Regional scale variability in the movement ecology of marine fishes revealed by an integrative acoustic tracking network

Running page head: Multi-species movement dynamics

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Abstract

Marine fish movement plays a critical role in ecosystem functioning and is increasingly studied with acoustic telemetry. Acoustic telemetry research traditionally has focused on single species and small spatial scales. However, integrated tracking networks are building the capacity to track multiple species over larger spatial scales. In this study we conduct a synthesis of tracking data for 29 species (889 transmitters), ranging from large top predators to small consumers, monitored along the west coast of Florida, USA, over three years (2016–2018). Space use of tracked species on the west coast of Florida was highly variable, with some groups using all monitored areas and others using only the area where they were tagged, with the most extensive space use found for Atlantic tarpon *Megalops atlanticus* and bull shark *Carcharhinus leucas*. Individuals' detection patterns clustered into four groups, ranging from occasionally detected long-distance movers to frequently detected adult or juvenile residents. Synchronized alongshore, long-distance movements were found for Atlantic tarpon, cobia *Rachycentron canadum* and a number of elasmobranch species, with movement predominantly northbound in spring and southbound in fall. Detections of top predators were highest in summer, except for

nearshore Tampa Bay where the most detections occurred in fall, coinciding with large red drum *Sciaenops ocellatus* spawning aggregations. We discuss the future of collaborative telemetry work on the west coast of Florida, including current limitations and potential solutions to maximize its impact for understanding movement ecology, conducting ecosystem monitoring, and supporting fisheries management.

Key words: Acoustic monitoring, Movement ecology, Ecosystem monitoring, iTAG, Collaboration

1. INTRODUCTION

There has been a push for unified approaches to studying animal movement ecology (Nathan et al. 2008) and using movement to understand ecosystem change (Hazen et al. 2019, Lowerre-Barbieri et al. 2019) and improve fisheries management (Link et al. 2020). Movement affects vulnerability to fishing and spatially explicit stressors (Lowerre-Barbieri et al. 2019) and variation in migration, movement, or location can result in perceived changes in marine populations of interest to managers (Link et al. 2020). In particular, a better understanding of top predator spatiotemporal abundance and movement patterns, is needed because they can serve as climate and ecosystem sentinels for which monitored attributes (including movement) indicate ecosystem change (Hays et al. 2016, Hazen et al. 2019). Additionally, habitat use of top predators can directly affect abundance and behavior of lower trophic levels (Hammerschlag et al. 2012, Shoji et al. 2017), an important consideration in fisheries management as many top predator populations are under threat from fisheries (Queiroz et al. 2019), while others are showing signs of recovery from overfishing (Peterson et al. 2017). A seasonal influx of predators to an area could lead to seasonal predation mortality patterns and, if coinciding with a high-discard rate fishing season, higher-than expected discard mortality levels.

Acoustic telemetry is a valuable tool for studying movement dynamics, migration, or centers of abundance of aquatic species (Abecasis et al. 2018) and has been widely used in marine and freshwater environments (Donaldson et al. 2014, Crossin et al. 2017). Acoustic telemetry uses underwater hydrophones (hereafter referred to as receivers), typically fixed in place and arranged in space and time within a specific ‘array’ of receivers according to research objectives (Brownscombe et al. 2019). Aquatic animals outfitted with acoustic transmitters are detected by receivers when they come within detection range, usually less than 500 m (Collins et al. 2008, Kessel et al. 2014b, Mathies et al. 2014). Research applications using acoustic telemetry has included studying life history aspects such as timing and location of spawning (Lowerre-Barbieri et al. 2016, Brownscombe et al. 2020), assessing levels of discard mortality (Bohaboy et al. 2020), studying the effects of artificial reefs on site fidelity and habitat connectivity (Keller et al. 2017), examining the effects of ecotourism on behavior (Hammerschlag et al. 2017), monitoring compliance with no-fishing zones (Tickler et al. 2019), and evaluating the design of protected areas (Lea et al. 2016, Griffin et al. 2020).

Acoustic tags can be detected on any receiver that records within the frequencies transmitted by the tags. Given the mobility of aquatic species and the connectivity of aquatic systems, acoustic tags are often opportunistically detected on outside receiver arrays (i.e. those deployed in other areas by researchers tracking a different set of animals). To facilitate the exchange of data between taggers and acoustic array owners, several regional tracking networks have formed, including the Australian Integrated Marine Observing System Animal Tracking Facility (IMOS ATF), Atlantic Cooperative Telemetry (ACT), FACT (including arrays from the

Carolinas to the Bahamas), and Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) networks. These networks expand the geographic area over which tagged animals can be tracked, thereby widening the scope of individual telemetry studies. Concurrently, conglomerates such as the Ocean Tracking Network (OTN) serve as data repositories and facilitators for the various tracking networks and telemetry studies. However, there is a need to better leverage the strength of acoustic telemetry tracking networks to address the challenges facing our ocean ecosystems (McGowan et al. 2017, Abecasis et al. 2018). A number of tools exist that facilitate such retrospective analyses (Udyawer et al. 2018), but there are often large differences in array design and transmitter settings that cannot be fully accounted for in data standardization and limit the scope of the questions that can be asked of these data.

The goal of this study was to evaluate how an integrative tracking approach can provide multi-species movement data to improve our understanding of movement ecology and ecosystem processes, with a specific focus on the seasonal movements of predators off the west coast of Florida. We analyzed three years of data (2016–2018) from 21 acoustic telemetry arrays within the iTAG network in the eastern Gulf of Mexico (Gulf) to investigate the following four hypotheses: (1) array coverage needed to track a given species varies based on movements and space use of that species, (2) movements vary due to external factors, motion capacity, and navigation capacity (Nathan et al. 2008); thus species, tagging location, and life stage affect observed movement patterns (3) there is commonality among species in seasonality and directionality of movement, indicating similar underlying biophysical movement drivers, and (4) top predator detection patterns show seasonal and spatial trends. Multiple analytical approaches were used to address these hypotheses, including quantification of detection metrics, clustering analysis, and predictive modeling.

2. MATERIALS & METHODS

2.1 Study areas

Data from 21 acoustic receiver arrays belonging to the iTAG regional tracking network in the eastern Gulf were used in this analysis (details about the individual iTAG arrays can be found in Supplement 1 and Table S1.1). These iTAG arrays, deployed on the west coast of Florida (WCF) during the study period (2016–2018), all consisted of Vemco receivers capable of detecting 69 kHz acoustic transmitters. Their locations covered the range of the entire WCF, but they were not evenly distributed. Because iTAG arrays were developed to address individual study-scale objectives, they exhibited a wide range of designs, varying in receiver number (3–60) and spatial receiver distribution (e.g., gate, grid), with the finest resolution coming from arrays set up as Vemco Positioning Systems (VPS).

It was necessary to regroup some iTAG arrays' receivers to form spatially distinct units of analysis, resulting in 22 meta-arrays (referred to hereafter as arrays) used in consequent analysis (Fig. 1, Table S2.1). These arrays were further aggregated into zones for some analyses presented here, in order to reduce the spatial bias created by heterogeneity in array distribution (Fig. 1). Throughout this paper, we refer to the arrays using the following three-character naming system: sub-region (N = north Florida, T = Tampa Bay area, C = Charlotte Harbor area, S = south Florida), sequential number within sub-region, and habitat (offshore[1] = o, nearshore = n, estuarine = e, riverine = r). For example, array T3o is an offshore array in the Tampa Bay sub-region, and it is also part of the Tampa Bay array zone that includes six arrays in close proximity

[1] We define 'offshore' as being located in federal waters, greater than 9 nautical miles away from shore, and 'inshore' as locations within state waters.

in and around the estuary (Fig. 1). Lastly, although not part of the WCF, receivers in the Florida Keys (Fig. S2.1) were included in the movement analysis portion of the study to capture movements into and out of the Gulf; the Keys array was considered part of the south Florida (SFL) array group.

2.2 Detection data

Transmitter-owner information from iTAG and the neighboring ACT and FACT telemetry network databases were used to identify transmitters. Unidentified transmitters detected on at least two iTAG arrays were sent to Vemco to help identify owners and species, and transmitters were included in this study only after receiving owner permission. For fish tagged in the WCF area, each individual was assigned to a tagging group based on a unique combination of species, tagging location, and life stage (juvenile or adult at the time of tagging; *a priori* assigned by transmitter owner). This was done to address species which demonstrated residency as juveniles and large scale movements as adults. Smalltooth sawfish *Pristis pectinata* (hereafter referred to as sawfish) large juveniles (2000–3400 mm stretched total length, STL) were treated as their own tagging group, given differences in movement ecology from smaller juveniles (Brame et al. 2019). Life stages were not distinguished for species tagged outside the WCF region as their detections within the Gulf were dependent on large scale movements.

Individual tracking data were aggregated at the array spatial scale and date temporal scale (i.e., 24 hours). This allowed us to: (1) control for differences in study design (e.g., different transmitters and transmitter delay programming; different array designs), (2) align with the scope of this study to assess movement across the entire WCF rather than at small spatial scales, and (3) avoid overlap with ongoing future analyses at the species-specific study scale. Animals with a known fate of shed transmitters, or mortality (as evidenced by lack of vertical or lateral movement or change in movement signature) were removed prior to analysis, as were any animals with less than a 10-day detection period (defined as the period from tagging date or study start date, whichever came first, until last detection date on the WCF or in the Florida Keys). Two detection filters, based on R package ‘glatos’ functions (Binder et al. 2018), were used to remove potentially spurious detections before analysis: for a detection to be considered valid, there had to be at least two detections within a zone in a 24-hour period; or for VPS arrays, at least two detections on a single receiver within a 24-hour period. This stricter validation for VPS arrays was chosen to avoid including spurious detections which were more likely to occur with overlapping receiver ranges and large numbers of high site fidelity animals tagged near receivers. Detection day (DD) is defined as a transmitter detected within an array on a calendar day. If a transmitter was detected at different arrays on the same day, multiple DDs were assigned. DD data were summarized and visualized using the ‘tidyverse’ R package collection (Wickham et al. 2019).

