

Confluences function as ecological hotspots: geomorphic and regional drivers can help identify patterns of fish distribution within a seascape

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ABSTRACT: Quantifying heterogeneity in animal distributions through space and time is a precursor to addressing many important research and management issues. Obtaining these distributional data is especially difficult for mobile organisms that use broader geographic extents. Here, we asked if the merger between 2 research directions — (1) quantifying spatial linkages between fish and geomorphic features (e.g. confluences) and (2) analyzing larger-scale, multi-metric organismal patterns — can provide a broader geographic context for ecological issues that depend on understanding dynamic fish distribution. To address these objectives, we collected data from 59 tagged striped bass *Morone saxatilis* that were detected by a 26 acoustic receiver array deployed within Plum Island Estuary, MA, USA. We examined these telemetry data using generalized linear mixed models and chi-squared, cluster, and network analyses. Geomorphic site types informed the estuary-wide distribution of striped bass in that tagged fish spent the most time at confluence junctions; however, they did not spend the same amount of time at all junctions. Relative to integrating multiple metrics, number of tagged fish, residence time, and number of movements were not the same across all receivers. When all 3 metrics were considered together, 4 distinct clusters of distributional patterns emerged. Network analyses connected geomorphology and multi-metric seascape patterns. Confluence junctions in the Rowley and Middle regions were the most connected (high centrality) and most used sites (high residence time). Although confluence junctions function as ecological hotspots, researchers and managers will benefit from interpreting geomorphology within a larger geographic context.

KEY WORDS: Striped bass · Geomorphic · Distribution · Confluence · Region

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1. INTRODUCTION

Quantifying patterns and drivers of organismal distribution and abundance are fundamental and persistent challenges for ecology (Stephens & Krebs 1986, Yackulic et al. 2011) and conservation (Mittermeier et al. 1998, Bond et al. 2012). In fact, identifying where mobile organisms are located is a precursor

to addressing important research and management issues for estuarine, coastal, and marine populations/communities. Yet understanding spatial patterns and drivers for animals that move frequently (e.g. fish) across broader geographic extents (i.e. aquatic landscapes) is difficult because researchers do not know where these mobile animals are located, how their location changes, or the distribution of the

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abiotic and biotic resources to which these organisms respond. To fill this gap, we asked if merging 2 research directions—(1) establishing spatial linkages between fish and geomorphic features (e.g. confluences; Fig. 1, box 1) and (2) quantifying larger-scale, multi-metric organismal patterns (Fig. 1, box 2)—can provide a broader geographic context for organism–environment relationships (Fig. 1, box 3) in a way that enhances our understanding of seascape-scale research and management (Fig. 1, arrow 4).

Locating ecologically influential geomorphic features, such as confluences, can reveal where mobile fish are located within an aquatic landscape. Confluences (areas where 2 smaller water bodies [arms] merge to form a single larger entity [junction]) are a dominant geomorphic feature (e.g. Poole 2002) that increase heterogeneity within aquatic ecosystems (e.g. Benda et al. 2004, Rice 2017). Confluences can alter biodiversity (Boddy et al. 2019) and create ecological hotspots for organisms through a variety of mechanisms (e.g. Rice et al. 2008). For example, tributaries funnel upstream productivity (stream and watershed) into confluence arms that subsequently merge to form a shared downstream confluence junction

(e.g. Kiffney et al. 2006). The resulting velocity-driven concentration of resources can provide predictable, high-energy rewards for animal foragers (see discussion in Kennedy et al. 2016). Confluences can also provide structural and physiological refuges from extreme physical conditions (e.g. temperature), resulting in animal aggregations (e.g. Breau et al. 2007, Brewitt et al. 2017). Relatively few previous studies have explicitly examined the role of within-confluence components (i.e. arms, junctions) or compared the ecological impact of variation across individual confluences (e.g. location, size, configuration) for mobile animals within the aquatic landscape. Addressing these gaps can advance our understanding of ecological and management issues related to larger-scale organism–environment interactions (Fig. 1, box 1).

Quantifying larger-scale fish distribution patterns using telemetry data can also inform seascape-scale organism–environment interactions. However, several difficulties impede the ability of environmental professionals to understand spatial patterns and drivers of highly mobile fish at larger scales. First, quantifying organismal distribution at larger scales is difficult because the location of mobile fish is often unknown, the fish typically do not stay in one place, and the wide range of sites that these fish might use make a whole-system assessment logistically problematic. Tracking acoustically tagged fish is a promising approach with which to address this larger-scale sampling problem, because telemetry can continuously detect the multi-scale distribution of tagged animals across a broad geographic expanse (e.g. Lowerre-Barbieri et al. 2019). Second, point-specific physical habitat variables such as depth (Torgersen & Close 2004, Jin et al. 2014) and substrate (Gratwicke & Speight 2005, Franca et al. 2012) can be important drivers of organism distribution (Albanese et al. 2004, Clark et al. 2004). However, these potentially important local factors can be difficult to measure intensively and representatively across larger geographic areas. An alternate indicator that can identify larger-scale physical drivers of organismal distribution—geomorphology—may eliminate this logistic difficulty (e.g. Dauwalter et al. 2008, Górski et al. 2013). Kennedy et al. (2016) showed that geomorphic discontinuities (i.e. drop-offs, sandbars, confluences) have a disproportionate effect on estuary-wide fish distribution. Addressing these gaps (i.e. what to measure, where, when, and why) can increase our understanding of mobile fish distributions at a larger, aquatic-landscape scale (Fig. 1, box 2).

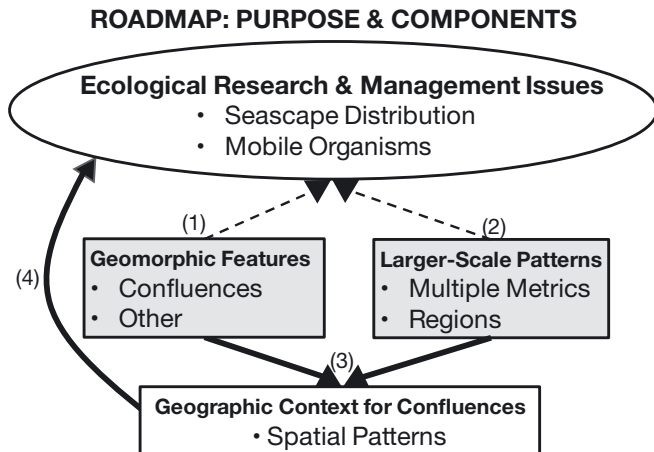


Fig. 1. Roadmap, purpose, and components of our research. Ultimately, we sought to understand research and management issues that focus on the distribution of mobile fish in the coastal and estuarine seascape. Towards this goal, we examined 2 related topics: (1) the role of geomorphic features (including confluences) using a generalized linear mixed model (box 1), and (2) multi-metric and regional larger scale landscape patterns of fish distribution revealed by chi-squared (Monte Carlo simulations) and cluster analyses (box 2). To integrate these 2 topics, we used network analysis to examine the importance of putting geomorphic features in a geographic context (box 3). Together, these 3 components identified new ways to understand research and management issues that depend on understanding mobile organism distributions at the seascape scale (arrow 4)

In this research, we examined confluences, multi-metric patterns, and the geographic context of organism–environment patterns using striped bass *Morone saxatilis* in Plum Island Estuary (PIE), MA, USA. Atlantic coast striped bass spawn in the Chesapeake, Delaware, and Hudson Bay estuaries. As sub-adults (2–4 yr) and as adults (>4 yr), some striped bass make a seasonal migration up the coast during the summer months (Mather et al. 2010) to feed in New England estuaries (Walter et al. 2003, Mather et al. 2009, Pautzke et al. 2010). Using a 26 unit acoustic telemetry receiver array, we asked 3 specific research questions about the estuary-wide distribution of acoustically tagged striped bass (Fig. 1, boxes 1–3). First, within PIE, do striped bass spend more time at confluences than other geomorphic site types (i.e. non-confluences, exits)? Second, based on 3 different distributional metrics (number of unique individuals, residence time, number of movements) and a combined, multi-metric response, do striped bass use some estuary locations and regions more than others? Third, do striped bass use individual confluences differently depending on their location within the estuary (i.e. what is the geographic context for confluences within the seascape)? The resulting insights can benefit scientific professionals who are addressing ecological and management issues that depend on understanding mobile fish distribution in an aquatic landscape (Fig. 1, arrow 4). Thus, the utility and broad relevance of our research is that without some knowledge of how mobile organisms are distributed throughout the larger ecosystem, our valued fish resources cannot be managed, conserved, or restored.

