Estuaries and Coasts (2026) 49:41
https://doi.org/10.1007/s12237-025-01657-3

Seasonal Residency and Movement Patterns of Bonnetheads (*Sphyrna tiburo*) in Two Subtropical Estuaries and Coastal Waters of the South Atlantic Bight

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Received: 19 March 2025 / Revised: 31 October 2025 / Accepted: 10 December 2025

Abstract

Tracking animal movements underpins our understanding of habitat linkages, stock definitions, and life-history vital rates. The bonnethead (*Sphyrna tiburo*) is abundant seasonally in southeastern United States (US) Atlantic coast estuaries; however, there is relatively little information regarding bonnethead ecology at the northern end of its distribution. We employed acoustic telemetry to document patterns of seasonal residency and movement for bonnetheads in North Carolina (NC) and Georgia (GA) estuaries, as well as other portions of the South Atlantic Bight (SAB). We acoustically tagged 21 bonnetheads in Beaufort Inlet Estuary, NC and 16 in Wassaw Sound, GA, and tracked those fish within estuarine arrays of 78 and 8 hydrophones in NC and GA, respectively. Bonnetheads were resident in NC and GA estuaries from March through November. Overall, detections were highly localized within individual estuaries, with most bonnetheads remaining in the area where they had been tagged, suggesting small core areas of movement (≤2 km) during seasonal residency. Conversely, 15 bonnetheads tagged in NC and 10 tagged in GA were detected in 14 other coastal hydrophone arrays in South Carolina, GA, and Florida (FL). The location and timing of these detections suggest that bonnetheads from distinct estuaries along the SAB overlap during late fall and winter months along the southeast US Atlantic coast, especially offshore of Brunswick, GA and Cape Canaveral, FL. Return rates for NC and GA bonnetheads were at least 25% and 19%, respectively, indicating a notable degree of estuarine-scale site fidelity.

Keywords Small coastal shark · Acoustic telemetry · Migration · Site fidelity

Introduction

Many animals perform diel, seasonal, and ontogenetic movements related to foraging, tracking preferential environmental conditions, risk avoidance, or reproduction; knowledge of which is crucial for predicting population and community dynamics (Morales et al., 2010). Among fishes, these movements can occur over a range of scales, such as across habitats, throughout coastal estuaries, or between management regions, as individuals attempt to maximize fitness (Mason & Brandt, 1996). For many estuarine-associated species, tracking seasonal movements or migrations of fishes capable of transiting between offshore spawning and inshore foraging habitats is critical for defining stock concepts, determining animal-habitat relationships, quantifying vital rates, and even understanding evolutionary patterns and potential mechanisms (Cadrin & Secor, 2009). Understanding how movement and habitat utilization (together referred to as behavior) affect population ecology of fishes is especially important as we move toward ecosystem-based approaches for managing coastal resources (Crowder & Norse, 2008).

Bonnetheads (*Sphyrna tiburo*) are abundant seasonally in southeastern US Atlantic and Gulf of Mexico (GOM) waters,

Communicated by Kevin M. Boswell

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Published online: 26 December 2025

including estuaries, and are potentially important predators on another key estuarine species, the blue crab (*Callinectes sapidus*) (Byers et al., 2017; Plumlee et al., 2023). Although demography, social behaviors, and estuarine habitat use of bonnetheads have been studied in the GOM and along Florida (FL) (Myrberg & Gruber, 1974; Cortés & Parsons, 1996; Heupel et al., 2006), comparatively little work has been undertaken north of FL. Previous work has detected latitudinal variation in growth rates of bonnetheads (Carlson & Parsons, 1997; Lombardi-Carlson et al., 2003), as well as regional differences in size-at-age (Frazier et al., 2014), highlighting the importance of understanding movement patterns throughout the entire range of this species, which could provide ecological context for observed differences (i.e., potential disparities in migrations to/from estuaries and overwintering grounds could be used to elucidate variation in growth seasons). A tagging study on female bonnetheads in South Carolina (SC) found evidence of site fidelity within specific estuaries across multiple years (Driggers et al., 2014), a pattern that remains to be confirmed from other locations within the northern extent of their range. Driggers et al. (2014) also reported that 90% of bonnetheads captured within five SC estuaries were female, suggesting a potential ecological tradeoff favoring the use of these estuaries by females, possibly related to reproduction.

Over the past several decades, the use of acoustic telemetry for the study of spatial ecology has grown exponentially, fueled by advances in technology including miniaturization of transmitters, battery life expansion, and software development (Hussey et al., 2015). Telemetry data have provided critical information on distribution and connectivity of a variety of marine taxa (e.g., fish, birds, mammals, turtles), utilized in management and conservation efforts, particularly site-based approaches such as the development of marine protected areas and identification of essential habitats (Hays et al., 2019). With the expansion of acoustic telemetry arrays in coastal regions and on offshore and mobile platforms there is an increasingly cost-effective opportunity to integrate tracking data across local-through-regional spatial scales to delineate migration patterns in highly-mobile marine megafauna, potentially informing collaborative conservation efforts across management jurisdictions (Hussey et al., 2015; Davies et al., 2021).

The objectives of this study were four-fold: (1) determine residency patterns (residency was gauged both in terms of the seasonal timing and duration of estuarine occupancy) of bonnetheads in two estuarine complexes along the South Atlantic Bight (SAB) – one in North Carolina (NC) and one in Georgia (GA); (2) assess within-estuary movement patterns of bonnetheads to explore the spatial scale of core areas of movement among individuals and spatial patterns of detections; (3) evaluate distribution and migration patterns of bonnetheads along the SAB during seasons in which fish emigrated from estuaries to gauge whether fish initially captured and tagged in separate estuaries remain spatially segregated year-round, or overlap while in the coastal ocean; and (4) quantify interannual return rates of individual bonnetheads to focal NC and GA estuaries to quantify the degree of estuarine-scale site fidelity among these fish.

