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

Claudia Friess , Susan K. Lowerre-Barbieri, Gregg R. Poulakis, Neil Hammerschlag, Jayne M. Gardiner, Andrea M. Kroetz, Kim Bassos-Hull, Joel Bickford, Erin C. Bohaboy, Robert D. Ellis, Hayden Menendez, William F. Patterson III, Melissa E. Price, Jennifer S. Rehage, Colin P. Shea, Matthew J. Smukall, Sarah Walters Burnsed, Krystan A. Wilkinson, Joy Young, Angela B. Collins, Breanna C. DeGroot, Cheston T. Peterson, Caleb Purtlebaugh, Michael Randall, Rachel M. Scharer, Ryan W. Schloesser, Tonya R. Wiley, Gina A. Alvarez, Andy J. Danylchuk, Adam G. Fox, R. Dean Grubbs, Ashley Hill, James V. Locascio, Patrick M. O'Donnell, Gregory B. Skomal, Fred G. Whoriskey, Lucas P. Griffin

SEDAR77-RD05

Received: 5/27/2021

Vol. 663: 157–177, 2021
https://doi.org/10.3354/meps13637

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 31

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

Claudia Friess[1,*,#], Susan K. Lowerre-Barbieri[1,2,#], Gregg R. Poulakis[3], Neil Hammerschlag[4], Jayne M. Gardiner[5], Andrea M. Kroetz[6], Kim Bassos-Hull[7], Joel Bickford[1], Erin C. Bohaboy[8], Robert D. Ellis[1], Hayden Menendez[1], William F. Patterson III[2], Melissa E. Price[9], Jennifer S. Rehage[10], Colin P. Shea[1], Matthew J. Smukall[11], Sarah Walters Burnsed[1], Krystan A. Wilkinson[7,12], Joy Young[13], Angela B. Collins[1,14], Breanna C. DeGroot[15], Cheston T. Peterson[16], Caleb Purtlebaugh[17], Michael Randall[9], Rachel M. Scharer[3], Ryan W. Schloesser[7], Tonya R. Wiley[18], Gina A. Alvarez[19], Andy J. Danylchuk[20], Adam G. Fox[19], R. Dean Grubbs[21], Ashley Hill[22], James V. Locascio[7], Patrick M. O'Donnell[23], Gregory B. Skomal[24], Fred G. Whoriskey[25], Lucas P. Griffin[20]

[1]Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL 33701, USA
Full author addresses are given in the Appendix

ABSTRACT: Marine fish movement plays a critical role in ecosystem functioning and is increasingly studied with acoustic telemetry. Traditionally, this research has focused on single species and small spatial scales. However, integrated tracking networks, such as the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network, are building the capacity to monitor multiple species over larger spatial scales. We conducted a synthesis of passive acoustic monitoring data for 29 species (889 transmitters), ranging from large top predators to small consumers, monitored along the west coast of Florida, USA, over 3 yr (2016–2018). Space use was highly variable, with some groups using all monitored areas and others using only the area where they were tagged. The most extensive space use was found for Atlantic tarpon *Megalops atlanticus* and bull sharks *Carcharhinus leucas*. Individual detection patterns clustered into 4 groups, ranging from occasionally detected long-distance movers to frequently detected juvenile or adult residents. Synchronized, alongshore, long-distance movements were found for Atlantic tarpon, cobia *Rachycentron canadum*, and several elasmobranch species. These movements were 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 research, 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 · Integrated Tracking of Aquatic Animals in the Gulf of Mexico · iTAG · Collaboration

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

There has been a call 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. 2019b) and improve fisheries management (Link et al. 2020). Movement affects vulnerability to fishing and spatially

*Corresponding author: elasmophile@gmail.com
#These authors contributed equally to this work

© Inter-Research 2021 · www.int-res.com

explicit stressors (Lowerre-Barbieri et al. 2019b), 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 by 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 have 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 many 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), Florida Atlantic Coast Telemetry (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 these 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 during standardization for data analysis 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 (WCF), USA. We analyzed 3 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 4 hypotheses: (1) array coverage needed to track a given species varies based on movements and space use by 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 AND 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 at www.int-res.com/articles/suppl/m663p157_supp/). These iTAG arrays, deployed on the 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 distribution (e.g. gate, grid), with the finest spatial resolution coming from arrays set up as Vemco Positioning Systems (VPS).

It was necessary to regroup the receivers of some iTAG arrays to form spatially distinct units for analysis, resulting in 22 meta-arrays (referred to hereafter as arrays) (Fig. 1; Table S2.1 in Supplement 2 at www.int-res.com/articles/suppl/m663p157_supp/). These arrays were further aggregated into nodes for some analyses to reduce the spatial bias created by heterogeneity in array distribution (Fig. 1). In the present study, we referred to the arrays using the following 3-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 = o, nearshore = n, estuarine = e, riverine = r, where we define 'offshore' as being located in federal waters, greater than 9 nautical miles away from shore, and 'nearshore' as locations within state waters). For example, array T3o is an offshore array in the Tampa Bay subregion, and it is also part of the Tampa Bay array node that includes 6 arrays in close proximity 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.

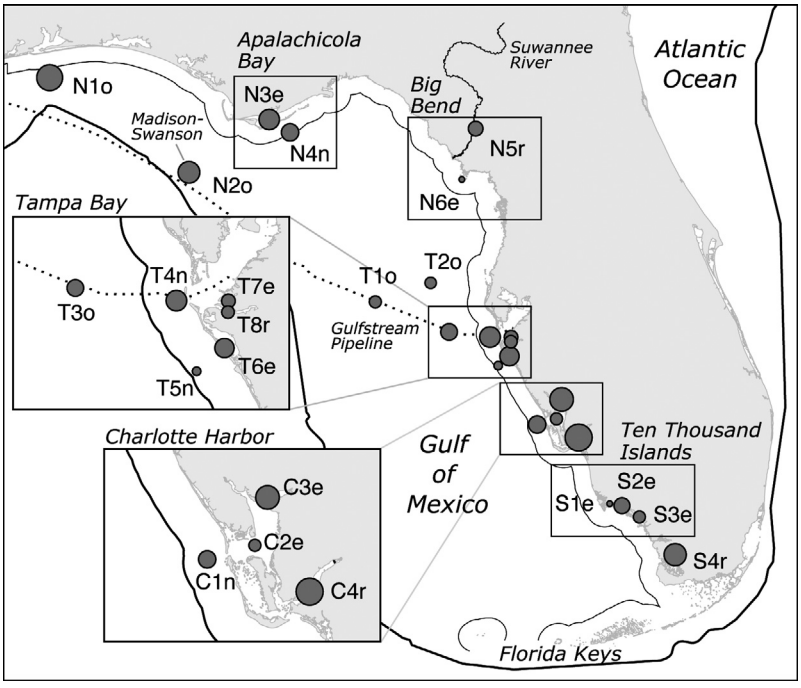


Fig. 1. Florida, USA, with west coast array locations indicated by circles. Symbol sizes are proportional to the number of receivers in each array (ranging from 3 to 60). Also shown are the state–federal waters boundary (thin black line), path of the Gulfstream gas pipeline (dotted line), and 200 m isobath (thick black line). Arrays grouped into the same node due to spatial proximity are within boxes. See Table S1.1 in Supplement 1 for corresponding iTAG array numbers and Section 2.1 for explanation of the 3-character naming system

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 2 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; assigned by transmitter owner *a priori*). This was done to address species which demonstrated residency as juveniles and large-scale movements as adults. Large juvenile (2.0–3.4 m stretch total length, STL) smalltooth sawfish *Pristis pectinata* (hereafter referred to as sawfish) 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 h). 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 and 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 d 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 2 detections within a node in a 24 h period; or for VPS arrays, at least 2 detections on a single receiver within a 24 h 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) was 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 mo to evaluate the detection period for potential seasonal effects. Clustering was performed using the fuzzy C-means 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 the 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 exploratory 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 on optimal cluster size (Table S2.2). The 4-cluster solution provided the clearest interpretability and was chosen due to the *a priori* expectation of 4 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 names *a posteriori* based on movement variable distributions.

