



## 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

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### ABSTRACT

Understanding the nature of migratory behaviors within animal populations is critical to develop and refine conservation and management plans. However, tracking migratory marine animals across life stages and over multiple years is inherently difficult to achieve, especially for highly migratory species. In this paper, we explore the use of acoustic telemetry to characterize the spatial ecology of Atlantic tarpon (*Megalops atlanticus*), elucidate the ecology of this poorly studied species, and ultimately inform conservation and management. Using the data from twenty-two acoustically tagged Atlantic tarpon, we found a diversity of tarpon migratory patterns, including spatial and temporal overlap for some individuals. We also reveal fine scale movements within specific ecosystems, as well as a range of distributions and connectivity across coastal waters of the southeastern United States of America. For tarpon with tracking durations greater than one month ( $n = 13$ ), we found heterogeneous space use and migratory connectivity with some tarpon remaining close to their capture location while others migrated hundreds of kilometers. In addition, we were able to identify a northern and southern limit for one migratory tarpon that had detections spanning over 365 days. We share analyses on Atlantic tarpon data, including model-driven approaches and network analysis, to investigate movement strategies and space use, which may be pertinent to other studies involving highly migratory species. The project was a collaborative effort involving several acoustic telemetry networks which enabled the monitoring of broad- and fine-scale movements for extended periods of time that would normally be difficult to achieve with other monitoring techniques. Although challenges exist with applying acoustic telemetry to monitor highly migratory species, we also discuss its value in enabling researchers to assess movements and space use beyond the focal species, such as cross-ecosystem comparisons and multi-species interactions.

### 1. Introduction

Globally, migratory species are declining due to anthropogenic habitat alteration and degradation, overexploitation, and shifts in climate (i.e., match-mismatch hypothesis) (Both et al., 2006; Wilcove and Wikelski, 2008; Robinson et al., 2009). Migrants facilitate important ecosystem services such as trophic interactions (e.g., predator-prey relationships), energy transfer, and nutrient transport that an ecosystem

would otherwise lack (Bauer and Hoye, 2014). In addition, migrant species are critical within coupled social-ecological systems as subsistence, economic value, or in part, as a cultural identity for communities (Daily, 1997; Reynolds and Clay, 2011). The largest hurdle to overcome in migratory species conservation is the lack of information on habitat requirements and migratory connectivity, such as the geographic cyclical overlap of disparate groups of individuals (Webster et al., 2002). Without an understanding of migratory connectivity

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across time and space (e.g., habitat), conservation strategies are difficult to develop and implement across political and cultural boundaries (Hansson and Åkesson, 2014).

The use of biotelemetry and biologging (i.e., receivers, transmitters, and archival loggers) to track individual animals has emerged as a technique in understanding the ecology and connectivity of migratory species (Cooke et al., 2004; Hussey et al., 2015). Biotelemetry and biologging has been most used with migratory terrestrial animals such as mammals (Ballard et al., 1998) and birds (Weimerskirch et al., 1993; Fuller, 2003; Weimerskirch et al., 2016), while applications of this technology are growing rapidly in the marine environment (Donaldson et al., 2014; Hussey et al., 2015; Crossin et al., 2017). Until recently, satellite biotelemetry (e.g., pop-up satellite tags [PSAT], fast-lock GPS, smart position and temperature transmitting [SPOT]) was the most used technology to study migratory marine species (Hussey et al., 2015), however this technology tends to be restricted to large free-swimming individuals and requires that the device (e.g., PSAT) or the animal (e.g., carrying a fast-lock GPS or SPOT) breaches the surface of the water such that the device can transmit data to satellites. Further, satellite tags are external and are buoyant which generates lift on the tagged individual (Grusha and Patterson, 2005), can become biofouled (Hays et al., 2007), and often are susceptible to tag failure and short retention times (Økland et al., 2013), thus inhibiting long-term monitoring of movements for migratory species (Musyl et al., 2011; Jepsen et al., 2015).

Over the past 25 years, passive acoustic telemetry has become a mainstream technology to answer conservation questions in the marine environment at ecologically meaningful spatial-temporal scales appropriate to informing management (Hussey et al., 2015; Crossin et al., 2017). Acoustic transmitters are generally less than 16 mm in diameter, less than \$350 (U.S.), with battery lives that can last 5–7 years. These benefits, have led to acoustic telemetry to become the most popular tracking method among marine researchers, with thousands of tags and receivers deployed to date (Heupel and Webber, 2012; Donaldson et al., 2014; Hussey et al., 2015). Capitalizing on the potential to ask and address new questions with acoustic telemetry brought on by the increase in telemetry studies and since hydrophone receivers can detect individuals tagged by other researchers, inter-institution and inter-agency collaborations have been established across the Gulf of Mexico and Western Atlantic. These participatory platforms include Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG), Florida Atlantic Coast Telemetry Array (FACT), and Atlantic Cooperative Telemetry Network (ACT) (Currier et al., 2015; Hussey et al., 2015; Whoriskey and Hindell, 2016).

The collaborative networks, consisting of hundreds or even thousands of receivers, enables researchers to track individual animals over a much broader geographic range than what can typically be achieved by an individual researcher (Whoriskey, 2015; Whoriskey and Hindell, 2016). As such, this opens up opportunities to monitor broad-scale individual variation in migratory behaviors, formulate cross-ecosystem comparisons, and test hypotheses of multi-species interactions. Here, we explore the use of acoustic telemetry to describe the movement patterns of a highly migratory coastal species, Atlantic tarpon.

### 1.1. Tracking highly migratory Atlantic tarpon using acoustic telemetry

Atlantic tarpon, *Megalops atlanticus*, is a renowned migratory gamefish that provides an important source of revenue for recreational and subsistence coastal communities across the Southeastern USA, Gulf of Mexico, and the greater Caribbean (Ault, 2008). The tarpon fishery began in Charlotte Harbor, FL in 1885, when the first tarpon ever caught on hook and line was recorded (White and Brennan, 2010). This led to the tarpon fishing tradition that continues to this day, with the most extensive recreational tarpon fishery existing in Florida. Today, the recreational tarpon fishery has rapidly expanded with fishing effort increasing along tarpon migratory routes, such as northern Gulf of

Mexico (e.g., Alabama, Louisiana) and in areas where there was little effort in the past (e.g., South Carolina, Georgia). While Atlantic tarpon are listed as vulnerable by the IUCN (Adams et al., 2012), management plans vary across international and national management jurisdictions making it difficult to adequately manage this migratory species (Adams et al., 2014; Adams and Cooke, 2015).

