

Tracking animal movements via collaborative acoustic telemetry  
networks: multiscale habitat use, phenology, and management insights

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Funding Information: This project was funded by the NOAA NMFS Chesapeake Bay Office award #NA21NMF4570525. Furey was also supported by the Class of 1937 Professorship in Marine Biology via the University of New Hampshire's School of Marine Science and Ocean Engineering. Funding for tags and the SERC acoustic receiver array was provided by Aramco Services Company (dusky shark, smooth dogfish), the Curtis and Edith Munson Foundation (cownose ray), the NOAA NMFS Chesapeake Bay Office award #NA18NMF4570255 (striped bass), and the Smithsonian Institution's Office of the Under Secretary for Science (acoustic receiver array, alewife, blue catfish, common carp, cownose ray, horseshoe crab).

## Abstract

Estuaries support diverse fish and invertebrate communities, including resident species that rely on estuarine habitats year-round and transient migratory species. The unique movement patterns of these animals connect habitats within and far beyond the estuary and are integrally linked to fisheries management objectives. With a focus on Chesapeake Bay, this study leveraged data from collaborative acoustic telemetry networks in the northwest Atlantic to assess habitat use and phenology of movements for seven species of fish (cownose rays, dusky sharks, smooth dogfish, alewife, striped bass, common carp, and blue catfish) and one invertebrate (horseshoe crabs). A total of 288 acoustically tagged individuals were detected >3.2 million times (6,743 to 2,095,717 detections per species) on receivers across ~20.5 degrees of latitude spanning the North American Atlantic seaboard from Florida, USA to New Brunswick, Canada. Common metrics of movement and phenology grouped these species as resident (common carp, blue catfish, horseshoe crabs), primarily resident in estuaries (juvenile striped bass), and coastal migrant (cownose rays, dusky sharks, smooth dogfish, alewife); maximum distance traveled varied by three orders of magnitude among these species. Further analysis of phenology for coastal migrants elucidated the timing and duration of these species' use of Chesapeake Bay. Collectively, movements linked habitats within Chesapeake Bay and connected the estuary to coastal ecosystems both to the north (e.g., alewife) and south (e.g., cownose rays), creating networks of fisheries management jurisdictions that varied in complexity and identified opportunities for enhancement to current management or co-management of some species. Our results elucidate the importance of estuaries to species with diverse movement behaviors, identify scales and pathways of habitat connectivity via animal movements, and highlight the utility of collaborative acoustic telemetry networks for quantifying movements relevant to both ecological research and fisheries management.

47

48 [Keywords](#)

49 acoustic telemetry, movement ecology, migration, habitat use, fisheries management,

50 connectivity

## 1. Introduction

Movements of animals, including fish, are fundamental to shaping ecosystem structure and function, and the causes and consequences of movement are profoundly diverse among species (Nathan et al. 2008; Cooke et al. 2022). An individual fish may move to seek out reproductive opportunities, find food, avoid predation, or remain within optimal habitat conditions (Chapman et al. 2015; Abrahms et al. 2021). The spatiotemporal scales of these movements vary among species and populations, ranging from residency and strong site fidelity to transoceanic migrations, which in turn influence ecological and biological phenomena at those scales (Papastamatiou et al. 2010; Block et al. 2011). Large-scale migrations are particularly influential in the transfer of energy among disparate habitats, such as the pulses of marine-derived nutrients to riverine spawning grounds transported by anadromous fishes (MacAvoy et al. 2000; Post and Walters 2009; Twining et al. 2017). For species that do not undergo migrations, especially those that are highly resident to a specific habitat or region, it is equally important to examine their space use patterns as they are particularly susceptible to local degradation and pressure (Clavel et al. 2011). Monitoring movements is also important for detecting shifts in phenology and habitat use due to climatic changes, both for species that are migratory (Crear et al. 2020; Shuert et al. 2022) and relatively resident (Williams et al. 2017). Given the immense diversity of movement ecology among species, and the equally diverse implications of those movements, multispecies assessments allow for uniquely informative ecological and management-related inferences across spatiotemporal scales (Friess et al. 2021).

For aquatic animals, acoustic telemetry is a common tool used to track underwater movements (Hussey et al. 2015; Matley et al. 2022). Acoustic tags, either implanted within or attached to an animal, emit a coded signal that is detected and logged by receivers. Multiple receivers are deployed in ‘arrays’ that monitor movement between locations over time. A major

strength of this method is the ability to track individuals, and determine the timing of their movements, which is key for quantifying phenology of migrations and shifts in habitat use (e.g., Massie et al. 2022). However, acoustic telemetry studies are often limited to relatively small spatial scales and low coverage of receivers, given the high cost and intensive labor associated with the deployment and maintenance of large-scale arrays. In response to these limitations, regional and continental-scale acoustic telemetry networks have developed and expanded in recent decades, which has revolutionized the field of aquatic animal tracking (Cooke et al. 2011; Abecasis et al. 2018; Krueger et al. 2018; Bangley et al. 2020b). These collaborative networks of researchers have emerged globally, including the northwest Atlantic and Gulf of Mexico (OTN, ACT, FACT, iTAG, Cooke et al. 2011; Boucek and Morley 2019; Bangley et al. 2020b; Young et al. 2020), the eastern Pacific (NEP, PIRAT, PATH, MIGRAMAR, Nalesso et al. 2019), Australia (IMOS, Taylor et al. 2017), the Laurentian Great Lakes (GLATOS, Krueger et al. 2018), South Africa (ATAP, Murray et al. 2022), and western Europe (ETN, Abecasis et al. 2018). By serving as platforms for data sharing and management, studies leveraging these networks have answered previously enigmatic questions in animal movement ecology, such as defining large-scale migration pathways and timing (Griffin et al. 2018; Ogburn et al. 2018; Bangley et al. 2020a). These networks can also increase the number of receivers in a specific area of interest (e.g., within an estuary), thus providing additional spatial coverage for species with moderate degrees of movement.

While acoustic telemetry has proven powerful for elucidating aspects of the ecology and biology of aquatic species, its value is also increasingly recognized as a management and conservation tool (Crossin et al. 2017; Ogburn et al. 2017a; Lowerre-Barbieri et al. 2019). Movement ecology is inherently linked to aquatic species management; for example, telemetry

data can delineate critical habitats to prioritize for conservation (Alós et al. 2011; Lea et al. 2016), document the responses of individuals and populations to environmental change (Ubeda et al. 2009), and estimate natural and fishery mortality across space and time (Lees et al. 2021). Acoustic telemetry can also inform delineation of management units and boundaries by assessing behaviors relevant to stock structure, including home range size, residency, migratory pathways, and individual variability in those metrics (e.g., Hussey et al. 2017). Particularly for highly migratory species, large collaborative telemetry arrays are critical to examining the nature and degree of movements between jurisdictions, which are integral to the development of cooperative management strategies (Huveneers et al. 2021; Lédée et al. 2021).

Chesapeake Bay, the largest estuary in the United States, has a long history of acoustic telemetry studies (e.g., Wolcott and Hines 1990), a high density of telemetry users who contribute to collaborative networks, and long-term monitoring arrays such as those coordinated by the National Oceanic and Atmospheric Administration (NOAA) Chesapeake Bay Office (NCBO 2022). Commercial and recreational fisheries are of high socioeconomic value to the Chesapeake Bay region, with commercial seafood industries in Maryland and Virginia contributing 1.61 billion US dollars in income and 45,795 jobs to the region's economy in 2020 (NMFS 2022). The estuary and coastal waters are managed by multiple state, cooperative, and federal agencies, including the state of Maryland, the commonwealth of Virginia, the Potomac River Fisheries Commission, and the National Marine Fisheries Service in the US Exclusive Economic Zone (EEZ). Balancing the needs of multiple stakeholders and management agencies is inherently challenging, but successful collaboration in fishery management among jurisdictions has occurred in Chesapeake Bay, especially for migratory species such as striped bass (Richards and Rago 1999) and blue crabs (Aguilar et al. 2008).

To assess the use of estuarine and adjacent coastal waters by fishes and invertebrates in the Chesapeake Bay region, and how some of those species link Chesapeake Bay to the rest of the northwest Atlantic, passive acoustic telemetry data were opportunistically compiled from studies of seven species of fish and one invertebrate: Cownose rays (*Rhinoptera bonasus*), dusky sharks (*Carcharhinus obscurus*), smooth dogfish (*Mustelus canis*), alewife (*Alosa pseudoharengus*), striped bass (*Morone saxatilis*), horseshoe crabs (*Limulus polyphemus*), common carp (*Cyprinus carpio*), and blue catfish (*Ictalurus furcatus*). These species represent a model assemblage for the diverse life histories of fish and invertebrates that use temperate estuaries, ranging from highly migratory to resident (Stuart and Jones 2006; Watson et al. 2016; Tuckey et al. 2017; Dell’Apa et al. 2018; Ogburn et al. 2018; Bangley et al. 2020a; Secor et al. 2020; Hare et al. 2021). Fishery management also differs among these species; Cownose rays are not currently managed, dusky sharks and smooth dogfish are managed federally in NOAA’s Highly Migratory Species group, striped bass, alewife and horseshoe crabs are managed by the Atlantic States Marine Fisheries Commission (ASMFC, a cooperative unit), and common carp and blue catfish are managed by individual states. Using data obtained via collaborative acoustic telemetry networks, the objectives of this study were to (1) assess these species’ habitat use patterns and phenology of movements with a focus on Chesapeake Bay, and (2) determine how these movements connect regions within Chesapeake Bay and fishery management jurisdictions along the Atlantic coast relative to current management strategies.

