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ORIGINAL PAPER

Spatial dynamics of three estuarine predatory fishes in a subtropical estuary

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Abstract
Understanding movement and habitat use patterns of co-occurring predatory fishes is crucial for effective conservation and management of estuarine ecosystems, where dynamic seasonal shifts and species interactions play crucial roles in shaping community structure. Using acoustic telemetry and network analysis, we compared the movements of alligator gar (*Atractosteus spatula*, $n=13$), bull sharks (*Carcharhinus leucas*, $n=12$), and Atlantic stingrays (*Hypanus sabinus*, $n=11$) within and outside the boundaries of a large estuary (Galveston Bay Complex, GBC) in the northwestern Gulf of Mexico. Habitat use varied seasonally for all species, though these patterns have been affected by tagging locations and receiver deployment. Alligator gar were detected year-round in the GBC, with seasonal variation likely driven by environmental conditions and prey availability. Bull sharks displayed seasonal migrations, with increased estuarine use during warmer months and a notable shift out of the GBC to southern bays in the winter. Atlantic stingrays exhibited restricted movement within the GBC during the summer, with few detections in other seasons potentially attributable to receiver coverage, tag retention and predation. Interspecific overlap in habitat use was highest between alligator gar and bull sharks, and lower with Atlantic stingrays. Intraspecific overlap was observed across all three species but was most extensive for bull sharks, suggesting that increased overlap may intensify competition, possibly driving size-based habitat partitioning. Our findings highlight the importance of habitat connectivity and seasonal dynamics for co-occurring predatory fishes within an estuary.

Keywords Acoustic telemetry · Estuarine predatory fishes · Movement · Network analysis · Habitat overlap

Introduction

Predatory fishes influence coastal ecosystems through top-down (Heithaus et al. 2008; Estes et al. 2016) and bottom-up processes (Schmitz et al. 2010). The exact nature of these roles varies based on how predators use these ecosystems in space and time, and how they interact with each other (Schmitz 2007). For example, interactions between species and conspecifics can strongly influence trophic niches and survival rates, thus affecting overall ecosystem functioning by affecting animal densities (Ritchie and Johnson 2009). Additionally, ontogenetic shifts can further modulate predator roles, as individuals may occupy distinct ecological niches throughout different life stages (Matich and Heithaus 2015). Therefore, investigating the habitat use of predatory fishes in coastal ecosystems provides critical insights into their ecological roles, which is especially relevant for estuarine environments subject to both natural and anthropogenic disturbances.

Estuaries are dynamic and highly productive, providing ecosystem services (e.g. food, protection) to predatory fishes (Barbier et al. 2011). Consequently, many estuaries host assemblages of multiple predators (Matich et al. 2017), including apex predators at the top of the food web (Wallach et al. 2015) and mesopredators that provide links between lower and higher trophic levels (Prugh et al. 2009). Despite the well-documented presence of predatory fishes in estuaries, our understanding of the mechanisms underlying their co-occurrence and resource partitioning remains limited, particularly with respect to their patterns of habitat use

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(Heupel et al. 2019). Estuaries are important nursery, reproductive, and feeding grounds, with many species displaying site fidelity (James et al. 2019; Whitfield 2020). Even large coastal transient sharks, such as bull (*Carcharhinus leucas*) and blacktip sharks (*Carcharhinus limbatus*) have been found to display long-term presence to discrete areas in estuaries (Curtis et al. 2011; Werry et al. 2011). Therefore, investigating spatial and temporal patterns of habitat use among co-occurring predatory fishes is essential to understanding the ecological processes that facilitate co-occurrence and maintain estuarine community structure.

Numerous studies have examined the movements of individual predatory fish species in estuarine environments, including both mesopredators (TinHan et al. 2018; Steffen et al. 2023) and large top predators (Drymon et al. 2014; Rider et al. 2021). In contrast, multispecies telemetry studies conducted in estuaries have predominantly focused on mesopredators (Dance and Rooker 2015; Moulton et al. 2017). As a result, there is limited insight into how co-occurring estuarine predators segregate or overlap in their habitat use (Friess et al. 2021; Livernois et al. 2025), with much of the current knowledge relying on multi-species syntheses of telemetry data from disparate studies (Brownscombe et al. 2022). Understanding movements and habitat use by multiple species is important for identifying and prioritizing areas for protection (Cook and Auster 2005; Moore et al. 2016) and this is particularly pertinent for estuarine predatory fishes, many of which are subject to both commercial and recreational exploitation (Cowley et al. 2022).

Acoustic telemetry has become a widely used tool in aquatic ecology for tracking fish movement and space use across ecologically meaningful spatial and temporal scales (Matley et al. 2022). This approach uses acoustic receivers to continuously monitor the presence of tagged individuals within the detection range of receiver arrays, allowing inference of movement patterns, habitat associations, and behavioral responses to environmental conditions (Hussey et al. 2015; Crossin et al. 2017). Recent developments in analytical techniques, such as network analysis, further enhance the interpretation of telemetry data by characterizing space use and movement corridors among individuals or species (Jacoby and Freeman 2016). Together, these advances make acoustic telemetry a powerful approach for elucidating the spatial and temporal behaviors of aquatic organisms (Matley et al. 2023).

The present study aimed to use acoustic telemetry and network analysis to examine habitat selection and spatial overlap among three commonly co-occurring predatory fishes in a large estuarine complex in the northwestern Gulf of Mexico, the Galveston Bay Complex (GBC), Texas: alligator gar (*Atractosteus spatula*), bull sharks (*Carcharhinus leucas*) and Atlantic stingrays (*Hypanus sabinus*). The three species display different life history strategies and are generally assumed to primarily occur in different regions of the estuary along the salinity gradient, ranging from low [Atlantic stingrays (Snelson Jr et al. 1988)] to high [alligator gar (Daugherty et al. 2018)] freshwater association, with bull sharks moving freely throughout estuaries and exhibiting size-specific affinities for certain salinities (Heupel and Simpfendorfer 2008; Froeschke et al. 2010). Additionally, the trophic ecology of these species differ, with alligator gar and bull sharks being primarily piscivorous (TinHan and Wells 2021; Marsaly et al. 2023; Fontaine et al. 2026) while Atlantic stingrays prey upon benthic invertebrates and small fishes (Cook 1994; Bradley 1996; Fontaine et al. 2026). Specific objectives of this study were to: 1) describe general movement patterns of alligator gar, bull sharks, and Atlantic stingrays across seasons and sub-bays in the estuary, (2) evaluate their spatial overlap, and (3) quantify the frequency and extent of movements beyond the GBC.

Materials and methods

Study area

This study was conducted in the GBC, Texas located in northwestern Gulf of Mexico (Fig. 1). GBC has four major sub-bays (Upper Galveston Bay, East Bay, Lower Galveston Bay and West Bay) that are characterized by unique physicochemical properties (Table. S1). On average, there is a northeast to southwest gradient of temperature and salinity from Upper Galveston Bay (lowest) to West Bay (highest). This gradient is driven by freshwater inputs from the Trinity and San Jacinto Rivers (Upper Galveston Bay) and Chocolate Bayou (West Bay), as well as saltwater exchange through Bolivar Roads (Lower Galveston Bay) and San Luis Pass (West Bay) (Villalon et al. 1998). The tidal current through the narrow outlets is strong despite a limited tidal range (mean of 0.3 m), which leads to strong tidal pumping (Du et al. 2019). The GBC is characterized by flat and shallow bottom (average 2 m), but deep, man-made ship channels in Lower Galveston Bay can reach a depth of 15 m (Lester et al. 2002). The waters of the GBC are usually turbid from inorganic suspended solids (Santschi 1995), and habitats found throughout the complex include salt marsh, seagrass, oyster reef, and non-vegetated substrate.