Without understanding the degree and scale of tarpon connectivity across fisheries management zones, current tarpon management plans may contradict one another and may be harmful for this fishery. For example, within the USA, harvest regulations vary widely across states (i.e., catch-and-release only, limited harvest, or no limits). Although tarpon harvest records within USA are data deficient, anecdotally, it occurs on a semi-regular basis in states that allow for harvest. Individuals are not often taken for consumption but rather as trophies, targeting the largest, oldest, and most fecund females in the population. Further, since the greatest threats to tarpon habitats are in coastal areas (wetlands, rivers, estuaries, beaches) there is an urgent need to know the extent of coastal habitat use by tarpon and how their movement patterns may be influenced by human alterations of habitats (e.g., habitat degradation, poor water quality, oil spills) (Ault, 2008). Understanding the degree of fish movement between states and regions is necessary to refine fisheries management plans from both harvest and habitat quality standpoints.

Given the economic importance of the Atlantic tarpon fishery across the region, a better understanding of tarpon movements and habitat use is needed to formulate and implement a management plan that can protect the species throughout its migrations that span state, federal, and international boundaries. Previous work with PSAT and SPOT tags revealed general seasonal migrations for tagged tarpon – northward from Florida or Mexico in spring, and a return southward in fall (Luo et al., 2008; Hammerschlag et al., 2012; Luo and Ault, 2012). However, early generation satellite transmitters were relatively large and required tarpon often larger than > 35 kg for tagging, reducing the capacity to study the movement patterns of a large portion of the population that are smaller than this body size threshold. Further, poor spatial resolution (> 100 km) and short tracking durations (mean  $54 \pm 43$  d SD) (Luo and Ault, 2012) only provide a coarse snapshot into the movement patterns of Atlantic tarpon.

The overarching objectives of this paper are to use results from the first two years of a long-term study on Atlantic tarpon to: 1) highlight and describe the diversity in tarpon migratory movements and connectivity across the coastal waters of the southeastern USA, 2) demonstrate methods that can be adopted in the future to examine the migratory connectivity, movements, and habitat use of both Atlantic tarpon and other mobile species throughout the nearshore waters of the Gulf of Mexico and Western Atlantic, and 3) provide insights related to studying migratory animals through an extensive collaborative framework of academic institutions, non-governmental conservation organizations, and government natural resource agencies.

## 2. Materials and methods

### 2.1. Receiver deployment and participatory data sharing platforms

Between 2015 and 2017, we deployed 92 autonomous fixed acoustic receivers (V2RW receivers, Vemco Inc., Halifax, NS, Canada) in Florida (Florida Keys, Charlotte Harbor, and Apalachicola), Georgia, and South Carolina. In the Florida Keys, local fishing guides provided important ecological knowledge of the areas, and aided and directed the placement of receivers in locations with high tarpon abundance and likely movement corridors. The majority of our receivers (79 of 92) spanned the Florida Keys. Specifically, receivers were primarily placed along shallow sandy contours, seagrass flats, and within deep channels ranging from 2 to 7 m in depth. Thirteen of the 92 receivers were loaned to other state agencies or academic institutions to facilitate collaboration and improve detection coverage by a series of acoustic detection

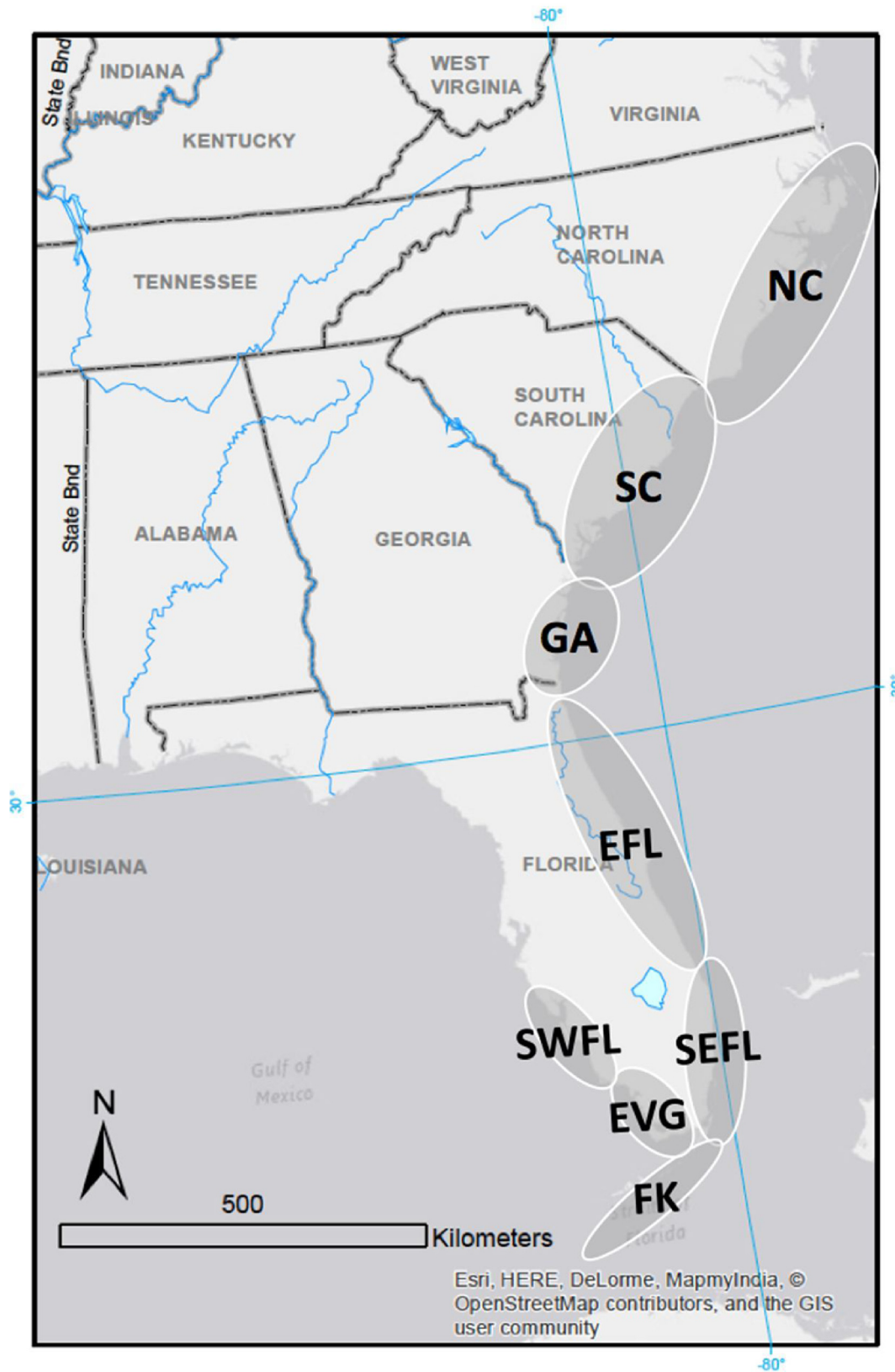


Fig. 1. Study area of South Eastern US overlaid with 8 detection regions (i.e., aggregate of receiver detections) corresponding to the area’s geography, including: Florida Keys (FK), Southwest Florida (SWFL), Everglades (EVG), Southeast Florida (SEFL), East Florida (EFL), Georgia (GA), South Carolina (SC), and North Carolina (NC).

gates (Charlotte Harbor, Apalachicola, Georgia, and South Carolina).

