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Individual variation and repeatability of Atlantic tarpon *Megalops atlanticus* migrations in the southern US: implications for conservation and management

Lucas P. Griffin[1] · Jacob W. Brownscombe[2] · Aaron J. Adams[3,4] · JoEllen K. Wilson[3] · Grace A. Casselberry[1] · Peter E. Holder[2] · Alex Filous[1] · Susan K. Lowerre-Barbieri[5,6] · Steven J. Cooke[2] · Andy J. Danylchuk[1]

Abstract

Individual fish movement patterns and behaviors influence population-level traits, and are important for understanding their ecology and evolution. Understanding these behaviors is key for managing and conserving migratory animal populations, including Atlantic tarpon (*Megalops atlanticus*), that support an economically important recreational fishery. Using acoustic telemetry, we tracked individual movement patterns of *M. atlanticus* inhabiting the eastern Gulf of Mexico and the southeast coast of the US over successive years. Net-squared displacement models revealed considerable individual-level variation in movement patterns with high individual-level repeatability in the timing of migrations and migratory pathways. Although distinct migratory subgroups existed, *M. atlanticus* generally migrate northward in the spring and summer to putative foraging grounds and remain in these areas for, on average, four months and then migrate southward in the fall. Subadult *M. atlanticus* exhibited similar migratory patterns as adults, while large juveniles exhibited either resident or nomadic behaviors. For migratory individuals, fish size did not influence movement patterns. Given that distinct migratory subgroups seasonally mixed in southern Florida for spawning activity, our study indicates that *M. atlanticus* along the eastern Gulf of Mexico and southeastern coast of the US should be considered a single interconnected stock. With that in mind, using *M. atlanticus* angler and guide knowledge, we assessed the vulnerability of *M. atlanticus* to potential threats across their range and along migratory pathways. Collectively, the far-ranging nature of *M. atlanticus* and their diversity in movement patterns highlights the need for more uniform and cohesive management and conservation efforts.

Keywords Movement ecology · Net-squared displacement · Local ecological knowledge · Phenology · Recreational fisheries · Stepping stones

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✉ Lucas P. Griffin
  lucaspgriffin@gmail.com

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

[2] Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada

[3] Bonefish & Tarpon Trust, Miami, FL 33133, USA

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

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

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

Introduction

Fishes have evolved a variety of movement and migration strategies that presumably optimize their fitness (Leggett 1977; Gross et al. 1988; Roff 1988; Dingle and Drake 2007). Both internal factors, such as genetics and physiology, and external factors, such as the physical environment and social interactions (e.g., predator–prey, density-dependent relationships), have shaped these strategies for fish (Chapman et al. 2011a; Tamario et al. 2019; Cooke et al. 2022). The diversity of individual traits and movement patterns collectively contribute to population-level characteristics of a given species (Dingemanse and Réale 2005; Mittelbach et al. 2014), while also playing a role in driving specialization influencing the size, shape, and configuration of ecological niches (Carlson et al. 2021). Ultimately, the variation and the repeatability

of individual-level differences in fish will affect how populations respond to anthropogenic disturbances (Killen et al. 2016).

A plethora of acute and chronic anthropogenic disturbances such as overharvesting, habitat loss and degradation, and associated changes in water quality and water regime shifts make fish extremely vulnerable (Rocha et al. 2015; Arthington et al. 2016). Indeed, many marine fish populations and their stocks have severely declined (Jackson et al. 2001; Pauly et al. 2002; Dulvy et al. 2003). Migratory fish species may be at even greater risk due to large energetic requirements, differing prey availability across distant areas, physical barriers that potentially disrupt critical life history events, and contrasting management regulations across their range (Meltzer 1994; Lascelles et al. 2014; Lennox et al. 2016). For example, Limburg and Waldman (2009) reported that 24 out of 35 diadromous fish species evaluated in North America and Europe had declined by more than 90% compared to their historic highs, with 13 of these species experiencing relative abundance declines of over 98%. Ultimately, because the scale and scope of risks along a migratory path can affect population-level processes and the viability of fish populations, understanding the migration patterns of individuals is a critical aspect of conservation and management (Secor 2015).

Information on the movement patterns and threats fish species face along their migratory routes can be valuable in determining the need for and, urgency of, implementing policy and management changes. For example, until recently, the Atlantic bluefin tuna (*Thunnus thynnus*), a highly migratory species, has experienced substantial population declines and regional fishery collapses since the 1960s due to over-exploitation (Safina and Klinger 2008; Cort and Abaunza 2015; Porch et al. 2019; Andrews et al. 2022). However, using tagging studies, stable isotope analysis, and genetics, research has provided fundamental and spatially explicit information on the population and stock structure of the species, leading to the implementation of a 15-year recovery plan in 2007 (Rodríguez-Marín et al. 2007). This plan successfully helped to recover the *T. thynnus* population, and in September 2021, the International Union for Conservation of Nature (IUCN) Red List of Threatened Species downgraded its status from "Endangered" to "Least Concern" (Collette et al. 2021). The success of this 15-year recovery plan for *T. thynnus* and the research that supported it demonstrates the effectiveness of management approaches inspired by movement ecology research for conserving and managing migratory species. Tailored management approaches that incorporate the complex movement patterns of fish populations, such as spatially explicit management or the establishment of inter-jurisdictional management zones (Runge et al. 2014; Hays et al. 2019; Lowerre-Barbieri et al. 2021), can be highly effective in targeting conservation and management

efforts to specific areas where they are most needed (Lascelles et al. 2014; Allen and Singh 2016).

The Atlantic tarpon (*Megalops atlanticus*) is a migratory mesopredator fish in the Megalopidae family, and occupies a wide range of habitats across the Eastern and Western Atlantic Ocean, including the Gulf of Mexico (GOM) and the Caribbean Sea (McMillen-Jackson et al. 2005). *Megalops atlanticus* have broad regional connectivity in the Western Atlantic Ocean, with seasonal ranges spanning hundreds to thousands of kilometers (Griffin et al. 2018; Luo et al. 2020). *Megalops atlanticus* are believed to migrate between spawning and foraging areas, moving northward to foraging grounds in the early summer following spawning predominantly in southern Florida (Griffin et al. 2018, 2022a; Luo et al. 2020; Drymon et al. 2021; Friess et al. 2021). Like many migratory species (Wilcove and Wikelski 2008), the *M. atlanticus* population abundance is likely decreasing (Adams et al. 2019; Griffin et al. 2023), and they are currently listed as "Vulnerable" by the IUCN (Adams et al. 2019). This decline is likely due to various anthropogenic impacts, including historic (commercial/subsistence) and contemporary fishing mortality (including harvest and catch-and-release mortality or depredation), degraded water quality, and habitat loss (Adams et al. 2014, 2019; Wilson et al. 2019; Luo et al. 2020; Fernandes et al. 2022; Griffin et al. 2022b, 2022c). The long life span, late maturation, and highly migratory behavior likely make the maintenance and recovery of *M. atlanticus* populations particularly vulnerable to exploitation and anthropogenic disturbances. *Megalops atlanticus* is also a highly prized gamefish that support a multimillion-dollar industry as a recreational fishery in the southeastern region of the United States of America (US) (Smith et al. 2022). Thus, declines in *M. atlanticus* stocks could not only affect the ecosystem services they provide (e.g., energetic connectivity, Shipley et al. 2023), but also negatively impact local economies. In fact, due to inadequate management, the collapse of the Texas *M. atlanticus* recreational fishery pre-1990s serves as an example of the economic and cultural consequences of such a decline (Stilwell 2011). To avoid additional regional fishery collapses, a better understanding of *M. atlanticus* migratory patterns and how they intersect with threats along their migratory routes (e.g., no tarpon harvest regulations in Louisiana vs. catch-and-release only in Florida) are needed to inform effective conservation strategies and management measures.

Acoustic telemetry is a widely used tool for tracking fish movements over a range of spatial and temporal scales (Hussey et al. 2015; Crossin et al. 2017; Matley et al. 2022). This method typically involves implanting a small acoustic transmitter into the fish, which emits an ID-coded ultrasonic (67–417 kHz) signal that can be detected by acoustic receivers placed in the water (Hellström et al. 2022). This technology can be used to determine the migratory patterns, habitat

use, and behavior of fish populations, and delineate stocks (Lennox et al. 2017; Lowerre-Barbieri et al. 2019; Lédée et al. 2021; Brownscombe et al. 2022). Targeted receiver deployments can also provide insights into how aquatic organisms respond to threats such as exploitation, pollution, and climate change, as well as assess the effectiveness of conservation and management efforts, such as habitat restoration and spatial management plans (Alós et al. 2022). To increase capacity for such endeavors, researchers in the US (and elsewhere) have established networks of acoustic receiver arrays [e.g., integrated Tracking of Aquatic Animals (iTAG) in the Gulf of Mexico, FACT Network, Atlantic Cooperative Telemetry (ACT), Ocean Tracking Network (OTN)] that enable tracking of highly migratory animals, including *M. atlanticus* (Griffin et al. 2018). Acoustic transmitters can have a long battery life (5–10 years), increasing the potential for tracking individuals over large spatial areas for multiple years, leading to a more comprehensive understanding of the variation in individual migration patterns, the repeatability of such migrations, and how these collectively contribute to population-level traits (Taylor and Cooke 2014).