Methods

Field Sampling

To monitor bonnethead movement behaviors and evaluate potential similarities and differences between estuaries, diffuse arrays of VR2W hydrophones (Vemco, Nova Scotia, Canada) were deployed in both NC and GA estuaries. The VR2W is an omni-directional hydrophone with a detection range of approximately 350 m in these shallow coastal systems based on onsite tests. The NC array consisted of 78 hydrophones placed in and around Beaufort Inlet and the lower estuary regions of the Newport and North Rivers. The specific hydrophone areas were: Ocean shipping channel, Atlantic Beach, Emerald Isle, Bogue Sound, Newport River, Beaufort Inlet, Morehead City shipping channel, Carrot Island, Middle Marsh, North River Marsh, Oscar Shoal, Back Sound, and Cape Lookout (Fig. 1). Of these, 20 hydrophones were placed within individual marsh complexes, as well as sand flats and deeper channels presumed to be travel corridors, to detect movement among salt marsh complexes (sensu Kenworthy et al., 2018). We also leveraged arrays from concurrent studies within this "Beaufort Inlet Estuary" complex, including the acoustic tracking of juvenile gag grouper and Gulf flounder within Middle Marsh and Oscar Shoal, with 21 hydrophones placed in sandflats and seagrass beds (Keller, 2018). Another acoustic tracking study of weakfish in and around the Morehead City shipping channel was leveraged that included 37 hydrophones attached to channel markers in deep channels and a porous gate of Beaufort Inlet (Krause et al., 2020). The GA array consisted of 8 hydrophones placed in and around several marsh creeks within lower Wassaw Sound including Romerly Creek, Bull River, and Tybee Cut, as well as the lower Wilmington and Skidaway Rivers surrounding Skidaway Island (Fig. 2). This array was much smaller due to the comparatively smaller size of the estuary, fewer tagged sharks at liberty, and the fact that it was not possible to gate the inlet with hydrophones, as in Beaufort Inlet. Hydrophones were placed in areas where sharks were caught and tagged; the inlet in this system was too large to provide any

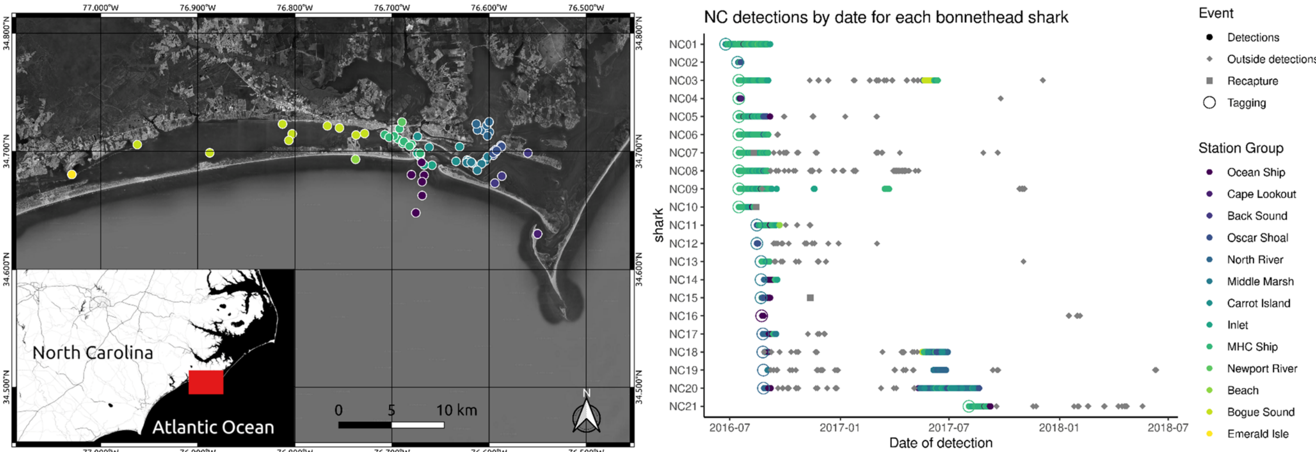

Fig. 1 Left pane contains map of study site in NC. Circles indicate locations of each of the 78 hydrophones in the NC array, used for tracking bonnethead shark movement during residency in 2016 and 2017. Color of circles indicates station grouping. Right pane contains abacus plot showing dates of all detections from each bonnethead shark tagged and detected in the NC array. Detections are color-coded by station grouping, aligned with station colors in the study site map. Also displayed are the dates of events such as the initial tagging (with location color-coded by station grouping), outside detections or detections from other arrays, and recapture reports from fishermen

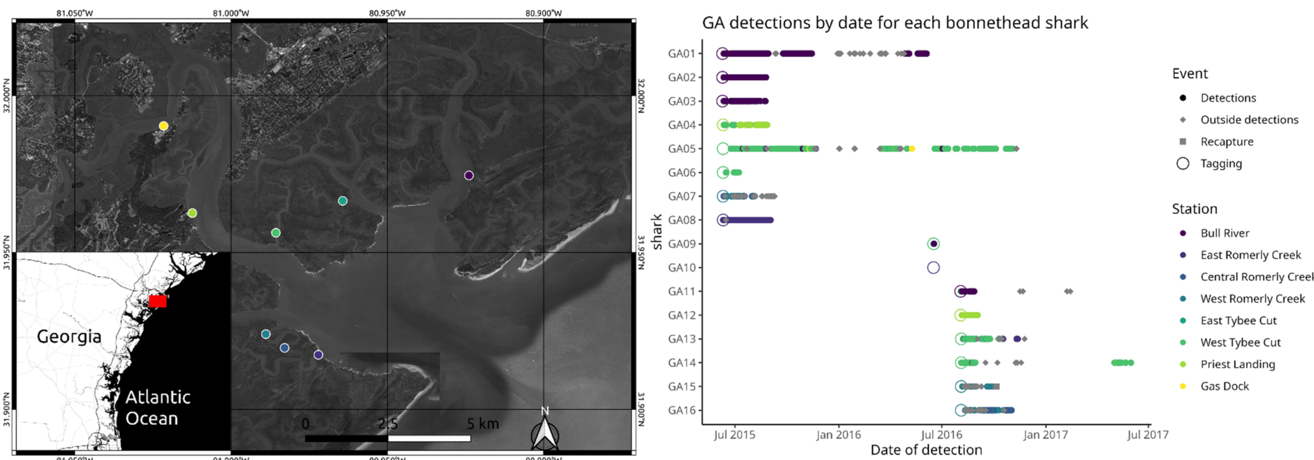

Fig. 2 Left pane contains map of study site in GA. Circles indicate locations of each of the 8 hydrophones in the GA array, used for tracking bonnethead shark movement during residency in 2016 and 2017. Color of circles indicates station. Right pane contains abacus plot showing dates of all detections from each bonnethead shark tagged and detected in the GA array. Detections are color-coded by station, aligned with station colors in the study site map. Also displayed are the dates of events such as the initial tagging (with location color-coded by station), outside detections or detections from other arrays, and recapture reports from fishermen

gate for detections. Acoustic arrays were maintained from June, 2016 through October, 2017 in NC and June, 2015 until June, 2019 in GA.