## 2. Materials and Methods

### 2.1 Study Area

This study focused on species occurring in the Chesapeake Bay and the adjacent continental shelf located in the temperate Mid-Atlantic region of the US East coast (Figure 1).

The estuary receives freshwater from a ~168,000 km<sup>2</sup> watershed, largely via the Susquehanna River but also through multiple other significant tributaries (Goetz et al. 2004). One primary inlet allows marine water to enter the low estuary, connecting the system to the coastal waters of Virginia. The oligohaline upper estuary is connected to a smaller adjacent estuary, Delaware Bay, through the continuously open Chesapeake and Delaware Canal.

## 2.2 Acoustic Telemetry Data Collection

All species were tagged with Innovasea 69-kHz transmitters (Table 1). Tagging occurred exclusively in Chesapeake Bay for striped bass, alewife, horseshoe crabs, and common carp (Figure 1). Cownose rays were primarily tagged in Chesapeake Bay, with the exception of one individual tagged approximately 150 km south in Pamlico Sound, North Carolina. Cownose rays were tagged with V13 (n = 62; 13-mm diameter, 31.5-mm length, est. battery life 653 days), V16 (n = 19; 16-mm diameter, 68-mm length, est. battery life 2435 days), and V9 tags (n = 1; 9-mm diameter, 27.5-mm length, est. battery life 802 days). Dusky sharks and smooth dogfish were captured and tagged in coastal waters north of the estuary, with the exception of one smooth dogfish that was tagged ~260 km south of Chesapeake Bay in Onslow Bay, NC (Figure 1). Twenty-four dusky sharks were tagged with V16 tags (est. battery life either 1825 days or 2435 days) and five were tagged with V13 tags, while all 21 smooth dogfish were tagged with V13 tags. All striped bass were tagged with V9 tags, and all alewife were tagged with V7 tags (7-mm diameter, 21.5-mm length, est. battery life 388 days). Common carp were tagged with V9 (n = 8) and V13 tags (n = 7), and all blue catfish were tagged with V13 tags. Horseshoe crabs were tagged with V9 tags within three distinct time periods; six individuals were tagged in 2016, five in 2021, and five in 2022. Additional details regarding tagged individuals and detections for each species are included in Table 1. Animals in this study were handled under Smithsonian Environmental Research Center (SERC) Animal Care and Use Committee proposal numbers:



SERC 06-24-13 (blue catfish and common carp), SERC 03-25-14 (cownose rays), SERC 12-02-16 (dusky sharks and smooth dogfish), SERC-2017-0512 (cownose rays, dusky sharks, smooth dogfish, SERC-2018-0426 (striped bass), and SERC-2020-0131 (alewife).

Detections of each species were retrieved from the Atlantic Cooperative Telemetry Network (ACT) database, ACT\_MATOS (<https://matos.asascience.com/>). This network leverages the deployment of acoustic receivers from North Carolina to Maine and those of the adjacent FACT Network and Ocean Tracking Network (OTN), with researchers uploading detections that are collated and downloaded in a standard format (Bangley et al. 2020b). Receivers that detected the tagged individuals in this study ranged from south Florida, USA to New Brunswick, Canada (Figures 1, 2). During the study period (2013 to 2023), Chesapeake Bay contained multiple receiver arrays, including several in critical locations related to the species of interest in this study. An array of 11 to 14 acoustic receivers, depending on the year, was deployed in the Rhode River, MD from 2015 to 2022 by SERC, capturing detections of striped bass, horseshoe crabs, and common carp which were tagged within this array. For alewife specifically, an array of eight receivers was deployed in the Choptank River, MD from February to June in 2022 and 2023. Receiver arrays were deployed in each of the rivers in which blue catfish were tagged, with individuals detected on 11 receivers in the Potomac River (2015 to 2017), 11 in the Patuxent River, MD (2013 to 2016), and 18 in the Marshyhope Creek and the Nanticoke River, MD (2014 to 2016). Of particular importance for understanding movements in Chesapeake Bay was the Chesapeake Bay acoustic telemetry “backbone” array, which consists of three lines of receivers across the mainstem of the estuary at the Chesapeake Bay Bridge, across the mid-bay near the Patuxent River, and across the estuary mouth (deployed from 2021 to present).

Detections retrieved from the ACT database for each tagged individual were combined with detection data that had not been uploaded to any regional databases (i.e., solicited directly from researchers with known arrays during the times of at-large tags who did not submit data to the ACT database), necessitating quality control to ensure compatibility. Data were checked for duplicate detections, station names and coordinates were checked and edited if necessary to eliminate any inconsistencies across deployments (e.g., obvious errors in latitude or longitude or minor changes to station names), and detections were mapped spatially to identify and remove any that were outside the realistic range of each species. Final filtered datasets were visualized to qualitatively identify spatiotemporal trends in space use by plotting detections of each species by date and latitude.

### 2.3 Common Movement Metrics

Although there are a variety of potential metrics that can be used to explore aspects of movement, phenology, habitat use, and connectivity with acoustic telemetry data (Kraft et al. 2023), this study required those that would be comparable among diverse species. Maximum distance traveled and a residency index were chosen due to their interpretability and validity for comparison among disparate species. To estimate the maximum distance traveled during the study for every tagged individual of each species, we iteratively calculated the distance between the tagging location and all receivers the individual was detected on using the Haversine method (R package ‘geosphere,’ Hijmans 2021). Maximum distance traveled was compared among species using a Kruskal-Wallis rank sum test and Pairwise Wilcoxon rank sum tests (with a false discovery rate p-value adjustment), given the non-normality and heteroscedasticity of the data.

A residency index (RI) was calculated for each species to examine space use among regions both within and outside the Chesapeake Bay. RI is a commonly used metric to summarize the duration of time a species spends in certain areas or habitats. Many equations

have been used to calculate RI, most often as a proportion of the number of days an animal was detected in a region divided by the number of days it was at liberty or the number of days the tag was active (Appert et al. 2023). However, the species monitored in the present study exhibited highly variable detection rates and tag lifespans, which could confound interpretations of RI. To account for this issue, the following RI equation was used:

$$RI = \frac{\text{Days present in region}}{\text{Total number of days detected}}$$

This RI represents the amount of time each individual spent in each region as a proportion of the total number of days they were detected anywhere, meaning differences in detection frequency among species is less influential on the RI value, but the metric is biased towards where receivers are placed. An RI was calculated for all individuals of each species within 12 regions (see inset Figure 4). Regions were delineated based on physicochemical and habitat regimes within Chesapeake Bay and the adjacent Delaware Bay and included larger regions north and south of these estuaries. The same equation was used to calculate RI for each species in each region across four seasons, winter (Dec-Feb), spring, (Mar-May), summer (Jun-Aug), and fall (Sep-Nov) to assess region-scale seasonality in space use. Seasonal RIs were calculated for male and female cownose rays and dusky sharks separately to assess sex-specificity in their habitat use patterns, considering known or suspected differences based on previous studies (e.g., Hoffmayer et al. 2014; Omori and Fisher 2017).

#### 2.4 Phenology of Coastal Migrations

We conducted further analyses for the coastal migratory species, including cownose rays, dusky sharks, smooth dogfish, and alewife, to assess the relative importance of Chesapeake Bay during their migrations. Dates of entry into and exit out of the Chesapeake Bay area were identified, including all receivers in the estuary and offshore near the mouth of the estuary

(region = Offshore Chesapeake, inset Figure 3). An “entry” represented the first detection of an individual within the Chesapeake Bay area after being detected elsewhere, while an “exit” represented the last detection of an individual within the Chesapeake Bay area before being detected elsewhere. This is a conservative approach to estimating entry and exit timing, given the requirement of a detection outside the area for the movement to be considered valid. However, absence from the Chesapeake Bay area was assumed for six individuals (one cownose ray, four dusky sharks, and one smooth dogfish) under specific circumstances: If an individual was detected in the Chesapeake Bay area, then not detected anywhere for at least four months, then detected in the area again, a dummy detection outside the estuary was added to the dataset to allow for the inclusion of the corresponding entry and exit dates. Sex specific entry and exit timing was calculated for cownose rays and dusky sharks.

## 2.5 Network Analyses

We employed network analyses to assess connectivity among habitats in the Chesapeake Bay and adjacent Delaware Bay, and to document movements among fishery management jurisdictions. Networks are well suited for acoustic telemetry data analysis because they consist of nodes connected by edges, which can intuitively represent movements (edges) between receivers (nodes; Dale and Fortin 2010, Finn et al. 2014, Whoriskey et al. 2019) and can be used to inform habitat connectivity, stock structure, and inter-jurisdictional fishery management (Lédée et al. 2021). For each species, we created two bidirectional (directed) weighted networks, one representing movements among regions within the Chesapeake Bay and adjacent Delaware Bay (hereby referred to as local networks), and another representing the relationships between each study species and the fishery management jurisdictions with which they interact (continental-scale networks). For local networks, regions within and near the Chesapeake Bay and adjacent Delaware Bay were retained, and some regions were partitioned further: “Rivers”

was separated into individual tributaries (see Figure 1 for river names and locations), and “Upper DE Bay” was separated into the Chesapeake and Delaware Canal and the Delaware River. For continental-scale networks, receiver stations were assigned the appropriate jurisdiction based on their location, using US state borders and the delineation of state vs. federally managed coastal waters (in the EEZ) based on the US Coastal Zone Management Act of 1972. For each network type, detections of each species were ordered by tag ID and datetime, and a to-from matrix was built to represent movements between and within regions or jurisdictions. Successive detections within the same region or jurisdiction were removed to eliminate self-loops in the resulting networks. Species-specific networks were weighted by the number of individuals detected in each node and edge. To describe the potential connectivity of habitats or management jurisdictions, the proportion of all nodes and edges used by each species within each network was calculated. Networks were created and visualized using the package ‘igraph’ (Csardi and Nepusz 2006) in R v. 4.4.0 (R Core Team 2024).

