Using geomorphology and animal “individuality” to understand ‘scape-scale predator distributions

by

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Abstract

Determining patterns and drivers of organismal distribution and abundance are fundamental and enduring challenges in ecology, especially for mobile organisms at a ‘scape scale. To address the problem presented by individuals whose distributions are dynamic across large geographic areas, here I tracked 59 acoustically-tagged migratory striped bass (*Morone saxatilis*) with an array of 26 stationary receivers in Plum Island Estuary (PIE), MA. Specifically, I asked (1) how these predators were distributed across the estuarine seascape, (2) if these fish used three types of geomorphic sites (exits, confluences, and non-confluences) differently, (3) if distinct types of individual distributional “types” existed, and (4) if fish within distinct distributional groups used geomorphic site types and regions differently. Based on three components of predator trajectories (site specific *numbers of individuals, residence time,* and *number of movements*), striped bass were not distributed evenly throughout PIE. Confluences attracted tagged striped bass although not all confluences or all parts of confluences were used equally. Use of non-confluences sites was more variable than exits or confluences. Thus, geomorphic drivers and regions link mobile organisms to physical conditions across the seascape. Based on spatial and spatial-temporal cluster analyses, these striped bass predators clustered into four seasonally-resident distributional types. These included the (1) *Rowley River* group (fish that primarily resided in the Rowley River), (2) *Plum Island Sound* group (fish that primarily resided in the Middle Sound region), (3) *Extreme Fidelity* group (fish that spent most of their time in PIE at a single receiver location), and (4) the *Exploratory* group (fish that showed no affiliation with any particular location). These distributional groups used geomorphic site types and regions differently. Thus, my data show a rare link between behavioral (i.e., individual

animal personalities) and field ecology (seascape geomorphology) that can advance the understanding of field-based patterns and drivers of organismal distribution.

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Chapter 1 - Geomorphic and regional drivers of seascape distribution for a mobile fish predator

Abstract

Patterns and drivers of organismal distribution and abundance are fundamental and enduring problems in ecology and resource conservation. These issues are especially challenging to address for mobile organisms at a ‘scape scale because their distributions are dynamic and cover a large geographic area. Integrating multiple whole-system responses can help quantify distribution for a range of mobile organisms at a variety of scales. In addition, geomorphic drivers (confluence, non-confluence, and exits) and region may link mobile organisms to physical conditions better than traditional point-specific physical habitat variables. Here, we used migratory striped bass (*Morone saxatilis*) on their feeding migration in Plum Island Estuary (PIE), Massachusetts, to develop a framework for quantifying whole-estuary distributional patterns and drivers of those seascape patterns. Specifically, we tracked 59 acoustically tagged striped bass within a 26 stationary receiver array from June 24, 2015 – October 26, 2015. This array included three types of geomorphic sites four exit receivers (egress to ocean), six non-confluence receivers, and 12 confluence receivers deployed at three locations within four confluences across four regions of the estuary the Upper, Middle, Lower Plum Island Sound, and Rowley River. Most tagged fish were detected monthly (June: 44 fish, 100%, July: 50 fish, 87% August: 48 fish, 81%) until they started to migrate south in the fall (September: 38 fish, 65% October: 8 fish, 13%). Based on three components of predator trajectories (site specific *numbers of individuals, residence time,* and *number of movements*), striped bass were not distributed evenly throughout PIE. By integrating three components of predator trajectories, we constructed an estuary-wide mosaic in which East-West Rowley River sites were associated with high residence and high movements, but low numbers of individuals and North-South mid-channel Sound sites were characterized by high numbers of individuals, but low residence and low movements. Confluences attracted tagged striped bass although not all confluences or all parts of confluences were used equally. Use of non-confluences sites was more variable than exits or confluences. Relative to region, more striped bass were detected in the Rowley River and Middle Sound regions (and spent more time there and moved among receivers more). Our research demonstrated how intensive spatial coverage of replicates of discrete types of geomorphic habitats can be used to inform ecology and fisheries management (i.e., where are the fish spending the most time, and why) and advance the field of movement ecology (i.e., characterize patterns and drivers of movements and distributions of mobile organisms at a seascape scale).

Introduction

Patterns and drivers of distribution and abundance are fundamental and enduring problems in ecology (Stephens and Krebs 1986; Yackulic et al. 2011) and resource conservation (Mittermeier et al. 1998; Bond et al. 2012). Understanding the distribution of fish predators is important ecologically (Heithaus 2008; Espinoza et al. 2016), for conservation (Sergio et al. 2005; Rous et al. 2017), and for management (Coleman et al. 2004; Crossin et al. 2017). In particular, many current scientific and management problems related to predators (e.g. Estes et al. 2011) depend on understanding ‘scape scale distributional patterns of these highly mobile organisms. However, understanding patterns and drivers of mobile organism distribution across a large geographic range, such as a seascape, is difficult because researchers and managers often don’t know where the animals are, when they are found, they don’t stay in one place, and their distribution frequently covers a large geographic area. Without some knowledge of how mobile organisms are distributed through time and space, we cannot study them, manage them, maintain them, or restore them. To address this broad and generalizable ecological and conservation problem, we use migratory striped bass (*Morone saxatilis*) predators feeding seasonally within Plum Island Estuary (PIE), Massachusetts, to construct a general framework for examining whole system distributional patterns and geomorphic and regional drivers of these patterns.

Distribution is important for fisheries and ecology and can change the outcome of many research questions and conservation / management issues (Crossin et al. 2017). Telemetry can be used to assess habitat (e.g. DeCelles and Cadrin 2010), survey use of marine protected areas (e.g. Espinoza et al. 2015), and monitor invasive species distributions (e.g. Binder et al. 2016). Other researchers have suggested how to use this distributional data to help with assessments of both hatchery fish (i.e. Boehler et al. 2012; Cram et al. 2013; Binder et al. 2016) and wild fish stocks (e.g. Bronte et al. 2007; Currey et al. 2014; Calihan et al. 2015). For example, imperiled and overfished species can be effectively protected by assessing site fidelity and activity (Currey et al. 2014). In ecology, understanding distribution is useful for predator-prey relationships (Burkholder et al. 2013; Kessel et al. 2016) and population modeling (Block et al. 2005; Shapeira et al. 2013). Specifically, quantifying cod distribution during iced and open water periods advances understanding of changes in the prey community (Kessel et al. 2016).

The distribution of predators is ecologically important. Predators can affect ecosystem energetics (Rosenblatt et al. 2013), are of social and economic interest (U.S. DOI et al. 2011), and are often at low population levels because of human impacts including harvest (Jackson et al. 2001; Estes et al. 2011). Distributions of predators can have consequences for local ecosystems through top down effects (Heithaus 2008; Altieri et al. 2012; Casini et al. 2012) and other direct and indirect impacts on the prey communities (Sergio et al. 2005; Fischer et al. 2012). For example, the absence of a predator is linked to the complete degradation of a marsh system (Altieri et al. 2012). Most of these predators are highly mobile. As such, predators can energetically connect spatially distant ecosystems (Webster et al. 2002; Mather et al. 2013), but they also require a seascape scale approach (Kennedy et al. 2016, 2017). New tracking tools can help inform ecological issues involving predators.

Understanding where fish are located, why, and if/how they aggregate is important to advance ecology and resource conservation. Physical habitat can be an important driver of organismal distribution (Albanese et al. 2004; Clark et al. 2004). For example, point-specific physical habitat variables (i.e. *depth*, Torgersen and Close 2004; Binsong et al. 2014; *substrate*, Gratwicke and Speight 2005; Franca et al. 2012) are often quantified to explain local distribution. However, these point-specific variables are difficult to measure over large geographic areas and may not be the variables to which mobile organisms react. Because these animals cover a large geographic area and their distribution frequently changes, regularly distributed, point-specific physical habitat variables may not effectively inform distributional patterns of mobile predators at larger scales. Geomorphology is another way of looking at physical drivers of distribution (Dauwalter et al. 2008; Johnson and Host 2010; Gorski et al. 2013). For example, Kennedy et al (2016, 2017) showed that physical “discontinuities” or rare, irregular physical features such as drop-offs, sandbars, depth variation, confluences, and islands have a disproportionate effect on seascape distribution of striped bass. We build on this geomorphic discontinuity organizing framework here.

Confluences, the junction where two bodies of water come together, is a common type of discontinuity in aquatic systems. An increasing body of ecological literature suggests that this particular type of geomorphic feature can be an ecological hotspot (Poole 2002; Benda et al. 2003; Rice et al. 2006; Rice et al. 2017)**.** Confluences have been examined relative to ecosystem processes (e.g. Rice et al. 2017). The confluence concept is increasingly being used to describe and understand organismal patterns (Hitt and Angermeier 2008; Osawa et al. 2011; Czegledi et al. 2016). For example, one use of the confluence concept, river network position, has been used to assess diversity in riverine ecosystems (Smith and Kraft 2005; Thornbrugh and Gido 2010; Kuglerova et al. 2015). Although important ecological effects are often attributed to confluences, many issues about confluence structure and function remain unknown. For example, do mobile organisms actually use confluences more than non-confluences? Does the effect of individual confluences vary within a system? Do different parts of a confluence function differently? These questions about confluences could help explain mobile fish predator distribution across a whole system.

Geographic region can also influence seascape scale distribution. Some research on organismal distribution has shown differential usage zones across regions (Murchie et al. 2013; Bultel et al. 2014; Kennedy et al 2016; Kessel et al. 2016). This regional scale of aggregation may be an important link between point habitat features and seascape geomorphic features. Specifically in PIE, Kennedy et al. (2016) showed that striped bass were concentrated in the middle region because of the interaction among discontinuities related to river and ocean processes.

Although an increasing body of telemetry data is accumulating, relatively few of these studies seek to understand patterns of seascape distribution and whole-system drivers of those patterns for fish predators. Using the keywords telemetry, acoustic, fish*, array, field, and distribution in Web of Science for a 5-year period 2013-2017, we identified 39 studies (Tab.

1.1). These studies included a variety of fish species in diverse ecosystems. Specifically, of these fish distributional studies, 29 (74%) focused on marine fish, two (5%) examined freshwater fish, and seven (18%) tagged anadromous fish. Fifteen (38%) of these studies were undertaken in estuaries, seven (18%) took place along the coast, eight (20%) researched coral reef fish, four (10%) were undertaken in freshwater ecosystems (1 reservoir, 3 rivers), and five (13%) tracked fish around islands. However, only four (10%) examined the whole system or explicitly noted that their studies were at the ‘scape scale. Few (10%) examined whether fish were evenly distributed across the study area. A small number of these studies linked fish distribution to point specific habitat (10, 26%), geomorphology (1, 3%), exits (7, 18%), regions (7, 18%) or confluences (0). Thus, although many researchers are tracking fish to understand distribution of mobile predator, a gap exists in that few studies connect fish predator distribution with whole systems, seascape scale, and geomorphic measures of habitat.

Striped bass are a model organism to address how to quantify patterns and drivers of mobile organisms related to geomorphic features across a seascape. Atlantic coastal migratory striped bass spawn in the Chesapeake, Delaware, and Hudson Bay estuaries. As subadults (2-4 yrs), they make a seasonal migration up the Atlantic coast into New England for the summer months (typically May-October; Walter et al. 2003; Mather et al. 2010; Pautzke et al. 2010) and may seasonally reside in New England estuaries (Mather et al. 2009; Pautzke et al. 2010; Kennedy et al. 2016). The uneven distribution of these fish has been linked to discontinuities (confluences, sand bars, islands, points, Kennedy et al. 2016), yet the role of individual geomorphologic features has not been systematically tested.

To fill these gaps in predator distribution and geomorphology, we asked three sets of specific research questions. First, relative to *patterns of whole system distribution,* did striped bass use the entire estuary study system (i.e., were they seen at all receivers), were they evenly distributed throughout PIE (i.e., did they use all locations equally), how were they distributed by number?; Did their distribution change with the distributional metric used (*number, residence time, number of movements*). Second, based on residence time, does *geomorphology* explain striped bass distribution? Specifically, are tagged fish more common at three different geomorphic types of sites (confluences, non-confluences, exits)?; are there differences in striped bass use of individual confluence sites, nonconfluence sites, and exits?; are there differences in where striped bass were detected within a confluence site?; are there differences in variability among geomorphic sites?; Third, are there differences in striped bass distribution related to *region* (Rowley River, Upper Sound, Middle Sound, Lower Sound)?

Methods

General Study Site

Plum Island Estuary (PIE) is a temperate estuary located within the cold-temperate Acadian Province on the northeastern coast of Massachusetts, USA (Fig. 1.1a-b). PIE is a bar-built coastal plain estuary with semi-diurnal tides that have an average tidal range of 2.9 m (Deegan and Garritt 1997). PIE includes three major rivers (Parker, Rowley, Ipswich Rivers), and a man-made connection to the Merrimack River (Plum Island River) (Fig. 1.2a). These rivers drain into an open water embayment, Plum Island Sound, characterized by a large central island, Middle Ground. The approximate length of the Sound is 13.2 km with a shoreline length of 262 km (Buchsbaum et al. 1997). This estuary has a surface area of 12.8 km^2 at low tide and 20.0 km^2 at high tide. Mean depth ranges from 1.4 m-5.7 m (http://pie-lter.ecosystems.mbl.edu/content/site-description). PIE has extensive areas of productive, tidal marshes as well as multiple non-vegetated, intertidal sand flats of varying sizes at low tide (7.2 km^2) (http://pie-lter.ecosystems.mbl.edu/content/site-description). Thus, PIE includes substantial heterogeneity in aquatic habitats that affect fish including confluences, depth variation, sand bars, and islands (Kennedy et al. 2016). Ocean access points include Plum Island River, which connects to the coastal Merrimack River and the southern entrance of Plum Island Sound, which connects directly to the Atlantic Ocean. The yearly water temperature ranges from -1.0-28°C and salinity ranges from 0 to 32 ppt.

PIE Geomorphic Features

PIE has seascape-scale geomorphic features that could affect striped bass distribution. Exits from Plum Island Sound include the four egress points on which we focus, Plum Island River, Parker River, Ipswich River, and the south end of Plum Island Sound (Fig 1.2a). PIE has many tidal creek confluences including our four focal confluences, West Creek, Rowley River, Third Creek, and Grape Island (Fig. 1.2b). West Creek is within the Rowley River network. Third Creek is the middle of Plum Island Sound and Grape Island is in the southern Sound near the main estuary access point. We identified three components of each confluence, two arms and a sweet spot nexus. Plum Island Sound also contains many non-confluence sites that may or may not be associated with physical discontinuities. For example, receiver 3 is located in the upper part of Plum Island Sound on a slightly curving marsh edge that contains no tidal creeks, whereas receivers 13 & 18 are on the northeast and southwest sides of a large salt marsh island called Middle Ground (Fig. 1.3a).

PIE Regions

In addition to geomorphology, the estuarine seascape can be divided into four regions: Rowley River, Upper Plum Island Sound, Middle Plum Island Sound, and Lower Plum Island

Sound (Fig. 1.2c) following the divisions used by Kennedy et al. (2016, 2017). Each region is physically different (Kennedy et al. 2016). The Lower region includes the deep mouth of the estuary, the Ipswich River confluence and Grape Island confluence (Fig. 1.2c). The Lower region is deeper and faster with fewer small confluences. The Middle region of Plum Island Sound has many confluences, including the Rowley River mouth, is dominated by salt marsh and tidal creeks, is relatively shallow, has a high proportion of sandbars, and a large salt marsh island, Middle Ground. Because of its size, we considered the Rowley River as its own region. The Rowley River region is dominated by salt marsh, is relatively shallow compared to the Plum Island Sound (<4 m maximum depth), has multiple smaller creeks flowing into it (small confluences), and has many tidal flats and sand bars exposed at low tide. The Upper region of the Plum Island Sound contains the Plum Island River confluence (i.e., an exit into the ocean via the Merrimack River), the Parker River confluence, and a mixture of shallow and deep locations with a few creek inputs.

Geomorphic and Regional Foci

In this research, we seek to understand how striped bass use three types of geomorphic features and four regions in Plum Island. The three geomorphic features are confluences, non-confluences and exits. To test confluences, we examined striped bass distribution in West Creek, Rowley River Mouth, Third Creek, and Grape Island (Fig 1.2b). In each confluence, we deployed three receivers (see details below). The non-confluences include six locations throughout the Plum Island Sound (Fig. 1.3a) and two locations adjacent to Middle Ground Island (Fig. 1.3a). The exits include Plum Island River, Parker River, Ipswich River, and the lower entrance to Plum Island Sound (Fig. 1.3a). The three regions are the Upper, Middle, Lower Plum Island Sound and Rowley River regions (Fig. 1.2c).

Stationary Array

We tracked acoustically tagged striped bass using a 26 stationary receiver array (VR2W-69kHz) (Fig. 1.3b) in which each receiver detected coded pings within a 500 m radius. Receivers were deployed from June 24, 2015 – October 26, 2015. We deployed four exit receivers (receiver numbers 1 - Plum Island River, 2 - Parker River, 25 - Spindle, & 26 - Ipswich River; Fig. 1.3a) and six non-confluence receivers (receiver numbers 3, 12, 13, 18, 19, 20). Non-confluences were chose in all regions based on locations away from confluences where fish were detected in past studies. Confluences of approximately the same size were chosen to span a range of distances from the ocean. Confluences (West Creek, Rowley River, Third Creek, and Grape Island) had three receivers each: West Creek (receivers 9, 10, & 11); Rowley River (receivers 5, 6, & 8); Third Creek (receivers 14, 15, &16); and Grape Island (receivers 21, 22, & 23). For all confluences, we placed one receiver in the central mixing area, i.e., the “sweet spot” (receivers 5, 9, 14, & 21). The other two receivers for each confluence were placed in the “arms” or the contributing rivers to the mixing basin of the confluence, (receivers 6, 8, 10, 11, 15, 16, 22, & 23). A few “neighborhood” receivers in the Rowley River and Plum Island Sound were deployed to detect fish in underrepresented areas and to provide greater spatial coverage of those locations. For example, receivers 7 (in the Rowley River) and 17 (in the Plum Island Sound). We deployed receivers in four regions (Upper, Middle, Lower, and Rowley River). The Upper region consisted of receivers 1-4. The middle region included receivers 13-19. The Rowley River region included receivers 5-12. The Lower region included receivers 20-26. In summary, the majority of receivers were placed in specific locations, across PIE regions, to provide replicates of specific geomorphic treatments across regions.

Fish Tagging

Subadult and adult striped bass (*n*=59; mean fish size = 524 mm, range = 434-623, SE = 5.85) were captured by fly angling with barbless hooks within our four focal confluences (West Creek, Rowley River Mouth, Third Creek, and Grape Island). We tagged fish on 11 days during two tagging events in the summer of 2015. Specifically, we tagged 44 angled striped bass on June 24 – June 29 and 15 striped bass on July 22 – July 26. All striped bass were released near capture locations. We tagged near equal numbers of fish from each location: 13 fish were caught, tagged, and released in West Creek, 14 fish were caught, tagged, and released in Rowley, 17 fish were caught, tagged, and released in Third Creek, and 15 fish were caught, tagged, and released in Grape Island.

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 2015). Tags were less than 2% of the body weight of all tagged fish (Bridger and Booth 2003). Individual fish were anesthetized with Aqui-S 30 mg-L until they lost orientation (mean = 2 min 18 sec). A 15-30 mm lateral incision was made below the pectoral fin, about ¾ of the way to the tip of the fin using surgical scalpels of size 12. The acoustic tag was sterilized using ethanol and inserted into the body cavity, then the incision was closed with 2-4 surgical sutures (Ethicon, braided, coated Vicryl, 3-0, FS-2, 19 mm 3/8c, reverse cutting; mean surgery time = 2:31). Post-surgery, all fish were intramuscularly injected with Liquamycin (0.1 mg/kg) and transferred to a recovery tank filled with ambient water. Fish were released once they regained orientation (mean recovery time = 6 min 15 sec).

Data and Response Metrics

Receiver data were downloaded into VEMCO's VUE software approximately monthly. Each individually coded tag detection was recorded as a single data line including information on receiver station number, date, time, and tag number. Data were compiled from VUE into Microsoft Excel. Data were summarized as three response metrics that quantified distribution of mobile predators*: numbers of unique individuals, residence time,* and *numbers of movements*.

The metric "*unique individuals*" was defined as the number of uniquely coded individual fish that visited a given location over a given time period. For this metric, each fish was counted only once even if it was detected multiple times.

The metric "*residence time*" quantified how much time each fish spent at each location. To calculate residence time, raw detection data from VUE were summarized with VTrack software (R 2.1.2 software; R Core Team; Campbell et al. 2012). Residence time at each receiver site was recorded when a tagged fish was detected twice until it was not detected anywhere for one hour or was detected at another receiver site. Residence time was then used to determine if fish favored certain locations over others (long vs. short residence times respectively).

The metric "*number of movements*" was calculated as the number of times a fish arrived or left a receiver site for a standard time period.

Statistical Analysis

Total *unique individuals*, average *residence time* for all fish at each receiver, and average *movement* for all fish at each receiver were calculated and plotted on a map of Plum Island Estuary to depict seascape patterns. All three response metrics observed at each receiver were compared to what would be expected to an even distribution. An even distribution was calculated as what would be expected if the same number of fish were present at each receiver (unique individuals), if fish resided for the same amount of time at each receiver (residence time), and if fish moved the same number of times at each receiver (number of movements). Observed was compared to expected using a Chi-square analysis with 2000 Monte Carlo simulations (‘chisq.test’ function, ‘stats’ package, R).

Whether geomorphology affected striped bass residence time was statistically tested using a one-way ANOVA (‘anova’ function, ‘stats’ package, R) in which geomorphic treatment (confluence, non-confluence, exit) was the independent variable and residence time per fish per receiver was the response. A one-way ANOVA was also used to compare differences among (a) individual confluences, (b) individual non-confluences, (c) individual exits, and (d) parts of confluences (arms vs sweet spots). For all of these geomorphic analyses, the individual fish at a receiver was the experimental unit. Zeros (i.e., all tagged fish were considered for all receivers) were included to test the entire tagged population. Data were log transformed to meet assumptions of normality. A post-hoc Tukey test (‘tukeyHSD’ function, ‘stats’ package, R) identified which geomorphic sites and regions were significantly different. A critical alpha value of $P < 0.05$ was used to determine statistical significance. A coefficient of variation was calculated for all confluences and non-confluences to compare variability across sites in geomorphic treatments.

Results

Overview

Across the six-month field season (June-November, 2015), we recorded 447,972 detections of tagged fish, for an average of 7,593 detections per individual tagged striped bass (range = 78-22,460; SE = 799; $n = 59$). In addition, during the summer, most tagged fish were detected monthly (June: 44 fish, 100%, July: 50 fish, 87% August: 48 fish, 81%) until fish started to migrate in the fall (September: 38 fish, 65% October: 8 fish, 13%). In 2015, tagged fish were detected at an average of 15 (of 26; 58%) receivers (range: 6-23, SE: 0.6). Overall, tagged fish spent on average 46 hours (range: 9.2-393.4 hours, SE: 16.4) at all receiver locations. Fish moved on average 167 times (range: .2-172.8, SE: 3.7) among all receiver locations. Fish were detected for 124 days, with an average of 69 days per fish (range: 4-117 days, SE: 4.43). In November, at the end of the first field season, all but 1 of the 59 (1.6%) tagged fish had left the estuary. After striped bass left, 37/59 (63%) of fish were seen outside of Plum Island.