2.3 Movement patterns

We used clustering to analyze movement patterns. Clustering was done on individual-based movement variables (see below) created from the networked telemetry data, which were first filtered for fish with potential detection periods of at least 12 months in order to evaluate the detection period for potential seasonal effects. Clustering was performed using the fuzzy C-means (FCM) clustering algorithm of Bezdek (1981) implemented in the R package ‘ppclust’ (Cebeci 2019). Two cluster validity indices were used to determine optimum cluster size for a given set of variables: the fuzzy silhouette index and modified partition coefficient index computed with the R package ‘fclust’ (Ferraro et al. 2019). The optimum number of clusters is that for which the index takes on the largest value. Clustering was done with different sets of candidate variables thought to capture the detection pattern variability among existing groups, and the final movement variables in the analysis were chosen such that both cluster validity indices agreed (Table S2.3). The four-cluster solution provided the clearest interpretability and was chosen due to the *a priori* expectation of four movement types ranging from highly resident to roaming or nomadic, similar to what has been described in the literature (Abrahms et al. 2017, Brodie et al. 2018). The resulting clusters were assigned *a posteriori* names based on movement variable distributions.

The five movement variables used in the analysis were a distance-related measure (the 99th quantile of distance traveled between successive detections), two detection frequency variables (the residence index and the 99th quantile of days between successive DD on the WCF), one seasonality indicator variable (a seasonality index), and one detection consistency index (the gap ratio defined as the 99th to 75th quantiles of days between successive DD; see Table S2.2 in Supplement 2 for variable summary statistics). Following Brodie et al. (2018), we used the 99th quantiles rather than 100th quantiles to provide better metrics of the movement data distribution. Residence index (RI) was the number of days an individual was detected on the WCF divided by the detection period. The seasonality index was calculated using time series decomposition of the number of DD per month over the detection period (see details in Supplement 2). The gap ratio is low for individuals lacking variation in temporal detection patterns and high for those characterized by periods of both increased and decreased numbers of DD, regardless of whether or not these follow a seasonal trend. For each tagging group, the proportion of individuals in each movement group was calculated, and within-tagging group variability in movement group was as estimated by calculating the deviation from the mode, which ranges from zero (no variability) to one (equal proportions).

2.4 Movement pathways

Seasonality and directionality in observed movement pathways was examined for species exhibiting long distance movements to and from the Florida Keys. Where species-specific data were insufficient, groupings of species with similar life history, movement ecology and shared taxonomy were created. This resulted in a ‘coastal sharks’ group consisting of great hammerhead *Sphyrna mokarran*, tiger *Galeocerdo cuvier*, lemon *Negaprion brevirostris*, and sandbar *Carcharhinus plumbeus* sharks. Movements were analyzed at the relatively coarse scale of calendar season[2] and zone. Even though movements were not expected to coincide perfectly with calendar season, these time bins allowed for comparisons of intra-annual patterns across species. Directed seasonal movement networks were created, and movements were classified according to alongshore directionality (northbound or southbound). To ensure the validity of seasonal comparisons, two successive observations were only counted as a movement if they occurred within a specific time period . This differed among species and was based on visual inspection of the time between DD quantiles for each group (see details in Supplement 2). Resulting cut-off values ranged from 57 days for cobia *Rachycentron canadum* to 80 days for Atlantic tarpon *Megalops atlanticus* (hereafter referred to as tarpon). Seasonal movement networks were constructed and visualized using the ‘igraph’, (Csardi et al. 2006), ‘ggplot2’ (Wickham et al. 2019), and ‘ggraph’ (Pedersen 2019) R packages.

[2] Winter = Dec-Feb, spring = Mar-May, summer = Jun-Aug, fall = Sep-Nov

Generalized linear models (GLMs) were used to detect differences in the number of movement pathways (i.e., network edges) observed by movement direction and season. For each species group, models with and without an interaction between season and movement direction were fitted. The response variable was edge weight, which was a count of the number of times a potential movement path (between two different arrays) was used. It was assumed to follow a negative binomial distribution. Since not all possible movement paths would be expected to be used by all species, a potential movement path was defined as a path that was observed to be traveled by that species, in either direction, during at least one season. Zero counts were assigned to unused potential movement paths. All models were fitted in the R package 'rstanarm' (Goodrich et al. 2020) which uses Stan (Carpenter et al. 2017) for back-end estimation. Some combinations of season and movement path direction had very low or no positive observations, causing separation in the data that led to estimation problems with standard GLMs using maximum likelihood. We, therefore, chose Bayesian inference with weakly informative priors which can help obtain stable regression coefficients and standard error estimates when separation is present in the data (Gelman et al. 2008). All models used four Markov chains with 2000 iterations each, discarding 1000 as "burn-in", and all priors were the default priors provided by rstanarm. These default priors are weakly informative, normally distributed (mean = 0, sd = 2.5). We assessed convergence by calculating the potential scale reduction ($\hat{R}$) statistic (ensuring that it was at most 1.1), inspecting trace plots, and ensuring effective sample sizes of at least 1000 for all parameters. Model fit was assessed using leave-one-out cross-validation functionality provided by the R package 'loo' (Vehtari et al. 2019), and the model with the higher weight was used for inference. Model fits were inspected graphically by conducting posterior predictive checks using the 'bayesplot' (Gabry and Mahr, 2020) and 'shinystan' (Gabry 2018) R packages.

Marginal mean effects were computed and contrasted using the R package 'emmeans' (Lenth 2019) to look for evidence of directional movement within season (pairwise contrast) and whether directional movements differed between seasons (i.e., comparing each season to the average over all other seasons). Hypothesis testing was done in the R package 'bayestestR' (Makowski et al. 2019a) by evaluating evidence for existence and significance of effects. Effect existence was assessed with the probability of direction (pd) metric, the probability that a parameter is strictly positive or negative, which is the Bayesian equivalent of the frequentist *p*-value (Makowski et al. 2019b). Any pd estimates above 97.5% were treated as strong evidence for effect existence. Effect significance was assessed by calculating and the portion of the full posterior density that falls within the region of practical equivalence (ROPE; the range of parameter values that is equivalent to zero). The ROPE range was set from -0.18 to +0.18, as is recommended for parameters expressed in log odds ratios, and values less than 5% in ROPE were considered significant (Makowski et al. 2019b). Overall, we considered an effect important if there was evidence for both effect existence and significance. We report observed trends in the data, and all explicitly stated comparisons constitute important effects.

2.5 Top predator hotspots

To test if top predator detections differed significantly by season or location, we fitted two GLMs to detection data for great hammerheads, bull *Carcharhinus leucas*, tiger, sandbar, lemon, and white *Carcharodon carcharias* sharks (individuals tagged as juveniles on the WCF were excluded to omit nursery habitat use from the analysis). The first model aimed to answer the question whether total top predator detection days varied by area (definition below) and season (DD model). The second model addressed whether the total number of unique individuals detected varied by area and season (n_{ind} model). For both models, we were particularly interested in the interaction effect between area and season. Only a few arrays had sufficient data to be included in this analysis and some needed to be combined to create four areas of comparison for this analysis: nearshore Charlotte Harbor (the C1n array), the northern shelf (arrays N1o and N2o), nearshore Tampa Bay (arrays T4n and T5n) and offshore Tampa Bay (arrays T2o and T3o). The response variable for the DD model was daily count of the number of individuals detected by area for each calendar day during the three-year study period. The response variable for the n_{ind} model was count of the number of unique individuals detected per month. Both were assumed to follow a Poisson distribution. The predictors for both models were area, season, number of transmitters available for detection, and study year (defined as December through November so as to not split winter across multiple years). Study year was included as a predictor to account for temporal changes in telemetry array configuration (most notably, the C1n array was mostly removed in 2018) and ecological effects (most notably, the exceptionally strong and long-lasting red tide event that affected coastal Tampa Bay, TB, and Charlotte Harbor, CH, areas in 2018). Number of available transmitters was included because some individuals were tagged after this study began (n_{start} = 24, n_{end} = 54). The models included interactions between area and season as well as area and study year, an offset for the number of available transmitters, and, for the DD model, a nested random effect for month within year to account for temporal autocorrelation patterns in the data. Specifying available transmitters as an offset variable results in modeling the response variable as rates rather than counts (i.e., number of animals detected per available transmitter). The models can be written as follows, where *i* represents calendar day for the DD model and month for the n_{ind} model:

$$y_i \sim Poisson(\mu_i)$$

$$E(y_i) = \mu_i \quad (1)$$

$$\log(\mu_i) = Area_i * Season_i + Area_i * StudyYear_i + \ln(Tags_i)$$

$$+ (1 \mid Year_i \,/\, Month_i) \qquad \text{(DD model only)}$$

$$Year_i \sim \mathrm{N}(0, \sigma^2_{year})$$

$$Month : Year_i \sim \mathrm{N}(0, \sigma^2_{month:year})$$

y_i is number of individuals observed per day for the DD model and number of unique individuals observed per month for the n_{ind} model and μ_i is the expected count. Models were fitted in glmmTMB (Brooks et al. 2017) which uses Laplace approximations to the likelihood via Template Model Builder (Kristensen et al. 2015). Temporal autocorrelation was checked visually using the R 'forecast' package (Hyndman & Khandakar 2008). Models were validated by simulating and testing residuals from the fitted models using the 'DHARMa' R package (Hartig 2019). Post-hoc analyses were conducted using the 'emmeans' R package, where marginal effects for the variables of interest (area and season) were calculated and contrasted to test for significance of season and study year effects within and among areas.

3. RESULTS

Detection data included in this study represent 889 fish from 29 species (Table 1). These species range in terms of management concerns from threatened species (Gulf sturgeon *Acipenser oxyrinchus desotoi*, and sawfish) to unmanaged species (hardhead *Ariopsis felis* and gafftopsail *Bagre marinus* catfish). Habitat use was similarly wide-ranging, from freshwater to offshore, with corresponding management responsibility divided between State and Federal agencies. The following list typifies the range from freshwater to a marine life cycles: the freshwater largemouth bass *Micropterus salmoides,* the diadromous common snook *Centropomus undecimalis* (hereafter referred to as snook), the primarily estuarine southern kingfish *Menticirrhus americanus*, estuarine-dependent species (e.g., tarpon and red drum *Sciaenops ocellatus*), reef fishes and elasmobranchs with estuarine nurseries (e.g., grey snapper *Lutjanus griseus* and blacktip shark *Carcharhinus limbatus*), to offshore species such as red snapper *Lutjanus campechanus* and white shark. The mean number of tagged fish per species was 31 but ranged from one fish (three species) to 163 individuals for sawfish (Table 1). Tagging dates varied over the study period, contributing to a range of detection periods from 1 to 899 days, with a relatively short mean detection period for all species (235 d).