## 3. Results

### 3.1 Common Movement Metrics

The final dataset consisted of approximately 3.2 million detections (6,743 to 2,095,717 detections per species) across ten years (1 to 9 years of detection time per species), with a total of 288 individuals being detected between latitudes of 25 to 45 degrees N (Figure 2, Table 1). Maximum distance traveled from tagging locations varied by three orders of magnitude among species (Kruskal-Wallis  $H = 167.69$ ,  $df = 7$ ,  $p < 0.001$ ), ranging from a median of 1061 km for cownose rays to 2.4 km for horseshoe crabs (Figure 2 inset). Similarities emerged among some species, such as the two sharks (dusky sharks and smooth dogfish, pairwise Wilcoxon  $p = 0.10$ ), two of the finfish (striped bass and alewife,  $p = 0.13$ ), and the two most resident species

(common carp and horseshoe crabs,  $p = 0.89$ , Figure 2 inset). Paths between tagging locations and the farthest detection highlighted the extent to which migratory species linked the Chesapeake Bay to far-reaching habitats along the eastern seaboard, while resident species remained within the estuary throughout the study duration (Figure 2).

Qualitative observation of detections by latitude over time (Figure 3) and quantitative seasonal residency indices (Figure 4) identified species groupings based on habitat use patterns and migratory behaviors: Horseshoe crabs, common carp, and blue catfish were highly resident, juvenile striped bass were primarily resident in the estuary, and cownose rays, dusky sharks, smooth dogfish, and alewife were coastal migrants. Highly resident species were primarily detected in the region in which they were tagged (mean RI > 90% summed among seasons). Horseshoe crabs were exclusively detected in the Rhode River during the winter, but these detections only consisted of three individuals (Figures 3, 4). Two individuals were detected in the upper bay region in the spring (Mar, May), summer (Jun – Aug), and fall (Nov, mean seasonal RIs from 11% to 25%, Figure 4). Common carp were not detected in the winter and were exclusively present in the Rhode River in the spring and fall, with infrequent movement into the upper bay in the summer (mean RI 0.3%, Figure 4). Blue catfish were not detected outside the rivers in which they were tagged. Juvenile striped bass used the Rhode River (tagging location) year-round (seasonal mean RIs from 37% to 86%, Figure 4), but also exhibited some distinct seasonal shifts in habitat use. In the spring, use of oligohaline regions by juvenile striped bass increased, including increased residency in other Chesapeake Bay rivers (mean RI 21%) and a transit to the upper DE Bay via the Chesapeake and Delaware Canal by eight individuals (mean RI 22%, Figure 4). In the winter, use of the lower bay increased (mean RI 40%). The only exceptions to estuarine residency were two individuals that migrated northward to coastal New

York and southern New England waters, and one individual that was detected at the mouth of Delaware Bay (Figures 3, 4). Six of the eight juvenile striped bass that transited the Chesapeake and Delaware Canal into the upper DE Bay subsequently returned to Chesapeake Bay, but one individual remained in the upper DE Bay until its final detection (June 2021) and the other migrated northward (one of the two migrants).

Within the coastal migratory group, differences emerged among species in the directionality and timing of their migrations and their degree of use of the Chesapeake Bay area. Cownose rays migrated south of Chesapeake Bay starting in the fall (RI South of Chesapeake Bay in winter 100%), before returning in the spring and using all regions within the estuary during the summer (sum of mean RI for regions within estuary F = 93%, M = 78%, Figure 4). Some northward movement beyond Delaware Bay occurred in the summer, primarily for males (mean RI North of DE Bay F = 2.7%, two individuals; M = 8.4%, five individuals, Figure 4). The migrations of dusky sharks and smooth dogfish were similar, whereby they moved south of Chesapeake Bay in the winter and north in the summer (thus passing by the estuary twice per year), but the timing and spatial scale of their migrations differed. Dusky sharks were detected at lower latitudes in both winter and summer compared to smooth dogfish (Figure 3, Table 1). Furthermore, smooth dogfish used coastal waters offshore of Chesapeake Bay and the mouth of Delaware Bay in the winter and spring (sum of mean RIs 50% and 64%, respectively), while dusky sharks primarily remained south of Chesapeake Bay (mean RI in winter 100%; in spring F = 83%, M = 86%, Figure 4). Dusky sharks then moved into the Chesapeake Bay region in the fall (mean RI F = 43%, M = 30%), while smooth dogfish remained farther north (sum of mean RIs = 91%, Figure 4) before moving into the area in the winter. For alewife, we captured one full annual migration from the Chesapeake Bay to the Gulf of Maine (Figures 3, 4). Individuals

exited through the mouth of Chesapeake Bay in the spring (mean RI in Lower Bay 5%), were exclusively detected north of the region in the summer and fall, and re-entered the following spring (mean RI in Mouth of Chesapeake 3%, Figure 4).

### 3.2 Phenology of Coastal Migrations

Identifying entry and exit dates determined the timing of movements of migratory fishes in and out of Chesapeake Bay (including nearshore waters; Figure 5). On average, female and male cownose rays entered the Chesapeake Bay at similar times in the spring (mean  $\pm$  sd entry day of year  $F = 147.4 \pm 36.5$ ,  $M = 144.6 \pm 33.3$ ; late May), but females exited the area later than males in the fall (mean exit day of year  $F = 262.1 \pm 45.1$ ,  $M = 246.9 \pm 46.9$ ; mid and early September, respectively). Exit dates were bimodally distributed for males, with some leaving the area in early summer and others leaving in early fall, while females exhibited a single peak in early fall (Figure 5). Dusky sharks entered and exited the Chesapeake Bay area twice per year, once in the spring and once in the fall. Entry timing in the spring was similar between the sexes ( $F = 156.7 \pm 10.0$ ,  $M = 157.0$  [one individual]; early June), and both sexes exited the Chesapeake Bay area within the following two weeks ( $F = 161.2 \pm 12.1$ ,  $M = 169.0$  [one individual]). In the fall, entry occurred slightly earlier for females ( $298.0 \pm 18.6$ ; late October) than males ( $305.3 \pm 6.4$ ; early November), but both exited within the following week ( $F = 302.7 \pm 13.6$ ,  $M = 300.5 \pm 12.4$ , Figure 5). Smooth dogfish exhibited a similar seasonal pattern to dusky sharks, but they entered and exited earlier in the spring (entry =  $117.8 \pm 12.8$ , exit =  $118.7 \pm 11.8$ ; late April) and later in the fall (entry =  $319.4 \pm 11.8$ , exit =  $321.7 \pm 9.1$ ; mid-November, Figure 5). Seventeen alewife exited Chesapeake Bay in the spring of 2022 ( $102.1 \pm 7.5$ ; late March to late April) and five individuals re-entered the following spring of 2023 ( $55.8 \pm 15.6$ ; mid-February to late March; Figure 5).



### 3.3 Network Analyses

With regions (notably rivers) delineated further, local networks revealed movements among distinct habitats within Chesapeake Bay and the adjacent Delaware Bay (Figure 6, Table 2). Cownose rays had the most complex network with movements occurring between 13 regions (68% of possible nodes) connected by 74 paths (22% of possible edges, Table 2). They were detected in eight tidal rivers in Chesapeake Bay, all other regions in the estuary mainstem, mouth, and offshore, and in Delaware Bay (Figure 6). Dusky sharks and smooth dogfish exhibited similar local networks, which exemplified their limited use of habitats in Chesapeake Bay (Figure 6). Dusky sharks were only detected moving between the mouth and offshore regions of Chesapeake Bay (11% of possible nodes and 0.3% of possible edges), while smooth dogfish moved between those two regions and Delaware Bay (16% of possible nodes and 1% of possible edges, Table 2, Figure 6). Alewife were primarily detected in the Choptank River where they were tagged, but one individual moved in and out of Tuckahoe Creek (a tributary of the Choptank River, Figure 6). For alewife, connections only occurred between the Choptank River, lower Chesapeake Bay, and the mouth of the estuary (21% and 2% of possible nodes and edges, respectively, Table 2). Striped bass exhibited the second most complex local network, consisting of 9 regions (47% of possible nodes) connected by 28 paths (8% of possible edges, Table 2). They moved between five tidal rivers in Chesapeake Bay, with the most traveled route between the Rhode River (tagging location) and the upper Chesapeake Bay. This network also highlighted movements between the upper Chesapeake Bay and the Delaware River through the Chesapeake and Delaware Canal (Figure 6). Blue catfish were isolated to the individual rivers in which they were tagged, but those tagged in the Nanticoke River moved in and out of a tributary to that river, Marshyhope Creek (Figure 6). Their local networks therefore consisted of four regions (21% of possible nodes) connected by two paths (0.6% of possible edges, Table 2). Horseshoe

crabs and common carp local networks were nearly identical, with both species moving solely from the Rhode River (tagging location) to the upper Chesapeake Bay (11% of possible nodes, 0.3% of possible edges, Table 2). One common carp and two horseshoe crabs underwent this movement, but none of those individuals returned to the Rhode River (Figure 6).