2. MATERIALS AND METHODS

2.1. Study area

PIE is a temperate, bar-built coastal plain estuary with large, semi-diurnal tides (mean range: 2.9 m; Deegan & Garritt 1997) located within the cold-temperate Acadian Province on the northeastern coast of Massachusetts, USA (Fig. 2A). PIE has extensive areas of productive tidal marshes as well as multiple non-vegetated sand flats of varying sizes that are exposed at low tide (Kennedy et al. 2016). PIE has 3 major rivers (Parker, Rowley, and Ipswich) and a man-made connection to the coastal Merrimack River (Plum Island River) (Fig. 2B). These rivers drain into a large, open-water embayment, Plum Island Sound (length: 13.2 km, shoreline length: 262 km;

Buchsbaum et al. 1998), in which a large central island, Middle Ground, is located. PIE connects to the Atlantic Ocean through the Plum Island River (via the coastal Merrimack River) and the southern ocean outlet (Fig. 2B).

We tested if striped bass distribution differed across 3 categories of geomorphic site types (exits from our study area, confluences, and non-confluences). We defined study area exits as egress points from the Rowley River–Plum Island Sound area. Our 4 study area exits included the 2 ocean access points (Plum Island River and south ocean outlet) as well as the mouths of the Parker and Ipswich rivers (Fig. 2B). For the confluence geomorphic site type, we examined 3 locations within each confluence (2 upstream arms and 1 downstream junction). Here, confluence arms are defined as the smaller, upstream contributing creeks that come together at the confluence junction or shared area (Fig. 2C). These 3 within-confluence locations were examined for 4 confluences (West Creek, Rowley River, Third Creek, and Grape Island; Fig. 2D). Our third category of physical sites, non-confluences, varied in physical conditions and location (Fig. 2D). PIE consists of 4 regions (Upper, Rowley River, Middle, and Lower; Fig. 2E) that differ in physical characteristics (Pautzke et al. 2010). More details on the study site and methods are provided elsewhere (Supplement 1; Supplements are available at www.int-res.com/articles/suppl/m629p133_supp.pdf).

2.2. Methods

Our research goal was to understand how tagged striped bass used 26 locations within 3 geomorphic site types across the 4 PIE regions, by placing telemetry receivers in deliberately chosen locations that provided replicates of site type and region (Fig. 3). Specifically, we tracked acoustically tagged striped bass using a 26 receiver stationary array (VR2W-69kHz) deployed from 24 June–26 October 2015 (Fig. 3A). We placed receivers at 4 Plum Island Sound exit sites (Fig. 3B, triangles). We chose 6 non-confluence sites that included a wide range of sites where tagged striped bass have been previously detected (Fig. 3B, circles; Kennedy et al. 2016). A total of 12 receivers were placed in 3 within-confluence locations (2 arms, 1 junction) across 4 confluences (Fig. 3B, squares). We placed a near equal number of receivers in each of the 4 PIE regions (Upper, Rowley River, Middle, and Lower Sound; Fig. 2E).

A total of 59 sub-adult and adult striped bass (mean \pm SE fish size: 524 ± 5.85 mm total length [TL]; range:

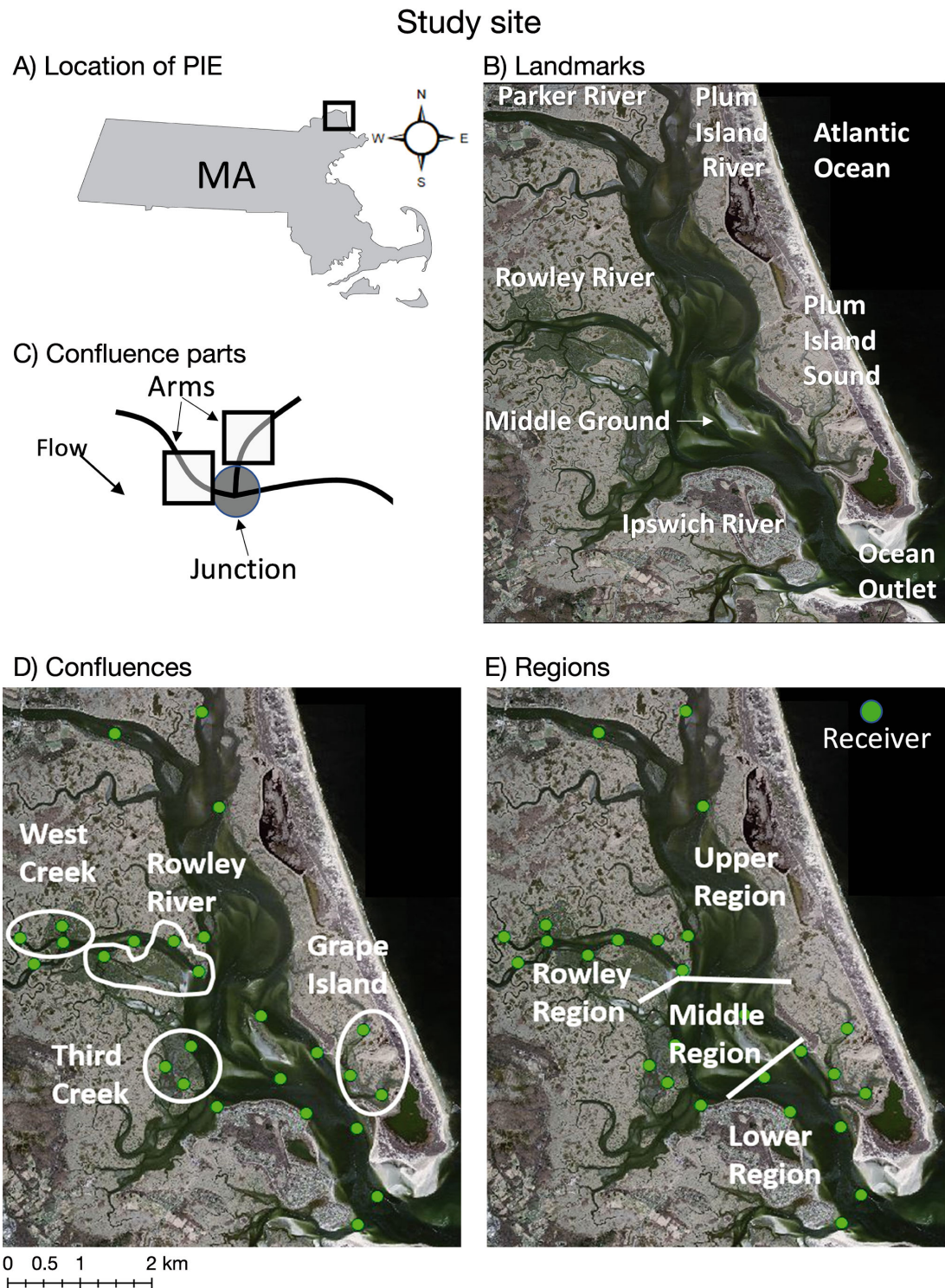


Fig. 2. (A) Plum Island Estuary (PIE), on the northeastern coast of Massachusetts and (B) its diverse geomorphic and bathymetric features. PIE has 3 major river inputs: Parker River, Rowley River, and Ipswich River. There is also an ocean outlet at the south end of Plum Island Sound and a man-made connection to the Merrimack River (and the Atlantic Ocean) through the Plum Island River. Other landmarks include a large salt marsh island called Middle Ground. (C) The confluence geomorphic site type consisted of 2 upstream confluence arms (smaller, upstream water bodies) and a downstream confluence junction. (D) Our study focused on West Creek, Rowley River, Third Creek, and Grape Island confluences. (E) PIE can be divided into 4 regions: Upper, Middle, Lower Sound, and Rowley River. Green dots in (D) and (E): receiver locations; ellipses in (D): confluences