The tracking network on the WCF varies in broad spatial acoustic monitoring coverage, array size (i.e., number of receivers) and habitat being monitored: riverine (n = 4), estuarine (n = 9), nearshore (n = 4) and offshore (n = 5) arrays (Fig. 1). Only 20% of the individuals in this study were observed in more than one zone, but these fish represented a fairly wide range of species: great hammerhead, blacktip, bull, lemon, sandbar, tiger, white sharks, tarpon, cobia, snook, goliath grouper *Epinephelus itajara*, Gulf sturgeon, red drum, sawfish, and white-spotted eagle ray *Aetobatus narinari* (hereafter referred to as eagle ray).

3.1 Large-scale space use

Fifty-five unique tagging groups were detected on the WCF (Fig. 2). Species with multiple tagging groups included: tarpon, bull shark, gag grouper *Mycteroperca microlepis*, goliath grouper, Gulf sturgeon, red drum, red snapper, sawfish, snook, blacktip shark, and eagle ray. Many tagging groups (49%) represented fish tagged within the WCF and detected on multiple arrays. Another 31% of the tagging groups were detected only in their study arrays, a pattern driven by both site fidelity and proximity of a study array to other arrays. These species included: most reef fishes, the catfishes, southern kingfish, sheepshead *Archosargus probatocephalus*, largemouth bass, and bonnethead *Sphyrna tiburo* (Fig. 2). Lastly, 18% of tagging groups were tagged outside of the WCF region, highlighting the role integrative tracking networks play for these species, which included a nurse shark *Ginglymostoma cirratum* as well as a number of top predators (great hammerhead, bull, lemon, sandbar, tiger, and white sharks), which prey on many of the resident species. The most expansive space use on the WCF was seen for adult tarpon tagging groups and bull sharks tagged in the Atlantic or CH area (Fig. 2).

3.2 Movement patterns

The four groups generated by clustering of movement variables for 554 individuals were characterized *a posteriori* as: long distance movers that were detected infrequently (‘movers’; n = 84), high-detection residents (‘HD residents’; n = 191), low-detection residents (‘LD residents’ n = 168), and ‘seasonals’ (n = 111). Both resident groups travelled short maximal distances between DD (LD residents mean 7.4 ± SE 1.45 km; HD residents mean 0.45 ± SE 0.36 km), but they differed in temporal detection patterns (Fig. 3). HD residents (represented best by red snapper, red grouper *Epinephelus morio*, and grey triggerfish *Balistes capriscus*) were detected consistently in monitored areas (gap ratio mean 1.93 ± SE 0.10, RI mean 0.91 ± SE 0.01, maximal days between DD mean 2.0 ± SE 0.11 days) whereas LD residents (represented by, e.g., some snook and largemouth bass) had less consistent temporal detections (gap ratio mean 17.0 ± SE 1.4, RI mean 0.36 ± SE 0.02, maximal days between DD mean 31.9 ± SE 2.64 days; Fig. 3; Fig. S3.1). Seasonals (represented best by eagle ray, some Gulf sturgeon, and TB red drum) had the largest seasonality index (mean 0.51 ± SE 0.02) and gap ratio (mean 49.6 ± SE 4.26). Movers (represented best by Atlantic-tagged sharks and cobia) traveled the greatest maximal distances between successive DD (mean 369 ± SE 25.2 km), had the smallest RI (mean 0.04 ± SE 0.005) and the second-highest seasonality index (mean 0.07 ± SE 0.01). Both movers and seasonals went long maximal periods without being detected on the WCF (mean 136 ± SE 15.2 days and mean 123 ± SE 10.1, respectively), but seasonals had periods of high detection frequencies in monitored areas, unlike the movers (Fig. 3; Fig. S3.1).

Intraspecific, large-scale movement patterns differed for some tagging groups but not for others. There were differences between life stages for tarpon and red drum, with the juveniles clustering as LD and HD residents while adults clustered predominantly as movers (tarpon), seasonals (TB red drum), and LD residents (CH red drum; Fig 4). In contrast, juvenile eagle ray movement patterns were like adults; both groups predominantly clustered as non-residents. However, sample size for juveniles was low (n = 2). The strongest intraspecific movement group differences among tagging groups were seen for sawfish. This difference was primarily between individuals tagged in SFL and those tagged in the CH area. SFL large juveniles (n = 3) and adults (n = 7) clustered exclusively as non-residents, while CH large juveniles (n = 13) were primarily residents. Small juveniles tagged in SFL (n = 6) clustered as seasonals and LD residents, whereas those tagged in CH (n = 77) clustered exclusively as LD or HD residents (Fig. 4). Additional species differences between tagging locations were seen for bull sharks, where all individuals tagged in the Atlantic (n = 22) but only 50% tagged off the central shelf (TB & CH, n = 4) clustered as movers. No stark differences between tagging locations were observed for red snapper or snook. Mild differences were seen for Gulf sturgeon and gag. Gulf sturgeon tagged in the Suwannee River (SR) clustered predominantly as seasonals and LD residents while those tagged further west, near Apalachicola Bay, also clustered as movers. Gag tagged in the southern offshore TB array where receivers were more densely arranged clustered predominantly as HD residents while those tagged in the northern offshore TB array, where receivers were more spread out, were evenly split between the two resident groups.

Within-tagging group variability for the 37 tagging groups in the analysis ranged from zero (for six roamer and three resident groups) to 0.833 for juvenile blacktip shark. Median variability among tagging groups was 0.444. Four tagging groups (SFL snook, SR Gulf sturgeon, TB red drum, and CH large juvenile sawfish) clustered in all four movement groups.

3.3 Movement pathways

The number of potential movement paths, number of movements, and number of individuals contributing to those movements differed among groups (Table S3.1). Number of movement paths ranged from eight for white and juvenile blacktip sharks to 38 for bull sharks, number of movements ranged from ten for white sharks to 182 for eagle rays, and the number of individuals in the analysis was lowest for white sharks (n = 7) and highest for bull sharks (n = 32). Predictions from the fitted models generally captured trends in the observed data (Fig. S3.2) The effect of movement direction on the number of observed movements differed among seasons (i.e., the season × movement direction interaction model was favored over the additive model) for all groups except juvenile blacktip shark, eagle ray, and white shark (see Tables S3.2–S3.4 in Supplement 3 for full model parameters and post-hoc test results). The overall pattern was that northbound movements dominated in spring and southbound movements in fall, winter movements were low, except for blacktip sharks, and summer patterns were more variable across species groups (Figs. 5 & 6). Cobia, bull shark, and the coastal sharks group (great hammerhead, lemon, tiger, and sandbar sharks) had more[3] northbound than southbound movements in spring, and tarpon, cobia, and bull sharks had more southbound than northbound movements in fall (Table S3.4). For tarpon, movements up the coast occurred later in the year compared to cobia, sharks, and sawfish: summer, not spring, movements differed by direction, and northbound movements were higher in summer than in other seasons. Northbound movements were higher in spring for cobia, bull shark, and sawfish and lower than in other seasons in fall for coastal sharks and sawfish (Table S3.3). More southbound movements were observed in fall than other seasons for tarpon, cobia, and bull sharks but also in summer for coastal sharks and cobia (Fig. 5). Generally, northbound movements in fall were short distance (<120 km; i.e., movement within central, north, or south Florida; Figs. 5 & 6) while those in spring were predominantly long distance for bull sharks, coastal sharks, cobia, and tarpon and short distance for the other species.

The species for which the models did not support a difference in movement direction by season were those with the fewest potential movement paths (Table S3.1). Blacktip shark had more movements in fall and winter, and fewer in summer than in other seasons, while more movements for white sharks were observed in spring than other seasons (Fig. 5, Table S3.3). No seasonal effects were supported for eagle rays.

While there was some commonality in spring and fall movement direction, there were also group-specific differences in space use that are apparent in individual movement networks (Fig. 6). For example, movement among SFL arrays occurred primarily for tarpon and sawfish, and movement to and from offshore arrays was seen primarily for bull sharks, coastal sharks, and cobia (also for white sharks; not shown). Furthermore, there was variation in movements

[3] Throughout this section, comparative language (e.g., more, higher, fewer) indicates statistically important effects whereas adjectives or superlatives (e.g., high, low, most) state an observed pattern that was not statistically important with respect to the two types of comparisons that were made (directional differences within season and seasonal differences within direction).

between species within the coastal sharks group: the only fall (southbound) movements observed were for great hammerhead (Fig. 6); southbound movements for lemon and tiger sharks occurred in summer (not shown).

3.4 Top predator hotspots

There were significant area and seasonal differences in top predator detections on the WCF. Seasonal trends were consistent across study years, while area trends differed among years. Detection days were highest in summer in north Florida (NFL), CH, and offshore TB, and highest in fall in nearshore TB (Fig. 7). Overall, the central shelf (TB & CH) had higher DD than NFL, but inter-annual variation was high, with 2018 being the lowest year for the central shelf and 2017 being the lowest year for NFL (Tables S3.7 and S3.8). The overall number of unique individuals detected was consistently highest in the offshore TB area in summer (Fig. 8). Within areas, significantly more unique individuals were detected in spring and summer offshore TB than in other seasons while nearshore TB it was spring and fall that had more unique individuals. In both TB areas, there were significantly fewer unique individuals detected in winter (Table S3.11). No significant seasonal effects were found for CH or NFL (Fig. 8). The highest number of DD across years and areas occurred in summer 2017 for the CH area, but no similar spike in the number of unique individuals was seen in that year and season (Figs. 7 & 8), suggesting repeat detections of the same individuals created the DD effect. In contrast, the detection data indicated that more unique individuals visit the offshore TB area each summer, with fewer DD per individual, either because they spend less time there or are present but not detected as frequently (see Tables S.3.45–S.3.12 in Supplement 3 for model parameters, diagnostics, and marginal means comparison results).