To understand bonnethead migration patterns outside of our estuarine arrays, we tapped into two collaborative networks, the Atlantic Cooperative Telemetry (ACT) Network and the Florida Atlantic Coast Telemetry (FACT) Network, comprised of approximately 418 and 1000 acoustic receivers, respectively. Combined, these two collaborative networks have a geographic scope of coverage that extends along the Atlantic coast from Maine to the FL Keys, including offshore areas such as the Gray's Reef National Marine Sanctuary and the Bahamas. These collaborative networks allowed us to receive detections from other researchers' arrays, greatly expanding the scale of our study through data sharing. Specifically, we received detections from the following locations: Myrtle Beach, (SC offshore), North Inlet (SC offshore), Charleston (SC offshore), St. Helena Sound (SC offshore), Hilton Head Island (SC estuarine/offshore), Savannah (GA estuarine), Rommerly Marsh Creek (GA estuarine) Ossabaw Sound (GA estuarine), Gray's Reef National Marine Sanctuary (GA offshore), Brunswick (GA offshore), St. Mary's River & St. John's River (FL estuarine/offshore), Indian River Lagoon (FL estuarine/offshore), Cape Canaveral (FL offshore), and Jupiter Beach (FL offshore).

A total of 21 bonnetheads in NC and 16 in GA were acoustically tagged for this study. Bonnetheads were captured using either hook and line, gill netting, cast net (1 individual), or bottom trawl (1 individual). In GA, sharks were tagged in June 2015 and June and August 2016, whereas in NC they were tagged between June and August 2016, with one additional individual tagged in August 2017 (Tables 1 and 2). Similar to a previous tagging study in SC (Driggers et al., 2014), all but one bonnethead we tagged were female (one male was captured by bottom trawl ~ 3.5 km outside of Beaufort Inlet, NC). A 50-mm external "roto" tag (Premier 1 Supplies, Iowa, USA) was attached to the first dorsal fin of each shark. We affixed Vemco V13 acoustic transmitters to external tags using marine epoxy. These 'coded' transmitters were set to transmit a signal from each shark (using a train of pings unique to each individual tag) randomly once every 3–5 min, throughout the life of the tag (~4 years). We chose to use external attachment as this reduced the handling time for each shark and was less invasive than surgery. Tags included our contact information in case of post-release recaptures, with a reward notice. We observed tagged sharks prior to being released to assess condition, only releasing individuals that showed no signs of distress, thereby avoiding tracking of individuals likely to expire.

Data Analyses

1) To determine patterns of seasonal residency of tagged bonnetheads in NC and GA estuaries, we were guided by previous efforts that suggested the sharks' use of inshore habitat during spring through fall, and equatorward movement (mostly offshore) during winter (Driggers et al., 2014). Within this framework, we analyzed patterns of occurrence within the NC and GA estuarine arrays, separately, to document the "first" (seasonal arrival) and "last" (seasonal departure) detection of individuals in each calendar year in each system as our metrics of seasonal residency patterns. Across all sharks and years, separately for NC and GA, we calculated the range of seasonal arrival and exit dates for each system, as well as the median arrival and departure dates for each system to examine the central tendency in these dates. To consider potential environmental correlates (putative triggers) for bonnethead entry and exit to/from our arrays, we collected temperature and photoperiod data. We obtained temperature data (sampling interval = 6 min) for the full range of departure and arrival dates for each array, separately, from the nearest NOAA

Table 1 Summary of 21 bonnethead sharks tagged with acoustic transmitters and tracked within the array of hydrophones surrounding Beaufort Inlet, NC. Shark IDs marked with an asterisk are sharks that returned in 2017. Tagging location indicates where fish were originally caught and tagged for this study: Carrot Island (CI), Morehead City shipping (MHCS), middle marsh (MM), ocean shipping (OS), North river (NR). Days in estuary are calculated as days between tagging date and date of last detection within NC array for tagging year. For previously tagged sharks returning in 2017, days between first and last detection within NC array during 2017 are used to compute the days in estuary for that year. % detections ≤ 2 km indicates proportion of detections within 2 km of tagging location

Shark ID	Tagging location	Tagging date	Sex	Fork length (mm)	Total detections	Hydrophones visited	Days in estuary 2016	Days in estuary 2017	% detections ≤ 2km year 1	% detections ≤ 2km year 2
NC01	CI	06/24/16	F	800	2843	15	74	NA	98	NA
NC02	CI	07/14/16	F	925	138	21	6	NA	22	NA
NC03*	MHCS	07/16/16	F	825	3785	23	49	24	94	56
NC04	MHCS	07/16/16	F	855	68	9	4	NA	81	NA
NC05	MHCS	07/16/16	F	885	2495	29	52	NA	93	NA
NC06	MHCS	07/16/16	F	955	3042	24	49	NA	92	NA
NC07	MHCS	07/16/16	F	NA	3527	13	49	NA	99	NA
NC08	MHCS	07/16/16	F	885	2529	30	48	NA	96	NA
NC09*	MHCS	07/16/16	F	845	3581	14	126	7	99	100
NC10	MHCS	07/16/16	F	785	1953	11	27	NA	100	NA
NC11	MM	08/15/16	F	830	2405	24	38	NA	1	NA
NC12	MM	08/15/16	F	870	81	10	2	NA	100	NA
NC13	MM	08/22/16	F	895	1057	26	14	NA	13	NA
NC14	MM	08/22/16	F	815	316	9	27	NA	34	NA
NC15	MM	08/22/16	F	865	541	31	15	NA	45	NA
NC16	OS	08/23/16	M	715	45	5	3	NA	0	NA
NC17	NR	08/25/16	F	835	528	21	22	NA	78	NA
NC18*	NR	08/25/16	F	865	837	33	9	43	62	62
NC19*	NR	08/26/16	F	930	112	2	7	21	100	100
NC20*	NR	08/26/16	F	850	1842	45	12	101	59	57
NC21	MHCS	08/03/17	F	860	2698	13	NA	36	98	NA

Table 2 Summary of 16 bonnethead sharks tagged with acoustic transmitters and tracked within the array of hydrophones surrounding Wassaw Sound, GA. Shark IDs marked with an asterisk are sharks that returned in 2016 or 2017. Tagging location indicates where fish were originally caught and tagged for this study: bull river (BR), priest landing (PL), West tybee cut (WTC), West Romerly entrance (WRC), East Romerly entrance (ERC). Days in estuary are calculated as days between tagging date and date of last detection within GA array for tagging year, for previously tagged sharks returning in 2016 and 2017 days between first and last detection within GA array are computed to reach days in estuary for that year. % detections ≤ 2 km indicates proportion of detections within 2 km of tagging location