Maps: Numbers of Unique Individuals

Numbers of unique individual tagged striped bass that visited individual receivers within PIE were unevenly distributed. The number of unique individuals detected was low at some sites (receivers 2, 10, 11, 12, 15, 16, 22, 23) and high at other sites (receivers 1, 3, 4, 5, 6, 9, 13, 14, 17, 18, 20, 24, 26; Fig. 1.4a). Based on the chi-square analysis, more fish than expected were present at some sites (receivers 1, 3, 4, 5, 6, 7, 13, 14, 17, 18, 19, 20, 24, & 26; $P<0.001$; $\alpha = 0.05$; $\chi^2 = 171.22$; Fig. 1.5a). Fewer individual striped bass than expected were detected at other locations (2, 8, 9, 10, 11, 12, 15, 16, 21, 23, & 25; ($P<0.001$; $\alpha = 0.05$; $\chi^2 = 171.22$; Fig. 1.5a). Even though fish were unevenly distributed, striped bass visited all receivers (Fig. 1.4a), suggesting that these mobile fish predators could and often did use the entire estuary ecosystem.

Map: Residence Time

Average residence time was extremely variable across receivers. Mean residence time for acoustically tagged striped bass was low at some sites (receivers 1, 2, 3, 6, 8, 10, 11, 15, 16, 20, 21, 22, 23, 24, 25, & 26) and high at others (receivers 4, 5, 7, 9, 12, 13, 14, & 17) (Fig. 1.4b). None of our 26 receivers had zero residence time. Residence times were not the same across receivers ($P<0.001$; $\alpha = 0.05$; Fig. 1.5b). Higher residence time than expected (i.e., all fish were spending the same amount of time at all receivers) occurred at some locations (receivers 4, 5, 7, 9, 12, 13, 14, & 17; $\chi^2 = 46270.33$; Fig. 1.5b). Lower residence time than expected was observed at all other locations (receivers 1, 2, 3, 6, 8, 10, 11, 15, 16, 20, 21, 22, 23, 24, 25, & 26; $\chi^2 = 46270.33$; Fig. 1.5b).

Map: Number of Movements

Average movements also varied across sites. Mean amount of movements for acoustically tagged striped bass in 2015 was low at some sites (receivers 1, 2, 3, 4, 10, 11, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, & 26) and high at others (receivers 5, 6, 7, 9, 12, 13, & 14; Fig. 1.4c). Numbers of movements of striped bass at all receivers within PIE were not the same at all receivers ($P<0.001$; $\alpha = 0.05$; Fig. 1.5c). More movements were made than expected at some locations (Receivers 5, 6, 7, 9, 12, 13, & 14; $\chi^2 = 15310.28$; Fig. 1.5c). Fewer movements were made than expected at all other locations (receivers 1, 2, 3, 4, 10, 11, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, & 26; $\chi^2 = 15310.28$; Fig. 1.5c).

Map: Integrated Responses

When all responses are considered together, intriguing seascape patterns emerged. First, more individuals use the central “highway” created by the channel (Fig. 1.6a). Second, fish are spending more time in the central basin of the Plum Island Sound and the Rowley River (Fig. 1.6b). Third, when we combine all responses, four different patterns were evident (Fig. 1.6c). The first pattern (red) shows areas with low numbers of individuals and low residence times (receivers 2, 6, 10, 11, 15, 16, 21, 22, 23, & 25; Fig. 1.6c). The second pattern (yellow) shows areas of receivers that have high numbers of individuals, but low residence times (receivers 1, 3, 18, 19, 20, 24, & 26; Fig. 1.6c). The third pattern (light green) shows areas that have low numbers of individuals, but high residence times (receivers 6, 7, 9, & 12; Fig 1.6c). The last pattern (dark green) shows areas that have both high numbers of individuals and high residence times (receivers 4, 5, 13, 14, & 17; Fig. 1.6c).

Geomorphic Type: Numbers

Numbers of unique striped bass varied across geomorphic site types. The exit sites (receivers 1, 2, 25, & 26) had moderate numbers of individuals (22-44 unique individuals) as almost all of these migratory striped bass left PIE for the ocean in the fall through an exit (Fig. 1.4a). Many tagged striped bass used the Rowley River confluence (receiver numbers 5, 6, & 8; average: 40 range: 14-50 unique individuals) (Fig. 1.4a). Numbers of fish were variable at Third Creek (receiver numbers 14-16; average: 25, range: 11-52 unique individuals) and West Creek (receivers 9-11; average: 21, range: 14-33 unique individuals) (Fig. 1.4a). Grape Island receivers (21-23) detected fewer unique individuals (average: 17, range: 5-43 unique individuals) (Fig. 1.4a). Detections of unique individual striped bass at non-confluence sites (receivers 3, 12, 13, 18, 19, 20) were highly variable (Average: 43, range: 44-56 unique individuals; Fig. 1.4a).

Geomorphic Type: Residence Time

Residence time varied across geomorphic site types and regions. The exit sites (receivers 1, 2, 25, & 26) had very low residence time (average: 2.38 hours, SE: 0.46, range: 1.76-3.56) because fish were detected by exit receivers briefly as they left the estuary during the southward fall migration. At the Rowley River confluence (receivers 5, 6, & 8), residence time varied from 6.5 hours – 62.9 hours on average (average: 25.67, SE: 5.59). West Creek (receivers 9-11) had high but variable residence times that ranged from 0.14-91.53 hours (average: 32.04, SE: 11.39). At Third Creek (receivers 14-16) times were intermediate, from 0.32 – 50.90 hours on average (average: 19.67, SE: 5.54). Grape Island (receivers 21-23) had lower residence times that ranged from 0.21-2.94 hours on average (average: 1.41, SE: 0.69). Residence times at non-confluence sites (receivers 3, 12, 13, 18, 19, 20), like unique individuals, were highly variable (average: 41.75, SE: 7.41, range: 6.66-85.22) (Fig. 1.4b).

Geomorphic Type: Movements

Movements of striped bass varied across geomorphic site types. The exit sites (receivers 1, 2, 25, & 26) had very low movements (average: 3.92, SE: 0.41, range: 1.14-7.14), as the fish exited infrequently. At the Rowley River confluence (Receivers 5, 6, & 8), movements varied from 21.5-36.17 on average (average: 28.13, SE: 2.83). West Creek (receivers 9-11) had high but variable movements that ranged from 1.7-61.29 (average: 38.44, SE: 5.28). At Third Creek (receivers 14-16) movements were intermediate, from 17.00 – 27.32 hours on average (average: 25.51, SE: 3.44). Grape Island (receivers 21-23) overall had lower movements that ranged from 1.25-5.15 movements on average (average: 4.51, SE: 0.74). In all four confluence sites, movements at the upper "arm" sites (receivers 6, 8, 10, 11, 15, 16, 22, & 23) were less than at the "sweet spots" (average: 3.75, SE: 0.90, range: 0.14-7.78; Fig. 1.5c). Residence times at non-confluence sites (receivers 3, 12, 13, 18, 19, 20), like unique individuals, were highly variable (average: 16.43, SE: 1.27, range: 1.25-23.3; Fig. 1.4c).

Test of Geomorphic Treatments

Striped bass residence times were different across geomorphic types (exits, confluences, non-confluences; Fig. 1.7a, $P<0.001$). Exit sites had significantly lower residence time than either confluence or non-confluence sites (Fig. 1.7a). Exits had little variation across sites because all exits had consistently low residence times (Fig. 1.7b). Residence times at confluence sites were lower than non-confluence sites (Fig. 1.7a) but higher than at exit sites. Confluences had an intermediate level of variation across sites (Fig. 1.7b). Non-confluences had highest mean residence time although non-confluences were also the most variable (Fig. 1.7b). Confluences had a higher coefficient of variation than non-confluences and exits (Fig. 1.7c).

All exit sites had low residence times and were not significantly different (Fig. 1.7d). Within the confluence category, tagged striped bass spent more time in West Creek than Rowley confluence or Third Creek compared to Grape Island ($P<0.05$; Fig. 1.7e). Within the non-confluence category, mean residence time at sites 3 and 20 were low but not very variable. Residence time at sites 18 and 19 were average but variable. Sites 12 and 13 had means above the estuary average but were highly variable ($P<0.05$; Fig. 1.7f).

Confluence Parts

At all four confluence sites, residence time at the upper “arm” sites (receivers 6, 8, 10, 11, 15, 16, 22, & 23) were less than at other confluence sites (average: 3.75, SE: 0.90, range: 0.14-7.78) (Fig. 1.4b). In all confluence sites, many fewer unique striped bass used the upper “arm” sites (receivers 6, 8, 10, 11, 15, 16, 22, & 23) than the “sweet spots” (average: 18, range: 5-42 unique individuals) (Fig. 1.4a). Striped bass did not use all parts of the confluence equally. Specifically, tagged striped bass had significantly higher residence times at “sweet spot” receivers than “arms” ($P<0.05$; Fig. 1.8). All “arm” sites were well below average residence time across the estuary ($P<0.05$; Fig. 1.9). All “sweet spot” sites were higher than average residence at all confluences across the estuary except Grape Island ($P<0.05$; Fig. 1.9).

Region

Residence time differed across regions. The Rowley, Upper, and Middle regions all had statistically higher residence time than the Lower regions ($P<0.05$; Fig. 1.10) with the Rowley and Middle regions having higher means than the Upper region.

Discussion

Take-home Message 1: High Resolution Telemetry Data

High resolution telemetry data can help link whole system fish distributions to seascape-scale physical conditions in a way that provides novel insights. Our study of seasonally resident fish predators (*n*=59 tagged striped bass) within an acoustic array of 26 stationary receivers deployed for 124 days resulted in high resolution distribution data (400,000 + detections; average: 7,593 per fish) for mobile fish predators that stayed within a 20.0 km^2 estuary for an average of 69 days. In contrast, many telemetry studies track fish for only a limited period of time in limited locations (e.g., 11 tagged fish, 120 days, Humston et al. 2005; 8 tagged fish, 29 days, Furey et al. 2013). Empirical trajectories are relatively rare because many impediments exist to collecting this type of data, i.e., many animals need to be tagged and the tagged animals need to be detected at many locations, move at regular intervals, but stay within the study system. This is especially difficult because researchers don't know where the animals are and where they go which makes setting up stationary arrays difficult. Often, telemetry arrays are placed within large open areas from which tagged animals come and go and full coverage is impossible (e.g. Humston et al. 2005; Dewar et al. 2008; Herbig and Szedlmayer 2016). This was not the case for our dataset. Consequently, with our high-resolution data, we were able to examine the three metrics *number of individuals*, *residence time*, and *movements* throughout the entire estuary for multiple fish.

Take-home Message 2: Integrated Metrics

Our three metrics revealed different pieces of information about the distribution of individual mobile organisms, which when integrated, revealed novel insights. All three metrics show higher values in certain areas than others. If these distribution metrics were examined in isolation, three contrasting (and erroneous) conclusions could be drawn. For example, receiver 3 had high numbers of individuals, low residence time, and high numbers of movements. Examining just the number of individuals, we might conclude that this is an important location for striped bass within the estuary. Using just residence time, we might conclude that this is not an important location. Using just numbers of movements, we might again conclude that this is an important location. Combining all three metrics, this location appears to be a transitional location where many fish (high number of unique individuals) pass through (high number of movements), but they are not spending time there (low residence time). This integrated insight is a very different interpretation than if number, residence, or movements were viewed in isolation.

Thus, using multiple metrics allowed us to look at seascape distributional patterns at individual sites and sites across the entire ecosystem. First, looking at the number of fish that visited each receiver allowed us to determine whether the entire population or just a few individuals used a location. Using the metric of *number of tagged fish* is common in telemetry studies (Humston et al. 2005; Dewar et al. 2008; Furey et al. 2013) and in traditional assessment sampling. *Residence time*, or how much time a single fish spends at a single location is measured less frequently, and often differently across studies (Reubens et al. 2013; Capello et al. 2015; Taylor et al. 2017). Finally, *movements*, or the number of times fish come and go from various locations are frequently discussed (Holland et al. 2003; Gerig et al. 2014; Gannon et al. 2015), but the way movements are quantified and the context in which they are discussed differs. Additionally, there are few studies that combine multiple metrics together to create a mosaic of site function metrics, as we have done here, to generate testable hypotheses.

Take-home Message 3: Geomorphic Features

At the seascape scale, geomorphic correlates of distribution provide insights into how physical habitat were used by mobile predators. Much research and ecological theory suggests that physical conditions are the stage on which biotic interactions play out (e.g. Levin 1992). Habitat research commonly uses point estimates of physical conditions (*depth*, Torgersen and Close 2004; Binsong et al. 2014; *substrate*, Gratwicke and Speight 2005; Franca et al. 2012). At the seascape scale, these point estimates may not reflect major influences on physical habitat. In fact, larger-scale, irregular physical features or discontinuities (confluences, sand bars, islands, points, Kennedy et al. 2016), may be more useful indicators of large scale physical variables that aggregate mobile organisms.

In PIE, geomorphology provided useful information about where striped bass spent more and less time. Exits were areas where striped bass spent little time. This is expected because these receiver locations were chosen to detect fish leaving the study system. Atlantic coastal striped bass are highly migratory (Waldman et al. 1997; Walter et al. 2003; Pautzke et al. 2010; Mather et al. 2013) and although contingents can remain within areas such as PIE for an entire season, other striped bass continue up the east coast as far north as Maine (Grothues et al. 2009; Able et al. 2012). At exits, we expected low residence times as these sites are only used as passage to leave the estuary. Other studies that track coastal migrations and other long distance movements (Mather et al. 2013; Kennedy et al. 2016) often put receivers at system exits, checkpoints, and other "forks in the road". However, ours is the first study to categorize exits as a functional site for fish.

Confluences attracted tagged striped bass, and, in many cases, tagged fish spent much time there and moved frequently to and from this type of geomorphic site. Confluences have been suggested to be ecological hotspots (Poole 2002; Benda et al. 2003; Rice et al. 2006). Confluences are increasingly a focus of organismal biodiversity studies (Hitt and Angermeier 2008; Torgersen et al. 2008; Osawa et al. 2011; Czegledi et al. 2016). However, many gaps still exist relative to how animals use confluences. For example, prior to this study it was unknown how different confluences affected predator individuals and populations. Striped bass used confluences in PIE differently. Striped bass spent much time at West Creek and Rowley River confluences, but little time at the Grape Island confluence. Other studies have rarely compared multiple confluences within a single system (e.g. but see Kennedy 2016). We were able to show that striped bass used the "sweet spot" significantly more than the upstream tributary "arms". Although other studies have examined biodiversity upstream vs downstream of confluences in river systems (Grenouillet et al. 2004; Hitt and Angermeier 2008; Czegledi et al.2016), no previous study has examined how predators used the parts of a confluence. Confluences were less variable than non-confluences meaning such that even when confluence sites did not offer the best conditions for a feeding striped bass, they were predictable in location, higher than average in quality, and a dependable food source (Benda et al. 2003; Rice et al. 2006) that offered "good-enough" payoffs. In summary, confluences are important geomorphic sites for fish predators. However, the profitability of a range of confluences within a seascape (as suggested by Rice 2017) merits further ecological investigation.

Non-confluences were also used by many fish, but were highly variable. For example, the highest average residence time for a non-confluence location (receiver 13) was 85.22 hours and this location was right in the Middle region of the estuary as well as near other features such as Middle Ground. In contrast, the lowest average residence time for a non-confluence location (receiver 20) was 6.66 hours. This location was within the Lower region of the estuary and not near any other geomorphic features. Kennedy et al. (2016) also found that non-confluence sites in PIE had the highest and lowest fish counts. In their study, the non-confluence sites that attracted large numbers of fish had multiple co-occurring discontinuities (e.g. sandbars, depth variation). Thus, non-confluence sites encompass a wide range of physical conditions (Torgersen and Close 2004; Franca et al. 2012; Binsong et al. 2014) and need additional refinement to understand the varied role they play as geomorphic drivers of fish distribution in the estuarine seascape.

Take-home Message 4: Region

At the seascape scale, geographic region within a system provided information about where animals spent more and less time. The Middle and Rowley River regions were the geographic areas at which tagged striped bass spent the most time. The Upper and Lower regions were the areas where fish spent the least amounts of time. This is likely because the greater Middle region in general (when combined with the Rowley River that is also located in the middle of the estuary) contains many discontinuities (Kennedy et al. 2016). Other studies have also broken larger seascapes into regions and found distinct differences in usage (Murchie et al. 2013; Bultel et al. 2014; Kennedy et al. 2016; Kessel et al. 2016).

Summary

By analyzing fish distribution patterns using telemetry, we have made a number of discoveries that advance field ecology and fish conservation. First, our research demonstrated how intensive spatial coverage of discrete areas within an entire ecosystem can be used to explore details of natural fish behavior in the field. Second, these high-resolution data can be broken into multiple metrics that, when integrated, can show novel insights into fish distribution. Third, we showed that measuring geomorphology rather than point habitat features can explain predator distribution at a larger scale. Relative to geomorphic features, we were also able to show that confluences are important features in the seascape. Although individual confluences differ, they are more predictable and less variable than non-confluences. Finally, as other studies have shown, striped bass use regions within a larger seascape differently. These findings can be broadly applied to any species of interest to provide more information on ‘scape scale distribution patterns. Specifically, the findings from this study can be used to inform fisheries management (where are the fish spending the most time, and why) and advance the field of movement ecology (how can we more specifically characterize movements and distributions?). Future research could attempt to integrate the metrics described in this paper and apply them to specific ecological theories (e.g. Central Place Foraging; Rosenberg and McKelvey 1999; Movement ecology, Nathan et al. 2008; Benkwitt 2016) or in support of fisheries goals (Crossin et al. 2017.

Literature Cited

Able, K. W. and T. M. Grothues (2007). Diversity of estuarine movements of striped bass (*Morone saxatilis*): a synoptic examination of an estuarine system in southern New Jersey. Fishery Bulletin 105(3): 426-435.

Able, K. W., et al. (2012). Distribution, movements, and habitat use of small striped bass (*Morone saxatilis*) across multiple spatial scales. Fishery Bulletin 110(2): 176-192.

Albanese, B., et al. (2004). Ecological correlates of fish movement in a network of Virginia streams. Canadian Journal of Fisheries and Aquatic Sciences 61(6): 857-869.

Altieri, A. H., et al. (2012). A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. Ecology 93(6): 1402-1410.

Bacheler, N. M., et al. (2015). Movement of invasive adult lionfish *Pterois volitans* using telemetry: importance of controls to estimate and explain variable detection probabilities. Marine Ecology Progress Series 527: 205-220.

Baguette, M., et al. (2013). Individual dispersal, landscape connectivity and ecological networks. Biological Reviews 88(2): 310-326.

Beguer-Pon, M., et al. (2015). Large-scale, seasonal habitat use and movements of yellow American eels in the St. Lawrence River revealed by acoustic telemetry. Ecology of Freshwater Fish 24(1): 99-111.

Benda, L., et al. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. Bioscience 54(5): 413-427.

Benkwitt, C. E. (2016). Central-place foraging and ecological effects of an invasive predator across multiple habitats. Ecology 97(10): 2729-2739.

Biggs, C. R. and R. S. Nemeth (2016). Spatial and temporal movement patterns of two snapper species at a multi-species spawning aggregation. Marine Ecology Progress Series 558: 129-142.

Binder, T. R., et al. (2016). Spawning site fidelity of wild and hatchery lake trout (*Salvelinus namaycush*) in northern Lake Huron. Canadian Journal of Fisheries and Aquatic Sciences 73(1): 18-34.

Binsong, J., et al. (2014). The impact of geomorphology of marsh creeks on fish assemblage in Changjiang River estuary. Chinese Journal of Oceanology and Limnology 32(2): 469-479.

Block, B. A., et al. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434: 1121-1127.

Boehler, C. T., et al. (2012). Within-stream release-site fidelity of steelhead trout from Lake Erie hatchery stocks. Journal of Great Lakes Research 38(2): 251-259.

Bond, M. E., et al. (2012). Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican barrier reef. PLoS ONE 7(3).

Brady, D. C. and T. E. Targett (2013). Movement of juvenile weakfish *Cynoscion regalis* and spot *Leiostomus xanthurus* in relation to diel-cycling hypoxia in an estuarine tidal tributary. Marine Ecology Progress Series 491: 199-219.

Braun, C. D., et al. (2015). Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. Marine Biology 162(12): 2351-2362.

Breve, N. W. P., et al. (2014). Explicit site fidelity of European catfish (*Silurus glanis*, L., 1758) to man- made habitat in the River Meuse, Netherlands. Journal of Applied Ichthyology 30(3): 472-478.

Bridger, C. J. and R. K. Booth. 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Reviews in Fisheries Science 11(1): 13-34.

Bronte, C. R., et al. (2007). Relative abundance, site fidelity, and survival of adult lake trout in Lake Michigan from 1999 to 2001: Implications for future restoration strategies. North American Journal of Fisheries Management 27(1): 137-155.

Buchsbaum, R., et al. (1998).The Marine Resources of the Parker River-Plum Island Sound Estuary: An Update after 30 Years.

Bultel, E., et al. (2014). Migration behaviour of silver eels (*Anguilla anguilla*) in a large estuary of Western Europe inferred from acoustic telemetry. Estuarine Coastal and Shelf Science 137: 23-31.

Callihan, J. L., et al. (2015). Sex-specific movement response of an estuarine sciaenid (*Cynoscion nebulosus*) to freshets. Estuaries and Coasts 38(5): 1492-1504.

Callihan, J. L., et al. (2015). Coastal migration and homing of Roanoke River striped bass. Marine and coastal fisheries 7(1): 301-315.

Callihan, J. L., et al. (2013). Sex differences in residency of adult spotted seatrout in a Louisiana estuary. Marine and Coastal Fisheries 5(1): 79-92.

Campbell, H.A., Watts, M.E., Dwyer, R.G., Franklin, C.E. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Marine and Freshwater Research, 63:815–820.

Capello, M., et al. (2015). A methodological framework to estimate the site fidelity of tagged animals using passive acoustic telemetry. PLoS ONE 10(8): e0134002.

Casini, M., et al. (2012). Predator transitory spillover induces trophic cascades in ecological sinks. Proceedings of the National Academy of Sciences of the United States of America 109(21): 8185.

Coleman, F. C., et al. (2004). The impact of United States recreational fisheries on marine fish populations. Science 305(5692): 1958-1960.

Cram, J. M., et al. (2013). Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. Environmental Biology of Fishes 96(1): 109-122.

Crossin, G. T., et al. (2017). Acoustic telemetry and fisheries management. Ecological Applications 27(4): 1031-1049.

Currey, L. M., et al. (2015). Assessing environmental correlates of fish movement on a coral reef. Coral Reefs 34(4): 1267-1277.