While our 79 receivers, along with receivers from Florida Fish and Wildlife Commission, were positioned to track localized movements in the Florida Keys, they also play an important role in filling detection gaps for other researchers studying transient animals that may occur or pass through the most southern portion of Florida. Including our receivers, the combined receivers across the collaborative institutional networks (ITAG, FACT, and ACT) includes ~1300 receivers across Gulf of Mexico and > 3000 receivers along coastal southeastern USA. Further, Ocean Tracking Network (OTN), dedicated to improving international researcher collaboration and marine monitoring, has provided aid to establish the existent data sharing platforms that facilitate sharing of detection data, and receivers to increase in-water detection coverage (Cooke et al., 2011). The data sharing platforms either use an orphan tag query (iTAG) or aggregate institutional-transmitter ownership information online (FACT and ACT) to facilitate sharing detections among researchers.

## 2.2. Tarpon capture and tagging

Tarpon were captured in Florida (i.e., Florida Keys, Everglades, Charlotte Harbor, Tampa Bay, and Apalachicola), Georgia (i.e., near Cumberland Island), and South Carolina (i.e., near Georgetown) using hook and line with either conventional or fly fishing gear. Fork length and girth (cm) were recorded and used to estimate weight (kg), fish estimated below 7 kg were not tagged. Acoustic tags (Vemco V16, 69 kHz, 16 mm diameter, 98 mm length, 17.3 g in air, min and max delay times 60–120 s, estimated battery life 1910 days; Vemco Inc., Halifax, NS, Canada) were surgically implanted in 48 tarpon between May 2016 and August 2017. To implant tags, one to two scales were removed from tarpon posterior to the pelvic fin and a 3 cm incision was made using a sterilized scalpel. The acoustic transmitter was then inserted into the coelomic cavity, and the incision closed with a single suture (PDS-II monofilament absorbable 3-0, model Z497G, Ethicon Inc., Somerville, NJ). Time to perform each surgery was < 5 min. Tarpon were carefully revived and released by slowly idling the boat forward with the fish held by the side or holding the fish stationary under the pelvic fins to allow for uninhibited buccal pumping.

### 2.2.1. Data analysis

**2.2.1.1. Cross-ecosystem comparisons and movement strategies.** For the three Atlantic tarpon with the longest tracking durations (11–13 months of detections), we display locational data that highlight the variability of movement patterns and the collaborative nature of the study. All maps were generated with the gmap package (Kahle and Wickham, 2016). In addition, using detection data from one individual tarpon, we demonstrate a model-driven approach using the package migrateR (Spitz et al., 2017), to show how tarpon movement strategies may be empirically assessed in the future (Bunnefeld et al., 2011; Spitz et al., 2017). Based on net squared displacement (NSD), that is the square of the straight-line distance between an animal's origin and successive relocations (Turchin, 1998), this method incorporates fitting non-linear *a priori* statistical movement models to the data and accessing the best fit using Akaike information criteria (AIC, Burnham and Anderson, 2001; Spitz et al., 2017). The selected "origin" for the models were selected using the findrloc function in the migrateR package which calculates the relative net squared displacement (rNSD) from each detected location and then uses a reference location as the origin that will produce the lowest AIC value for the top model. The five movement models were: mixed migrant, migrant, disperser, nomad and resident (see review by Bunnefeld et al., 2011; Spitz et al., 2017). After selecting the top movement model, location data was grouped into ranges (e.g., southern or northern ranges or summer versus winter season) based on timing of movement parameter estimates from the model using the function spatmig in the migrateR package.

### 2.2.2. Network analysis and connectivity

We used network analysis to demonstrate how the variability in tarpon space use and connectivity across different regions may be assessed. Network Analysis, based in graph theory, provides a means to easily interpret and analyze the linked connections between individual movements and receivers. Following Dale and Fortin (2010) and Finn et al. (2014), bipartite graphs were generated to represent linkages from individual tarpon to regions visited (receiver aggregates). We aggregated detections into eight regions that correspond to the area's geography, including: Florida Keys (FK), Southwest Florida (SWFL), Everglades (EVG), Southeast Florida (SEFL), East Florida (EFL), Georgia (GA), South Carolina (SC), and North Carolina (NC) (Fig. 1). To highlight connectivity across regions, we used individual Atlantic tarpon with tracking durations greater than one month (i.e., date captured through the last date of detection). In total, data for 13 Atlantic tarpon were used for network analyses. Bipartite graphs connect tarpon to their detected regions or "nodes" using weighted links or "edges" (i.e., number of detections in each region by individual). The package igraph was used to generate network graphs (Csardi and Nepusz, 2006). The Fruchterman and Reingold force-directed layout algorithm (Fruchterman and Reingold, 1991) was applied on bipartite graphs making attractive and repulsive forces among the regions (nodes) proportional to the weight of the edges connecting adjacent nodes (Finn et al., 2014). While little or no attraction between nodes would arrange the bipartite graph into an equidistant circle, strong attraction between nodes would arrange the graph into heavily weighted edges with tight connections, forming potential network communities (Finn et al., 2014).

To show the extent of network communities (i.e., heterogeneous space use) across the 13 fish, we applied six community detection algorithms (CDAs), including: 'Leading-Eigenvector' (Newman, 2006a,b), 'Walk-Trap' (Pons and Latapy, 2006), 'Fast-Greedy' (Newman and Girvan, 2004; Clauset et al., 2004), 'Spin-Glass' (Reichardt and Bornholdt, 2006), 'Label-Propagation' (Raghavan et al., 2007), and 'Multilevel' (Blondel et al., 2008; Finn et al., 2014). The strength and quality of the potential network communities or "modules" detected were assessed by a calculated modularity score for each community detection algorithm (Newman and Girvan, 2004). Modularity scores are calculated using the proportion of edges within selected groups minus the expected proportion if edges were distributed randomly, given the degree (number of edges) of each node (Finn et al., 2014). Modularity is a useful metric for determining the quality of module divisions created by the algorithms. Considering this is a demonstrative technique with limited detections over time, no normalization or statistical tests (i.e., Wilcoxon sum-rank test) occurred that would evaluate if modules were significant, i.e., if nodes were more linked to one another within the module than with other modules or the entire network (Song and Singh, 2013).

## 3. Results

Movement data were examined from 22 tarpon ( $27.23 \pm 7.71$  kg weight,  $134.68 \pm 14.60$  cm FL) captured from Florida Keys (FK,  $n = 15$ ), Southwest Florida (SWFL,  $n = 1$ ), Everglades (EVG,  $n = 1$ ), Georgia (GA,  $n = 3$ ), and South Carolina (SC,  $n = 2$ ). Tracking duration (i.e., date captured to last detection) for these 22 fish ranged between 4–396 d ( $108 \pm 138$ ), however these fish will continue to be tracked for up to five years.