Shark ID	Tagging location	Tagging date	Sex	Fork length (mm)	Total detections	Hydrophones visited	Days in estuary 2015	Days in estuary 2016	Days in estuary 2017	% detections ≤ 2km year 1	% detections ≤ 2km year 2
GA1*	BR	06/09/2015	F	820	11,248	1	158	39	NA	100	100
GA2	BR	06/09/2015	F	790	4988	1	77	NA	NA	100	NA
GA3	BR	06/09/2015	F	840	816	2	76	NA	NA	99	NA
GA4	PL	06/10/2015	F	830	245	2	78	NA	NA	79	NA
GA5*	WTC	06/10/2015	F	900	4502	6	164	231	NA	98	98
GA6	WTC	06/10/2015	F	890	51	1	28	NA	NA	100	NA
GA7	WRC	06/10/2015	F	900	2239	4	56	NA	NA	99	NA
GA8	ERC	06/10/2015	F	890	3400	1	84	NA	NA	100	NA
GA9	WTC	06/16/2016	F	820	13	2	NA	1	NA	0	NA
GA10	ERC	06/16/2016	F	780	0	0	NA	NA	NA	NA	NA
GA11	BR	08/03/2016	F	880	258	2	NA	24	NA	98	NA
GA12	PL	08/03/2016	F	700	25	1	NA	30	NA	100	NA
GA13	WTC	08/04/2016	F	830	2484	4	NA	100	NA	95	NA
GA14*	WTC	08/04/2016	F	880	2168	3	NA	25	29	99	NA
GA15	WRC	08/04/2016	F	880	1827	2	NA	57	NA	99	NA
GA16	WRC	08/04/2016	F	800	8940	6	NA	89	NA	99	NA

Tides and Currents Stations (station 8656483 – Beaufort, Duke Marine Lab for NC and station 8670870 – Fort Pulaski for GA) (NOAA Center for Operational Oceanographic Products and Services, 2024). We computed the minimum, maximum, and mean temperatures for both departure and arrival periods, separately, for each array. We also obtained sunrise and sunset hours for each array from the NOAA Solar Calculator (NOAA Global Monitoring Laboratory, 2024), and from this calculated photoperiod, which we summarized in terms of the minimum, maximum, and mean photoperiod for both departure and arrival periods, separately, in NC and GA. Finally, we calculated days in estuary for each individual in each estuary – separately for NC and GA – using the dates of each fish's arrival (or tagging date in the year of fish's initial capture) and departure from the estuary in each year. We made this calculation of days in estuary separately for each consecutive year (i.e., the clock is reset for each year) for sharks that were detected in multiple years.

2) To assess the within-estuary movements, i.e. the size of core areas of movement, for bonnetheads tracked within NC and GA arrays, distances between each hydrophone location and tagging location were calculated as a straight-line distance for each detection and for each bonnethead, separately, using the R package geosphere (Hijmans, 2024). We then computed overall detection density for each array as a function of distance from tagging location (number of detections from any tagged shark at specific distances from tagging location) in 1 km increments or bins, generating a histogram to evaluate the overall scale of core areas of movement in each array. We calculated the minimum distance between adjacent hydrophones for each hydrophone in our NC and GA arrays, separately, using the R package sf (Pebesma, 2018). We then computed the average (mean) for each array, to quantify differences in distances between hydrophones within the NC and GA arrays. Because hydrophones in GA were further spaced (an average of 2 km between adjacent stations), to better compare individual patterns of core areas of movement between NC & GA arrays, we also calculated the proportion of detections occurring within 2 km of tagging location for each bonnethead, separately. In addition, detections were plotted as a function of time (abacus plots), color-coded by station for GA or station group for NC (hydrophones grouped by specific areas within our study site), to determine if there were differences in spatial patterns of detections.

3) To evaluate the distribution and migration patterns of bonnetheads along the SAB during seasons in which fish emigrated from their tagging/home estuaries, we evaluated detections of our tagged sharks from other arrays that were shared with us from areas in SC, GA, and FL. Detections were first examined to filter out suspected false detections, including detections occurring far outside the known distribution range for bonnetheads (e.g., Europe or Nova Scotia, Canada) and single

detections that seemed highly unlikely (e.g., 1 shark from GA that was only detected once outside of Pensacola, FL). The coordinates (latitude and longitude) of hydrophones outside of the array where each shark was tagged, as well as date/time detected were compiled from all detections, for each bonnethead, separately. We then computed average daily positions for each day that a shark was detected outside of its array, which was the arithmetic mean of latitude and the arithmetic mean of longitude across all hydrophones detecting each shark for all days they were detected (sensu Ogburn et al., 2018). We also computed monthly mean positions with the same procedure except averaging positions over monthly intervals.

Straight-line distances from tagging location were calculated for each daily average position of each bonnethead, separately, to determine the maximum distance each shark travelled outside of its array of origin. Average daily positions for each shark were then ordered chronologically and classified as southward or northward migration to examine each phase of migrations separately. All daily positions occurring before and including the maximum distance travelled outside of the array for each shark were classified as southward migration (if multiple average daily positions were at the maximum distance we used the last instance), with all subsequent positions classified as northward migration. Likewise, monthly mean positions were classified as southward or northward migration based on whether they occurred before or after the maximum distance travelled. Average daily position and monthly mean position coordinates for all sharks across both NC and GA arrays were plotted using QGIS (QGIS.org, 2024) for both southward and northward migrations (separately) to examine areas of overlap between NC- and GA-tagged sharks. Average daily position data were also exported as web maps (see Online Resources 1 & 2) using the QGIS plugin qgis2o.gis (O.GIS, (O.GIS. 2025).

4) To quantify interannual return rates to the estuaries in which bonnetheads were tagged as a measure of estuarine-scale fidelity, we tracked the number of sharks returning to the estuary (defined here as the entire receiver array at each of our sites) in which they were released each following year for the NC and GA estuarine arrays, separately. We present the data as the proportion returning out of all tagged sharks in each system. Based on the timing and duration of hydrophone array deployments and the recency of tag deployments, these calculations were made for one year (2017) in NC and two years (2016 and 2017) in GA. All statistical analyses were performed in (R Core Team, 2024).

Results

1) We recorded a total of 34,423 detections within the NC array and 43,204 detections from the GA array. In NC, an average of 1,639 ± 1,340 (standard deviation) detections per shark were recorded from the 21 tagged sharks. In GA, there was an average of 2,880 ± 3,367 detections per shark recorded for 15 tagged sharks (1 tagged GA shark was never detected). Individual sharks in NC visited ~ 19 out of 78 total hydrophones, on average, and individual sharks in GA visited an average of ~ 2 out of 8 total hydrophones. In NC, 20 sharks were recorded within the array between 2 and 126 days, with an average of 32 ± 30 days in estuary, during 2016. During 2017, 6 NC-tagged sharks were recorded within their array between 7 and 101 days, with an average of 39 ± 33 days in estuary (Table 1). In GA, 8 sharks were recorded within the array between 28 and 164 days, with an average of 90 ± 47 days in estuary, during 2015. During 2016, 9 GA-tagged sharks were recorded within their array between 0 and 231 days (1 shark was tagged, but never detected), with an average of 60 ± 69 days in estuary. Finally, during 2017 only 1 shark was recorded within the GA array, with 29 days in estuary (Table 2).