Continental-scale networks identified if and how these species moved among fishery management jurisdictions (Figure 7, Table 2). Cownose rays exhibited the most connectivity among jurisdictions; individuals were detected in 11 different jurisdictions (73% of possible network nodes) and had 53 unique linkages between those jurisdictions (25% of possible network edges, Table 2). The most interconnected jurisdiction (greatest number of individuals moving in and out) was US EEZ waters, and the most important jurisdiction (used by the greatest number of individuals) was Virginia (Figure 7). Alewife, smooth dogfish, striped bass, and dusky sharks were each detected in 8 jurisdictions (53% of possible nodes), but the number of linkages between jurisdictions differed (18 (9%), 17 (8%), 16 (8%), and 14 (7%), respectively, Figure 7, Table 2), indicating different extents of connectivity. The US EEZ was the most interconnected and most important jurisdiction for dusky sharks and smooth dogfish. Maryland was the most important jurisdiction for striped bass and alewife, primarily because tagging occurred there, but the most interconnected was Maryland for alewife and New Jersey for striped bass. Common carp and horseshoe crabs were only detected in Maryland (7% of possible nodes), where they were tagged, and while Maryland was also the most important jurisdiction for blue catfish, one individual was detected moving into Delaware waters within the Nanticoke River (20% of possible nodes and 1% of possible edges, Figure 7, Table 2).

## 4. Discussion

Collaborative acoustic telemetry networks made it possible to describe patterns of habitat use, phenology, and connectivity for a diverse assemblage of eight species ranging from estuarine residents to coastal migrants, with scales of movement varying by three orders of magnitude and across ~20.5 degrees (~2,650 km) of latitude. Using metrics that were informative across species, we quantified gradients in the duration, timing, and use of estuarine habitats. Some species exclusively inhabited fresh and brackish regions in Chesapeake Bay and were highly resident (blue catfish, common carp, horseshoe crabs), some only used coastal waters at the estuary mouth for brief periods of time and were highly migratory (dusky sharks, smooth dogfish), and others moved within and among multiple habitats in the estuary ranging from moderately resident (striped bass) to highly migratory (cownose rays, alewife). These variable movement dynamics have broad implications for ecological and biological phenomena and inform how each species interacts with fishery management jurisdictions.

Network analysis quantified connectivity among fishery management jurisdictions ranging from single states (e.g., horseshoe crabs, common carp) to interjurisdictional movements among state, federal, and international waters (e.g., cownose rays, alewife), and generally aligned with current management strategies. For example, the common carp examined in this study were only detected within the state of Maryland and were not observed moving outside of the Rhode River and upper Chesapeake Bay. Common carp are managed by individual states, and our results suggest this is likely appropriate and sufficient given their relatively high residency. Alewife and striped bass are managed cooperatively by states via the Atlantic States Marine Fisheries Commission (ASMFC), and the complex networks produced from their detections offered insight into possible beneficial changes to current management schemes. Juvenile striped bass moved among five tidal rivers, estuary mainstem habitats, and a canal

within a single jurisdiction (Maryland), separated by a distance of approximately 200 km, suggesting that largely resident size classes still make substantial seasonal movements that should be considered in management. On a larger scale, one individual alewife crossed an international border by entering Atlantic Canada during its northward migration in August 2022 (further details in Ogburn et al. 2024). Currently, the US and Canada do not cooperatively manage alewife or other anadromous river herring, but our results support the consideration of binational discussions for collaborative management (Harrison et al. 2018; Hare et al. 2021). Cownose rays are not currently managed, however in 2017 the state of Maryland approved the development of a fishery management plan (Senate Bill 268). Jurisdictional network analysis of cownose rays suggests that cooperative management among multiple state and US federal agencies would be appropriate, given their high degree of interjurisdictional movement. The potential applications of acoustic telemetry data for fishery management are much greater than presented here (Table 3), but our results particularly emphasize the importance of large-scale collaborative networks when using telemetry data to improve and develop fishery management strategies.

Fisheries managers have historically relied upon data from traditional gears such as trawls, gillnets, longlines, and seines to collect information on species' distribution and abundance. Although foundational for fisheries management, these monitoring programs provide snapshots of populations at specific points in time and space. Acoustic telemetry is a strong complementary tool for assessing aquatic animal populations for management objectives (Table 3) given its ability to track individual variability in movements over time (up to 10 years for large species) and determine connectivity between habitats. For example, acoustic telemetry data were used in the 2017 benchmark stock assessment for Atlantic sturgeon (*Acipenser oxyrinchus*)

conducted by the ASMFC (ASMFC 2017). Acoustic telemetry data from various sources identified migratory pathways and phenology, delineated critical spawning habitats, enhanced the accuracy of survival estimates, and elucidated spatial differences in habitat use (e.g., Altenritter et al. 2017; Balazik et al. 2012; Breece et al. 2016; Hightower et al. 2015; Wippelhouser et al. 2017), serving as a model for implementing acoustic telemetry data as a complementary tool alongside traditional data sources. Our network analysis exemplifies how acoustic telemetry data from disparate studies across diverse species can be aggregated and opportunistically used for management-relevant questions.

In addition to highlighting the utility of acoustic telemetry data for assessing fishery management, the movements of these study species provided inferences into their biology and ecology. For highly migratory species (cownose rays, dusky sharks, smooth dogfish, and alewife), the observed within-estuary and continental-scale movements exemplified much of the diversity and scale of migratory behaviors of fishes along the US East Coast and delineated the extent to which they use the Chesapeake Bay area. Of the coastal migrants, cownose rays exhibited the greatest connectivity among tidal rivers and mainstem regions while in Chesapeake Bay. For about half of each year, they use estuarine habitats extensively for reproduction and foraging (Smith and Merriner 1985; Fisher et al. 2013), and our results indicate they move between coastal, mainstem, and multiple tidal river habitats during this period. The timing of their migrations to the estuary were sex-specific, which aligned with previously identified differences between males and females in their response to exogenous (sea surface temperature, photoperiod) and potentially endogenous (day of year) migration cues (Bangley et al. 2021). Some males exited Chesapeake Bay earlier and used a broader suite of habitats than females, which primarily resided in the low estuary and tidal rivers. Females therefore likely experienced

warmer temperatures in the estuary throughout the spring, summer, and fall, during which they pup, mate, and begin to develop the next embryo (Fisher et al. 2013). This pattern aligns with observations from satellite tagging (Omori and Fisher 2017) and acoustic telemetry (Bangley et al. 2021), suggesting that females prioritize warmer conditions for embryonic development while males exploit additional habitats and resources in the summer.

Dusky sharks and smooth dogfish exhibited similar migration pathways, using estuarine and coastal waters near Chesapeake Bay in the spring (traveling northward) and fall (traveling southward) with minimal use of habitat in Chesapeake Bay. This is the first description of the migratory behavior of smooth dogfish using acoustic telemetry and aligns with mark-recapture data and habitat suitability models (Kohler et al. 2014; Dell’Apa et al. 2018). Migrating dusky sharks moved farther south (Florida, USA) relative to observations in the first two years after tagging (South Carolina, USA) reported by Bangley et al. (2020a). One distinct difference emerged between these two sharks: smooth dogfish were present in the Chesapeake Bay area earlier in the spring and later in the fall compared to dusky sharks, aligning with smooth dogfish’s general association with lower water temperatures than dusky sharks (Dell’Apa et al. 2018; Bangley et al. 2020a).

Similarly, entry and exit timing of alewife aligned with known temperature-dependence of their migrations (Ogburn et al. 2017b, Legett et al. 2021). Alewife in Chesapeake Bay enter in the early spring (Feb – Mar) and exit approximately one month later (~April), remaining within a thermal window of 9 to 21°C (Legett et al. 2023). We observed very little movement among regions within Chesapeake Bay during the spawning period, other than the directed migration to and from their spawning river through the lower estuary. These migratory movements were captured primarily by the Chesapeake Bay “backbone” array, which is maintained in partnership

with local researchers and managers in the upper bay (Maryland Department of Natural Resources), mid-bay (University of Maryland Center for Environmental Sciences), and southern bay (Virginia Marine Resources Commission), and all data are shared through the ACT network. These backbone receivers provide an opportunity for repeated tag deployments in alewife (or other migratory species) to monitor potential changes to migratory pathways and phenology due to anthropogenic effects such as increasing temperatures and habitat degradation, as have been observed for alewife in the southern extent of their range (North Carolina, USA; Lombardo et al. 2020).