Tagging and tracking

Acoustic receivers (Innovasea, Inc. VR2W, VR2Tx), were deployed in East Bay ($n=6$), Lower Galveston Bay ($n=8$), and West Bay ($n=13$, Fig. 1) and were primarily distributed along the shoreline (mean depth = 1.6 m). Because sub-bays

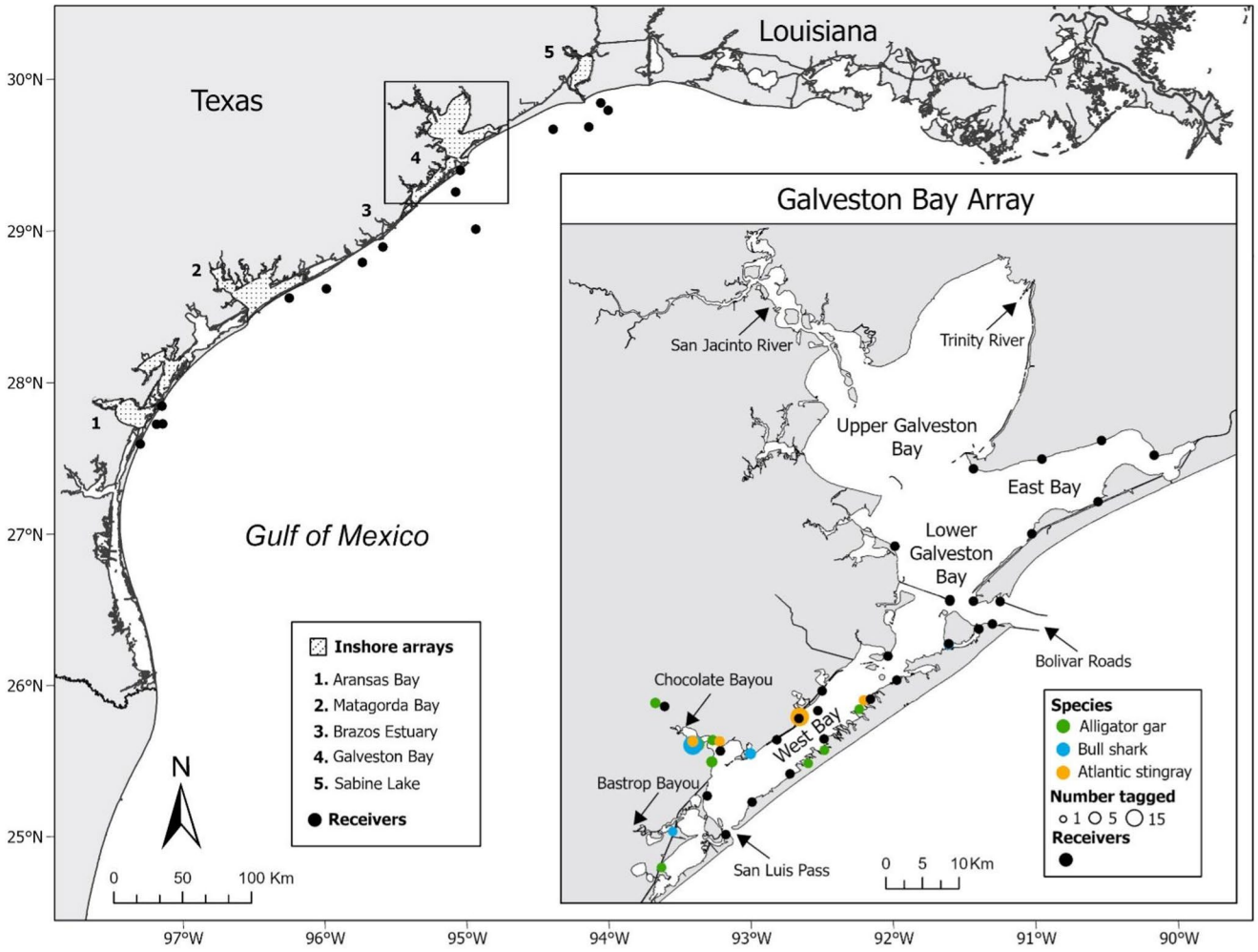

Fig. 1 Locations of inshore acoustic receiver arrays and coastal receivers along the Texas coastline, USA. Locations of receivers in the Galveston Bay Complex (GBC) (inset). Labels represent the four major sub-bays within the GBC. Arrows represent dominant freshwater and saltwater sources for the GBC. Black circles indicate receiver locations and outlined circles represent the number of individuals acoustically tagged at each location. No receivers were deployed in Upper Galveston Bay

differ in basin extent, receiver coverage was not uniform, with West Bay having the highest receiver coverage (0.061 receivers/km^2), followed by Lower Galveston Bay (0.028 receivers/km^2) and East Bay (0.021 receivers/km^2). The higher receiver coverage in West Bay reflects the fact that all individuals were tagged in West Bay and adjacent waterbodies of Chocolate Bayou and Bastrop Bayou, and this allocation was intended to maximize detection probability. Therefore, differences in basin size, receiver distribution, and tagging effort may influence observed spatial patterns and should be considered when interpreting results, as they could contribute to apparent variation in habitat use that does not necessarily reflect true ecological differences. Detection data were continuously recorded from September 2023 to September 2025.

We elected to focus receiver deployment in lower estuarine zones to capture patterns of habitat use and spatial overlap among study predators in areas of higher salinity, as previous studies have demonstrated a strong reliance of both alligator gar and bull sharks on the low salinity Upper Galveston Bay (Livernois et al. 2021; Fontaine et al. 2024). West Bay is ecologically distinct from other sub-bays within the GBC because it is hydrologically isolated from major freshwater inputs, resulting in higher salinity levels and a unique habitat gradient (Villalon et al. 1998). This gradient ranges from more saline, marine-influenced conditions near San Luis Pass (~30 psu) to slightly lower salinity levels closer to freshwater tributaries (i.e., Chocolate Bayou and Bastrop Bayou, ~ 10 psu). Because predators in West Bay can experience both freshwater and marine habitats within a limited spatial scale, this area provides an ideal context for assessing ecological dynamics across different salinity gradients and determining whether tagged individuals actively utilize the region or exhibit transient behavior.

Alligator gar and bull sharks were collected using large-mesh multifilament entanglement nets (3 × 100 m, 15 cm mesh width). A subset of individuals was also caught using hook-and-line fishing (4/0 treble hooks). Atlantic stingrays were caught using bag seine tows (18.3 m long x 12.2 m) conducted parallel to the shoreline. Upon capture, each fish was secured onboard in a tank filled with aerated water for the duration of the procedure. Size was measured for each individual (total length 'TL' and disc width 'DW'- cm) and sex was determined for bull sharks and Atlantic stingrays based on presence or absence of claspers. Alligator gar sex was not recorded, as reliable determination requires invasive internal inspection. Life stages (i.e., juvenile and mature) was inferred from TL for alligator gar and bull sharks and DW for Atlantic stingrays, based on published size at maturity (Snelson et al. Jr 1988; Natanson et al. 2014; Binion et al. 2015). For alligator gar and bull sharks, a small incision (approximately 1–2 cm long) was made along the ventral region and an acoustic tag (V16-4x,69 kHz, 40–80 s delay, estimated battery life = 1613 days; Innovasea) was implanted in the peritoneal cavity through the incision. The incision was then closed using one or two interrupted sutures with PDO II monofilament absorbable suture material (Oasis US, LLC). For Atlantic stingrays, a single acoustic tag (V9T-2x, 69 kHz, 180 s delay, estimated battery life = 414 days; Innovasea) was externally attached by securing nickel pins through the posterior dorsal side of the left wing and fastening them ventrally with a disc to minimize irritation (Meese et al. 2025). Each acoustically tagged individual was equipped with an external identification tag: alligator gar with BFIM-96 tags (12.0 cm, Floy Tag), bull sharks with rodeo tags (4.8 cm, Q-flex), and Atlantic stingrays with spaghetti tags (3.5 cm, Floy Tag). Once all tagging procedures were complete, individuals were then held in the water from the side of the boat and monitored until swimming equilibrium was regained, at which point they were released at the location of capture. All procedures involving the capture, handling, tagging, and release of fish were conducted in compliance with the Institutional Animal Care and Use Committee (IACUC) at Texas A&M University under protocol no. IACUC 2024-0031.

Data analysis and statistical methods

Spatiotemporal habitat use patterns within the GBC

Suspected false detections from the receiver data were removed using the *glatos* package (Holbrook et al. 2021). Detections were first reviewed for implausible movement patterns and deployment inconsistencies, after which the "short interval" criteria (Pincock 2012) was applied. Detections separated from others of the same code on a single receiver by 30 times the nominal delay of each transmitter model were omitted. This two-step approach follows recommendations to avoid over-filtering valid detections. Collectively, these filters removed 320 detections, representing 2% of the total dataset. One individual alligator gar was also removed from the analysis because it was detected only once, precluding meaningful movement inference of movement pattern. Detection data were categorized into seasonal periods: winter (1 December–28/29 February), spring (1 March–31 May), summer (1 June–31 August), and fall (1 September–30 November). Spatial network analysis was used to examine the movement patterns and space use of tagged individuals for each season, and a social network approach to identify overlap between individuals within the GBC. Networks and network metrics were generated using the *igraph* (Csardi and Nepusz 2006), *tidygraph* (Pederson 2022) *ansipe* (Farine 2013) and *spatsoc* (Robitaille et al. 2018) packages in R (R Core Team 2025).

In addition to network analysis, movement rates of individuals were calculated using the straight-line distance between consecutive detections from two different receiver stations, divided by the time elapsed between those detections. Distance between receiver stations were computed using the *geosphere* package (Hijmans et al. 2017). Time intervals were calculated in days and steps with impossible longs gaps between detection (> 7 days) were excluded to avoid or overestimating movement rates. This calculation provides the lowest possible estimate of movement rates, as it assumes a direct, straight-line path between receiver stations, which may not reflect the true movement behavior of the fish. Nonetheless, this metric enables comparison of mobility across species and seasons, complementing the spatial and social network analysis by offering an additional perspective on movement dynamics.