Bonnetheads left the NC array between July 20th and November 19th in the year they were tagged, with half of tagged sharks having departed the array by September 3rd. Tagged sharks that returned to the NC array arrived between March 16th and June 5th of the following year, with half of those sharks returning by May 17th (Fig. 1). During the fall departure from the NC array, temperatures ranged between 12.7 and 29.7 °C with a mean temperature of 23.9 °C, while photoperiods ranged between 10.2 and 14.2 h with a mean photoperiod of 12.2 h. During the spring arrival temperatures ranged between 7.8 and 25.7 °C with a mean temperature of 18.7 °C, while photoperiod ranged between 12 and 14.4 h with a mean photoperiod of 13.3 h. In the GA array, bonnetheads departed the array between June 17th and November 21 st on the year tagged, with half of tagged sharks having departed the array by August 29th. The sharks that returned to the GA array arrived between March 17th and May 2nd the year following tagging, with half of those sharks returning by April 26th (Fig. 2). During the fall departure from the GA array, temperatures ranged between 16 and 31.3 °C with a mean temperature of 26.7 °C, while photoperiods ranged between 10.4 and 14.25 h with a mean photoperiod of 12.6 h. During the spring arrival temperatures ranged between 13.3 and 25.5 °C with a mean temperature of 19.6 °C, while photoperiod ranged between 12.1 and 13.5 h with a mean photoperiod of 12.8 h.

2) Within the GA array, detection density was highest within 1 km of tagging location, with 99% of detections falling within this range. Detection density within the NC array was also relatively high (37%) within 1 km of tagging location; however, in NC, detection density was highest at a distance between 1 and 2 km, with 47% of detections occurring within this range. Detection densities at distances above 2 km from tagging location were generally low for both arrays (<2.5%), with the exception of the distance of 6–7 km in the NC array, where 11% of detections occurred (Fig. 3), most of which were associated with Beaufort Inlet and surrounding waters. The average distance between adjacent hydrophones was 803 m in NC, whereas in GA it was 2,310 m. Individual bonnethead detection densities ≤ 2 km from tagging location in NC were generally high the year of tagging, with 11 of 21 sharks having detection densities above 90% at this distance. Of the 4 sharks that returned to the NC array the following year, 2 were detected within 2 km of their tagging location 100% of the time (Table 1). In GA, individual bonnethead detection densities ≤ 2 km from tagging location were also high the year of tagging, with 12 of 16 sharks having detection densities above 95% at this distance. Both sharks that returned to the GA array the following year had detection densities above 95% within the same core areas of movement from the previous year (Table 2).

3) Thirteen of the 21 bonnetheads tagged in the NC array were detected outside of that array between the dates of 08/27/16 and 05/19/18. All 13 bonnetheads were detected in SC (estuarine and offshore waters), 11 of them were detected in GA (offshore waters), and six were detected in FL (offshore waters). Nine of the 16 bonnetheads tagged in the GA array were detected outside of that array between the dates of 07/22/15 and 02/13/17. Nine of these bonnetheads were detected in GA (estuarine and offshore waters) and four were detected in FL (offshore waters). There were 10 NC-tagged sharks and 5 GA-tagged sharks detected off of Brunswick, GA between the months of September 2016 and April 2017, as well as 5 NC-tagged sharks and 1 GA-tagged shark detected off Cape Canaveral, FL between the months of September 2016 and January 2017, with some overlap of NC- and GA-tagged sharks within the same month in both locations (Fig. 4, Online Resources 1 & 2). Notably, no GA-tagged bonnethead was ever detected in any of the sites from SC or NC (i.e., farther north than tagging location), while NC-tagged fish were detected in these sites (Figs. 4 and 5).

4) At least one quarter of bonnetheads tagged in this study returned to NC in the year following tagging, with 5 of 20 sharks tagged in our NC study system during 2016 detected again in our NC array during 2017. There was one shark tagged in 2017 that was detected outside of the NC array during 2018, but was never detected within the array that year (Table 1; Fig. 1). In GA, approximately 20% of tagged bonnetheads returned in the year following tagging, with 2 of 8 sharks tagged in our GA array during 2015 returning to our GA study system in 2016, and 1 of the 8 sharks tagged in 2016 returning in 2017. None of the bonnetheads tagged in GA during 2015 or 2016 returned to our GA array in 2018–2019 (Table 2; Fig. 2).

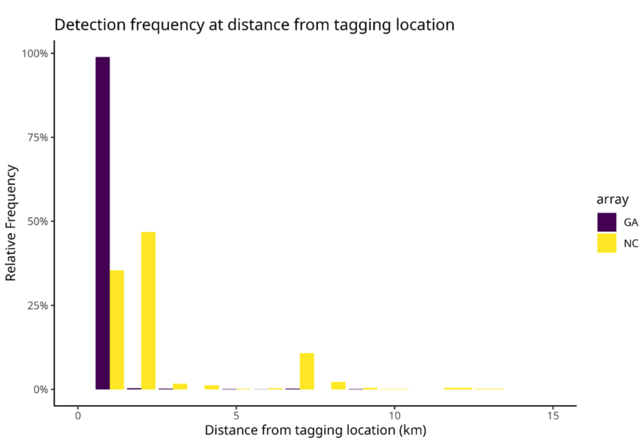

Fig. 3 Histogram displaying proportion of detections for all bonnethead sharks tracked acoustically in the GA and NC arrays (separately as denoted by colors) by distance from tagging location. Detections are aggregated in bins of width equal to 1 km. For ease of viewing, detection densities above 15 km, which combined totaled 0.1% of detections, have been cut from the x-axis scale

Discussion

We documented residency patterns and site fidelity of bonnetheads for two subtropical estuaries on seasonal and inter-annual time scales and build upon previous studies in the region by revealing individual patterns of movement ecology. Moreover, by highlighting and delimiting core areas of movement for bonnetheads in their seasonal estuarine habitats, our results contribute novel information important to the management of this species. These data also offer qualified support of previous research which has suggested mixing of bonnetheads across the southeastern US Atlantic Coast (Escatel-Luna et al., 2015; Díaz-Jaimes et al., 2021). We note that this spatial overlap occurs during fall and winter off the coast of GA and FL, while evidence of overlap during summer was not recorded (i.e., NC and GA tagged fish were not recorded outside of their