Our study aimed to quantify individual migratory patterns of *M. atlanticus* inhabiting the coastal waters of the eastern GOM and southeastern US using acoustic telemetry. By evaluating the movement patterns across successive years, we aimed to quantify the connectivity among coastal regions and the consistency of movement behaviors. We then used the migratory patterns of individuals to assess their vulnerability to known risks that vary regionally along the coastline (i.e., water quality, habitat decline, forage prey decline, angling pressure, angler ethics, insufficient regulations, differing harvest/kill regulations, shark predation, and non-angling activities). Collectively, the results of this study will shed light on the evolved diversity in migratory patterns for *M. atlanticus* along the eastern GOM and southeastern coast of the US, as well as inform effective conservation strategies and management actions necessary to curb the recent declines of *M. atlanticus*.

Materials and methods

Capture, tagging, and monitoring

Capture and tagging were conducted from May 2016 to June 2021. *Megalops atlanticus* were captured by hook and line in South Florida (e.g., Florida Keys, 24.61 N, −81.48 W), Southwest Florida (e.g., Charlotte Harbor, FL, 26.72 N, −82.2 W; Tampa Bay, FL, 27.61 N, −82.67 W), Florida Panhandle (e.g., Apalachicola, FL, 29.65 N, −84.93 W), Northeast Florida (e.g., Amelia Island, FL, 30.84 N, −81.42 W), and Central South Carolina (e.g., Charleston,

SC, 33.06 N, −79.33 W) (Fig. 1, Fig. SI). Upon capture, fork length (FL) and girth (cm) were recorded and an acoustic transmitter (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; Innovasea, Amirix Inc., Bedford, NS, Canada) was surgically implanted through a 3–4 cm incision posterior to the pelvic fin that was made with a sterilized scalpel. When environmental conditions allowed and low predator density was apparent, a single suture (PDS-II monofilament absorbable, 3–0, model Z497G, Ethicon Inc., Somerville, NJ) was used to close the incision. Fish were released at the site of capture. Adult maturity was defined as having a FL greater or equal to 128.5 cm based on Crabtree et al. (1997), who reported size of maturity estimates at 117.5 cm for males and 128.5 cm for females. When fish were less than 129.5 cm FL, they were assigned as a sub-adult/large juvenile. There were no small juveniles (<30 cm) tagged in this study, which are ontogenically distinct from coastal nearshore areas (Wilson et al. 2019).

Megalops atlanticus detections were collected from approximately 1000 fixed acoustic receivers (VR2RW and VR2Tx models, Amirix Inc., Bedford, NS, Canada) deployed across the GOM and southeastern US. These detections were shared through collaborative institutional networks, including iTAG (https://itagscience.com/track
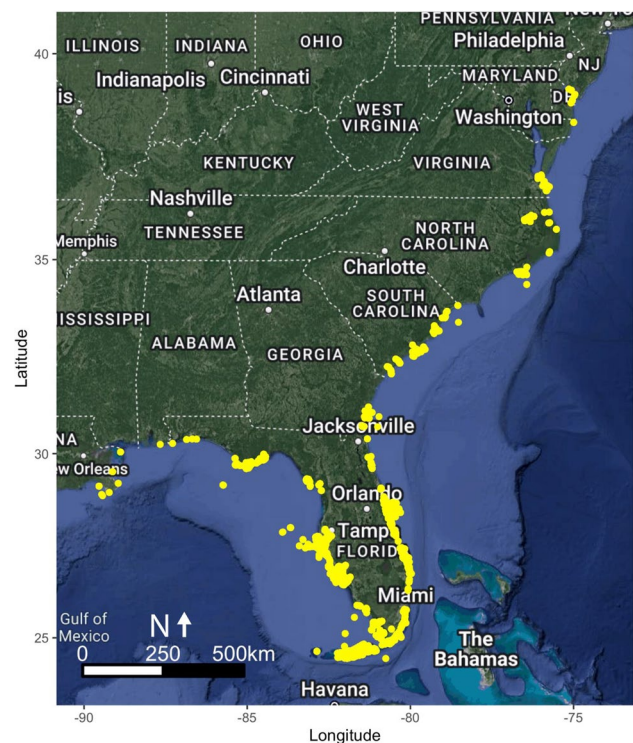

Fig. 1 Atlantic tarpon (*Megalops atlanticus*) detections (yellow) from 2016 to 2022 across the eastern Gulf of Mexico and southeastern USA

ing/), FACT (https://secoora.org/fact/), and ACT (https://www.theactnetwork.com). The Ocean Tracking Network (https://oceantrackingnetwork.org also provided receiver loans and data-sharing capabilities to collect and aggregate *M. atlanticus* detections. Collectively, despite being dependent on variable receiver deployment and locations, these networks enabled the tracking of *M. atlanticus* across the GOM and southeastern US (Griffin et al. 2018).

Data analysis

All statistical analyses were conducted using R 3.6.2 (R Core Team 2022). Raw detection records were examined for anomalies such as unrealistic or lack of movement, e.g., expelled tag, potential mortality (Klinard and Matley 2020), and when found, were removed. All *M. atlanticus* with tracking durations of 14 days or less were removed from all analyses. For all analyses, detections refer to the daily averaged latitude and longitude for each individual.

Regional connectivity

We assessed adult *M. atlanticus* connectivity across different regions through network analysis. To ensure detection logs capture the movements across an entire annual cycle at a minimum, connectivity was assessed for *M. atlanticus* with tracking durations greater than 365 days. Based on graph theory, network analysis connects individuals and regions (Fig. SI 1) as determined by their movements (Dale and Fortin 2010; Jacoby et al. 2012; Jacoby and Freeman 2016). In this case, bipartite, meaning two nodes, network graphs generated via the *igraph* package (Csardi and Nepusz 2006) comprised nodes (individual *M. atlanticus* and regions) and weighted edges (connections). Subsequently, we applied a Fruchterman–Reingold force-directed layout algorithm (Fruchterman and Reingold 1991) to the network graphs that proportionally aggregate or repulse nodes to the weight of the edges connecting adjacent nodes (Finn et al. 2014). More aggregated nodes are more similar, while repulsed nodes are more dissimilar. If nodes were not similar, this algorithm would arrange nodes into an equidistant circle. However, network communities may emerge when weighted edges have tight connections to one another.

To explore if network communities existed among individual fish and regions (Griffin et al. 2018), we applied six community detection algorithms that generate groups of nodes, known as modules (see Finn et al. 2014). The six algorithms included: 'Leading-Eigenvector' (Newman 2006a, b), 'Walk-Trap' (Pons and Latapy 2005), 'Fast-Greedy' (Clauset et al. 2004; Newman and Girvan 2004; Reichardt and Bornholdt 2006), 'Spin-Glass' (Reichardt and Bornholdt 2006), 'Label-Propagation' (Raghavan et al. 2007; Blondel et al. 2008), and 'Multilevel' (Blondel et al. 2008).

The modularity scores of each algorithm were assessed to determine the division quality between the potential network communities. Ranging from 0 (low-quality division) to 1 (high-quality division), modularity scores are the proportion of edges within selected modules minus the proportion that would be expected if edges were randomly distributed across nodes (Finn et al. 2014). Subsequently, we performed a Wilcoxon rank-sum test to determine if the nodes within each cluster were more linked to one another than outside the cluster. If significant, these clusters are defined as network communities (Finn et al. 2014).

Lastly, we examined the proportion of individuals that moved between the broader regions of south Florida (S. FL; defined as the Florida Keys and The Everglades), the GOM, and the Atlantic (southeastern US coast). Detections from each region were collapsed to better account for the heterogeneous distribution of receivers across the study area. Network plots were then produced and examined for each category, again using the Fruchterman–Reingold force-directed layout algorithm.

Adult and subadult/large juvenile movement patterns

Each detection log of successive daily detections was examined, and direction-specific migration was identified and cataloged as separate "bursts," e.g., distinct northward or southward movements. Per methods outlined in Griffin et al. (2018), multiple non-linear a priori statistical movement models, e.g., mixed migrant, migrant, disperser, nomad, and resident (Bunnefeld et al. 2011; Spitz et al. 2017), were then fitted to each *M. atlanticus* burst. Akaike information criteria (Burnham and Anderson 2004; Spitz et al. 2017) then determined which movement model fit best (Spitz et al. 2017). This approach, facilitated through the *migrateR* package (Spitz et al. 2017), is based on net-squared displacement and is defined as the square of the straight-line distance between an animal's starting location and each successive relocation (Turchin 1998). The origin location for each model was selected through manual selection or through the 'findrloc' function in the *migrateR* package that determines the best origin location that minimizes the Akaike information criteria value. Subsequently, movement parameter estimates from each model, in this case migrant and mix-migrant models, were extracted and summarized. Interpreted movement parameters included delta (δ, the distance separating seasonal ranges; km^2), theta (θ, the midpoint of departing movement; days), theta2 (θ_2, the midpoint of arriving movement; days), phi (φ, the time required to complete ½ to ¾ of the migration; days), phi2 (φ_2, the time required to complete ½ to ¾ of the return migration; days), and rho (ρ, the duration spent in the area the animal migrated to; days). To standardize across parameters and consistent with Griffin et al. (2022a), confidence intervals surrounding migration start and stop dates were calculated with 01 March

defined as day 0. Lastly, some *M. atlanticus* made multiple early migrations prior to moving and remaining northward; these relatively quick (generally less than 10 days) northward and then southward migrations were believed to be associated with *M. atlanticus* spawning periods in the Florida Keys (Griffin et al. 2022a). We defined the two movement patterns as "early" and "typical" and separated the two for summary and plotting purposes, further, typical movement patterns were separated into spring (e.g., April–July) and fall (e.g., September–November) migrations.