Currey, L. M., et al. (2014). Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish. Marine Biology 161(9): 2155-2166.

Czegledi, I., et al. (2016). The scales of variability of stream fish assemblages at tributary confluences. Aquatic Sciences 78(4): 641-654.

Dauwalter, D. C., et al. (2008). Biogeography, ecoregions, and geomorphology affect fish species composition in streams of eastern Oklahoma, USA. Environmental Biology of Fishes 82(3): 237-249.

Deegan, L. A. and R. H. Garritt (1997). Evidence for spatial variability in estuarine food webs. Marine Ecology Progress Series 147(1-3): 31-47.

Dewar, H., et al. (2008). Movements and site fidelity of the giant manta ray, *Manta birostris,* in the Komodo Marine Park, Indonesia. Marine Biology 155: 121-133.

Escalle, L., et al. (2015). Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters. Journal of Fish Biology 87(2): 323-341.

Espinoza, M., et al. (2016). Evidence of partial migration in a large coastal predator: Opportunistic foraging and reproduction as key drivers? PLoS ONE 11(2).

Espinoza, M., et al. (2015). Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. Ecological Applications 25(8): 2101-2118.

Espinoza, M., et al. (2015). Movement patterns of silvertip sharks (*Carcharhinus albimarginatus*) on coral reefs. Coral Reefs 34(3): 807-821.

Estes, J. A., et al. (2011). Trophic downgrading of planet earth. Science 333(6040): 301-306.

Ferguson, A. M., et al. (2013). A herbivore knows its patch: Luderick, *Girella tricuspidata*, exhibit strong site fidelity on shallow subtidal reefs in a temperate marine park. PLoS ONE 8(5).

Ferguson, A. M., et al. (2016). Herbivore abundance, site fidelity and grazing rates on temperate reefs inside and outside marine reserves. Journal of Experimental Marine Biology and Ecology 478: 96-105.

Fischer, J. D., et al. (2012). Urbanization and the predation paradox: The role of trophic dynamics in structuring vertebrate communities. Bioscience 62(9): 809-818.

Fox, R. J. and D. R. Bellwood (2014). Herbivores in a small world: network theory highlights vulnerability in the function of herbivory on coral reefs. Functional Ecology 28(3): 642-651.

Franca, S., et al. (2012). Predicting fish community properties within estuaries: Influence of habitat type and other environmental features. Estuarine Coastal and Shelf Science 107: 22-31.

Furey, N. B., et al. (2013). Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. Journal of Fish Biology 82(5): 1469-1483.

Gahagan, B. I., et al. (2015). Partial migration of striped bass: revisiting the contingent hypothesis. Marine Ecology Progress Series 525: 185-197.

Gannon, R., et al. (2015). Fine-scale movements, site fidelity and habitat use of an estuarine dependent sparid. Environmental Biology of Fishes 98(6): 1599-1608.

Gardiner, N. M. and G. P. Jones (2016). Habitat specialisation, site fidelity and sociality predict homing success in coral reef cardinalfish. Marine Ecology Progress Series 558: 81-96.

Gerber, K. (2015). Tracking blue catfish: quantifying system-wide distribution of a mobile fish predator throughout a large heterogeneous reservoir. Master’s thesis, Kansas State University, Manhattan, KS.

Gerber, K. M., M. E. Mather, J. Smith. (2017). A suite of standard post-tagging evaluation metrics can help assess tag retention for field-based fish telemetry research. Reviews in Fish Biology and Fisheries 27 (3): 651-664.

Gerig, B., M.J. Dodrill, and W.E. Pine. 2014. Habitat selection and movement of adult Humpback Chub in the Colorado River in Grand Canyon, Arizona, during an experimental steady flow release. North American Journal of Fisheries Management 34(1): 39-48.

Getz, W. M. and D. Saltz (2008). A framework for generating and analyzing movement paths on ecological landscapes. Proceedings of the National Academy of Sciences of the United States of America 105(49): 19066-19071.

Gould, A. L., et al. (2014). Host preference, site fidelity, and homing behavior of the symbiotically luminous cardinalfish, *Siphamia tubifer* (Perciformes: Apogonidae). Marine Biology 161(12): 2897-2907.

Gratwicke, B. and M. R. Speight (2005). Effects of habitat complexity on Caribbean marine fish assemblages. Marine Ecology Progress Series 292: 301-310.

Grenouillet, G., et al. (2004). Within-basin fish assemblage structure: the relative influence of habitat versus stream spatial position on local species richness. Canadian Journal of Fisheries and Aquatic Sciences 61(1): 93-102.

Grothues et al. (2009). Migration patterns of striped bass throughout nonnatal estuaries of the U.S. Atlantic coast. American Fisheries Society Symposium 69: 135-150

Gorski, K., et al. (2013). Geomorphology and flooding shape fish distribution in a large scale temperate floodplain. River Research and Applications 29: 1226-1236.

Harasti, D., et al. (2014). Ontogenetic and sex-based differences in habitat preferences and site fidelity of White's seahorse *Hippocampus whitei*. Journal of Fish Biology 85(5): 1413-1428.

Harrison, P. M., et al. (2015). Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). Behavioral Ecology 26(2): 483-492.

Haulsee, D. E., et al. (2016). Implantation and recovery of long-term archival transceivers in a migratory shark with high site fidelity. PLoS ONE 11(2).

Heithaus, M. R. (2008). Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution 23(10): 537.

Heithaus, M. R., et al. (2002). Habitat use and foraging behavior of tiger sharks (*Galeocerdo cavier*) in a seagrass ecosystem. Marine Biology 140(2): 237-248.

Herbig, J. L. and S. T. Szedlmayer (2016). Movement patterns of gray triggerfish,*Balistes capriscus*, around artificial reefs in the northern Gulf of Mexico. Fisheries Management and Ecology 23(5): 418-427.

Hitt, N. P. and P. L. Angermeier (2008). Evidence for fish dispersal from spatial analysis of stream network topology. Journal of the North American Benthological Society 27(2): 304-320.

Humston, R., et al. (2005). Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. Marine Ecology Progress Series 291: 237-248.

Jackson, J. B. C., et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530): 629-638.

Johnson, L. B. and G. E. Host (2010). Recent developments in landscape approaches for the study of aquatic ecosystems. Journal of the North American Benthological Society 29(1): 41-66.

Kennedy, C. G., et al. (2017). Quantifying site-specific physical heterogeneity within an estuarine seascape. Estuaries and Coasts 40(5): 1385-1397.

Kennedy, C. G., et al. (2016). Discontinuities concentrate mobile predators: quantifying organism-environment interactions at a seascape scale. Ecosphere 7(2).

Kessel, S. T., et al. (2016). Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. Polar Biology 39(6): 1057-1068.

Kneebone, J., et al. (2014). Movements of striped bass between the exclusive economic zone and Massachusetts state waters. North American Journal of Fisheries Management 34(3): 524-534.

Knope, M. L., et al. (2017). Site fidelity and homing behaviour of intertidal sculpins revisited. Journal of Fish Biology 90(1): 341-355.

Kuglerova, L., et al. (2015). Local and regional processes determine plant species richness in a river-network metacommunity. Ecology 96(2): 381-391.

Levin, S. (1992). The problem of pattern and scale in ecology. Ecology 73(6): 1943-1967.

Li, X., et al. (2015). Three-dimensional tracking of juvenile salmon at a mid-reach location between two dams. Fisheries Research 167: 216-224.

Lowerre-Barbieri, S. K., et al. (2016). Assessing reproductive behavior important to fisheries management: a case study with red drum, *Sciaenops ocellatus*. Ecological Applications 26(4): 979-995.

Lowerre-Barbieri, S. K., et al. (2013). Site fidelity and reproductive timing at a spotted seatrout spawning aggregation site: individual versus population scale behavior. Marine Ecology Progress Series 481: 181-197.

Malard, L. A., et al. (2016). Site fidelity, size, and morphology may differ by tidal position for an intertidal fish, *Bathygobius cocosensis* (Perciformes-Gobiidae), in Eastern Australia. PeerJ 4.

Mather, M. E., et al. (2009). Use of non-natal estuaries by migratory striped bass (*Morone saxatilis*) in summer. Fishery Bulletin 107(3): 329-338.

Mather, M. E., et al. (2010). Diversity in destinations, routes and timing of small adult and sub-adult striped bass *Morone saxatilis* on their southward autumn migration. Journal of Fish Biology 77: 2326-2337.

Mather, M., et al. (2013). What happens in an estuary doesn’t stay there: Patterns of biotic connectivity resulting from long term ecological research. Oceanography 26(3): 168-179.

Mittermeier, R. A., et al. (1998). Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conservation Biology 12(3): 516-520.

Moore, M., et al. (2013). A floating bridge disrupts seaward migration and increases mortality of steelhead smolts in Hood Canal, Washington State. PLoS ONE 8(9).

Murchie, K. J., et al. (2013). Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, The Bahamas. Fisheries Research 147: 404-412.

Nathan, R., et al. (2008). A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105(49): 19052-19059.

Osawa, T., et al. (2011). The role of river confluences and meanderings in preserving local hot spots for threatened plant species in riparian ecosystems. Aquatic Conservation: Marine and Freshwater Ecosystems 21(4): 358-363.

Ozgul, A., et al. (2015). Preliminary study on the use of the Vemco Positioning System to determine fish movements in artificial reef areas: a case study on *Sciaena umbra* Linnaeus, 1758. Journal of Applied Ichthyology 31: 41-47.

Pautzke, S. M., et al. (2010). Seasonal use of a New England estuary by foraging contingents of migratory striped bass. Transactions of the American Fisheries Society 139: 257-269.

Piper, A. T., et al. (2013). Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. Ecological Engineering 57: 88-96.

Poole, G. C. (2002). Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47(4): 641-660.

Poulakis, G. R., et al. (2013). Movements of juvenile endangered smalltooth sawfish, *Pristis pectinata*, in an estuarine river system: use of non-main-stem river habitats and lagged responses to freshwater inflow-related changes.

Rechisky, E. L., et al. (2013). Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean. Proceedings of the National Academy of Sciences of the United States of America 110(17): 6883-6888.

Reubens, J. T., et al. (2013). Residency, site fidelity and habitat use of Atlantic cod (*Gadus morhua*) at an offshore wind farm using acoustic telemetry. Marine Environmental Research 90: 128-135.

Revilla, E., et al. (2004). Effects of matrix heterogeneity on animal dispersal: From individual behavior to metapopulation-level parameters. American Naturalist 164(5): E130-E153.

Rice, S. P. (2017). Tributary connectivity, confluence aggradation and network biodiversity. Geomorphology 277: 6-16.

Rice, S. P., et al. (2006). Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63(11): 2553-2566.

Rosenblatt, A. E., et al. (2013). The roles of large top predators in coastal ecosystems new insights from long term ecological research. Oceanography 26(3): 156-167.

Roshier, D. A., et al. (2008). Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. Oecologia 156(2): 465-477.

Rous, A. M., et al. (2017). Telemetry-determined habitat use informs multi-species habitat management in an urban harbour. Environ Manage 59(1): 118-128.

Rueger, T., et al. (2014). Relationships between pair formation, site fidelity and sex in a coral reef cardinalfish. Behavioural Processes 107: 119-126.

Scheiner, S. M. and M. R. Willig (2005). Developing unified theories in ecology as exemplified with diversity gradients. American Naturalist 166(4): 458-469.

Shapiera, M., et al. (2014). Season and site fidelity determine home range of dispersing and resident juvenile Greenland cod *Gadus ogac* in a Newfoundland fjord. Marine Ecology Progress Series 503: 235-246.

Selby, T. H., et al. (2016). Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. Ecology and Evolution 6(14): 4823-4835.

Sergio, F., et al. (2005). Top predators and biodiversity. Nature 436(7048): 192-192.

Siceloff, L. and W. H. Howell (2013). Fine-scale temporal and spatial distributions of Atlantic cod (*Gadus morhua*) on a western Gulf of Maine spawning ground. Fisheries Research 141: 31-43.

Smith, T. A. and C. E. Kraft (2005). Stream fish assemblages in relation to landscape position and local habitat variables. Transactions of the American Fisheries Society 132(2): 430-440.

Stephens, D. and J. Krebs (1986). Foraging Theory. Princeton, NJ, Princeton University Press.

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7: 533-555.

Taylor, B. M. and J. S. Mills (2013). Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. Coral Reefs 32(4): 1077-1087.

Taylor, M. D., et al. (2017). Feels like home: homing of mature large-bodied fish following translocation from a power-station canal. Ices Journal of Marine Science 74(1): 301-310.

Teesdale, G. N., et al. (2015). Patterns of home ranging, site fidelity, and seasonal spawning migration of barred sand bass caught within the Palos Verdes Shelf Superfund Site. Marine Ecology Progress Series 539: 255-269.

Tetard, S., et al. (2016). Poor oxic conditions in a large estuary reduce connectivity from marine to freshwater habitats of a diadromous fish. Estuarine Coastal and Shelf Science 169: 216-226.

Thornbrugh, D. J. and K. B. Gido (2010). Influence of spatial positioning within stream networks on fish assemblage structure in the Kansas River basin, USA. Canadian Journal of Fisheries & Aquatic Sciences 67: 143-156.

Thwaites, L., et al. (2014). Glenelg River Judas Carp Tracking Program. An interim report to the Glenelg Hopkins Catchment Management Authority. SARDI Research Report Series - South Australian Research and Development Institute (802): VII + 27 pp.-VII + 27 pp.

Torgersen, C. E. and D. A. Close (2004). Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biology 49(5): 614-630.

Torgersen, C. E., et al. (2004). Pattern detection in stream networks: quantifying spatial variability in fish distribution. GIS/Spatial Analyses in Fishery and Aquatic Sciences: 405-420.

U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau. 2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation.

Villegas-Rios, D., et al. (2013). Home range and diel behavior of the ballan wrasse, *Labrus bergylta*, determined by acoustic telemetry. Journal of Sea Research 80: 61-71.

Villegas-Rios, D., et al. (2017). Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. Animal Behaviour 124: 83-94.

Waldman, J. R., et al. (1997). An empirical comparison of stock identification techniques applied to striped bass. Transactions of the American Fisheries Society 126(3): 369-385.

Walker, A. M., et al. (2014). The home range and behaviour of yellow-stage European eel *Anguilla anguilla* in an estuarine environment. Aquatic Conservation-Marine and Freshwater Ecosystems 24(2): 155-165.

Walter, J. F. I., et al. (2003). Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. Fisheries Management and Ecology 10: 349-360.

Ward, A. J. W., et al. (2013). Site fidelity and localised homing behaviour in three-spined sticklebacks (*Gasterosteus aculeatus*). Behaviour 150(14): 1689-1708.

Webster, M. S., et al. (2002). Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution 17(2): 76-83.

Wolfe, B. W. and C. G. Lowe (2015). Movement patterns, habitat use and site fidelity of the white croaker (*Genyonemus lineatus*) in the Palos Verdes Superfund Site, Los Angeles, California. Marine Environmental Research 109: 69-80.

Yackulic, C. B., et al. (2011). One size does not fit all: flexible models are required to understand animal movement across scales. Journal of Animal Ecology 80: 1088-1096.

Zemeckis, D. R., et al. (2014). Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: implications for population structure and rebuilding. Ices Journal of Marine Science 71(6): 1356-1365.

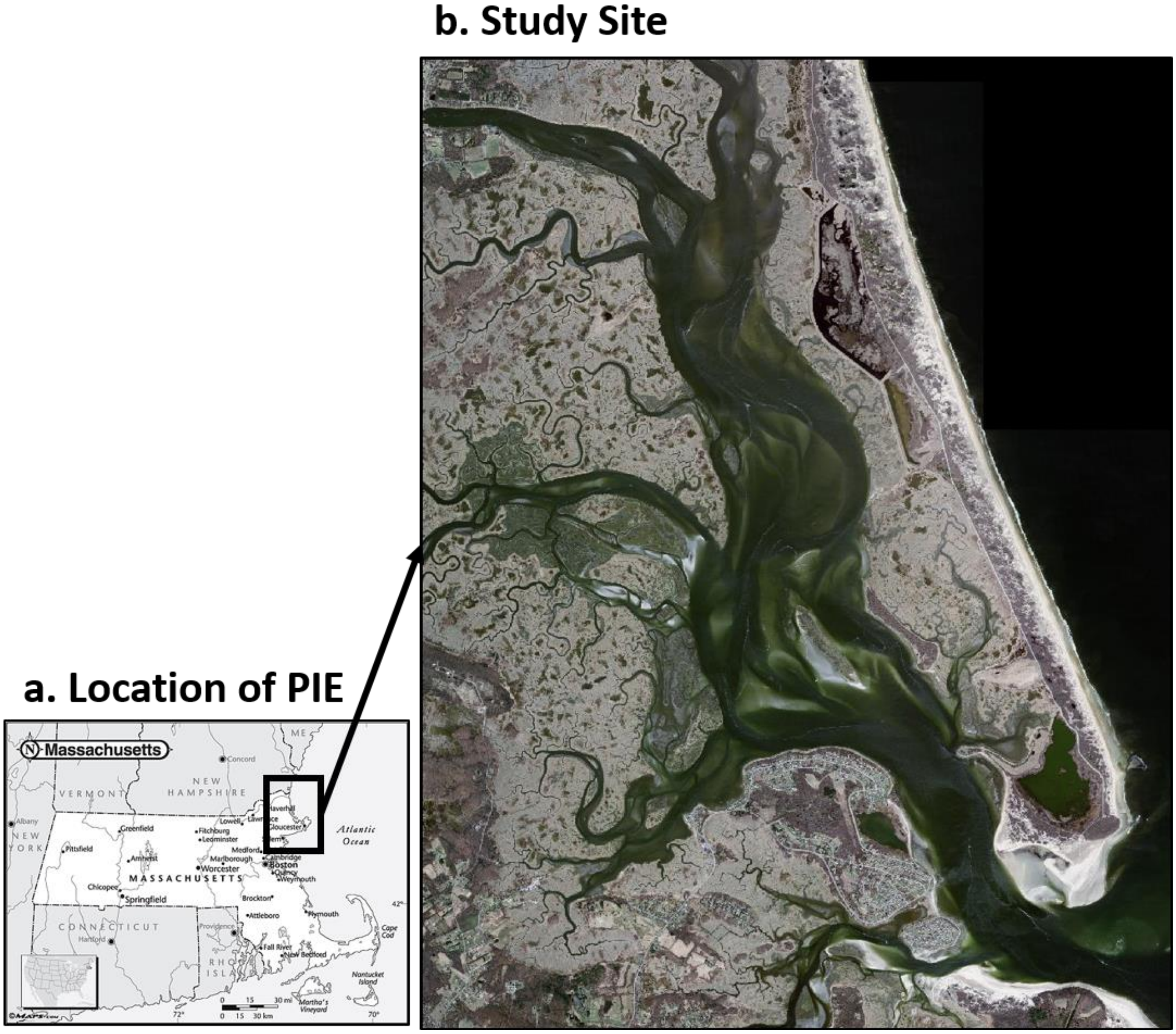
Zhang, Y., et al. (2015). Short-term fidelity, habitat use and vertical movement behavior of the black rockfish *Sebastes schlegelii* as determined by acoustic telemetry. PLoS ONE 10(8).

Table 1.1: Summary of the literature review on studies using acoustic telemetry.

No.	Citation		Focus		Ecological Questions - Linked to								Data Resolution & Extent						Metrics Used							
	Year	Author	System	Fish	Whole System?	Distribution?	Point specific habitat?	Geomorphology?	Exits / connectivity	Confluences?	Region?	Site fidelity?	# Receivers	Time Period (Mo)	# Fish Tagged	% Fish Detected	Total Detections	Detections/fish/mo	Residence	Vtrack	By Day	Detections	Movement	V track	By Day	Other (Homing
21	2015	Beguer-Pon et al.	FW - River	Fresh.		X						X	103	8	67	64	10,965	20								
22	2015	Bacheler et al.	Coast	Marine		X							9	7	25	80						X				
23	2014	Walker et al.	Estuary	Marine			X							6	14	86	115,027	1,369				X				
24	2014	Kneebone et al.	Coast	Anadr.										24	125	95						X				
25	2014	Fox et al.	Coral Reef	Marine					X			X	13	12	20	100										
26	2014	Currey et al.	Coral Reef	Marine									52		60	80			X		X					
27	2014	Bultel et al.	Estuary	Marine					X		X		31		51	98										
28	2013	Villegas-Rios et al.	Island	Marine								X	12	3	25	100	822,251	10,963	X		X					
29	2013	Taylor and Mills	Coral Reef	Marine								X	33	10	18	100	575,849	3,199								
30	2013	Siceloff et al.	Coast	Marine									6	2	26	92										
31	2013	Rechisky et al.	Estuary	Anadr.										36	800	83										
32	2013	Poulakis et al.	Estuary	Marine							X	X	33	27	35	69										
33	2013	Piper et al.	Estuary	Anadr.			X						19	12												
34	2013	Murchie et al.	Island	Marine							X	X	27	39	47	68	324,242	177								
35	2013	Moore et al.	Estuary	Anadr.										48	157	60										

Table 1.1 (continued)

No.	Citation		Focus		Ecological Questions - Linked to								Data Resolution & Extent						Metrics Used							
	Year	Author	System	Fish	Whole System?	Distribution?	Point specific habitat?	Geomorphology?	Exits / connectivity	Confluences?	Region?	Site fidelity?	# Receivers	Time Period (Mo)	# Fish Tagged	% Fish Detected	Total Detections	Detections/fish/mo	Residence	Vtrack	By Day	Detections	Movement	V track	By Day	Other (Homing
36	2013	Lowerre-Barbieri et al.	Estuary	Marine	X							X	18	6	32	97	169,928	885								
37	2013	Ferguson et al.	Estuary	Marine			X					X	20	6	14	86			X		X					
38	2013	Calihan et al.	Estuary	Marine					X			X	60	29	172	84	659,838	132								
39	2013	Brady et al.	Estuary	Marine			X						11	12	30	100										
		Taylor et al.	**Estuary**	**Anadr.**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**29**	**5**	**59**	**100**	**447,972**	**1,519**	**X**	**X**		**X**	**X**	**X**		
Total		40			4	4	10	1	7	0	7	16							15	2	13	5	1	0	1	1
Average													34	16	212	86	308158	1521								



b. Study Site

a. Location of PIE

Figure 1.1: (a) Plum Island Estuary, MA is located on the Northeastern coast of Massachusetts and (b) has diverse geomorphic and bathymetric features.