4. DISCUSSION

This study used collaborative acoustic telemetry data from the iTAG network to show that (1) space use of tracked species on the WCF was highly variable, with some groups using all monitored areas and others using only the area where they were tagged, (2) telemetry-derived movement types differed among tagging groups (life stage and tagging location) for some but not all species, but differences between tagging locations cannot be conclusively attributed to biological differences due the confoundment of observation and process effects, (3) there was commonality in seasonal movement directionality for tarpon, cobia, bull sharks, coastal sharks, and sawfish moving primarily northward in the spring and southward in the fall, and (4) top predator detections showed consistent spatiotemporal patterns that differed between season and area.

4.1 Large-scale space use

The value of iTAG for monitoring highly migratory species was expected and confirmed in this study. Additionally, we showed that the tracking network helps to fill data gaps in movement information for species monitored in a specific area for part of their annual migration or during early life stages. This includes species with strong seasonal patterns such as eagle ray, red drum, and Gulf sturgeon; movers such as tarpon; and juvenile elasmobranchs such as blacktips, bull shark, and sawfish as they leave their nursery areas and transition from residents to a different movement pattern. The network allows researchers studying these animals to ask new questions they would not have otherwise been able to ask (Griffin et al. 2018).

Individuals tagged outside the WCF that have observations in this data set were almost exclusively tagged in the Atlantic (including the east coast of Florida, the Bahamas, and the northeastern U.S.A.). The only individual in this data set tagged in the western Gulf was a sandbar shark. This is probably due in part to the greater acoustic tagging effort in the Atlantic than the western Gulf, but also the observed pattern of a biogeographical break between the eastern and western Gulf (Chen 2017), with many fish in the western Gulf migrating south to Mexico rather than east toward the WCF (Rooker et al. 2019).

There was a somewhat surprising lack of reef fish detections, particularly red snapper, among arrays located near the Gulfstream pipeline. Pipeline construction created artificial hard bottom habitat on and near the pipeline as part of the damage mitigation process from pipeline construction. It was hypothesized that the pipeline and these artificial hardbottom spots could contribute to the expansion of red snapper into the eastern Gulf by serving as steppingstones (Cowan et al. 2011). Red snapper were tagged on three offshore reefs near the pipeline (arrays N1o, N2o, and T1o), but none of the over 300 tagged red snapper were detected anywhere but on their study arrays. Perhaps receiver arrays in closer proximity to each other along the pipeline artificial reefs can help resolve the question of whether red snapper do use them as stepping stones for range re-expansion to areas occupied prior to intense fishing, or perhaps the three-year time period used in this synthesis was insufficient to detect such movement.

4.2 Movement patterns

Multi-species clustering of movement patterns would not be possible with data from only a small number of arrays. The results of the clustering analysis are dependent on the spectrum of movement ecologies represented in the sample of tagged animals as well as the observation system in place, and of course the variables included in the analysis. We found that results were sensitive to the choice of clustering variables, a result also reported in studies conducting similar analyses (Brodie et al., 2018). Even though there were a number of differences in our movement type clustering analysis compared to Brodie et al. (2018) (different systems, different movement variables, shorter study period, fewer species and tagged individuals), three of the four groups generated in this study were equivalent to those reported in the Australian study ('HD residents' ≈ 'residents', 'LD residents' ≈ 'occasionals', and 'movers' ≈ 'roamers'). Our 'seasonals' group was not previously reported, which is not surprising given that we used a seasonality index variable specifically to distinguish that group. It should be noted here that many individuals or entire groups that clustered as movers in our analysis are known to undertake seasonal migrations to and from the Gulf (Biesiot et al. 1994, Reyier et al. 2014, Skomal et al. 2017) but detections were so infrequent that they could not be distinguished from more nomadic movement patterns. Our analysis identified individuals that spent a lot of time in areas with acoustic monitoring coverage (e.g., eagle ray) when seasonally present on the WCF, whereas movers seasonally often travel even further into the Gulf and spend less time in monitored areas, perhaps also using habitats in deeper waters without acoustic monitoring coverage.

Networked telemetry data extends the spatial scope of observation but at the cost of disparate observation capacity between monitored regions. Changes to the telemetry infrastructure, especially the kinds that would allow more detections along migratory routes, could change the set of variables needed to discriminate amongst movement groups. Thus, movement type clustering is a snapshot in time and results must be interpreted with care, as apparent intraspecific variability in movement patterns may be due to the observation infrastructure and not true population trends. For example, receiver density is likely what was driving the differences between movement types (as high vs. low detection residents) for gag tagged in two different offshore TB areas. Similarly, the observed differences in movement patterns between tagging locations for sawfish are likely due to a combination of ontogenetic changes in habitat use, sample size, habitat complexity, and receiver density. A total of 84% of the 89 sawfish tagged in the Charlotte Harbor estuarine system were small juveniles (< 2 m STL), known to spend most of their time within their natal estuarine nurseries, some of which include extensive creek and canal habitats (Poulakis et al. 2013, 2016, Scharer et al. 2017). As individuals exceed 2 m STL, they begin leaving the nurseries and moving to and from SFL (Graham et al. In press) where fewer fish (n = 16) were tagged and included in the clustering analysis, and most (n = 10, 62.5%) were > 2 m. Consequently, within the CH area, where there were two dense arrays of receivers compared to SFL, some small juveniles were almost constantly within receiver range and clustered as HD residents, while other small juveniles as well as large juveniles, went undetected for longer periods and clustered as LD residents. These apparent differences in movement ecology by tagging location identified in this study highlight the limitations of this multi-species approach and show that detailed knowledge of local arrays and species-specific research is needed to address nuances in the data (e.g., habitat complexity), to validate the results and fully understand complex life histories that encompass the entire eastern Gulf and beyond.

4.3 Movement pathways

The seasonal large-scale movement patterns reported here are congruent with existing literature. Tarpon generally move north in spring and summer, and south in fall (Luo et al. 2020) and cobia move from the Florida Keys into the northern Gulf in spring (Franks et al. 1999).

Large juvenile and adult sawfish are known to undergo seasonal migrations, consisting of spring and summer northward and fall and winter southbound movements (Graham et al. In press), and seasonal, temperature-related residence patterns for sharks have been described off southeast Florida (Kessel et al. 2014a, Hammerschlag et al. 2015, Guttridge et al. 2017). Large sharks are found in deeper waters in fall and winter (Ajemian et al. 2020), which is consistent with the reduced movements we found in those seasons, as deep-water sites are poorly monitored.

Our analysis failed to detect statistically relevant differences in movement direction by season for juvenile blacktips and white sharks. This was surprising given that previous research revealed seasonal movements into the Gulf in winter and spring for white sharks (Skomal et al. 2017), and previous tag-recapture data also suggested a pattern of seasonal movements for WCF juvenile blacktip sharks (Hueter et al. 2005). Our results are most likely attributable to low sample sizes, suggesting the WCF telemetry network did not adequately monitor long-distance migrations for those species or not enough tagged individuals were available for detection during our study period. Unlike cobia, which had an equal ratio of south to northbound movements in the data, one movement direction exceeded the other one by a factor of two for blacktips and white sharks. It is unclear whether this skew in the data is an artifact of low sample size or represents a real trend of systematically failing to detect directional movements. Juvenile blacktip sharks are vulnerable to predation and fishing mortality in the nursery (Heupel & Simpfendorfer 2002). Mortality rates on their migratory routes may also be high, which might be partially responsible for more observed movements leaving the nursery and heading south than returning back north. White sharks might use deeper waters with little receiver coverage when migrating from the Gulf back to the Atlantic resulting in fewer records of those movements in the telemetry data.

Additional factors that could lead to failure to detect interaction effects are 1) individual variation in timing of migrations that could, at the population level, give the appearance of bidirectional movements in the same season, and 2) inclusion of shorter distance, within-season movements (particularly between the TB and CH areas) that may or may not be part of long-distance migration tracks. Those factors likely contributed to the finding of no significant movement direction effects for eagle rays. Eagle rays are known to occur off the west coast of Florida in spring, summer, and fall, and are hypothesized to migrate to offshore and southern areas when water temperatures decrease (Bassos-Hull et al. 2014). There was a lot of individual variability in eagle ray movement direction but inspection of seasonal eagle ray movement networks revealed patterns that the GLM was not set up to detect: a latitudinal progression of movement activity, from the southern part of the coast in winter to the northern part in summer (Fig. S3.3).

The commonality in movement directionality over coarse spatiotemporal scales observed for tarpon, cobia, and most elasmobranchs supports the existence of shared biophysical movement drivers. Although identifying the precise drivers is beyond the scope of this study, some likely contributors are temperature, which is known to be a major factor for ectothermic organisms (Lear et al. 2019b), reproduction (i.e., movement to and from spawning, mating, and nursery areas), foraging (Lear et al. 2019a), and predation. Some sharks likely follow the migration routes of their prey, a phenomenon called migratory coupling (Furey et al. 2018), others change their movements in response to reef fish spawning aggregations (Pickard et al. 2016, Rhodes et al. 2019), and, while most potential shark prey species prefer to avoid their predators, some, such as cobia, are known to associate with large elasmobranchs (Shaffer & Nakamura 1989).

4.4 Top predator hotspots

We found seasonal trends of top predator detections that differed by area and were consistent across study years. Top predator DDs were highest in most analyzed areas in the summer, which is consistent with the finding of movement from the Florida Keys into the Gulf in spring. Nearshore TB was the exception to the pattern in that fall was the season of highest detections. This could be driven by the large red drum spawning aggregations that form in fall at the mouth of TB (Lowerre-Barbieri et al. 2018) which also attract smaller shark species such as blacknose shark *Carcharhinus acronotus* (pers. obs., J. Bickford). A seasonal influx of predators into the Gulf could result in seasonally fluctuating predation rates, resulting in high depredation levels in high-discard recreational fisheries, such as red snapper. The federal recreational red snapper season is in the summer, coinciding with highest shark detections on the WCF.