To examine whether fish size influenced movement patterns, we implemented four separate general linear mixed models (GLMM) with fish size as the independent variable in each and with δ, ρ, and the ordinal dates for the onset of northern and southern migrations as the dependent variables separately. Each GLMM had a Gaussian error structure and fish ID as the random effect for repeated measures. These models were implemented only for "typical" movement patterns using the *glmm_TMB* (Brooks et al. 2017) package. The performance (Lüdecke et al. 2021) and *sjPlots* (Lüdecke 2021) packages were used to evaluate model assumptions and visualize the marginal effects. A log transformation was applied to the dependent variables (δ, ρ, and the starting spring and fall migration dates). Further, because many of the subadult/large juveniles ($<$128.5 cm FLs) detection profiles were sparse in frequency and did not exhibit clear migratory behaviors, some movement models could not converge and could not be included in the above analyses. To address this gap, we examined and plotted subadult/large juvenile movement patterns and net-squared displacement metrics. The size differences between subadult/large juvenile that exhibited migratory behaviors rather than nomadic or resident behaviors, as determined by the plots, were assessed with a Welch two-sample *t* test.

Repeatability of migration patterns

To determine if typical migratory patterns were repeatable across years for individuals, we first filtered the dataset for *M. atlanticus* with multiple years of tracking data. We then extracted movement parameter model estimates and their associated ordinal dates from each individual and their multiple bursts. Then based on detections, we categorically assigned when *M. atlanticus* were either present or absent across general areas of the southeastern US and GOM (Fig. SI 1). Subsequently, we performed multivariate analysis (factor analysis of mixed data) with the 'FAMD' function in the *FactoMineR* package (Lê et al. 2008) to reduce the dataset into two dimensions. Additional interpretation and plotting were performed with the *factoextra* package (Kassambara and Mundt 2021). Unlike principal component analysis and correspondence analysis, factor analysis of mixed data allowed for the simultaneous inclusion of

multiple data types, i.e., numeric (i.e., movement parameter estimates) and categorical (i.e., locations visited). Numeric input variables included the ordinal dates of θ, θ_2, the ordinal dates for when migrations began and ended (both south to north and north to south), δ, φ, φ_2, and ρ. Categorical input variables included the presence or absence of *M. atlanticus* in the Florida Keys, Everglades, southeastern Florida, eastern Florida, Georgia, South Carolina, North Carolina, Virginia, Maryland, southwestern Florida, central western Florida, northwestern Florida, and northern GOM.

We estimated the repeatability (R) (Sokal and Rohlf 1981) of migration patterns using the first- and second dimension scores of each migration as derived from the FAMD analysis. The scores were separately assessed using linear mixed-effects models (LMMs) with individual as a random effect via the 'rpt' function in the *rptR* package (Nakagawa and Schielzeth 2010; Stoffel et al. 2017). Here, the estimation of R is the proportion of total variation in the dimension scores within and between individuals. While an R-value of 0 suggests zero consistency, a value of 1 suggests complete consistency (Sokal and Rohlf 1981; Lessells and Boag 1987). Further, we used the *rptR* package (Stoffel et al. 2017) to derive statistical significance at the alpha level of 0.05 and 95% confidence intervals from 1000 parametric bootstraps.

Vulnerability

To assess the vulnerability of adult *M. atlanticus* (with tracking durations $>$365 days), we examined the proportion of time spent across three distinct regions (i.e., Mid-Atlantic, northern GOM, and Florida) and compiled the varying threats that *M. atlanticus* may encounter in these areas. Informed by community network analysis, which was based on *M. atlanticus* movements (see "Regional connectivity"), we classified *M. atlanticus* belonging to two separate groups, "GOM" and "southeastern US coast," and calculated their residence proportions individually. The regions were categorized as Mid-Atlantic (Delaware, Maryland, Virginia, North Carolina, South Carolina, Georgia), northern GOM (Apalachicola, FL and westward, including Alabama, Mississippi, Louisiana), and Florida (all of Florida excluding Apalachicola, Florida and westward). All detections from Florida were labeled as Florida except for detections that occurred in areas surrounding Apalachicola and westward (Fig. SI 1). These detections were labeled as northern GOM since receiver coverage was minimal in the surrounding states (e.g., Alabama, Mississippi, Louisiana), thus likely to miss *M. atlanticus* detections. Further, the exploratory analysis indicated that some *M. atlanticus* likely continue westward after reaching Apalachicola. The proportion of time spent in each region was calculated using the 'detection_events' function in the *glatos* package (Holbrook et al. 2020) that organizes detections into separate events based

on when an individual is detected at a different location. Because Florida contained the highest number of receivers and was positioned to best detect *M. atlanticus*, we defined a departure event starting at the last detection within Florida and an arrival event as the first detection within Florida.

Threats and their severity level (very low, low, medium, high, and very high) were constructed from *M. atlanticus* angler and guide survey data (see Griffin et al. 2023) and was based on the questions "Which factors represent threats to the current status of Atlantic tarpon populations?" and on where respondents primarily angled *M. atlanticus* (again, responses from the Apalachicola region were assigned as northern GOM). Respondents were asked to rank each threat (water quality, habitat decline, angling pressure, angler ethics, insufficient regulations, differing harvest/kill regulations, shark predation, and non-angling activities/pleasure) as a very low, low, medium, high, or very high threat. We selected the severity for each threat and region based on whichever severity category had the highest number of responses (see Table 1). Lastly, the threat "forage fish decline" was not an option within the survey question, but due to growing concern within the angler community (A. Adams pers. comm.), we provided a ranking for each of the three regions based on the authors' collective knowledge.

Results

A total of 200 M. *atlanticus* were tagged between 2016 and 2021, and after the removal of all detection logs with less than 14 days, movement data were collected and analyzed from 109 M. *atlanticus* (28.2 ± 13.8 kg weight, 132.8 ± 27.2 cm FL) captured from South Florida ($n = 53$), Southwest Florida ($n = 34$), Florida Panhandle ($n = 8$), Northeast Florida ($n = 11$), and Central South Carolina ($n = 3$) (Fig. 1, Table 2). Tracking duration (i.e., date captured to last detection) ranged between 15 and 1912 d (971 ± 582 d) (SI Table S1).

Regional connectivity

For adult *M. atlanticus* with tracking durations greater than 365 days (32.9 ± 8.3 kg weight, 146.2 ± 12.4 cm FL, 1298 ± 420 d tracking duration, $n = 56$), network analysis revealed heterogeneous space use among *M. atlanticus* and

Table 2 Number of Atlantic tarpon (*Megalops atlanticus*) by capture location and life stage (adult, ≥ 128.5 cm; subadult/large juvenile, < 128.5 cm fork length) used for analysis

Capture location	Life stage	Count
Central South Carolina	Adult	2
Central South Carolina	Subadult/large juvenile	1
Florida Panhandle	Adult	6
Florida Panhandle	Subadult/large juvenile	2
Northeast Florida	Adult	9
Northeast Florida	Subadult/large juvenile	2
South Florida	Adult	36
South Florida	Subadult/large juvenile	17
Southwest Florida	Adult	22
Southwest Florida	Subadult/large juvenile	12

Table 1 Threats and their rankings for adult Atlantic tarpon (*Megalops atlanticus*) across Florida, Mid-Atlantic (Georgia, South Carolina, North Carolina, Delaware, Maryland), and northern Gulf of Mexico (Apalachicola, Florida and westward, including Mississippi, Alabama, Louisiana)

Threat	Water quality	Habitat decline	Forage prey decline	Angling pressure	Angler ethics	Insufficient regulations	Differing harvest/kill regulations	Shark predation	Non-angling activities/pleasure
Description	e.g., pollution, freshwater flows, red tide, cruise-line industry	e.g., mangroves, seagrass, reefs	e.g., reduction in important prey sources for *M. atlanticus*	e.g., angler boat traffic, number of anglers	e.g., handling, motoring after *M. atlanticus* schools, etc	e.g., handing practices, harvest limits, lack of enforcement	e.g., across states and countries	related to angling events	e.g., boat traffic, jet skis, sandbar crowds etc
Threat ranking by location									
Florida	5	4	3	4	3	3	3	3	3
Mid-Atlantic	4	4	5	3	3	3	2	3	3
Northern Gulf of Mexico	5	4	5	4	3	2	2	3	3

Threat rankings were compiled from an *M. atlanticus* angler and guide survey (see Griffin et al. 2023) and from expert opinion. Threat ranking ranged from very low (1) to very high (5)

regions with substantial mixing primarily occurring in south Florida (e.g., the Florida Keys and The Everglades) (Fig. 2). Community analysis confirmed the division between distinct and significant network communities for fish that primarily used the GOM coast vs. the southeastern US coast (Fig. 3). Modularity scores ranged from 0.19 to 0.32, and algorithms identified between two to three modules per algorithm (SI Table S2). Four algorithms (Leading-Eigenvector, Fast-Greedy, Spin-Glass, and Multilevel) had the highest modularity scores of 0.32. All algorithms similarly separated space use between the GOM and the southeastern US coast.