Network analysis is a robust method for quantifying movement patterns from acoustic telemetry data and is well-suited for evaluating animal movements (Jacoby and Freeman 2016; Kraft et al. 2023) and spatial overlap relative to estuary boundaries (Tecchio et al. 2015; Lilly et al. 2020). Based on graph theory, networks consist of nodes (receiver station) and edges (fish movements) between receiver stations (Ledee et al. 2015, 2016). These networks visualize spatial connectivity among receiver stations but do not imply direct travel paths, as actual fish trajectories may follow more circuitous routes. However, the abstraction of movement as straight-line edges does not compromise the utility of network analysis. Edges were weighted according to the total number of recorded movements between each pair of receiver stations, providing a measure of movement intensity. Two-dimensional spatial network visualizations were generated to represent fish movements across the study area. To evaluate spatial overlap among individuals, a social

network framework based on co-occurrence was employed. Co-occurrence was defined as detections of different tagged individuals at the same receiver station within a 24-hour period (Farine and Whitehead 2015). A 24-hour temporal interval was selected because previous telemetry studies indicate that alligator gar, bull sharks, and Atlantic stingrays can exhibit site fidelity within estuarine habitats for multiple days, and potentially for weeks to months (Buckmeier et al. 2013; Drymon et al. 2014; Meese et al. 2025). Accordingly, multiple tagged individuals may remain within the detection range of a single receiver station over this period.

Two node-based centrality metrics, degree centrality and eigenvector centrality, were used to quantify space use trends for each fish species. Degree centrality describes important connection centers within each spatial network and functions as a frequency use metric (Jacoby et al. 2012), and nodes with high eigenvector centrality values represent preferred space use areas within a movement network (Espinoza et al. 2015). For each seasonal network, degree centrality was calculated as the number of edges connected to each receiver node. Nodes with many connections represent areas more frequently used by tagged individuals, while nodes with fewer or no connections reflect infrequently or unused areas. Receiver nodes without any detections (i.e., no edges) were assigned to a degree value of zero. Eigenvector centrality was computed for all nodes with degree values greater than zero. Eigenvector centrality quantifies a node's influence within a spatial network by measuring its connections to other highly connected nodes. Together, degree centrality and eigenvector centrality provided complementary insights into the spatial behavior of tagged fish, helping to identify areas of potential ecological importance.

To evaluate temporal and spatial variation in fish movement throughout the tracking period, degree centrality was analyzed as the response variable within a hurdle model framework. Species, season, and sub-bay were treated as fixed categorical explanatory variables, while receiver and year period (i.e., first, second and third year) were included as categorical random effects to account for repeated measures and variability in detections across seasonal periods. A hurdle model with a negative binomial error distribution and log link function was selected as the most suitable approach, given the overdispersion and zero-inflation present in the degree centrality count data.

To examine variations in space use among species, generalized linear mixed models (GLMMs) were developed for degree centrality and beta regression models for eigenvector centrality, derived from spatial networks of alligator gar, bull sharks, and Atlantic stingrays. Season and sub-bay were included as fixed categorical explanatory variables, with receiver station and year period treated as categorical random effects. Degree centrality was modeled as the response variable in a GLMM with a negative binomial error distribution and a log link function, while eigenvector centrality was modeled in a beta regression (to accommodate the 0–1 bounded nature of eigenvector centrality values) with a logit link function. To assess overlap, co-occurrence was calculated using the simple ratio index (SRI) from the *spatsoc* package in R (Robitaille et al. 2018; R Core Team 2025). SRI values range from 0 (no co-occurrence) to 1 (constant co-occurrence). To investigate temporal variation in overlap, SRI was modeled as a response variable in a zero-augmented beta regression with a logit link function to account for the bounded nature of SRI values. Co-occurrence type (i.e., categorical co-occurrences between tagged individuals- alligator gar, bull sharks, and Atlantic stingrays and all combinations therein), season and sub-bay were included as fixed categorical explanatory variables, with receiver station and year period as random effects. All models were generated using the *glmmTMB* package in R (Brooks et al. 2017; R Core Team 2025).

Model adequacy was assessed using residual diagnostic plots generated via the *DHARMa* package (Hartig 2016). Likelihood ratio (LR) tests were employed to evaluate the relative support for each model compared to a null model (Royall 2017). The contribution of individual explanatory variables was quantified using analysis of deviance (ANODEV) through nested LR tests. For GLMMs with a negative binomial distribution, marginal R^2 (R^2_m,variance explained by fixed effects) and conditional R^2 (R^2_c, variance explained by both fixed and random effects) were reported (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017). As formal variance partitioning metrics are not well-defined for hurdle models or mixed-effects beta regressions, pseudo-R^2 values for beta regressions (Ferrari and Cribari-Neto 2004) were reported instead. These include pseudo-R^2_f (fixed effects only) and pseudo-R^2_{fr} (combined fixed and random effects). For hurdle and zero-augmented beta regression models, a correlative proxy R^2 was reported, calculated as the squared correlation between observed and predicted values, for models with fixed effects only (proxy-$R^2_{corr–f}$) and with both fixed and random effects (proxy-$R^2_{corr–fr}$), as implemented in the *performance* package in R (Lüdecke et al. 2021; R Core Team 2025).

Movement outside the GBC

Alligator gar and bull sharks were detected on acoustic receiver stations located outside the GBC, including other estuarine systems and sites along the Texas coastline (Fig. 1). These detections were also filtered following the two-step approach previously described, resulting in the removal of 8 detections (1.6% of the total dataset). To visualize the long-distance movements of these species, raw

detection counts per season (i.e., number of detections per receiver station for each season) were plotted for all individuals detected outside the GBC.

Results

Spatiotemporal habitat use patterns within the GBC

Between September 2023 and September 2025, 13 of 20 tagged alligator gar (mean TL = 120.1 cm; size range = 86.4–172.0 cm), 12 of 20 tagged bull sharks (mean TL = 122.2 cm; size range = 92.6–152.0 cm, sex ratio = 1.4:1 females to males), and 11 of 20 tagged Atlantic stingrays (mean DW = 28.6 cm; size range = 22.2–31.9 cm, sex ratio = 4.5:1 females to males), were detected in the GBC (Fig. 2), accumulating a total of 16,048 valid detections. Alligator gar tagged included 5 juveniles and 8 adults, bull sharks were exclusively juveniles, and Atlantic stingrays were all adults. Bull sharks accounted for the largest number of detections (% total, mean, min–max = 75%, 1010, 189–2141) compared to alligator gar (22%, 271, 27–943) and Atlantic stingrays (3%, 37, 3–150). Bull sharks were detected on the most receivers (mean, min–max = 7, 2–14), followed by alligator gar (3, 1–10) and Atlantic stingrays (2, 1–6). Bull sharks had the longest average tracking duration for individual fish (mean, min–max = 401, 105–737 days, referring to number of days detected in the array), followed by alligator gar at 252, 45–529 days and Atlantic stingrays at 26, 1–188 days. Days at liberty (i.e., days from tagging date to last detection date) were longest for bull sharks (mean, min–max = 401 ,776–107 days), followed by alligator gar (285, 46–530 days) and Atlantic stingrays (66, 6–282). Mean daily movement rates differed among species, with Atlantic stingrays exhibiting the highest average movement (mean ± SD = 1.1 ± 1.8 km day^{-1}), followed by alligator gar (0.35 ± 0.72 km day^{-1}) and bull sharks (0.32 ± 0.37 km day^{-1}). Variation in detection histories among tagged individuals was likely influenced, in part, by differences in tag models and deployment methods, with alligator gar and bull sharks internally tagged using V16-4x transmitters, and Atlantic stingrays externally tagged using V9T-2x transmitters. Additional individual-level tagging and detection data are provided in supplementary information (Table S2, Fig. S1).