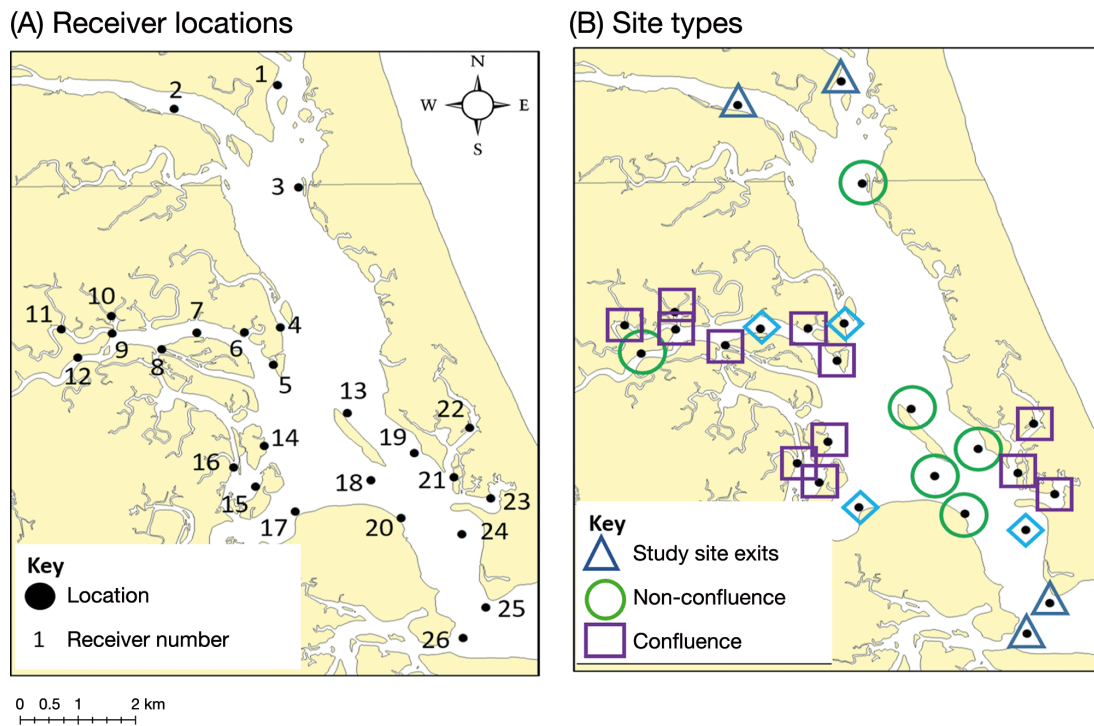


Fig. 3. Stationary receiver (A) locations and (B) site types within Plum Island Estuary, shown by 3 physical site type symbols: (1) exit sites that bound the study area (between sound and ocean and sound and non-study area rivers) (triangles), (2) confluences (squares), and (3) non-confluences (circles). In previous research, tagged fish did not use areas in the Upper Sound between receivers 3 and 4. Neighborhood receivers (diamond symbols) fill in potential gaps in array coverage and were not treated as a specific site type

434–623 mm) were captured by fly angling with barbless hooks within our 4 focal confluences on 11 d during 2 tagging events in the summer of 2015 (44 fish: 24–29 June; 15 fish: 22–26 July). Tagged fish were released near capture locations. All fish ($n = 59$) were internally implanted with VEMCO V13 acoustic tags (length: 36–48 mm, weight in air: 11–13 g, weight in water: 6–6.5 g; Gerber et al. 2017, 2019a). Tags were less than 2% of the body weight of all tagged fish (Bridger & Booth 2003). Individual fish were anesthetized with Aquí-S 30 mg l⁻¹ until they lost orientation (mean: 2 min 18 s). A 15–30 mm lateral incision was made below the pectoral fin, about 3/4 of the way to the tip of the fin, using a size 12 surgical scalpel. The acoustic tag was sterilized using ethanol and inserted into the body cavity. The incision was closed with 2–4 surgical sutures (Ethicon, braided, coated Vicryl, 3-0, FS-2, 19 mm, 3/8, reverse cutting; mean surgery time: 2 min 31 s). Post-surgery, all fish were injected intramuscularly with Liquamycin (0.1 mg kg⁻¹). Fish were held in a tank of ambient water during the tagging process and were released following recovery (mean recovery: 6 min 15 s).

Fish detection data were summarized as 3 receiver site-specific response metrics (number of unique

individuals, residence time, and number of movements). We intentionally chose these 3 conservative fish telemetry responses because they are ecologically informative but less influenced by fine-scale variability than raw detection data. We integrated data across the same combination of diel periods, tide stages, and days for all receivers. Number of unique individuals was calculated as a receiver-site-specific total only. Residence time and number of movements were calculated both as (1) the mean of all fish detected at a receiver site and (2) receiver-site, fish-specific totals.

The first metric, number of unique individuals, was defined as the total number of uniquely coded individual fish that visited a given receiver site during our 5 mo study season. For this first metric, each fish was counted only once even if a specific individual was detected multiple times. The second metric, residence time, quantified how much time (h) an individual fish spent at each of our 26 stationary receiver sites. To calculate residence time, we aggregated raw detection data for a specified fish, site, and time period ('VTrack' v.2.1.2 package in R; Campbell et al. 2012). The calculation for each segment of residence time started when a tagged fish was detected twice

at a site and ended when a tagged fish was not detected at that site for 1 h or was detected at another site (Chamberlin et al. 2011). All residence time segments were summed for each fish at each receiver to determine if site-specific behavior differed (high vs. low residence time). The third metric, number of movements, was calculated as the number of times a fish arrived or left a receiver site over the course of the field season and represented an index of across-site activity.

2.3. Role of geomorphic site types and regions

We tested whether physical site type and region (treatment variables) affected striped bass residence time (response variable). For this test, we used a generalized linear mixed model with a Poisson distribution and log-link function in which individual fish (our experimental unit) were treated as a random effect ('lme4' package in R; Bates et al. 2015). In choosing this analysis, we considered 3 underlying distributions: Gaussian, Poisson, and gamma. We decided not to use a gamma distribution because this distribution does not allow for the zero values that occurred in our data set. We ran additional analyses with both Gaussian and Poisson distributions. We chose the Poisson distribution based on 3 pieces of information: (1) our use of residence time was a count of time, (2) both the Gaussian and the Poisson distributions gave similar results, and (3) the Gaussian distribution provided confidence intervals that were negative, which was problematic for our variable that was bounded by zero. In our generalized linear mixed model, we tested if residence time differed across individual sites for 3 types of effects: (1) within each category of physical site types (i.e. replicates of study area exits, confluences, and non-confluences), (2) across physical site types (exits vs. confluences vs. non-confluences), and (3) between within-confluence locations (arms vs. junctions). In a separate generalized linear mixed model, we tested if residence time for the same 3 types of effects differed by geographic region. We focused on residence time because how long fish use a site is a critically important component of foraging behavior. Post hoc multiple comparison tests ('multcomp' package in R; Hothorn et al. 2008) were used to identify which treatments were significantly different. To identify if the site-specific receiver range affected our ecological conclusions, the same statistical procedures were applied to fish metrics that were divided by site-specific detection range (data set 2; Supplement 2).

2.4. Multi-metric distribution patterns

Total number of unique individuals, mean residence time, and mean number of movements at each receiver site were plotted on maps of PIE to depict whole-estuary patterns. All 3 observed site-specific responses were compared to what would be expected from an even distribution (i.e. if the same number of fish were present at each receiver [number of unique individuals]; if fish resided for the same amount of time at each receiver [residence time]; if fish moved the same number of times at each receiver [number of movements]). To compare our observed whole-system distribution data to these expected values, we used a chi-squared analysis based on 2000 Monte Carlo simulations ('chisq.test' function, 'stats' package in R). Of course, other expected values could also be used. When patterns for residence time and number of movements were similar, only residence time is shown.