At the broader regional scale (i.e., Atlantic, GOM, and S. FL), a considerable portion of fish moved across these areas at least once. The network plots for each region revealed that most movements were limited to either the GOM and S. FL or the Atlantic and S. FL (Fig. 4a). Specifically, 21.4% ($n = 12$) of the fish were detected in all three broad regions. In comparison, 39.3% ($n = 22$) were detected only in the Atlantic and S. FL regions, and 33.9%

($n = 19$) were detected only in the GOM and S. FL regions (Fig. 4b). Notably, only two fish were never detected outside the Atlantic region, and one was never detected beyond the GOM region.

Megalops atlanticus captured and tagged along the southeastern US coast (i.e., northeastern Florida and central South Carolina) were detected only along the Atlantic coast and S. FL (Fig. 4a). Similarly, fish that were tagged in the Florida Panhandle were never detected on the Atlantic coast. For fish that were tagged in southern Florida, a proportion of them were detected across all three regions.

Adult and subadult/large juvenile movement patterns

From 57 M. *atlanticus* (48 adult, 32.5 ± 7.2 kg weight, 145.3 ± 11.6 cm FL, 1347 ± 382 d tracking duration, 9 subadult/large juvenile, 17.3 ± 3.8 kg weight, 113.9 ± 7.4 cm FL, 1124 ± 439 d tracking duration), movement parameter
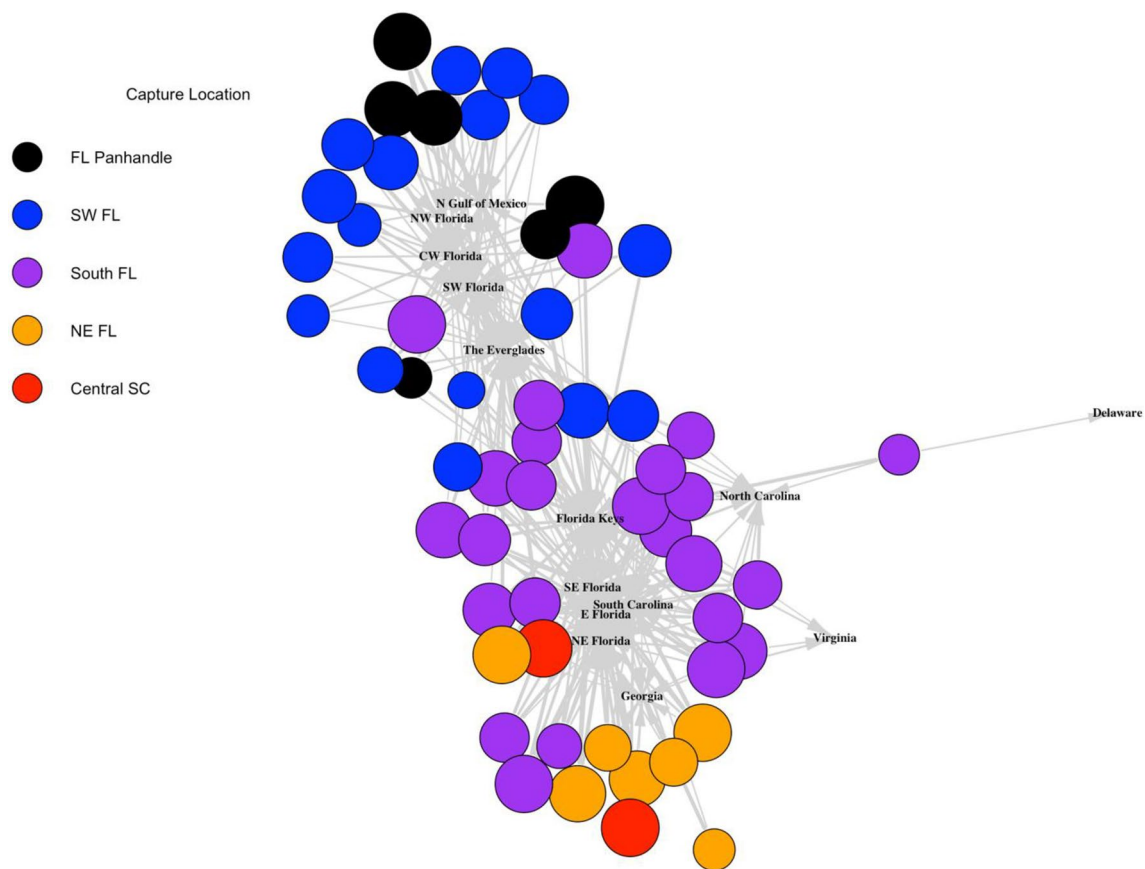

Fig. 2 Bipartite graph of Atlantic tarpon (*Megalops atlanticus*) regional network with Fruchterman–Reingold force-directed layout algorithm. *Megalops atlanticus* (nodes) are colored based on tagging location, node size is proportional to the duration of tracking (i.e., larger nodes have longer tracking durations than a smaller nodes). Links (edges) connect *M. atlanticus* to regions visited, and their width is proportional to the number of unique detection days at each region per individual. The Fruchterman–Reingold force-directed layout algorithm places nodes in space proportional to the weight of edges connecting adjacent nodes. Groups of *M. atlanticus* that visit similar areas are closer together

Fig. 3 Atlantic tarpon (*Megalops atlanticus*) community network plot from Leading-Eigenvector community detection algorithm overlaid on *M. atlanticus* regional bipartite graph with significant network communities largely divided by use of the Gulf of Mexico (blue) and southeastern US Atlantic coast (red)
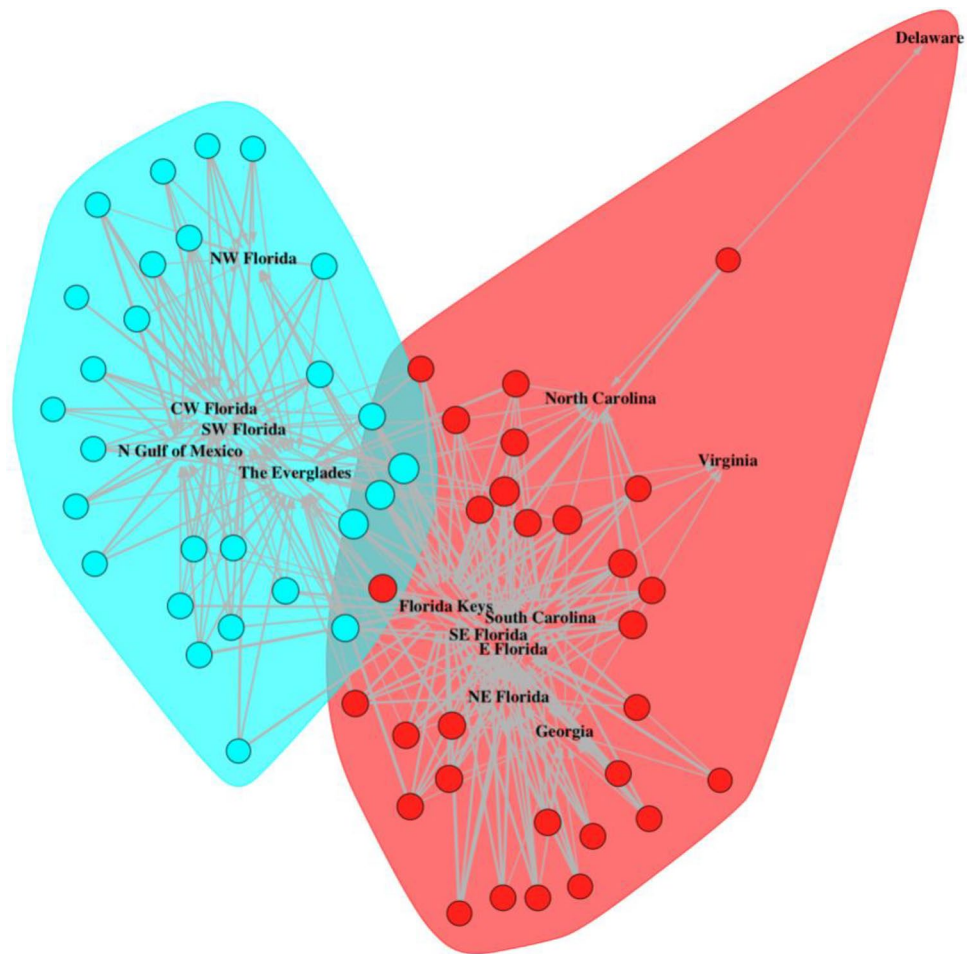
estimates were derived from a total of 136 typical movement pattern bursts (from 48 adults and 9 subadult/large juveniles) and 19 early (from 10 adults only) movement pattern bursts (Table S3). During typical movement patterns, *M. atlanticus* on average remained in their northern migratory areas (ρ) for 124 d ($\pm$ 65 d). Further, the southern and northern seasonal ranges were separated by 525 km^2 ($\pm$ 525 km^2). Alternatively, *M. atlanticus* that displayed early migratory movements northward in April-June, on average remained in these areas for only 6 d ($\pm$ 5 d) before returning southward. These early movements occurred from the Florida Keys to northeast Florida and Georgia (Fig. 5a).

Using the lower and upper 95% CI bounds for the migratory beginning and end dates (ordinal), the average onset and ending for migrations occurred between 24 April and 22 May (mean date: 08 May) for early migrations, 06 June and 08 July (mean date: 22 June) for typical spring migrations, and 19 September and 07 November (mean date: 14 October) (Fig. 5b) for typical fall migrations.

