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Stock composition and movement patterns of striped bass in the Saco River Estuary, Maine, USA, using acoustic telemetry

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A B S T R A C T

Diversity in fish migration across space and time can buffer populations against environmental variability and promote long-term resilience. Considerable effort has been focused on understanding anadromous mixed-stock populations of striped bass on the east coast of the United States; yet a key knowledge gap remains in identifying which spawning populations contribute to northern habitats during seasonal migrations. Here, we used acoustic telemetry and network analyses to investigate the migratory behavior of striped bass utilizing northern habitats. We compared fine-scale movements and broad coastal migrations of striped bass populations present within southern Maine, USA. Our specific goals were to identify spawning populations present in Southern Maine, characterize estuarine habitat use, and compare migratory patterns among populations. Results revealed a mixed-stock assemblage in the Saco River Estuary composed primarily of Hudson River, New York, USA (42.3 - 59.6%) and Delaware Bay, Delaware and New Jersey, USA (5.8 - 32.7%) origin fish, with fewer fish from the Chesapeake Bay population, Maryland and Virginia, USA (1.9 - 3.8%), and 3.8% of individuals whose spawning population origin could not be confidently estimated. Fine-scale habitat use varied among individuals and size classes and shifted seasonally, with fish exhibiting both long- and short-term residency. Despite overlapping seasonal residency within the estuary, network analyses indicated that Hudson River and Delaware Bay striped bass largely maintained distinct migratory pathways (8-20% network similarity) and habitat connections, converging within shared northern foraging habitats. These findings demonstrate that Maine provides important seasonal habitat for multiple Atlantic coast spawning populations and highlight population-specific differences in movement, habitat connectivity, and site fidelity.

1. Introduction

In the north Atlantic, anthropogenic activities are increasingly exerting both direct and indirect pressure on fish populations including overfishing, habitat destruction, bycatch mortality, climate change, and the introduction of invasive species (Brander, 2013; Peer and Miller, 2014; Free et al., 2019; Plagányi, 2019). This pressure is often exacerbated by inadequate fisheries management leading to the depletion of fish stocks, disruption of marine ecosystems, and declines in biodiversity (Rosenberg et al., 2006; Hilborn et al., 2020). Collectively, this can result in an increased risk of population collapse, undermining the long-term sustainability of commercial and recreational fisheries (Lewin et al., 2019), underscoring the need to better understand population dynamics and behavior to protect vulnerable species.

Along the United States (U.S.) East Coast, striped bass (*Morone saxatilis*), are especially vulnerable to anthropogenic stressors (Richards and Rago, 1999). The species is primarily targeted by recreational anglers using hook-and-line gear, with recreational harvest regularly exceeding commercial harvest; in 2024, striped bass ranked among the most heavily harvested recreational species, with an estimated 15 million pounds harvested (ASMFC, 2024). Recent assessments showing declining female spawning stock biomass (Appelman et al., 2023; ASMFC, 2024) and poor young-of-year (YOY) recruitment indices (Buchanan et al., 2022; New York State Department of Environmental Conservation, 2024) mark uncertainty for the sustainability of the coast-wide stock. These declines likely stem from the species complex life history strategies (e.g., distinct spawning populations, variable migration patterns, and broad geographic ranges), driven by the need to reach specific spawning habitats, utilize productive nursery areas, and exploit seasonal foraging grounds (Secor, 1999; Morris et al., 2003;

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Hasegawa et al., 2022). A key knowledge gap for northern fisheries like those in Maine is identifying which spawning populations contribute to coastal catches and how these populations utilize northern habitats during seasonal migrations. Understanding migratory behavior, seasonal presence, and habitat use in northern systems is important for identifying when and where different spawning populations overlap.

Striped bass are managed as a single coastal migratory stock; however, this stock is composed of several genetically distinct spawning populations associated with major river systems along the U.S. Atlantic Coast (Hasegawa et al., 2022; ASMFC, 2024), including the Hudson River, Delaware Bay, Chesapeake Bay, and Albemarle Sound (Roanoke River; Gauthier et al., 2013, Callihan et al., 2015; Hasegawa et al., 2022; Buchanan et al., 2022; Maryland Department of Natural Resources, 2024). These populations migrate northward during the spring and summer along the Atlantic coast and intermingle as they pass through or inhabit coastal and estuarine habitats (Kneebone et al., 2014; Hollema et al., 2017). The relative contribution of spawning populations to coastal habitats varies spatially and seasonally, with recent evidence suggesting that Hudson and Delaware populations may contribute more broadly to northern coastal fisheries than previously recognized (Kneebone et al., 2014; Secor et al., 2020; Hasegawa et al., 2022). Southern spawning populations, such as those from North Carolina and South Carolina, are generally considered non-contributors to northern coastal fisheries, including those in Maine, as fish from those populations are not known to undergo broad-scale coastal migrations (Hasegawa et al., 2022; Doll and Marsik, 2023). Consequently, understanding the movement and habitat use of mixed-origin striped bass is important for fisheries management, particularly in northern coastal areas such as Maine that may serve as seasonal foraging or transitional habitat for multiple populations (Grothues et al., 2009).

Acoustic telemetry is a key tool in understanding the migratory behavior of striped bass and other coastal migratory species (Hussey et al., 2015; Jacoby and Piper, 2023), at various temporal and spatial scales. Historically, telemetry studies have been primarily descriptive, focusing on characterizing the movements of individual fish or summarizing broad seasonal patterns. Telemetry data alone only provides raw movement records that require robust analytical frameworks to uncover patterns of connectivity and migration. Advances in computational methods have enabled more complex, quantitative investigations of these data (e.g., kernel density estimation, mark-recapture modeling, network analysis, machine learning–based classification, and Bayesian hierarchical modeling; Hussey et al., 2015; Whoriskey et al., 2019; Jacoby and Piper, 2023). One approach in interpreting such patterns is network analysis, a method in movement ecology that models fish movements as connections between nodes (individual receivers or receiver groups), allowing for the quantification of complex migratory behaviors and stock interconnections (Espinoza et al., 2015; Lédée et al., 2015; Casselberry et al., 2020). By analyzing metrics describing global, node, or edge specific characteristics, network analysis can reveal the link between stock structure and habitat use patterns relevant to fisheries management (Jacoby et al., 2012; Lédée et al., 2015, 2021).

This study aims to characterize the stock composition, seasonal occurrence, movement patterns, and habitat use of acoustically tagged migratory striped bass in the Saco River Estuary and adjacent coastal waters of southern Maine. Specifically, we (1) estimate the relative contribution of major spawning populations to striped bass using the Saco River Estuary, (2) evaluate differences in habitat use and movement behavior among fish assigned to different spawning populations, and (3) characterize the coastal migratory pathways of tagged striped bass along the U.S. East Coast. We hypothesize that striped bass using the Saco River Estuary will primarily originate from the Hudson River spawning population, with smaller contributions from the Delaware Bay and Chesapeake Bay spawning populations (Wirgin et al., 1993). We further hypothesize that movement patterns and habitat use will differ among spawning populations, reflecting differences in migratory behavior and the energetic costs associated with alternative coastal migration pathways (Bernatchez and Dodson, 1987; Roff, 1991). By characterizing the seasonal presence, movement patterns, and habitat use of mixed-origin striped bass in Maine waters, this study provides insight into the connectivity between striped bass spawning populations and northern coastal habitats.

2. Methodology

2.1. Study site: Saco River Estuary & U.S. Coast

The Saco River Estuary (comprised of the Saco River and adjacent coastal waters of Saco Bay at its mouth; Fig. 1), located along the western Gulf of Maine, has historically served as an important habitat for striped bass in southern Maine (Little, 1995). The tidal portion of the Saco River is approximately 7 km, from mouth to dam, and is no more than 0.5 km wide at any point. The Cataract Dam represents an impenetrable boundary for striped bass preventing their movement upstream to habitat dominated by freshwater (Grothues et al., 2009). As such, the Saco River is not known as a current spawning habitat for striped bass and has no known evidence of young-of-year capture. The Saco River has a stratified, salt-wedge profile during periods of low river input (Brothers et al., 2008; Tilburg et al., 2011). However, during times of high river discharge, such as the spring, the freshwater plume can extend beyond the river mouth into Saco Bay (Tilburg et al., 2011). As a result, the river offers a variety of salinity gradients, habitats, and bathymetric features. The river mouth is considered polyhaline, with salinity values around 30 practical salinity units (PSU), while the upriver sections near the dam exhibit salinity near 1-5 PSU (Grothues et al., 2009). The Saco River transitions from shallow, sandy and rocky areas near the mouth to salt marsh-lined embankments, deeper rocky channels with scattered rock islands upstream, and returning to shallow, sandy conditions near the dam (Grothues et al., 2009; Novak et al., 2017). The river and surrounding coastal waters of the Saco Bay function as an interface between estuarine and marine habitats used by migratory striped bass moving between riverine systems and the broader coastal ocean. This area therefore constitutes the fine-scale study area, whereas the broader study area encompasses the wider U.S. Atlantic coast.