### 3.1. Cross-ecosystem comparisons and movement strategies

In total, 22 tarpon were detected on receiver networks of 15 different institutions. In many instances when tarpon were detected at other institutional receivers, they were only detected briefly (< 10 detections), while for other locations (i.e., Florida Keys, Everglades, Miami, and Cape Canaveral) tarpon displayed resident-like behaviors

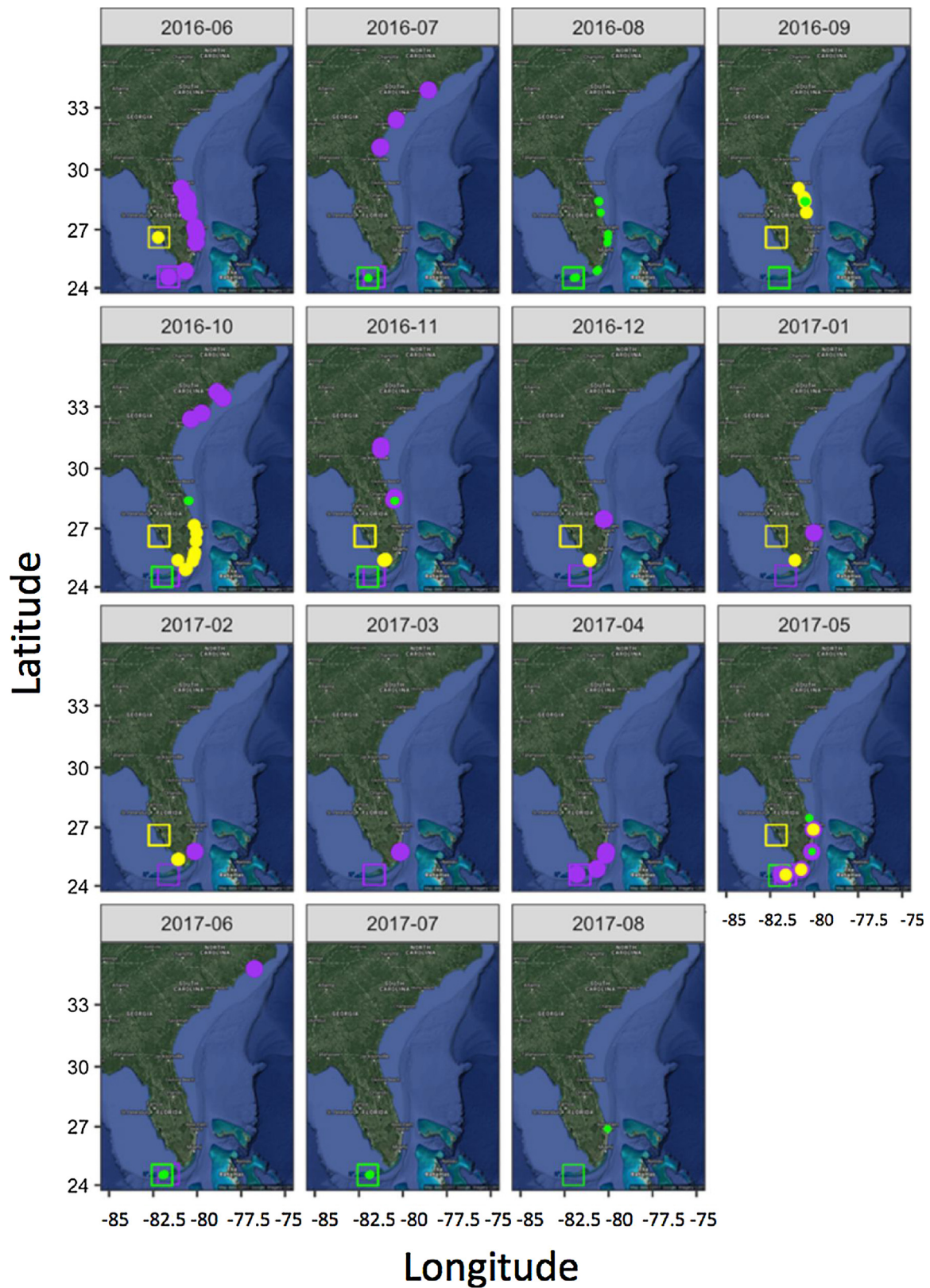


Fig. 2. Detections (dots) for three tarpon, ID 18574 (purple), ID 18565 (yellow), ID 18576 (green) across June 2016–May 2017. Capture locations (squares) specific to each fish are listed in only months that have detections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