Seasonal variation in detection patterns was evident across tagged individuals (Fig. 2, Table S3). Alligator gar exhibited highest detection frequencies in spring (1269

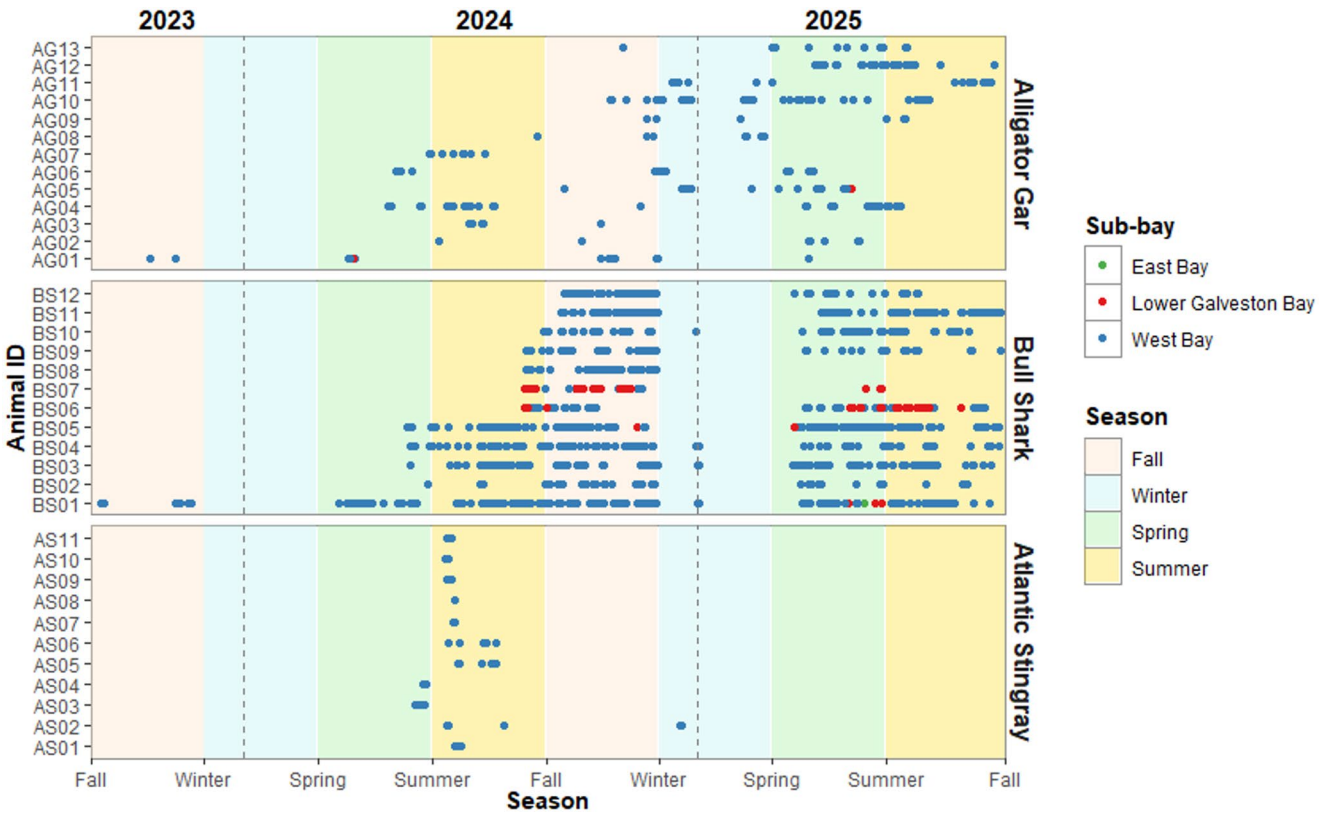

Fig. 2 Presence plot illustrating the detection history for each tagged fish in the Galveston Bay Complex (GBC) over the study period (2023–2025). Each dot mark on the y-axis corresponds to an individual fish. Colored circles represent where detections took place with respect to the GBC. Colored background panels indicate seasons: Fall (Sep-Nov), Winter (Dec-Feb), Spring (Mar-May) and Summer (Jun-Aug)

Table 1 Analysis of deviance through nested likelihood ratio (LR) tests of the hurdle model with degree centrality as a function of species, season, and sub-bay and a LR calculated for each parameter

Parameter	df	X^2	*p*-value	LR
Species	2	34.75	<0.001	27.22
Season	3	18.67	<0.01	6.87
Sub-bay	2	19.00	<0.001	16.95

$R^2_{fcorrected-f} = 0.246$ and $R^2_{corrected-fr} = 0.659$

detections, 36.1% of species-specific detections) followed by winter (965, 27.4%), summer (904, 25.7%), and fall (380, 10.8%). Bull sharks were predominantly detected during fall (5230, 43.1%) and summer (4464, 36.8%), with fewer detections in spring (2386, 19.7%) and minimal presence in winter (44, < 1%). Atlantic stingrays detections were predominantly recorded during summer (335, 82.5%), with lower detections in spring (61, 15.0%) and winter (10, 2.5%), and no detections observed during fall. Seasonal variation in detection patterns was likely influenced by tagging periods for Atlantic stingrays, with 88.2% of detections recorded within the first two months post-tagging, while alligator gar and bull sharks exhibited lower proportion of detections during the same interval (17.4% and 19.3%, respectively). Mean daily movement also varied among seasons for each species with alligator gar exhibiting the highest movement rates during spring (mean ± SD = 0.52 ± 0.97 km day^{-1}) and the lowest during winter (0.14 ± 0.19 km day^{-1}). Bull sharks showed the greatest movement rates in fall (0.46 ± 0.46 km day^{-1}), whereas Atlantic stingrays exhibited the highest overall movement rates in spring (1.34 ± 1.90 km day^{-1}), although this estimate is based on only two individuals. Spatially, most detections occurred in West Bay, consistent with the initial tagging locations and receiver deployment. Atlantic stingrays detections were restricted to West Bay (100%), and alligator gar (98.5%) and bull sharks (97.2%) also had high proportions of detection within this area. Alligator gar and bull sharks were additionally detected in Lower Galveston Bay (1.53% and 2.72%, respectively). Only one bull shark was detected in East Bay (< 1%), and it was recorded at a single receiver station adjacent to the Lower Galveston Bay.

Variation in degree centrality was significantly associated with differences in species, season and sub-bay (ANODEV, $\chi2 = 34.75$, LR = 27.22, $\chi2 = 18.67$, LR = 6.87, and $\chi2 = 19.00$, LR = 16.95 respectively, Table 1). Relatively high LRs for species and sub-bay suggested that models including these variables were substantially more likely than the null model. This result supports distinct spatial use patterns among tagged individuals, driven primarily by species, followed by differences across sub-bays and seasons. Space use differences among species were investigated using separate models for both degree and eigenvector centrality for alligator gar, bull sharks, and Atlantic stingrays. This approach enabled direct comparisons of spatial behavior across species by isolating patterns within each network structure. Because only one individual bull shark was detected in East Bay, this sub-region was excluded from spatial network maps to enhance interpretability and visual clarity.

For alligator gar, variation in degree and eigenvector centrality was more closely associated with differences among sub-bays (ANODEV, $\chi2 = 11.16$, LR = 35.97, and $\chi2 = 8.10$, LR = 7.96 respectively, Table 2) relative to seasons (ANODEV, $\chi2 = 12.35$, LR = 13.13, and $\chi2 = 1.54$, LR = 1.57, respectively). Alligator gar accumulated a relatively high degree and eigenvector centralities in West Bay throughout the study period reflecting their sustained use of this sub-bay as a core area for movement (Figs. 2 and 3). Alligator gar had large degree and eigenvector centrality throughout West Bay in the spring, highlighting more frequent use of the sub-bay during this season. In contrast, during summer, degree and eigenvector centrality were comparatively low and largely restricted to the inner zone of Chocolate Bayou, a pattern that persisted over two consecutive years.

Table 2 Analysis of deviance through nested likelihood ratio (LR) tests of the generalized linear mixed model for degree centrality and of the beta regression for eigenvector centrality as a function of season and sub-bay for alligator gar, bull shark, and Atlantic stingray and a LR calculated for each parameter

Species	Parameter	Degree centrality				Eigenvector centrality			
		df	X^2	*p*-value	LR	df	X^2	*p*-value	LR
Alligator gar	Season	3	12.35	<0.01	13.13	3	1.54	0.67	1.57
	Sub-bay	2	11.16	<0.01	35.97	2	8.10	<0.05	7.96
R^2_m=0.474 R^2c=0.584 $R^2_{fcorrected-f} = 0.133$,$R^2_{corrected-fr}$=0.362									
Bull shark	Season	3	2.57	0.46	41.67	3	33.20	<0.001	22.33
	Sub-bay	2	49.32	<0.001	75.62	2	29.00	<0.001	27.02
R^2_m=0.488, R^2_c=0.696 $R^2_{fcorrected-f} = 0.239$,$R^2_{corrected-fr}$=0.427									
Atlantic stingray	Season	3	6.53	0.73	18.64	3	3.31	0.34	3.28
	Sub-bay	2	4.35	0.23	12.22	2	3.31	0.19	3.11
R^2_m=0.347, R^2_c=0.478 $R^2_{fcorrected-f} = 0.214$,$R^2_{corrected-fr}$=0.289									