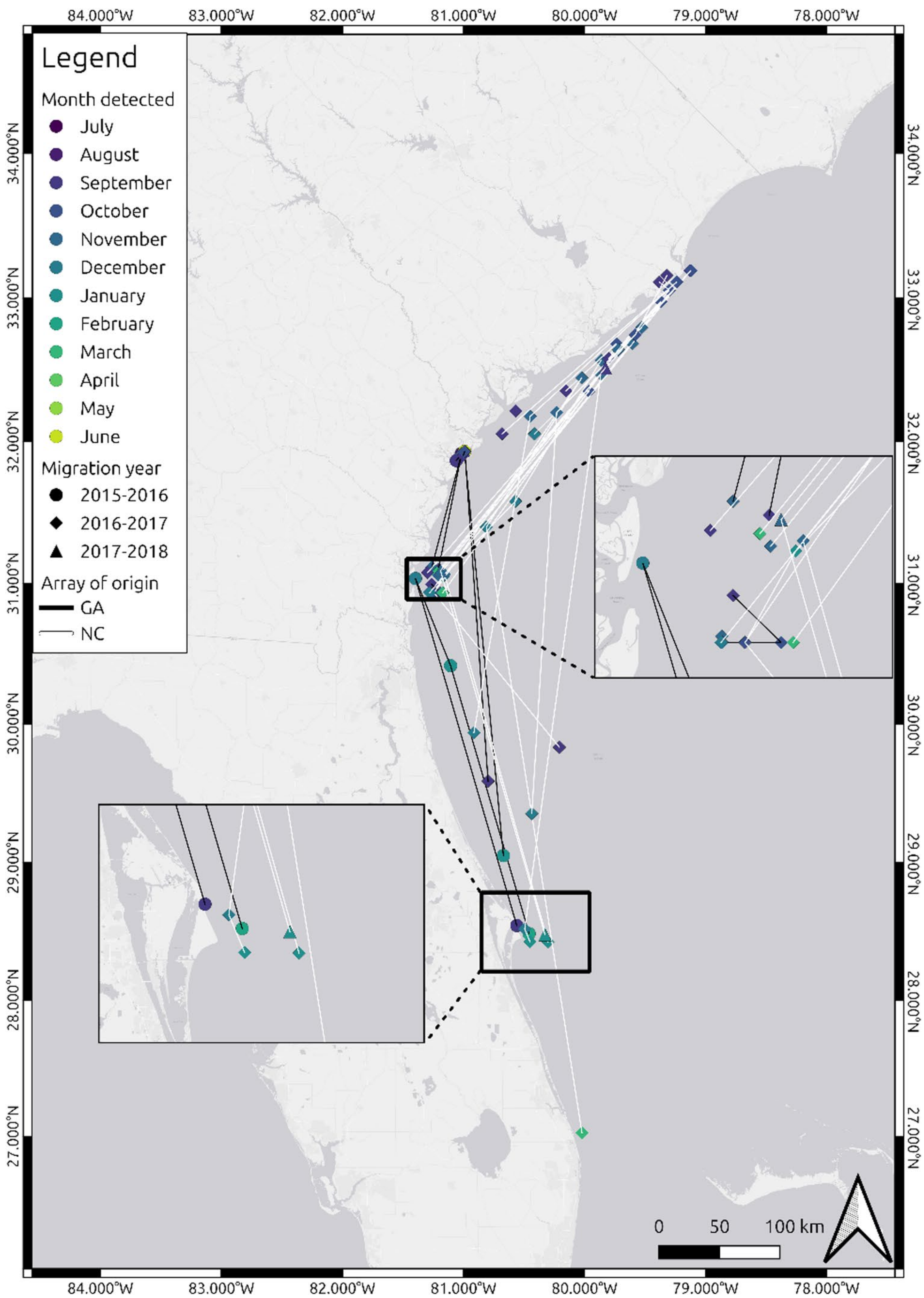

Fig. 4 Tracks of bonnetheads emigrating and migrating southward. Monthly mean positions for all bonnethead sharks tagged in both NC and GA study sites are plotted for all dates prior to and including the last day detected at the greatest distance from tagging location (i.e., southward migration). Symbols are color-coded by month of detections and shapes represent the migration year. Lines are drawn for each individual bonnethead shark connecting monthly mean positions in chronological order and color-coded by array of origin or where the individual sharks were tagged (i.e., GA or NC). Insets show areas of overlap between NC- and GA-tagged sharks (Brunswick, GA and Cape Canaveral, FL)

arrays at distances greater than 12 km from their tagging locations during summer months [Jun-Aug]).

Bonnetheads exhibited seasonal residency during summer months in both NC and GA estuaries, although there was a slight difference in timing of arrival between the two groups, potentially due to differences in water temperatures. An alternative explanation is that the GA-tagged sharks simply reached GA waters sooner, however by this reasoning we would expect that NC-tagged sharks would have left their estuary earlier in the fall or arrived at overwintering areas significantly later than GA-tagged sharks, which our analyses suggest was not the case (Figs. 4 and 5). While the range and central tendency of departure dates from the array and photoperiods were similar between NC- and GA-tagged sharks, NC-tagged sharks displayed a delay of ~1 month for both the latest arrival and the central tendency of arrivals the following year. The range and central tendency of temperatures were more similar during this arrival period than during the fall departure period. These results suggest that bonnetheads may share migratory cues known to