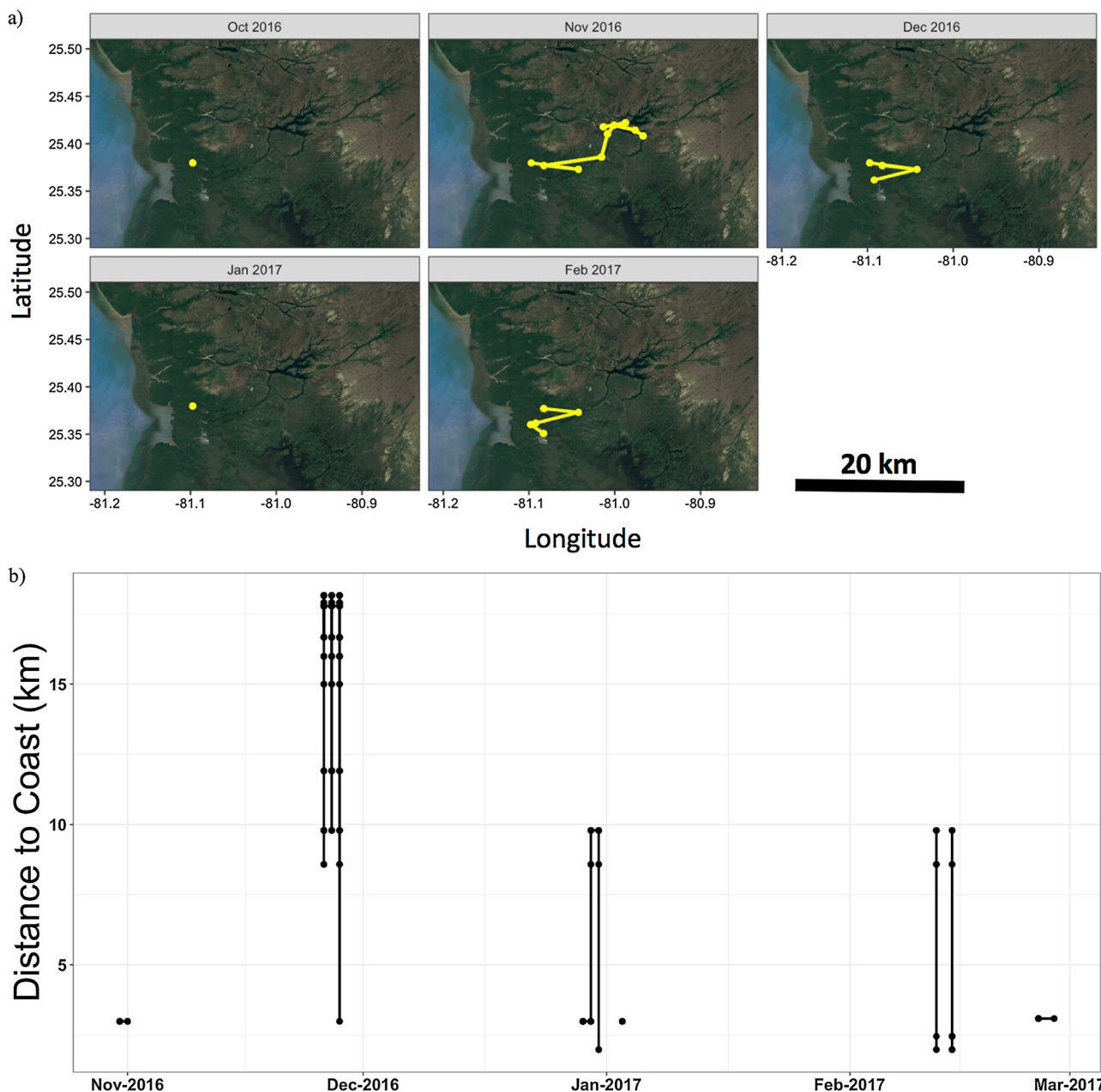
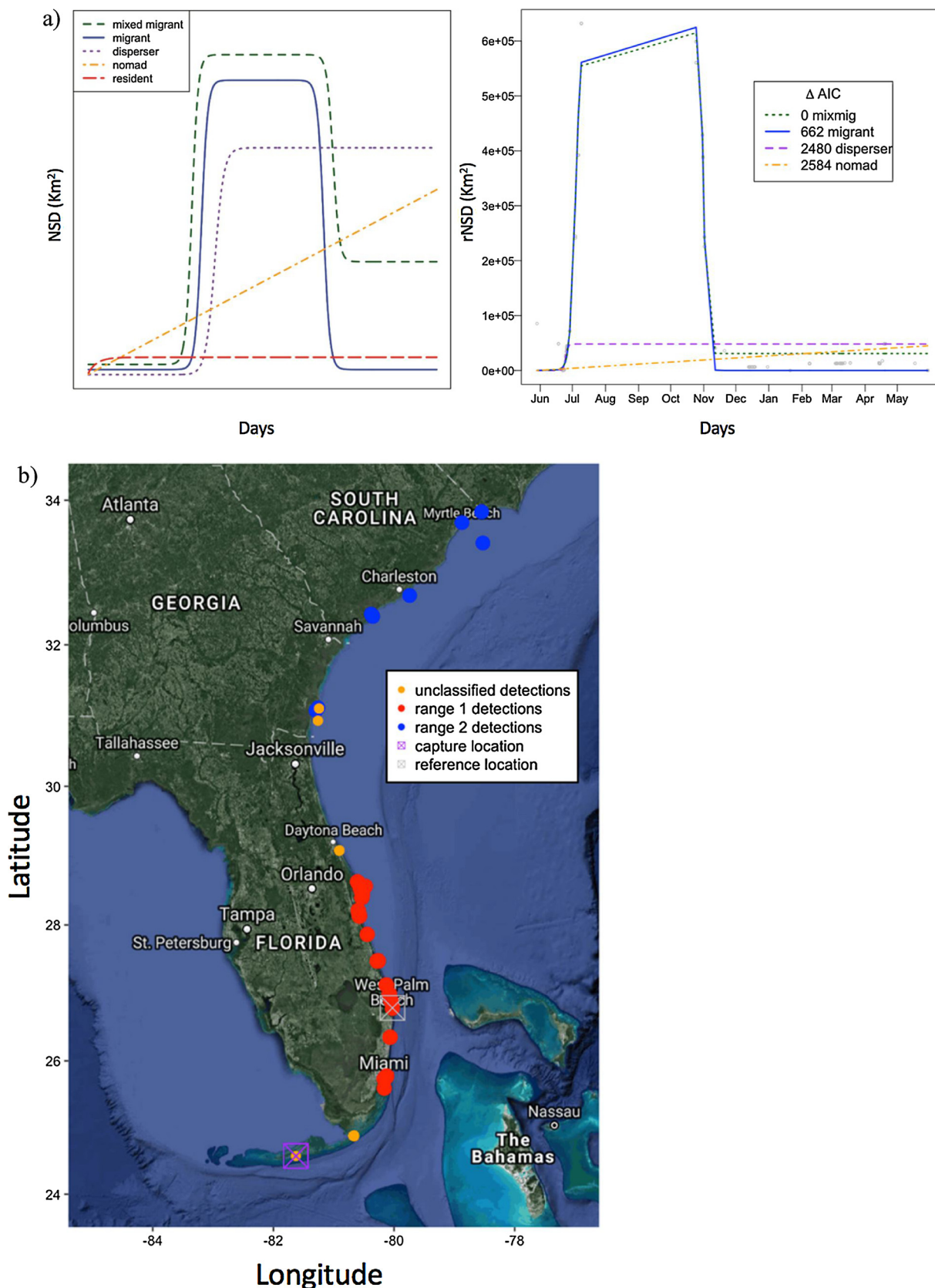


Fig. 3. a) Detections (dots) for ID 18565 (yellow) in the Shark River, Everglades, managed by Florida International University, across October 2016–February 2017. b) Plot showing distance from coast movements corresponding with ID 18565 detection data in Shark River, Everglades. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