The 5 movement variables used in the analysis were: 1 distance-related measure (the 99th quantile of distance traveled between successive detections), 2 detection frequency variables (the residence index and the 99th quantile of days between successive DDs on the WCF), 1 seasonality indicator variable (a seasonality index), and 1 detection consistency index (the gap ratio defined as the 99th to 75th quantiles of days between successive DDs; see Table S2.3 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 DDs mo^{-1} 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 DDs, 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 estimated by calculating the deviation from the mode, which ranges from 0 (no variability) to 1 (equal proportions).

2.4. Movement pathways

Seasonality and directionality in observed movement pathways were 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 (winter = December–February, spring = March–May, summer = June–August, fall = September–November) and node. 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, 2 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 and Fig. S2.2). Resulting cut-off values ranged from 57 d for cobia to 80 d for Atlantic tarpon (hereafter referred to as tarpon). Seasonal movement networks were constructed and visualized using the R packages 'igraph' (Csardi & Nepusz 2006), 'ggplot2' (Wickham et al. 2019), and 'ggraph' (Pedersen 2020).

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 2 different nodes) 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 1 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. Therefore, we 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 4 Markov chains with 2000 iterations each, discarding 1000 as 'burn-in,' and all priors were the default priors provided by 'rstanarm' (weakly informative, normal priors with mean 0 and standard deviation 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. 2017), and the model with the higher weight was used for inference. Model fits were inspected graphically by conducting posterior predictive checks using the R packages 'bayesplot' (Gabry & Mahr 2020) and 'shinystan' (Gabry 2018).

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 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 probability of direction estimates above 97.5% were treated as strong evidence for effect existence. Effect significance was assessed by calculating the portion of the full posterior density that fell within the region of practical equivalence (ROPE; the range of parameter values that is equivalent to 0). 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 2 GLMs 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 address 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 particu-

larly 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, resulting in 4 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 a daily count of the number of individuals detected by area for each calendar day during the 3 yr study period. The response variable for the n_{ind} model was a count of the number of unique individuals detected mo^{-1}. 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 largely 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:

$$y_i \sim \text{Poisson}(\mu_i)$$

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

$$\log(\mu_i) = \text{Area}_i \times \text{Season}_i + \text{Area}_i \times \text{StudyYear}_i + \log(\text{Tags}_i) + (1|\text{Year}_i/\text{Month}_i) \quad \text{(DD model only)}$$

$$\text{Year}_i \sim N(0, \sigma^2_{\text{year}})$$

$$\text{Month:Year}_i \sim N(0, \sigma^2_{\text{month:year}})$$

where y_i is number of individuals observed d^{-1} for the DD model and number of unique individuals observed mo^{-1} for the n_{ind} model, μ_i is the expected count, and $\log(\text{Tags}_i)$ is the offset term for number of available transmitters. Models were fitted in the R package '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 package 'forecast' (Hyndman & Khandakar 2008). Models were validated by simulating and testing residuals from the fitted models using the R package 'DHARMa' (Hartig 2019). Post-hoc analyses were conducted using the R package 'emmeans,' where marginal effects for the variables of interest (i.e. 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 represented 889 fish from 29 species (Table 1). These species range in terms of management concerns from threatened and endangered species (Gulf sturgeon *Acipenser oxyrinchus desotoi* and sawfish, respectively) to unmanaged species (e.g. 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 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), reef fishes and elasmobranchs with estuarine nurseries (e.g. gray snapper *Lutjanus griseus* and blacktip shark *Carcharhinus limbatus*), to offshore species such as red snapper *L. campechanus* and white shark. The mean number of tagged fish $species^{-1}$ was 31 but ranged from 1 (3 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 d, 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 15% of the individuals were observed in more than 1 node, but these fish represented a fairly wide range of species: great hammerhead, blacktip, bull, lemon, sandbar, tiger, and white sharks, tarpon, cobia, snook, goliath grouper *Epinephelus itajara*, greater amberjack *Seri-*

Table 1. Species detection summary. Detection day metrics are transmitter-based. DD: detection days, DP: detection period (d)

Common name	Scientific name	No. of transmitters	Total DD	Mean DD	Mean DP
Atlantic tarpon	*Megalops atlanticus*	34	2101	62	274
Blacktip shark	*Carcharhinus limbatus*	17	1431	84	245
Bonnethead	*Sphyrna tiburo*	4	78	20	63
Bull shark	*Carcharhinus leucas*	40	1351	34	471
Cobia	*Rachycentron canadum*	18	84	5	202
Common snook	*Centropomus undecimalis*	126	17264	137	316
Gafftopsail catfish	*Bagre marinus*	12	413	34	117
Gag grouper	*Mycteroperca microlepis*	29	2686	93	119
Goliath grouper	*Epinephelus itajara*	14	951	68	106
Gray snapper	*Lutjanus griseus*	44	3948	90	106
Great hammerhead	*Sphyrna mokarran*	5	50	10	255
Greater amberjack	*Seriola dumerili*	17	1363	80	134
Grey triggerfish	*Balistes capriscus*	13	1749	135	136
Gulf sturgeon	*Acipenser oxyrinchus desotoi*	82	7341	90	400
Hardhead catfish	*Ariopsis felis*	8	84	11	100
Largemouth bass	*Micropterus salmoides*	45	3830	85	284
Lemon shark	*Negaprion brevirostris*	2	48	24	809
Nurse shark	*Ginglymostoma cirratum*	1	1	1	1
Red drum	*Sciaenops ocellatus*	44	1704	39	303
Red grouper	*Epinephelus morio*	26	11238	432	499
Red snapper	*Lutjanus campechanus*	91	13672	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	18164	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
Whitespotted eagle ray	*Aetobatus narinari*	33	3067	93	428

ola dumerili, Gulf sturgeon, red drum, sawfish, and whitespotted eagle ray *Aetobatus narinari* (hereafter referred to as eagle ray).

3.1. Large-scale space use

We detected 55 unique tagging groups 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 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 4 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 traveled short maximal distances between DDs (LD residents: mean ± SE = 7.4 ± 1.45 km; HD residents: 0.45 ± 0.36 km), but they differed in temporal detection patterns (Fig. 3). HD residents (represented best by red snapper, red