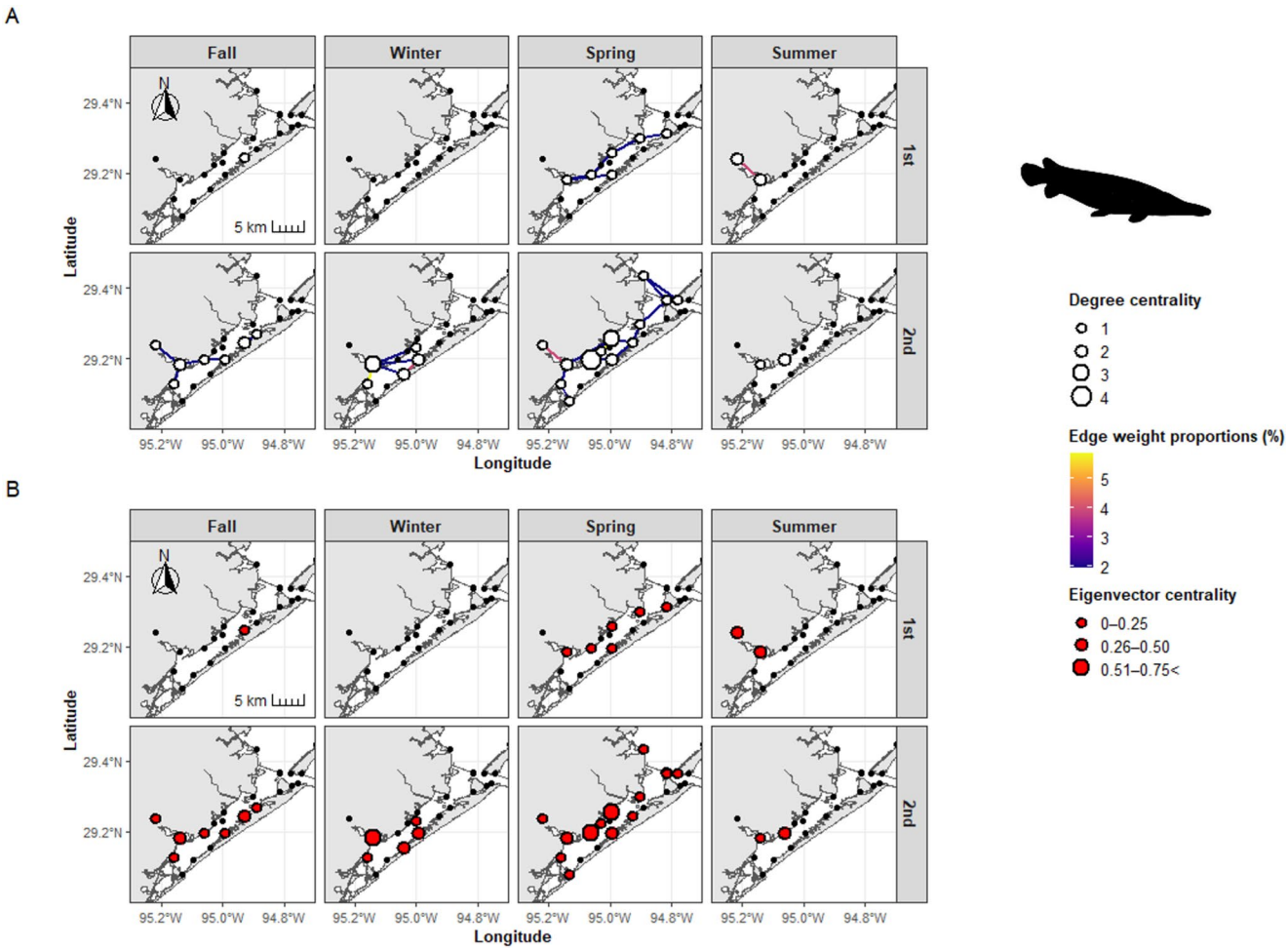

Fig. 3 Spatially oriented movement networks of alligator gar across four seasons: spring (March–May), summer (June–August), fall (September–November), and winter (December–February). (A) Receiver node size is scaled to degree centrality, with edge opacity representing the relative frequency of movements between nodes. (B) Receiver node size is scaled to eigenvector centrality, emphasizing nodes connected to other well-connected nodes. Black circles indicate the geographic locations of inactive acoustic receivers (i.e., receivers with zero degree of centrality for alligator gar). Horizontal facets refer to the correspondingly ordered seasons (i.e., first and second, fall, winter, spring and summer) over the duration of the study

For bull sharks, degree and eigenvector centrality did not exhibit consistent patterns. Variation in degree centrality was more closely associated with differences among sub-bays (ANODEV, $\chi2=49.32$, LR = 75.62, Table 2) relative to seasons (ANODEV, $\chi2=2.57$, LR = 41.67). Bull sharks had higher degree centrality in West Bay compared to other sub-bays, suggesting greater presence and movement in this region (Figs. 2 and 4).Variation in eigenvector centrality was closely related to both differences among seasons (ANODEV, $\chi^2 = 33.20$, LR = 22.33, Table 2) and sub-bays (ANODEV, $\chi^2 = 29.00$, LR = 27.02). Bull sharks exhibited particularly high eigenvector centrality in West Bay during the fall of the second year, indicating sustained connectivity to key locations within this sub-bay during that period. The absence of degree and eigenvector centrality in the GBC during winter indicates that bull sharks were likely not present in the system during that period.

For Atlantic stingrays, variation in degree and eigenvector centrality did not show significant variation across seasons (ANODEV, $\chi^2 = 6.53$, LR = 18.64, and $\chi^2 = 3.31$, LR = 3.28, respectively, Table 2) or sub-bays (ANODEV, $\chi^2 = 4.35$, LR = 12.22, and $\chi^2 = 3.31$, LR = 3.11, respectively). All detections were confined to West Bay, and any apparent seasonal differences in degree and eigenvector centrality should be interpreted cautiously given the limited data (Figs. 2 and 5). Some individuals were detected on multiple receivers within West Bay, indicating occasional movement within the sub-bay.

Patterns in overlap among tagged individuals were evident over the tracking period (Fig. 6). Variations in SRI values were associated with co-occurrence type ($\chi2=12.83$, LR = 10.50, Table 3), seasons ($\chi2=12.14$, LR = 11.60), and sub-bays ($\chi2=4.44$, LR = 4.05). Co-occurrence events between alligator gar and bull sharks were the most frequent