While we have provided evidence for predictable spatiotemporal fluctuations in predator presence on the WCF, quantifying any potential predation effect to be useful for management would require further study and the use of additional tools and data sources (Hammerschlag 2019). For example, Bohaboy et al. (2020) used fine-scale movement monitoring in a high-resolution acoustic telemetry array to estimate that 83 % of red snapper and 100 % of grey triggerfish discard mortality was due to predation by large pelagic predators. Predator-prey interactions could also be studied with predation transmitters (Halfyard et al. 2017) or Vemco Mobile Transceivers (Haulsee et al. 2016). In addition, there could be other areas on the WCF that are important shark hot spots but are currently not acoustically monitored, particularly in deeper waters. Spatial fisheries-dependent and independent data could be evaluated to determine potential locations for additional arrays to expand top predator monitoring capabilities.

Long-term monitoring of inter-annual differences in movements and space use is needed to understand ecosystem health. In order to make temporal comparisons from networked telemetry data, consistency in telemetry infrastructure over time is needed. Without this consistency, process and observation effects become confounded in the data. We explicitly considered year effects in analyzing spatiotemporal top predator detection patterns, and there are process as well as observation factors explaining the strong inter-annual differences we observed. Of the three years analyzed, 2018 stood out as having lower DD in all central Florida areas. This was the year of an abnormally strong and long-lasting red tide event that affected nearshore central Florida. Unfortunately, the removal of receivers from the nearshore CH array and offshore TB arrays in 2018 made it impossible to attribute this effect to red tide in those areas. The nearshore TB array, however, was mostly consistent across years and the reduction in DD and number of unique individuals detected here in 2018 should not be due to changes in observation capacity, making it likely that this was a signal from the red tide event.

One noteworthy caveat of the movement paths and predator hot spots GLMs we fitted is that the data consisted of repeated observations of the same individuals, thereby violating independence assumptions. Repeated observations of the same individuals could give the appearance of strong population trends that may or may not hold if sample size was increased.

5. CONCLUSIONS

Fisheries science, like other sciences, is assessing how best to use the emerging field of “technoecology” (Allan et al., 2018) and incorporate non-extractive sampling into standard monitoring schemes. Telemetry networks collect extensive information about the movements of tagged marine animals, but the value of networked telemetry data synthesis studies to practical fisheries management is very limited at this point. This is for two reasons. First, changes in detectability over time cannot currently be separated from changes in behavior due to frequent changes in array configuration. Unlike Australia's IMOS ATF, the WCF currently does not have any state, federal, or consortium-funded permanent receiver arrays in place. A network of strategically placed, permanent receivers would enable temporal comparisons of movement patterns and space use without the confounding influences of changing observation capacity. Second, the fisheries assessment and management process is currently not capable of accepting outputs from telemetry studies, much less telemetry syntheses, unless these outputs come packaged in the form of a standard stock assessment parameter such as natural mortality. Changing this will likely require the system to move beyond management based on maximum sustainable yield and its analogues, and there are currently no operational alternatives.

Telemetry synthesis studies have potential value for ecology that is yet to be fully realized. If done unplanned and without consistent telemetry infrastructure, options are largely limited to exploratory data analysis methods such as clustering and pattern recognition, which perhaps confirm what is already known but can also lead to hypothesis development. For example, future research questions inspired by our work include: (1) Are spawning aggregations the drivers of a seasonal predator influx to the WCF?; (2) Are there seasonal, spatially specific fluctuations in predation mortality of WCF resident fishes?; (3) Are the differences between high-and-low site fidelity residents observed in this study artifacts of the observation system or do they reflect true behavioral differences within populations?; and (4) How can observation effects (e.g., differences in spatiotemporal detection probability over time) be formally incorporated into inference from networked acoustic telemetry data? For iTAG it fully realize its potential for hypothesis-driven ecological inquiry will necessitate long-term funding to support standardized monitoring infrastructure, coordinated multi-species tagging, a Gulf-wide database, and the personnel needed to oversee membership, database management, workshops, and the website (https://itagscience.com).

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Tables

Table 1. Species detection summary. Detection day metrics are transmitter-based. DD = detection days, DP = detection period.

Common Name	Scientific Name	Number of Transmitters	Total DD	Mean DD	Mean DP
Atlantic tarpon	*Megalops atlanticus*	34	2,101	62	274
Blacktip shark	*Carcharhinus limbatus*	17	1,431	84	245
Bonnethead	*Sphyrna tiburo*	4	78	20	63
Bull shark	*Carcharhinus leucas*	40	1,351	34	471
Cobia	*Rachycentron canadum*	18	84	5	202
Common snook	*Centropomus undecimalis*	126	17,264	137	316
Gafftopsail catfish	*Bagre marinus*	12	413	34	117
Gag grouper	*Mycteroperca microlepis*	29	2,686	93	119
Goliath grouper	*Epinephelus itajara*	14	951	68	106
Great hammerhead	*Sphyrna mokarran*	17	1,363	80	134
Greater amberjack	*Seriola dumerili*	44	3,948	90	106
Gray snapper	*Lutjanus griseus*	5	50	10	255
Grey triggerfish	*Balistes capriscus*	13	1,749	135	136
Gulf sturgeon	*Acipenser oxyrinchus desotoi*	82	7,341	90	400
Hardhead catfish	*Ariopsis felis*	8	84	11	100
Largemouth bass	*Micropterus salmoides*	45	3,830	85	284
Lemon shark	*Negaprion brevirostris*	2	48	24	809
Nurse shark	*Ginglymostoma cirratum*	1	1	1	1
Red drum	*Sciaenops ocellatus*	44	1,704	39	303
Red grouper	*Epinephelus morio*	26	11,238	432	499
Red snapper	*Lutjanus campechanus*	91	13,672	150	156
Sandbar shark	*Carcharhinus plumbeus*	2	10	5	25
Scamp	*Mycteroperca phenax*	1	106	106	106
Sheepshead	*Archosargus probatocephalus*	1	262	262	274
Smalltooth sawfish	*Pristis pectinata*	163	18,164	111	210
Southern kingfish	*Menticirrhus americanus*	3	152	51	111
Tiger shark	*Galeocerdo cuvier*	3	27	9	440
White shark	*Carcharodon carcharias*	11	40	4	113
White-spotted eagle ray	*Aetobatus narinari*	33	3,067	93	428

Figure captions

Figure 1. Map of Florida with west coast array locations indicated by circles. Symbol sizes are proportional to the number of receivers in each array. Also shown are the state-federal waters boundary (thin black line), path of the Gulfstream gas pipeline (dotted line), and 200 m isobath (thick black line). Arrays grouped into the same zone due to spatial proximity are within boxes. See table S1.1 for corresponding iTAG array numbers.

Figure 2. Overview of tagging groups detected on west coast of Florida acoustic telemetry arrays between 2016 and 2018. Species is indicated on the left (with down arrows indicating the same species as the one above the arrow) and tagging location and life stage, if not adult, are identified on the right. The number of detected transmitters in each tagging group is shown in parentheses. Box color indicates proportion of detection days (min = $9x10^{-5}$ = white; max = 1 = dark blue). Boxes with bold black borders indicate the study array for that tagging group; general tagging locations are shown with hashes. Arrays are ordered on the x-axis by geographic location, with the northwestern most array on the far left and the southernmost on the far right. CH = Charlotte Harbor, NFL = north Florida, SFL = south Florida, TB = Tampa Bay, ATL = Atlantic, MS = Madison-Swanson, SR = Suwannee River, DT = Dry Tortugas, PL = Pipeline, WGOM = western Gulf of Mexico, EGOM = eastern Gulf of Mexico.

Figure 3. Distribution of covariates for movement pattern clustering analysis. The horizontal line is the median, upper and lower hinges show the 25^{th} and 75^{th} percentiles, and whiskers extend from the hinge to the smallest (lower) and largest (upper) value no further than 150% of the interquartile range; values outside that range are separate. Groups are M = low-detection, long

distance movers, S = seasonals, LR = low-detection residents, HR = high-detection residents. Max time is the 99^{th} quantile of days between successive detection days, distance is the 99^{th} quantile of kilometers between successive detection days, and the detection consistency index is the ratio of 99^{th} to 75^{th} quantiles of days between detection days.

Figure 4. Movement pattern clustering results by tagging group showing the proportion of animals (within tagging group) in each movement group. The scale ranges from zero (white) to one (black). Species is indicated on the left axis (with down arrows indicating the same species as the one above the arrow) and tagging location and life stage (if not adult) are identified on the right. Groups are M = low-detection, long distance movers, S = seasonals, LR = low-detection residents, HR = high-detection residents. Numbers in parentheses indicate number of transmitters included in the analysis for each group. Of the 889 animals included in this study, 548 were included in the movement network analysis; most of the censoring occurred due to insufficient potential detection periods (≤12 months). Only tagging groups represented by at least two animals are shown. CH = Charlotte Harbor, NFL = north Florida, SFL = south Florida, TB = Tampa Bay, ATL = Atlantic, MS = Madison-Swanson, SR = Suwannee River, PL = Pipeline, EGOM = eastern Gulf of Mexico.

Figure 5. Mean number of observed movements (bars) and standard deviations (error bars) by species or species group, season, and movement direction, relative to the maximum for each group. (a) = juvenile and adult bull shark, (b) = juvenile and adult coastal sharks (great hammerhead, sandbar, lemon, and tiger sharks), (c) = cobia, (d) = adult Atlantic tarpon, (e) = large juvenile and adult smalltooth sawfish, (f) = juvenile and adult white shark, g = juvenile

blacktip shark, (h) = juvenile and adult white-spotted eagle ray. n_p = number of unique potential movement paths. Generalized linear models were fitted to number of movements (see methods for details) for each group and results from *post-hoc* comparisons of marginal means are indicated where there was strong evidence for both existence (probability of direction > 97.5%) and significance (<5% in region of practical equivalence) of effects (see Tables S3.1-S3.3 for full model results): panels highlighted with grey backgrounds indicate seasons within which the marginal means between northbound and southbound movements differed, and asterisks mark the season for which a marginal mean for the indicated movement direction (blue = south, red = north) differed from the mean over the other seasons. Bicolored asterisks were used to note seasons that differed for those models where the data did not support direction-specific seasonal effects. Every group was observed on west coast of Florida arrays in every season, even though movements, as defined in this study, were not observed for every season-group combination.