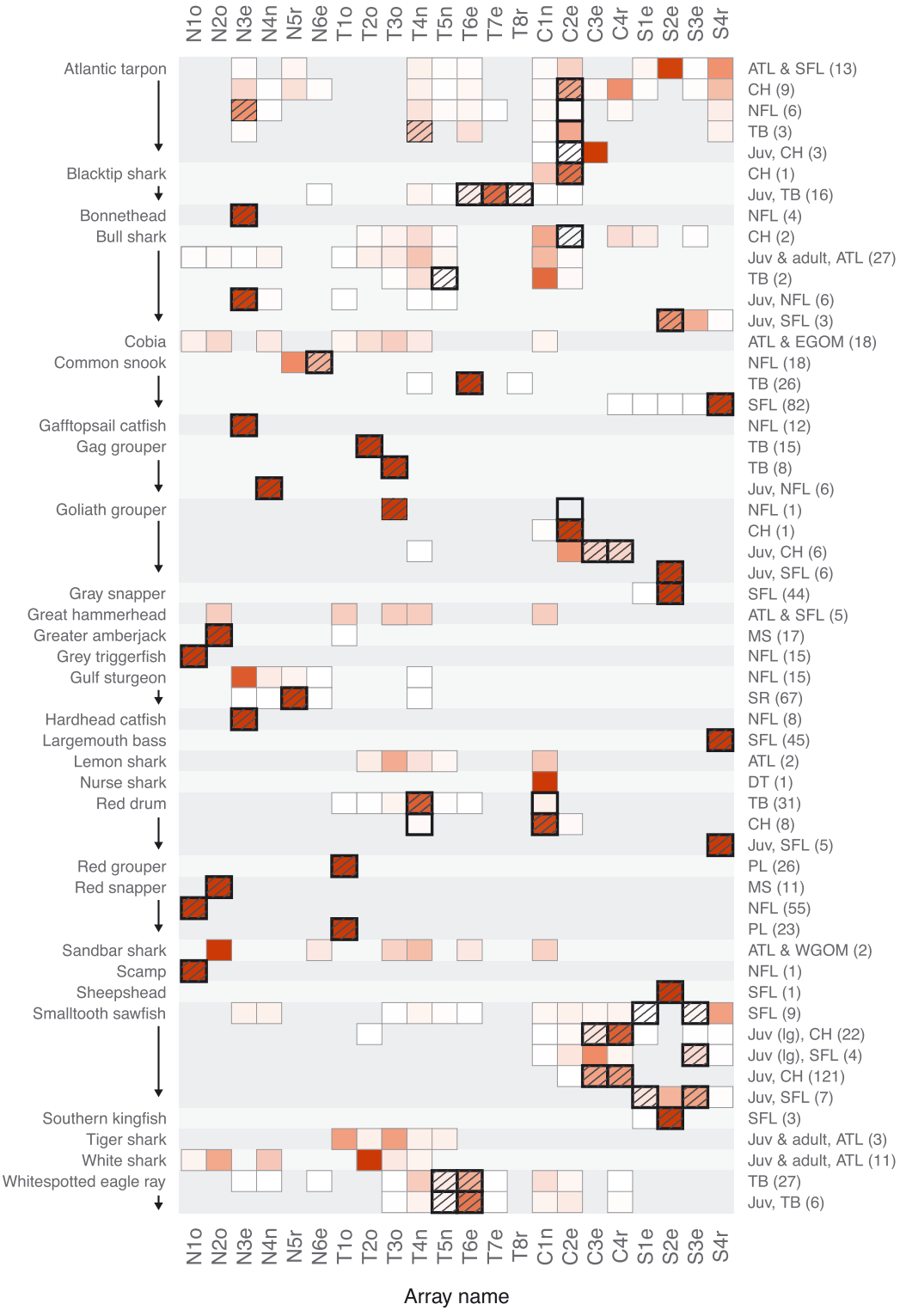


Fig. 2. Overview of tagging groups detected on west coast of Florida acoustic telemetry arrays between 2016 and 2018. Species is indicated on the left (with down arrows indicating the same species as the one above the arrow), and tagging location and life stage, if not adult, are identified on the right. The number of detected transmitters in each tagging group is shown in parentheses. Box color indicates proportion of detection days (min = 9×10^{-5} = white; max = 1 = dark red). 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 northwesternmost 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, Juv: juvenile, lg: large

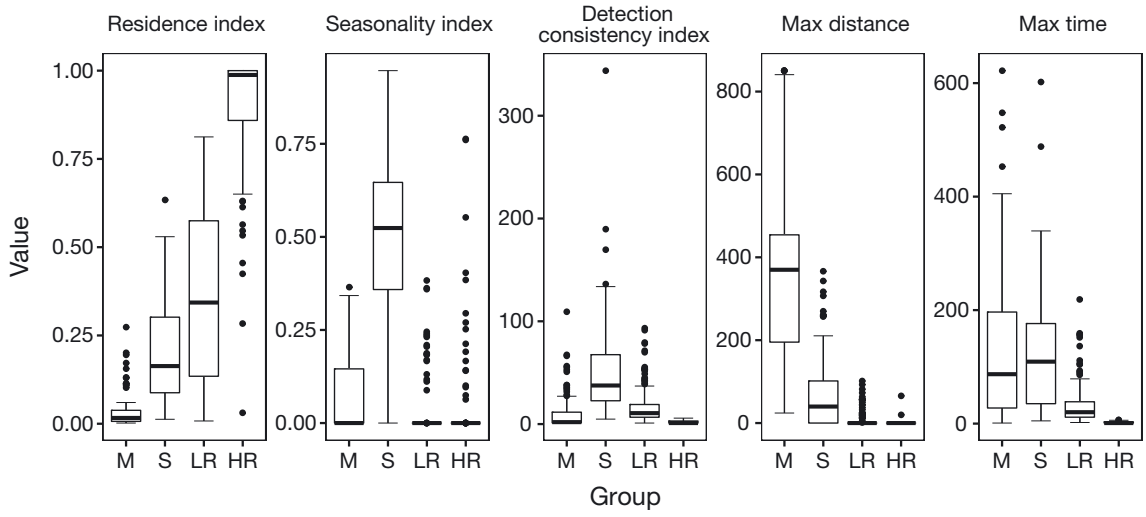


Fig. 3. Distribution of covariates for movement pattern clustering analysis. The horizontal line is the median, upper and lower hinges show the 25th and 75th percentiles, and whiskers extend from the hinge to the smallest (lower) and largest (upper) value no further than 150% of the interquartile range; values outside that range are shown as black dots. Groups are M: low-detection, long distance movers, S: seasonals, LR: low-detection residents, HR: high-detection residents. Max time is the 99th quantile of days between successive detection days, distance is the 99th quantile of kilometers between successive detection days, and the detection consistency index is the ratio of 99th to 75th quantiles of days between detection days

grouper *Epinephelus morio*, and grey triggerfish *Balistes capriscus*) were detected consistently in monitored areas (gap ratio mean: 1.93 ± 0.10; RI mean: 0.91 ± 0.01; maximal days between DD mean: 2.0 ± 0.11 d) whereas LD residents (represented by, e.g., some snook and largemouth bass) had less consistent temporal detections (gap ratio mean: 17.0 ± 1.4; RI mean: 0.36 ± 0.02; maximal days between DD mean: 31.9 ± 2.64 d; Fig. 3; Fig. S3.1 in Supplement 3 at www.int-res.com/articles/suppl/m663p157_supp/). Seasonals (represented best by eagle rays, some Gulf sturgeon, and TB red drum) had the largest seasonality index (mean 0.51 ± 0.02) and gap ratio (mean 49.6 ± 4.26). Movers (represented best by Atlantic-tagged sharks and cobia) traveled the greatest maximal distances between successive DDs (mean 369 ± 25.2 km), had the smallest RI (mean 0.04 ± 0.005) and the second-highest seasonality index (mean 0.07 ± 0.01). Both movers and seasonals went long maximal periods without being detected on the WCF (means 136 ± 15.2 and 123 ± 10.1 d, 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 (i.e. fish tagged in different locations or in different life stages) 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 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 the CH area (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 and CH, n = 4) clustered as movers. No clear 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 2 resident groups.

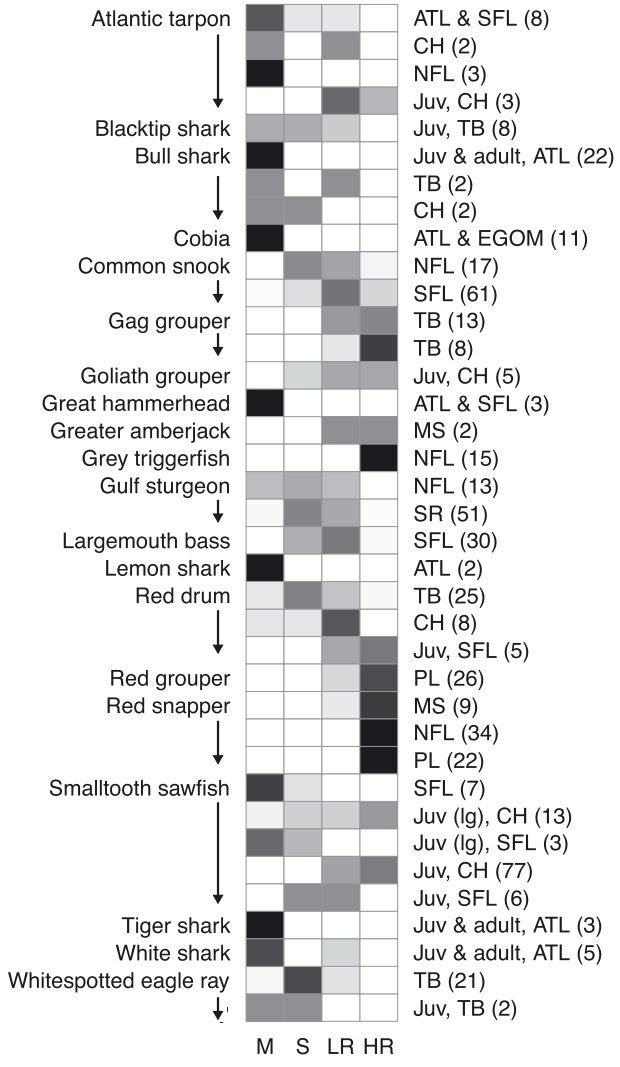


Fig. 4. Movement pattern clustering results by tagging group, showing the proportion of animals (within tagging group) in each movement group. The scale ranges from 0 (white) to 1 (black). Species is indicated on the left axis (with down arrows indicating the same species as the one above the arrow), 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, 554 were included in the movement network analysis; most of the filtering occurred due to insufficient potential detection periods (≤12 mo). Only tagging groups represented by at least 2 animals are shown. Site abbreviations as in Fig. 2