There was no significant effect of fish size on the extracted movement parameters (δ, ρ, and dates of the northern and southern migrations (Table S3). Beyond examining

movements from those only with parameter estimates, *M. atlanticus* with FLs less than 128.5 cm (13.5 $\pm$ 5.7 kg weight, 101.8 $\pm$ 17.0 cm FL, 1013 $\pm$ 447 d tracking duration, $n = 26$) displayed varying migratory tendencies ranging from highly migratory to residential (Fig. SI 1). Of the 26 subadult/large juvenile *M. atlanticus*, there was a significant difference (Welch two-sample *t* test, $T = 4.0$, DF $= 23.0$, $P < 0.001$) in size between the six migratory subadult/large juveniles (tag IDs: 16674, 15923, 16678, 16690, 9682, 18582; 115.8 $\pm$ 6.0, 107.0–124.0 cm FL) and the 20 non-migratory subadult/large juveniles (97.7 $\pm$ 17.1, 69.0–119.0 cm FL). The migrant subadults were observed annually moving between the Florida Keys and northern locations such as Virginia or the northern GOM. Conversely, the large juveniles were largely resident or nomadic in or around the region they were tagged in, e.g., the Florida Keys, central western Florida, and southwestern Florida (Fig. 6).

Repeatability of migration patterns

Using 120 migrations (2.9 $\pm$ 0.96 migrations, max $= 5$, min $= 2$) from 41 M. *atlanticus* (30.7 $\pm$ 7.8 kg weight,

Fig. 4 **a** Bipartite graphs of Atlantic tarpon (*Megalops atlanticus*) regional networks for fish that were detected across different regions (i.e., Atlantic, Gulf of Mexico, and South Florida). The Fruchterman–Reingold force-directed layout algorithm was applied. *Megalops atlanticus* (nodes) are colored based on tagging location. Links (edges) connect *M. atlanticus* to regions visited and their width is proportional to the number of unique detection days at each region per individual. The Fruchterman–Reingold force-directed layout algorithm places nodes in space proportional to the weight of edges connecting adjacent nodes. Groups of *M. atlanticus* that visit similar areas are closer together. **b** Corresponding detections, again, classified belonging to the regions: Atlantic, Gulf of Mexico, and South Florida. Only adult *M. atlanticus* (≥ 128.5 cm fork length) with tracking durations greater than 365 days are shown
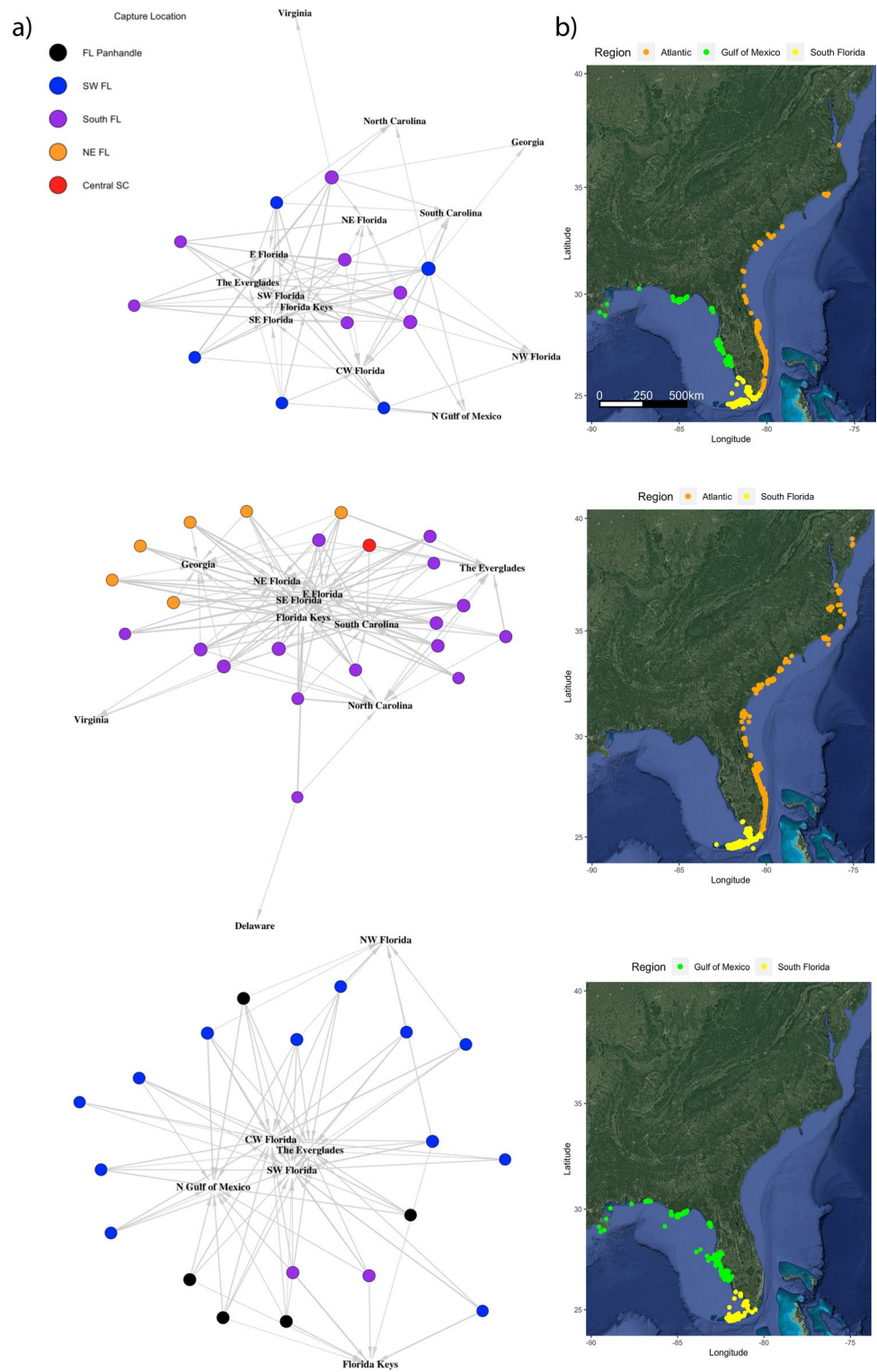
142.1 ± 13.5 cm FL, 1417 ± 347 d tracking duration) (Fig. 7), factor analysis of mixed data reduced migration parameters into five dimensions explaining 66.6% of the variance. The first and second dimensions explained 26.1% and 15.9% of the variance, respectively. The top greatest variable contributions for the first dimension

were if fish were detected or not in southeastern Florida, central western Florida, or eastern Florida (Fig. 8a). Separation of these variables across dimensions highlighted that when fish were detected in southeastern Florida or eastern Florida they would be unlikely to be detected in central western Florida and vice versa (Fig. 8b). The
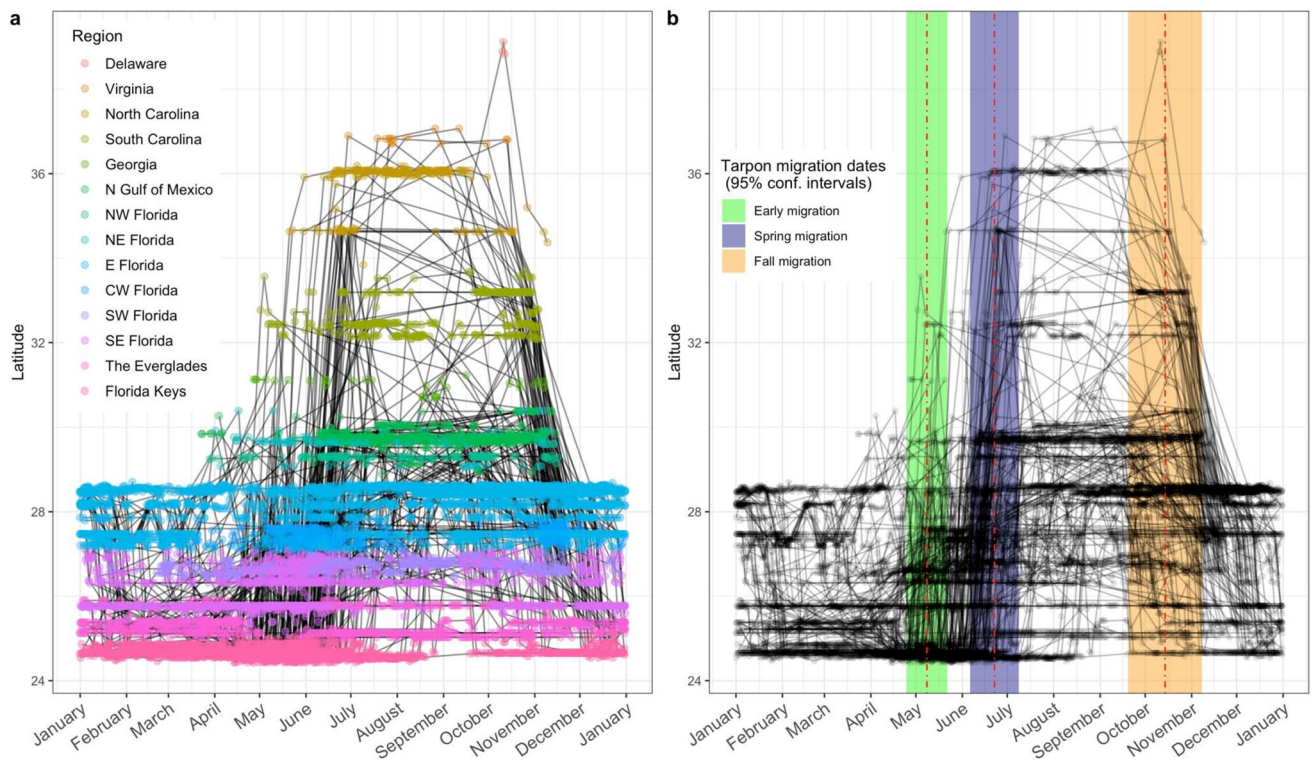
Fig. 5 **a** Migration patterns across latitude and month for individual adult Atlantic tarpon (*Megalops atlanticus*) with black paths connecting detections (colored dots indicate detection origin). **b** Constructed from the parameter estimates of 57 M. *atlanticus*, lower and upper 95% CI bounds for the migratory beginning and end dates (ordinal) were plotted by migration period on top of individual adult *M. atlan-*

ticus detections. Early migration period is shown in green, spring migration shown in blue, and fall migration shown in red. The average ordinal date for each migration period was plotted (red dashed line). Due to primarily adults migrating, only adult *M. atlanticus* detections are displayed

greatest variable contributions for the second dimension were the ordinal dates of θ_2 (midpoint of arriving movement), when north to south migrations ended and began, and δ (the distance separating seasonal ranges) (Fig. 8c). When distances separating seasonal ranges increased, northward to southward migration began and ended later with θ_2 increasing as well (Fig. 8d).