To quantitatively compare the combination of all 3 metrics across receiver locations, we used a cluster analysis applied to a Euclidean distance matrix created from site-specific measurements of our 3 distributional responses. Specifically, we used the non-hierarchical 'PAM' (partitioning around medoids) function in R ('cluster' package) to determine if there were groups of sites with distinct patterns of total number of unique individuals, mean residence time, and mean number of movements across receivers. The optimal number of clusters was determined by maximizing the mean silhouette width (Kaufman & Rousseeuw 1990). We used Jaccard bootstrap mean values >0.75 to identify stable clusters ('clusterboot' function, 'fpc' package in R; Hennig 2008). Box plots for the 3 response variables were created to interpret cluster patterns.

2.5. Geographic context for confluences within the seascape

We used a network analysis to examine how the shared use of specific receivers across individual tagged fish was connected through geomorphology, region, and general estuary location. Network analysis was performed using the 'igraph' package in R (Csardi & Nepusz 2006). Our network analysis used a data matrix of individual fish residence times at each individual receiver to calculate a centrality coefficient that quantified the importance of individual receivers or how often each receiver was included in an individual tagged fish's receiver network. Addi-

tional details of this analysis are provided in the relevant figure legend. Results are presented as mean (\pm SE) values, unless otherwise stated.

3. RESULTS

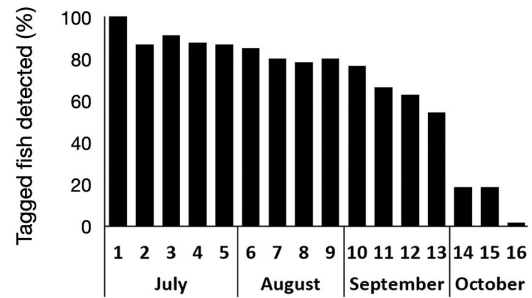
3.1. Overview

Across our 5 mo field season, tagged striped bass were detected in PIE for 69 ± 4.43 d fish⁻¹ (range: 4–117 d). From July through November 2015, we recorded 447 972 detections, resulting in 7593 ± 799 detections fish⁻¹ (range: 78–22 460). Most tagged fish were detected monthly in PIE (July: $n = 50$ fish, 87 % of the original number of tagged individuals; August: $n = 48$, 81 %) until fish started to migrate in the fall (September: $n = 38$, 65 %; October: $n = 8$, 13 %; Fig. 4A). By November, all but 1 of our 59 tagged fish (1.6 %) had left the estuary. In addition, 63 % of tagged individuals (37 of 59 tagged fish) were detected at receivers outside of PIE. In 2015, tagged fish were detected by 15 ± 0.6 of the 26 receivers (58 % of all receivers; range: 6–23) for 46 ± 16.4 h (range: 9.2–393.4 h), and moved 167 ± 3.7 times (range: 2–172.8). The above described detection metrics satisfy criteria suggested by Gerber et al. (2017) to evaluate telemetry data set quality. In general, many individual tagged striped bass used the entire estuary during their seasonal residence, as illustrated by detection tracks created by 2 individual fish trajectories (latitude and longitude = x -, y -axes, time = z -axis; Fig. 4B,C).

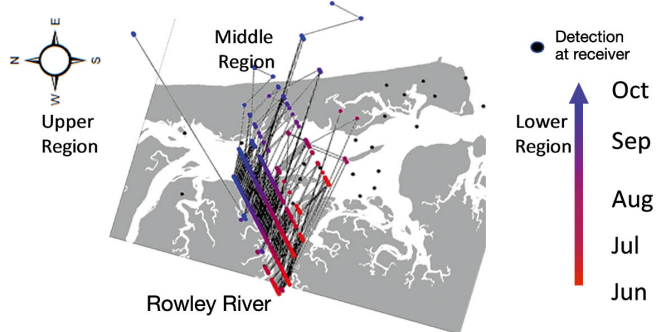
3.2. Role of geomorphic site types and regions

Striped bass use of geomorphic site types varied. Residence times were much higher at confluence junctions than in confluence arms ($p < 0.001$; Fig. 5A vs. 5B). Striped bass did not spend the same amount of time at the junctions of the 4 individual PIE confluences (Fig. 5A); residence time was much higher at the West Creek confluence junction than the Grape Island confluence junction, whereas the time spent in Rowley and Third Creek confluence junctions was intermediate ($p < 0.001$; Fig. 5A). When only the confluence arms were considered, residence times at all confluence sites were low but variable (Fig. 5B). Striped bass had low and relatively similar residence times at all exit sites (Fig. 5C). Use of non-confluence sites was highly variable (Fig. 5D). Within the non-confluence physical site type, mean residence times

(A) Tagged fish detected (%)



(B) Trajectory of detections (Fish 57609)



(C) Trajectory of detections (Fish 57613)

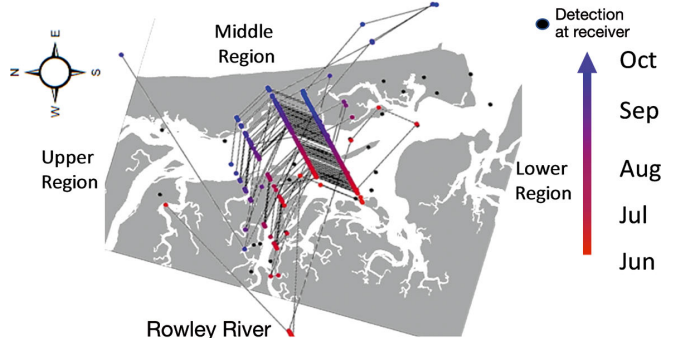


Fig. 4. (A) Tagged striped bass (% of 59 individuals with multi-year tags) detected by sample weeks post-tagging (1–16) in 2015. Fish migrated out of Plum Island Estuary (PIE), in October–November and were detected elsewhere along the Atlantic coast. (B,C) Examples of trajectories by 2 individuals: raw detection data that shows integrated space use within PIE. On these trajectories, the x - and y -axes are latitude and longitude, respectively (i.e. the maps are rotated 90° anticlockwise to the conventional geographic orientation); z -axis is time. Points are detections. These graphics depict the complexity of spatial distribution for mobile fish like striped bass and the need for multiple distributional metrics such as the 3 responses we present here

at Sites 3, 18, 19, and 20 were very low while mean residence times at Sites 12 and 13 were higher but still variable. The mean amount of time striped bass spent across geomorphic site types differed ($p < 0.001$; Fig. 5E); study area exit sites had the lowest