Within-tagging group variability for the 37 tagging groups in the analysis ranged from 0 (for 6 roamer and 3 resident groups) to 0.833 for juvenile blacktip sharks. 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 4 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 8 for white and juvenile blacktip sharks to 38 for bull sharks; number of movements ranged from 10 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 sharks, eagle rays, and white sharks (see Tables S3.2–S3.4 for full model parameters and post-hoc test results). The overall pattern was that northbound movements dominated in spring, southbound movements dominated in fall, winter movements were low, except for blacktip sharks, and summer patterns were more variable across species groups (Figs. 5 & 6). Within season, cobia, bull sharks, and the coastal sharks group (great hammerhead, lemon, tiger, and sandbar sharks) had more northbound than southbound movements in spring, and tarpon, cobia, and bull sharks had more southbound than northbound movements in fall (Table S3.4; note that 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 2 types of comparisons that were made, i.e. directional differences within season and seasonal differences within direction). 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. Within movement direction, northbound movements were higher than in other seasons 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).

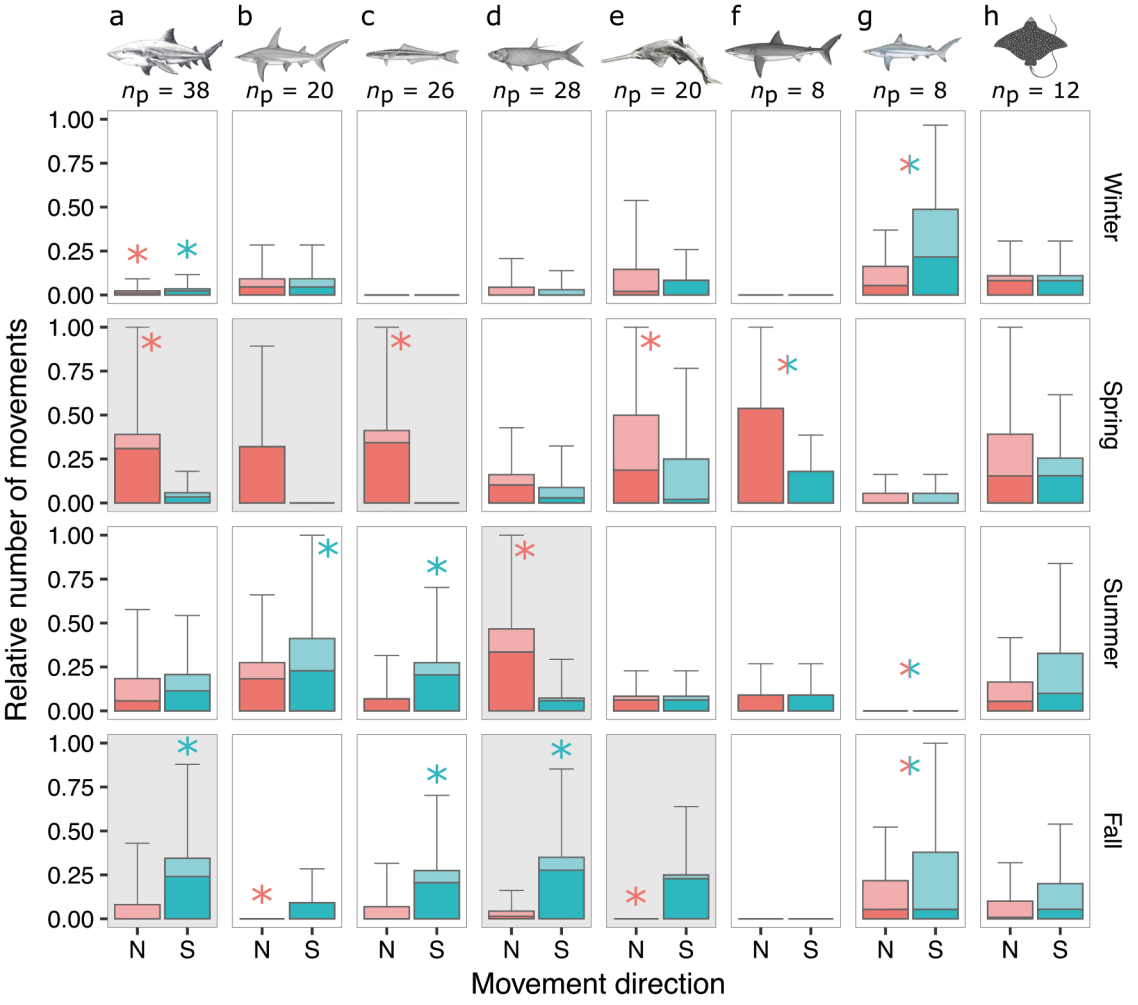
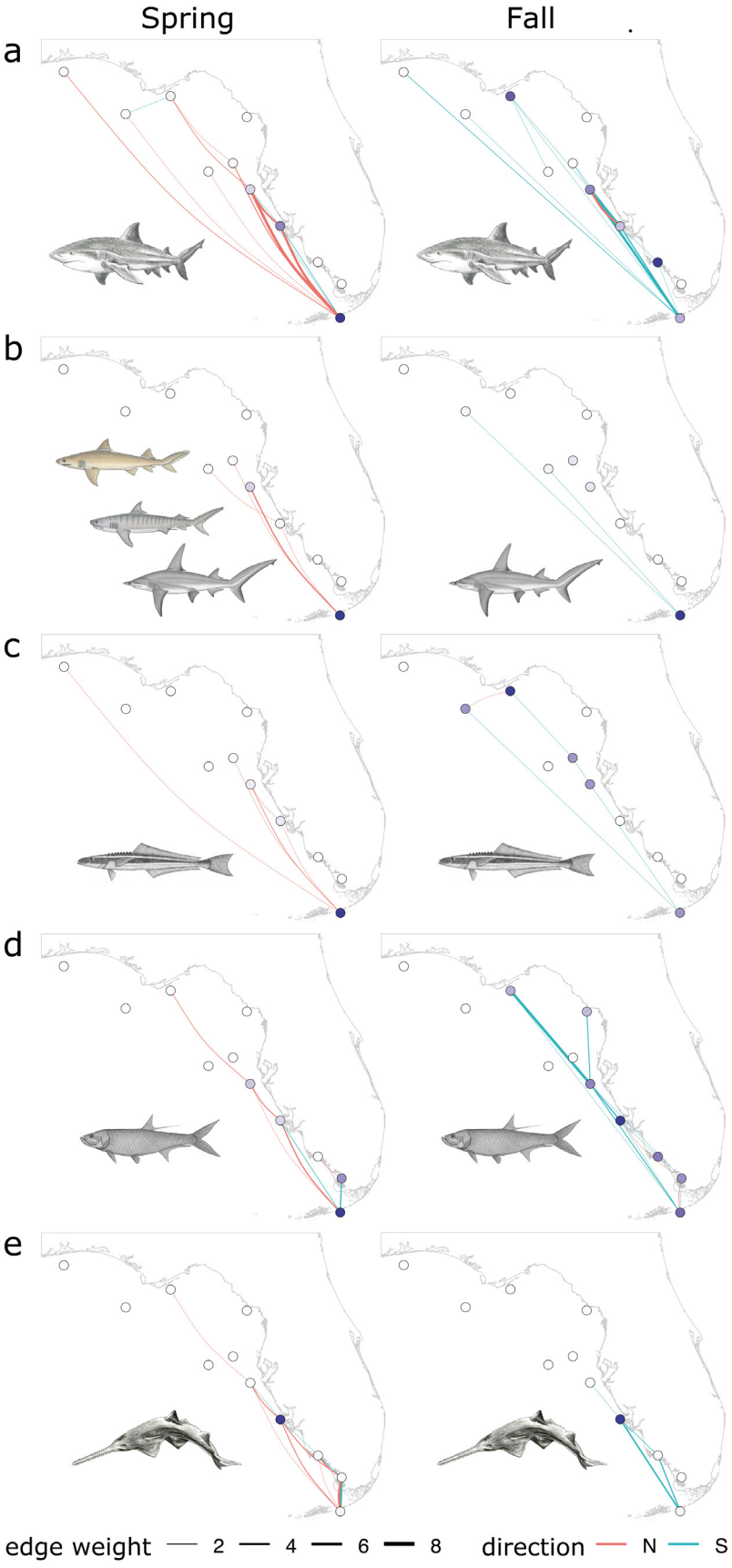