In addition to describing large-scale migrations, our results elucidated within- and among-estuary movements of resident species, including juvenile striped bass. Individual striped bass of the size tagged in this study ( $0.35 \text{ m} \pm 0.07 \text{ m TL}$ ) primarily inhabit oligohaline up-estuary regions year-round (Wingate et al. 2011; Able et al. 2012), and this was generally confirmed by the observed detection patterns. Juvenile striped bass used brackish habitats in all seasons, such as the Rhode River and upper bay, but they increased their riverine occupancy in the spring and moved among five tidal rivers. Furthermore, eight individuals transited the Chesapeake and Delaware Canal (C&D) into the adjacent Delaware River. This movement pathway has been documented in the context of egress during the northward migrations of adults (Secor et al. 2020), but movements of adult migrants were unidirectional (outward). The bidirectional movement through the C&D Canal observed in the present study suggests juvenile striped bass remain within oligohaline regions in the spring, such that the Delaware River represents an important additional habitat for juvenile striped bass using Chesapeake Bay as a nursery area. Our results also support the differential migration paradigm for striped bass in Chesapeake Bay, whereby only two individuals of this relatively small size class ( $0.35 \text{ m} \pm 0.07$

m total length) underwent the northward migration typical of larger individuals ( $\geq 0.80$  m, Secor et al. 2020). The most common exit pathway for migrating adult striped bass is through the lower Chesapeake Bay (Secor et al. 2020), which aligns with the observed RI increase for juvenile striped bass in that region during the winter (pre-migration) period in the present study.

While striped bass were largely resident in estuarine waters, three species exhibited even higher residency. Common carp and horseshoe crabs were infrequently detected outside of the Rhode River, and rarely (never for common carp) detected during the winter. In lakes, common carp form winter aggregations (Bajer et al. 2011) so it is possible individuals in this study aggregated outside the range of deployed receivers and did not travel far enough to be detected on other Chesapeake Bay receiver arrays that were a few to 10s of km away. Horseshoe crabs reduce their movement rate and home range size during winter in New England, USA estuaries (Moore and Perrin 2007; Watson et al. 2016), and our results support a similar restriction of movements within or just outside the Rhode River during winter. Blue catfish were exclusively detected in the rivers in which they were tagged, so we did not observe any movement between rivers or into the estuary mainstem. This species is invasive in Chesapeake Bay tributaries, having increased dramatically in abundance since their introduction in the 1970s (Fabrizio et al. 2021). Large blue catfish likely disperse throughout much of Chesapeake Bay during low salinity periods (Nepal and Fabrizio 2019), but we did not have any active acoustic telemetry tags in blue catfish during low salinity periods that might have enabled us to observe dispersal events.

Despite the value of employing acoustic telemetry to answer management-related and ecological questions demonstrated in this study, there are several considerations for applying this multispecies framework to other ecosystems and designing future studies. First, the arrangement and spatiotemporal scale of an acoustic receiver array inherently influences patterns of detection



and the resulting inferences that can be made (Carlisle et al. 2019; Ellis et al. 2019).

Collaborative acoustic telemetry networks consist of multiple arrays designed for unique research programs, so it is important to carefully examine when and where receivers were present and absent while analyzing and interpreting detections. Specifically designed, optimized receiver deployments could improve the efficacy of cooperative acoustic telemetry networks and provide stronger datasets, such as long-term, strategically arranged “curtains” (Taylor et al. 2017), grid-based arrays (Kraus et al. 2018), or distance-based gradients around areas of interest (e.g., wind farm sites; Methratta 2020). The sample size of tagged individuals and the spatiotemporal distribution of tag deployments are also important to consider. This study used data across species with various sample sizes ( $n = 15$  to 82, Table 1), and we were able to conduct more detailed analyses across longer timescales for species with greater sample sizes (e.g., cownose rays, especially those with long-lasting tags) compared to those with fewer tagged individuals (e.g., common carp) or shorter tag life (e.g., alewife). Furthermore, this study highlights the importance of, and challenges inherent to, choosing data analyses that are comparable among species and account for the aforementioned sample size and array design considerations. For example, the residency index equation we used was specifically designed to reduce the influence of days when individuals were not detected, which were far greater for migratory species that transited areas with relatively low receiver coverage (e.g., dusky sharks) compared to those that generally remained within small areas with high coverage (e.g., blue catfish). However, the quality (quantity) of data produced for a given species does affect the confidence with which we can interpret these metrics. Complementing these RI metrics with other analyses, such as entry and exit dates and network analyses, can provide an enhanced understanding of habitat use patterns, especially for species with limited detection quantities.

Leveraging collaborative acoustic telemetry networks allowed us to quantify connectivity among habitats within Chesapeake Bay, document how migratory movements link the estuary to coastal habitats at a continental scale, and explore the implications of those movements for fisheries within and among management jurisdictions. By using a multispecies analysis framework, we highlight the diversity in scale of movements among fishes and invertebrates that use estuarine habitats. We documented previously enigmatic migration pathways and timing, including dusky sharks migrating farther south than previously recorded using acoustic telemetry, smooth dogfish traveling along the US Atlantic coast, alewife migrations into Canadian waters, and two striped bass migrating to New England at smaller sizes than previously observed. Within Chesapeake Bay, we observed varying degrees of movement, and thus connectivity of habitats, among species ranging from highly migratory to resident within tagging regions. Furthermore, network analysis allowed us to identify potential enhancements to current fishery management strategies, both within a given jurisdiction and across international borders. We suggest continued, if not increased, participation in collaborative acoustic telemetry networks and support for long-term spatially stable receiver arrays to enhance the quantity and quality of acoustic telemetry data. We also urge resource managers to implement acoustic telemetry studies in combination with traditional data collection efforts to increase the knowledge base for developing fishery management strategies that are effective and adaptable over time.

## 5. Acknowledgements

This project was funded by the NOAA NMFS Chesapeake Bay Office award #NA21NMF4570525. Furey was also supported by the Class of 1937 Professorship in Marine Biology via the University of New Hampshire's School of Marine Science and Ocean

Engineering. Funding for tags and the SERC acoustic receiver array was provided by Aramco Services Company (dusky sharks, smooth dogfish), the Curtis and Edith Munson Foundation (cownose ray), the NOAA NMFS Chesapeake Bay Office award #NA18NMF4570255 (striped bass), and the Smithsonian Institution's Office of the Under Secretary for Science (acoustic receiver array, alewife, blue catfish, common carp, cownose ray, horseshoe crab). The authors thank Charles Bangle, Robert Fisher, Michael Goodison, Jim Gartland, and the VIMS Shark Monitoring and Assessment Program crew, Rob Latour, Carmen Ritter, Paige Roberts, Mark Sampson, and the crew of the F/V Fish Finder, and SERC interns and volunteers for their assistance in capturing and tagging some of the animals in this study. We thank Wilmelie Cruz Marrero, Mike O'Brien, Kevin Schabow, Dave Secor, Ethan Simpson, and Chuck Stence for coordinating and providing tag detections from the Chesapeake Bay backbone and Chesapeake Bay Interpretive Buoy System acoustic telemetry arrays. Most importantly, this study would not have been possible without the many tag detections provided by members of the Atlantic Cooperative Telemetry Network, FACT Network, and Ocean Tracking Network. Illustrations of each species used in the figures were created and provided by Chloe Pearson.

## 6. Author Contributions

Conceptualization: M.B.O., N.B.F., H.D.L. Data collection: M.B.O., H.D.L., K.D.R., R.A., K.H. Data analysis: M.C.L., N.B.F. Preparation of figures and tables: M.C.L., M.B.O. Writing: M.C.L., N.B.F., M.B.O., H.D.L., K.D.R., R.A.