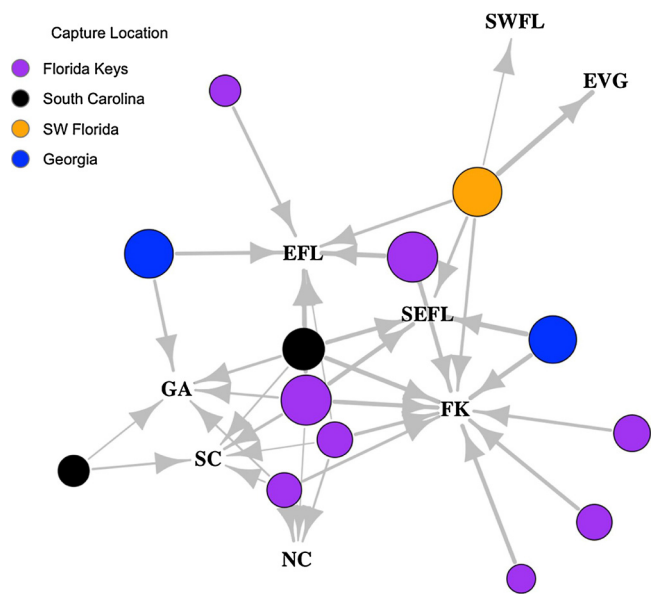
with detections spanning multiple months. The movements of three tarpon with > 340 days of detections (i.e., ID 18576, ID 18565, and ID 18574) suggests spatiotemporal differences in individual use across regions (Fig. 2). Although individual fish were unaccounted for (i.e., no detections) between two and four months, there was some spatial-temporal overlap of detections, meaning similar residency periods (within a month) in a general location. For example, ID 18565 and ID 18576 were both detected near Cape Canaveral in September 2016, ID 18574 and again ID 18576 were detected near Cape Canaveral in November 2016, and all three fish were detected between West Palm Beach and Miami in May 2017. In contrast to large, broad-scale movements for ID 18565 (captured in Charlotte Harbor, FL), fine-scale detection data for this individual was also collected for over 5 months within the Everglades (Fig. 3a), including a series of large intra-tidal river movements ranging from 5 to 20 km inland from the coast into waters of very low salinity (< 10 PSU, USGS hydrostation SRS3)

(Fig. 3b).

Using the NSD model-driven approach, we assessed the movement strategy for ID 18574, which was captured in the Florida Keys May 29, 2016, and detected for 392 days (Fig. 4a). This fish reached its furthest detection (N 33.84145, W -78.5474) from its capture location near the border of South Carolina and North Carolina in July 2016 and its 2017 furthest detection (N 34.6932, W -76.7375) at Pamlico sound, North Carolina in late June 2017. To ensure NSD movement models were fit correctly, tracking data was subset to one year’s length of data (i.e., the first 365 days), which partially removed the second movement to North Carolina in June 2017. Using the first 365 days of tracking, this fish traveled an estimated minimum distance of nearly 1300 km to its farthest northern detection in 41 days, averaging ~31 km per day. There were no detections for three months (likely as the fish continued north) until detected again at its furthest north detection in October 2017, and then returned southward eventually being detected in the



**Fig. 4.** a) Left, categorization of non-linear movement models (mixed migrant, migrant, disperser, nomad, resident) generated from theoretical net square displacement (NSD) movements adopted from Spitz et al. (2017). Right, NSD model approach using detection data from ID 18574 with reference location optimized, Akaike information criteria produced lowest value for mixed migrant movement strategy. b) Detections (dots) for ID 18574 across southeastern US coast between May 2016–May 2017, detections are color coordinated to ranges which were generated via migraton timing parameter estimates. Unclassified relocations (orange), range 1 (red), range 2 (blue), capture location (purple), and reference location (grey) are plotted respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Bipartite graph of tarpon-region network in southeastern US with Fruchterman-Reingold force-directed layout algorithm. The network links (edges) tarpon (nodes) to regions visited (region acronyms). The width of edges is proportional to the number of detections at each region per individual and the diameter of each fish node is proportional to the duration of tracking (i.e., larger node has a longer tracking duration than a smaller node). The Fruchterman-Reingold force-directed layout algorithm balances attractive and repulsive forces among nodes which are proportional to the weight of edges connecting adjacent nodes (i.e., similar space use by individuals would be clustered together). Individuals are clustered more closely together in their respective captured regions (e.g., Florida Key captured individuals (purple nodes) with Florida Key region node). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mid Florida Keys in April 2017 (~90 km north of its capture location). The findrloc function selected a detection on June 22, 2016 south of West Palm Beach, FL as the rNSD model’s origin. All models converged except for the resident model. Using the lowest AIC value to select the top model, mixed migrant movement strategy was chosen with migrant as the second best potential model (Fig. 4a). Using the parameter estimates from the mixed migrant model for ID 18574, range 1 was selected as the southern range while range 2 was selected as the northern range (Fig. 4b), further, range 1 was associated with detections from late-November to mid-June and range 2 with detections from July to early-November. Relocation data south of range 1 and in between range 1 and range 2 remained unclassified.

**Table 1**

Capture information on tarpon with tracking durations greater than one month and their connections across regions as determined via network analysis methods.

ID	Weight (kg)	FL (cm)	Capture Loc.	Date Tagged	Tracking Dur.	Regions Det.
15921	32	142	FK	4/23/17	62	FK, GA, SC, NC
15929	39	155	FK	5/10/17	30	FK
16671	25	130	FK	5/28/17	41	EFL
16678	14	107	FK	5/4/17	68	FK
16680	25	137	SC	9/27/16	141	FK, SEFL, EFL, GA, SC
16682	27	132	FK	4/29/17	78	FK
16685	30	137	SC	9/28/16	40	GA, SC
16687	34	152	FK	4/28/17	68	FK, EFL, SC, NC
18565	25	129	SWFL	6/12/16	343	SWFL, EVG, FK, SEFL, EFL
18572	23	130	GA	8/18/16	331	EFL, GA
18573	30	146	GA	8/18/16	286	FK, SEFL
18574	30	141	FK	5/29/16	392	FK, SEFL, EFL, GA, SC, NC
18576	30	142	FK	7/8/16	396	FK, SEFL, EFL