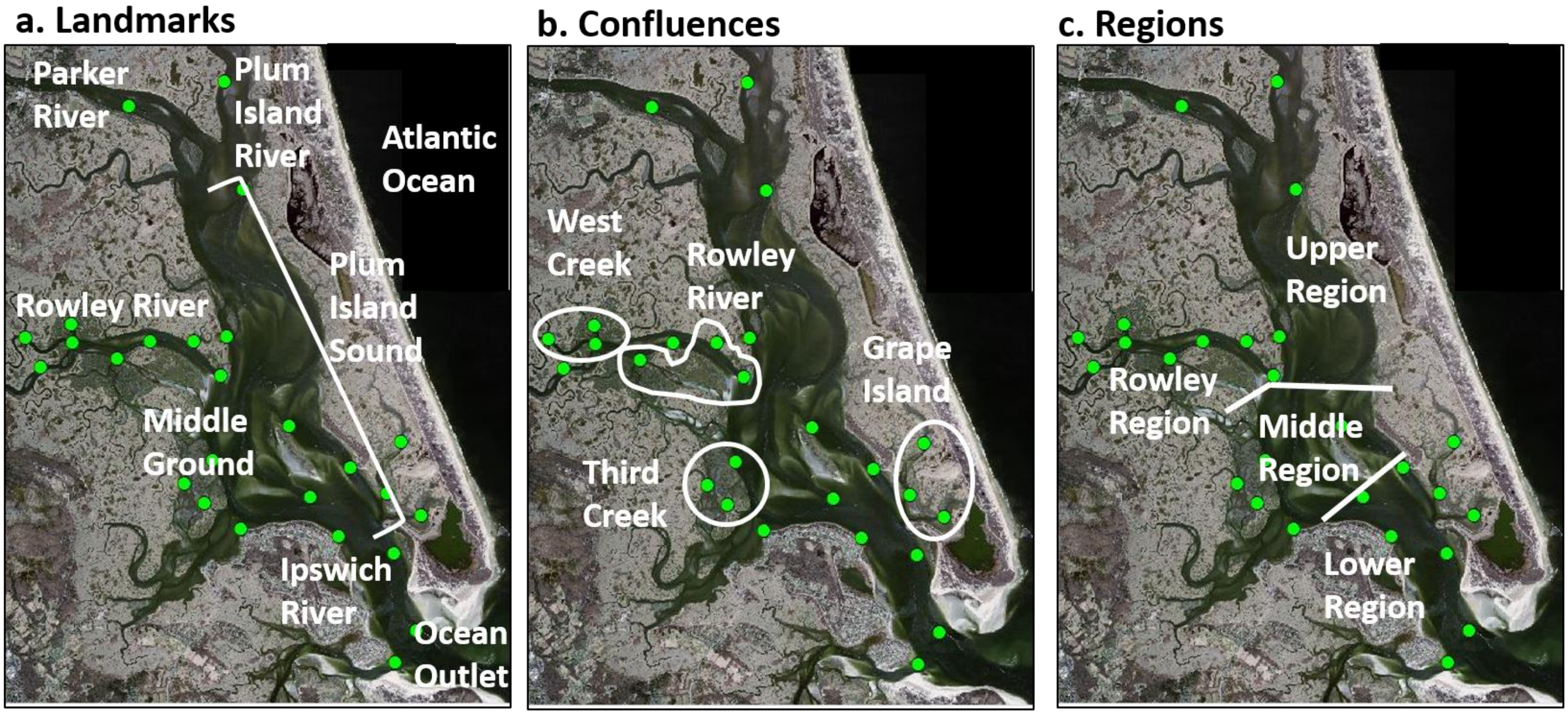
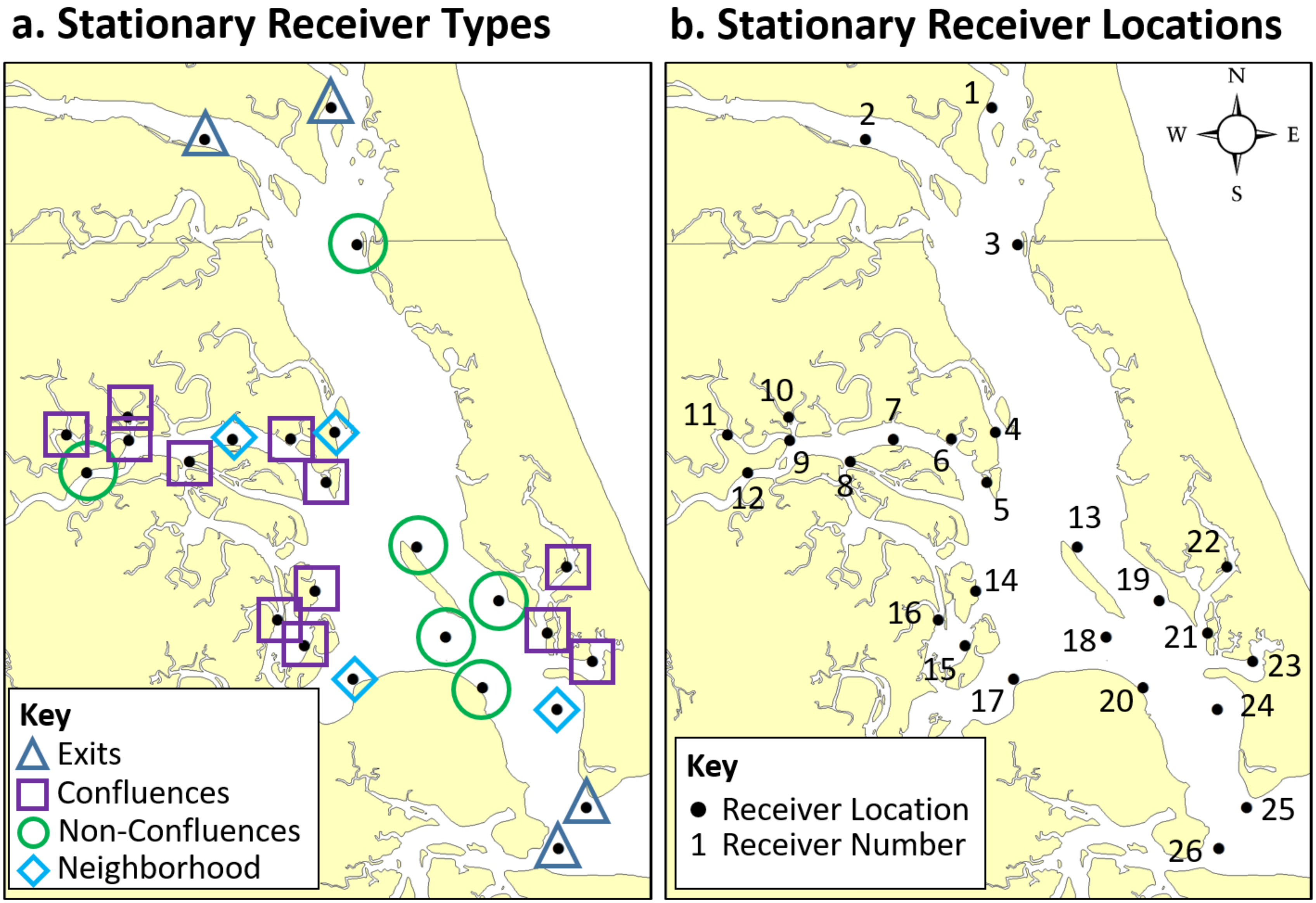


Figure 1.2: (a) Plum Island Estuary has three major river inputs; Parker River, Rowley River, and Ipswich River, one outlet into the Atlantic Ocean, and one man-made connection to the Merrimack River; Plum Island River. Landmarks include a large salt marsh Island called Middle Ground. (b) Multiple tidal creek confluences are present, of which our study will focus on West Creek, Rowley River, Third Creek, and Grape Island. (c) The estuary can be broken into four main regions, Upper, Middle, Lower, and Rowley.


a. Stationary Receiver Types

b. Stationary Receiver Locations

Figure 1.3:(a) Stationary receiver distribution within Plum Island Estuary, MA. Shapes indicate the categories of receiver types. (b) Receiver locations and numbers are shown.

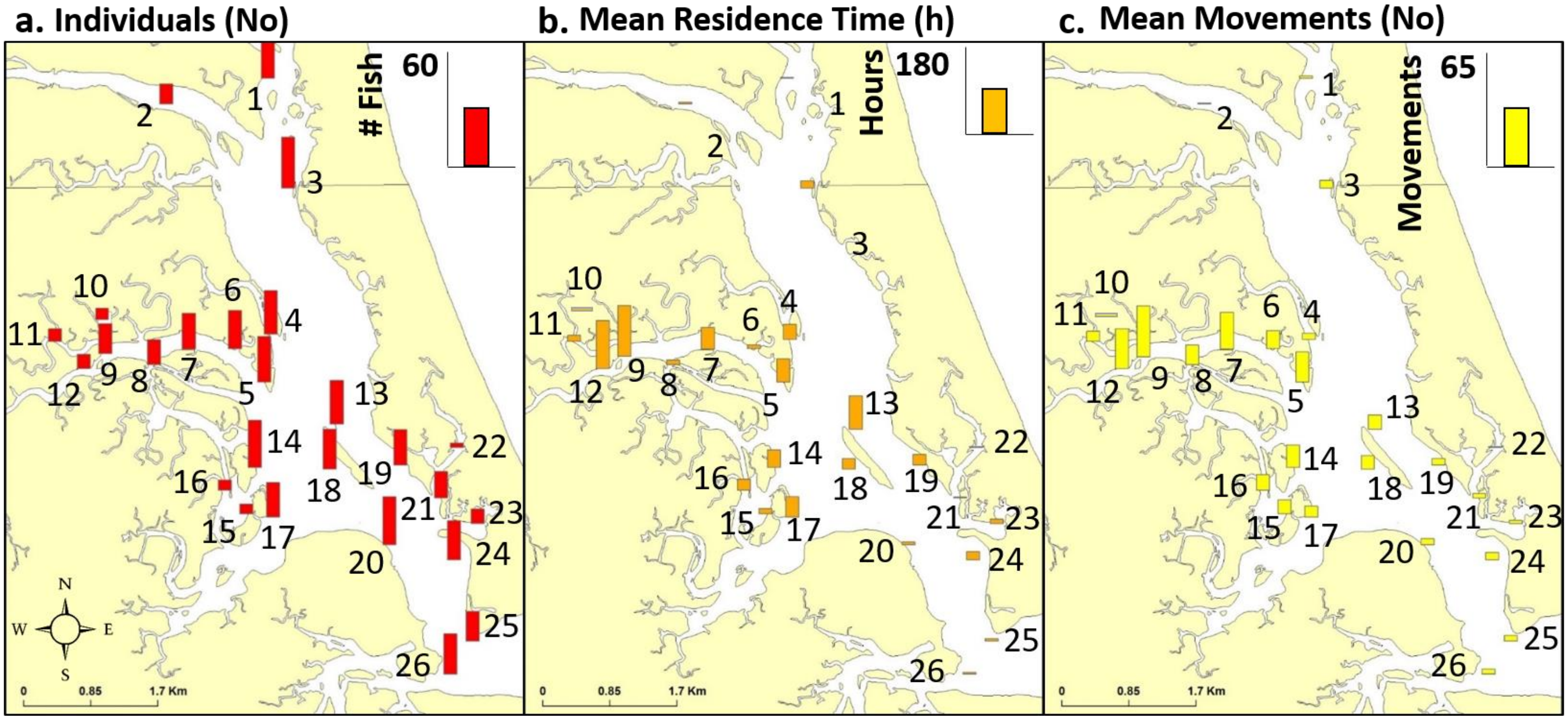


Figure 1.4:The spatial distribution of (a) numbers of individuals, (b) average residence time, and (c) average number of movements in Plum Island Estuary, MA for 59 tagged striped bass at 26 receivers. Receiver numbers are indicated next to the associated bars. A scale bar is in the right top corner of each plot. Figures 1.4 and 1.5 are related.

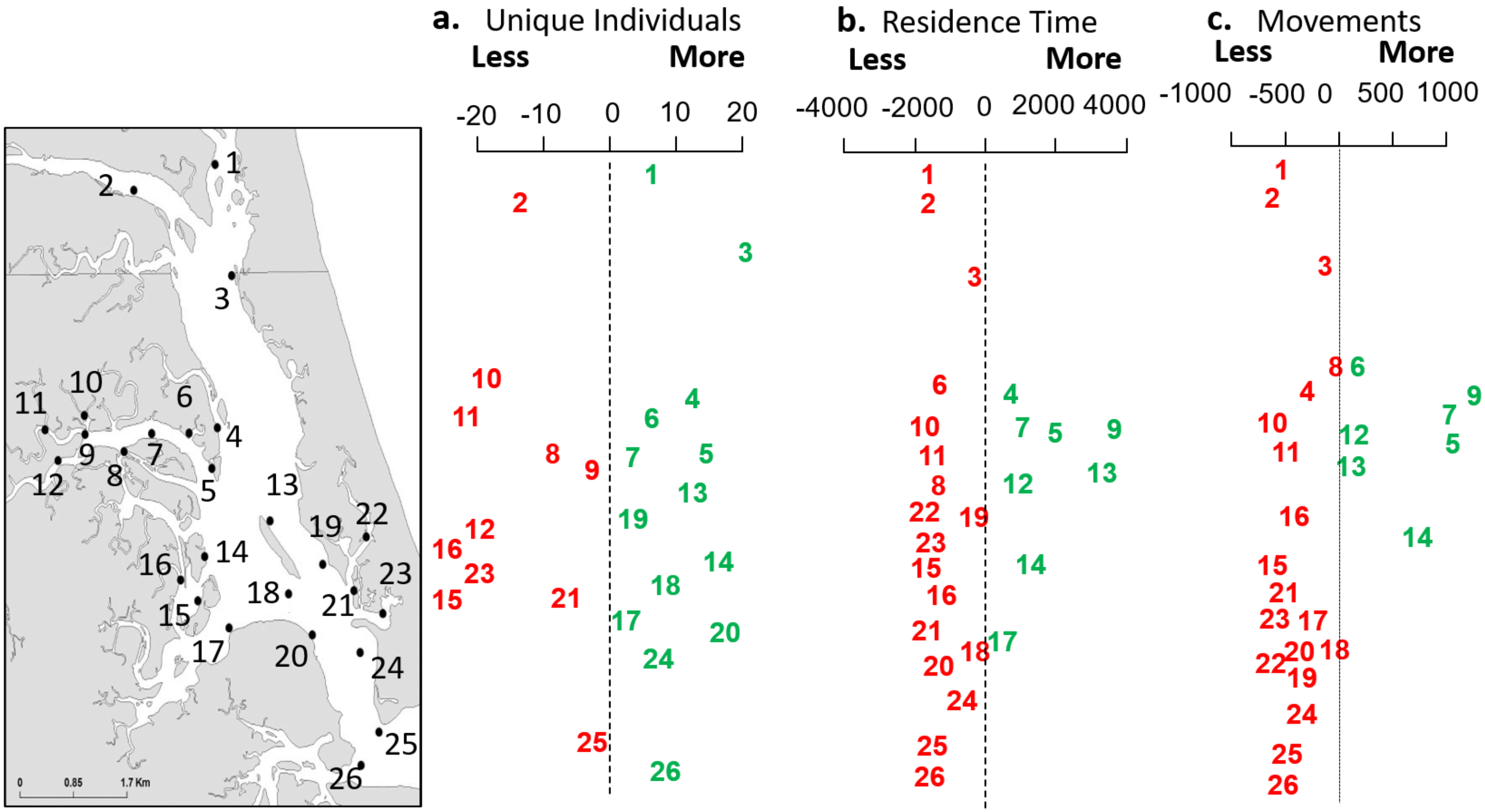


Figure 1.5: Results of a Chi-square analysis that identified (a) which receivers saw more individuals than expected and which receivers saw less individuals than expected. The expected is based on an even distribution (i.e. the same amount of individuals at all receivers). (b) At which receivers fish spent more or less time than expected based on an even distribution, and (c) at which receivers fish moved more or less than expected based on an even distribution.

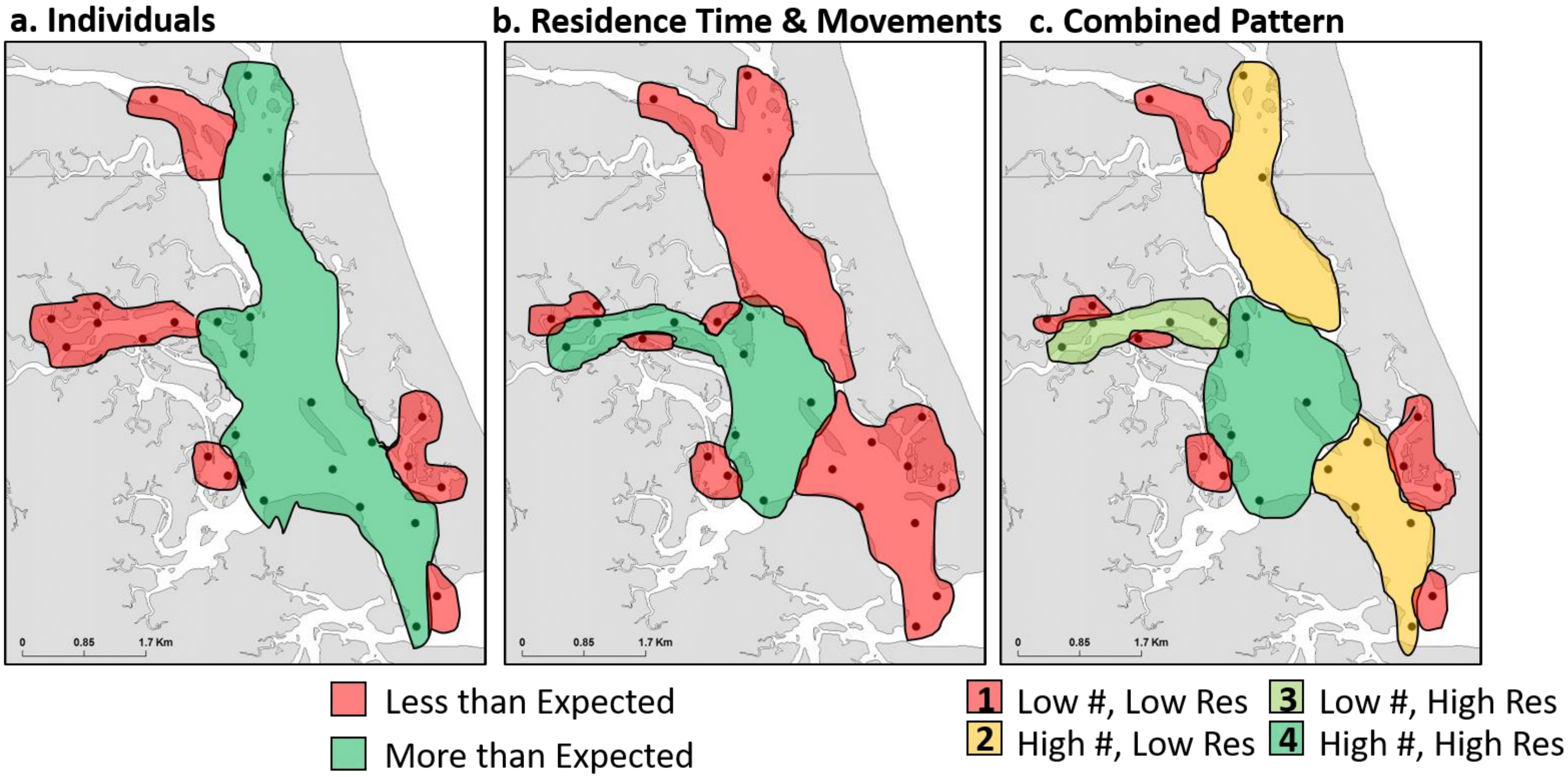


Figure 1.6: A map of mosaics indicating areas for (a) where there were more individuals than expected based on an even distribution (red) and where there were less individuals than expected based on an even distribution (green), (b) where there was higher residence times than expected based on an even distribution (red) and where there was lower residence times than expected based on an even distribution (green), and (c) the combined patterns from a and b where red indicates areas with low numbers of individuals and low residence times, yellow indicates areas with high numbers of individuals but low residence times, light green indicates areas with low numbers of individuals but high residence times, and dark green indicates areas with both high numbers of individuals and high residence times.