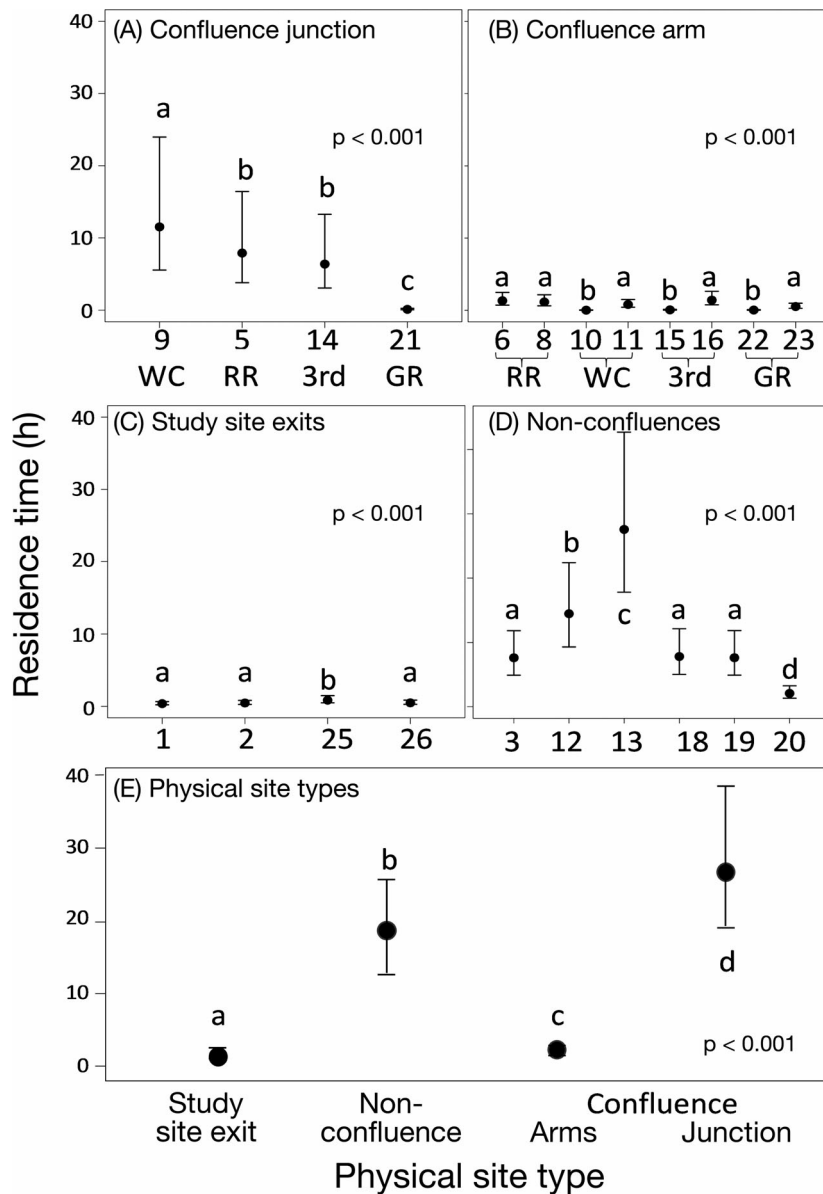


Fig. 5. Mean ($\pm 95\%$ CI) residence time for striped bass by physical site categories: (A) confluence junctions, (B) confluence arms, (C) study site exits, (D) non-confluence sites, and (E) a comparison of all physical site categories. WC: West Creek; RR: Rowley River; 3rd: Third Creek; GR: Grape Island. Receiver site numbers are shown on some panels. For confluence arms (B), statistically significant residence times were unlikely to be ecologically meaningful because of the very low numerical values of these data

residence times of all physical site types; residence times at confluence arms were also low. Non-confluence sites, on average, had intermediate residence times, while confluence junctions had the highest residence times.

Residence times also differed across PIE regions ($p < 0.001$; Fig. 6). Striped bass spent the least amount of time at receivers in the Lower region, followed by

sites in the Upper region; residence time was highest in the Middle and Rowley River regions. Results for physical site types and regions, calculated with range-adjusted data (data set 2), were similar (Supplement 2).

3.3. Multi-metric distribution patterns

The number of unique individual striped bass were not evenly distributed throughout the estuary ($\chi^2 = 171.22$; $p < 0.001$; Fig. 7A); number detected was higher than expected at some sites (receivers 3, 4, 5, 13, 14, 18, 20, 24, and 26; Fig. 7A; green bars) and lower than expected at others (receivers 2, 8–12, 15–16, 21–23, 25; Fig. 7A; red bars). Even though the number of unique individuals was highly variable, some striped bass individuals visited all receivers (Fig. 7A), suggesting that these mobile fish used the entire estuary.

Mean site-specific residence time was also highly variable and uneven across the estuary ($\chi^2 = 46270.33$; $p < 0.001$; Fig. 7B). Mean residence time for acoustically tagged striped bass was higher than expected at some sites (receivers 4, 5, 7, 9, 12, 13, 14, 16, 17, 18, and 19; Fig. 7B; green bars) and lower than expected at other sites (receivers 1, 2, 6, 8, 10, 20–23, and 25–26; Fig. 7B; red bars). Mean number of movements also varied across sites and reflected different location-specific patterns of across-site activity (Fig. 7C). Despite the above-described differences in receiver-specific fish behavior, none of our 26 receivers recorded zero residence time or zero number of movements (Fig. 7B,C).

When all 3 distributional responses were considered together, intriguing patterns emerged. First, more individuals used the central 'highway' created by the north–south channel that intersects the east–west axis of the open sound (Fig. 8A; green circles). Second, in general, tagged striped bass spent more time in the Middle region that intersects the north–south axis of Plum Island Sound, as well as the adjacent Rowley

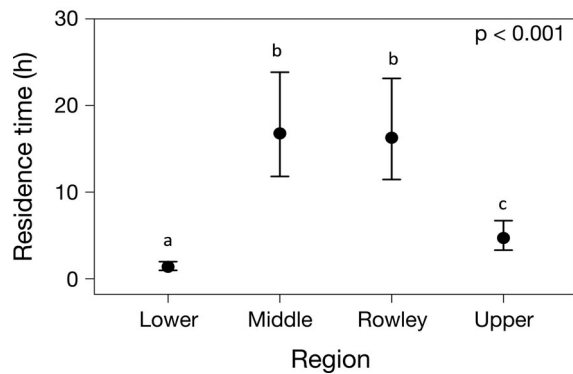


Fig. 6. Statistical differences in striped bass residence time among Plum Island Estuary regions

River region (Fig. 8B; green circles). Third, when these responses were combined, 4 different spatial patterns emerged (Fig. 8C) that formed statistically stable clusters (Jaccard scores ≥ 0.88 ; Fig. 9).

The first cluster (C1) contained open sound sites that were centrally located along an east–west axis (yellow circles, Fig. 8C; Sites 1, 3, 4, 6, 17–21, and 24–26, Fig. 9A). Sites in this cluster generally had high num-

bers of unique individuals (Fig. 9B) that stayed at each site for a relatively brief time (low or moderately low residence times; Fig. 9C) and moved little between receivers (low across-receiver number of movements; Fig. 9D). When all metrics were considered together, these sites were used briefly by many fish.

The second cluster (C2) contained sites at the edge of our study area (relative to both north–south and east–west axes) and included confluence arms (red circles, Fig. 8C; Sites 2, 8, 10, 11, 15, 16, 22, and 23, Fig. 9A). This cluster included sites with low numbers of unique individuals (Fig. 9B), low receiver-specific residence times (Fig. 9C) and low (or relatively low) across-receiver number of movements (Fig. 9D). When all metrics were considered together, these sites were used little by few fish.

The third cluster (C3) included sites in the middle of PIE (green circles, Fig. 8C; Sites 5, 7, 13, and 14, Fig. 9A). These sites had high numbers of unique individuals (Fig. 9B), relatively high residence times (Fig. 9C), and relatively high across-receiver number of movements (Fig. 9D). When all metrics were considered together, these sites were heavily used