2.2. Acoustic telemetry

A total of 52 striped bass (mean size = 61.4 cm fork length [FL; range, 43.1 – 100.0 cm]) were included in this analysis, including 41 individuals tagged as part of this study and 11 fish tagged by external partners. The 11 fish were tagged across multiple years and locations as part of independent studies; however, all individuals were detected within the Saco River or adjacent coastal waters of Saco Bay and were therefore considered part of the defined Saco River Estuary study area. Fish were caught using conventional rod and reel tackle with artificial lures with approval for animal research from the University of New England IACUC 061422-006. As fish included in this study were tagged across multiple independent efforts, a combination of Innovasea acoustic transmitters (Innovasea, Halifax, Nova Scotia, Canada), including V13 tags (69 kHz; low-power, ~915-day battery life at 40-s delay), V13AP tags (69 kHz; low-power, ~915-day battery life at 40-s delay, with integrated acceleration and depth sensor), and V16-4H tags (69 kHz; high-power output, ~1834-day battery life with 50–130 s randomized delay), all programmed with unique ID codes for detection by the Atlantic Cooperative Telemetry (ACT; www.theactnetwork.com) coastal receiver network, were utilized (Table 1). Detection data from August 2022 to August 2025 were used in this analysis; auxiliary sensor data (e.g., acceleration, pressure) were not considered. Upon capture, total and fork length (cm) were recorded, and fish were placed in a buffered anesthetic bath containing 141.5 mg L^{-1} tricaine methanesulfonate (MS-222) and 141.5 mg L^{-1} sodium bicarbonate ($NaHCO_3$) (5.66 g of each dissolved in 40 L of water) until a narcotic state was observed (Grothues et al., 2009). Once immobile, an incision

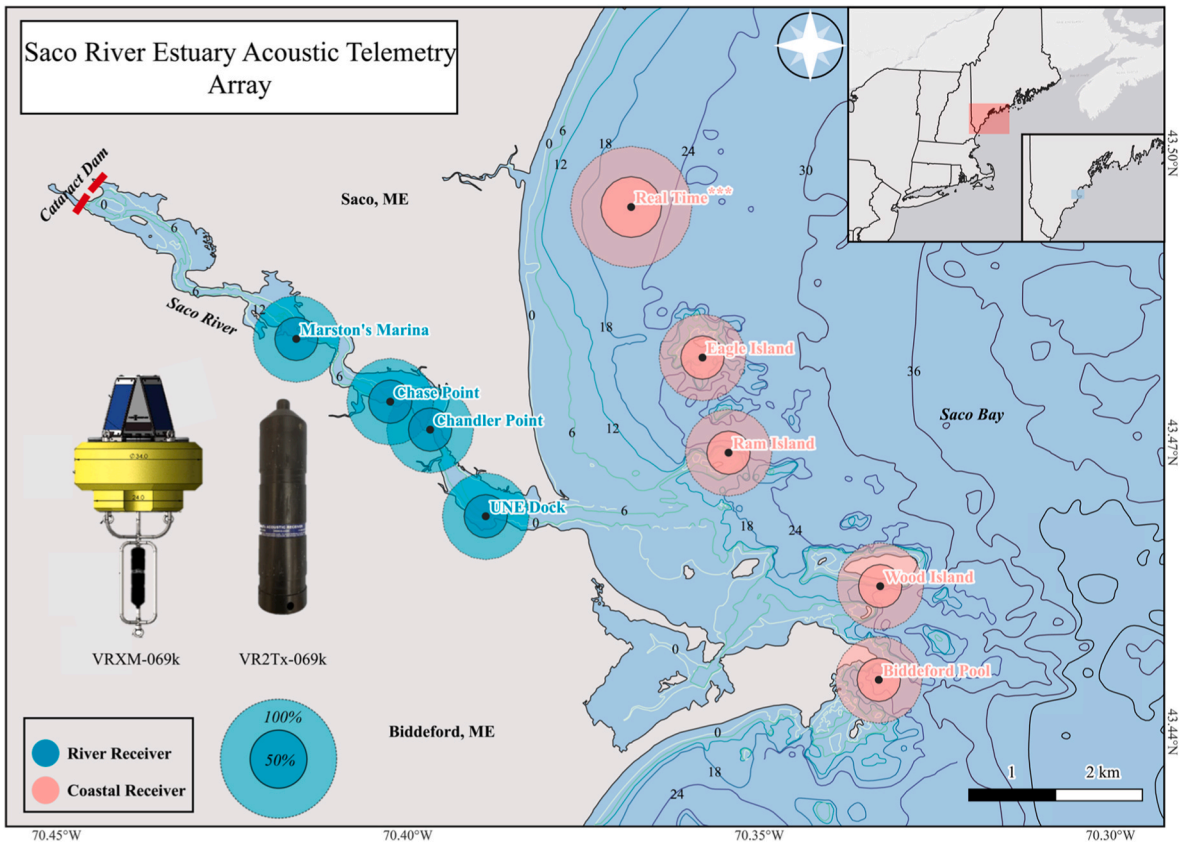

Fig. 1. Acoustic receiver array deployed in the Saco River and Saco Bay, Maine (UNESACOBAY–ACT). The array consisted of eight Innovasea VR2Tx (69 kHz) receivers and one CB-450 VRXM (69 kHz) receiver. Blue symbols denote riverine receiver locations, and red symbols denote coastal receiver locations. The VRXM receiver is indicated by asterisks (***). All receivers were surface-mounted on custom moorings approximately 0.5 m below the surface. Estimated detection ranges (radius) are shown for each receiver type (VR2Tx: 50% ≈ 250 m, maximum ≈ 500 m; VRXM: 50% ≈ 350 m, maximum ≈ 700 m). Coastal receiver locations at Wood and Ram Islands were maintained year-round to provide continuous acoustic coverage. Depth measurements (ft) are referenced to mean high water (MHW). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Tagging locations, sample sizes, FL range (mean ± SD in parentheses), and acoustic transmitter specifications for striped bass (*Morone saxatilis*) captured and tagged during 2020 –2024.

Year	Location	*n*	Fork Length (cm)	Innovasea Tag Model	Nominal Delay (s)	Battery Life (d)
2020	Island Beach State Park, NJ	1	55.5	V16-4H	50 -130	1834
2021	Fire Island Inlet & Montauk, NY	8	43.1 - 74.0 (56.5 ± 10.9)	V13AP	40	915
2022	Saco River Estuary, ME	9	45.5 - 52.8 (48.5 ± 2.7)	V13	40	915
2023	Saco River Estuary ME; Island Beach State Park NJ	19; 2	56.0 - 100.0 (67.1 ± 14.2); 47.0 – 55.0 (51.0 ± 5.6)	V13; V16-4H	40; 50 -130	915; 1834
2024	Saco River Estuary, ME	13	57.2 - 88.3 (70.6 ± 9.1)	V13	40	915
Summary		52	43. 1 - 100.0 (61.4 ± 13.1)			

approximately 2 cm in length was made immediately lateral to the ventral midline, between the pelvic fins and the anus, of each fish. Each fish was surgically implanted with an acoustic tag and sutured using absorbable suture material. The fish were also tagged with an external Hallprint plastic tipped dart tag with contact information in the event of recapture (Grothues et al., 2009; Kneebone et al., 2014).

Movement of all tagged individuals within the Saco River Estuary were monitored using a fixed array of acoustic receivers from August 2022 to August 2025. The Saco River Estuary array utilized eight VR2Tx receivers at 69 kHz (Innovasea, Halifax, Nova Scotia, Canada) in addition to a real time passive receiver (CB-450, VRXM Series; Innovasea, Halifax, Nova Scotia, Canada; Fig. 1). All receivers were surface mounted to custom moorings roughly 0.5 m below the surface (See S1 for mooring specifications). Beginning in August 2022 (initial deployment established the full array), receivers were moored within the Saco River and coastally around the river mouth in Saco Bay to provide comprehensive coverage of the study area. Four receivers were within the Saco River to detect tagged individuals from the mouth to mid river, and five were set near the islands surrounding the river mouth within Saco Bay (Fig. 1). In subsequent years, seven of the nine receivers were deployed seasonally in early spring and removed in late fall due to ice rafting and harsh winter conditions, while two coastal receivers (Wood

and Ram Island locations) remained deployed year-round to maintain continuous acoustic coverage. Estimated detection ranges (radius) varied by receiver type (VR2Tx: 50% ≈ 250 m, maximum ≈ 500 m; VRXM: 50% ≈ 350 m, maximum ≈ 700 m; Kessel et al., 2014; Anderson et al., 2026). Movements of acoustically tagged striped bass outside of the primary array in the Saco River Estuary and along the U.S. East Coast were monitored through collaboration with the ACT & Atlantic White Shark Conservancy (AWSC) Networks (Mather et al., 2010; Kneebone et al., 2014; Rothermel et al., 2020). The ACT Network is a collaborative coastal acoustic telemetry network spanning the northeastern and mid-Atlantic United States, from Maine through North Carolina, with receiver density varying geographically among participating arrays (see ACT Network website, www.theactnetwork.com, for current array locations and receiver density).

Following manufacturer's recommendations, a stationary test was conducted from 1600 on 16 June 2022 until 1600 on 17 June 2022 within the Saco River. Two VR2Tx receivers equipped with transmitters were set approximately 250m apart (manufacturer estimated 50% maximum detection range) and allowed to "listen" to each other for 24 h. One receiver was set to transmit at very high power, while the other was programmed at medium power. Detection efficiency was calculated by counting the number of detections on each receiver of the other receiver's transmitter and dividing those values by the number of expected detections. Upon completion of the 24-h trial, the receivers were recovered, and data was downloaded into VEMCO User Environment (VUE) software for analysis. Detection efficiency was higher at high power (62%) compared to medium power (28%), making high power the preferred setting for use throughout the study (See S2). As acoustic detection efficiency can vary with environmental conditions such as depth, salinity, temperature, turbidity, ambient noise, biofouling, and tidal fluctuations (tidal range ~4 m in the study area), environmental parameters were recorded (temperature, tide height, tilt angle) and plotted using Innovasea's range testing software. Tide height was overlayed against the tilt angle for each receiver and demonstrated a clear correlation between incoming and outgoing tidal fluxes and increased tilt angle. Detection efficiency also varies with transmitter type and output power; for example, Kessel et al., (2014) reported that approximately 40–60% of V13 and V16 tag transmissions are detected at a distance of 500 m, with detection rates at 250 m estimated at 88.4% for V13 tags and 27.7% for V16 tags. The substantial change in water depth, tilt, and salinity across tidal cycles and differences in tag power are likely to influence detection efficiency.