3.2. Network analysis and connectivity

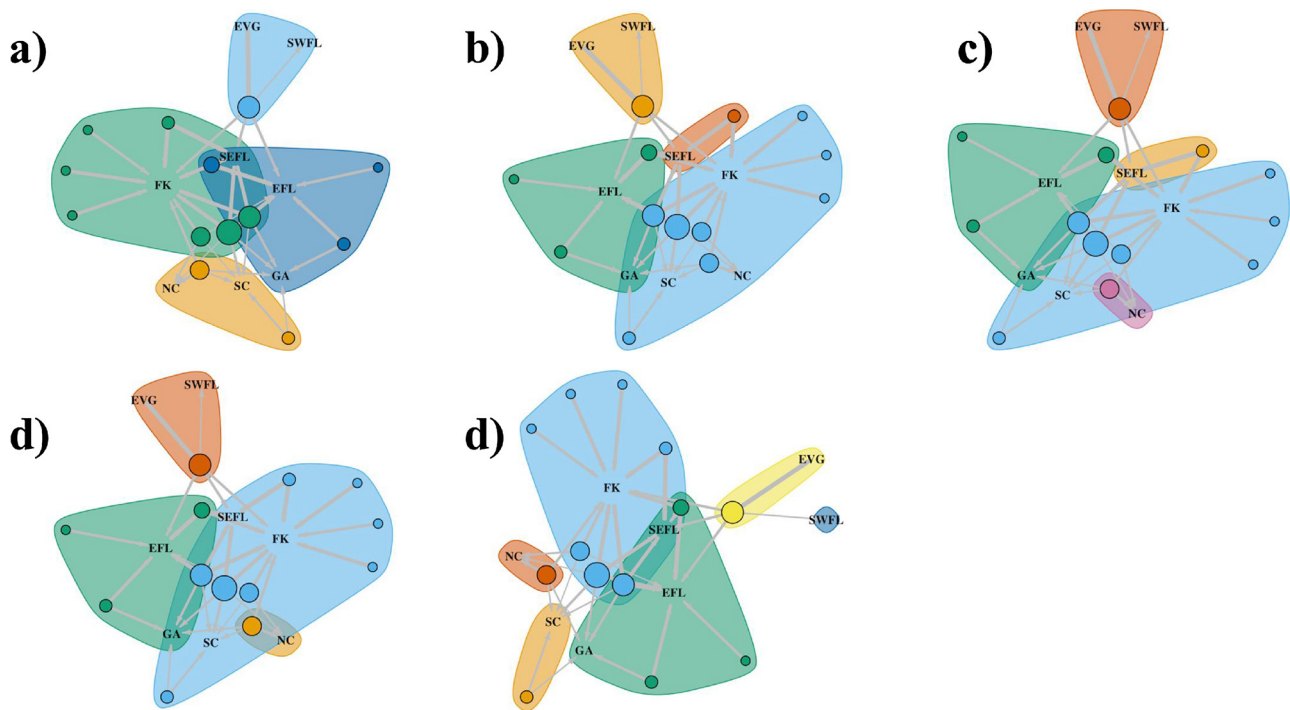
Using the Fruchterman-Reingold force directed layout algorithm and data from tarpon with tracking durations greater than one month (n = 13), the bipartite graph highlights heterogeneous space use among tarpon and associated regions (Fig. 5). Although limited in sample size and duration of tracking, tarpon with greater than one month of tracking data displayed wide variability in connectivity across regions (Fig. 1, Table 1). Some tarpon with shorter tracking periods (between one and three months, n = 5, 78 ± 20 d), were arranged near the region of capture, however others with equally limited tracking durations (n = 2, 65 ± 4 d) were positioned in the middle by the algorithm, suggesting high connectivity across regions in a relatively short amount of time. Atlantic tarpon with longer tracking durations (> 3 months, n = 6, 315 ± 94 d) generally had much wider connectivity with many linkages across regions and were positioned in the middle of the bipartite graph. The single fish captured in SWFL (Charlotte Harbor, 25 kg, tracking duration of 343 days; shown in orange) had high connectivity to multiple regions across EFL, SEFL, FK, and the EVG, some of which were unvisited by the other 12 fish.

Network communities derived from the bipartite graph by six CDAs highlighted some of the potential similarities and differences among tarpon space use (Fig. 6). Using modularity scores (a measure of strength and quality of the modules) as a performance metric across CDAs, some CDAs produced better divisions and thus a greater insight into tarpon space use than CDAs with lower modularity scores. Two of the six CDAs, Fast-Greedy and Multilevel, produced four identical module groups with the highest modularity score of 0.495 (Fig. 6b, Table 2). Modularity scores from the four other CDAs were similar with Spin-Glass (0.494 modularity), Leading Eigenvector (0.491 modularity), Label Propagation (0.491 modularity), and Walktrap (0.490 modularity). All CDAs had four modules detected other than Spin-Glass and Walktrap which had 6 modules detected each with one module forming around the SWFL region itself.

4. Discussion

Acoustic telemetry offers the promising capacity to track tarpon over time and space for a broad range of life stages. Long-term tracking may provide insight into migratory connectivity, potential inter-annual site fidelity and behaviors, and ontogenetic shifts that is necessary for effective conservation and management. These data collected from acoustically tagged tarpon suggest broad and heterogeneous connectivity among individuals and across regions. Management should be expanded across state lines to meet conservation end points, including adjusting harvest regulations considering that individuals move freely over jurisdictional lines. Tarpon are unique in that they use inshore (wetlands), coastal (estuaries, coastlines), and offshore habitats through their life history, and are also capable of migrating among distinct





**Fig. 6.** Community networks, produced via six community detection algorithms (CDAs), overlaid on tarpon-region bipartite graphs. a) four modules detected using Leading-Eigenvector CDA, b) four identical modules detected using Fast-Greedy and Multilevel CDAs, c) six modules detected using Spin-Glass CDA, d) four modules detected using Label-Propagation CDA, and e) six modules detected using Walktrap CDA.

**Table 2**

Results from the six community detection algorithms applied to the bipartite graph (13 tarpon with > 1 month tracking duration across 8 regions). Modularity indicates the community detection algorithms ability to partition the bipartite graph. Scores are calculated using the proportion of edges within selected modules minus the expected proportion if edges were distributed randomly, given the degree (number of edges) of each node. Higher modularity scores indicate better formation and division across modules.

Community detection algorithm	Modularity	Modules detected
Leading Eigenvector	0.491	4
Fast-Greedy	0.495	4
Spin-Glass	0.494	6
Label Propagation	0.491	4
Walktrap	0.490	6
Multilevel	0.495	4

segments of marine ecosystems. Examining the three fish with tracking durations greater than 340 days highlighted this pattern with variable residency times across geographic regions. As such, strategies for habitat restoration and protection that best suits tarpon should be thought of across multiple scales and regions (e.g., Florida Everglades, Florida Keys, coastal river deltas in South Carolina). While additional data will continue to build upon our understanding of connectivity and space use, an important future management question that requires spatio-temporal data to answer is: do local tarpon fisheries rely on the same individuals each year or are there new individuals cycling among fisheries each year? By using acoustic telemetry data made available because of collaborative participatory networks, many more fundamental and applied questions could be addressed that will inform the management of Atlantic tarpon.

Although we currently present movement data for the first two years of a long-term study on Atlantic tarpon, this work already extends beyond what was previously revealed by other movement studies for the species. For example, satellite tracking of Atlantic tarpon provided data for an average of 54 d for PSAT tags (Luo and Ault, 2012) and 25 d

for SPOT tags (Hammerschlag et al., 2012). Further, the mean weight of tarpon tagged with acoustic transmitters in our current study was 30.48 kg with a range between 6.8 kg and 72.57 kg, a far wider range than possible with satellite tags. The internal, smaller, and less expensive tags provide a viable option for those wishing to track migratory species across longer periods of time and sizes.

This study features the emerging collaborative (i.e., iTAG, FACT, and ACT) success of acoustic telemetry to track migratory marine fish and highlights some developing techniques to analyze the data. Examining the spatial visualizations of individual tarpon provide a simple yet useful way to observe general spatiotemporal use. The data for three fish collected via 15 institutional receiver networks suggest different movement strategies, but all fish underwent a general migration that included extended periods of times in specific areas and variable overlap with one another. Similarly, Mather et al. (2013) observed that all acoustically tagged striped bass (*Morone saxatilis*) underwent long distance migrations with extended periods of seasonal overlap but intra-individual differences existed across movement strategies. Just as with striped bass, tarpon that use specific routes may have varying across-system coastal impacts via exporting nutrients and energy in the form of biomass.