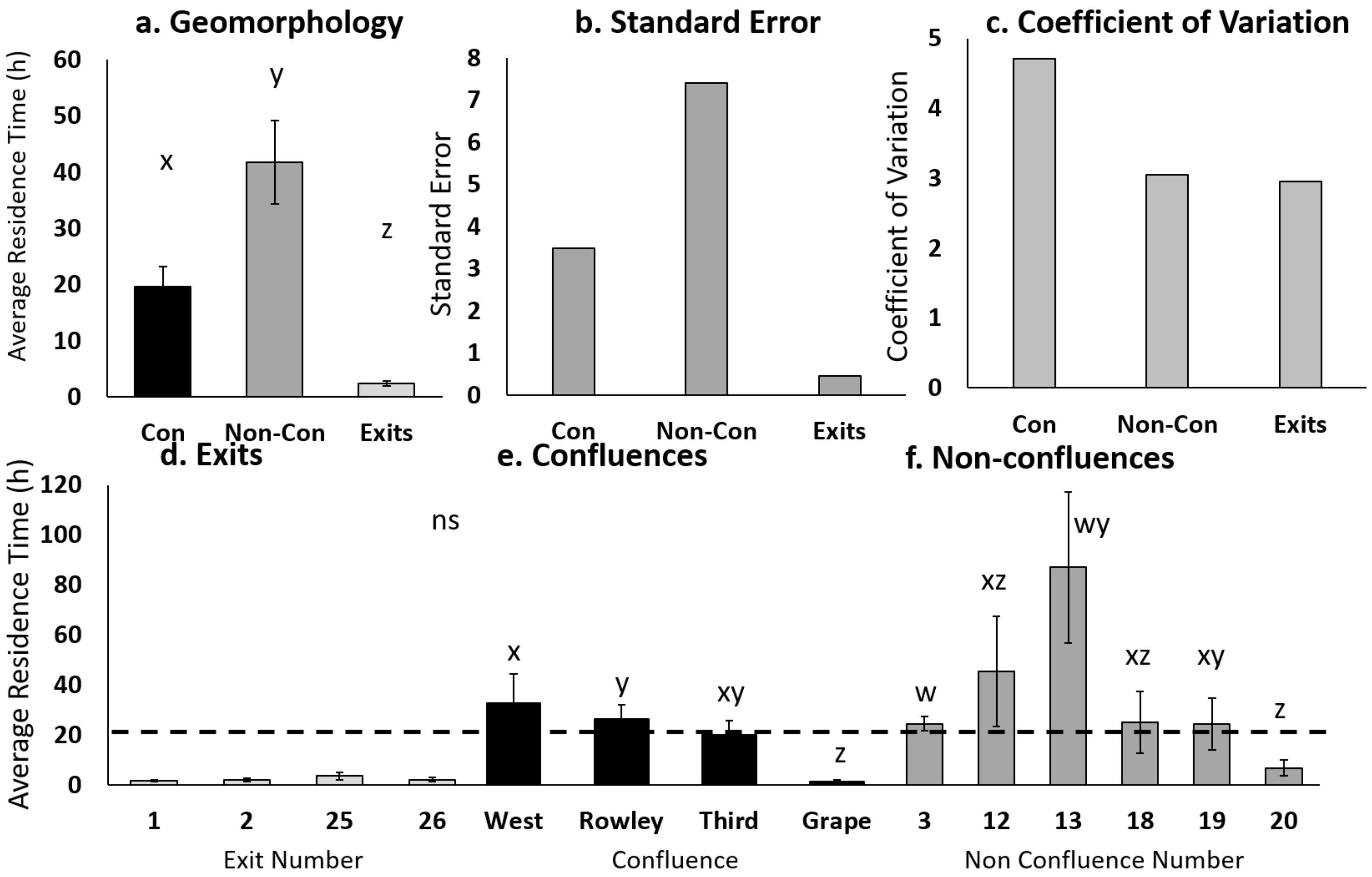


Figure 1.7: Bar graphs depicting mean and standard error (a) geomorphology types (confluences, non-confluences, and exits), (b) standard error of geomorphic types, (c) coefficient of variation of geomorphic types, mean and standard error of (d) exits,

(e) confluences, and (f) non-confluences. The dotted line is the estuary mean. Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

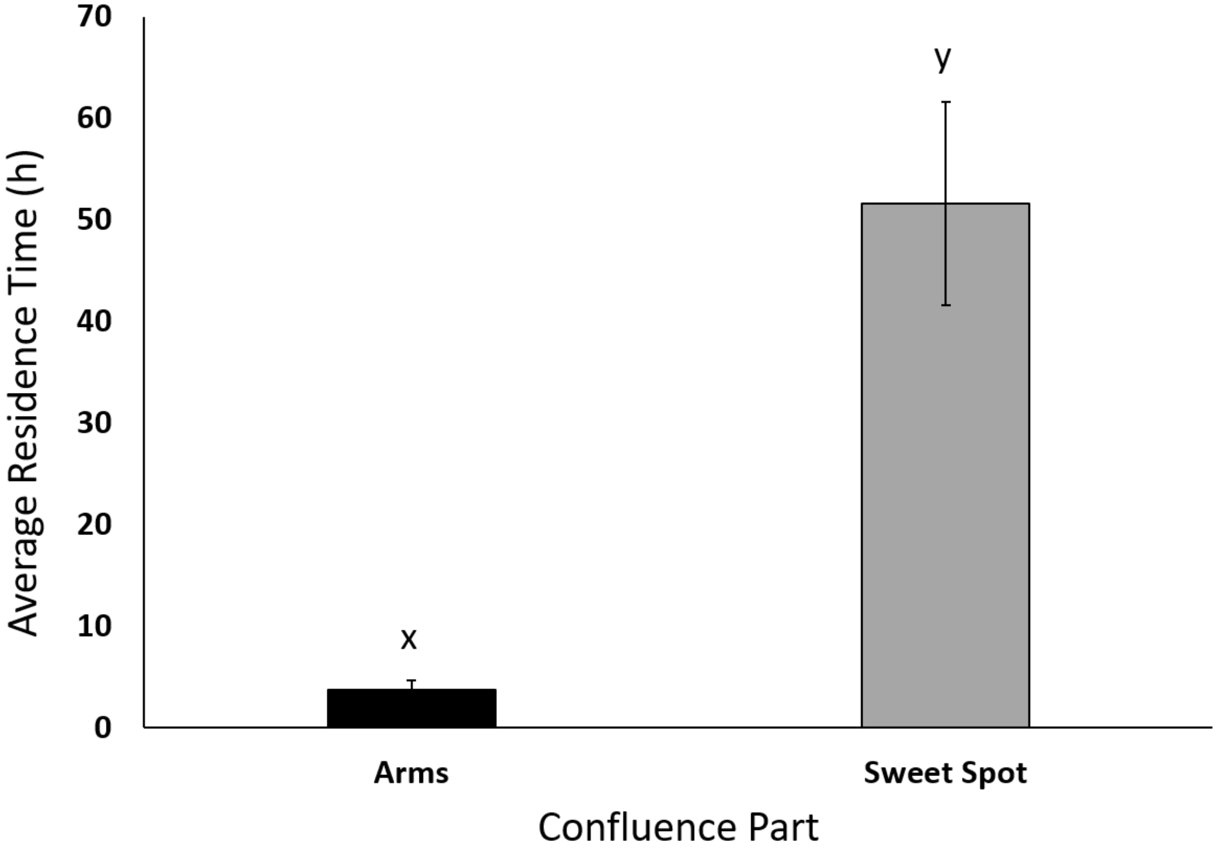


Figure 1.8: Bar graphs depicting residence time (mean +/- 1 SE) for confluence parts in 2015. Letters indicate the results of Tukey post hoc comparisons. P<0.05 was used to determine significance.

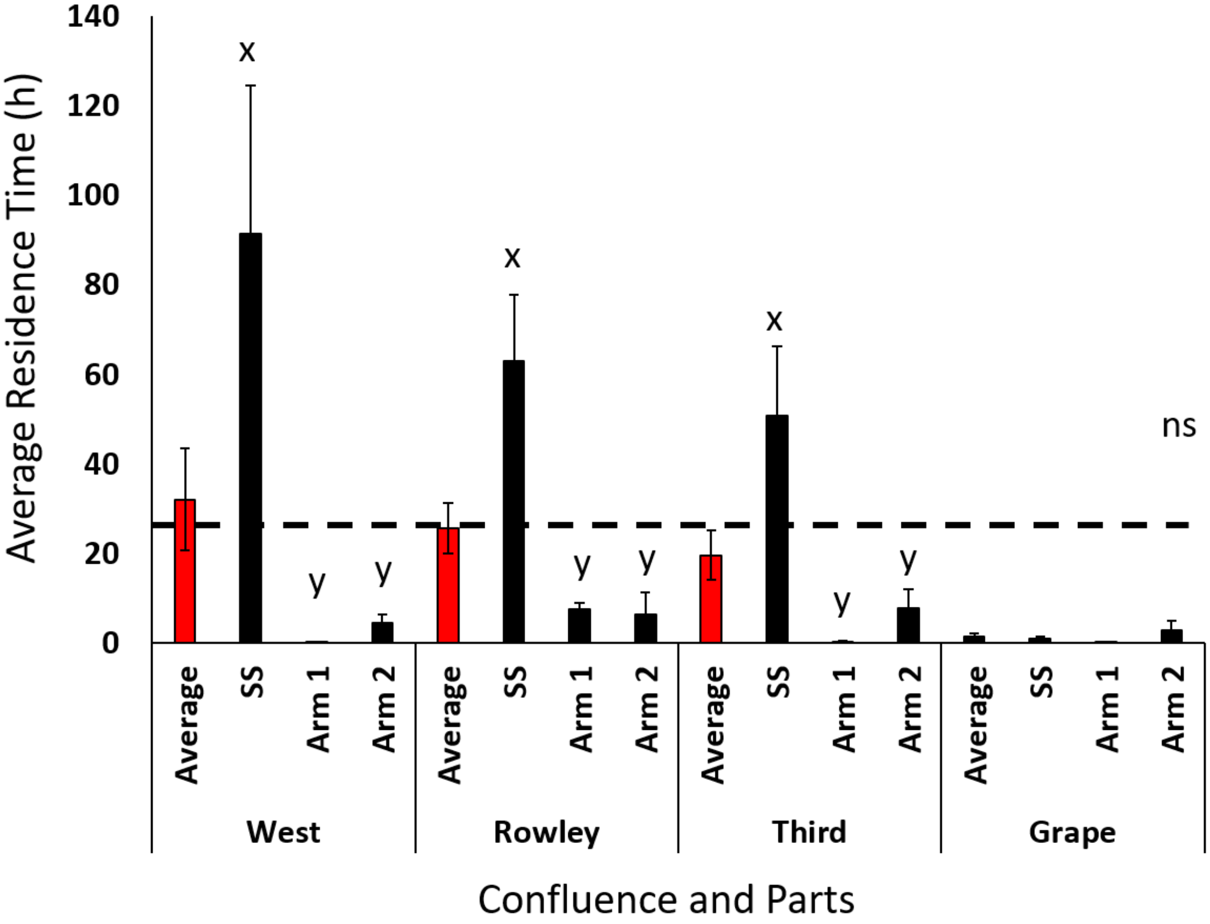


Figure 1.9: Bar graphs depicting the differences among the confluences, their overall averages, and their corresponding parts ("arms" and "sweet spot"). Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

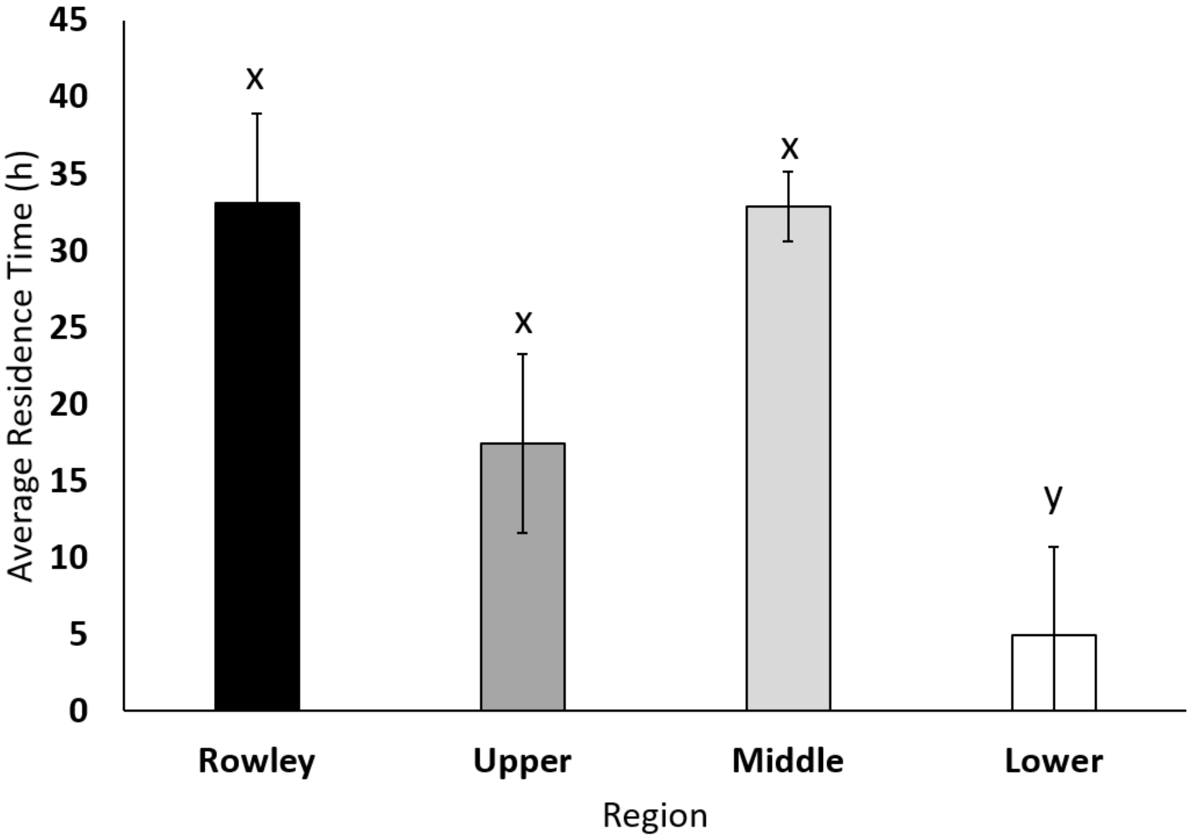


Figure 1.10: Bar graph depicting the differences in residence time between regions in 2015. Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

Chapter 2 - How individual variation in distributional groups provides insights into geomorphic and regional drivers of seascape distribution for a mobile predator

Abstract

The examination of within-population individuality (also known as discrete individual variation or behavioral syndromes) is a rapidly growing area of ecological and evolutionary research that has the potential to reduce previously-unexplained within-population variation for many attributes of natural populations. However, few studies of individuality link a discrete type of individual variation to distribution, movement, and habitat use in the field. Identifying discrete behavioral types can have important implications for understanding patterns and drivers of organismal distribution in the field if individuals within a discrete group behave similarly to each other but differently from other groups. Here, we used spatial and temporal-spatial cluster analyses to test if distinct types of distributional groupings existed for migratory striped bass (*Morone saxatilis)* predators feeding seasonally in Plum Island Estuary (PIE), MA. We also tested if fish within distinct distributional groups or clusters used geomorphic habitat types and regions differently. If a link between individual group and field behavior exists, then identifying and categorizing individuality can add to our understanding of patterns and drivers of field distribution. To advance this issue, we tracked striped bass, (*n*=59) with a 26 stationary acoustic receiver array between June 24, 2015 and October, 26, 2015. Based on multiple locational metrics, these fish predators clustered into five discrete types, hereafter referred to as "distributional groups." One distribution group, "*short-timers*" spent less than 30 days in PIE and were not analyzed further. The four seasonal-resident discrete distributional groups included

the (1) *Rowley River* distributional group (fish that primarily resided in the spatial region of the Rowley River), (2) *Plum Island Sound* distributional group (fish that primarily resided in the spatial Middle Sound region), (3) *Extreme Fidelity* distributional group (fish that spent most of their time in PIE at a single receiver location), and (4) the *Exploratory* distributional group (fish that showed no affiliation with any particular location). These discrete distribution groups used geomorphic habitat types and regions differently. For example, the Rowley River distributional group used more confluence habitats, whereas the Plum Island Sound and Extreme Fidelity distributional groups used more non-confluence habitats. Regionally, the Rowley River distributional group used the Rowley River region more, but the Extreme Fidelity and Plum Island Sound distribution groups favored the Middle region. These data show a rare link between individuality and field distribution patterns that can connect animal behavior to field ecology.

Introduction

The problem. Determining patterns and drivers of the distribution of mobile organisms at a seascape scale is an important ecological and conservation issue (Stephens and Krebs 1986; Mittermeier et al. 1998; Crossin et al. 2017), but is challenging to address because the location of mobile organisms changes frequently and often unpredictably across a large spatial scale. Elsewhere we determined that geomorphic habitat features can explain patterns of distribution for migratory striped bass (*Morone saxatilis)* foraging seasonally in an estuarine seascape (Taylor et al 2017; Chapter 1). However, much variation in these distributional patterns still exists for these seasonally resident migratory fish predators. An increasing amount of literature on individuality and behavioral syndromes has described discrete types of variation in individual behaviors within populations (e.g. Bell 2007; Sih et al. 2004). This literature shows promise for providing insights into unexplained variation in patterns and drivers of field distribution, but has not been well linked to field patterns yet. Here, we use high resolution telemetry data to quantify individuality in distributional groups for striped bass predators in an estuarine seascape (Plum Island Estuary, MA), then we assess if identifying distinct individuality increases the understanding of geomorphic and regional drivers of distribution.

Importance of distribution. Patterns and drivers of predator distribution have a range of important research and management implications. Predator presence can cause trophic cascades (Frank et al. 2005; Estes et al. 2011; Altieri et al. 2012; Casini et al. 2012). Their high mobility allows predators to make energetic connections between spatially distant food webs (Walter et al. 2003; Bestley et al. 2010; Casini et al. 2012; Mather et al. 2013; Rosenblatt et al. 2013). Thus, how predators are distributed can have ecosystem effects, societal and economic implications (for sportfish or seafood), and conservation consequences (Coleman et al. 2004).

Many factors can influence where and how animals are distributed. Habitat characteristics can be especially important drivers (Albanese et al. 2004; Clark et al. 2004). Many abiotic factors link to organismal distributions (e.g. depth, Torgerson and Close 2004; Binsong et al. 2014; substrate Bouska and Whitledge 2014). However, a larger view of physical conditions, or geomorphology, is an alternate approach to habitat. For example, aspects of geomorphology, such as confluences, are larger-scale physical habitat features that can create potential ecosystem hotspots (Poole 2002; Benda et al. 2003; Rice et al. 2006). Select examples exist of how this discontinuity is linked to general organismal (Osawa et al. 2011) and fish distributions (Hitt and Angermeier 2008; Kennedy et al,. 2016; Czegledi et al. 2016), but much about how this and other geomorphic features affect seascape scale biotic distributions remains unknown.

Importance of individuality. Individuality and behavioral syndromes are the focus of much ecological and evolutionary research (e.g., Sih et al. 2004; Dall et al. 2012; Wolf and Weissing 2012). Behavioral syndromes are defined as "a suite of correlated behaviors" (Sih et al. 2004) that by explaining non-optimal behaviors can have impacts on population and distributions (Sih et al. 2004; Dingemanse et al. 2009; Wolf and Weissing 2012). For example, differences in activity syndromes (active vs inactive individuals) can affect the tradeoff between feeding and predator avoidance choices and consequently species distributions (Sih et al. 2004). Landscapes of fear (Laundre et al. 2014) can also be caused by behavioral syndromes where individuals that show more predator avoidance will have different distributions than individuals that are more bold.

Scope of current research. The recent literature on individuality is diverse and rapidly expanding**.** Using the keywords animal personalit* or behavioral syndrome in the title for a Web of Science search between 2011-2017 (5 years), we identified an objective subsample of 43 select papers (Tab. 2.1). The behaviors that are most often examined include very specific traits such as aggression (19%; 8), boldness (19%; 8), activity level (16%; 7), exploration (16%; 7), or feeding (12%; 5) (Tab. 2.1). Of the 43 studies, 51% were reviews or commentaries not empirical studies. Of the remaining 49%, 21 tested discontinuous, often discrete behavioral differences across individuals. However, of these 21 empirical tests, 40% were undertaken in labs or cages and only 9% (4) of the empirical studies on behavior were undertaken in the field (Tab. 2.1). Even for empirical or field research in animal behavior, however, few of these behavioral studies (35%; 15) mention ecological links (Tab. 2.1), and even fewer address consequences for ecological distributions (7%; 3) or organismal movement (16%; 7).

Thus, missing from the existing individuality literature is how individual differences impact wild animals in the field, and, especially how they link to ecological effects or distribution/movement patterns. The four field studies in the above described sample of 43 papers (Briffa and Greenaway 2011; Carter et al. 2012; Kazama et al. 2012; Fresneau et al. 2014) tested ecological ties (e.g. mating, feeding, adaptivity, and response to invasive organisms) on a variety of species (birds, mammals, and anemones) (Tab. 2.1). As an example, Kazama et al. (2012) demonstrated differences in nesting and mating behaviors related to aggression and feeding syndromes in a wild gull population across varying environmental conditions. As one of the few examples of how animal behavior links with distribution (e.g. Monceau et al. 2015; Pruitt and Modlmeier 2015), invasive insect species outperformed the natives on traits measured in the lab (Monceau et al. 2015).

In field ecology, evidence for discrete groups is increasing. Discrete individual groups or behavioral contingents in fish have been detected in multiple studies using telemetry (DeCelles and Cadrin 2010; Pautzke et al. 2010; Gerber 2015). For example, Gerber (2015) showed that groups of blue catfish make different types of seasonal movements within a reservoir. Some researchers have begun to associate these contingents with habitat use (Harcourt et al. 2009; Revilla et al. 2008; Rosenblatt et al. 2013; Fodrie et al. 2015; Hirsch et al. 2017). For example, Harcourt et al. (2009) were able to show how contingents of sticklebacks make different shoaling decisions. Hirsch et al. (2017) showed group differences in the probability of crossing an in-stream barrier. Outside of the contingent literature, individuality or behavioral syndromes have largely developed in isolation from distributional or movement data. Clearly, more explicit connections between behavioral research and field ecology related to distribution is needed.

Specific questions. In the past, technology has not existed that would provide high-resolution data needed to explore individual personalities related to field distribution of fish. With acoustic telemetry and an estuary-wide array of stationary receivers, we asked three specific research questions. First, do ***individual*** striped bass of the same size systematically vary in discrete types of ***distributional groups***? Second, are ***types*** of ***distribution groups*** linked to ***geomorphologic habitat and ecosystem region***? Three, does personality help us understand mobile predator distribution in the field?

Methods

PIE and Geomorphology

This study was conducted in Plum Island Estuary (PIE) located on the northeastern coast of Massachusetts, USA. PIE is an estuary with a diverse set of geomorphic features (confluences, non-confluences, and exits) across four regions (Upper, Middle, Lower, and Rowley). All aspects of the study system and tagging methods are described in detail elsewhere (Taylor et al. 2017; Chapter 1). Below, some of these methods are briefly summarized.

Tagged Fish and Stationary Arrays

In 2015, variation in striped bass distribution was assessed using a stationary array of 26 Vemco VR2W acoustic receivers deployed across three geomorphic types of sites (confluences, non-confluences, and exits) throughout four estuarine regions. In 2015, 59 subadult striped bass were implanted with Vemco V13 acoustic transmitters and released near the location where they were captured.

Data and Response Metrics

The metric *"residence time"* was quantified by summing the amount of time each fish spent at each location using VTrack software (R 2.15.2 software; R Core Team; Campbell et al. 2012). The metric, *"proportion of time"* was calculated by taking the amount of time a fish spent at a single receiver and dividing it by the total time a fish was detected across the entire array.

Cluster Analyses

To identify individual striped bass distributional groups, two separate spatial and temporal-spatial hierarchical cluster analyses were run using Ward's linkage on a Euclidian distance matrix ('cluster' package, R). Fish that stayed <30 days ("short-timers") were classified as a distinct cluster, but excluded from further analyses. To determine the optimal number of clusters, the average silhouette width was maximized (Kaufman and Rousseeuw 1990). Jaccard bootstrap mean values >0.60 ('clusterboot' function, 'fpc' package, R) were used as criteria for distinct and cohesive cluster groups (Hennig 2008).

The first spatial cluster analysis used the metric "*proportion of time*" at each of the 26 receivers and isolated the Rowley distributional group removed. A second, temporal-spatial cluster analysis on the remaining Plum Island Sound fish used five additional distributional metrics. The first temporal-spatial metric, *total days in Plum Island*, was measured as the days between an individual fish's first detection and its last. We expected fish that stayed a short period of time to behave differently than seasonally-resident fish. The second metric, *total receivers visited,* was a measure of mobility that was calculated by counting the number of unique receivers each fish visited. A fish that visited many receivers was likely more active than a fish that stayed close to the same few receivers. The third temporal-spatial metric, *total movements*, was another measure of activity that was calculated by summing the numbers of times fish came or went from one receiver to another. The fourth temporal-spatial metric, *highest proportion of time spent at a single receiver*, was a measure of fidelity and was calculated by selecting the highest proportion of time that each fish spent at any single receiver. A fish that stayed in the same place would have a high value of this metric compared to a fish that spent time at different receivers throughout the estuary. The final temporal-spatial metric, *coefficient of variation*, measured variation in within estuary distribution, and was calculated as the coefficient of variation of residence times across all receiver locations for a single fish. A fish that was not attached to a limited set of locations would have a low coefficient of variation of residence time compared to a fish that favored just a few receivers and did not visit other receivers at all.

These two spatial and temporal-spatial cluster analyses grouped individual fish into four distinct seasonally resident distributional groups. All metrics were examined as boxplots to visualize the differences among distributional group clusters. Differences in metrics across distributional groups were tested using a Kruskal-Wallis nonparametric ANOVA test (‘kruskal.test’ function, ‘stats’ package, R) with a post-hoc Mann Whitney U multiple comparisons.