Using 120 dimension 1 and dimension 2 scores assigned to each burst and corresponding individual, we calculated overall significant repeatability values for both dimensions (dimension 1: repeatability, $R = 0.85$, 95% CI 0.76–0.91, $P < 0.001$; dimension 2: repeatability, $R = 0.59$, 95% CI 0.40–0.73, $P < 0.001$). The significant and high R values suggest migration consistency and repeatability at the individual level.

Vulnerability

To determine the degree *M. atlanticus* encountered potential threats we evaluated their residence time in each region, and compared these values to perceived threats (Griffin et al. 2023). On average, "southeastern US coast" *M. atlanticus*

$(30.9 \pm 6.4$ kg weight, 142.0 ± 9.9 cm FL, tracking duration 1354 ± 434 d, $n = 29$) had a residence of 76% in Florida and 24% in the Mid-Atlantic. Conversely, "GOM" *M. atlanticus* $(35.1 \pm 9.5$ kg weight, 150.6 ± 13.5 cm FL, tracking duration 1238 ± 404 d, $n = 27$) had an average residence of 68% in Florida, 31% in northern GOM, and 1% in the Mid-Atlantic (Fig. 9).

Derived from a previously conducted survey (Griffin et al. 2023), data from 730 respondents (Florida = 625, Mid-Atlantic = 56, northern GOM = 49) (Fig. SI 3) were assessed. While the majority of ranked severities were similar (Fig. SI S3, Table 1), water quality, habitat decline, forage prey decline, and angling pressure were ranked as the highest threat severities. More specific to high and very high threats and region similarities and differences, water quality was identified as a very high threat in both Florida and the northern GOM, while being categorized as a high threat in the Mid-Atlantic region. Habitat decline was equally a high threat across all regions. Additionally, forage prey decline was rated as very high in the northern GOM and the Mid-Atlantic but was only considered a medium threat in Florida. Lastly, angling

Fig. 6 Detection patterns across latitude and year for Atlantic tarpon (*Megalops atlanticus*) that were less than 128.5 cm in fork length (colored dots indicate detection origin). Tagging latitude is shown in black with shapes indicating migrant (circle) or non-migrant (triangle) classifications

pressure was assessed as a high threat in the northern GOM and Florida, but was only a medium threat in the Mid-Atlantic.

Discussion

This study provides valuable insights into the movement patterns and spatial dynamics of *M. atlanticus*, a highly migratory teleost, with a focus on regional connectivity and their perceived vulnerability across the GOM and southeastern US coastal regions. Network analysis revealed heterogeneous space use among regions, with mixing primarily occurring in south Florida, specifically The Everglades and the Florida Keys in spring. Furthermore, while *M. atlanticus* displayed varying movement patterns among individuals, there was low inter-annual variability by individuals, suggesting that individual *M. atlanticus* tend to exhibit consistent and repeatable movement patterns. For fish that migrated, we found no effect of size on the extracted movement parameter metrics, further supporting that once reaching maturity or joining migratory adults, individuals will remain consistent in migratory behaviors. Additionally, while some subadults displayed highly migratory behaviors similar to adults, larger juvenile *M. atlanticus* predominantly exhibited resident or nomadic behaviors.

Collectively, the far-ranging nature of *M. atlanticus* and their diversity in movement patterns across individuals, life stages, seasons, and regions, highlight the need for more uniform and cohesive management and conservation efforts across jurisdictions.

Regional connectivity

Our data support the existence of a single interconnected stock unit of *M. atlanticus* in the US Atlantic coast and eastern GOM (McMillen-Jackson et al. 2005; Luo et al. 2020). While the stock is connected through both larval and adult dispersal, our tracking data demonstrated that the stock is also spatially structured with distinct subgroups that migrate either primarily along the eastern GOM or southeastern US coastlines. Considering no *M. atlanticus* were detected moving beyond the Mississippi Delta, Louisiana, there is a further likelihood that an additional subgroup or stock exists for the western GOM, as supported by other tracking studies (Luo et al. 2020; Drymon et al. 2021). While boundaries appear to exist for subgroups of fish, adult mixing and gene flow are likely to occur along each regional edge. In this study, considerable mixing of adult *M. atlanticus* occurred in the Florida Keys during the spring months, when spawning occurs (Crabtree 1995; Luo et al. 2020; Lowerre-Barbieri et al. 2021; Griffin et al. 2022a). For fish that migrate along
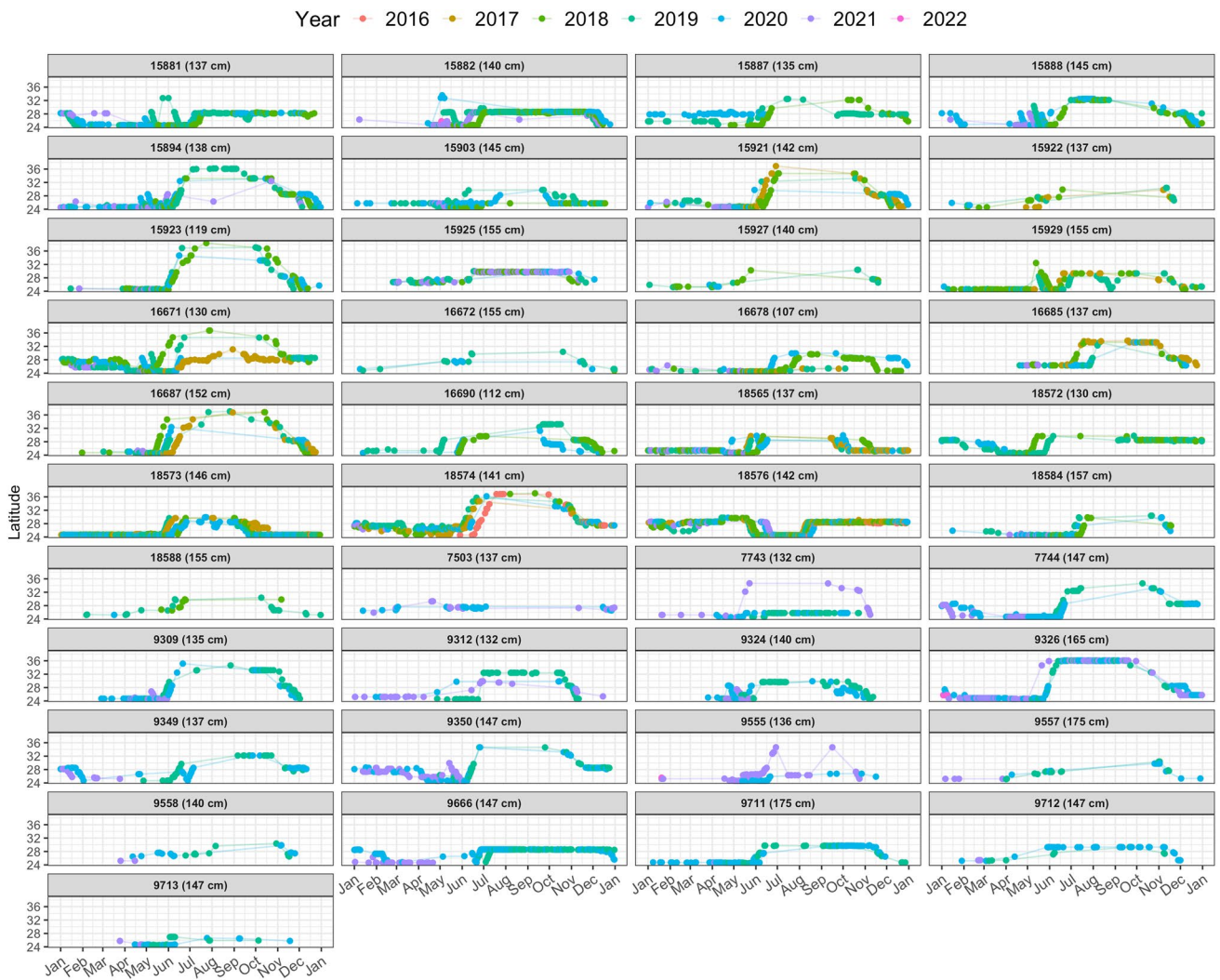
Fig. 7 Migration patterns across latitude and month for individual adult Atlantic tarpon (*Megalops atlanticus*) with colored paths connecting detections (colored paths indicate detection year)

the eastern GOM coast and onward toward Louisiana, an additional mixing location is likely (Luo et al. 2020) and may, in part, be attributed to spawning (Stein III et al. 2012, 2016; Graham et al. 2017; Luo et al. 2020).