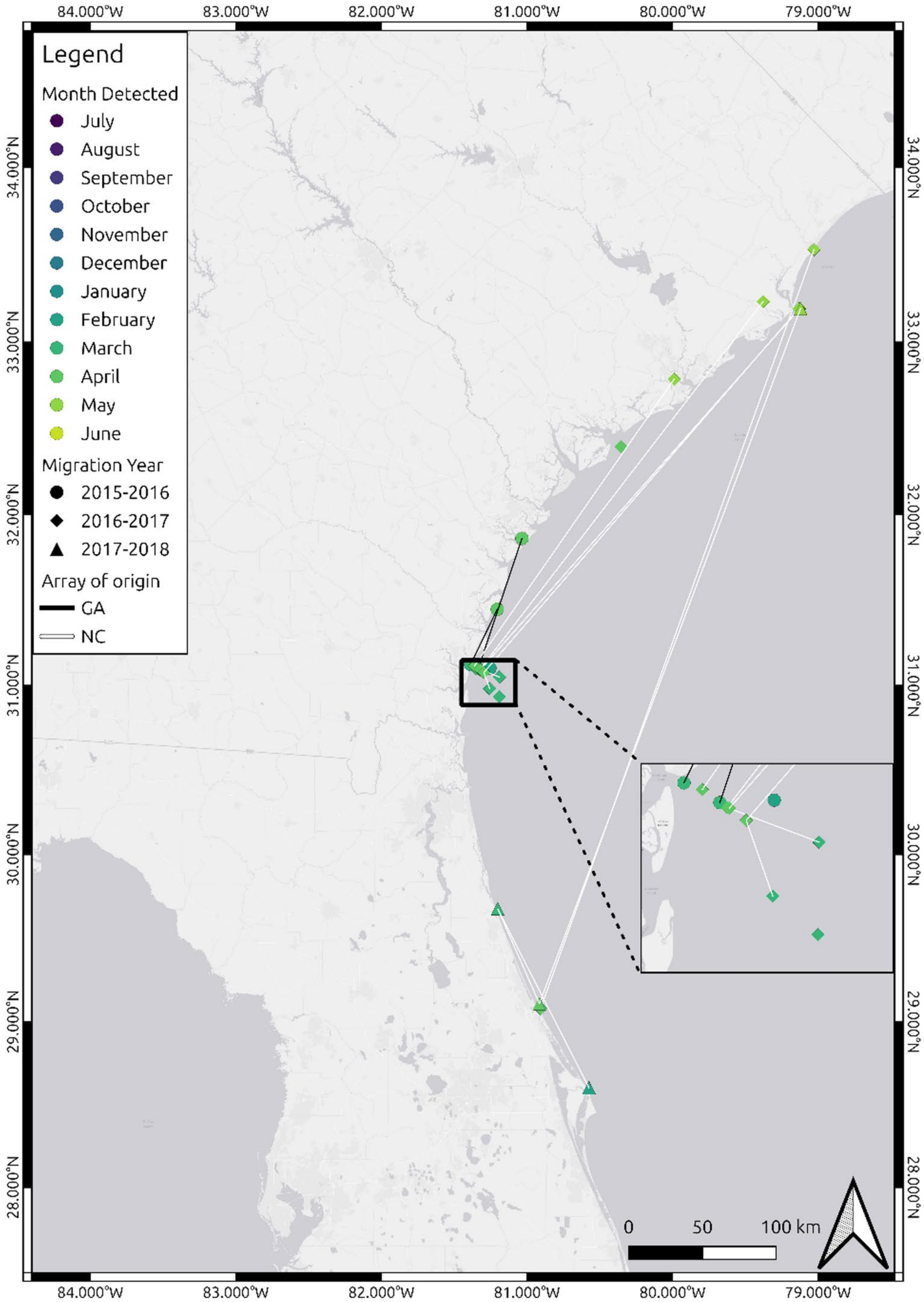

Fig. 5 Tracks of bonnetheads migrating northward and returning. Monthly mean positions for all bonnethead sharks tagged in both NC and GA study sites are plotted for all dates subsequent to the last day detected at the greatest distance from tagging location (i.e., northward migration). Symbols are color-coded by month of detections and shapes represent the migration year. Lines are drawn for each individual bonnethead shark connecting monthly mean positions in chronological order and color-coded by array of origin or where the individual sharks were tagged (i.e., GA or NC). Inset shows area of overlap between NC- and GA-tagged sharks (Brunswick, GA)

be used by other species such as sandbar sharks, which are hypothesized to initiate migrations based on photoperiod; however, they wait to enter the estuary until water temperatures are warmer (Grubbs et al., 2007). Seasonal residency in estuaries and temperature-dependent onset of ingress/egress has also been described in several estuarine fishes in the Mid-Atlantic Bight, suggesting that bonnetheads follow a seasonal migration pattern broadly consistent with many estuarine fishes along the US Atlantic coast (Able et al., 2014). It is important to note that we use departure/arrival dates from each array as proxies for understanding egress/ingress patterns to the respective estuaries; however, we expect that these might not be identical since we were not able to gate all entry and exit points. Similarly, we note that our days in estuary calculation for each shark is dependent on tagging date for the year, with less days in estuary in sharks that were tagged later in the year, simply due to the logistics of tagging.

Individual bonnetheads in both NC and GA displayed affinity to specific areas within estuaries in which they were seasonal residents, suggesting the potential for intraspecific habitat partitioning during periods of seasonal residency. Overall, detection densities for bonnetheads in GA were highest at ≤1 km from tagging location, although it is important to note that most hydrophones were spaced at least 2 km apart in this array. In NC, when integrating detection densities across distances ≤2 km from tagging location to account for this difference in hydrophone spacing, detection density was also high (84%) (Fig. 3). Most bonnetheads were detected primarily at sites where they were tagged or nearby (≤2 km); importantly, this individual pattern of habitat use within their respective estuaries was conserved interannually for the sharks that returned the year following tagging (Tables 1 and 2; Figs. 1 and 2). Kenworthy et al. (2018) showed that another large mobile fish found in NC estuaries (red drum) did not range all around the estuaries, suggesting that perhaps this is a somewhat general pattern in temperate estuaries. These results contrast with those of another acoustic telemetry study for bonnetheads, however, which found that bonnetheads that returned in years subsequent to tagging did not return to specific areas within a FL GOM estuary (Heupel et al., 2006). That study deployed a hydrophone array in only one portion of Charlotte Harbor (Pine Island Sound), thus it is possible that on a larger (estuarine) scale returning bonnetheads did exhibit site fidelity to this specific area of Charlotte Harbor estuary (i.e., they exhibited site fidelity to Pine Island Sound or the area encompassed by their overall array). Alternatively, this could indicate differences in movement patterns between US Atlantic and GOM bonnethead populations.

Over broader scales, particularly within our NC array, bonnetheads appeared to prefer areas that were located near an inlet. Overall, detections were high at distances ≤2 km from tagging location in our NC array, with 84% of detections falling in this range (Fig. 3), and many of the sharks were tagged at sites near Beaufort Inlet (Table 1; Fig. 1). Importantly, the only other notable peak in detection density occurred at 6–7 km, where 11% of detections occurred (Fig. 3), which is largely attributed to detections in and around Beaufort Inlet (station groups Inlet, MHC Ship, and Ocean Ship [Figure 1]) from 7 sharks (NC 11, 13–15, 17–18, 20 [Table 1]) that were tagged at roughly this distance from the inlet (station groups Middle Marsh and North River [Figure 1; i.e., fish that then moved to area around the inlet]). This suggests that the inlet is an important feature in NC, restricting bonnethead distribution during seasonal residency. In GOM estuaries, highest capture rates of bonnetheads have also been near tidal inlets, suggesting this distribution pattern is characteristic for the species (Froeschke et al., 2010). Proximity to inlets may be related to foraging since bonnetheads are known to feed primarily on blue crabs, making up greater than 70% of their diet by net weight and occurrence (Cortés et al., 1996). Female blue crabs migrate from low salinity estuarine regions to high salinity regions near the ocean, specifically areas surrounding Beaufort Inlet in NC, using ebb-tide transport, to release larvae during summer months (Carr et al., 2004). The findings of this study therefore would be consistent with the hypothesis that bonnetheads use southeast US estuaries as seasonal foraging habitat, exploiting energetically-rich ovigerous blue crabs to meet higher energetic demands associated with reproduction (Driggers et al., 2014).