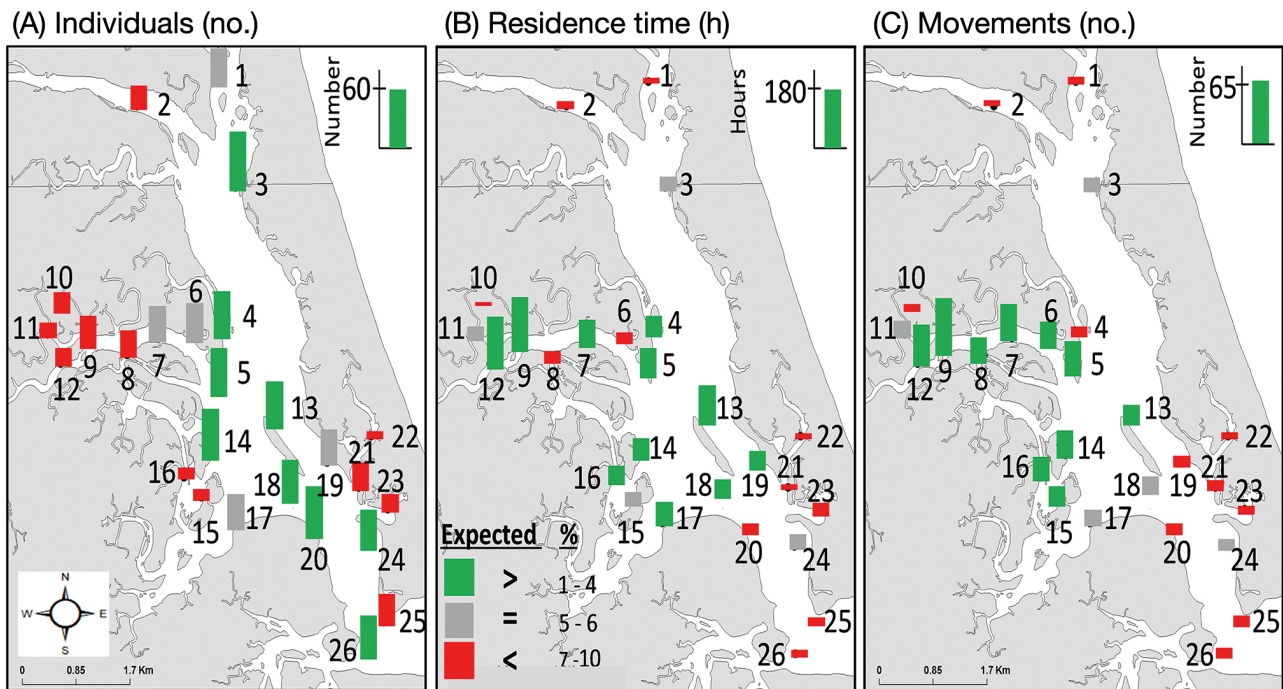


Fig. 7. Spatial distribution of acoustically tagged striped bass within Plum Island Estuary, July–September 2015. (A) Numbers of unique individuals detected at each receiver, (B) mean site-specific residence time, and (C) mean number of movements across receivers. Receiver numbers indicated next to bars; a scale bar is shown in the right top corner of each plot. Colors illustrate how site use differed: green: highest data points (1–39% of ranked data); gray: middle data points (40–59%); red: lowest data points (60–100%). This color scheme generally corresponds to the greater than expected values that would occur if tagged fish were evenly distributed (green); as expected if fish were evenly distributed (gray), and less than expected if fish were evenly distributed (red). Predictions for an even distribution (same numbers across receivers) were determined from the chi-squared analysis with Monte Carlo simulations

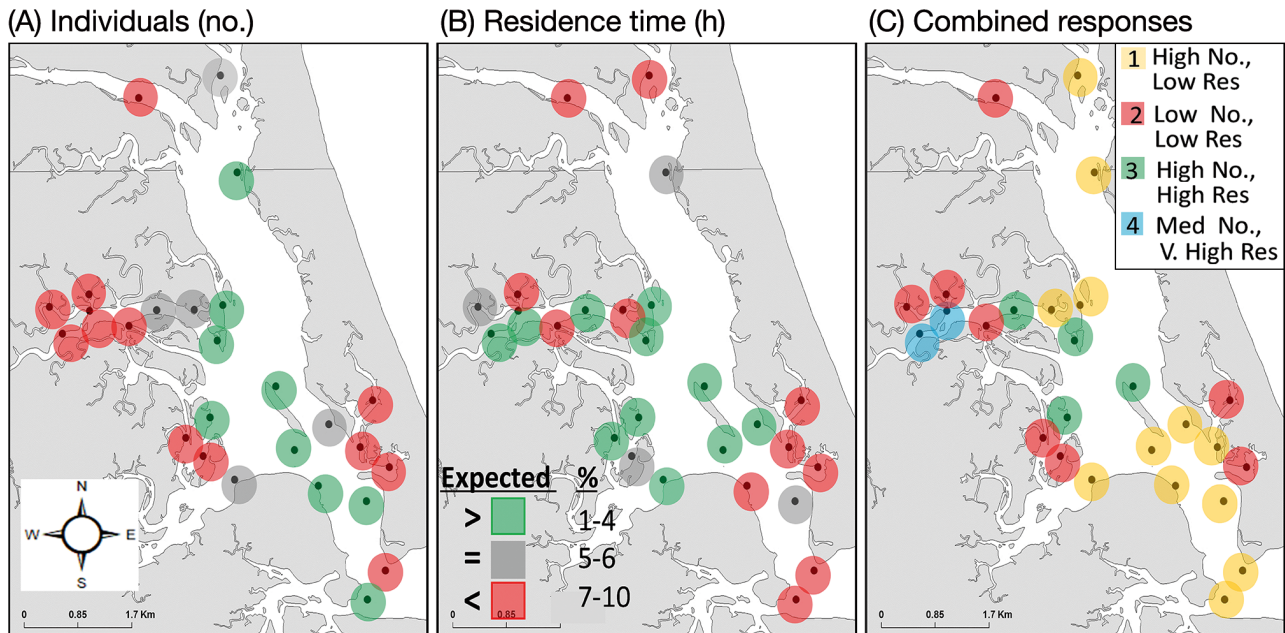


Fig. 8. Areas within Plum Island Estuary where (A) more (green) or less (red) numbers of unique striped bass individuals were present; (B) individuals resided for more (green) or less (red) time; and (C) combined metric patterns from the cluster analysis (C1: high numbers of unique individuals but low residence times; C2: low numbers of unique individuals and low residence times; C3: high numbers of unique individuals and moderately high residence times; and C4: moderate numbers of unique individuals with very high residence times. Metrics by clusters associated with these data are shown in Fig. 9. Number of movements most often mirrored residence time

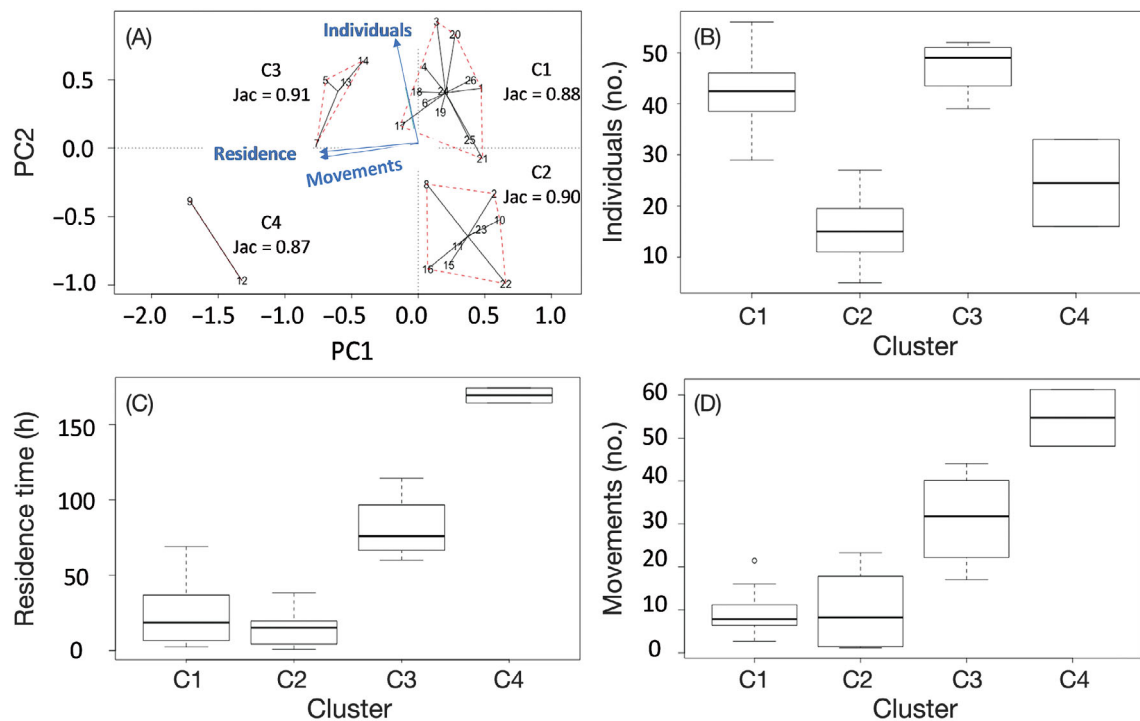


Fig. 9. Cluster analysis of our 3 striped bass telemetry responses (number of unique individuals, residence time, and number of movements across receivers) for 26 receiver sites. Shown are: (A) silhouette plots for clusters 1–4 (C1–C4) with Jaccard values, and (B) number of unique individuals, (C) residence time, and (D) number of movements. Boxes: 1st and 3rd quartiles; mid-line: median; whiskers: $\pm 1.5 \times$ interquartile range; points: outliers

(residence and movement) by many fish.