Adult and subadult/large juvenile movement patterns

Movement patterns of *M. atlanticus* varied in timing, duration, and distance traveled among individuals. At the population level, mechanistic movement models determined *M. atlanticus* migrate northward during spring (mainly in June–July) and southward in the fall (mainly in September–November). Although no adult exhibited resident behavior (i.e., no movement beyond one location), similar to the findings of Luo et al. (2020), this study highlighted some degree of partial migration (i.e., intraspecific differences in

migration patterns; (Chapman et al. 2012), with some individuals traveling many thousands of kilometers and others relatively shorter distances. For instance, some individuals were only detected within the borders of Florida.

Regardless of the distance traveled, the northward movements of *M. atlanticus* are believed to be foraging migrations aimed at recovering energy stores after overwintering and spawning. Similar to another migratory species, *T. thynnus*, state-dependent energy allocation models have shown the energetic trade-offs between migration distance, timing, and net energy intake (Chapman et al. 2011b). Interestingly, as the distance between migratory ranges for *M. atlanticus* increased, the time spent in their northern migratory range decreased, but southward migrations in the fall began and ended later. As seen in avian biology, this dynamic highlights the complex energetic trade-off that migratory species face between energetically
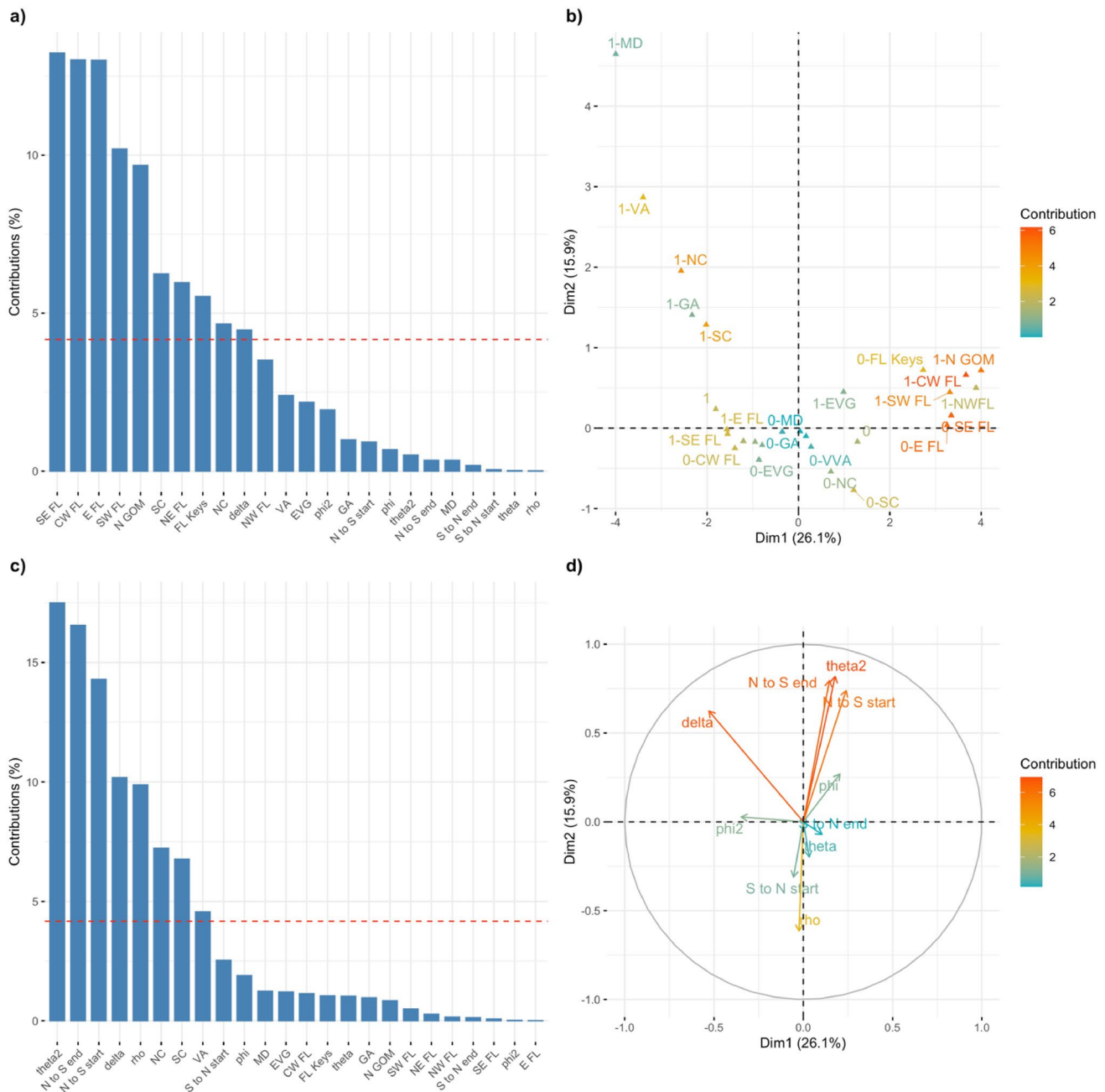
Fig. 8 Factor analysis of mixed data output using movement model parameter estimates and locations where *M. atlanticus* were detected and not; **a** contribution of variables to dimension one, **b** contribution of categorical variables (locations visited and not visited) across dimension 1 and 2, **c** contribution of variables to dimension 2, and **d** contribution of numeric variables (locations visited) across dimension 1 and 2. The red dashed line in panels a and c indicate the expected average value, if the contributions were uniform

costly long-distance migrations and the search for temporally and spatially stable prey sources that require less effort for locating and capture when reliably available (Parrish 2000). For *M. atlanticus*, these areas include productive estuarine systems extending from northern Florida (June and Chamberlin 1959; Dame et al. 2000; Chanton and Lewis 2002), to Virginia (Roman et al. 2005) or Louisiana (Grimes 2001). Supporting this, Drymon

et al. (2021), using satellite telemetry transmitters on *M. atlanticus*, found that the Mississippi River Delta, which is known for its high productivity (Grimes 2001), exhibited the lowest movement persistence rates for tagged *M. atlanticus*. While our biological understanding of *M. atlanticus* is limited, our data indicates that they typically remain within their northern migratory ranges for approximately four months. Consequently, these areas hold significant
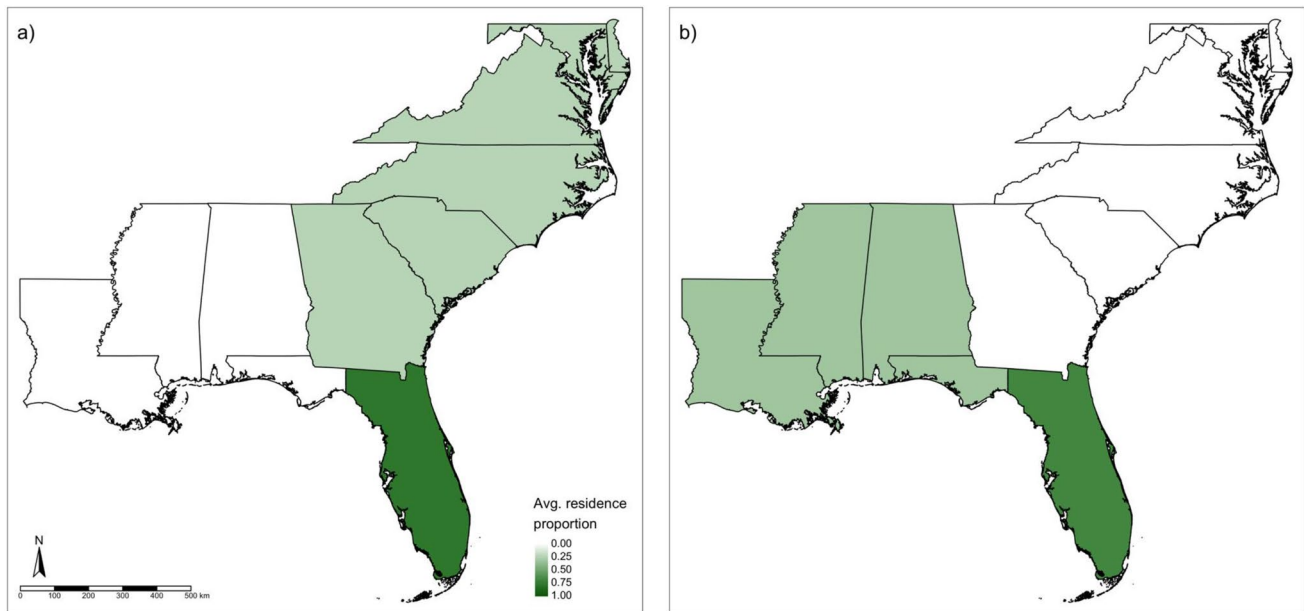
Fig. 9 Averaged proportion of time spent in each region by Atlantic tarpon (*Megalops atlanticus*), darker colors indicate higher residence times on average. Using the community groupings from network analysis and from the Leading-Eigenvector algorithm, **a** shows the proportion spent for *M. atlanticus* that were assigned to the 'southeastern US coast' community group, while **b** shows the proportion spent for *M. atlanticus* that were assigned to the 'Gulf of Mexico' community group

importance for *M. atlanticus* and serve as critical components of their life history patterns and underscore the importance of migration timing in relation to the phenology and abundance of seasonal prey availability.