Figure 6. Spring (left panel) and fall (right panel) movement networks for groups with season-specific movement direction differences. (a) = juvenile and adult bull shark, (b) = juvenile and adult coastal sharks (great hammerhead, sandbar, lemon, and tiger sharks), (c) = cobia, (d) = adult Atlantic tarpon, (e) = large juvenile and adult smalltooth sawfish. Arrays in zones were grouped to focus on longer distance movements. Southbound movements are drawn in straight, blue lines and northbound movements in curved, red lines. Node color is indicative of network degree, with darker shades indicating higher degree (degree calculations included consecutive detections days at the same array, which are not shown). Line width corresponds to edge weight (number of times a path was used). Species contributing to the spring movement paths for the

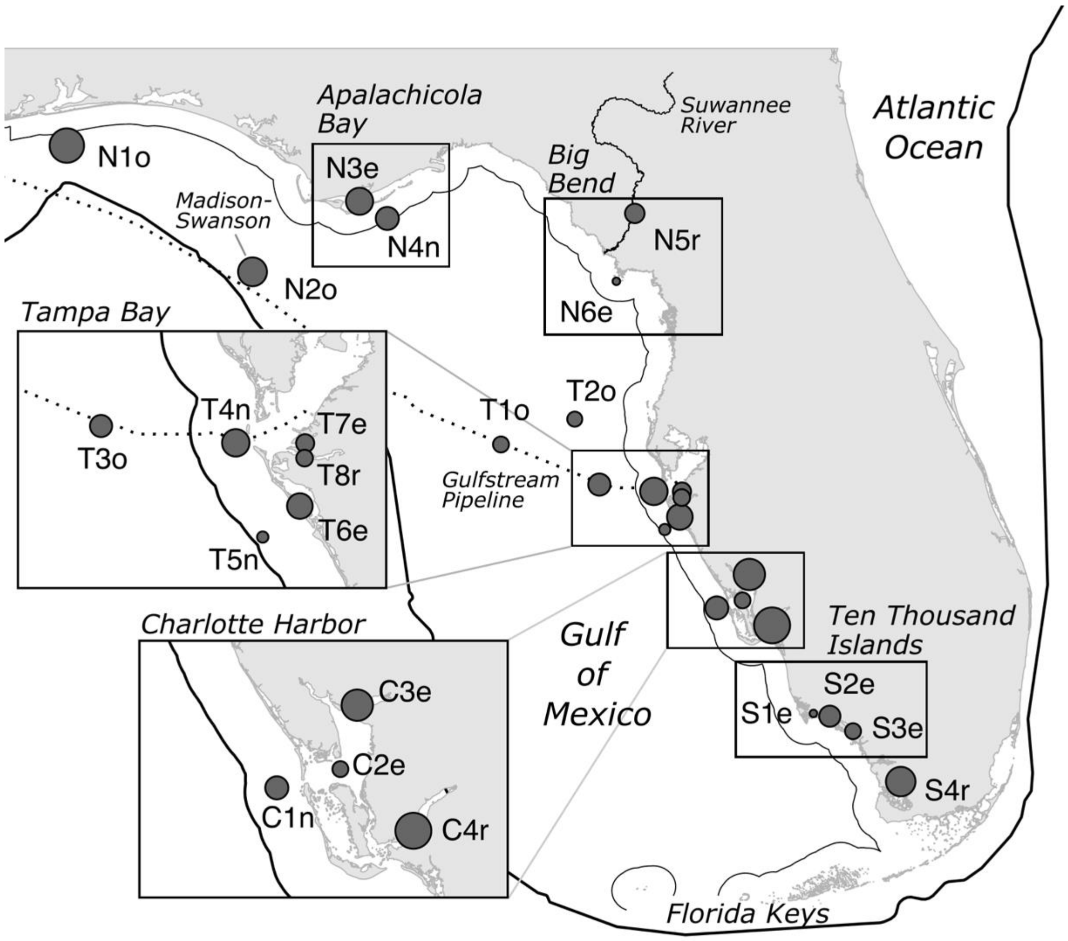
sharks group were (great hammerhead, tiger, and lemon sharks), while only great hammerheads were detected moving in fall.

Figure 7. Observed (grey bars) and predicted (boxplots) number of top predators (great hammerheads, bull, white, tiger, sandbar, and lemon sharks; excluding juveniles tagged on the west coast of Florida) detected per day, summed by season and averaged over study year. Within area, seasons that had significantly ($p \leq 0.05$) lower detection days are indicated by blue boxplots, those with significantly higher estimates are red, and significantly higher or lower study years are highlighted with > and <, respectively (<< = $p \leq 0.01$, < = $p \leq 0.05$, < = $p = 0.055$).

Figure 8. Observed (grey points) and predicted (boxplots) number of unique top predator individuals (great hammerheads, bull, white, tiger, sandbar, and lemon sharks; excluding juveniles tagged on the WCF) detected per month, averaged over study year. Within area, seasons that had significantly ($p \leq 0.05$) lower unique individuals detected are indicated by blue boxplots, those with significantly higher estimates are red, and significantly higher or lower study years are highlighted with > and <, respectively (<< = $p \leq 0.01$, < = $p \leq 0.05$).

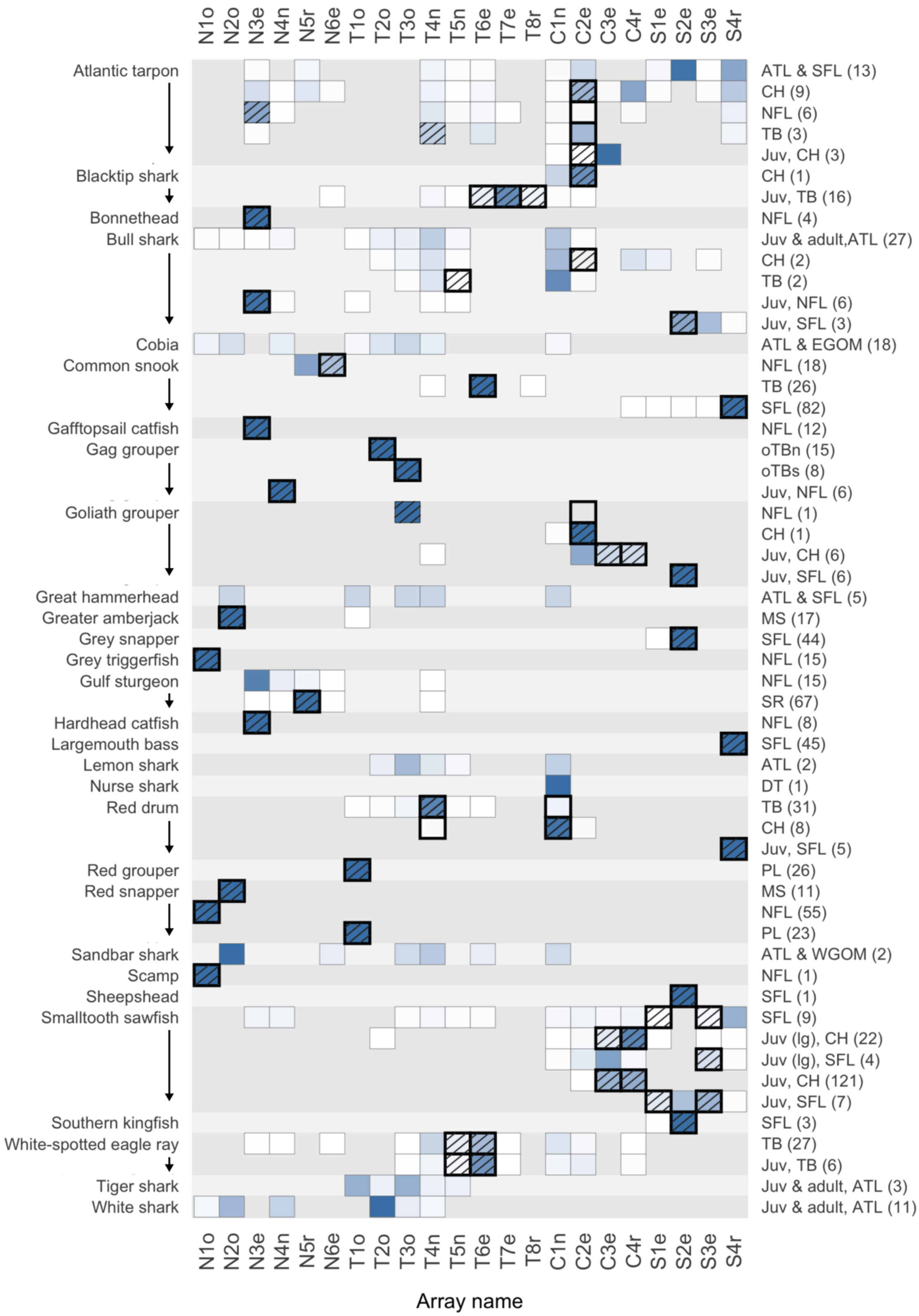
1 **Figures**

2



3

4 Figure 1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Atlantic tarpon
Blacktip shark
Bonnethead
Bull shark
Cobia
Common snook
Gafftopsail catfish
Gag grouper
Goliath grouper
Great hammerhead
Greater amberjack
Grey snapper
Grey triggerfish
Gulf sturgeon
Hardhead catfish
Largemouth bass
Lemon shark
Nurse shark
Red drum
Red grouper
Red snapper
Sandbar shark
Scamp
Sheepshead
Smalltooth sawfish
Southern kingfish
White-spotted eagle ray
Tiger shark
White shark
ATL & SFL (13)
CH (9)
NFL (6)
TB (3)
Juv, CH (3)
CH (1)
Juv, TB (16)
NFL (4)
Juv & adult,ATL (27)
CH (2)
TB (2)
Juv, NFL (6)
Juv, SFL (3)
ATL & EGOM (18)
NFL (18)
TB (26)
SFL (82)
NFL (12)
oTBn (15)
oTBs (8)
Juv, NFL (6)
NFL (1)
CH (1)
Juv, CH (6)
Juv, SFL (6)
ATL & SFL (5)
MS (17)
SFL (44)
NFL (15)
NFL (15)
SR (67)
NFL (8)
SFL (45)
ATL (2)
DT (1)
TB (31)
CH (8)
Juv, SFL (5)
PL (26)
MS (11)
NFL (55)
PL (23)
ATL & WGOM (2)
NFL (1)
SFL (1)
SFL (9)
Juv (lg), CH (22)
Juv (lg), SFL (4)
Juv, CH (121)
Juv, SFL (7)
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TB (27)
Juv, TB (6)
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Juv & adult, ATL (11)
Array name