Relationship Between Geomorphic Site and Distributional Groups

We also tested whether geomorphic type (confluence, nonconfluence, and exit) and striped bass distributional groups (the four above-described clusters) affected receiver-specific residence time using two 2-way ANOVAs (‘anova’ function, ‘stats’ package, R). In these analyses, geomorphic type and distribution group were the independent variables, and residence time was the response. The individual fish was the experimental unit. Data were log transformed to meet statistical assumptions. A post-hoc Tukey test (‘tukeyHSD’ function, ‘stats’ package, R) identified pairs of significantly different treatments. For these analyses, all fish were included (i.e., zero values were included) to test how the fish behaved as an entire tagged population. A value of $P < 0.05$ was used to determine statistical significance. The above statistical procedure was repeated after substituting the treatment, region, for geomorphic site.

Results

Types of Distributional Groups

In addition to fish that were in PIE < 30 days, the cluster analysis identified four seasonal resident distributional groups for striped bass in PIE. These four clusters resulted from the spatial (one cluster; Fig. 2.1) and temporal spatial (three clusters; Fig. 2.2) cluster analysis. The four distributional clusters were distinct based on Jaccards mean values > 0.6. In addition, many metrics were statistically different among clusters (see below).

Nine fish, the Short-Timers, stayed in PIE <30 days and are excluded from future analyses (Fig. 2.3). Seventeen tagged fish (detected within PIE for 51-117 days) clustered with the first Rowley River distributional group (Fig. 2.1; Fig. 2.3). Thirteen tagged striped bass (detected within PIE for 72-111 days) represented the second Plum Island Sound distributional group (Fig. 2.2; Fig. 2.3). Thirteen tagged fish (detected within PIE for 68-102 days) were classified into the third Extreme Fidelity distributional group (Fig. 2.2; Fig. 2.3). Seven tagged fish (detected within PIE for 6-52 days) fit the fourth Exploratory distributional group. (Fig. 2.2; Fig. 2.3). Below, we use boxplots (Fig. 2.4) to show differences across all four distributional groups for all metrics. Then, we show one example of each seasonal resident group in detail using a single representative fish (Fig. 2.5 – Fig. 2.8).

Differences in Distributional Group Metrics

For the metric *Total Days*, the Exploratory distributional group had a significantly lower number of days spent in PIE than the Extreme Fidelity, Rowley River, and Plum Island Sound distribution groups ($P<0.05$; Fig. 2.4a). For the metric *Total Receivers Visited*, the Rowley River and Plum Island Sound distribution groups visited significantly more receivers than the Extreme Fidelity group ($P<0.05$; Fig. 2.4b). For the metric *Total Movements*, the Rowley River and Plum Island Sound distribution groups had significantly more movements than the Exploratory and Extreme Fidelity distribution groups ($P<0.05$; Fig. 2.4c). For the metric *Highest Proportion of Time Spent*, the Extreme Fidelity distribution group spent a significantly higher proportion of time at any one receiver than all other distribution groups ($P<0.05$; Fig. 2.4d). For the metric *Coefficient of Variation of Residence Time*, the Extreme Fidelity distribution group had a significantly higher coefficient of variation of residence time than the other three distribution groups ($P<0.05$; Fig. 2.4e).

Rowley River Distributional Group

The Rowley River distributional group (Fig. 2.5) was-characterized by trajectories with movements within the Rowley River (Fig. 2.5a) where the highest proportion of time was spent at receivers 5-12 (Fig. 2.5b), and residence times were highest at Rowley River receivers (Fig. 2.5c). The Rowley River distributional group was seasonally resident in PIE (average: 88.35 days, SE: 5.01 Fig. 2.4a), visited a *high number of receivers* (average: 18.47, SE: 0.69; Fig. 2.4b), had very high but variable *numbers of movements* (average: 451.88, SE: 43.52; Fig. 2.4c), had a high but variable *highest proportion of time spent at a single receiver* (average: 0.55, SE: 0.04; Fig. 2.4d), and had a low *coefficient of variation of residence time* (average: 3.07, SE: 0.16; Fig. 2.4e). Individual fish in the Rowley River distributional group visited a lot of receivers and moved a lot, but primarily within the Rowley River resulting in them spending a lot of time at a subset of receivers. This distributional group varied in how much time was spent at each receiver, but as a group they primarily used the Rowley River over their entire residence in PIE.

Plum Island Sound Distributional Group

The Plum Island Sound distributional group's (Fig. 2.6) trajectories showed a combination of movements and residence events within the Sound (Fig. 2.6a), they spent the most time at receivers 13-18 (Fig. 2.6b), and had the highest residence time at receivers within the Sound (Fig. 2.6c). The Plum Island Sound distributional group was seasonally resident in PIE (average: 89.08 days, SE: 4.32; Fig. 2.4a), visited a high *number of receivers* (average: 17.62, SE: 0.53; Fig. 2.4b), had an intermediate *number of movements* (average: 270.00, SE: 32.40; Fig. 2.4c), had a variable *highest proportion of time spent at a single receive*r (average: 0.48, SE: 0.06; Fig. 2.4d), and had a low *coefficient of variation of residence time* (average: 2.68, SE: 0.24; Fig. 2.4e). Individual fish within the Plum Island Sound varied with some fish spending more time around Middle Ground and other fish spending more time in the southern end of the estuary. As a distributional group, the Plum Island Sound fish seldom used the Rowley River, but visited multiple Sound receivers, resulting in low variation in residence time across receivers.

Extreme Fidelity Distributional Group

The-Extreme Fidelity distributional group (Fig. 2.7) was characterized by trajectories that show one long residence event with very few movements (Fig. 2.7a), an extremely high proportion of time at only one or two receivers (e.g. 17; Fig. 2.7b), and high residence times at a few receivers (Fig. 2.7c). The Extreme Fidelity distributional group was seasonally resident in PIE (average: 87.92 days, SE: 3.19; Fig. 2.4a), visited a low *number of receivers* (average: 11.77, SE: 0.71; Fig. 2.4b), made a low *number of total movements* (average: 109.08, SE: 20.12; Fig.

2.4c), had a high *highest proportion of time a single receiver* (average: 0.82, SE: 0.03; Fig. 2.4d), and had a high *coefficient of variation of residence time* across receivers (average: 4.21, SE: 0.14; Fig. 2.4e). Fish in the Extreme Fidelity distributional group spent the majority of their time at one or two receiver locations although the specific receivers varied by fish. These fish made very few forays to any other receivers until they left PIE at the end of the season. All fish were observed leaving at the end of the summer-fall season.

Exploratory Distributional Group

The Exploratory distributional group was characterized by trajectories that showed very few residence events and many movements (Fig. 2.8a), low proportions of time spent at multiple receivers across the estuary (Fig. 2.8b), and low residences across the estuary (Fig. 2.8c). The Exploratory distributional group spent a low *number of days in PIE* (average: 34.28, SE: 6.79; Fig. 2.4a), had a high *number of receivers visited* (average: 14.00, SE: 1.56; Fig. 2.4b), made a low *number of total movements* (average: 71.29, SE: 8.89; Fig. 2.4c), had a low but variable *highest proportion of time spent at a single receiver* (average: 0.50, SE: 0.08; Fig. 2.4d), and had a low *coefficient of variation of residence time* (average: 2.80, SE: 0.35; Fig. 2.4e). The Exploratory group was a roaming behavioral group that did not devote time to any specific region or receiver.

Geomorphic Drivers of Distributions

Incorporating intra-population distribution groups provided new insights into geomorphic and regional drivers for the population (Taylor et al. 2017 Chapter 1). Striped bass in all distributional groups spent very little time at exit locations (Fig. 2.9). Striped bass in the Rowley River distributional group had the highest residence time at confluences ($P<0.05$; Fig. 2.9). The Plum Island Sound distributional group had intermediate high residence times at confluences

(*P*<0.05; Fig 2.9). The Extreme Fidelity and Exploratory distributional groups spent little time at confluences (P<0.05; Fig 2.9). Tagged striped bass in the Extreme Fidelity and Estuary groups had higher mean residence times at non-confluence sites than confluence sites although these highly variable differences were not significant (Fig 2.9).

Region

By region, the Rowley River distributional group spent significantly more time in the Rowley River region (*P*<0.05; Fig. 2.10). No distributional group spent much time in the Upper region (Fig. 2.10). The Middle region was used more by both the Extreme Fidelity distributional group and the Plum Island Sound distributional group than the Exploratory or Rowley River distributional groups (*P*<0.05; Fig. 2.10). The Lower region had very low residence time for all distribution groups (Fig. 2.10).

Discussion

Take-home Message 1: Discrete Distributional Groups

Discrete and predictable distributional groups existed for striped bass in PIE during their seasonal foraging migration. Individual fish clustered into four different seasonal-resident groups based on where fish were located (spatial dimension) and how they behaved within each location (temporal-spatial dimension). As one example, the Rowley River distributional group used the Rowley River for the whole season. Although almost 1/3 of the tagged fish (the 17 fish in the Rowley River distributional group) spent almost the entire season there (Average residence time: 108 hours), the rest of the tagged population spent no more than six hours in this same location. Other research has found behavioral contingents of fish (DeCelles and Cadrin 2010; Pautzke et al. 2010; Gerber 2015) and some have even linked these contingents with general site fidelity groups (Gahagan et al. 2015; Atkins et al. 2016; Espinoza et al. 2016). However, these previous studies of fish distribution have not grouped fish into as many statistically distinct distributional groups as we show here. Thus, we have extended the connection between the animal behavior literature and fish distribution literature in a way that can benefit both research areas.

Take-home Message 2: Distributional Groups and Geomorphology

The four seasonally resident distribution groups had specific associations with geomorphic sites. These distributional groups added to the understanding of how striped bass use geomorphic sites and regions. For example, the Rowley River distributional group used confluences more than the other geomorphic sites. In related research, we expected confluences to be ecological hotspots (Poole 2002; Benda et al. 2004; Rice et al. 2006) and these geomorphic sites were commonly used. However, our previous whole population analysis showed that not all fish used these discontinuities (Taylor et al. 2017 - Chapter 1). When just the Rowley River distribution group is considered, though, confluence use is high.

Regionally, we also saw large differences between the distribution groups. The Rowley River fish showed the highest usage of the Rowley River. The Middle region was dominated by both the Extreme Fidelity fish and the Plum Island Sound fish. Regional aggregations have been found in the literature (Gahagan et al. 2015; Zhang et al. 2015; Kennedy et al. 2015; Kessel et al. 2016) but we show how these can be related to distinct distribution groups within a population. The animal behavior literature is just beginning to explore how individual differences link to habitat use in the field (e.g. Monceau et al. 2015; Pruitt and Modlmeier 2015). Our research on geomorphic site types and regions adds to this literature.

Take-home Message 3: Site Fidelity

Site fidelity is one explanation for the patterns displayed by these four seasonally-resident distribution groups. Site fidelity is defined as “the tendency to return to a previously occupied location” (Switzer 1993). All four seasonally resident distributional groups stayed in PIE over 30 days and thus are site fidel to the estuary (our largest scale). The Rowley River distribution group is site fidel to the intermediate-sized Rowley River region. Although fish in this distribution group move a lot within the Rowley River, they stay within this area, and if they leave, they return. The Extreme Fidelity group are site fidel to specific receiver locations (our smallest scale) and rarely leave the range of these single receivers. Elsewhere, site fidelity has been found to occur at many different scales. For example, the size of a site can be from a single holdfast where a seahorse grips (Harasti et al. 2014), the same coral colony (Gardiner and Jones 2016), or even as large as an entire bay area (Atkins et al. 2016). However, to our knowledge, we are the first to show multi-scale site-fidelity (estuary, region, site) by a single population that co-occurs in a single ecosystem. Thus, identifying distinct distributional groups has also provided insights into site fidelity.

Summary

Intra-population variation (i.e. individuality and behavioral syndromes) is a growing field of research that can benefit from better connections between field ecology and animal behavior. Field ecology has made great strides in explaining organismal distributions. However, unexplained variation in distribution is still substantial and could be related to individual differences. Animal behavior research is on the forefront of animal individuality research but needs a stronger connection to ecological implications in nature. With our large database of high resolution telemetry data, we were able to make these links by both identifying behavioral syndromes and showing how these syndromes help explain variation in field distribution of mobile fish.

Literature Cited

Able, K. W. and T. M. Grothues (2007). Diversity of estuarine movements of striped bass (*Morone saxatilis*): a synoptic examination of an estuarine system in southern New Jersey. Fishery Bulletin 105(3): 426-435.

Altieri, A. H., et al. (2012). A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. Ecology 93(6): 1402-1410.

Atkins, S., et al. (2016). Net loss of endangered humpback dolphins: integrating residency, site fidelity, and bycatch in shark nets. Marine Ecology Progress Series 555: 249-260.

Bell, A. M. (2007). Evolutionary biology - Animal personalities. Nature 447(7144): 539-540.

Benda, L., et al. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. Bioscience 54(5): 413-427.

Bestley, S., et al. (2010). Predicting feeding success in a migratory predator: integrating telemetry, environment, and modeling techniques. Ecology 91(8): 2373-2384.

Binsong, J., et al. (2014). The impact of geomorphology of marsh creeks on fish assemblage in Changjiang River estuary. Chinese Journal of Oceanology and Limnology 32(2): 469-479.

Bouska, K. L. and G. Whitledge (2014). Habitat associations of fish assemblages in the Cache River, Illinois. Environmental Biology of Fishes 97(1): 27-42.

Brady, D. C. and T. E. Targett (2013). Movement of juvenile weakfish *Cynoscion regalis* and spot *Leiostomus xanthurus* in relation to diel-cycling hypoxia in an estuarine tidal tributary. Marine Ecology Progress Series 491: 199-219.

Briffa, M. and J. Greenaway (2011). High in situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). PLoS ONE 6(7)

Bultel, E., et al. (2014). Migration behaviour of silver eels (*Anguilla anguilla*) in a large estuary of Western Europe inferred from acoustic telemetry. Estuarine Coastal and Shelf Science 137: 23-31.

Burkholder, D. A., et al. (2013). Groups of top-down control in a seagrass ecosystem: could a roving apex predator induce a behavior-mediated trophic cascade? Journal of Animal Ecology 82(6): 1192-1202.

Callihan, J. L., et al. (2015). Sex-specific movement response of an estuarine sciaenid (*Cynoscion nebulosus*) to freshets. Estuaries and Coasts 38(5): 1492-1504.

Campbell, R. E., et al. (2015). Flow-related disturbance creates a gradient of metacommunity types within stream networks. Landscape Ecology 30(4): 667-680.

Carere, C. and F. Gherardi (2013). Animal personalities matter for biological invasions. Trends in Ecology & Evolution 28(1): 5-6.

Carter, A. J., et al. (2012). Evaluating animal personalities: do observer assessments and experimental tests measure the same thing? Behavioral Ecology and Sociobiology 66(1): 153-160.

Casini, M., et al. (2012). Predator transitory spillover induces trophic cascades in ecological sinks. Proceedings of the National Academy of Sciences of the United States of America 109(21): 8185.

Cerqueira, M., et al. (2016). Thermal preference predicts animal personality in Nile tilapia *Oreochromis niloticus*. Journal of Animal Ecology 85(5): 1389-1400.

Coleman, F. C., et al. (2004). The impact of United States recreational fisheries on marine fish populations. Science 305(5692): 1958-1960.

Cram, J. M., et al. (2013). Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. Environmental Biology of Fishes 96(1): 109-122.

Crossin, G. T., et al. (2017). Acoustic telemetry and fisheries management. Ecological Applications 27(4): 1031-1049.

Currey, L. M., et al. (2015). Assessing environmental correlates of fish movement on a coral reef. Coral Reefs 34(4): 1267-1277.

Czegledi, I., et al. (2016). The scales of variability of stream fish assemblages at tributary confluences. Aquatic Sciences 78(4): 641-654.

Dall, S. R. X., et al. (2012). An evolutionary ecology of individual differences. Ecology Letters 15(10): 1189-1198.

DeCelles, G. R. and S. X. Cadrin. 2010. Movement groups of Winter Flounder (*Pseudopleuronectes americanus*) in the southern Gulf of Maine: observations with the use of passive acoustic telemetry. Fishery Bulletin 108(4): 408-419.

Dingemanse, N. J., et al. (2009). Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. Proceedings of the Royal Society B-Biological Sciences 276(1660): 1285-1293.

Dingemanse, N. J. and D. Reale (2005). Natural selection and animal personality. Behaviour 142: 1159-1184.

Dosmann, A. and J. M. Mateo (2014). Food, sex and predators: animal personality persists with multidimensional plasticity across complex environments. Animal Behaviour 90: 109-116.

Downey, N. J., et al. (2010). An investigation of the spawning behaviour of the chokka squid *Loligo reynaudii* and the potential effects of temperature using acoustic telemetry. Ices Journal of Marine Science 67(2): 231-243.

Espinoza, M., et al. (2016). Evidence of partial migration in a large coastal predator: Opportunistic foraging and reproduction as key drivers? PLoS ONE 11(2).

Estes, J. A., et al. (2011). Trophic downgrading of planet earth. Science 333(6040): 301-306.

Ferry, K. H. and M. E. Mather (2012). Spatial and temporal diet groups of subadult and small adult striped bass in Massachusetts estuaries: Data, a synthesis, and trends across scales. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4(1): 30-45.

Fodrie, F. J., et al. (2015). Measuring individuality in habitat use across complex landscapes: approaches, constraints, and implications for assessing resource specialization. Oecologia 178(1): 75-87.

Frank, K. T., et al. (2005). Trophic cascades in a formerly cod-dominated ecosystem. Science 308(5728): 1621-1623.

Fresneau, N., et al. (2014). A sex-specific behavioral syndrome in a wild passerine. Behavioral Ecology 25(2): 359-367.

Gahagan, B. I., et al. (2015). Partial migration of striped bass: revisiting the contingent hypothesis. Marine Ecology Progress Series 525: 185-197.

Gardiner, N. M. and G. P. Jones (2016). Habitat specialisation, site fidelity and sociality predict homing success in coral reef cardinalfish. Marine Ecology Progress Series 558: 81-96.

Goodchild, C. G., et al. (2017). Animal personality explains among-individual variation in antipredator strategies. Integrative and Comparative Biology 57: E274-E274.

Harasti, D., et al. (2014). Ontogenetic and sex-based differences in habitat preferences and site fidelity of White's seahorse *Hippocampus whitei.* Journal of Fish Biology 85(5): 1413-1428.

Harcourt, J. L., et al. (2009). Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. Animal Behaviour 77(6): 1501-1505.

Haulsee, D. E., et al. (2016). Implantation and Recovery of Long-Term Archival Transceivers in a Migratory Shark with High Site Fidelity. PLoS ONE 11(2).

Hennig, C. 2008. Dissolution point and isolation robustness: robustness criteria for general cluster analysis methods. Journal of Multivariate Analysis 99, 1154-1176.

Hirsch, P. E., et al. (2017). An approach to incorporate individual personality in modeling fish dispersal across in-stream barriers. Ecology and Evolution 7(2): 720-732.

Hitt, N. P. and P. L. Angermeier (2008). Evidence for fish dispersal from spatial analysis of stream network topology. Journal of the North American Benthological Society 27(2): 304-320.

Isaak, D. J., et al. (2007). Chinook salmon use of spawning patches: Relative roles of habitat quality, size, and connectivity. Ecological Applications 17(2): 352-364.

Juette, T., et al. (2014). Animal personality and the ecological impacts of freshwater non-native species. Current Zoology 60(3): 417-427.

Kalinkat, G. (2014). Bringing animal personality research into the food web arena. Journal of Animal Ecology 83(6): 1245-1247.

Kaufman, L. and P.J. Rousseeuw. 1990. Partitioning around medoids (program pam). Pages 68-125 in John Wiley & Sons, Inc., editors. Finding groups in data: an introduction to cluster analysis, John Wiley & Sons, Inc., Hoboken, New Jersey

Kazama, K., et al. (2012). Consistent individual variations in aggressiveness and a behavioral syndrome across breeding contexts in different environments in the Black-tailed Gull. Journal of Ethology 30(2): 279-288.

Kennedy, C. G., et al. (2016). Discontinuities concentrate mobile predators: quantifying organism-environment interactions at a seascape scale. Ecosphere 7(2).

Kessel, S. T., et al. (2016). Distinct groups of Arctic cod (Boreogadus saida) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. Polar Biology 39(6): 1057-1068.

Lapiedra, O., et al. (2017). Urbanization and biological invasion shape animal personalities. Global Change Biology 23(2): 592-603.

Laundre, J. W., et al. (2014). The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology 95(5): 1141-1152.

Lichtenstein, J. L. L. and J. N. Pruitt (2015). Similar groups of frequency-dependent selection on animal personalities emerge in three species of social spiders. Journal of Evolutionary Biology 28(6): 1248-1256.

Marsh, P. C., et al. (2013). Diel cover use and local site fidelity of a large southwestern cyprinid, bonytail *Gila elegans*, in a lower colorado river backwater. Western North American Naturalist 73(2): 211-218.

Mazue, G. P. F., et al. (2015). Boldness-exploration behavioral syndrome: interfamily variability and repeatability of personality traits in the young of the convict cichlid (*Amatitlania siquia*). Behavioral Ecology 26(3): 900-908.

Mittermeier, R. A., et al. (1998). Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conservation Biology 12(3): 516-520.

Modlmeier, A. P., et al. (2015). Integrating animal personality into insect population and community ecology. Current Opinion in Insect Science 9: 77-85.

Monceau, K., et al. (2015). Behavioral syndrome in a native and an invasive hymenoptera species. Insect Science 22(4): 541-548.

Neat, F., et al. (2015). Site fidelity, survival and conservation options for the threatened flapper skate (*Dipturus cf. intermedia*). Aquatic Conservation-Marine and Freshwater Ecosystems 25(1): 6-20.

Ng, C. L., et al. (2007). Habitat use, site fidelity, and movement of adult striped bass in a Southern New Jersey estuary based on mobile acoustic telemetry. Transactions of the American Fisheries Society 136(5): 1344-1355.

Osawa, T., et al. (2011). The role of river confluences and meanderings in preserving local hot spots for threatened plant species in riparian ecosystems. Aquatic Conservation: Marine and Freshwater Ecosystems 21(4): 358-363.

Pautzke, S. M., et al. (2010). Seasonal use of a New England estuary by foraging contingents of migratory striped bass. Transactions of the American Fisheries Society 139: 257-269.

Piper, A. T., et al. (2013). Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. Ecological Engineering 57: 88-96.

Poole, G. C. (2002). Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47(4): 641-660.

Poulakis, G. R., et al. (2013). Movements of juvenile endangered smalltooth sawfish, *Pristis pectinata*, in an estuarine river system: use of non-main-stem river habitats and lagged responses to freshwater inflow-related changes. Environmental Biology of Fishes 96(6): 763-778.

Pruitt, J. N. and A. P. Modlmeier (2015). Animal personality in a foundation species drives community divergence and collapse in the wild. Journal of Animal Ecology 84(6): 1461-1468.

Quinn, J. L. (2015). Animal personality meets community ecology: founder species aggression and the dynamics of spider communities. Journal of Animal Ecology 84(6): 1457-1460.