The movements of subadult/large juvenile *M. atlanticus* were also highly variable, with larger subadults appearing to migrate like adults, and large juveniles remaining resident or nomadic. This result supports Kurth et al. (2019), who found that ontogenetic shifts from the upper estuary to coastal waters occur at or near maturity (~ 140 cm total length). These data also highlight that even subadult or small adult *M. atlanticus* can make long-distance migrations. For migrant *M. atlanticus*, there was no relationship between fish size and observed migration patterns, suggesting migratory tendencies are likely linked to individual behaviors rather than size.

Repeatability of migration patterns

While some variability existed, *M. atlanticus* displayed significant repeatability in their movement patterns from year to year, including movement parameter estimates (distance, timing) and the locations they visited. These results align with those of Griffin et al. (2022a), who found that *M. atlanticus* often consistently arrived in the Florida Keys at similar times each year. Additionally, Kurth et al. (2019) found consistent isotopic signatures on *M. atlanticus* eye lenses, indicating that they migrate to the same coastal system annually.

These consistent movement patterns, coupled with a lack of size–migration relationship among migrants, align well with the entrainment hypothesis (Petitgas et al. 2006; ICES 2007), which suggests younger fish learn migration routes and patterns from adults, leading to multi-generational conservatism in habitat use.

Understanding this repeatability offers insight into how *M. atlanticus* may balance the trade-off between energetics and survival. For example, as demonstrated with sea trout (*Salmo trutta*), consistency in the arrival timing and duration of time spent in freshwater compared to marine environments can also indicate a trade-off between decreased fitness and safer conditions (Birnie-Gauvin et al. 2021). Similarly, *M. atlanticus* may weigh these factors when deciding whether to migrate to highly productive, but energetically expensive far-ranging estuarine systems, or to remain in nearby, less productive areas. The risk of predation from great hammerhead (*Sphyrna mokarran*) and bull (*Carcharhinus leucas*) sharks, both known to actively target *M. atlanticus* (Griffin et al. 2022b), must also be considered in these migratory decisions.

Known as the portfolio effect (Schindler et al. 2010, 2015), the diversity in life history strategies for *M. atlanticus* could enhance population stability by spreading risk across time and space. This is particularly evident in the Florida Keys, where some individuals may undergo multiple, energetically expensive migrations in the spring before undergoing foraging migrations. These individuals were found to quickly migrate away from the Florida Keys, presumably

via the Gulf Stream due to the speed and lack of detections along the coastline, only to return a few days later. While this behavior could be related to real or false spawning runs in early May, it highlights the extreme energetic costs some individual *M. atlanticus* may incur each year. Further research into these behaviors is necessary to better understand its implications for *M. atlanticus*' survival, fitness, and conservation.

Conservation and management implications

The highly migratory and interconnected *M. atlanticus* population spans multiple management regions and habitats. This highlights the necessity of implementing a unified management approach to ensure the conservation of *M. atlanticus* throughout their extensive geographic range. Proportionally, *M. atlanticus* spent most of their time in Florida, where the severity of threats such as water quality degradation, habitat decline, and angling pressure is especially high. The decline in prey emerged as a major concern for *M. atlanticus* in the northern GOM and Mid-Atlantic regions. A comprehensive *M. atlanticus* management plan should incorporate and address several key components, including fishery regulations (harvest limitations, catch-and-release mandates), angler education on best angling and handling practices (Brownscombe et al. 2017), shark depredation and post-release mortality (Guindon 2011; Luo et al. 2020; Griffin et al. 2022b; Horowitz et al. 2023) and habitat and water quality (e.g., harmful algal blooms Griffin et al. 2022c), protection and restoration (Wilson et al. 2019). In addition, this plan should also consider the potential overharvest of putatively important prey sources, like menhaden (*Brevoortia patronus*, *Brevoortia tyrannus*), and protect the habitats they rely on (Gillson 2011; Broadley et al. 2022).

One of the most pervasive threats to *M. atlanticus* is the potential impact of climate change resulting in phenological mismatches (Miller-Rushing et al. 2010). These mismatches have implications at multiple levels for *M. atlanticus*. For instance, as observed in some avian species (Both et al. 2009; Zhemchuzhnikov et al. 2021), if *M. atlanticus* prey sources change phenology at faster rates than *M. atlanticus*, this trophic mismatch may lead to reductions in growth and survival. Alternatively, phenological mismatches may occur within estuaries (Chevillot et al. 2017), which play a vital role in supporting the early life stages of *M. atlanticus* (Wilson et al. 2019) and their prey sources (Kurth et al. 2019). In addition, marine ecosystem-wide phenological changes are increasing (Edwards and Richardson 2004; Staudinger et al. 2019), and as sea surface temperatures continue to rise (IPCC 2021), these changes will undoubtedly affect *M. atlanticus* (Danylchuk et al. 2023). Indeed, respondents from an *M. atlanticus* angler and guide survey noted an earlier

seasonal arrival timing of *M. atlanticus*, suggesting that climate change is already impacting this species (Griffin et al. 2023). The repetitive nature and high site fidelity exhibited by *M. atlanticus* could further exacerbate these potential anthropogenic-driven changes and phenological mismatches (Merkle et al. 2022). Along with proactive management strategies, their ability to adapt and exhibit behavioral plasticity will be critical in determining their resilience in the face of these changes (Killen et al. 2016).

Despite the economic importance of *M. atlanticus* (Smith et al. 2022) and the concerning evidence of declines in their abundance (Adams et al. 2019; Griffin et al. 2023), formal management plans are still lacking. However, by raising awareness and actively involving stakeholders in conservation and management efforts, it is possible to generate grassroots pressure for policy and management changes focused on *M. atlanticus* and their habitats (Sawchuk et al. 2015; Sterling et al. 2017; Raynal et al. 2020; Shephard et al. 2022). As a charismatic species with cultural significance (Kokomoor 2010; Mill et al. 2010; Davis 2017), *M. atlanticus* are an ideal candidate to serve as flagship species and to rally support for conservation efforts. Promoting awareness and conservation actions for *M. atlanticus* will create a broader platform to advocate for the protection of their habitats and the ecosystems they inhabit (Wilson et al. 2023). A successful example of stakeholder involvement in management was documented with permit (*Trachinotus falcatus*), another valuable recreational fishery. Brownscombe et al. (2019) demonstrated how collaboration among scientists, managers, and stakeholders, facilitated by a non-governmental conservation organization, led to the implementation of a seasonal harvest closure based on *T. falcatus* movement data. This example highlights the importance of strong relationships and communication channels to translate research findings into actionable management measures for recreational fisheries.

To effectively conserve *M. atlanticus*, it will be essential to implement management strategies that go beyond traditional fishery management techniques. Drawing inspiration from the concept of flyways for waterfowl (Anatidae family) management (Bolen 2000), it becomes evident that *M. atlanticus* exhibit distinct and segregated annual northward and southward movements. In the case of waterfowl, a decline in populations can be attributed to the degradation and fragmentation of habitat networks, which leads to a loss of functional connectivity (Xu et al. 2019). Similarly, for *M. atlanticus*, it will be important to establish and recognize interconnected networks, ranging from spawning sites to northern foraging areas, in order to enhance conservation and management efforts. Additionally, framing conservation efforts around these networks should enable *M. atlanticus* to better adapt to the challenges posed by climate change. By

identifying and focusing on key features for *M. atlanticus*, such as estuaries and associated prey sources, these areas can also serve as climatic stepping stones (Hodgson et al. 2012; McGuire et al. 2016), preserving functional habitat connectivity across their range and facilitate potential expansion and subsequent entrainment (Petitgas et al. 2006). This approach, that focuses on safeguarding the stepping stones, aligns with the positive outcomes observed in avian conservation efforts (Huntley et al. 2006; Saura et al. 2014; Stralberg et al. 2019), underscoring the necessity of considering broader ecological dynamics when developing management plans for *M. atlanticus*.

Conclusion

This multi-year acoustic telemetry study aimed to gain a comprehensive understanding of *M. atlanticus* movement patterns. By examining individual movement patterns and behaviors, we were able to determine there are two distinct migratory subgroups along the eastern GOM and southeastern US coast, which predominantly converge in South Florida for spawning in the spring, with individuals from each group displaying consistent and repeatable migratory behaviors from year to year. Our data also highlight that relatively smaller *M. atlanticus*, young adults or subadults, can make distant migrations to reach more productive northern foraging areas. Considering migrant *M. atlanticus* remain in these more northern areas for an average of four months, future research should aim to better understand the importance of prey from these regions. Furthermore, additional genetic analyses (Ward et al. 2004) is needed to confirm if *M. atlanticus* in the GOM and Atlantic seaboard constitute a single stock. Collectively, the findings of this multi-year acoustic telemetry study reveal the complexity of *M. atlanticus* movement patterns, characterized by widespread connectivity across the eastern GOM and southeast US, diverse movement patterns among individuals, and consistency within each individual. *Megalops atlanticus* populations face numerous threats from human activities, and without proper and unified management efforts, the trend of declining population abundance is likely to persist (Adams et al. 2019, 2023).

Declarations

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