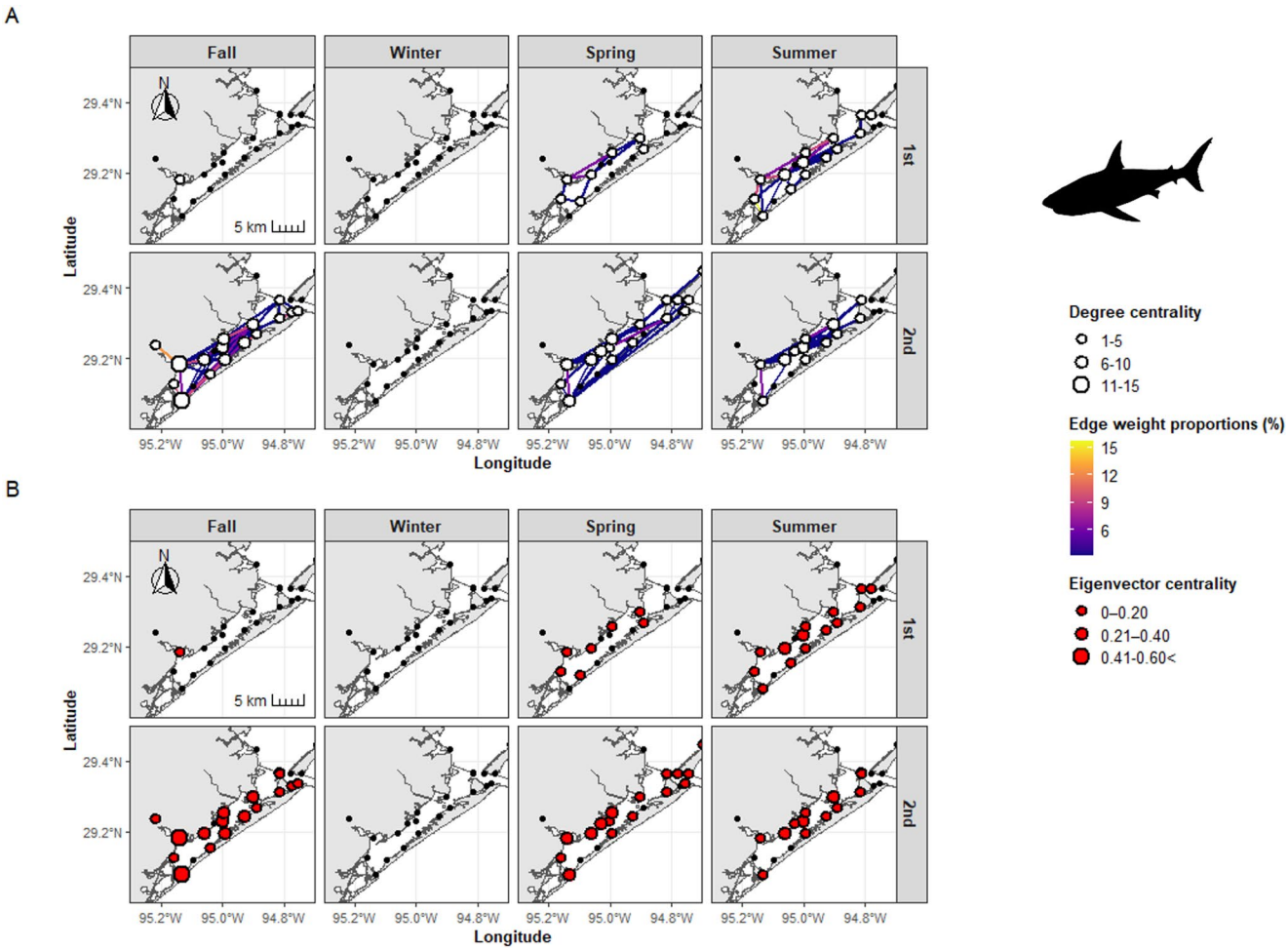

Fig. 4 Spatially oriented movement networks of bull shark across four seasons: spring (March–May), summer (June–August), fall (September–November), and winter (December–February). (A) Receiver node size is scaled to degree centrality, with edge opacity representing the relative frequency of movements between nodes. (B) Receiver node size is scaled to eigenvector centrality, emphasizing nodes connected to other well-connected nodes. Black circles indicate the geographic locations of inactive acoustic receivers (i.e., receivers with zero degree of centrality for bull shark). Horizontal facets refer to the correspondingly ordered seasons (i.e., first and second, fall, winter, spring and summer) over the duration of the study

(73 events, 88% of interspecific co-occurrence detections), and these events were observed during all seasons except winter. Bull sharks and Atlantic stingrays also co-occurred, but exclusively during the summer and at lower frequencies (8 events, 10% of interspecific co-occurrence detections). Only two instances of co-occurrence were recorded between alligator gar and Atlantic stingrays, both during winter (2% of interspecific co-occurrence detections). Intraspecific co-occurrence was observed for all three species. Bull sharks exhibited the highest frequency of intraspecific co-occurrence events (160 events, 90.0% of intraspecific co-occurrence detections), with simultaneous detection observed during all seasons. Alligator gar and Atlantic stingrays demonstrated moderate intraspecific co-occurrence (10 and 7 events, 6% and 4% of intraspecific co-occurrence detections, respectively), with co-occurrence events observed throughout all seasons for alligator gar, it was restricted to spring and summer months for Atlantic stingrays.

Movement outside the GBC

Two alligator gar (i.e., AG03 and AG02) were detected in the Brazos Estuary, accounting for a total of 377 detections, with AG03 traveling upriver approximately 18 km into the Brazos River (Fig. 7a). Detections of alligator gar outside the GBC were predominantly observed in spring, representing 88% of all detections in these areas, with the remaining detections occurring during winter. Alligator gar that entered the Brazos Estuary were not subsequently detected in the GBC during the study period.

Seven bull sharks (35% of the tagged individuals) were detected outside the GBC, for a total of 106 detections, with all detections occurring in areas south of GBC, including

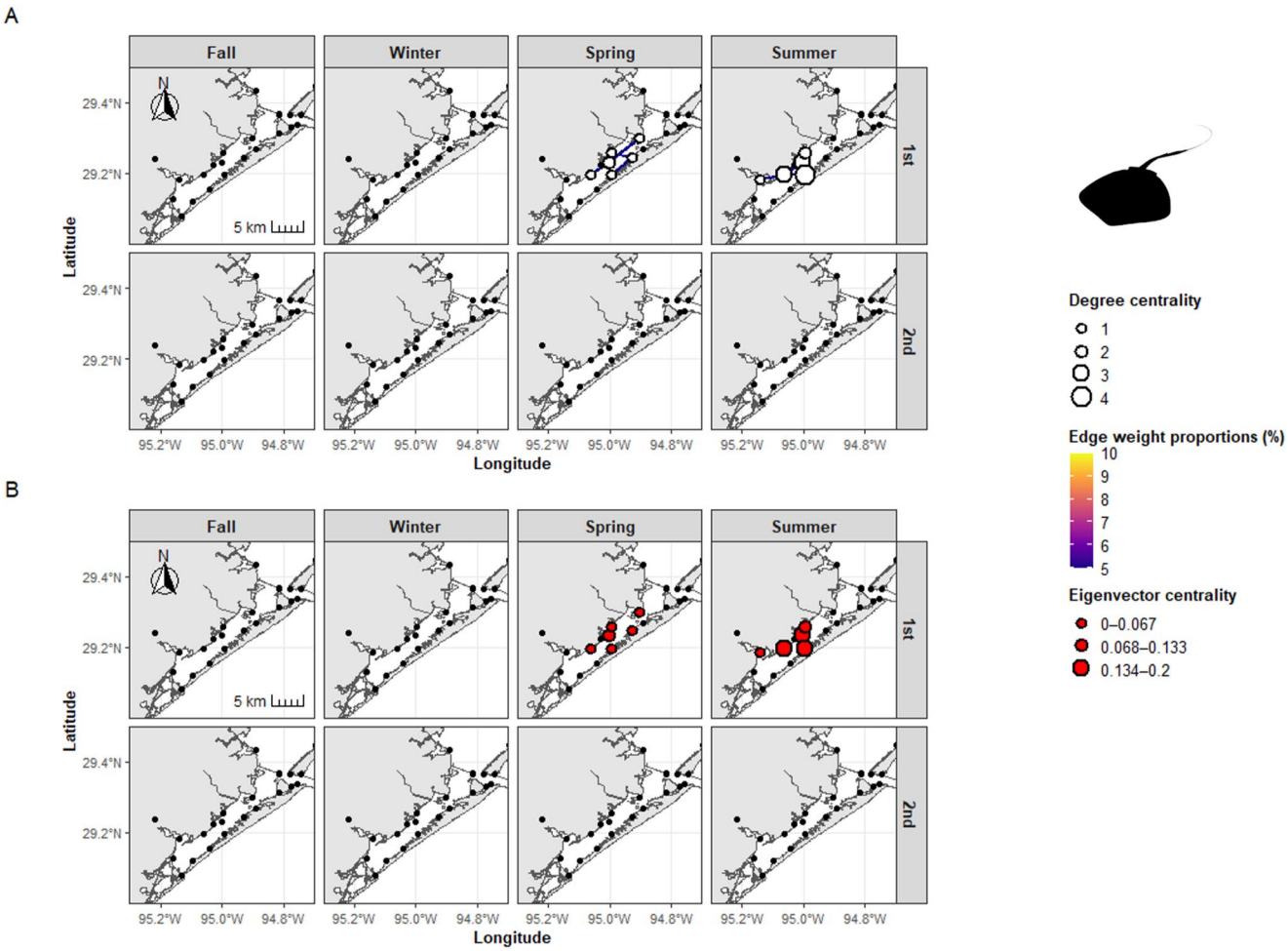

Fig. 5 Spatially oriented movement networks of Atlantic stingray across four seasons: spring (March–May), summer (June–August), fall (September–November), and winter (December–February). (A) Receiver node size is scaled to degree centrality, with edge opacity representing the relative frequency of movements between nodes. (B) Receiver node size is scaled to eigenvector centrality, emphasizing nodes connected to other well-connected nodes. Black circles indicate the geographic locations of inactive acoustic receivers (i.e., receivers with zero degree of centrality for Atlantic stingray). Horizontal facets refer to the correspondingly ordered seasons (i.e., first and second, fall, winter, spring and summer) over the duration of the study

Matagorda Bay and Aransas Bay (Fig. 7b). The longest recorded distance traveled by an individual bull shark in this study was 259 km, reaching Aransas Bay. Detections outside the GBC occurred during all seasons. Regardless of their movement outside the GBC, bull shark detections within the GBC were minimal during winter months (Fig. 2). Notably, 57% of bull sharks detected outside the GBC subsequently returned. For example, bull shark (BS01, 103.5 cm TL at time of tagging), tagged in West Bay in July 2023, was last detected in the GBC in October 2023 (Fig. 2) before being subsequently detected in Matagorda Bay in December 2023. The individual was later detected again in the GBC in March 2024 and was last observed in August 2024. Although it was not detected again outside the GBC during winter, it was subsequently detected in the GBC in March 2025.