Fig. 5. Mean + SD by species or species group, season, and movement direction, relative to the maximum for each group. (a) Juvenile and adult bull sharks, (b) juvenile and adult coastal sharks (great hammerhead, sandbar, lemon, and tiger sharks), (c) cobia, (d) adult Atlantic tarpon, (e) large juvenile and adult smalltooth sawfish, (f) juvenile and adult white sharks, (g) juvenile blacktip sharks, (h) juvenile and adult whitespotted eagle rays. n_p: number of unique potential movement paths. Generalized linear models were fitted to number of movements (see Section 2 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 S3.2–S3.4 in Supplement 3 for full model results): panels highlighted with grey backgrounds indicate seasons within which the marginal means between northbound (N) and southbound (S) movements differed, and asterisks mark the season for which a marginal mean for the indicated movement direction (green = 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

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 sharks 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 nodes occurred primarily for tarpon and sawfish, and movement to and from off-



shore nodes was seen primarily for bull sharks, coastal sharks, and cobia (also for white sharks; not shown). Furthermore, there was variation in movements among species within the coastal sharks group: the only fall (southbound) movements observed were for great hammerheads (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. DDs 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 and CH) had higher DDs 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 & 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

Fig. 6. Spring and fall movement networks for groups with season-specific movement direction differences. (a) Juvenile and adult bull sharks, (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 nodes were grouped to focus on longer-distance movements. Southbound movements are drawn in straight green 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 node, which are not shown). Line width corresponds to edge weight (i.e. 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

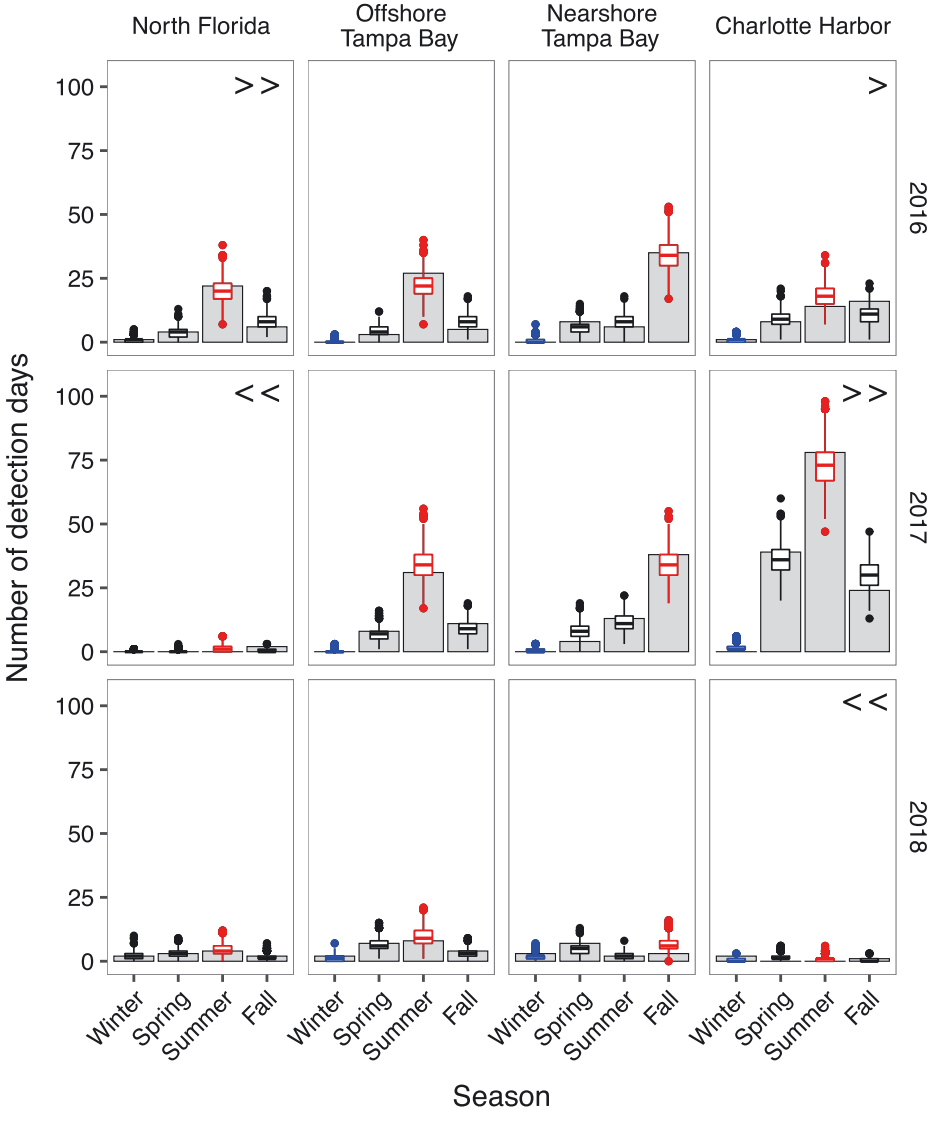


Fig. 7. Observed (grey bars) and predicted (boxplots) number of top predators (great hammerheads, bull, white, tiger, sandbar, and lemon sharks; excluding juveniles tagged on the west coast of Florida) detected per day, summed by season. Within area, seasons that had significantly ($p \leq 0.05$) lower 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 (<< = $p \leq 0.01$, < = $p \leq 0.05$). Representations of mid-line, hinges, and whiskers are as in Fig. 3

unique individuals were detected in spring and summer offshore of TB than in other seasons, while in nearshore TB, spring and fall 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 DDs 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 DD data indicated that more unique individuals visited the offshore TB area each summer, with fewer DDs ind.$^{-1}$, either because they spend less time there or are present but not detected as frequently (see Tables S3.5–S3.12 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