While collaborations among institutions provide a means to track broad scale migratory movements (e.g., within and across regions), it can also facilitate the tracking of fine-scale movements if individuals are readily detected within a localized network for an extended period of time. Observed detection data at finer scales can allow for novel comparisons across ecosystems and for individual-level variation in movement in an otherwise unobservable ecosystem, such as for the large intra-tidal river movements within the Everglades between October and February for ID 18565. This network of receivers is over 75 km from our nearest receiver in the Florida Keys and represents an entirely different ecosystem than is covered by another network of receivers.

Finally, we demonstrated how to assess movement strategies and ranges empirically through the use of NSD movement models. Future analysis of movement strategies may highlight the importance of

specific pre-spawn aggregation sites, northern productive estuary systems (e.g., Mississippi, Carolinas, Chesapeake Bay), and thermal refuges. Observed individual movement strategies and seasonal ranges across years and size classes will provide important biological information on habitat use and migrations; as well as insight into how climate change or other anthropogenic threats may alter behaviors.

Network analysis was a useful tool to examine tarpon migratory connectivity across the southeastern U.S., with tagged individuals displaying heterogeneous space use. Derived from the bipartite graph and CDAs, two of the six CDAs produced the same network communities consisting of identical modules and the highest modularity score (Fig. 6b). Using these two CDA's with the highest modularity scores, it suggests while tarpon have tight connections to some locations (i.e., southern Florida), some individuals readily move among regions (e.g., from the Florida Keys to North Carolina). Regional nodes in closer proximity to one another (e.g., FK and SEFL) were often grouped within the same modules. Tarpon movements and space use across regions are diverse with no consistent movement yet to be observed. Future network analysis applied to data with longer tracking durations, an increased sample size, and diversity in capture locations will provide a better representation of migratory connectivity for this population. The further inclusion of size and seasonal components into network analysis methods may offer additional insights into tarpon life history strategies. While network analysis has become an emergent technique to interpret movement patterns (Jacoby et al., 2012; Finn et al., 2014; Jacoby and Freeman, 2016), our results highlight the novel ability for its use for migratory marine species in combination with acoustic telemetry. Ultimately, this approach will show the extent of individual variability within the overall population patterns and may highlight evolutionary implications of partially migratory populations (Chapman et al., 2011).

The scale at which fisheries are managed often do not adequately match the ecology of the focal species, presenting challenges to effective fisheries management plans (Cumming et al., 2006). This disconnect has had large impacts on the Atlantic tarpon fishery, a species characterized as long-lived, late age-of-sexual maturity, highly fecund, and having complex habitat-ontogeny (Adams et al., 2012). For example, using genetic markers, it was recently determined that tarpon comprise only one distinct genetic population across the entire Atlantic (i.e., from the U.S. to Brazil and Africa) (Wallace et al. pers. comm.). These combined life history characteristics illustrate the critical importance of conserving tarpon at the regional and international level, in a way that ensures the protection of this species across political jurisdictions and geographic boundaries. This is especially important since subsistence and commercial tarpon harvest are prevalent across Mexico and the Caribbean (Adams et al., 2012). Thus, tarpon that support economically important fisheries in a region with strict harvest regulations may migrate through locations that make them vulnerable to harvest. Even within the USA., management strategies do not match tarpon ecology: regulations in states range from enforced catch-and-release only tarpon fisheries (e.g., Florida, Virginia), to limited harvest (e.g., Texas, Alabama, Georgia, South Carolina, North Carolina), to no limits at all (e.g., Louisiana, Mississippi). For example, four of the eight tarpon tagged in the Florida Keys with tracking durations greater than a month moved across Florida state-lines, where they are more vulnerable to harvest. More problematic is that habitat degradation and water quality issues occur at multiple scales (Adams and Cooke, 2015, e.g., watershed, state, regional level), which may challenge connectivity across areas (Adams et al., 2012). Long-term and comprehensive tracking of tarpon, along with future larval connectivity and isotope analyses, may help elucidate the vulnerability and need to protect these species at a greater scale than they are currently managed for in the U.S.

#### 4.1. Lessons learned in using acoustic telemetry to study migratory species

Although acoustic telemetry is a promising technology to study highly migratory coastal species there are some inherent challenges

associated with collaborative networks and extensive acoustic telemetry data sets. Collaborative networks such as iTAG, FACT, and ACT provide a means to track fish beyond one's own receiver coverage; however, the utility of these networks are completely dependent on researchers sharing detection data. Non-members and network members may decide to not participate and actively share detections for multiple reasons (Nguyen et al., 2017). These reasons include that they study sedentary species and do not find value in sharing data, they may have conflicts with other researchers (e.g., personal or study the same species), or are limited by time to enter or disseminate orphan detections. Even if a member does participate in sharing data, acoustic data must first be downloaded from receivers (may occur monthly or annually) and then organized into a sharable form (e.g., upload into iTAG query database or email researchers directly via FACT and ACT). This process leads to intermittent reporting and sometimes extremely backlogged data that will not be available to the tag owner for a long period. Backlogged data creates uncertainties with fish that are not yet detected. This issue may be more of a concern with highly migratory species or species that regularly make long distance movements compared to species that are sedentary and generate high detections within localized receiver networks. Given these limitations, we recommend that researchers proceed with caution when interpreting shorter duration datasets because this could lead to inaccurate or misrepresented movement patterns.

Ultimately, to realize the full potential of the collaborative networks, it is important to maintain a semi-constant receiver network across large areas of coast so that we may reliably monitor individuals across greater extents of space and time. We believe these current issues (i.e., participation, backlogged data, receiver network gaps) are not large enough challenges to deter researchers from using acoustic telemetry to study migratory species

## 5. Conclusion

Data from the first two years of a long-term acoustic telemetry study highlight the diversity in tarpon migratory movements and the complex patterns of regional connectivity across the coastal waters of the southeastern USA. The acoustic telemetry participatory collaborative platforms enabled the tracking of tarpon at multiple and meaningful spatiotemporal scales. Further, we share emerging model-driven approaches and network analyses that can be used to investigate movement strategies, habitat use, and connectivity not only with Atlantic tarpon but with other studies involving highly migratory species. While challenges exist with using acoustic telemetry data to track highly migratory species, such as intermittent data reporting or the continuance of a semi-constant receiver network along USA coasts, we believe the advances in acoustic telemetry technology, analytical methods, and collaborations across institutions far outweigh the limitations. As acoustic telemetry continues to gain traction among researchers to address marine conservation issues, so will its ability to provide valuable insight into migratory species, such as the Atlantic tarpon, at a range of spatiotemporal scales.

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## Conflicts of interest

The authors declare no conflict of interest exists.

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