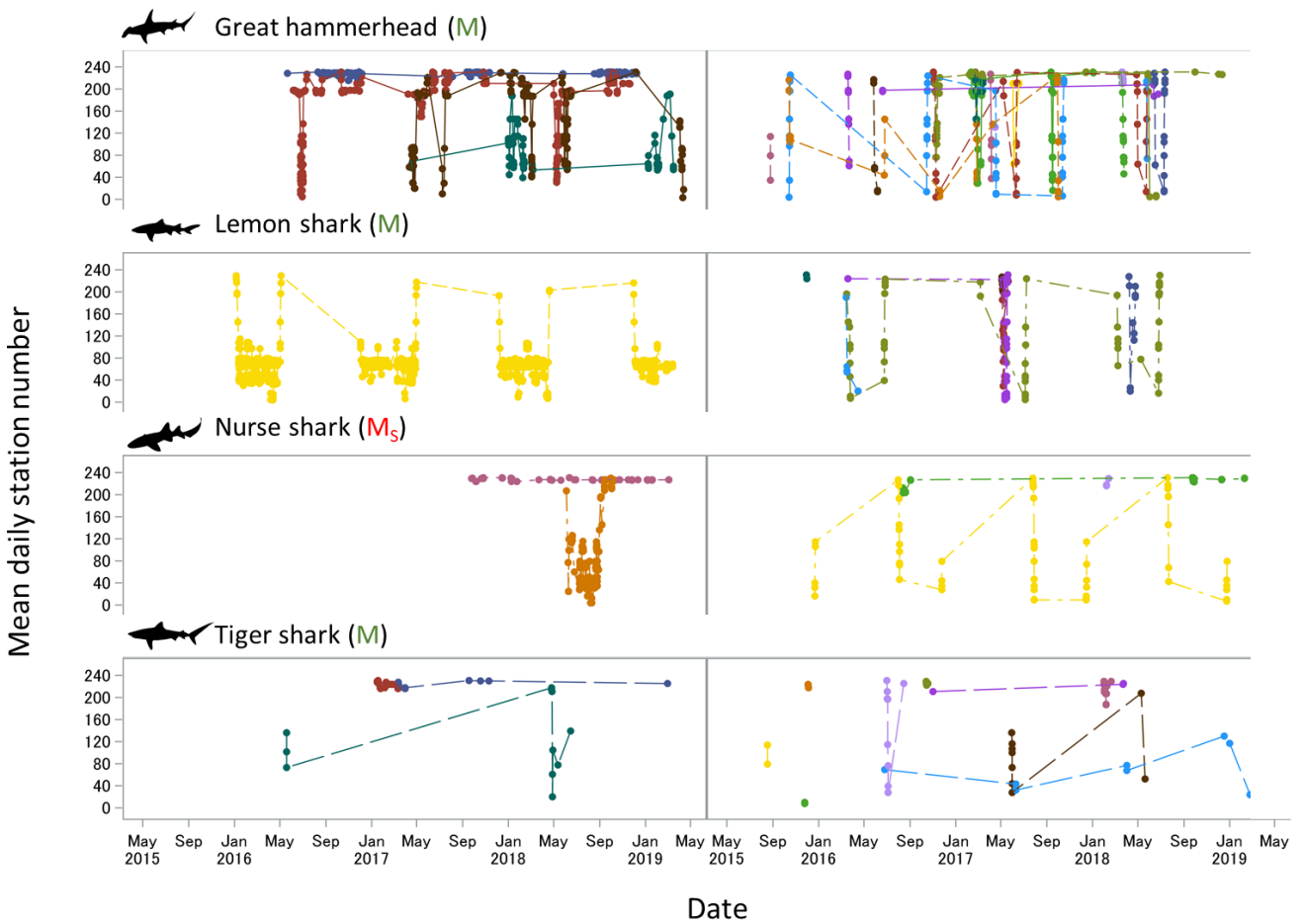
1253 make it easier to see shifts in location, but do not necessarily indicate a direct movement from

1254 one location to another. Cluster analysis movement types are indicated in parenthesis after

1255 species names (M = migrant, MS = seasonal migrant, RH = high site fidelity resident, R =

1256 resident) and colored-coded.

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