2.3. Spawning population identification

As individuals tagged in this study were from varying spawning locations, determining the spawning population for each fish required analysis of movement patterns, including timing of entry into spawning sites, and size at tagging. Spawning population assignments were made using confirmed detections of fish in spawning regions during spawning periods (see Kneebone et al., 2014). However, to increase assignments, a broad movement-based approach was also used to consider delayed or incomplete ACT MATOS network uploads, the presence of immature fish, and individuals that may skip spawn. In this approach, when individuals were not detected within known spawning rivers, spawning origin was inferred from repeated detections in locations and during periods consistent with established spawning population characteristics. For example, individuals exhibiting pre-spawning staging behavior, such as repeated detections in estuaries or coastal areas in the weeks preceding spawning periods, post-spawning detections in the same regions were considered indicative of association with specific spawning populations. This allowed inclusion of fish that were not directly detected at spawning sites or times but whose movement behaviors aligned with known spawning population characteristics. Fish that did not meet any spawning criteria were classified as originating from an "Unknown" population (Kneebone et al., 2014). Each spawning population assignment was categorized as high, moderate, or low confidence based on the type, strength, and consistency of supporting evidence, with assignment criteria and confidence levels defined in Table 2. Sensitivity analyses were conducted by excluding indirectly assigned individuals and repeating key population-specific analyses to assess the robustness of results to uncertainty in spawning population assignment. Overall, 48% of individuals were assigned to spawning populations based on direct detections within known spawning rivers, while 48% were assigned using broad movement-based criteria, and 4% remained unassigned (S3). As such, inferred assignments therefore represent levels of support based on observed movement patterns rather than definitive classifications of spawning origin.

2.4. Data processing

All acoustic telemetry data was processed and analyzed in R ver. 4.3.2 (R Foundation for Statistical Computing, 2024; Vienna, Austria) using the *glatos* package (Holbrook et al., 2017). All statistical tests were conducted using a significance threshold of $\alpha = 0.05$. Prior to analysis, all detection data was examined for any false detections which were removed (0.42%; 5125 detections) using criteria established by the equipment manufacturer. Single detections that were temporally and/or spatially isolated (e.g., a single transmitter code detected on only one receiver within a period of 30 times the average transmitter delay interval) were excluded, as were detections of transmitter sensor codes without accompanying identification codes.

2.5. Detection visualization and system use classification

Abacus plots were generated to visualize acoustic telemetry detections over time at specific receiver locations. Individual use metrics including total days detected, maximum consecutive detection days, number of estuarine visits, and proportion of the monitoring period spent in the system were z-score standardized and used as input variables in hierarchical clustering analysis (Ward's method, Euclidean distance; Ward, 1963; Ferreira and Hitchcock, 2009) to identify behavioral groupings reflecting patterns of system use. The number of estuarine visits was defined based on detections across the entire receiver array (river and coast). A visit was defined as a discrete period of presence within the full array, separated by periods of no detection (1 day). The optimal number of clusters determined by silhouette (maximizing average silhouette width) methods (Sagala and Gunawan, 2022). Silhouette analysis evaluates how well each observation fits within its

Table 2
Criteria used to assign spawning population and associated confidence levels for acoustically tagged striped bass. Assignments were categorized based on the type, strength, and consistency of spatial and temporal movement evidence.

Assignment evidence	Description	Assignment strength
Direct spawning detection	Fish detected within a known spawning river during the documented spawning period	High
Repeated pre-spawning staging & subsequent movement	Repeated detections in characteristic staging areas/timing followed by movement consistent with a known spawning population	Moderate
Repeated seasonal movement pattern	Repeated detections across locations and periods consistent with the established migratory behavior of a spawning population	Moderate
Single/limited detection consistent with population	Limited detections occurring in a location/time consistent with a spawning population but lacking additional supporting movement evidence	Low
No population-specific evidence	No detections or movement pattern sufficient to support an assignment	Unknown

assigned cluster relative to other clusters, with average silhouette widths ranging from −1 to 1 and higher values indicating better-defined clustering. The optimal *k* is selected as the number of clusters that maximizes the average silhouette width.

2.6. Residency patterns across spawning populations

Residency patterns were analyzed for each spawning population using a Kessel residence index (RI): calculated as the number of days an individual fish was detected at each receiver station divided by the total number of days the fish was detected anywhere on the acoustic array (Kessel et al., 2016) and then grouped by Saco River Estuary habitat (river vs. coast) and size (threshold of 600 mm FL). RI values were calculated at the level of individual fish by aggregating detections across all receiver stations within each habitat type (river vs. coastal) over the full monitoring period, such that each RI value represents a single, independent observation per individual. A 600 mm FL was used to classify individuals by body size to assess whether residency patterns differed between smaller and larger individuals (Nelson et al., 2025). RI was used over raw number of detections as it reduces the potential bias of many detections at a given station being generated by a low number of individuals. To account for the non-normal distribution of the response variables, we employed non-parametric permutation ANOVAs (10,000 permutations) using r package *coin* (Hothorn et al., 2008) to test for differences in RI among stocks.

2.7. Machine learning models of spawning population-specific presence

To evaluate and compare the ability of supervised classification models to predict weekly striped bass presence within the Saco River Estuary, and to assess the relative contribution of spawning population, habitat (Saco River vs. Saco Bay), and week to predicted occurrence, we developed supervised classification models using the *tidymodels* framework in R (Kuhn and Wickham, 2020). This analysis was intended primarily as a comparative predictive framework rather than as an alternative to traditional inferential approaches for estimating individual predictor effects. The dataset consisted of weekly presence/absence observations for each tagged individual within the complete Saco River Estuary receiver array, along with associated predictor variables (spawning population, habitat, and week). Weekly presence–absence observations were generated separately for each tagged individual and habitat for each week during which the individual was available for detection, resulting in repeated observations for individual fish across weeks. Individual identity was retained during data processing but was not included as a predictor in the classification models because the objective was to evaluate the relative influence of spawning population, habitat, and week on occurrence at the population level. Data were randomly partitioned into training (70%) and testing (30%) sets to enable independent model evaluation and reduce overfitting. Because presence and absence observations were imbalanced, the majority class (absence) was randomly down sampled within the training dataset to improve model performance. Categorical predictors were converted to numeric format using dummy encoding, and numeric predictors were standardized to ensure comparability among variables. We implemented three supervised machine learning algorithms for model comparison: random forest (ranger engine), extreme gradient boosting (XGBoost), and an artificial neural network (ANN, nnet engine). Hyperparameters for each model were tuned using a grid search approach with 5-fold cross-validation, and model performance was evaluated using accuracy (proportion of correctly classified observations), area under the receiver operating characteristic curve (ROC-AUC; discrimination ability across thresholds), and F-measure (F1 score; harmonic mean of precision and recall), all ranging from 0 to 1 with higher values indicating better performance (Liu et al., 2011; Li and Wang, 2013; Norberg et al., 2019). Among the three algorithms tested, the random forest model consistently outperformed the other model types and achieved the highest average performance (accuracy = 0.756, ROC-AUC = 0.853, F1 = 0.855) and was selected for final inference. A final random forest model was fit using the best-performing hyperparameters identified during tuning. Predictor importance scores were extracted from the fitted model to assess the relative influence of spawning population, habitat, and week on predicted presence (S4). To further evaluate the temporal effect of week, partial dependence plots (PDPs) stratified by spawning population were generated and compared using multifactor ANOVA (Kuhn and Wickham, 2020).

2.8. Broad scale network analysis

Network analysis along the U.S. East Coast was undergone to better define regions of importance such as migratory hubs and transit points and to determine differences in seasonal migratory movements between spawning populations. Saco River Estuary primary array detections were combined with detection data obtained from the ACT and AWSC coastal networks and analyzed by employing spatial network analysis using *igraph* package (Csardi and Nepusz, 2006) and visualized using QGIS (QGIS Development Team, 2024) and Gephi (Bastian et al., 2009). Network nodes were defined as 56 grouped regions (Kneebone et al., 2014; Secor et al., 2020), with node weight ranging from 0 to 1 (with higher values indicating higher residency) and calculated as the proportion of days an individual was detected in that region divided by total number of days, reflecting the fine scale residence index. Additional node specific network metrics, i.e., eigenvector centrality (measure of node influence; ranging from 0 to 1 with higher values indicating higher network influence) and raw betweenness centrality (degree of node flow; arbitrary number based on size of network of shortest paths passing through a node with higher values indicating greater control of network flow), were calculated to better define regions of importance such as migratory hubs and transit points (King et al., 2024). For clarity, these metrics capture complementary aspects of network structure: eigenvector centrality reflects node influence or "prestige," where nodes are important if they are connected to other highly connected nodes, whereas betweenness centrality identifies nodes that function as bridges linking otherwise weakly connected or disconnected regions of the network. In this context, eigenvector centrality describes what a node is connected to, while betweenness centrality describes where a node is positioned within the network. To address differences in regional importance between spawning populations, paired t-tests were used to compare node specific network metrics (node weight, eigenvector centrality, betweenness centrality; S5) in overlapping regions between spawning populations.