Discussion

Using acoustic telemetry and network analysis, this study revealed differences in space use and movement patterns among three estuarine predatory fishes at local scales (within the GBC) and documented longer-distance movement beyond the GBC. Seasonal variations in space use were observed across all species, likely mediated by temporal fluctuations in abiotic conditions (i.e., temperature and salinity), and biological processes (i.e., prey availability and reproduction), although these mechanisms were not explicitly evaluated in this study. Within the GBC, all species demonstrated a marked reliance on West Bay, but this pattern should be considered with caution, as it may have been influenced by the study design. Observed overlaps in habitat use among alligator gar, bull sharks, and Atlantic stingrays

Fig. 6 Simple ratio index (SRI) values of co-occurrences among alligator gar, bull shark, and Atlantic stingray at acoustic receivers. SRI values are displayed based on co-occurrence types plotted across sub-bays and colored by seasons

Table 3 Analysis of deviance through nested likelihood ratio (LR) tests of the zero-augmented beta regression for simple ratio index values as a function of co-occurrence type, season, and sub-bay with a LR calculated for each parameter

Parameter	df	X^2	*p*-value	LR
Co-occurrence type	5	12.83	< 0.05	10.50
Season	3	12.14	< 0.01	11.60
Sub-bay	2	4.44	< 0.05	4.05

$R^2_{fcorrected-f} = 0.249$ and $R^2_{corrected-fr} = 0.384$

indicated that these species use similar resources, providing insight into their ecological interactions and functional roles within estuarine ecosystems.

Species-specific spatial dynamics

Alligator gar

Alligator gar were detected year-round in West Bay, with some movement into Lower Galveston Bay during spring. During the spring, alligator gar expanded their habitat use throughout West Bay, moving from the primary source of freshwater input (i.e., Chocolate Bayou) to more brackish habitats (Villalon et al. 1998). In contrast, during summer, their range contracted, with individuals primarily relying on areas inside or closer to the bayou. In this study, alligator gar is the most freshwater-associated species, and this seasonal shift in habitat use is likely driven by increased freshwater inflows during spring, which lower salinity (~22 psu) and expand habitat suitability across West Bay (Livernois et al. 2021). While the mechanisms underlying habitat selection by alligator gar remain speculative and require further field validation, we suggest that, in addition to freshwater discharge, variation in water temperature and availability of foraging opportunities may also influence their habitat use.

Water temperatures are generally lower in river systems (i.e., Chocolate and Bastrop Bayou, ~ 20 °C) than in adjacent estuarine areas (i.e., West Bay, ~22 °C), and as a poikilothermic species, temperature fluctuations strongly influence alligator gar physiology (Allen et al. 2017). Consistent with these physiological constraints, alligator gar were frequently detected in West Bay during the colder months (winter and early spring), a pattern also observed in riverine systems where individuals occupy warmer off-channel habitats as thermal refuge (Kluender et al. 2017; Wegener et al. 2017). Prey abundances may also vary as a response to changes in water temperature. Based on long-term monitoring data in the GBC, Livernois et al. (2021) showed that the abundance of prey species (i.e., Atlantic croaker, Gulf menhaden, and brown shrimp) was greatest during spring in comparison to fall suggesting that alligator gar select habitats that optimize their net energetic gain in response to the combined influence of environmental conditions and prey availability.

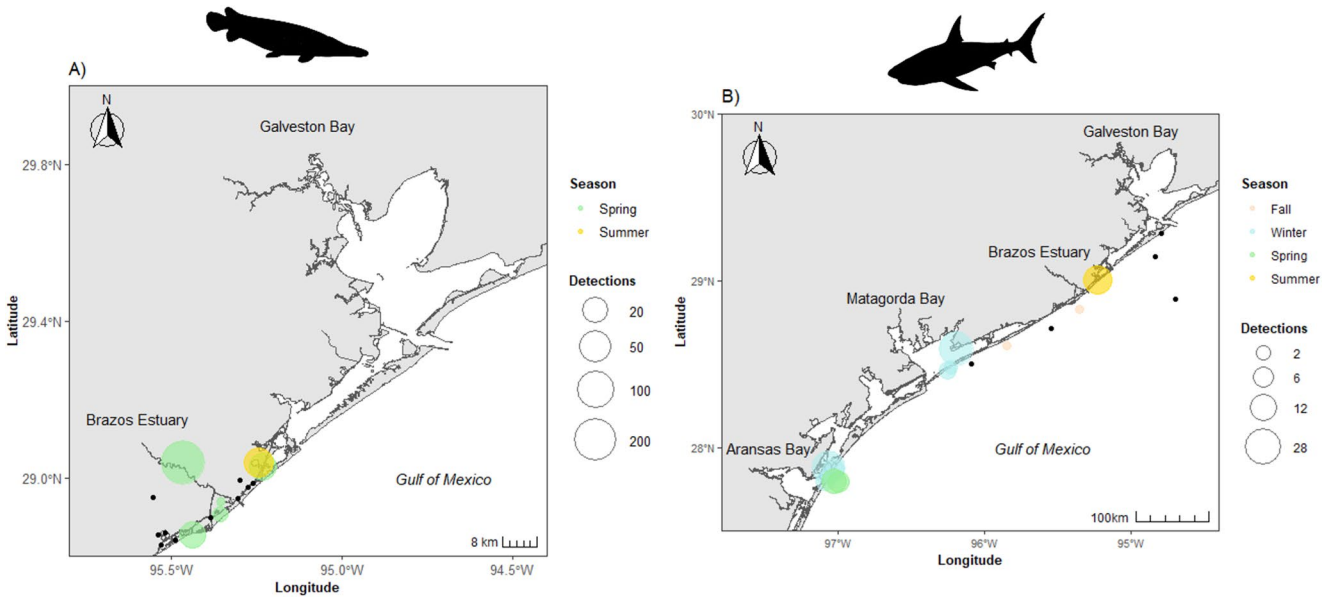

Fig. 7 Detection counts for (a) alligator gars and (b) bull sharks on receivers outside of the Galveston Bay Complex (GBC). Bubble size represents the total number of detections per receiver, as defined in each legend. Black circles indicate the geographic locations of inactive acoustic receivers (i.e., receivers without detections)

In this study, alligator gar movements were largely confined to West Bay, suggesting that these individuals belonged to a localized sub-population within the lower region of the GBC (i.e., West Bay and adjacent waterbodies), rather than individuals dispersing from the estuarine sub-population previously identified near the base of the Trinity River (Buckmeier et al. 2013). This hypothesis is further supported by the observed movement rate of 0.35 km²/day, which is relatively low and consistent with localized residency rather than widespread dispersal across the GBC (Reyier et al. 2020). However, limited receiver coverage in our study may have constrained detections, and it cannot be excluded that some individuals moved outside the monitored array (i.e., Upper Galveston Bay). This is particularly possible given that two individuals exhibited long-distance movements into the Brazos Estuary, while others displayed high movement rates (> 1.0 km²/day). Thus, population segments of alligator gar appear to exhibit distinct patterns in resource use that may lead to more complex life histories and ecological roles than initially suspected for this freshwater-associate predator.

Otolith microchemistry has also been employed to assess habitat use and movements of alligator gar in Gulf Coast rivers, providing complementary evidence of connectivity among freshwater and estuarine habitats. In both the Guadalupe River–San Antonio Bay (Daugherty et al. 2017) and Trinity River–Galveston Bay systems (Daugherty et al. 2019), otolith chemistry indicated the presence of multiple alligator gar stocks that differ in their relative prevalence across freshwater and estuarine habitats, including river-residents, transient individuals, and bay-residents that exclusively occupy saltwater habitats. In this study, individual alligator gar tagged demonstrated a distinct set of habitat preferences and behavioral patterns that are reflective of their adaptation to saltwater environments within the estuary. However, it remains difficult to ascertain whether these individuals are bay residents, transients, or a combination of both based solely on acoustic telemetry data. It is, however, clear that they are widespread in estuarine habitats, potentially filling the niche of other estuarine predators like bull sharks when they are largely absent from the system.

Bull shark

Bull sharks were consistently detected in West Bay, with occasional detections in Lower Galveston Bay and East Bay. Pronounced movements of bull sharks in West Bay were observed during summer and fall months, and their presence was markedly reduced during winter. Reduction of detections in West Bay during winter coincided with increased detections on receiver stations located outside the GBC, indicating that a significant portion of tagged individuals migrate outside the GBC during winter to move throughout the northern Gulf of Mexico, as oberved in other nurseries (Heupel and Simpfendorfer 2008; Drymon et al. 2014).

Bull shark is one of few elasmobranchs able to tolerate freshwater indefinitely (Gausmann 2021), allowing them to access habitats such a rivers and brackish waters (Heupel and Simpfendorfer 2008; Plumlee et al. 2018). This

adaptation allows juvenile bull sharks to thrive in estuarine environments, where they experience higher survival rates compared to juvenile sharks of other species (Heupel and Simpfendorfer 2011; Matich et al. 2020). Estuaries play a critical role as nursery habitats for juvenile bull sharks, with their seasonal distributions and migratory patterns strongly influenced by water temperatures and a mix of other factors including dissolved oxygen, prey availability and predation risk (Drymon et al. 2014; Matich and Heithaus 2015; Lofthus et al. 2024).