The last cluster (C4) included select Rowley River sites (blue circles, Fig. 8C; Sites 9, 12, Fig. 9A). These sites had medium numbers of unique individuals (Fig. 9B), extremely high residence times (Fig. 9C), and extremely high across-site movements (Fig. 9D). When all metrics were considered together, these sites were major use areas (residence and movement) for a select group of individual fish.

Categorical data map classifications (Fig. 8A,B) and continuous data clusters (Figs. 8C & 9B–D) generally agreed. However, some sites were differentially classified (e.g. were intermediate values, had opposing trends for residence and movements, or were located at the edge of clusters) because of the 2 modes of calculation. Trends for the same metrics calculated using range-adjusted data set (data set 2) were ecologically similar (Supplement 2).

3.4. Geographic context for confluences within the seascape

Network analysis refined our understanding of the importance of confluence junctions, confirming that most fish were detected at most receivers at least briefly (many arrows; Fig. 10A), but that the amount of time tagged fish spent at each receiver location was variable (different bubble sizes; Fig. 10A). However, the most connected receiver sites (i.e. high centrality) were not always the most visited (i.e. high residence time). Middle and Rowley River region receivers were used by many fish (high centrality: Middle receivers 13, 14, 17, 18, and 19; Rowley: 5, 6, 7, and 9), but not always for a long period of time (high residence time: Middle: 13 and 14; Rowley: 5 and 9; Fig. 10B). However, confluence junctions in the Rowley and Middle regions (receivers 5, 9, and 14) were both connected (high centrality) and heavily used (high residence time) (Fig. 10B).

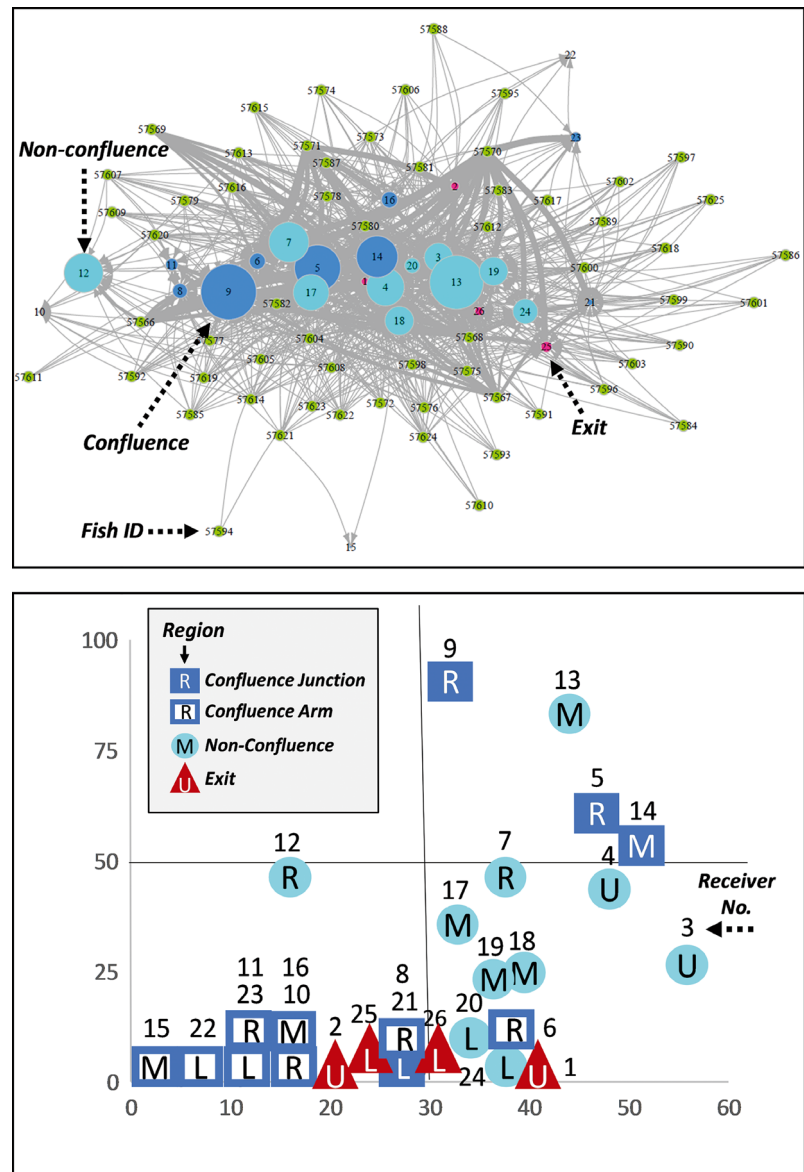


Fig. 10. (A) A network analysis of time, examined common use of 26 telemetry receiver sites by 59 tagged striped bass in Plum Island Estuary. Green dots and related numbers: individual fish IDs; circles: receivers (receiver numbers indicated within the symbol); colors: site types (blue: confluence; aqua: non-confluence; red: exits). Black dotted arrows: examples of these site types. Receiver circle size: magnitude of residence times per receiver for all fish that visited that receiver; arrow thickness: number of fish that visited each receiver. If individual fish did not visit multiple receivers, the network bubble plot would have few arrows. If groups of fish visited different groups of receivers, distinct clusters would exist in the data. If only where the fish were located was important, resident time bubbles would be similar across receivers. (B) To understand the geographic context of confluences, especially whether certain geomorphic site types in specific regions grouped together, we plotted each receiver by network centrality and residence. Geomorphic site types are indicated by color and shape (solid blue square: confluence junction; unfilled blue square: confluence arms; filled aqua circle: non-confluence; filled red triangle: exit). Region is indicated within the symbol (U: Upper; M: Middle; L: Lower; R: Rowley); receiver numbers are next to the symbol. Perpendicular black lines at 50% of the x- and y-axes create 4 quadrants of residence-centrality values

4. DISCUSSION

4.1. Roadmap

Our research identified take-home messages that can inform research and management issues for seascape distribution of mobile organisms in estuarine, coastal, and marine ecosystems (Fig. 1). These take-home messages fell into 2 categories — (1) the important role of confluences and (2) insights from multi-metric spatial patterns — which, taken together, led to a third summary insight about the value of a geographic context for site-specific geomorphic features. We discuss each category and associated discoveries in detail below. In so doing, we note how our study fills existing gaps and points to the next generation of research questions.

4.2. Role of confluences

Our understanding of the importance of confluences arose from comparisons of tagged fish across multiple geomorphic site types including confluences, non-confluences, and exits. Many individual striped bass visited but spent little time at PIE exits. We would expect that many coastal migrants would enter and leave PIE during exploratory coastal movements, and, in so doing, would spend little time at these transitional exit sites. Non-confluences were used for highly variable time periods (e.g. highest mean residence time for a non-confluence location [receiver 13]: 85.22 h; lowest [receiver 20]: 6.66 h). Kennedy et al. (2016) also found that non-confluence sites in PIE had both the highest and lowest fish counts. This variation is probably a consequence of the wide range of physical conditions that characterize non-confluences (Torgersen & Close 2004, Franca et al. 2012, Jin et al. 2014).

Confluence junctions acted as ecological hotspots for striped bass. Confluences are geomorphically important in aquatic ecosystems (e.g. Poole 2002, Benda et al. 2004, Rice et al. 2006) and are an increasingly common focus of ecological studies (e.g. Osawa et al. 2011, Czegledi et al. 2016, Boddy et al. 2019). Confluences can increase biodiversity through higher habitat heterogeneity, better feeding opportunities, and physiological refuges from stressful environments (e.g. Breau et al. 2007, Brewitt et al. 2017). The confluence is a multi-faceted interactive landscape feature. Specifically, an individual confluence includes one or more upstream tributary arms that flow together into the shared downstream junction.