Furthermore, overall network structure was compared between spawning populations, utilizing the graph edit distance as a baseline similarity measure, quantifying the minimum-cost set of operations (e.g., insertion, deletion, substitution of weighted nodes or edges) needed to transform one network into another (SolÉ-Ribalta et al., 2012; Stauffer et al., 2017; Liu et al., 2024). As edit distance depends on network size, the values are arbitrary in nature. Therefore, a similarity index (SI) was used to normalize edit distance, expressing similarity on a standardized scale from 0 to 100%, where higher values indicate greater structural similarity using equation (1).

$$SI = (1 - (E_{distance} / E_{max})) * 100 \quad \text{[eq1]}$$

Where $E_{distance}$ is edit distance of the two networks, and E_{max} is the maximum possible edits of the two networks given the size and structure of the networks, representing the total number of edits required to completely transform one network into the other (Evans and Graham, 2019). To further evaluate overall movement patterns differences between spawning populations, separate networks were previously constructed for each population were subsequently combined into a unified comparative framework. In this framework, edges, defined as movements between node regions, were classified as either shared (present in

both population-specific networks) or unique (present in only one population). The number of shared and unique edges, along with the percentage of overlapping nodes (Lédée et al., 2021), were calculated to provide a more detailed understanding of network structure and potential habitat partitioning between mid-Atlantic populations.

2.9. Sensitivity analysis of spawning population assignment

To assess the robustness of network comparisons to uncertainty in spawning population assignment and unequal sample sizes, a sensitivity analysis was conducted using only individuals assigned to spawning populations based on direct detections within known spawning rivers. First, network similarity was calculated using the full directly assigned dataset (22 Hudson River and 3 Delaware Bay individuals). Because the number of directly assigned Hudson River individuals was greater than the number of Delaware Bay individuals, the larger Hudson River group was repeatedly subsampled to match the sample size of the Delaware Bay group (3). Network construction and calculation of the network similarity index were then repeated for each random subsample. This resampling procedure was repeated 1540 times, generating a distribution of similarity index values that reflects the expected variability in network similarity associated with the unequal sample sizes. The observed similarity index from the complete inferred dataset was compared with the distribution generated from the resampling procedure to evaluate whether conclusions regarding network similarity were sensitive to sample size and population assignment.

3. Results

Detection patterns were highly variable both within the Saco River Estuary and along the broader U.S. Atlantic coast. A total of 1.22 million valid detections of 52 tagged striped bass were detected, with 382,000 detections within the Saco River Estuary and 838,000 along the U.S. Atlantic coast between August 2022 and August 2025. Every fish was observed participating in migration following release, demonstrating that the tagging procedure did not lead to mortality (average days = 98 ± 77; across U.S. Atlantic coast). Within the Saco River Estuary (river and coast), detections varied widely among individuals and spawning populations, with fish exhibiting high site fidelity and extended estuarine presence both seasonally and interannually, while others displayed more transient patterns. Cluster analysis (Fig. 2) suggested that there were two distinct behavioral groups with the strongest statistical separation (silhouette width: = 0.81; S6), corresponding to prolonged non-natal residency (average days = 153 ± 24), and short-term non-natal estuarine occupancy (average days = 8 ± 11). Interannual detections within the Saco River Estuary were observed in 26 of 52 individuals (50%), confirming multi-year Saco River Estuary habitat (river and coast) use across tagged individuals. Residency within the Saco River Estuary ranged from 1 to 177 days per individual (37 days ± 59 days), with 40 of 52 fish (77%) detected at multiple receiver locations within the river and coast (Fig. 3). Of the 52 individuals, 26 were detected within the Saco River Estuary for five days or fewer, whereas nine fish exhibited prolonged estuarine use, being detected for more than 100 days belonging to the prolonged non-natal residency cluster. No detections were recorded within the Saco River Estuary during winter months (November – April), as southern migrations occurred resulting in consistent detections along the U.S. Mid-Atlantic coast during the same period. In total, fish were detected on 1132 different days throughout the study (S7).

3.1. Fine scale: Saco River Estuary

Using broad inferred movement-based criteria, 50 of 52 fish were assigned to a mid-Atlantic spawning population with 31 (59.6%) from the Hudson, 17 (32.7%) Delaware, and 2 (3.8%) Chesapeake. Of these, 22 Hudson River and 3 Delaware Bay individuals were assigned based on direct detections within known spawning rivers, while the remaining assignments were based on movement patterns. Due to the limited sample size from the Chesapeake spawning group (n = 2), comparative analyses were restricted to the Hudson River and Delaware Bay populations. Within these two populations, Hudson River fish were predominantly <600 mm FL, with only 10 of 31 individuals (32%) classified as ≥600 mm FL, whereas Delaware Bay fish had a substantially higher proportion of individuals ≥600 mm FL at 13 of 17 fish (76%). Fine-scale RI within the Saco River Estuary differed strongly by habitat type (coast vs. river; permutations = 10,000, $p < 0.05$), with individuals exhibiting higher residency in riverine habitats (mean RI = 0.373 ± 0.314) relative to coastal habitats (mean RI = 0.102 ± 0.235) across spawning populations (Fig. 4). Spawning population alone did not significantly influence RI (permutations = 10,000, $p = 0.355$). A significant habitat × size class interaction was found (permutations = 10,000, $p < 0.05$), indicating that smaller individuals (<600 mm FL) exhibited disproportionately higher mean residency in riverine habitats compared to coastal habitats, whereas larger individuals showed a reduced contrast between river and coastal residency (Fig. 4). Variable importance metrics identified week and habitat as the top predictors of fish presence, week consistently ranking highest. The random forest model (classification accuracy = 0.756) further highlighted the importance of habitat type rather than population, as partial dependence plots revealed insignificant differences

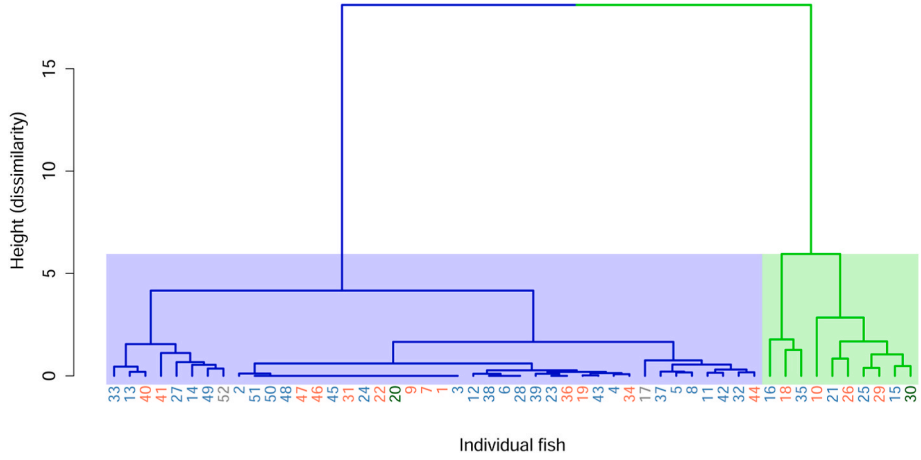

Fig. 2. Wards hierarchical clustering of residency strategies of striped bass (*Morone saxatilis*) in the Saco River Estuary (River and Coast) from August 2022 – August 2025. Individual fish numbering coloring is designated by spawning population with assigned Hudson River fish in Blue, Delaware Bay in Orange, Chesapeake Bay in Green, and unknown in Grey. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

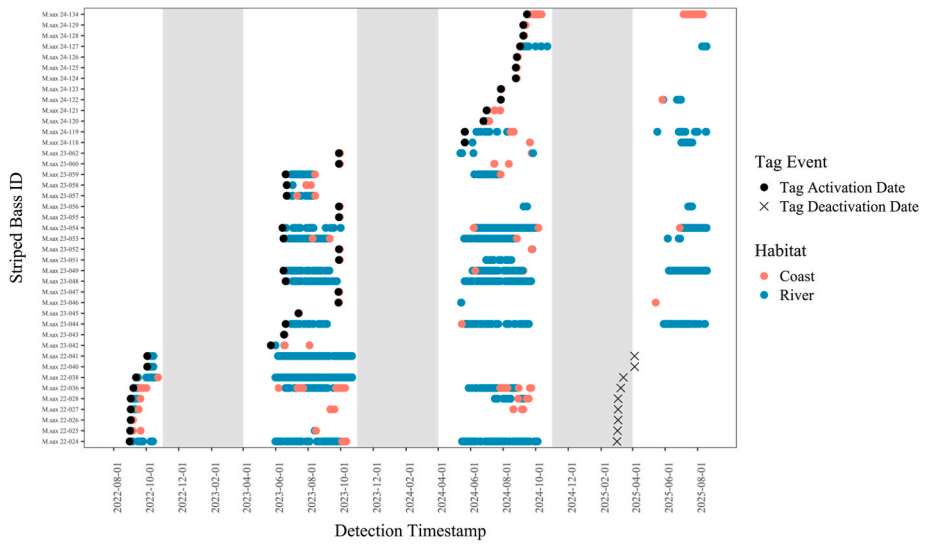

Fig. 3. Detection history of acoustically tagged striped bass (*Morone saxatilis*) in the Saco River Estuary, Maine organized by Habitat (Saco River vs. coastal Saco Bay). Marston's Marina, Chase Point, Chandler Point, and UNE Dock represent river receiver habitat locations, while Biddeford Pool, Real Time, Eagle Island, Ram Island, and Wood Island represent coastal receiver habitat locations (Fig. 1). Black circles indicate acoustic tag activation dates, and black X's mark estimated tag battery expiration dates. Shaded grey areas indicate winter periods (November to April) when tagged fish were absent from the array. Seven of the nine receivers were deployed seasonally in early spring and removed in late fall due to ice rafting and harsh winter conditions, while two coastal receivers remained deployed year-round to maintain continuous acoustic coverage.