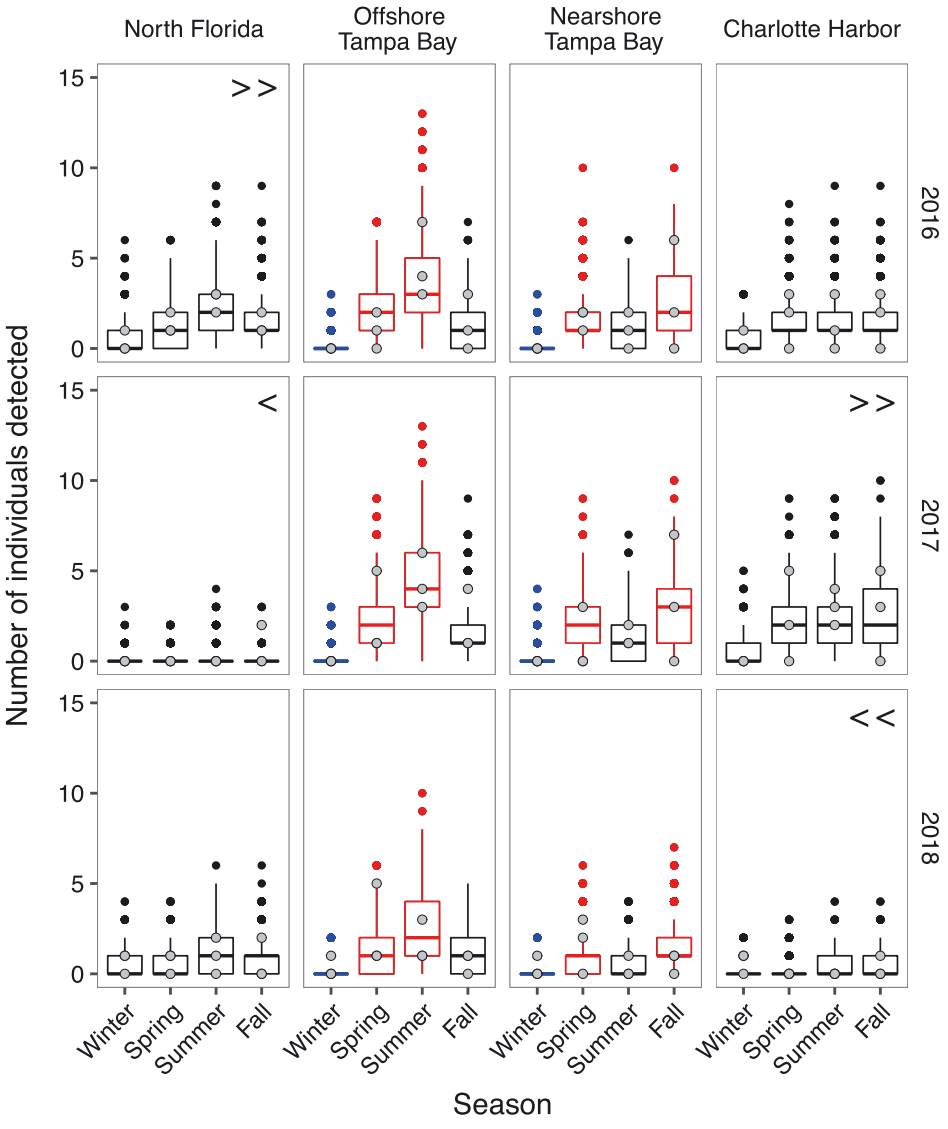


Fig. 8. Observed (grey points) and predicted (boxplots) number of unique top predator individuals (great hammerheads, bull, white, tiger, sandbar, and lemon sharks; excluding juveniles tagged on the west coast of Florida) detected per month, averaged by season. Within area, seasons that had significantly ($p \leq 0.05$) 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 (<< = $p \leq 0.01$, < = $p \leq 0.05$). Representations of mid-line, hinges, and whiskers are as in Fig. 3

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

It was expected and confirmed in the present study that the iTAG network was a valuable source for monitoring highly migratory species. 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 rays, red drum, and Gulf sturgeon; movers such as tarpon; and juvenile elasmobranchs such as blacktips, bull sharks, and sawfish as they leave their nursery areas and transi-

tion 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 (Griffin et al. 2018). Tracking networks benefit not only researchers studying highly mobile animals but also those focused on resident fishes. For example, collaborative work with network taggers can provide insights into predation on resident species by migratory predators (Bohaboy et al. 2020). Additionally, many resident fishes exhibit spawning movements which could result in detections on other network arrays, and tracking networks allow for the potential to discover previously unknown transient behavior or shifts in space use over time.

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 USA). The only individual 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 3 offshore reefs near the pipeline (i.e. arrays N1o, N2o, and T1o), but none of the over 300 tagged fish were detected anywhere but on their study arrays. Perhaps 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 steppingstones for range re-expansion to areas occupied prior to intense fishing, or perhaps the 3 yr time period of 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 were dependent on the spectrum of movement ecologies represented in the sample of tagged animals as well as the observation system, and the variables analyzed. Results were sensitive to the choice of clustering variables, a result also reported by Brodie et al. (2018) for Australian telemetry arrays. Even though there were a number of differences in our movement type clustering analysis compared to theirs (e.g. different systems, different movement variables, shorter study period, fewer species and tagged individuals), 3 of the 4 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 rays) 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 extend 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 observation error rather than true movement patterns, especially in species using habitats with low receiver coverage. For example, receiver density is likely what was driving the differences between movement types (as high vs. low detection residents) for gag tagged in 2 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. Most (84 %) sawfish tagged in the CH estuarine system (n = 89) were small juveniles (<2 m STL), which

are known to be primarily resident 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. 2021) 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 2 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 highlight the limitations of the multi-species clustering 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 undergo seasonal migrations, consisting of spring and summer northward and fall and winter southbound movements (Graham et al. 2021), 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 blacktip 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 that the WCF telemetry network did not adequately monitor long-distance migrations for those species or that 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, blacktip and white sharks were predominantly observed moving in 1 direction (south for blacktips and north for white sharks). It is unclear whether this skew is an artifact of low sample size or represents a real trend of systematically failing to detect directional movements for these species. 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. 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.

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 finding no significant movement direction effects for eagle rays. Eagle rays occur off the WCF in spring, summer, and fall, and are hypothesized to migrate to offshore and southern areas when water temperatures decrease (Bassos-Hull et al. 2014, DeGroot et al. 2021). 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 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 aggrega-

tions (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. 2019a) which also attract smaller shark species such as the blacknose shark *Carcharhinus acronotus* (J. Bickford pers. obs.). A seasonal influx of predators into the Gulf could mean seasonally fluctuating predation rates, resulting in high predation 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 hotspots 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. 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 3 years analyzed, 2018 stood out as having lower DDs in all central Florida areas. In this year, an abnormally strong and long-lasting red tide event affected nearshore central Florida waters. 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, has been maintained since 2012. Thus, the reduction in DDs 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 hotspot 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 currently limited, for 2 reasons. First, changes in detectability over time cannot currently be separated from changes in behavior due to frequent changes in array configuration. Unlike the Australian IMOS ATF, the WCF currently does not have any state, federal, or consortium-funded permanent receiver arrays. 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, although they may be most valuable for exploratory data analysis and 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? (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 to move beyond opportunistic data and fully realize its potential for hypothesis-driven ecological inquiry, it will require long-term funding to support permanent 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).

Acknowledgements. We thank all researchers, technicians, and institutions that have contributed to collecting the data used in this manuscript by tagging fish or maintaining acoustic receiver arrays. We thank the following people for giving permission to use their transmitter data in this study: Debra Abercrombie, Judd Curtis, Tobey Curtis, Keith Dunton, Joe Heublein, Adam Kaeser, Matt Kendall, Frank Parauka, and Wes Pratt. We are grateful to Ray Simpson and Lindsay Henderson for providing the fish artwork, and to J. Walter and 2 anonymous reviewers whose comments strengthened the manuscript. The Ocean Tracking Network and Vemco provided receivers for some iTAG arrays. S.K.L.-B. was funded by NOAA CIMAS grant NA15AR4320064. Grant F-59 from the US Fish and Wildlife Service Sport Fish Restoration program helped to fund iTAG, iTAG workshops, and personnel to oversee the running of iTAG. The views and conclusions are those of the authors and do not necessarily reflect the opinions or policies of the US government or any of its agencies. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

LITERATURE CITED

Abecasis D, Steckenreuter A, Reubens J, Aarestrup K and others (2018) A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. Anim Biotelem 6:12

Abrahms B, Seidel DP, Dougherty E, Hazen EL and others (2017) Suite of simple metrics reveals common movement syndromes across vertebrate taxa. Mov Ecol 5:12

Ajemian MJ, Drymon JM, Hammerschlag N, Wells RJD and others (2020) Movement patterns and habitat use of tiger sharks (*Galeocerdo cuvier*) across ontogeny in the Gulf of Mexico. PLOS ONE 15:e0234868

Allan BM, Nimmo DG, Ierodiaconou D, Vanderwal J, Koh LP, Ritchie EG (2018) Futurecasting ecological research: the rise of technoecology. Ecosphere 9:e02163

Bassos-Hull K, Wilkinson KA, Hull PT, Dougherty DA and others (2014) Life history and seasonal occurrence of the spotted eagle ray, *Aetobatus narinari*, in the eastern Gulf of Mexico. Environ Biol Fishes 97:1039–1056

Bezdek JC (1981) Pattern recognition with fuzzy objective function algorithms. Plenum Press, New York, NY

Biesiot PM, Caylor RE, Franks JS (1994) Biochemical and histological changes during ovarian development of cobia, *Rachycentron canadum*, from the northern Gulf of Mexico. Fish Bull 92:686–696