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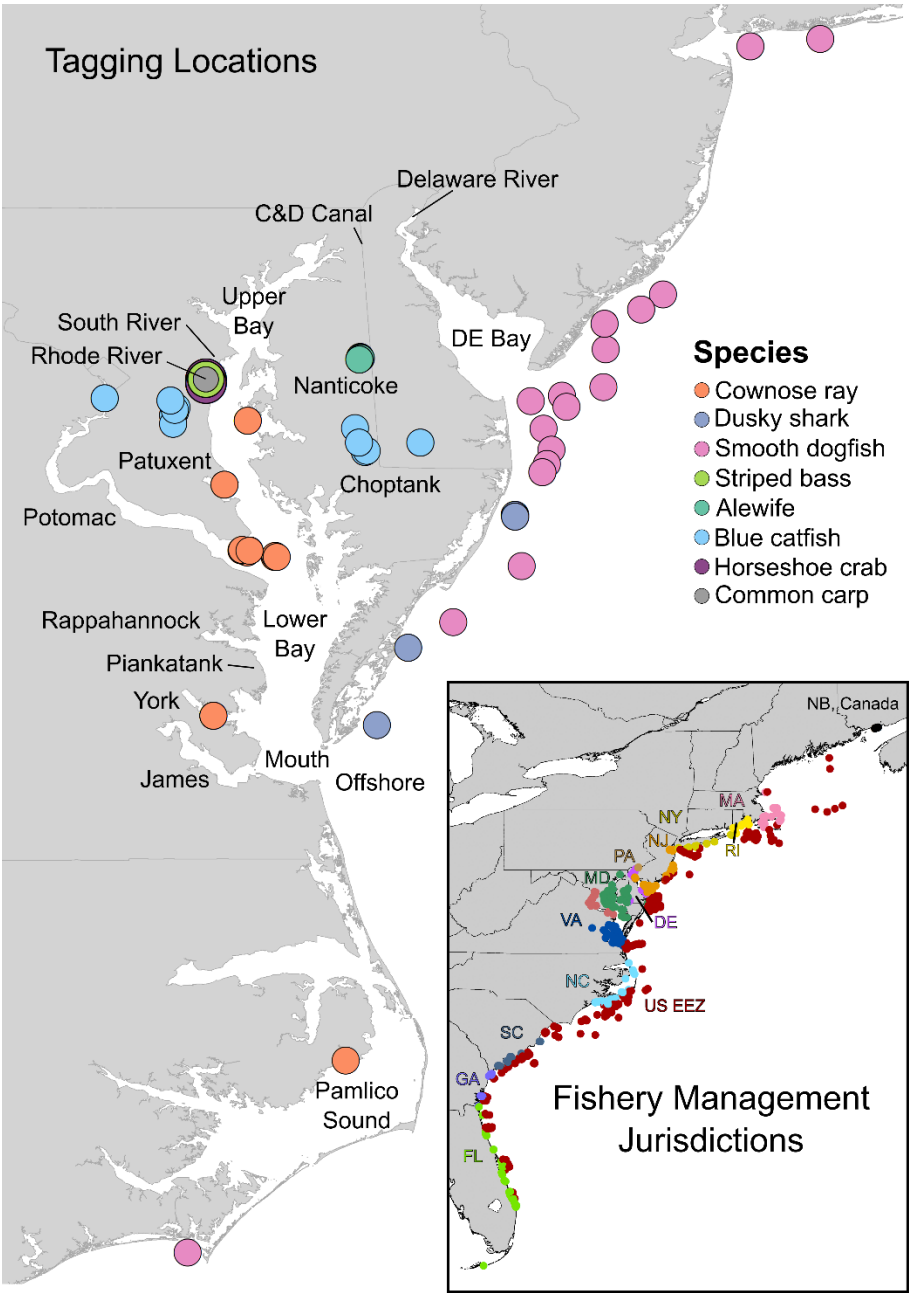
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Fig 1. Study area and tagging locations of each species, with notable regions and tidal rivers labeled. Inset includes locations of all receivers that detected a tagged animal of any species, and the corresponding fishery management jurisdiction in which it belongs (color coded with labels).

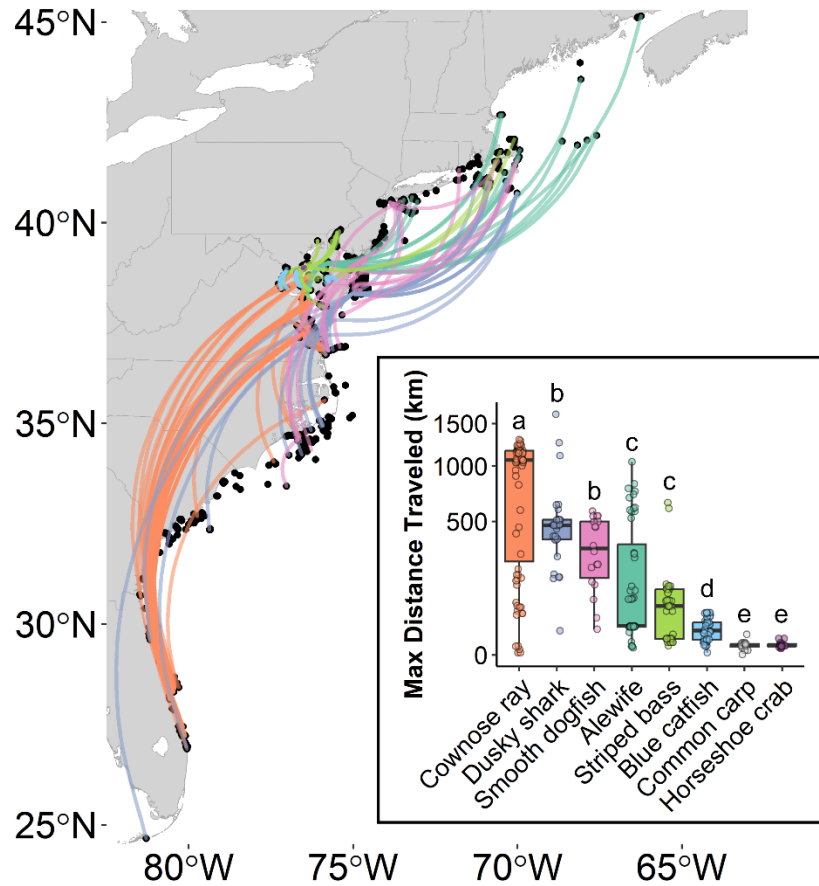


Fig 2. Locations of all receivers that detected a tagged animal of any species (black circles) and path from release site to farthest detection away from release site for each tagged individual (color coded by species). Inset depicts farthest detection away from tagging location by species, calculated as the maximum Haversine distance from tagging location to each detection location (y-axis scaled to square root). Letters represent pairwise differences between species via Wilcoxon rank sum tests.

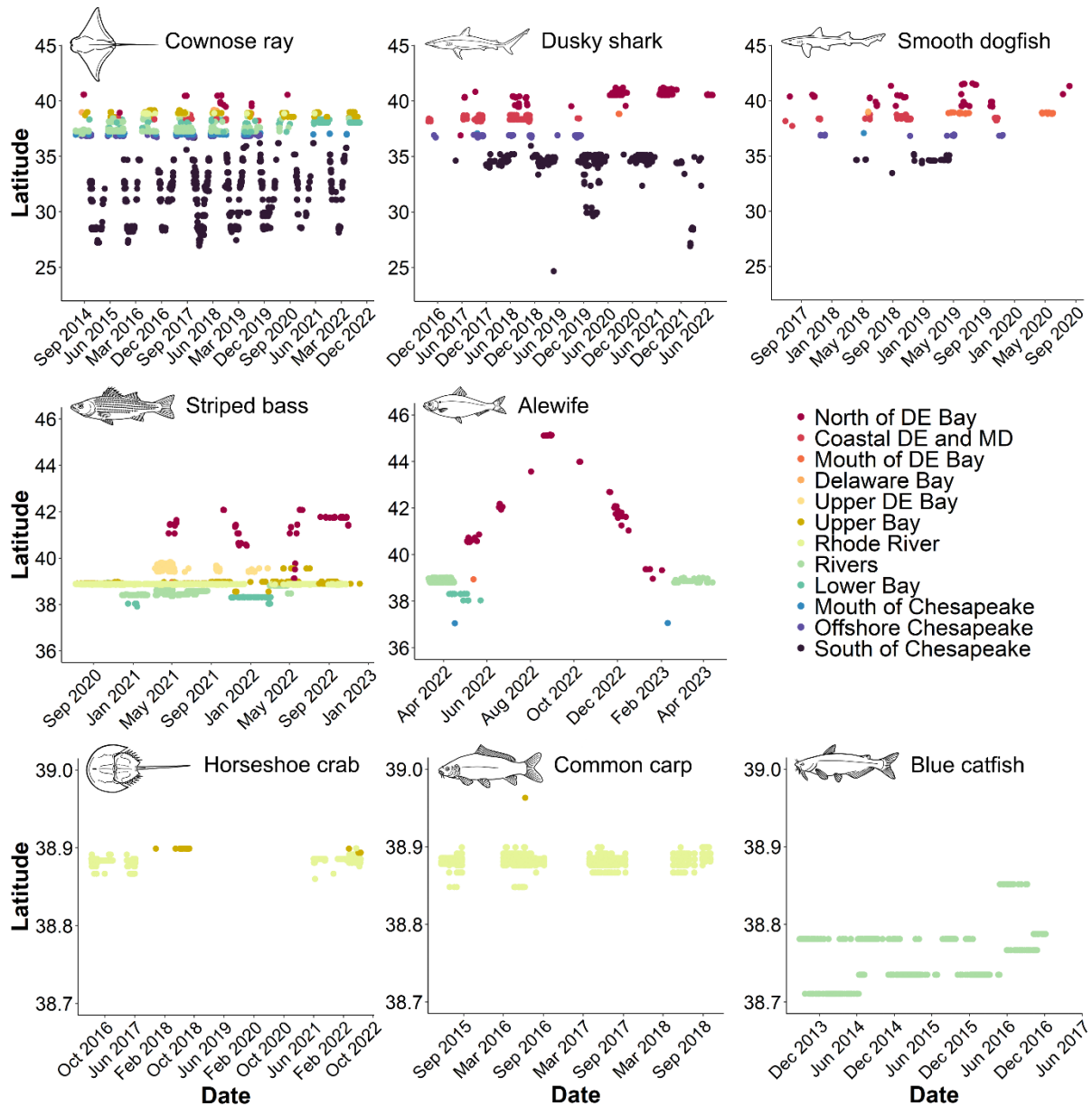


Fig 3. The spatiotemporal distribution of combined detections for all individuals of each species, with each point representing a single detection plotted by date and latitude. Colors represent general regions of detection location (see inset map in Fig 4 for details).



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1107 Fig 4. Residency indices by region and season for each species. Sex-specific panels are included  
 1108 for cownose rays and dusky sharks. Inset map depicts receiver locations in each region within the  
 1109 Chesapeake Bay and Delaware Bay. The region “North of DE Bay” extends from the New Jersey  
 1110 coast to Canada, while “South of Chesapeake Bay” extends to the Florida Keys.