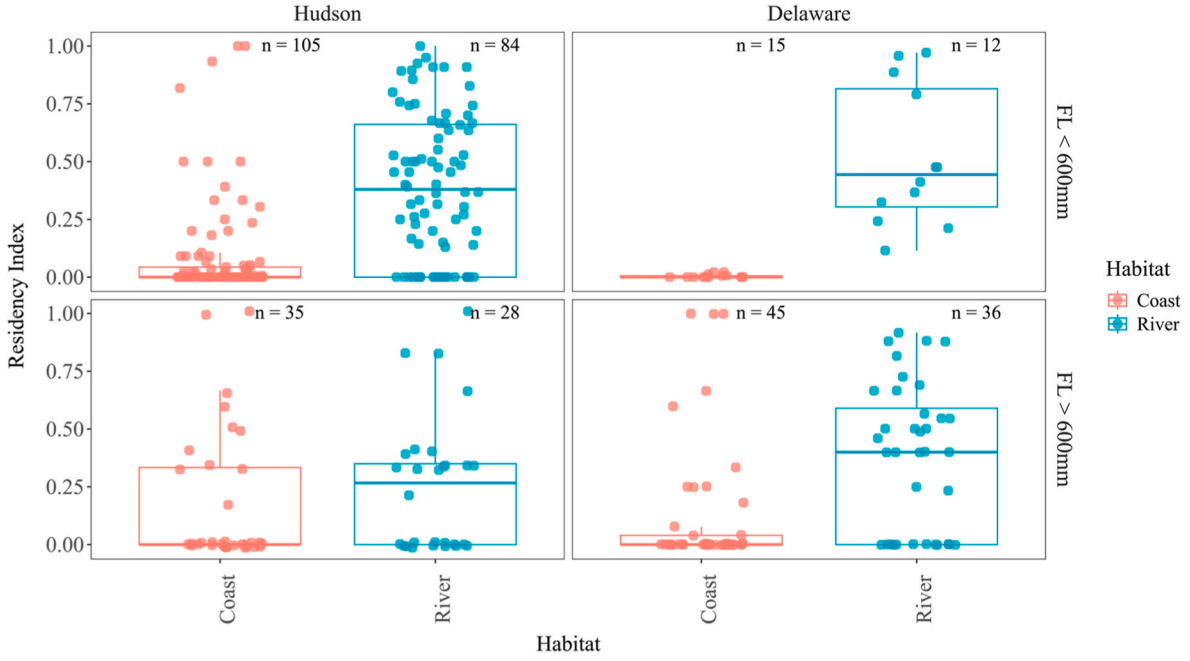

Fig. 4. Spawning population-specific residency index of acoustic tagged striped bass (*Morone saxatilis*) detected in the Saco River Estuary and adjacent coastal waters, separated by habitat (coast vs. river), natal spawning population: (left) Hudson and (right) Delaware, and size: (top) FL < 600 mm and (bottom) FL > 600 mm. Boxplots represent the distribution of individual fish residency indices, with the center line indicating the median and points indicating individual fish values at acoustic receivers. Residency index values calculated from following Kessel et al. (2016) as number of days an individual fish was detected at each receiver station divided by the total number of days the fish was detected anywhere on the acoustic array. Values range from 0 (no residency) to 1 (maximum residency). Sample sizes are indicated in each panel.

between spawning populations in habitat usage across time ($F = 1.74$, $p = 0.161$). In contrast, habitat was an important predictor of occurrence ($F = 2.98$, $p = 0.032$), with river sites showing early-season peaks in predicted probability of weekly fish detection followed by a slight decline and a subsequent increase in coastal sites seasonally (Fig. 5).

3.2. Broad scale: U.S. Coast network analysis

Spatial network analysis of Hudson River and Delaware Bay striped bass revealed differences in spatial patterns of connectivity, movement bottlenecks, and regional importance in use of the U.S. Atlantic coast. Each network represented movements among 56 distinct spatial regions, though the number of receivers per region varied due to differences in

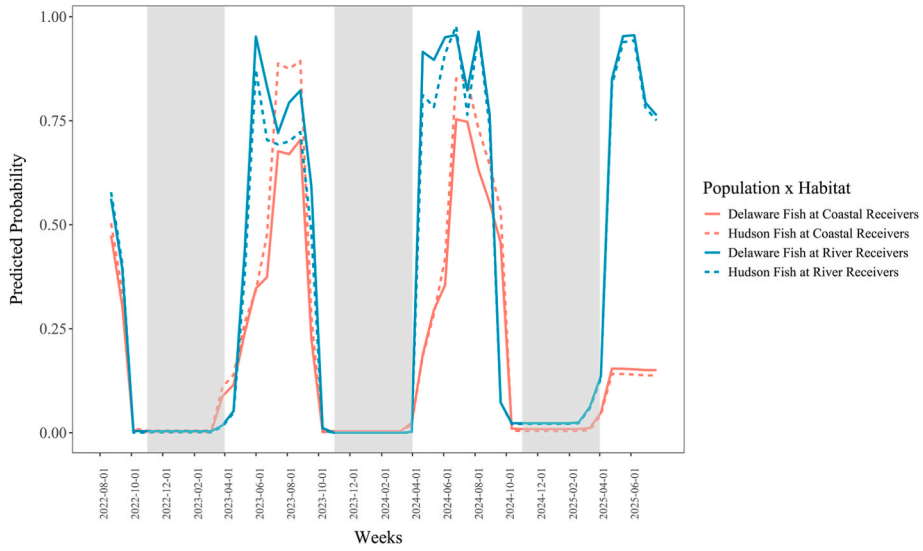

Fig. 5. Partial dependence of predicted probability of weekly fish detection for acoustic tagged striped bass (*Morone saxatilis*) in the Saco River Estuary, Maine, using random forest machine learning model, separated by spawning population (Hudson: blue, Delaware: red) and habitat (coast, river). Solid lines represent river detections and dashed lines represent coastal detections. Shaded grey areas indicate winter periods (November to April) when tagged fish were absent from the estuary. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

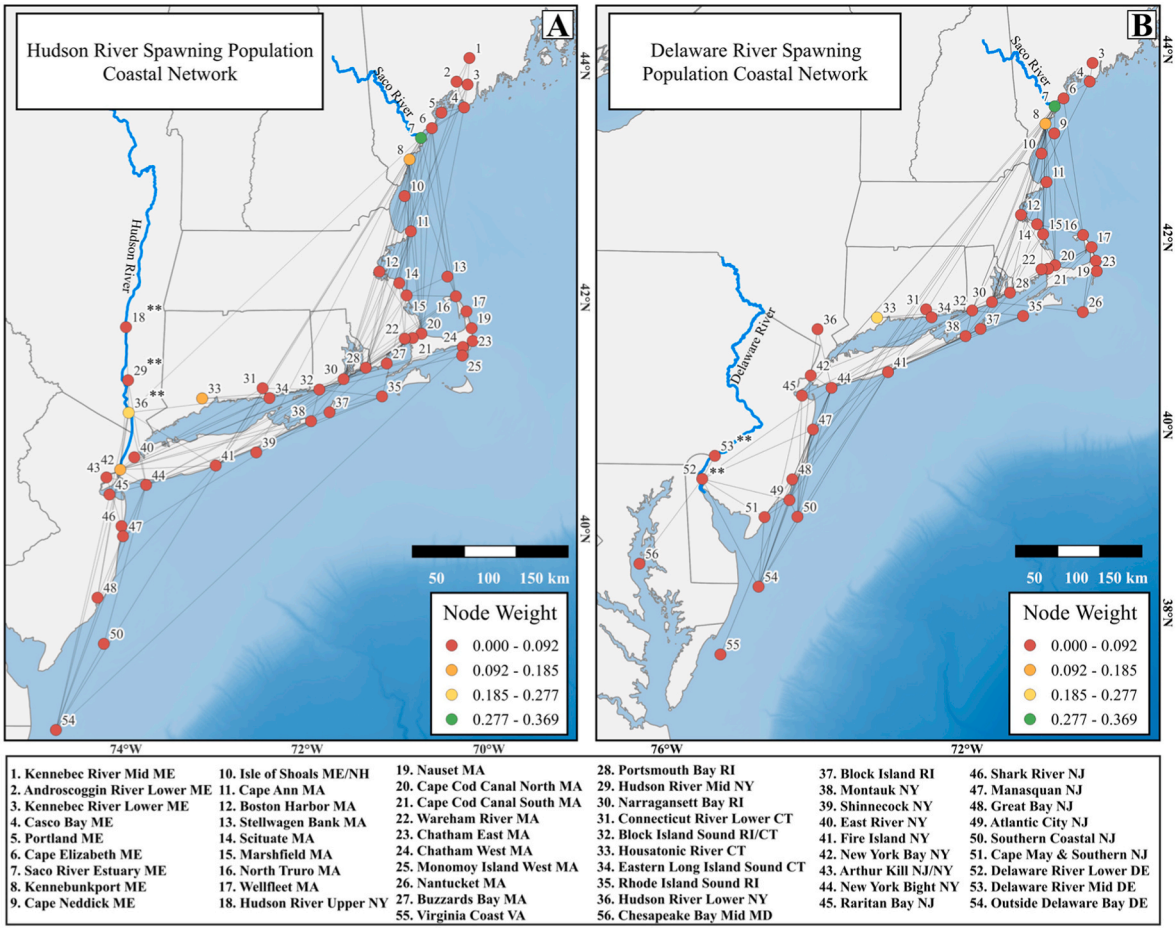

Fig. 6. Undirected spatial networks of Atlantic coastal movements for (A) Hudson River and (B) Delaware Bay spawning populations of striped bass (*Morone saxatilis*). Nodes (dots) represent regional receiver array groupings labeled by name, with numbering assigned in order of decreasing latitude. Node color reflects node weight (the proportion of days an individual was detected relative to the total number of days monitored). Edges (black lines) represent movements between regions, indicating spatial connectivity, not direct migratory route. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