Binder TR, Hayden TA, Holbrook C (2018) glatos: an R package for the Great Lakes Acoustic Telemetry Observation System. R package version 2.0. https://gitlab.oceantrack.org/GreatLakes/glatos

Bohaboy EC, Guttridge TL, Hammerschlag N, Van Zinnicq Bergmann MP, Patterson WF III (2020) Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. ICES J Mar Sci 77:83–96

Brame AB, Wiley TR, Carlson JK, Fordham SV and others (2019) Biology, ecology, and status of the smalltooth sawfish *Pristis pectinata* in the USA. Endang Species Res 39:9–23

Brodie S, Lédée EJI, Heupel MR, Babcock RC and others (2018) Continental-scale animal tracking reveals functional movement classes across marine taxa. Sci Rep 8:3717

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brownscombe JW, Lédée EJI, Raby GD, Struthers DP and others (2019) Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. Rev Fish Biol Fish 29:369–400

Brownscombe JW, Griffin LP, Morley D, Acosta A and others (2020) Seasonal occupancy and connectivity amongst nearshore flats and reef habitats by permit *Trachinotus falcatus*: considerations for fisheries management. J Fish Biol 96:469–479

Carpenter B, Gelman A, Hoffman MD, Lee D and others (2017) Stan: a probabilistic programming language. J Stat Softw 76:1–32

Cebeci Z (2019) Comparison of internal validity indices for fuzzy clustering. J Agric Bioinform 10:1–14

Chen Y (2017) Fish resources of the Gulf of Mexico. In: Ward C (ed) Habitats and biota of the Gulf of Mexico: before the Deepwater Horizon oil spill (Vol 2). Springer, New York, NY, p 869–1038

Collins AB, Heupel MR, Simpfendorfer CA (2008) Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. Estuaries Coasts 31:1174–1183

Cowan JH Jr, Grimes CB, Patterson WF III, Walters CJ and others (2011) Red snapper management in the Gulf of Mexico: science- or faith-based? Rev Fish Biol Fish 21:187–204

Crossin GT, Heupel MR, Holbrook CM, Hussey NE and others (2017) Acoustic telemetry and fisheries management. Ecol Appl 27:1031–1049

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal Complex Syst 1695:1–9

DeGroot BC, Bassos-Hull K, Wilkinson KA, Lowerri-Barbieri S, Poulakis GR, Ajemian MJ (2021) Variable migration patterns of whitespotted eagle rays *Aetobatus narinari* along Florida's coastlines. Mar Biol 168:18

Donaldson MR, Hinch SG, Suski CD, Fisk AT, Heupel MR, Cooke SJ (2014) Making connections in aquatic ecosystems with acoustic telemetry monitoring. Front Ecol Environ 12:565–573

Ferraro MB, Giordani P, Serafini A (2019) Fclust: an R package for fuzzy clustering. R J 11:198–210

Franks JS, Warren JR, Buchanan MV (1999) Age and growth of cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico. Fish Bull 97:459–471

Furey NB, Armstrong JB, Beauchamp DA, Hinch SG (2018) Migratory coupling between predators and prey. Nat Ecol Evol 2:1846–1853

Gabry J (2018) shinystan: interactive visual and numerical diagnostics and posterior analysis for Bayesian models. R package version 2.5.0. https://CRAN.R-project.org/package=shinystan

Gabry J, Mahr T (2020) bayesplot: plotting for Bayesian models. R package version 1.7.2. https://mc-stan.org/bayesplot

Gelman A, Jakulin A, Pittau MG, Su YS (2008) A weakly informative default prior distribution for logistic and other regression models. Ann Appl Stat 2:1360–1383

Goodrich B, Gabry J, Ali I, Brilleman S (2020) rstanarm: Bayesian applied regression modeling via Stan. R package version 2.19.3. https://mc-stan.org/rstanarm

Graham J, Kroetz AM, Poulakis GR, Scharer RM and others (2021) Large-scale space use of large juvenile and adult smalltooth sawfish *Pristis pectinata*: implications for management. Endang Species Res 44:45–59

Griffin LP, Brownscombe JW, Adams AJ, Boucek RE and others (2018) Keeping up with the silver king: using cooperative acoustic telemetry networks to quantify the movements of Atlantic tarpon (*Megalops atlanticus*) in the coastal waters of the southeastern United States. Fish Res 205:65–76

Griffin LP, Smith BJ, Cherkiss MS, Crowder AG and others (2020) Space use and relative habitat selection for immature green turtles within a Caribbean marine protected area. Anim Biotelem 8:22

Guttridge TL, Van Zinnicq Bergmann MPM, Bolte C, Howey LA and others (2017) Philopatry and regional connectivity of the great hammerhead shark, *Sphyrna mokarran* in the US and Bahamas. Front Mar Sci 4:3

Halfyard EA, Webber D, Del Papa J, Leadley T, Kessel ST, Colborne SF, Fisk AT (2017) Evaluation of an acoustic telemetry transmitter designed to identify predation events. Methods Ecol Evol 8:1063–1071

Hammerschlag N (2019) Quantifying shark predation effects on prey: dietary data limitations and study approaches. Endang Species Res 38:147–151

Hammerschlag N, Luo J, Irschick DJ, Ault JS (2012) A comparison of spatial and movement patterns between sympatric predators: bull sharks (*Carcharhinus leucas*) and Atlantic tarpon (*Megalops atlanticus*). PLOS ONE 7: e45958

Hammerschlag N, Broderick AC, Coker JW, Coyne MS and others (2015) Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. Ecology 96: 2117–2126

Hammerschlag N, Gutowsky LFG, Gallagher AJ, Matich P, Cooke SJ (2017) Diel habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high use area exposed to dive tourism. J Exp Mar Biol Ecol 495:24–34

Hartig F (2019) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.4. https://CRAN.R-project.org/package=DHARMa

Haulsee DE, Fox DA, Breece MW, Brown LM, Kneebone J, Skomal GB, Oliver MJ (2016) Social network analysis reveals potential fission–fusion behavior in a shark. Sci Rep 6:34087

Hays GC, Ferreira LC, Sequeira AM, Meekan MG and others (2016) Key questions in marine megafauna movement ecology. Trends Ecol Evol 31:463–475

Hazen EL, Abrahms B, Brodie S, Carroll G and others (2019) Marine top predators as climate and ecosystem sentinels. Front Ecol Environ 17:565–574

Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Can J Fish Aquat Sci 59:624–632

Hueter RE, Heupel MR, Heist E, Keeney DB (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fish Sci 35: 239–247

Hyndman RJ, Khandakar Y (2008) Automatic time series for forecasting: the forecast package for R. J Stat Softw 27: 1–22

Keller K, Smith JA, Lowry MB, Taylor MD, Suthers IM (2017) Multispecies presence and connectivity around a designed artificial reef. Mar Freshw Res 68:1489–1500

Kessel ST, Chapman DD, Franks BR, Gedamke T and others (2014a) Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). Mar Ecol Prog Ser 514:175–190

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014b) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218

Kristensen K, Nielsen A, Berg CW, Skaug H, Bell B (2015) TMB: automatic differentiation and Laplace approximation. J Stat Softw 70:1–21

Lea JS, Humphries NE, von Brandis RG, Clarke CR, Sims DW (2016) Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. Proc R Soc B 283: 20160717

Lear KO, Poulakis GR, Scharer RM, Gleiss AC, Whitney NM (2019a) Fine-scale behavior and habitat use of the endangered smalltooth sawfish (*Pristis pectinata*): insights from accelerometry. Fish Bull 117:348–359

Lear KO, Whitney NM, Morgan DL, Brewster LR and others (2019b) Thermal performance responses in free-ranging elasmobranchs depend on habitat use and body size. Oecologia 191:829–842

Lenth R (2019) emmeans: stimated marginal means, aka least-squares means. R package version 1.4.3.01. https://CRAN.R-project.org/package=emmeans