Our findings support previous research showing the influence water temperature has on bull shark distributions. In shallow temperate and subtropical estuaries, juvenile bull sharks routinely migrate to higher-salinity coastal waters during winter to avoid low temperatures, to maintain body condition and optimize growth during early life stages despite increased predation risk (Matich and Heithaus, 2012; Lear et al., 2020). In the GBC, previous study suggests that episodic freshwater inflows during fall create prohibitively cold conditions, forcing bull sharks to find refuge in warmer waters of West Bay (Livernois et al. 2021; Fontaine et al. 2024), and this study support this hypothesis. Bull shark detections and movement rates were highest during fall in West Bay (~22 °C) but dropped sharply during the winter (~16 °C). Fall cold-fronts may trigger this response before winter water temperatures fall below the species' preferred theshold of approximately 20 °C for juveniles (Matich et al. 2024).

However, warming temperatures associated with climate change affect the seasonal migration patterns of bull sharks (Bangley et al. 2018; Matich et al. 2024). This is particularly relevant in West Bay, where warming water temperature are enabling juvenile bull sharks to remain for extended periods, delaying autumn migrations and shortening overwintering periods, which may utilmately eliminate the need for Gulf overwintering (Matich et al. 2024). In the present study, four bull sharks (i.e., BS01, BS03, BS04, and BS10) were detected during winter months, suggesting that water temperatures in West Bay remained favorable enough to support their presence beyond the typical overwintering period. These findings underscore the influence for climate-driven temperature shifts to influence bull shark migratory behavior, potentially altering their ecological roles in estuarine ecosystems and affecting recruitment into the adult population. It remains unclear whether estuarine food webs will be able to support shifting residency patterns as climate change may also affect the spawning success of key forage species, which could, in turn, influence the availability of prey for bull sharks and other estuarine predators (Matich et al. 2024; Mullins et al. 2024).

Atlantic stingray

Atlantic stingrays were exclusively detected in West Bay, although their number of detections were relatively low over the study period, limiting conclusions for this species. Limited detections for Atlantic stingrays were likely attributed to smaller, externally attached transmitters (V9T-2x) with shorter battery life and higher risk of detachment compared to larger, internal tags (V16-4x) used for the other study species. Consequently, detection histories for stingrays may not be directly comparable to those of alligator gar and bull sharks. Additionally, the acoustic receiver array in West Bay may not have been optimally positioned to detect Atlantic stingray presence, as their slow-moving benthic lifestyle and tendency to bury in sediment (Rosenberger 2001) likely reduce detection probability by limiting movement within receiver detection ranges and increasing the risk of tag detachment or signal attenuation.

Atlantic stingrays exhibited site fidelity within West Bay, with detections concentrated near tagging locations, likely reflecting localized space use within the home ranges of tagged individuals. Although detections at other receiver stations indicate occasional movements beyond their primary area of use and likely contributed to the observed variability in movement rates (1.1 km²/day), no individuals were recorded at the West Bay inlet (i.e., San Luis Pass), suggesting high residency, consistent with previous studies (Ramsden et al. 2017; Meese et al. 2025). Seasonal detections peaked in summer and were minimal in winter; however, low detection frequency limits interpretation, and the observed patterns may reflect both environmental influences and detection constraints.

Overlap in habitat use patterns

As co-occurring estuarine predators, alligator gar, bull sharks, and Atlantic stingrays likely exhibit interspecific interactions that influence their spatial and temporal movements. The highest spatial overlap occurred between alligator gar and bull sharks, which coincides with their similar habitat preferences (Livernois et al. 2021) and co-occurrence patterns (Fontaine et al. 2024). Alligator gar showed increased movement during the cold season, when bull sharks displayed reduced presence in the system. While these contrasting seasonal movement patterns are likely influenced by abiotic factors (Barletta et al. 2008; Childs et al. 2008), they could also reflect resource segregation (Kroetz et al. 2017; Livernois et al. 2020). Although these species exhibit trophic overlap, spatial partitioning may facilitate their coexistence by reducing direct competitive interactions (Marsaly et al. 2023; Livernois et al. 2024; Fontaine et al. 2026). Our findings corroborate this hypothesis,

demonstrating that when these species co-occur, alligator gar reduced their use of higher salinity habitats, potentially as a tactic to minimize overlap in resource use with bull sharks.

In contrast to alligator gar and bull sharks, which both feed at higher trophic positions, Atlantic stingrays primarily consume benthic crustaceans and other invertebrates (Cook 1994; Bradley 1996; Fontaine et al. 2026), potentially explaining the limited habitat overlap between this species and the other two predators (Fontaine et al. 2024). Some spatial overlap with bull sharks was observed during summer; however, given the limited number of stingray detections, this pattern should be interpreted cautiously. While the present data do not allow mechanistic inference, it is possible that predation by bull sharks on stingrays may have occurred, as documented along the Texas coast (TinHan and Wells 2021). The relatively low detection rate for Atlantic stingrays is therefore likely driven by a combination of detection constraints, species-specific behavior, and potentially unobserved mortality.

Beyond interspecific dynamics, interactions among conspecifics may also shape movements of these predators. Intraspecifc overlap among bull sharks was the most pronounced, occuring consistently across seasons and sub-bays (i.e., West Bay and Lower Galveston Bay). Within estuarine environments, juvenile bull sharks exhibit size-based habitat partitioning, with smaller individuals (< 121 cm TL) utilizing brackish and freshwater habitats and larger juveniles (> 135 cm TL) found in higher-salinity environments (Heupel and Simpfendorfer 2011; Matich et al. 2020). Such spatial segregation reduce encounters between size classes, minimizing predation (Simpfendorfer et al. 2005) and competition (Heupel and Simpfendorfer 2008). The mean size of bull sharks detected for this study (mean TL = 122.2 cm), suggests that individuals were whitin the size range typically associated with the transition to higher-salinity habitats. For bull sharks, parturition occurs in late spring to summer, after which neonates recruit into estuarine nursery habitats where they grow and progressively shift habitat use as they increase in size (Werry et al. 2011). The consistent overlap of bull sharks in West Bay likely reflects localized salinity gradients or habitat preferences linked to ontogenetic shifts, with similar sized individuals occupying the same areas. However, the broad size range (92.6–152.0 cm), combined with the predominance of intraspecific overlap occurring during fall (40% of bull shark intraspecific co-occurrence events), suggests that individuals across size classes may converge in West Bay during this season, supporting the hypothesis that West Bay serves as a seasonal refuge for juvenile bull sharks.

Conversely, alligator gar and Atlantic stingrays displayed less pronounced intraspecific overlap compared to bull sharks. Fontaine et al. (2024) determined that salinity was the most important variable influencing the co-occurrence of alligator gar based on gillnet sampling, with higher co-occurrence observed in lower saline areas. The same study also noted that when co-occurrence was reported, the average size of alligator gar was below the recorded length at maturity (Fontaine et al. 2024). Given that West Bay is characterized by high salinity levels (20.6–25.6 psu), and the mean size of individuals (120.1 cm) detected in our study was above the recorded length at maturity, these factors potentially contribute to the observed low co-occurrence. However, given that both juvenile and adult individuals were detected, we do not exclude the possibility that, under physiologically and behaviorally favorable conditions (i.e., expansive low salinity waters during spring), conspecifics may periodically overlap in West Bay.

Although intraspecific overlap among Atlantic stingrays was primarily observed during summer, this pattern should be interpreted with caution because most individuals had relatively short tracking periods after being tagged in summer, potentially biasing the seasonal distribution of detections. Given the limited temporal coverage for many individuals, further year-round tracking across multiple tagging seasons is required to determine whether this pattern reflects true seasonal behavior or is primarily an artefact of the study design. If representative of true spatial behavior, summer overlap may be linked to favorable foraging conditions (Furst 2011; Pini-Fitzsimmons et al. 2021) and potentially increased opportunities for mating (Chaikin et al. 2020) and other social interactions (Thonhauser et al. 2013).

Conclusion

The present study highlights the utility of acoustic telemetry and network analysis for identifying broad-scale movement and spatial distributions of estuarine predatory fishes. Seasonal shifts in habitat use were observed for all species; however, these patterns should be interpreted with caution, as they may have been influenced by the study design (i.e., tagging location and receiver deployement). To our knowledge, this study is the first to assess the spatial dynamics of alligator gar tagged exclusively in the lower portion of an estuary and suggest that some individuals may stongly rely on these environments in the northern Gulf of Mexico. Bull sharks were absent from the estuary during winter, and the long-distance movements observed for this species suggest connectivity between estuarine and coastal environments. Site fidelity observed for Atlantic stingrays underscores the importance of specific habitats for this species and their susceptibility to declines in habitat quality compared to species that have larger home ranges and use a greater variety

of habitats. Overlaps in habitat use were evident over the tracking period, indicating potential intercations among and witihn species. Given the emphasis placed on ecosystem-based management, there is a growing need for studies that incorporate multi-species approaches to more effectively identify and protect habitats that are essential to ecosystem function (Hussey et al. 2015). Here we demonstrate the importance of habitat connectivity and seasonal dynamics for co-occurring predatory fishes within an estuary.

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Data availability The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Declarations

Conflict of interest The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Ethics statement The study was conducted in accordance with the local legislation and institutional requirements.

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