Figure 2

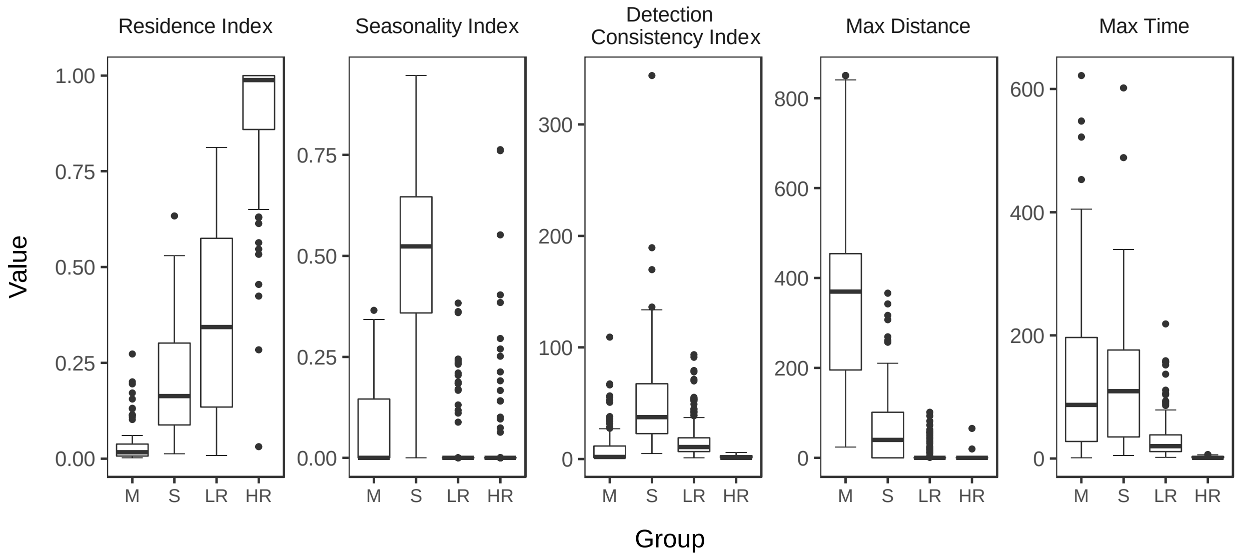

Residence Index
Seasonality Index
Detection
Consistency Index
Max Distance
Max Time
Value
1.00
0.75
0.50
0.25
0.00
0.75
0.50
0.25
0.00
300
200
100
0
800
600
400
200
0
600
400
200
0
M
S
LR
HR
Group

Figure 3

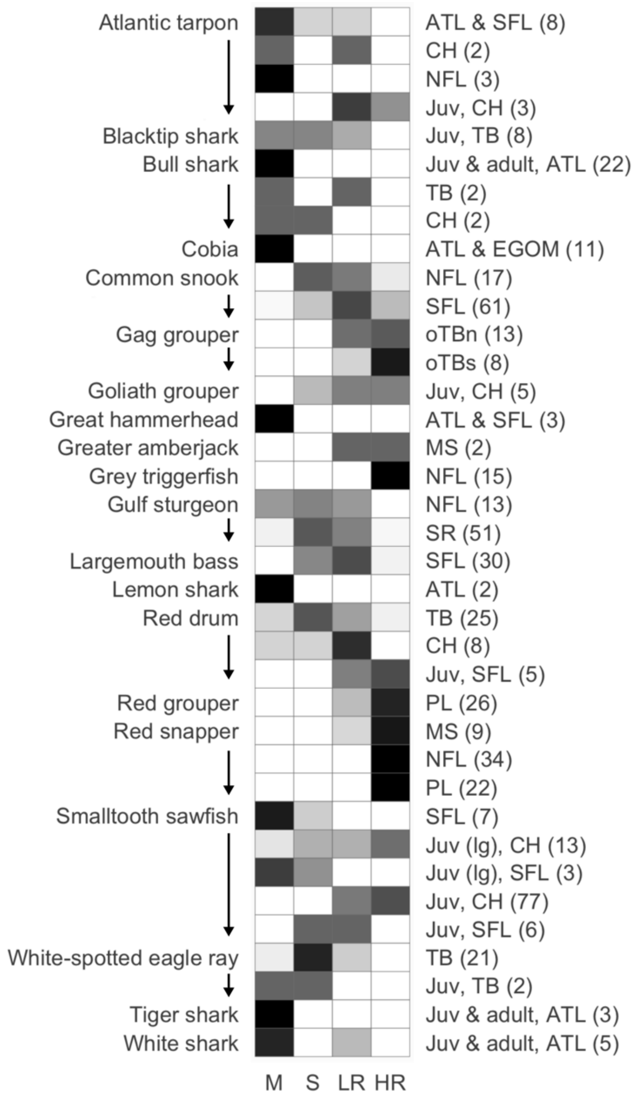
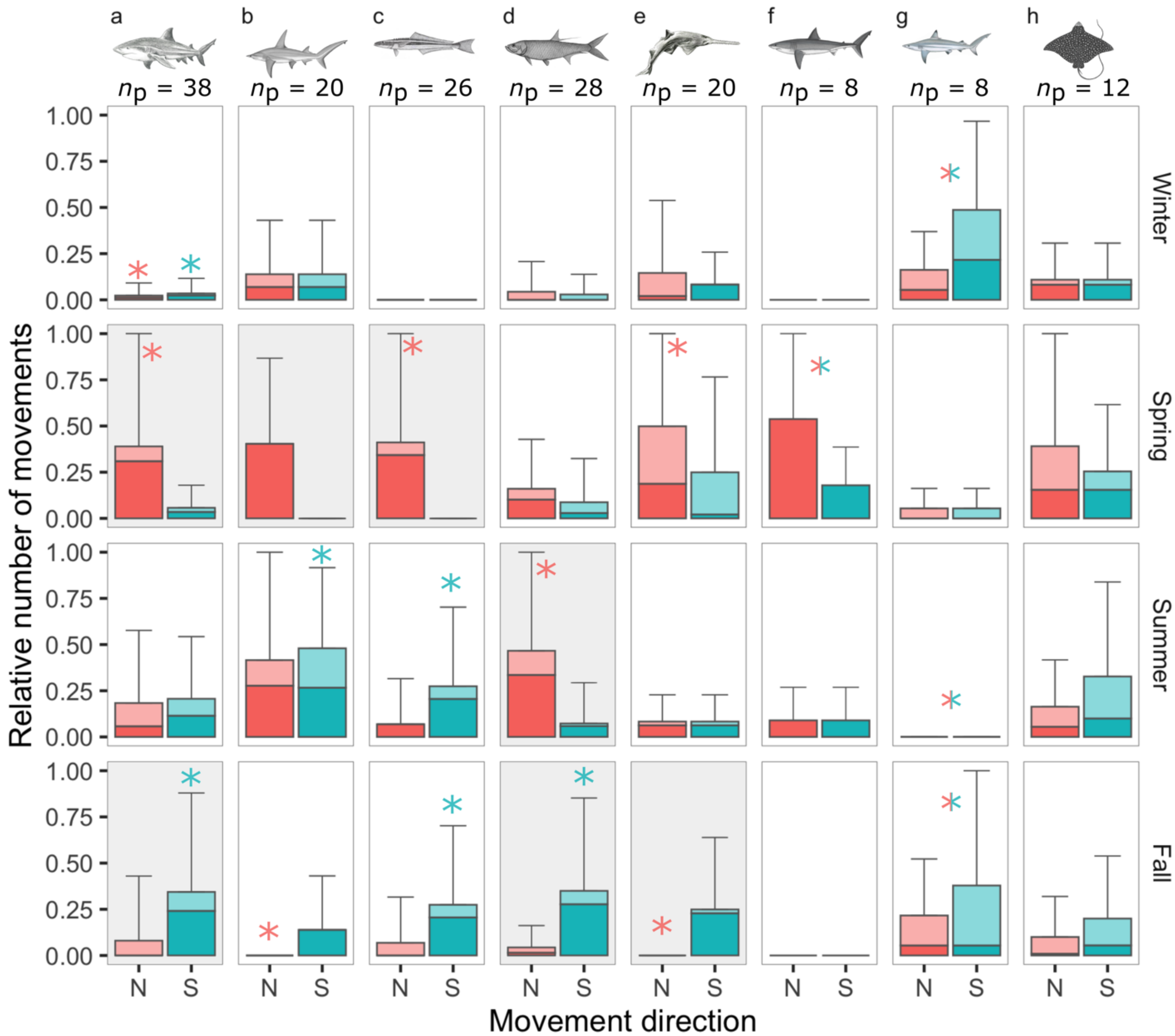

Atlantic tarpon
Blacktip shark
Bull shark
Cobia
Common snook
Gag grouper
Goliath grouper
Great hammerhead
Greater amberjack
Grey triggerfish
Gulf sturgeon
Largemouth bass
Lemon shark
Red drum
Red grouper
Red snapper
Smalltooth sawfish
White-spotted eagle ray
Tiger shark
White shark
ATL & SFL (8)
CH (2)
NFL (3)
Juv, CH (3)
Juv, TB (8)
Juv & adult, ATL (22)
TB (2)
CH (2)
ATL & EGOM (11)
NFL (17)
SFL (61)
oTBn (13)
oTBs (8)
Juv, CH (5)
ATL & SFL (3)
MS (2)
NFL (15)
NFL (13)
SR (51)
SFL (30)
ATL (2)
TB (25)
CH (8)
Juv, SFL (5)
PL (26)
MS (9)
NFL (34)
PL (22)
SFL (7)
Juv (lg), CH (13)
Juv (lg), SFL (3)
Juv, CH (77)
Juv, SFL (6)
TB (21)
Juv, TB (2)
Juv & adult, ATL (3)
Juv & adult, ATL (5)
M
S
LR
HR