Rankin, P. S., et al. (2013). Effect of hypoxia on rockfish movements: implications for understanding the roles of temperature, toxins and site fidelity. Marine Ecology Progress Series 492: 223-234.

Revilla, E. and T. Wiegand (2008). Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proceedings of the National Academy of Sciences of the United States of America 105(49): 19120-19125.

Rey, S., et al. (2013). Combining animal personalities with transcriptomics resolves individual variation within a wild-type zebrafish population and identifies underpinning molecular differences in brain function. Molecular Ecology 22(24): 6100-6115.

Rice, S. P., et al. (2006). Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63(11): 2553-2566.

Rosenblatt, A. E., et al. (2013). Intra-population variation in activity ranges, diel groups, movement rates, and habitat use of American alligators in a subtropical estuary. Estuarine Coastal and Shelf Science 135: 182-190.

Rous, A. M., et al. (2017). Telemetry-determined habitat use informs multi-species habitat management in an urban harbour. Environ Manage 59(1): 118-128.

Rueger, T., et al. (2014). Relationships between pair formation, site fidelity and sex in a coral reef cardinalfish. Behavioural Processes 107: 119-126.

Sih, A., et al. (2004). Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19(7): 372-378.

Stephens, D. and J. Krebs (1986). Foraging theory. Princeton, NJ, Princeton University Press.

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7: 533-555.

Torgersen, C. E. and D. A. Close (2004). Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biology 49(5): 614-630.

Tupper, M. and K. W. Able (2000). Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. Marine Biology 137(5-6): 1049-1058.

Villegas-Rios, D., et al. (2013). Home range and diel behavior of the ballan wrasse, *Labrus bergylta,* determined by acoustic telemetry. Journal of Sea Research 80: 61-71.

Walter, J. F. I., et al. (2003). Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. Fisheries Management and Ecology 10: 349-360.

Way, G. P., et al. (2015). Sex differences in a shoaling-boldness behavioral syndrome, but no link with aggression. Behavioural Processes 113: 7-12.

Wolf, M. and F. J. Weissing (2012). Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution 27(8): 452-461.

Table 2.1: Summary of the literature review on animal behavior and personality studies.

No.	Citation		Focus				Traits Measured						Ecology Links		
	Year	Author	Empirical Test?	Review?	Field Study?	Organism	Aggressiveness	Boldness	Activity Level	Exploration	Feeding	Other	Distribution	Movement	Ecology Mentioned?
1	2017	Perals et al.	X			Bird		X	X	X				X	
2	2017	Lapiedra et al.	X			Lizard	X	X		X	X	X		X	X
3	2017	Briffa, M.		X											
4	2017	Beekman and Jordan		X											
5	2016	Roche, et al.		X											
6	2016	Michelangeli, et al.	X			Lizard		X	X	X	X	X		X	
7	2016	David and Dall		X											
8	2016	Cerqueira, et al.	X			Fish					X	X		X	X
9	2016	Briffa and Sneddon		X											
10	2015	Way, et al.	X			Fish	X	X				X			
11	2015	Sih, et al.		X											
12	2015	Rey, et al.	X			Fish						X			
13	2015	Quinn, J. L.		X		Insect	X						X	X	X
14	2015	Pruitt and Modlmeier	X			Insect	X						X	X	X
15	2015	Monceau, et al.	X			Insect		X	X	X			X	X	X
16	2015	Monceau, K.		X											
17	2015	Modlmeier, et al.		X		Insect									
18	2015	Mauze, et al.	X			Fish		X		X					X
19	2015	Lichtenstein, and Pruitt	X			Insect	X								X
20	2015	Hans and Dingemanse		X											
21	2015	Dosmann, et al.	X			Mammal			X	X		X			X
22	2015	Dosmann, et al.	X			Mammal			X	X		X			X
23	2015	Briffa, et al.		X											
24	2014	Wright, et al.	X			Insect	X								X
25	2014	Pruitt, J. N.		X											
26	2014	Kalinkat, G.		X											
27	2014	Juette, et al.		X											
28	2014	Ingley and Johnson		X											
29	2014	Fresneau, et al.	X		X	Bird						X			X
30	2014	Dosmann and Mateo	X			Mammal						X			X
31	2014	Dirienzo and Hendrick		X											

Table 2.1 (continued)

No.	**Citation**		**Focus**				**Traits Measured**						**Ecology Links**		
	Year	Author	Empirical Test?	Review?	Field Study?	Organism	Aggressiveness	Boldness	Activity Level	Exploration	Feeding	Other	Distribution	Movement	Ecology Mentioned?
32	2013	Zipser, et al	X			Mammal						X			
33	2013	Rey, et al.	X			Fish	X	X	X		X				X
34	2013	Carter et al.		X											
35	2013	Carere and Gherardi		X											
36	2013	Brommer, J. E.		X											
37	2012	Wolf and Weissing		X											
38	2012	Wilson and Krause		X											
39	2012	Kazama et al.	X		X	Bird	X				X	X			X
40	2012	Gherardi et al.		X		Crustacean									
41	2012	Carter et al.	X		X	Mammal		X							
42	2011	Brodin and Drotz	X			Insect			X			X			X
43	2011	Briffa and Greenaway	X		X	Cnidarian						X			
		Taylor et al.	**X**		**X**	**Fish**			**X**	**X**			**X**	**X**	**X**
	Total		21	22	4		8	8	7	7	5	13	3	7	15

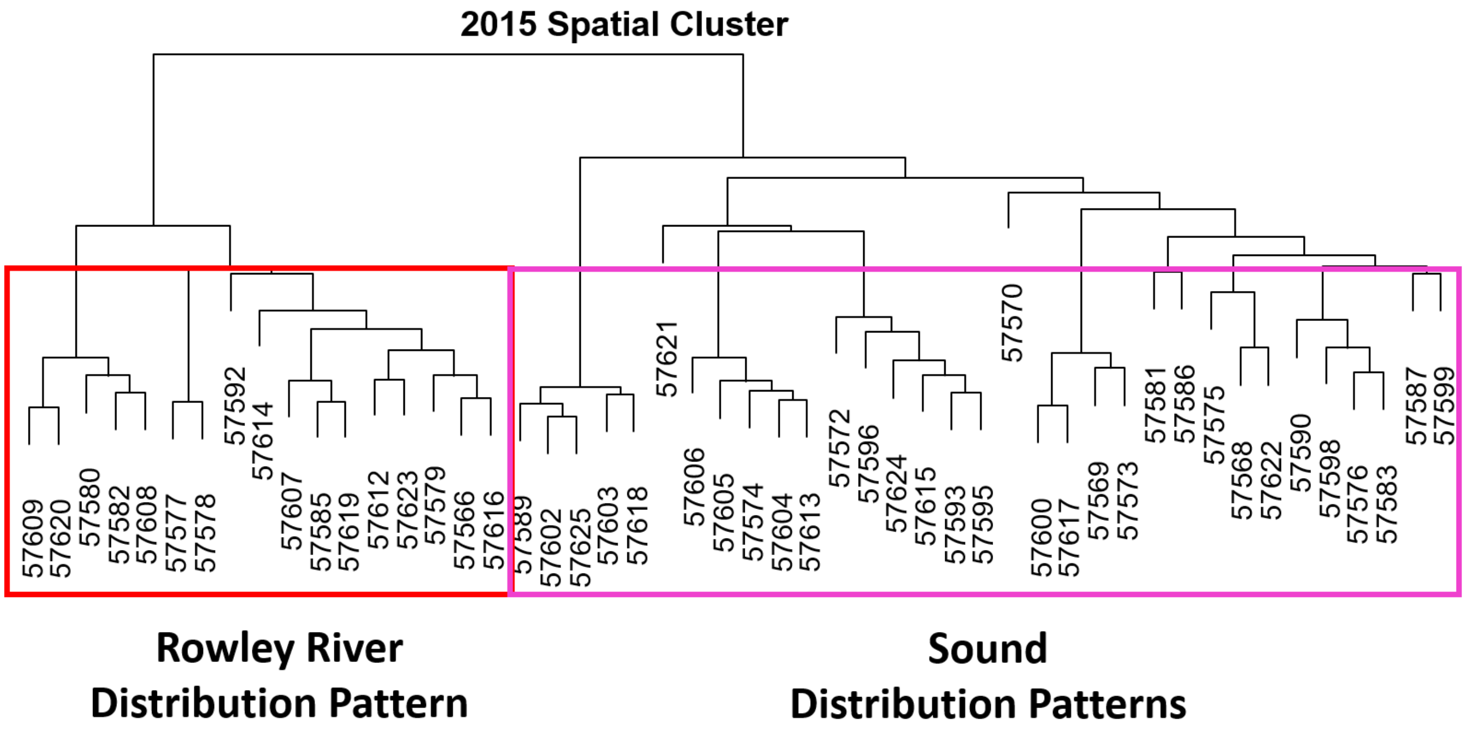


Figure 2.1: Spatial cluster dendrogram based on proportion of time spent at each receiver. The red box indicates fish within the Rowley River Distribution Group. The purple box indicates Non-Rowley Distribution Groups. Each number indicates an individual fish.

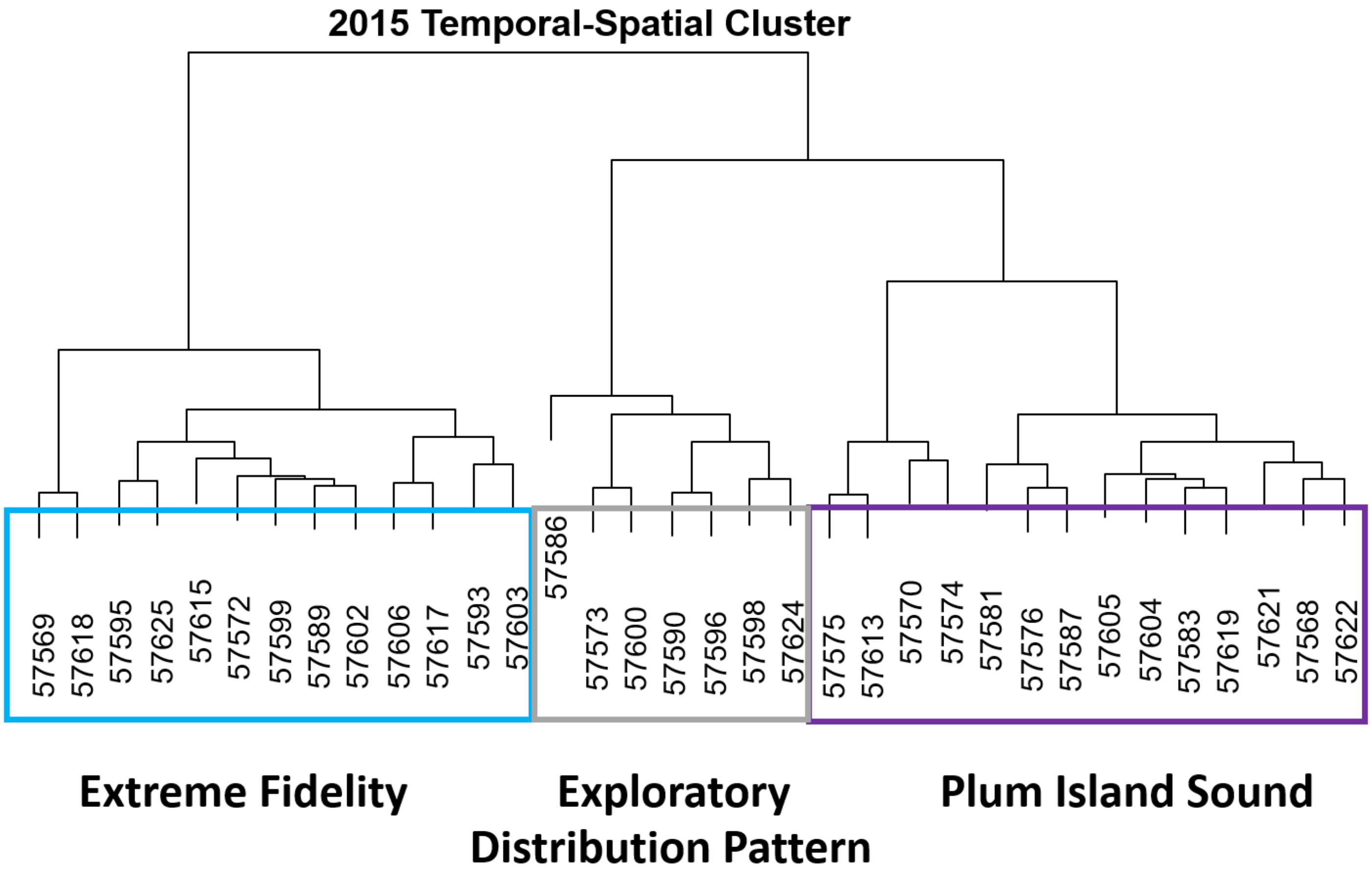


Figure 2.2: Temporal-spatial cluster dendrogram using the *total number of days* in PIE, total *number of receivers visited, total movements, highest proportion of time spent at a single receiver,* and *standard error of residence time*. Each number indicates an individual fish. The Rowley River Distribution Group (spatial cluster 1) is excluded.

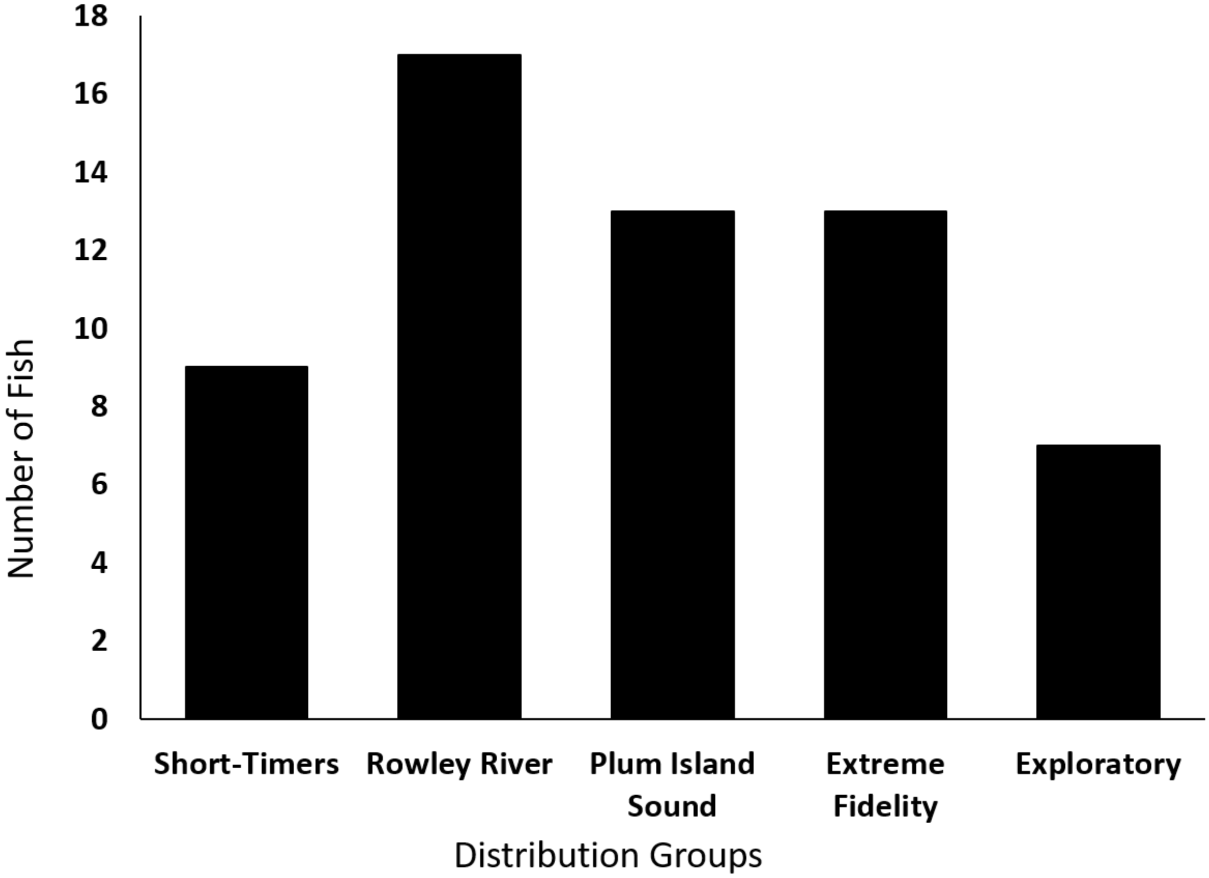


Figure 2.3: Bar graphs illustrating the number of tagged fish in each distribution group. Short-timers were excluded from subsequent analysis.

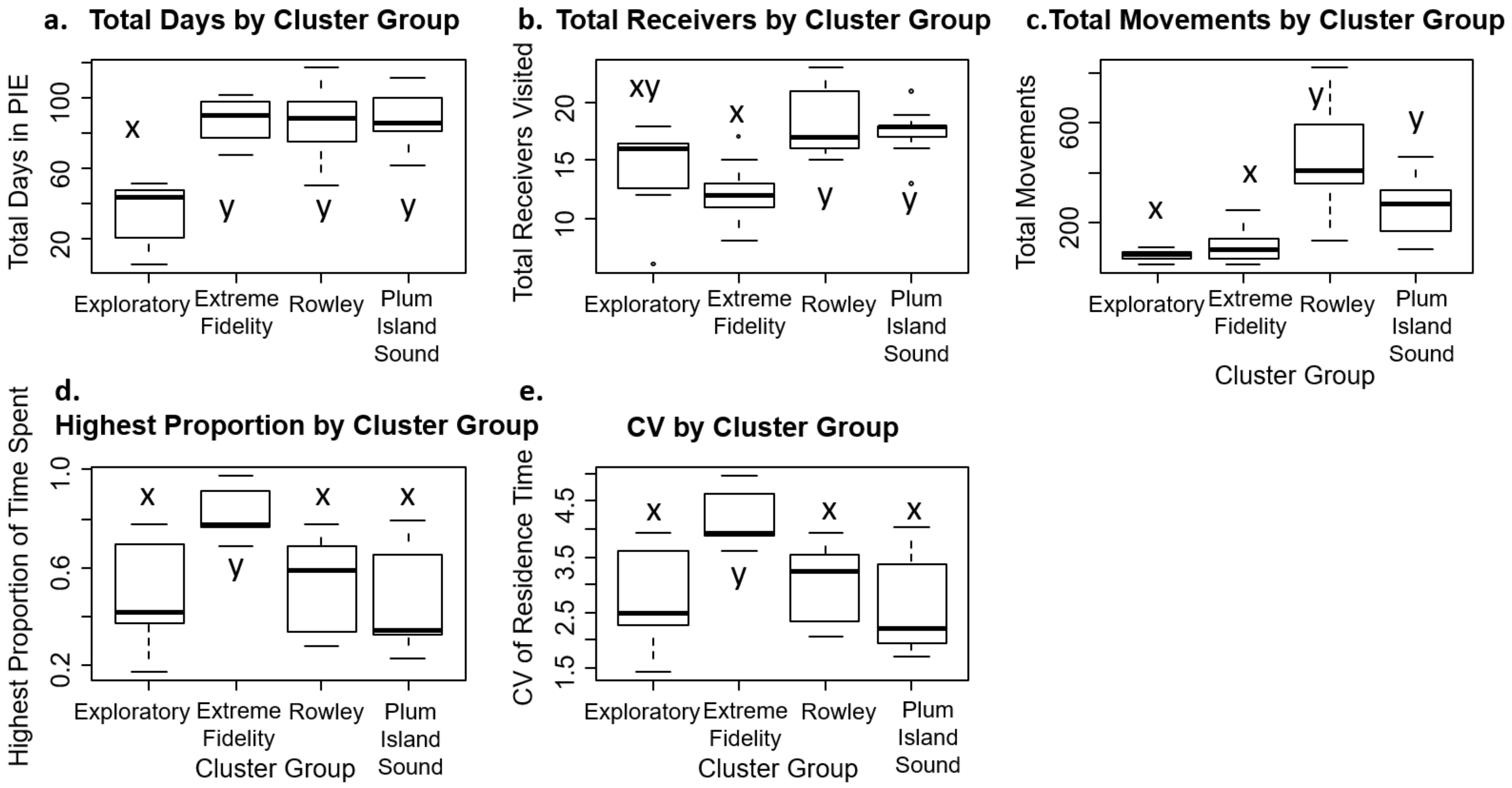


Figure 2.4: For the four cluster groups (X Axis), shown are the box plots (Y axis) of (a) *total days in PIE*, (b) *total receivers visited,* (c) *total number of movements,* (d) *highest proportion of time at a single receiver,* and (e) *standard error of residence time*. Letters indicate statistical differences.

Rowley River Distribution Group

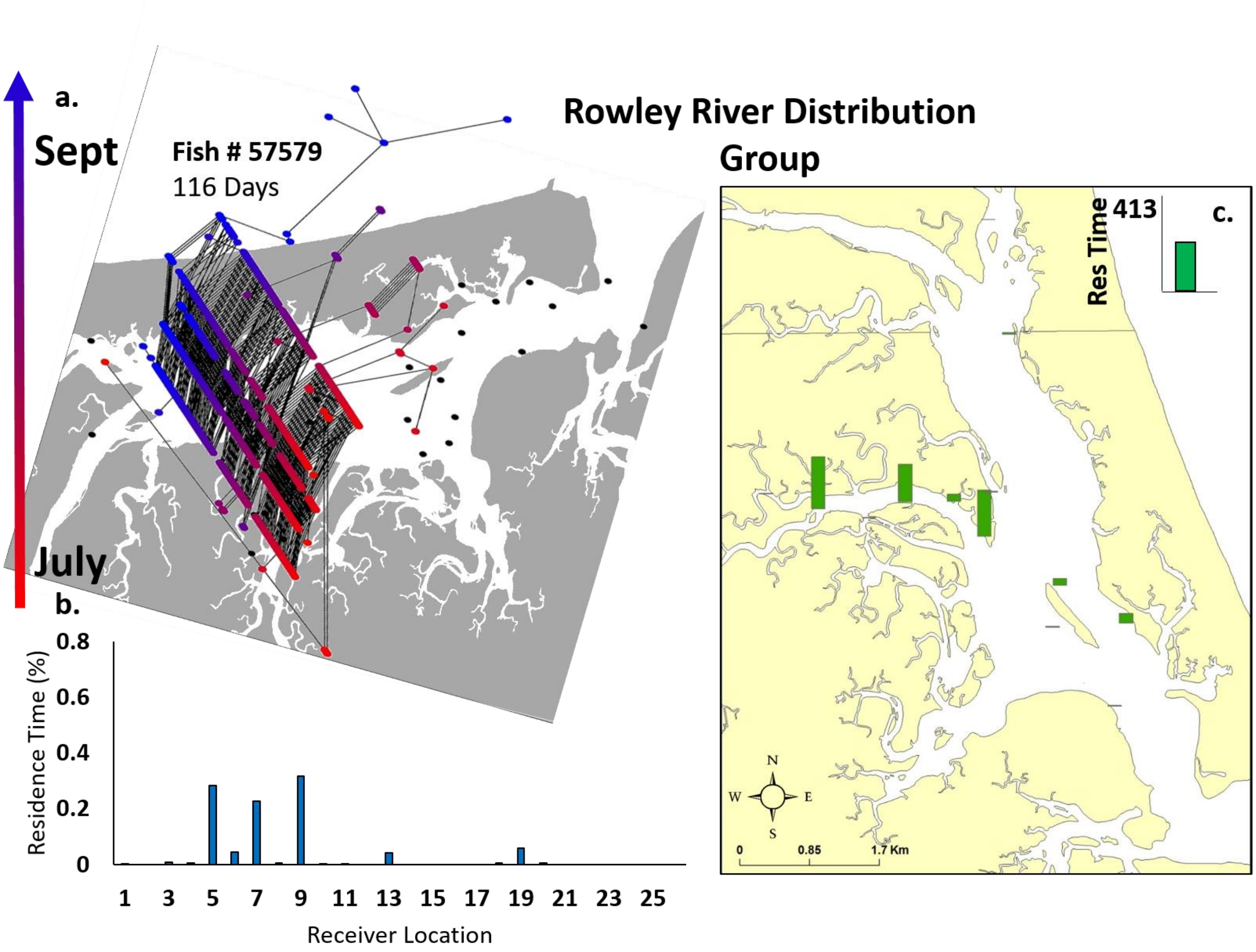


Figure 2.5: An example of a fish from the Rowley River distribution group showing (a) a trajectory displaying detections and movements among receivers over the entire study period, (b) a bar graph indicating the proportion of residence time this fish spends at each receiver location, and (c) a map of the average residence time that this fish spends at each receiver location. The red asterisk denotes the same locations.