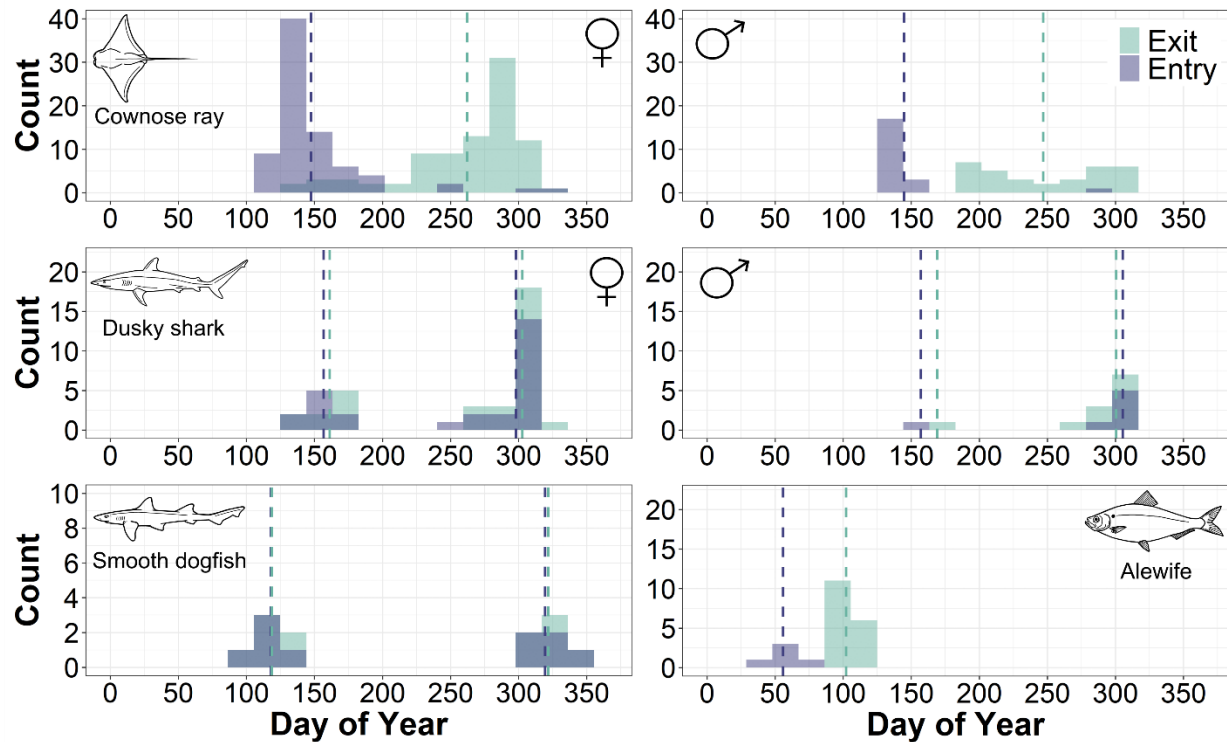


Fig 5. Dates of entry and exit in and out of the Chesapeake Bay area, including detections in the “Offshore Chesapeake” region (the estuary plume), for each species and sex, if applicable. Entry is considered the first detection in the Chesapeake Bay area after the individual was detected elsewhere, and exit is considered the last detection in the Chesapeake Bay area before the individual is detected elsewhere. Dashed lines represent average entry and exits dates across all individuals of each species and sex, if applicable.

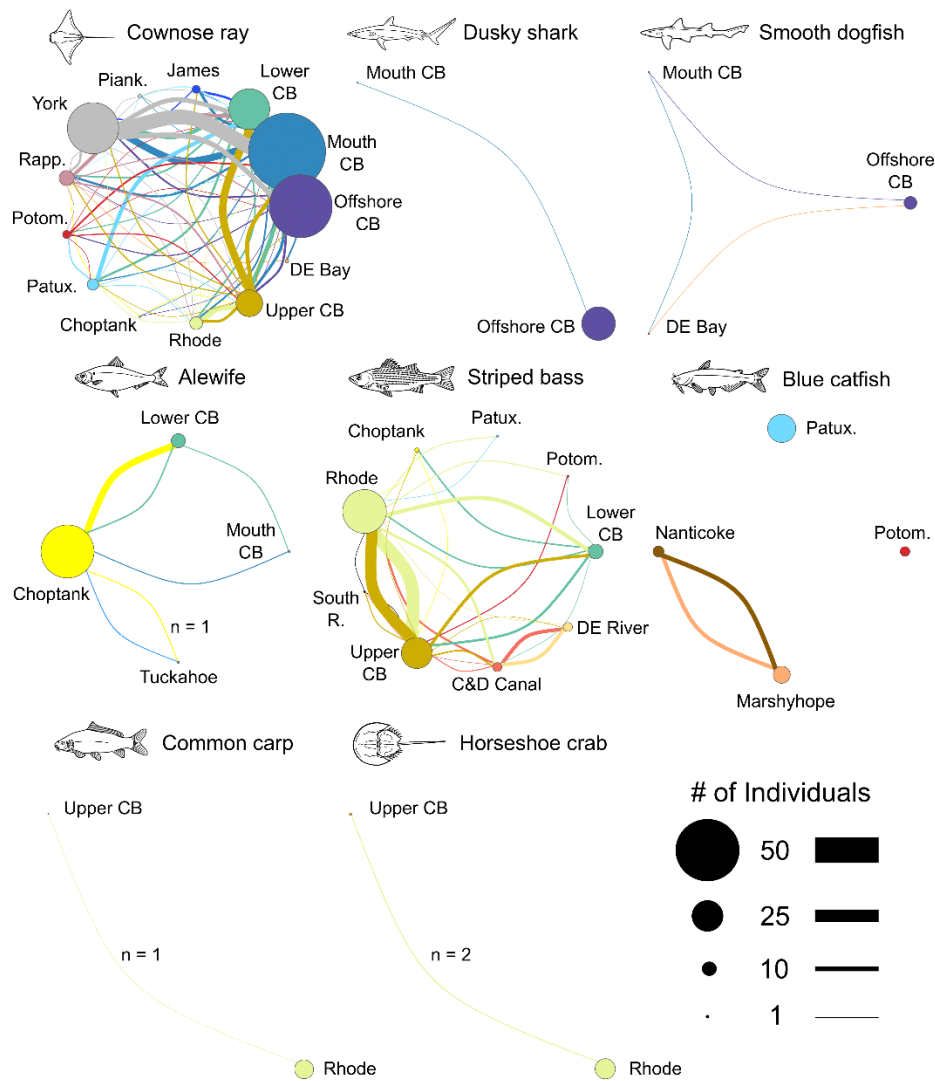


Fig 6. Networks representing movements of individuals of each species among regions within and near Chesapeake Bay, including the mouth and areas offshore Chesapeake Bay and Delaware Bay (referred to in text as local networks). Regions are described in Figure 1, and include major sections of the Chesapeake Bay (upper and lower), tributaries of Chesapeake Bay and Delaware Bay, and the Chesapeake and Delaware Canal (CD Canal). Size of nodes (points) represent the number of individuals detected in each region, and width of edges (lines) represents the number of individuals moving between regions (see legend for scale). Edges are colored by the region the path begins in.