Figure 4


a
b
c
d
e
f
g
h
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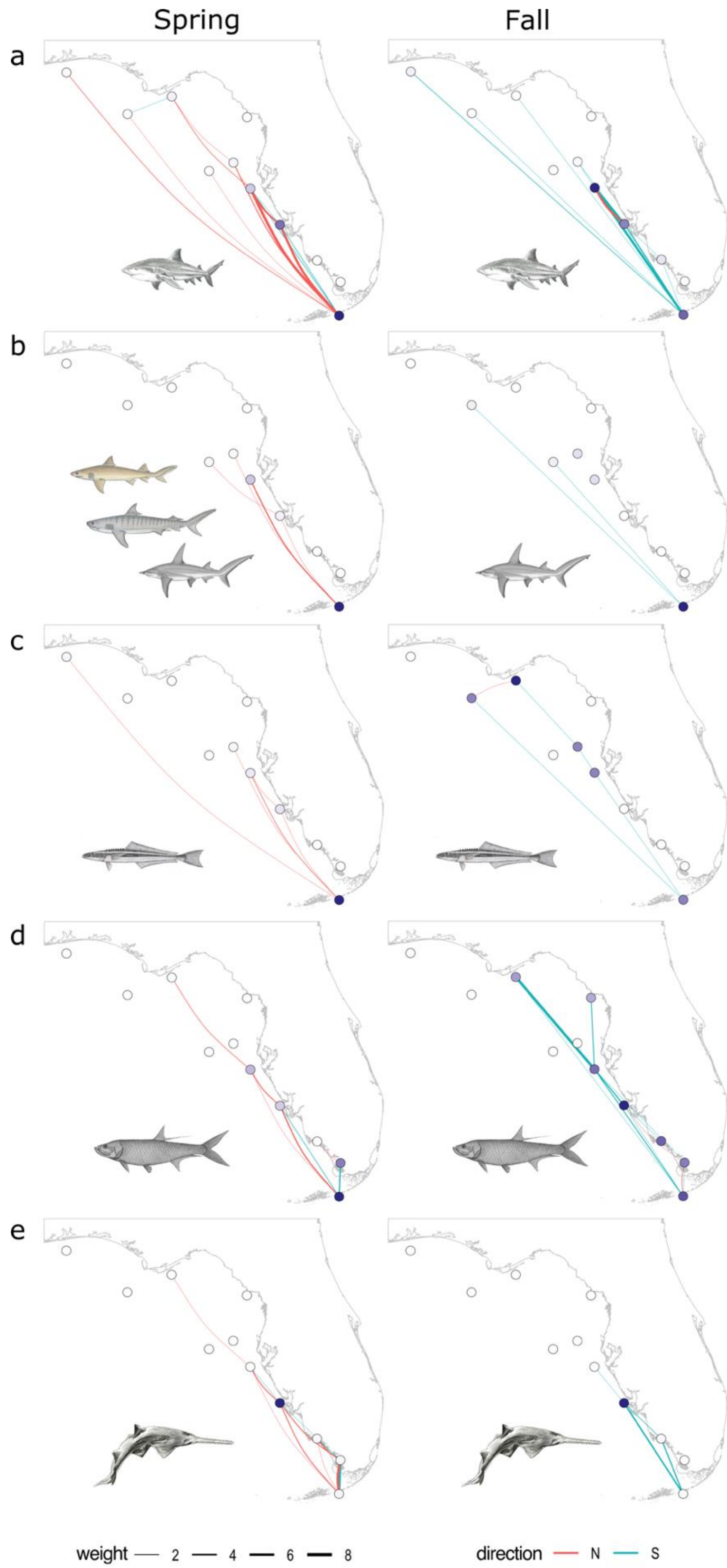
n_p = 28
n_p = 20
n_p = 8
n_p = 8
n_p = 12
1.00
0.75
0.50
0.25
0.00
Winter
Spring
Summer
Fall
Relative number of movements
N
S
Movement direction

Figure 5



1

2 Figure 6

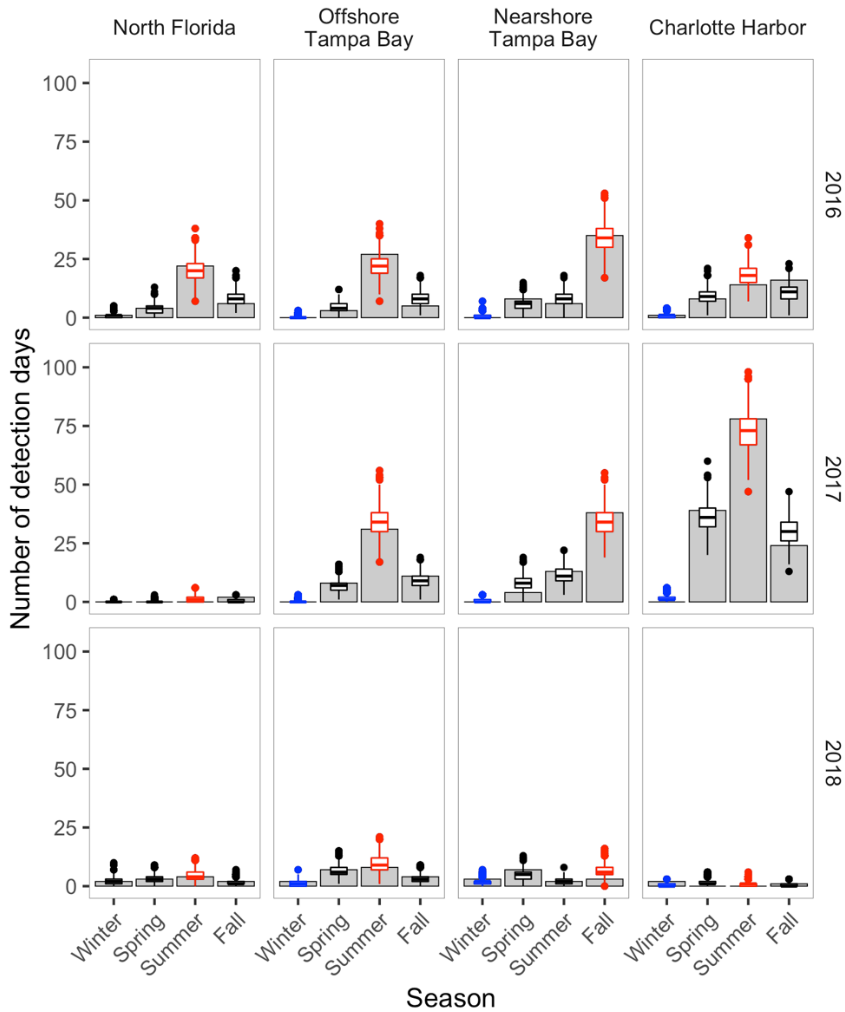

North Florida
Offshore Tampa Bay
Nearshore Tampa Bay
Charlotte Harbor
2016
2017
2018
Number of detection days
100
75
50
25
0
Winter
Spring
Summer
Fall
Season

Figure 7

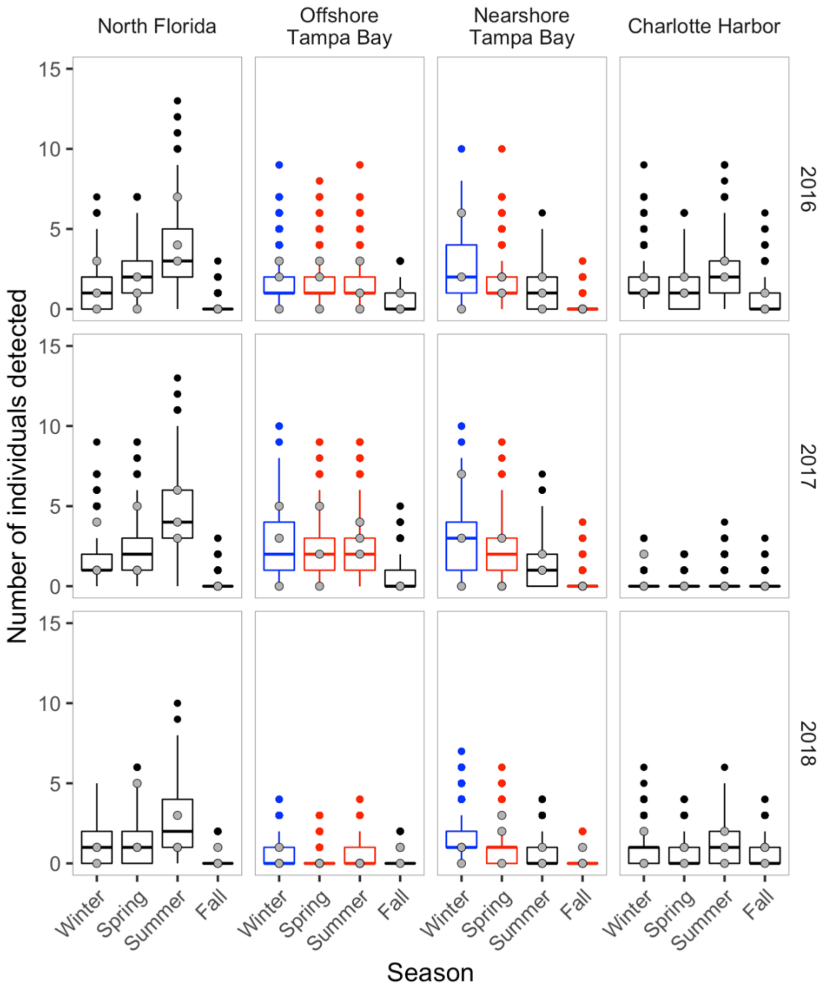

North Florida
Offshore Tampa Bay
Nearshore Tampa Bay
Charlotte Harbor
2016
2017
2018
Number of individuals detected
0
5
10
15
Winter
Spring
Summer
Fall
Season

Figure 8