Link JS, Huse G, Gaichas S, Marshak AR (2020) Changing how we approach fisheries: a first attempt at an opera-

tional framework for ecosystem approaches to fisheries management. Fish Fish 21:393–434
Lowerre-Barbieri SK, Burnsed SLW, Bickford JW (2016) Assessing reproductive behavior important to fisheries management: a case study with red drum, *Sciaenops ocellatus.* Ecol Appl 26:979–995
Lowerre-Barbieri SK, Tringali MD, Shea CP, Walters Burnsed S, Bickford J, Murphy M, Porch C (2019a) Assessing red drum spawning aggregations and abundance in the eastern Gulf of Mexico: a multidisciplinary approach. ICES J Mar Sci 76:516–529
Lowerre-Barbieri SK, Kays R, Thorson JT, Wikelski M (2019b) The ocean's movescape: fisheries management in the biologging decade (2018–2028). ICES J Mar Sci 76:477–488
Luo J, Ault JS, Ungar BT, Smith SG and others (2020) Migrations and movements of Atlantic tarpon revealed by two decades of satellite tagging. Fish Fish 21:290–318
Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D (2019a) Indices of effect existence and significance in the Bayesian framework. Front Psychol 10:2767
Makowski D, Ben-Shachar MS, Lüdecke D (2019b) BayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. J Open Source Softw 4:1541
Mathies NH, Ogburn MB, McFall G, Fangman S (2014) Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. Mar Ecol Prog Ser 495:27–38
McGowan J, Beger M, Lewison RL, Harcourt R and others (2017) Integrating research using animal-borne telemetry with the needs of conservation management. J Appl Ecol 54:423–429
Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059
Pedersen TL (2020) ggraph: an implementation of grammar of graphics for graphs and networks. R package version 2.0.3. https://CRAN.R-project.org/package=ggraph
Peterson CD, Belcher CN, Bethea DM, Driggers WB III, Frazier BS, Latour RJ (2017) Preliminary recovery of coastal sharks in the south-east United States. Fish Fish 18:845–859
Pickard AE, Vaudo JJ, Wetherbee BM, Nemeth RS, Blondeau JB, Kadison EA, Shivji MS (2016) Comparative use of a Caribbean mesophotic coral ecosystem and association with fish spawning aggregations by three species of shark. PLOS ONE 11:e0151221
Poulakis GR, Stevens PW, Timmers AA, Stafford CJ, Simpfendorfer CA (2013) Movements of juvenile endangered smalltooth sawfish, *Pristis pectinata*, in an estuarine river system: use of non-main-stem river habitats and lagged responses to freshwater inflow-related changes. Environ Biol Fishes 96:763–778
Poulakis GR, Stevens PW, Timmers AA, Stafford CJ and others (2016) Long-term site fidelity of endangered smalltooth sawfish (*Pristis pectinata*) from different mothers. Fish Bull 114:461–475
Queiroz N, Humphries NE, Couto A, Vedor M and others (2019) Global spatial risk assessment of sharks under the footprint of fisheries. Nature 572:461–466
Reyier EA, Franks BR, Chapman DD, Scheidt DM, Stolen ED, Gruber SH (2014) Regional-scale migrations and habitat use of juvenile lemon sharks (*Negaprion brevirostris*) in the US South Atlantic. PLOS ONE 9:e88470
Rhodes KL, Baremore I, Graham RT (2019) Grouper (Epinephelidae) spawning aggregations affect activity space of grey reef sharks, *Carcharhinus amblyrhynchos*, in Pohnpei, Micronesia. PLOS ONE 14:e0221589
Rooker JR, Dance MA, Wells RJD, Ajemian MJ and others (2019) Population connectivity of pelagic megafauna in the Cuba–Mexico–United States triangle. Sci Rep 9:1663
Scharer RM, Stevens PW, Shea CP, Poulakis GR (2017) All nurseries are not created equal: large-scale habitat use patterns in two smalltooth sawfish nurseries. Endang Species Res 34:473–492
Shaffer RV, Nakamura EL (1989) Synopsis of biological data on the cobia *Rachycentron canadum* (Pisces: Rachycentridae). NOAA Tech Rep NMFS 82. FAO Fish Synop 153. http://www.fao.org/3/ap958e/ap958e.pdf
Shoji J, Mitamura H, Ichikawa K, Kinoshita H, Arai N (2017) Increase in predation risk and trophic level induced by nocturnal visits of piscivorous fishes in a temperate seagrass bed. Sci Rep 7:3895
Skomal GB, Braun CD, Chisholm JH, Thorrold SR (2017) Movements of the white shark *Carcharodon carcharias* in the North Atlantic Ocean. Mar Ecol Prog Ser 580:1–16
Tickler DM, Carlisle AB, Chapple TK, Curnick DJ, Dale JJ, Schallert RJ, Block BA (2019) Potential detection of illegal fishing by passive acoustic telemetry. Anim Biotelem 7:1
Udyawer V, Dwyer RG, Hoenner X, Babcock RC and others (2018) A standardised framework for analysing animal detections from automated tracking arrays. Anim Biotelem 6:17
Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput 27:1413–1432
Wickham H, Averick M, Bryan J, Chang W and others (2019) Welcome to the Tidyverse. J Open Source Softw 4:1686

Appendix. Full list of author addresses

Claudia Friess[1,*,#], Susan K. Lowerre-Barbieri[1,2,#], Gregg R. Poulakis[3], Neil Hammerschlag[4], Jayne M. Gardiner[5], Andrea M. Kroetz[6], Kim Bassos-Hull[7], Joel Bickford[1], Erin C. Bohaboy[8], Robert D. Ellis[1], Hayden Menendez[1], William F. Patterson III[2], Melissa E. Price[9], Jennifer S. Rehage[10], Colin P. Shea[1], Matthew J. Smukall[11], Sarah Walters Burnsed[1], Krystan A. Wilkinson[7,12], Joy Young[13], Angela B. Collins[1,14], Breanna C. DeGroot[15], Cheston T. Peterson[16], Caleb Purtlebaugh[17], Michael Randall[9], Rachel M. Scharer[3], Ryan W. Schloesser[7], Tonya R. Wiley[18], Gina A. Alvarez[19], Andy J. Danylchuk[20], Adam G. Fox[19], R. Dean Grubbs[21], Ashley Hill[22], James V. Locascio[7], Patrick M. O'Donnell[23], Gregory B. Skomal[24], Fred G. Whoriskey[25], Lucas P. Griffin[20]

[1]Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL 33701, USA

[2]Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32653, USA

[3]Charlotte Harbor Field Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Port Charlotte, FL 33954, USA

[4]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA

[5]Division of Natural Sciences, New College of Florida, Sarasota, FL 34243, USA

[6]Riverside Technology, Inc. for NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City, FL 32408, USA

[7]Mote Marine Laboratory, Sarasota, FL 34236, USA

[8]National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, HI 96818, USA

[9]U.S. Geological Survey Wetland and Aquatic Research Center (USGS-WARC), Gainesville, FL 32653, USA

[10]Institute of Environment, Florida International University, Miami, FL 33199, USA

[11]Bimini Biological Field Station Foundation, South Bimini, Bahamas

[12]Chicago Zoological Society's Sarasota Dolphin Research Program c/o Mote Marine Laboratory, Sarasota, FL 34236, USA

[13]Tequesta Field Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Tequesta, FL 33469, USA

[14]University of Florida IFAS Extension, Florida Sea Grant, Palmetto, FL 34221, USA

[15]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL 34946, USA

[16]Florida State University, Tallahassee, FL 32306, USA

[17]Senator George Kirkpatrick Marine Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Cedar Key, FL 32625, USA

[18]Havenworth Coastal Conservation, Palmetto, FL 34221, USA

[19]Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

[20]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA 01003, USA

[21]Florida State University Coastal and Marine Laboratory, St. Teresa, FL 32358, USA

[22]Lynker Technologies for NOAA, National Ocean Services, Office of Response and Restoration, Marine Debris Division, Silver Spring, MD 20910, USA

[23]Rookery Bay National Estuarine Research Reserve, Naples, FL 34113, USA

[24]Massachusetts Division of Marine Fisheries, New Bedford, MA 02744, USA

[25]Ocean Tracking Network, Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada

Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA
Reviewed by: J. Walter and 2 anonymous referees

Submitted: September 9, 2020
Accepted: January 11, 2021
Proofs received from author(s): March 17, 2021