array density and yearly changes across the ACT MATOS Network. Key coastal regions with elevated residency, inferred from node weight, were relatively similar between spawning populations ($t = 1.24$, $p = 0.221$) and were generally concentrated in northern foraging habitats and mid-Atlantic spawning and staging locations (Fig. 6). For both spawning populations, northern residency was heavily centered within and around the Saco River Estuary, including at Kennebunkport, ME, which accounted for a substantial proportion of habitat use (node weights of 0.153 for the Hudson River population and 0.180 for the Delaware Bay population), while approximately one-third of total residency occurred directly within the Saco River Estuary itself (node weights of 0.301 and 0.369, respectively). The Housatonic River, CT, exhibited moderate residency across both populations, suggesting consistent habitat use in these regions regardless of assigned spawning origin. In contrast to shared northern foraging areas, residency within spawning habitats and adjacent areas differed between spawning populations. For Hudson River fish, the key spawning area, the lower Hudson River, NY, had a high residency (node weight of 0.2292), while the Delaware Bay's fish core spawning region, the lower Delaware River, DE, showed low residency (node weight of 0.0586). Adjacent regions such as New York Bay, NY (0.1439 for Hudson) exhibited moderate residency rates that differed between spawning populations, despite their geographic proximity to spawning locations (Fig. 6).

Movement bottlenecks (nodes that act as key connectors or movement corridors within the network), inferred from high betweenness centrality (BC), were largely consistent between spawning populations, although differences in node-level BC values between populations approached significance ($t = 1.98$, $p = 0.054$; Fig. 7). For the Hudson spawning population, Narragansett Bay, RI (BC = 645.3), Kennebunkport, ME (BC = 464.8), and North Truro, MA (BC = 368.4) were dominant, highlighting a strongly connected New England corridor. For the Delaware spawning population, two of these nodes were shared (Kennebunkport, ME, BC = 416.8; Narragansett Bay, RI, BC = 336.7), with Block Island Sound, RI/CT (BC = 306.2) as a third key node. These patterns indicate that the Hudson and Delaware populations utilize partially overlapping movement corridors within northern and Southern New England waters. Core migratory hubs, inferred from high eigenvector centrality (EC), differed between spawning populations ($t = 2.26$, $p = 0.036$; Fig. 7). High EC values indicate well-connected regions that serve as key hubs maintaining broad-scale stock connectivity. New England sites like the Saco River Estuary (EC = 1.000), Kennebunkport ME (EC = 0.844), and Narragansett RI (EC = 0.697) were most important for fish assigned to the Hudson River spawning population, whereas mid-Atlantic areas, particularly areas in New York (EC = 0.955 – 1) and New Jersey (EC = 0.743 – 0.919) emerged as key hubs for fish assigned to the Delaware spawning population.

Although node specific patterns of EC, BC, and node weight along the U.S. Atlantic coast only differed in EC, overall network comparisons revealed large differences between assigned spawning populations of the Hudson River and Delaware Bay. The combined Hudson and Delaware network contained 56 nodes and 222 edges, of which only 17% of edge connections were shared between spawning populations (S8). This

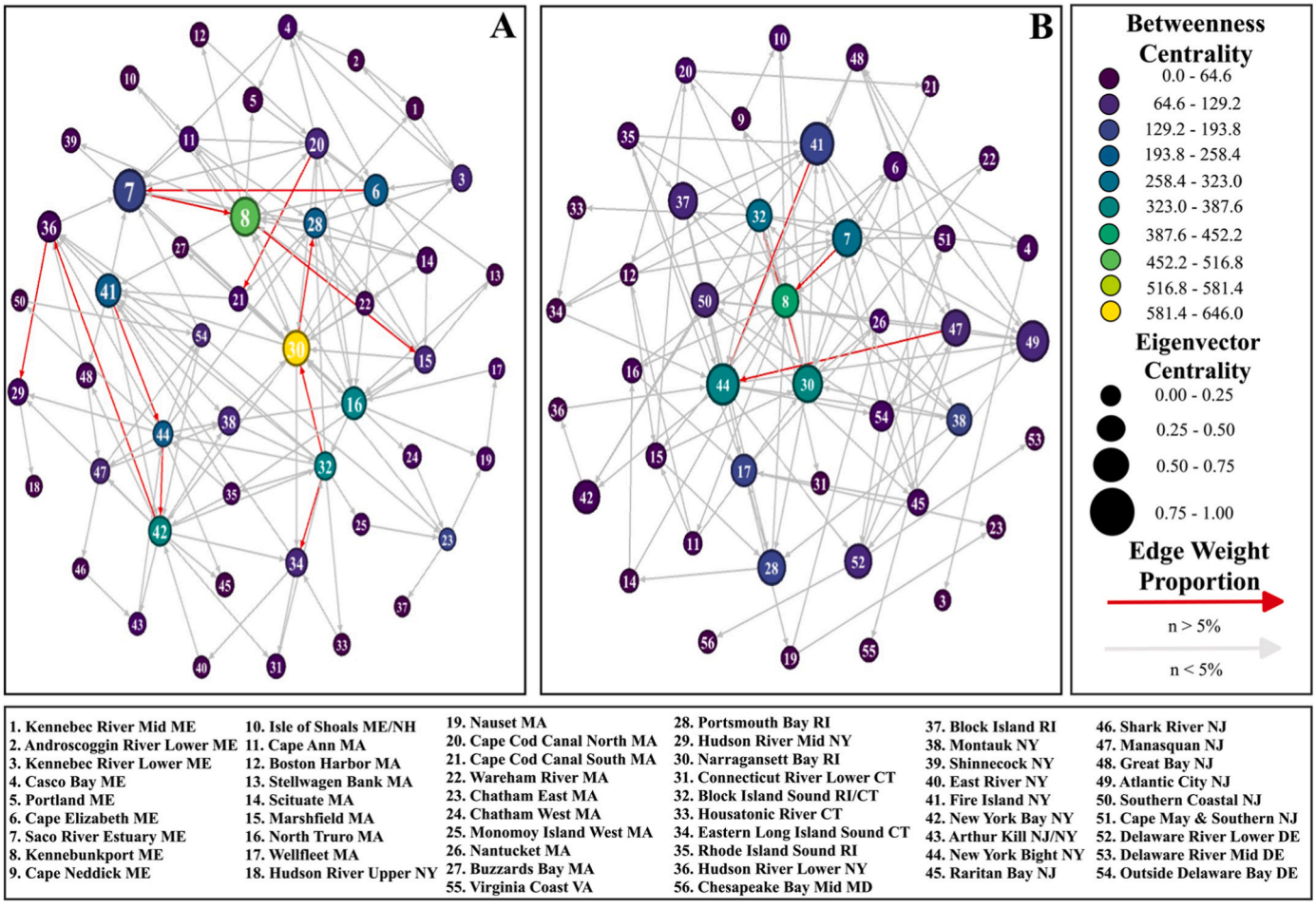

Fig. 7. Directed networks of Atlantic coastal movements for (A) Hudson River and (B) Delaware Bay spawning populations of striped bass (*Morone saxatilis*). Nodes (dots) represent regional receiver groupings with names labeled. Node color indicates betweenness centrality, and node size indicates eigenvector centrality. Edges represent movement pathways, with red edges denoting pathways comprising more than 5% of total movements among all edges, and grey edges denoting less frequently used pathways (<5%). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

minimal overlap is also supported by a network similarity index of just 8% (edit distance: 257, maximum possible edits: 279), indicative that assigned Hudson and Delaware striped bass largely use separate networks and display limited spatial connectivity along the U.S. coast. However, network similarity estimates varied depending on spawning population assignment and sample composition (S9). Using the full dataset of fish assigned through direct and movement-based criteria, the network similarity index was 0.08 (8%). When the analysis was restricted to the 25 individuals assigned based on direct detections (22 Hudson River and 3 Delaware Bay), the similarity index increased to 21%. To account for the unequal sample sizes of the directly assigned populations, the 22 Hudson River individuals were repeatedly subsampled to match the Delaware Bay sample size ($n = 3$). Across 1540 resampling iterations, the mean and median similarity indices were approximately 20%, with a 95% resampling interval of 14%–27%. The similarity index from the full inferred-assignment dataset (8%) fell below the lower bound of the resampling interval, indicating that the lower similarity observed in the primary analysis was not reproduced when analyses were restricted to directly assigned individuals and standardized for sample size.

4. Discussion

4.1. Stock composition

Using acoustic telemetry and network analyses, this study provides evidence that striped bass using the Saco River Estuary, in Southern Maine, are primarily from Hudson and Delaware spawning populations, underscoring the continued importance of northern habitats to the Atlantic Coast Mixed Stock fishery. Particularly, the presence of Delaware Bay fish in southern Maine highlights the recovery of the Delaware Bay spawning population from 1979 to 2016. This is important given that historically (pre-moratorium) Delaware Bay populations were on the brink of collapse (Shepherd et al., 1979; Kahn et al., 1998). Previous investigations of Atlantic Coast Mixed Stock composition during the pre- (before 1985) and post-moratorium (after 1990) periods (Richards and Rago, 1999) suggested that contributions varied widely across both space and time (Berggren and Lieberman, 1978; Fabrizio, 1987), with evidence that by the early 1990s that the Hudson population contributed more than the Chesapeake Bay (Wirgin et al., 1993) to mid-Atlantic and southern New England regions. Earlier management and scientific assumptions long held that fish from the Chesapeake Bay dominated coastal fisheries. Even recently, in the coastal waters of Massachusetts, stock composition was dominated by Chesapeake Bay-origin fish (55–67%), with fewer fish from the Delaware (14–20%) and Hudson (12–18%) systems (Kneebone et al., 2014). Further south, in Montauk, NY, evidence from microsatellite DNA mixture analysis revealed that stocks were comprised primarily of Chesapeake-Delaware fish (78-86%), with minimal contributions from both the Hudson River (8.5–12%), and the Roanoke River (5.5–12%) (Hasegawa et al., 2022). However, findings from this study suggest that the northern areas like southern Maine are dominated by fish primarily from the Hudson River, indicating that more southern spawning populations (e.g., Chesapeake Bay) may not migrate as far north as Hudson River fish. These differences highlight the importance of preserving all contributing spawning populations, as changes in the productivity of any single region can directly alter the composition and resilience of the mixed-stock fishery.