Tributaries that form the confluence arms can drain a substantial watershed area such that terrestrial-associated nutrients and detritus can fuel aquatic productivity within and downstream of confluences (e.g. Kiffney et al. 2006, Rice et al. 2008). These components of the confluence interact bidirectionally both through the upstream-to-downstream delivery of productivity from the arms to the junction and through the creation of a downstream-to-upstream corridor that mobile consumers can use for exploration and feeding.

Within-confluence position affected striped bass distribution, in that tagged striped bass spent much more time at confluence junctions than confluence arms. Thus, confluence junctions are where mobile fish, such as striped bass, aggregate. In our research, both arms and junctions were spatially adjacent and within the geographic area commonly used to delineate a confluence. Although other studies have examined biodiversity near confluences in river systems (e.g. Hitt & Angermeier 2008), few previous studies have examined how mobile fish use confluence components as we have done here. Viewing confluences as a complex entity with multiple components (i.e. arms, junctions) is a useful approach for understanding how they influence fish distribution. Our insights on within-confluence location can be used to standardize future sampling and analysis (i.e. identify the same within-confluence location across studies), conceptualize future studies that examine the ecological role of confluences for mobile organisms, and apply network dynamics to aquatic animal ecology (e.g. identify how confluence junctions act as network nodes).

Not all confluence junctions in PIE functioned the same way relative to striped bass distribution. The amount of time tagged fish spent at individual confluences of a similar size varied dramatically. For example, West Creek was used much more than Grape Island. Specific characteristics of the arm and junction components of confluences can differ (e.g. location, physical conditions, productivity, complexity, connectivity; Kennedy et al. 2017). Anecdotal observations on fish distribution at confluences are common. Investigations of how confluences affect fish at a landscape scale are increasing (e.g. Czegledi et al. 2016, Boddy et al. 2019); however, relatively few previous studies have explicitly compared physical differences across multiple confluences relative to the physical habitat characteristics that are important to mobile fish. Our results emphasize the need to understand structure and function of across-confluence variation and the ecological consequences of this

variation for mobile organisms (e.g. what characteristics of Grape Island caused this confluence to attract and retain so few striped bass?).

Variation in fish use of individual confluences may depend on the relative menu of abiotic and biotic conditions available to fish across the buffet of accessible sites (i.e. confluence and neighboring habitat patches). Elsewhere, examining habitat mosaics reveals a different pattern of organismal diversity than the pattern shown by examining a single, isolated habitat type (Hitchman et al. 2018). Likely, relative foraging profitability, resource predictability, and abiotic compatibility influenced how much time striped bass spent at individual confluences. The most profitable individual confluence junctions (Rowley, West Creek) may offer these fish a dependable and predictable food source in a consistently identifiable location with acceptable biotic conditions. Relative to foraging profitability, the increased and predictable productivity associated with the confluence (described above) can include the preferred prey of striped bass. Relative to resource predictability, striped bass can readily and repeatedly locate the geographically fixed confluence junction. Relative to abiotic compatibility, confluences may or may not be more physiologically more hospitable than neighboring estuary locations. Our prediction that confluences may be ecological hotspots because of their cumulative benefits compared to the neighboring mosaic of patches to which mobile fish have access is an intriguing and testable focus for future research.

4.3. Multi-metric distribution patterns

Each distributional metric provided a different piece of information about spatial heterogeneity for striped bass within our estuarine seascape. First, the number of unique individuals that visited each receiver site identified whether the entire tagged population or just a few individuals used a location. This metric (number of unique individual fish) is common in traditional assessment sampling and telemetry studies (e.g. Humston et al. 2005, Dewar et al. 2008, Furey et al. 2013). Residence time showed whether a fish stayed at a site or was just passing through. Residence time is an ecologically useful metric for understanding fish distribution and behavior (e.g. for identifying contingents and metapopulations; Childs et al. 2015) and is measured with increasing frequency in the telemetry literature, albeit with different methodologies across studies (e.g. Reubens et al. 2013, Capello et al. 2015, Taylor et al. 2017). Finally,

number of movements between receivers is frequently calculated (e.g. Holland et al. 1993, Gerig et al. 2014, Gannon et al. 2015), but the general utility of movement metrics can be limited by different definitions and interpretations of this metric across studies.

When integrated, our 3 distributional metrics revealed novel insights. All 3 metrics showed higher values at some sites than others. If these distribution metrics were examined in isolation, contrasting (and potentially erroneous) conclusions could be drawn. For example, receiver 3 had high numbers of unique individuals, low residence times, and high numbers of movements. Examining just the number of unique individuals, we might conclude that this was an important location for striped bass within the estuary. Using just residence time, however, we might conclude that Site 3 was an unimportant location for striped bass. Using just number of movements, we might again conclude that this is an important location for striped bass across-site activity. Combining all 3 metrics, this location appears to be a transitional location that was used briefly by many fish. By using integrated metrics to categorize sites across the entire estuary, we detected not just transitional sites (C1), but also little-used sites (C2), sites with a large active aggregation of striped bass (C3), and sites with a small active aggregation of striped bass with high site fidelity (C4). Elsewhere, residence and movement have been examined together to assess size- and sex-specific habitat use (Chin et al. 2016), stopovers (Hollema et al. 2017), spawning aggregations (Lowerre-Barbieri et al. 2013, Biggs & Nemeth 2016), and ecological responses (e.g. home range, site fidelity, spawning migration, habitat specialization, and social traits; Teesdale et al. 2015, Gardiner & Jones 2016). In general, few telemetry studies combine all 3 metrics at sites across an ecosystem as we have done here (but see Gerber et al. 2019b).

4.4. Summary: providing a geographic context for geomorphic effects

Understanding where mobile animals are located and why is critically important for addressing many research and management issues in estuaries and other ecosystems (Switzer 1993, Roshier et al. 2008, Rous et al. 2017). Relative to research, the impact of top predators is important to ecosystems in general (Estes et al. 2011). In addition, predator distribution can change ecosystem energetics (Rosenblatt et al. 2013), initiate top-down effects (Heithaus 2008, Altieri et al. 2012, Casini et al. 2012), impact prey communi-

ties (Sergio et al. 2005, Altieri et al. 2012, Fischer et al. 2012), and spatially connect distant ecosystems (Webster et al. 2002, Mather et al. 2013). Relative to management, knowledge about the distribution of mobile fish can inform decisions about habitat use and protection (e.g. DeCelles & Cadrin 2010), estimate angler impact (Coleman et al. 2004), aid fisheries management (Crossin et al. 2017), make recommendations about marine protected areas (e.g. Espinoza et al. 2015, Filous et al. 2017), assess invasive species distribution and impact (e.g. Binder et al. 2016), evaluate the success of hatchery fish stocking (Boehler et al. 2012, Cram et al. 2013, Binder et al. 2016), and assist with assessments of wild fish stocks (e.g. Bronte et al. 2007, Currey et al. 2014, Callihan et al. 2015).

Using a stationary telemetry array, we made important discoveries about where mobile fish are located within an estuarine seascape. First, intensive spatial coverage of fish telemetry receivers within discrete areas across an entire ecosystem was a useful way to explore mobile fish behavior. Second, the resulting high-resolution telemetry data can be broken into multiple metrics that, when integrated, reveal intriguing patterns of fish distribution. Third, telemetry methods (fish response, research design, statistical analysis) need to be tailored to specific research goals. For example, calculations with and without detection range provided similar results (above vs. Supplement 2). Fourth, organismal distributions can be linked to physical conditions at larger spatial scales through geomorphology. Fifth, confluences acted as ecological hotspots for striped bass but not all confluences had the same effect. Finally, our network analysis showed that seascape location can provide a geographic context for site-specific data that can improve our understanding of the importance of geomorphology across the estuary-wide distribution of striped bass. This insight on the interaction between geomorphology (especially confluence junction) and region (especially Rowley and Middle) shows that researchers and managers will lose valuable information if they do not interpret the role of geomorphic features within a larger geographic context.

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