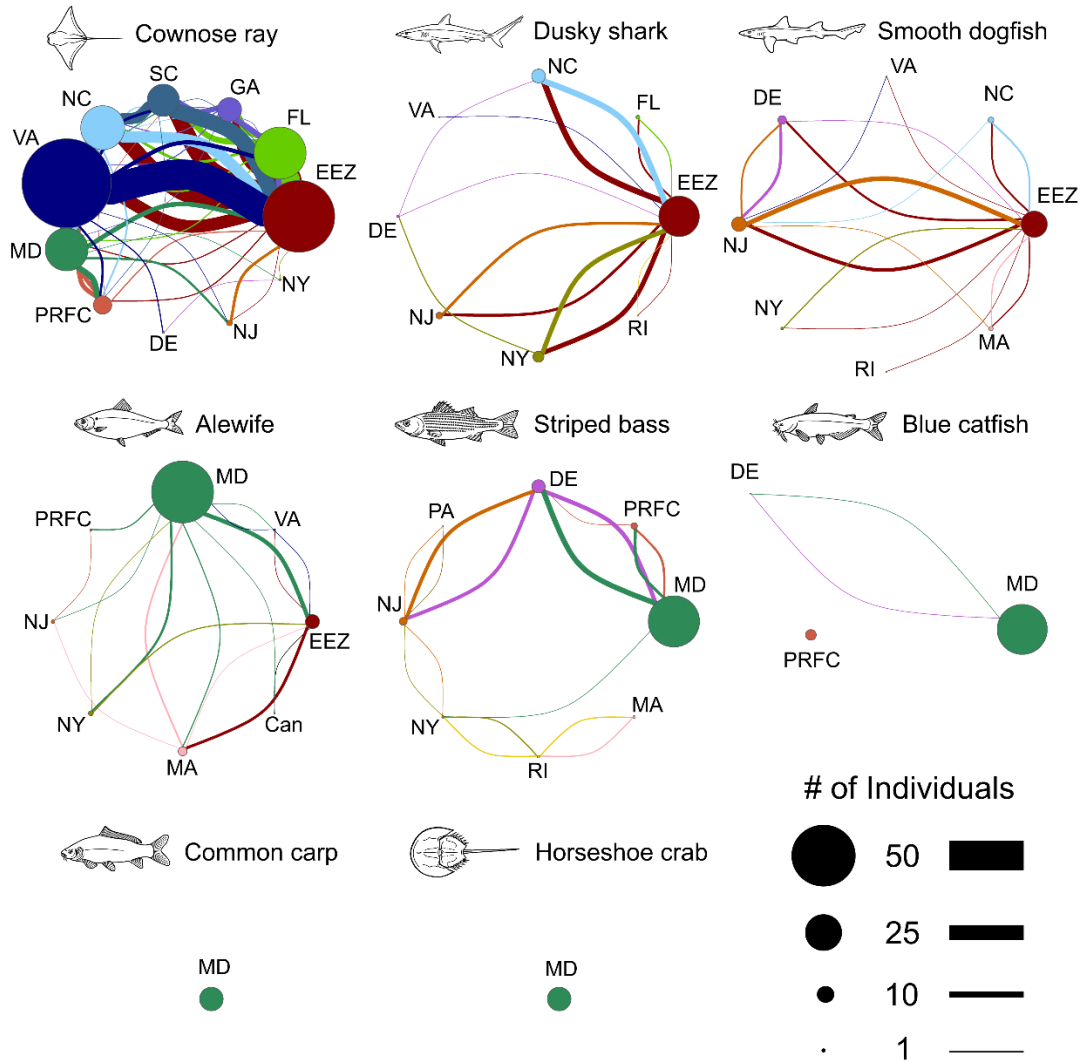


Fig 7. Networks representing movements of individuals of each species between fishery management jurisdictions (referred to in text as “continental-scale networks”). Fishery management jurisdictions are described in Figure 1 (inset), and include United States state agencies (represented by the state abbreviation), US federal (outside of state waters within the EEZ), the Potomac River Fisheries Commission (PRFC), and the Canadian province of New Brunswick (Canada). Size of nodes (points) represent the number of individuals detected in each jurisdiction, and width of edges (lines) represents the number of individuals moving between jurisdictions (see legend for scale). Edges are colored by the jurisdiction the path begins in.



## Tables

Table 1. Tagging and detection data for each species: The number of tagged individuals and the sizes of tags used (in parentheses, e.g., 9 = Innovasea V9), the number of individuals detected and remaining in filtered datasets and the percentage of those tags that were detected for at least one full year (in parentheses), years when tagging occurred, years in which detections were recorded, total length in meters (mean  $\pm$  1 SD) for all but cownose rays and horseshoe crabs (disk width and carapace width, respectively), number of male and female individuals detected if applicable, total number of detections in filtered datasets, and minimum and maximum latitudes of detection per species.

Species	Tagged (tag size)	Detected (% >1yr)	Years Tagged	Years Detected	Size (m)	M F	Total Dets.	Latitude (min/max)
<b>Cownose ray</b>	82 (9/13/16)	79 (49%)	2014-2019	2014-2022	0.77 $\pm$ 0.23	20 59	79620	26.94 / 40.57
<b>Dusky shark</b>	29 (13/16)	29 (83%)	2016-2019	2016-2022	1.46 $\pm$ 0.31	10 19	16168	24.66 / 41.20
<b>Smooth dogfish</b>	21 (13)	18 (39%)	2017-2018	2017-2020	0.98 $\pm$ 0.11	1 17	11360	33.44 / 41.55
<b>Striped bass</b>	40 (9)	38 (42%)	2020	2020-2022	0.35 $\pm$ 0.07	NA	831594	37.91 / 42.08
<b>Alewife</b>	50 (7)	48 (8%)	2022	2022-2023	0.28 $\pm$ 0.02	23 25	6743	37.05 / 45.15
<b>Horseshoe crab</b>	16 (9)	16 (6%)	2016, 21, 22	2016-19, 2020-22	0.25 $\pm$ 0.05	7 9	91743	38.86 / 38.90
<b>Common carp</b>	15 (9/13)	15 (47%)	2015-2016	2015-2018	0.68 $\pm$ 0.13	NA	90784	38.85 / 38.96
<b>Blue catfish</b>	47 (13)	45 (60%)	2013-2015	2013-2017	0.57 $\pm$ 0.11	NA	2095717	38.35 / 38.89

Table 2. Metrics for each species' local (Chesapeake and Delaware Bay regions) and continental-scale (jurisdictional) network analysis, including the number of observed nodes (regions/jurisdictions in which one or more individual was detected) and edges (movements between regions/jurisdictions). Values in parentheses are the proportion of observed to possible nodes or edges; local network = 19 possible nodes and 342 possible edges, continental-scale network = 15 possible nodes and 210 possible edges.

Species	Local Networks		Continental-scale Networks	
	Nodes (%)	Edges (%)	Nodes (%)	Edges (%)
<b>Cownose ray</b>	13 (0.68)	74 (0.22)	11 (0.73)	53 (0.25)
<b>Dusky shark</b>	2 (0.11)	1 (0.003)	8 (0.53)	14 (0.07)
<b>Smooth dogfish</b>	3 (0.16)	3 (0.01)	8 (0.53)	17 (0.08)
<b>Striped bass</b>	9 (0.47)	28 (0.08)	8 (0.53)	16 (0.08)
<b>Alewife</b>	4 (0.21)	6 (0.02)	8 (0.53)	18 (0.09)
<b>Horseshoe crab</b>	2 (0.11)	1 (0.003)	1 (0.07)	0 (0)
<b>Common carp</b>	2 (0.11)	1 (0.003)	1 (0.07)	0 (0)
<b>Blue catfish</b>	4 (0.21)	2 (0.006)	3 (0.20)	2 (0.01)

Table 3. Applications of acoustic telemetry data for fishery management

Management Action	Research Goal	Relevant Methods, Analyses & Metrics	Examples
Conserve and restore critical habitats	Identify critical habitats and evaluate responses to restoration	Residency index	Reubens et al. 2013; Rous et al. 2017; this study; reviewed by Appert et al. 2023
		Euclidean distance-based analysis	Furey et al. 2013; Moulton et al. 2017; Rooker et al. 2018
		Center of activity	Simpfendorfer et al. 2002; Alós et al. 2011
		Core use area (kernel density, minimum convex polygon, Brownian bridge, etc.)	Topping and Szedlmayer 2011; Tinhan et al. 2018; Edwards et al. 2022
		Habitat selection index	Topping et al. 2005; Zhang et al. 2015
		Continuous time residency	Capello et al. 2015
		Bayesian state-space models	Semmens 2008
Adapt management for climate change	Determine environmental associations and model responses to climate change	Modeling frameworks (GLM, GAM, BRT, RF, etc.)	Kneebone et al. 2012; Bangle et al. 2020a
		Center of activity	Ubeda et al. 2009
Design spatiotemporal management (protected areas, time-area closures)	Identify phenology of space use and migration pathways	Entry and exit dates	Sackett et al. 2007; Able et al. 2014; Secor et al. 2020; this study
		Seasonal residency index	Kessel et al. 2014; Wingate et al. 2011; this study
		Modeling frameworks	Bangle et al. 2021
		Detection at checkpoint receivers	Hayden et al. 2014
Evaluate effectiveness of protected areas	Quantify movements within and surrounding protected areas	Core use area (KDE, MCP, BB)	Lippi et al. 2022; van Zinnicq Bergmann et al. 2022
		Network analysis	Garcia et al. 2015; Lea et al. 2016
		Residency index	Novak et al. 2020
Identify interjurisdictional management opportunities and effectiveness	Determine connectivity among regions or habitats	Network analysis	Lédée et al. 2021; Espinoza et al. 2021; this study
		Connectivity plot	Heupel et al. 2015
		Residency index	Hussey et al. 2017

Appropriately define stock units	Examine spatial scale of potential reproductive mixing	Network analysis	Lédée et al. 2021
		Stock assignment	Kneebone et al. 2014
Explore size-based management actions for migratory species	Identify ontological shifts in space use and partial migration patterns	Modeling frameworks (GLMM, GAMM)	Papastamatiou et al. 2013; Secor et al. 2020
		Multivariate analyses (PCA)	Gahagan et al. 2015
		Residency index, connectivity plot	Espinoza et al. 2016
Restore migration passageways for diadromous fishes	Determine effects of barriers on fish passage and response to restoration	Proportion of passage success or survival	Roscoe et al. 2011; Piper et al. 2017; Leander et al. 2021
		Modeling frameworks (GLM)	Raabe et al. 2019; Davies et al. 2023
Enhance accuracy of mortality estimates in stock assessments	Estimate natural mortality	Bayesian multistate models	Ellis et al. 2017; Block et al. 2019; Nelson and Powers 2020
		Mark-recapture methods	Bacheler et al. 2009; Dudgeon et al. 2015; Clark et al. 2016; ASMFC 2017; reviewed in Lees et al. 2021
		Detection at checkpoint receivers	Raby et al. 2015; Flávio et al. 2020
Determine influence of catch-and-release fishing pressure	Estimate post-release mortality	Comparison to dead controls	Yergey et al. 2012; Capizzano et al. 2016
		Three-dimensional geopositioning or acceleration/depth tags	Curtis et al. 2015; Bohaboy et al. 2020
Sex-specific management objectives and methods	Examine sex-specific differences in space use	Any herein, calculated for each sex or included as a covariate	Callihan et al. 2013; Espinoza et al. 2021; this study