In interpreting present-day stock contributions in Maine, it is also important to consider historical stocking practices. From 1982 to 1989, Maine DMR stocked more than 187,000 Hudson River–origin striped bass into the Kennebec River, which successfully reestablished local spawning activity by the late 1980s (Maine Department of Marine Resources, 2020). Although wild YOY continued to be detected intermittently through the 1990s, recruitment has since become highly variable, and no recent evidence indicates persistent, self-sustaining reproduction at levels comparable to major Mid-Atlantic systems (Rulifson and Laney, 1999). As a result, contemporary detections of Hudson-origin fish in Maine likely reflect natural coastal migration rather than ongoing local production, but the legacy of stocking remains relevant when comparing historical and modern stock compositions. Consistent with this interpretation, the detection histories of our tagged individuals do not align with the geographic location, seasonal timing, or duration of residency expected for Kennebec-origin spawners. Instead, their spring movements, coastal transit patterns, and presence in known Mid-Atlantic spawning regions correspond closely with established Hudson River migration phenology, strongly suggesting that these fish are participants in the Mid-Atlantic spawning migration rather than remnants of historic Kennebec stocking.

Importantly, the contrasts in stock compositions between historical (pre- and post-moratorium) studies and present-day patterns illustrate how spawning population contributions shift with both population recovery and regional context, providing critical insights for interpreting current patterns and anticipating future changes under ongoing management and environmental pressures (Pan et al., 2023; ASMFC, 2024). This not only emphasizes the ecological importance of northern estuaries as critical habitats for migratory populations but also highlights the management need to account for regional variability in stock contributions when evaluating harvest strategies and long-term sustainability. Stock composition in migratory populations are not static; rather, the relative contributions of each spawning population shifts through time and region, highlighting the need for continual updates to stock-specific information. Such changes may also reflect underlying differences in spawning population productivity or health, emphasizing the importance of monitoring how each population contributes to the mixed stock coastal fisheries.

4.2. Fine scale estuary use and residency patterns

Patterns of fine-scale estuarine use in the Saco River highlight the importance of both coastal and riverine habitats as dynamic components of striped bass migratory behavior. Residency indices and random forest modeling revealed significant differences in habitat use throughout the system. River sites supported earlier-seasonal peaks in presence, followed by later shifts to coastal areas, suggesting a flexible strategy in which striped bass exploit brackish and low-salinity regions as a temporary, and assumed, foraging habitat before transitioning to marine environments as seasonal conditions and ecological needs change (Ferry and Mather, 2012; Pan et al., 2023). This pattern was consistently observed in 2023 and 2024, aligning with previous work demonstrating that striped bass exhibit considerable behavioral flexibility, adjusting habitat use over time (Coutant and Benson, 1990; Murphy et al., 2022). In 2025, data was analyzed up until August, prior to the typical September–October coastal migration period so it was not possible to test for this trend. This habitat progression likely reflects known environmental preferences, as striped bass distribution within estuaries is often structured by temperature, bathymetry, and prey availability (Coutant and Benson, 1990; Able and Grothues, 2007; Wingate and Secor, 2007; Ng et al., 2007). In many systems, striped bass show a greater affinity for riverine and nearshore habitats where thermal conditions are favorable and prey such as forage fish and invertebrates are abundant (Nelson et al., 2003; Walter and Austin, 2003; Murphy et al., 2022). This seasonal progression culminates in the onset of fall migration (colloquially known by fishers as the “fall run”), when a clear shift from riverine to coastal habitat use was observed, suggesting that striped bass treat the Saco River Estuary's coastal corridor as a migratory highway while using the river system primarily as a seasonal feeding ground—a strategy also documented in other Saco River species such as Atlantic sturgeon (Novak et al., 2017). Notably, no significant differences in temporal estuarine habitat use were detected between Hudson- and Delaware-origin fish, indicating that spawning population identity was less important than regional habitat type in shaping estuary use. This pattern aligns with previous evidence that striped bass from multiple

spawning populations intermingle and opportunistically exploit non-natal estuaries rather than through stock-based habitat partitioning (Boreman and Lewis, 1987; Fabrizio, 1987; Rulifson et al., 2008; Pautzke et al., 2010; Kneebone et al., 2014). More globally, shared habitat usage among multiple fish stocks is a relatively common phenomenon (Fujiwara et al., 2011; Kerr et al., 2017), as migratory species like bluefin tuna (*Thunnus thynnus*) and yellowfin tuna (*Thunnus albacares*; ICCAT, 2014; Minte-Vera et al., 2024), Atlantic cod (*Gadus morhua*; Knutsen et al., 2018; Schade et al., 2022), Atlantic herring (*Clupea harengus*; Bekkevold et al., 2011), and hake (*Merluccius sp.;* Wilhelm et al., 2015) often converge in productive foraging or overwintering areas driven by similar environmental cues and resource availability.

Findings from this study contribute to a growing body of evidence that striped bass frequently utilize non-natal estuaries along the U.S. Atlantic coast, both as destinations during coastal migrations and as habitats briefly occupied while moving between systems (Able and Grothues, 2007; Ng et al., 2007; Grothues et al., 2009; Pautzke et al., 2010; Hollema et al., 2017). Prior studies have described a range of estuarine behaviors, including individuals that establish seasonal "home ranges," those that exhibit short-term exploratory visits, and others that remain highly mobile between systems (Grothues et al., 2009; Pautzke et al., 2010; Hollema et al., 2017). This is illustrated by the high variability in Saco River estuarine residence time (37 days ± 59 days) with 26 fish detected for five days or fewer, whereas nine fish exhibited prolonged estuarine use, being detected for more than 100 days. This is further supported by cluster analysis supporting 2 groups, indicating the existence of long and short term non-natal residents. Exploration of cluster residency metrics in relation to size class revealed pronounced differences in estuarine use, with smaller individuals exhibiting substantially greater riverine residence and longer detection periods within the Saco River Estuary compared to larger fish. Additionally, although overall RI did not differ between size classes, smaller individuals (<600 mm FL) exhibited disproportionately higher riverine residency relative to coastal habitats, whereas larger individuals showed a weaker contrast between habitat types. This pattern suggests that riverine habitats within non-natal estuaries may function as particularly important foraging or refuge areas for smaller, likely immature fish, consistent with size-based tradeoffs in predation risk, energetic demand, and habitat selection, while larger individuals appear less constrained and more evenly distributed across riverine and coastal habitats. Together, these results indicate that observed behavioral groups may reflect not only flexible movement strategies but also size -related habitat specialization.

Additionally, the observed short- and long-term patterns of non-natal estuarine use across both spawning populations may reflect underlying behavioral plasticity and provide evidence for the presence of coastal migratory contingents, first defined in striped bass as groups of fish which engage in a distinct pattern of seasonal migration not shared by other fish (Clark, 1968). Contingent structure in striped bass is well established, particularly in the Hudson River system, where Clark (1968) first described three distinct migratory groups: the Hudson River estuary contingent, the western Long Island Sound contingent, and the Atlantic coastal contingent. Later work has refined these categories into groupings such as upper- and lower-estuary residents, coastal migrants (Gahagan et al., 2015) or, through otolith chemistry, into resident, mesohaline, and coastal contingents (Secor et al., 1995). Previous work in the Great Bay Estuary, NJ by Able and Grothues (2007), identified behavioral types (resident, seasonal inlet, seasonal estuary, and seasonal river) without explicitly using the term "contingents," while Grothues et al. (2009) suggested that striped bass in Saco River Estuary, ME and Great Bay Estuary, NJ were likely migratory contingents originating elsewhere. Given that the present study examines the same Saco River Estuary system, the patterns observed here are consistent with, and likely reflect, the presence of such migratory contingents. Moreover, the high rates (50%) of individual returns across years indicate that these behaviors are not isolated events but are repeated annually, consistent with other studies documenting strong site fidelity and repeated habitat use across seasons (Kneebone et al., 2014). The variability in habitat usage time provides supporting evidence of migratory contingents within a non-natal estuary in the Gulf of Maine, supporting the idea that northern systems like the Saco River Estuary's function as seasonal adult habitats for migratory striped bass.