Approximately one quarter of bonnetheads tagged in this study were observed to return to NC or GA estuaries across years, suggesting that at least some individuals of this species establish annual migration patterns of returning to the same estuaries (Figs. 4 and 5). Other studies have documented patterns of inter-annual site fidelity of bonnetheads to specific estuaries in SC using mark-recapture and acoustic telemetry, finding some individuals returned to the same estuary multiple times, up to 9 years after tagging (Driggers et al., 2014; Keller et al., 2025). Reciprocally, to our knowledge none of the sharks we tagged in any given year showed fidelity to a different estuarine system in the following year(s). This contrasts with the findings from a recent study on bonnetheads from SC, which found that one shark tagged there returned to NC the following summer, although they attributed this to having likely tagged a shark on its migration path from NC, where it was already showing site fidelity (Keller et al., 2025). Similar patterns of site fidelity have been seen in other species such as summer flounder (*Paralichthys dentatus;* Sackett et al., 2007). The fidelity rates we calculated for bonnetheads returning to these estuaries may be underestimates because tag shedding or fishing mortality are two likely possibilities. In fact, two acoustic transmitters attached to individuals caught within the NC array were returned to us by fishermen, who indicated they found the transmitters within their fishing gear (i.e., gillnets). Thus, the functional lifespan of these acoustic transmitters may be significantly reduced when attached externally. Keller et al. (2025) found much higher return rates using internal attachment, with all bonnetheads believed to be living and displaying site fidelity to the tagging site (North Edisto River estuary) returning in years subsequent to tagging (~70% of all tagged animals), highlighting the potential for the attachment method to influence our ability to record the full extent of site fidelity at our sites. In a recent study on seasonal residency and movement of Greenland sharks (*Somniosus microcephalus*) in an arctic fjord system, however, similar return rates (25%) were found with internal tag attachment, which they suggested could have been the result of fishing mortality or that species' nomadic life-history strategy (Edwards et al., 2022).

Our results also suggest connectivity among populations of bonnetheads along the southeastern US Atlantic coast. Areas of proximity in timing and location between NC- and GA-tagged bonnetheads during migrations were identified in the waters offshore of Brunswick, GA and Cape Canaveral, FL. Keller et al. (2025) examined the effect of sea surface temperatures on bonnethead migration distance and found that in the warmest year of the study, 2016–2017, 10 of 11 sharks ended their winter migrations in GA, whereas in other years they tended to exhibit longer migrations (generally to FL waters). While we did not specifically examine the effect of sea surface temperature on migration distance, our results would appear to confirm this finding, with more bonnetheads showing the greatest maximum distance travelled in GA during the 2016–2017 migration year, compared with other years (Figs. 4 and 5). Both NC and GA bonnetheads were only detected in arrays along the Atlantic coast of the US, with the exception of one shark (GA04) that had a single detection outside of the GA array in the GOM, although this was deemed a false detection given the low probability of this occurrence. This is consistent with the notion that US Atlantic and GOM coast populations are functionally separate (Frazier et al., 2014). These results are also in concordance with recent studies examining mitochondrial and nuclear markers of bonnetheads sampled from the US Atlantic and eastern GOM coasts, finding that populations show high levels of genetic divergence between these two regions, but little divergence within US Atlantic coast populations (Escatel-Luna et al., 2015; Portnoy et al., 2015; Díaz-Jaimes et al., 2021). This pattern of isolation between US Atlantic and eastern Gulf populations has been described in several species of fish (e.g., Bowen & Avise, 1990; Gold & Richardson, 1998), as well as other coastal shark species including the blacknose shark (*Carcharhinus acronotus;* Portnoy et al., 2014; Dimens et al., 2019), the finetooth shark (*Carcharhinus isodon*; Portnoy et al., 2016), the bull shark (*Carcharhinus leucas*; Karl et al., 2011; Laurrabaquio-A et al., 2019), and the scalloped hammerhead (*Sphyrna lewini*; Daly-Engel et al., 2012). This general pattern has been attributed to biogeographic processes originating from geologic or oceanographic features separating the two regions (Portnoy et al., 2014).

Conversely, the differences in timing and distance traveled during migrations between bonnetheads that are seasonal residents in NC and GA suggests that migrations could serve to partition resources during seasonal residencies. Although bonnetheads in NC and GA both migrated south during colder months and overlapped in the waters of GA and FL, only NC-tagged sharks were detected north of GA, in SC (Figs. 4 and 5). Notably there were no detections for any sharks between our array in NC and Myrtle Beach, SC, however this can be explained by the lack of any receiver arrays that would likely be in the paths of bonnetheads migrating from NC; this gap in coverage was also documented in the NC-resident shark tagged in SC (Keller et al., 2025). This pattern has interesting implications for stock structure and dynamics of bonnetheads seasonally inhabiting different estuaries along the US Atlantic coast. Bonnetheads from the US Atlantic coast are thought to mate during fall months (late September-October; Gonzalez de Acevedo, 2020), which falls within the period of seasonal residency reported for several of the sharks in this study, indicative that perhaps reproductive isolation may be occurring. Combined with the latitudinal variation in life-history traits reported in this species from other areas (Lombardi-Carlson et al., 2003), this suggests the possibility of local adaptations originating from differing habitat and resource use and selectively being passed on, supported by small, but statistically robust genetic differences reported between bonnetheads from SC and FL (Díaz-Jaimes et al., 2021).

Bonnetheads display behaviors common to many estuarine fishes, including seasonal residency, migrations on a range of scales in time/space, and site fidelity. This study highlights the importance of considering the full range of habitat available to a species or stock. Bonnetheads show fidelity to specific areas within estuaries across years, although future work could bolster sample sizes on this issue. Our findings contribute critical information on their seasonal migrations, including the distance traveled, routes taken, and their overlap with other bonnethead populations. All of this information contributes to our understanding of bonnethead ecology as well as migratory patterns of estuarine species more generally.

Acknowledgements We thank Maxwell Tice-Lewis, Amy Yarnall, Danielle Keller, Richard Mahoney, Jeff Beauvais, Julie Blaze, and Kaitlin Kinney for assistance in the field. Charles Peterson, Johanna Rosman, and Nathan Bacheler aided with data analyses and comments on the manuscript.

Author Contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Martin T. Benavides and Matthew D. Kenworthy. The first draft of the manuscript was written by Martin T. Benavides and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The authors also guarantee that the manuscript has been prepared according to the instructions for authors.

Funding This project was funded by a North Carolina Aquarium Society Conservation Grant (Award# 2015-03) and Martin T. Benavides was supported by a PhD scholarship from the Peruvian National Council for Science, Technology and Technological Innovation (CONCYTEC).

Data Availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics Approval and Consent to Participate Fieldwork was conducted under Research Permit #7-2016 issued by the N.C. Coastal Reserve and National Estuarine Research Reserve and IACUC ID #15-134.0-C from the University of North Carolina at Chapel Hill.

Consent for Publication Not applicable.

Competing Interests The authors declare that they have no competing interests.

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