4.3. Broad-scale stock specific migratory variability

Although striped bass migration and within-stock contingent variability have been well documented (Clark, 1968; Secor et al., 1995; Secor, 1999; Gahagan et al., 2015), comparatively few studies have examined how migratory behaviors differ among spawning populations across the U.S. Atlantic coast. The present analysis extends this framework by identifying, spawning population-specific connectivity patterns between Hudson River and Delaware Bay fish. While both spawning populations occupied broadly similar spatial patterns of connectivity (EC), movement bottlenecks (BC), and residency (node weight), their overall movement networks were largely distinct. Both comparisons of single and combination networks resulted in markedly low network similarity index (8%) and shared edges (17%). It is important to note that these comparisons reflect aggregate movement pathways and do not incorporate temporal structure; thus, an edge may be shared if used by one population during northward migration and by another during southward migration. As such, seasonal differences in migration timing and geographic distribution are not explicitly resolved here, and network structure would likely differ if partitioned into northward and southward migratory periods. Furthermore, sensitivity analysis indicated that estimates of network similarity were sensitive to spawning population assignment and sample composition. The similarity index from the full inferred-assignment analysis (8%) fell below the interval from direct assignment, indicating that the lower similarity observed in the primary analysis was unlikely to be explained solely by unequal sample sizes. Rather, the difference suggests that the inclusion of indirectly assigned individuals influenced estimates of network similarity, highlighting the importance of assignment uncertainty when interpreting population-specific movement patterns. Given the small number of directly assigned Delaware Bay individuals, however, these results should be interpreted cautiously and are best viewed as evidence of sensitivity rather than definitive differences in migratory network structure. Despite this, the minimal overlap present (8-20% similarity) in the multi-year networks indicate that Hudson and Delaware striped bass largely maintain separate overall migratory pathways and habitat connections, even while exploiting some common habitats.

Moreover, while both spawning populations exhibited broadly similar spatial patterns of connectivity and shared key northern foraging habitats (e.g., Saco River Estuary, Kennebunkport, Narragansett Bay), differences in network structure were evident in the relative importance of specific regions. In particular, EC indicated that New England habitats functioned as more influential connectivity hubs for Hudson River fish, whereas mid-Atlantic regions, particularly in New York and New Jersey, played a greater role in maintaining connectivity for Delaware Bay fish. These findings suggest that, although movement corridors and high-use areas overlap substantially between populations, the underlying structure of connectivity differs in how regions contribute to overall network organization. This pattern is consistent with previous studies indicating that northern migratory fish undertake extended foraging migrations and exhibit strong use of northern estuarine habitats (Pautzke et al., 2010; Kneebone et al., 2014; Hollema et al., 2017). At the same time, the greater influence of mid-Atlantic hubs for Delaware-origin fish suggests continued reliance on southern portions of the range, even as individuals utilize northern habitats, perhaps driven by more thermally stable migratory loops optimized for energy conservation and consistent prey access (Bernatchez and Dodson, 1987; Roff, 1991; Walter et al., 2003; Able et al., 2018). Together, these results indicate that

spawning population identity influences not only spawning location but also the relative importance of regions within broader migratory networks. The strong use of northern estuaries by both populations supports the hypothesis that these systems function as important seasonal foraging habitats for mixed-origin stocks (Ng et al., 2007; Pautzke et al., 2010; Hollema et al., 2017), while differences in network structure may reflect variation in migration extent, habitat use strategies, and environmental preferences across populations.

4.4. Limitations

Several methodological considerations should be acknowledged when interpreting these results. Within the Saco River Estuary, Saco River and Bay receiver deployment schedules varied seasonally, with most receivers removed during winter months due to ice and redeployed in spring, which may have reduced detection probability during periods of southward migration and limited the ability to fully resolve seasonal movement patterns. Paired with deployment, receiver spacing, array configuration, and the use of multiple transmitter types and power outputs (e.g., V13, V13AP, V16) may have affected the likelihood of detecting fish movements, particularly in areas with lower receiver density around the coast where inter-receiver distances exceeded effective detection ranges. Detection probability may also have varied over shorter temporal and environmental scales. Range-testing conducted within the Saco River Estuary indicated that detection efficiency was influenced by tidal stage, receiver orientation, and transmitter type, with differences in detection performance among tag models and environmental conditions. These results indicate that individual detections were not equally likely across all locations and times. Consequently, periods of reduced detections may reflect reduced detection efficiency rather than true changes in fish presence, potentially leading to underestimation of residency duration or habitat use in areas or periods with lower detection efficiency. This limitation is particularly relevant when interpreting differences in habitat use among spawning populations, as differences in transmitter type or the environmental conditions experienced by fish could contribute to variation in observed detections. Variable detection probability may also influence the observed structure of the coastal movement networks. Regions with higher receiver density or more favorable detection conditions may have been more likely to capture movements, whereas movements through areas with lower receiver density or reduced detection efficiency may have been underrepresented. Thus, the network analyses represent observed movement connectivity rather than a complete representation of all movements undertaken by tagged fish. Although detection probability was not explicitly incorporated into subsequent analyses, the use of detections accumulated over multiple years and across the ACT and AWSC coastal receiver network provides a broad representation of movement pathways. Future studies incorporating spatially and temporally explicit detection-probability models could further distinguish true differences in habitat use and connectivity from variation attributable to imperfect detection.

Importantly, we inferred spawning population origin from detections during spawning periods, consistent with prior approaches (Kneebone et al., 2014), on the basis that migratory striped bass are rarely present in these systems outside of spawning activity. Meaning that an observation (detection) of fish in a spawning region does not directly confirm that spawning activity occurred. However, our population assignments represent the best available estimates. Individuals in this study were tagged across a range of life stages, and as a result, not all were of spawning age, and some may have skipped spawning in a given year. We broadened our assignment approach beyond strict detections at spawning sites to incorporate movement patterns, seasonal timing, and spatial behaviors consistent with known spawning population characteristics. This method allowed us to classify individuals that were not directly observed in spawning habitats but whose movement trajectories strongly suggested spawning population membership. From a management perspective, this means that while our approach provides an ecologically grounded estimate of spawning population contributions, the assignments should be interpreted as estimates rather than definitive classifications. The possibility of misclassification cannot be excluded, particularly for younger fish or those exhibiting atypical migratory behaviors. Future studies would benefit from integrating genetic assignments or genomic stock-identification tools to validate telemetry-based classifications and reduce uncertainty in spawning population origin. Nonetheless, the convergence of movement-based criteria across multiple individuals supports the reliability of our estimates, which remain informative for identifying broad-scale patterns of population mixing and coastal habitat use. In addition, sex and age are potential co-variates that should be considered in future research as potential influencers of migratory behavior.

4.5. Management implications

While stock estimates carry some inherent uncertainty, the results of this study provide several important insights for fisheries management. Current striped bass management under the Atlantic States Marine Fisheries Commission primarily relies on coastwide benchmarks of fishing mortality, spawning stock biomass, and recruitment indices such as young-of-year surveys to set harvest regulations. Recent management measures, such as Addendum III, which implemented a recreational 28–31-inch slot limit, were designed to reduce fishing mortality and protect spawning potential. Despite this, ongoing concerns about weak year classes and low likelihood of recovering the fishery by 2029 have prompted discussions of further adjustments to the fishery. These assessments are complicated by strong year-class variability, poor predictive power of young-of-year indices, and challenges in linking local abundance with coastwide population trends. Management actions should prioritize protecting shared foraging habitats and incorporating mixed-stock dynamics into assessment models to ensure that exploitation rates and rebuilding targets reflect the distinct contributions and vulnerabilities of each spawning population. Our findings add value to these efforts by demonstrating that stock compositions in northern systems like the Saco River Estuary are different from earlier management and scientific assumptions of a Chesapeake Bay dominated coastal fishery.

Management of striped bass in freshwater and estuarine systems already varies substantially among states, reflecting the recognized importance of spawning population and size-structured vulnerability. In New York, striped bass in northern sections of Hudson River are managed under a distinct tidal freshwater regulation, including a reduced slot size (23–28 in) and a seasonal harvest window (April 1–November 30), explicitly designed to protect spawning fish and regulate freshwater exploitation. Similarly, New Jersey applies specific regulations to the Delaware River and its tributaries, including seasonal closures during peak spawning (April–May) and a standardized coastal slot size (28–31 in), while also requiring the use of non-offset circle hooks when fishing with bait to reduce post-release mortality in all waters under ASMFC guidance. Similar hook requirements have also been adopted in Maine, including the Kennebec and Saco Rivers, further reflecting a coast-wide management emphasis on minimizing release mortality in freshwater and estuarine striped bass fisheries. These measures prove that existing management framework (which already exhibits some degree of spawning population specific management) could be further refined through improved understanding of mixed-stock dynamics.

In this way, network-based approaches that track spawning populations can complement existing age-structured models and help managers design more spatially nuanced strategies that better address population mixing and variable stock statistics. Furthermore, the implications of this work extend beyond striped bass management to other mixed-stock fisheries where overlapping distributions obscure spawning group-specific dynamics. In such systems, spatially explicit approaches

that integrate telemetry, genetic, or chemical tagging data can help disentangle population structure and identify where and when stocks co-occur. Recognizing and quantifying these interactions is critical for developing management frameworks that move beyond uniform coast-wide quotas toward stock-informed harvest strategies. Ultimately, incorporating mixed-stock dynamics into assessment and management can improve sustainability by ensuring that more vulnerable or less productive spawning groups are not disproportionately impacted by broad-scale regulations.

CRediT authorship contribution statement

Benjamin P. Gowell: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alexa Cacacie:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Jessica B. Maguire:** Writing – review & editing, Methodology. **Ashley M. Nicoll:** Writing – review & editing, Methodology. **Michael G. Frisk:** Writing – review & editing, Methodology. **Keith J. Dunton:** Writing – review & editing, Methodology. **Craig Tennenhouse:** Writing – review & editing, Methodology, Conceptualization. **Jason Doll:** Writing – review & editing, Methodology, Conceptualization. **John A. Mohan:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **William Kochtitzky:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition. **Michelle Caputo:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Funding acquisition.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2026.110225.

Data availability

Acoustic telemetry data used in this study were collected as part of a collaborative receiver network and are subject to data-sharing agreements among participating institutions. Data supporting the findings of this study are available from the corresponding author upon reasonable request, pending approval from data owners.

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