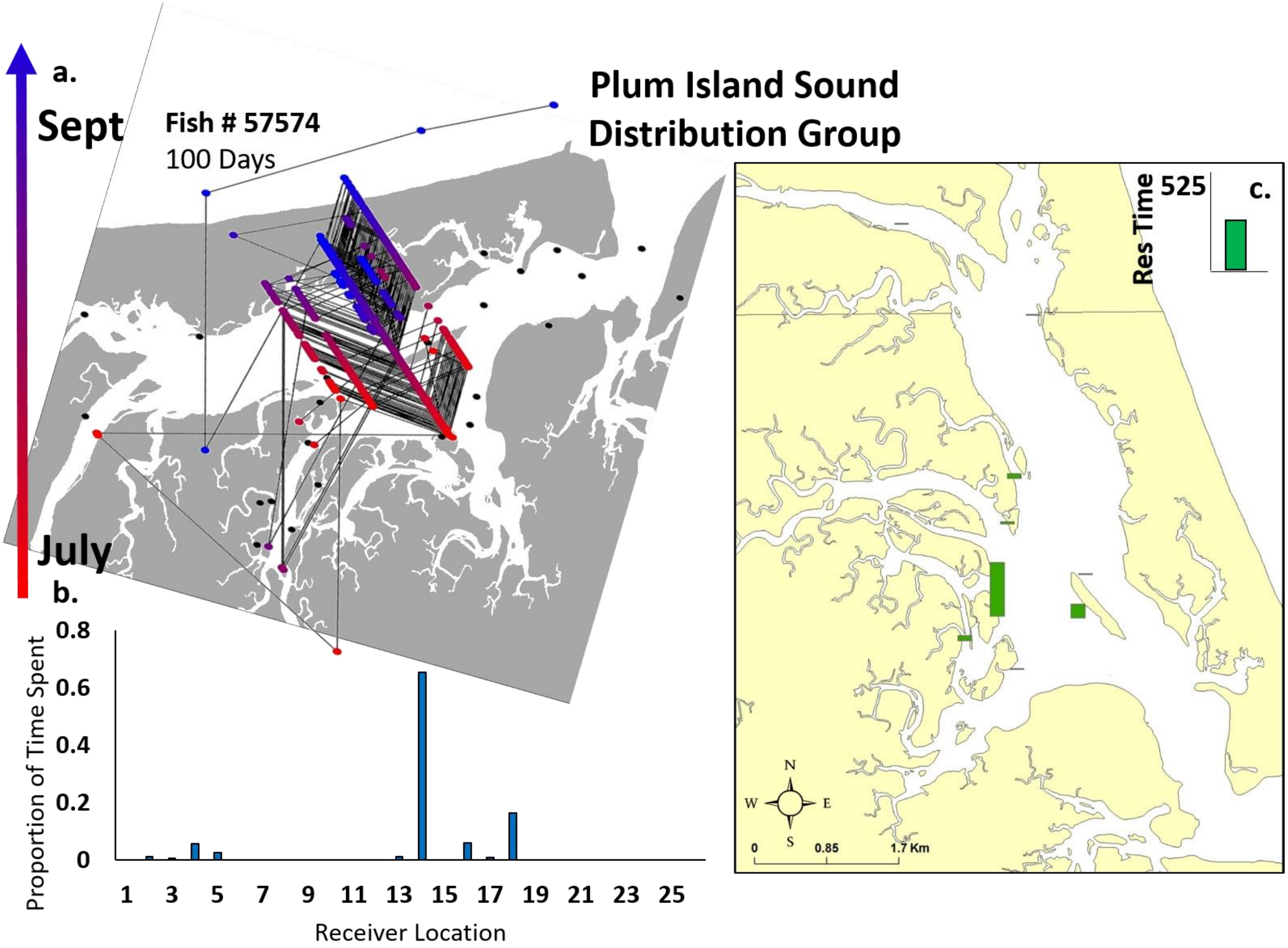

a.
Sept
July
Fish # 57574
100 Days
Plum Island Sound
Distribution Group
b.
Proportion of Time Spent
0.8
0.6
0.4
0.2
0
1
3
5
7
9
11
13
15
17
19
21
23
25
Receiver Location
c.
Res Time
525
N
W
E
S
0
0.85
1.7 Km

Figure 2.6: An example a fish from the Plum Island Sound distribution group showing (a) a trajectory displaying detections and movements among receivers over the entire study period, (b) a bar graph indicating the proportion of residence time this fish spends at each receiver location, and (c) a map of the average residence time that this fish spends at each receiver location. The red asterisk denotes the same locations.

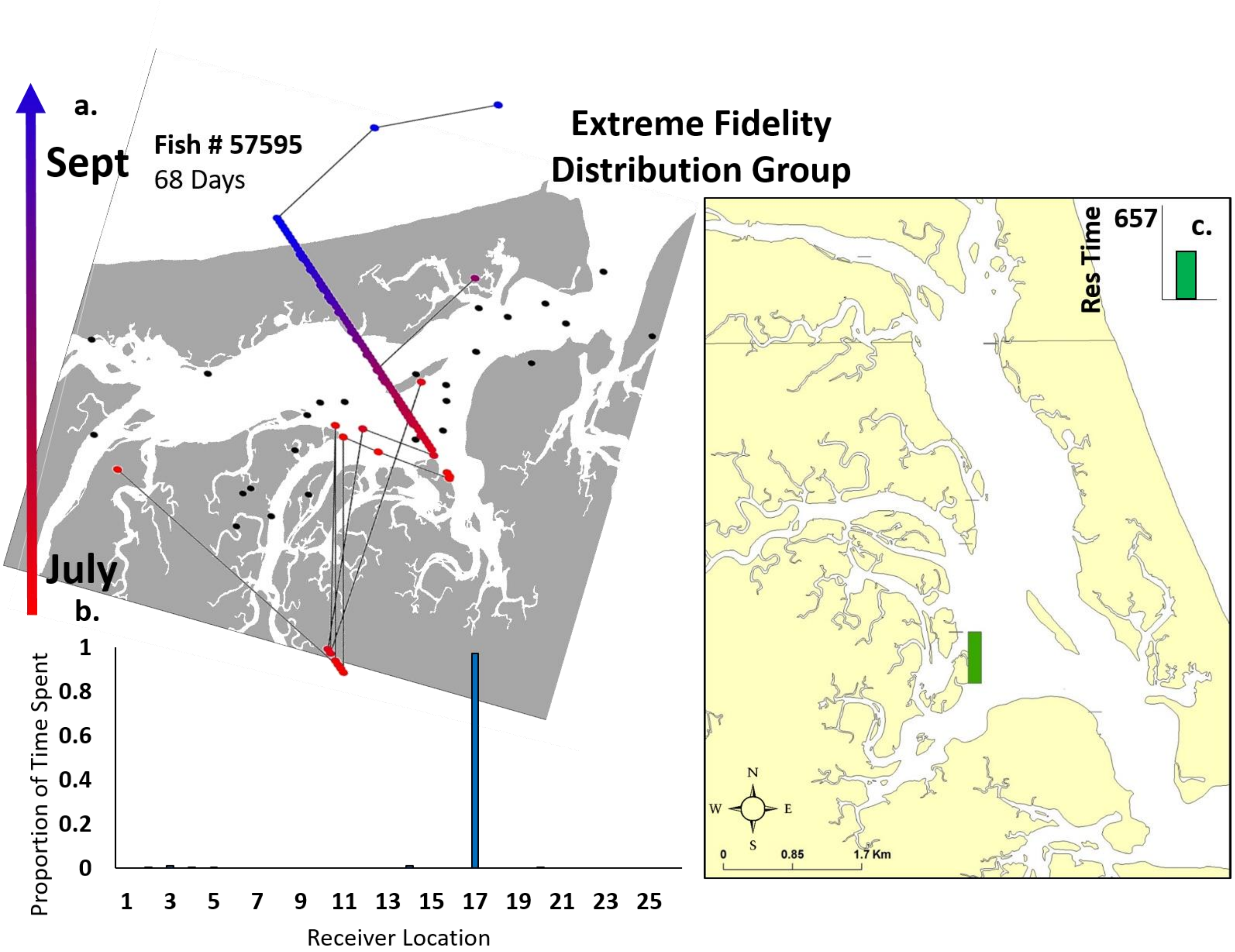

Extreme Fidelity
Distribution Group
a.
Sept
July
Fish # 57595
68 Days
b.
Proportion of Time Spent
1
0.8
0.6
0.4
0.2
0
1
3
5
7
9
11
13
15
17
19
21
23
25
Receiver Location
c.
Res Time
657
N
W
E
S
0
0.85
1.7 Km

Figure 2.7: An example of a fish from the Extreme Fidelity distribution group showing (a) a trajectory displaying detections and movements among receivers over the entire study period, (b) a bar graph indicating the proportion of residence time this fish spends at each receiver location, and (c) a map of the average residence time that this fish spends at each receiver location. The red asterisk denotes the same locations.

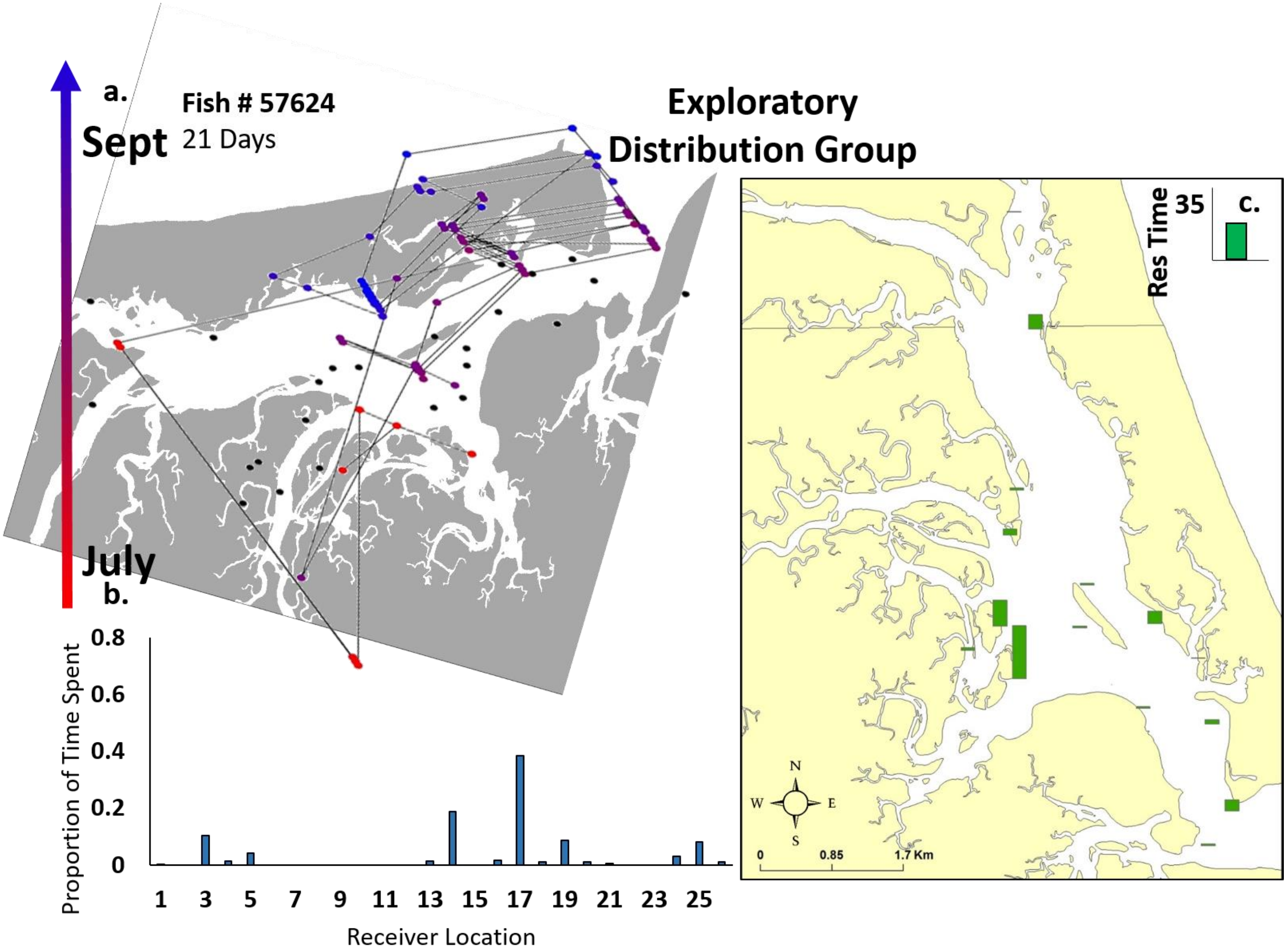

a.
Fish # 57624
21 Days
Exploratory
Distribution Group
Sept
July
b.
0.8
0.6
0.4
0.2
0
Proportion of Time Spent
1
3
5
7
9
11
13
15
17
19
21
23
25
Receiver Location
c.
35
Res Time
N
W
E
S
0
0.85
1.7 Km

Figure 2.8: An example of a fish from the Exploratory distribution group showing (a) a trajectory displaying detections and movements among receivers over the entire study period, (b) a bar graph indicating the proportion of residence time this fish spends at each receiver location, and (c) a map of the average residence time that this fish spends at each receiver location. The red asterisk denotes the same locations.

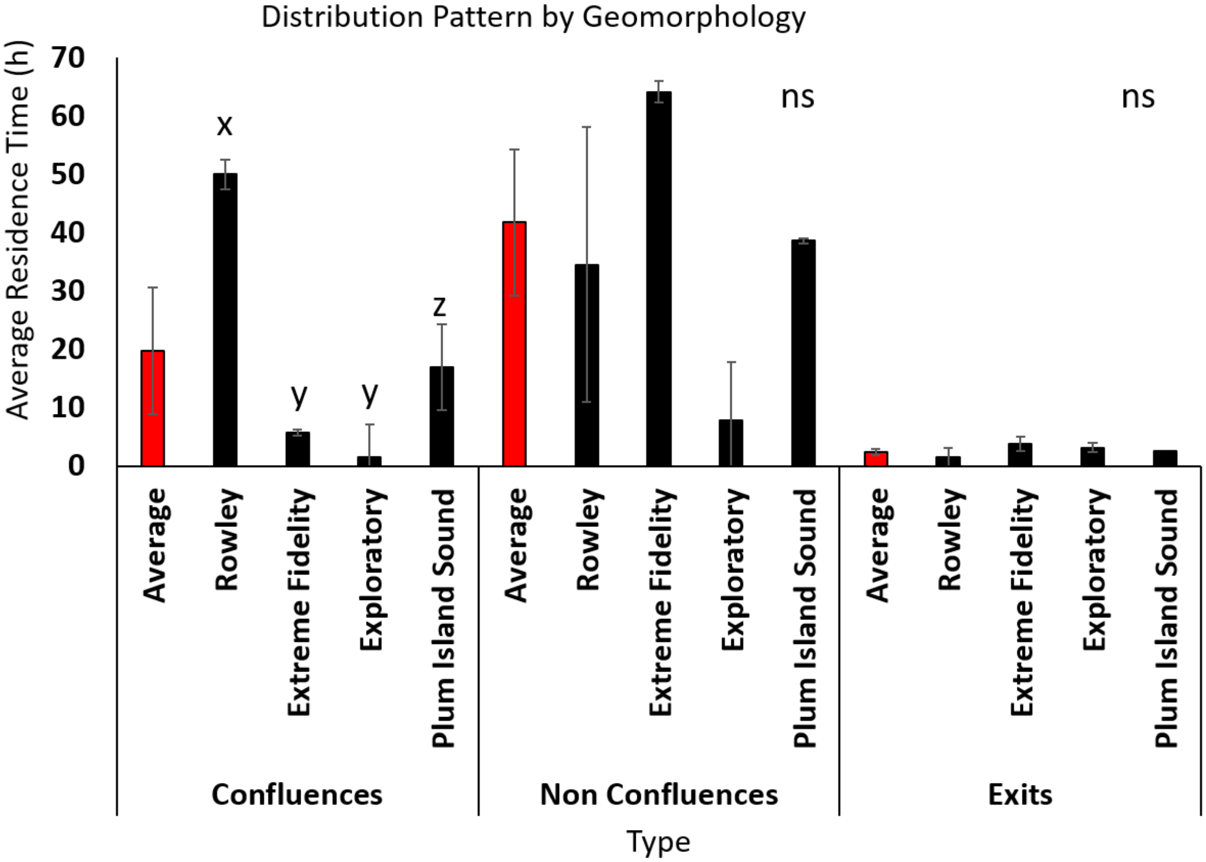


Figure 2.9: Bar graphs depicting the average residence time (h) (Y axis) for each distribution group (X axis) by geomorphic type (confluence, nonconfluence, exit). Letters indicate statistical differences.

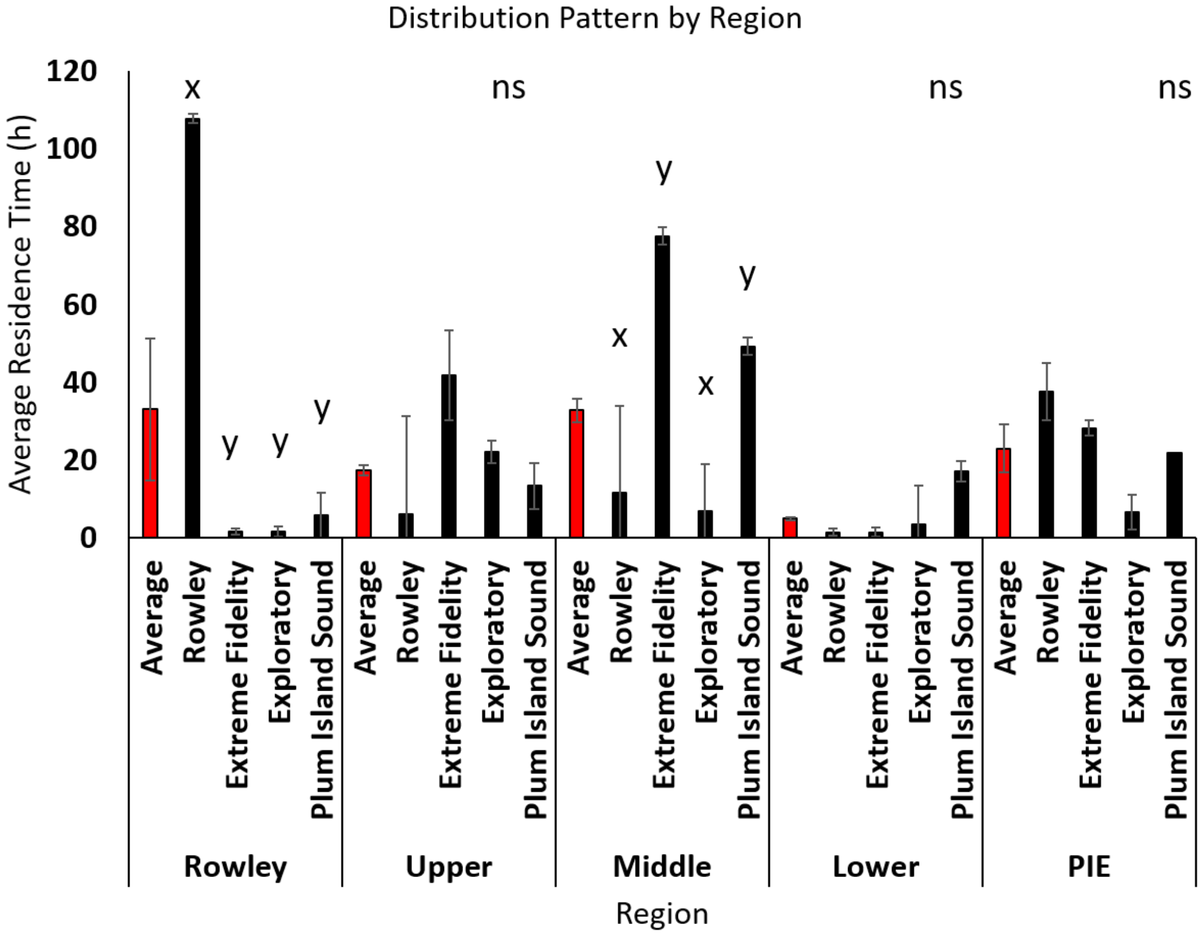


Figure 2.10: Bar graphs depicting the average residence time (h) (Y axis) for each distribution group (X axis) by region. Letters indicate statistical differences.

Appendix A - General Data Trends

Fish were tagged (*n*=59) during two tagging events over 11 days in the summer in 2015. Average fish length was 524.42 mm (range: 434-623; SE: 5.85; Fig. A.1a). Average fish weight was 1.46 kg (range: 0.79-2.85; SE: 0.05; Fig. A.1b).

By sampling week, an average of 67% of our fish were seen weekly in 2015 (Fig. A.2a). In 2016, after 33 fish returned (56%), an average of 30% of fish were seen weekly (Fig. A.2b).

In 2015, tagged fish spent an average of 69 total days in Plum Island (Fig. A.3a). In 2016 fish also spent an average of 69 days in Plum Island (Fig. A.3b).

Outside of Plum Island, the majority of fish were seen elsewhere along the East Coast (Fig. A.4). The location farthest south was the Chesapeake Bay (three fish) and the location farthest north was the Kennebec River (one fish). The most unique individual fish seen in a location outside Plum Island was 50 fish in the Massachusetts Bay area.

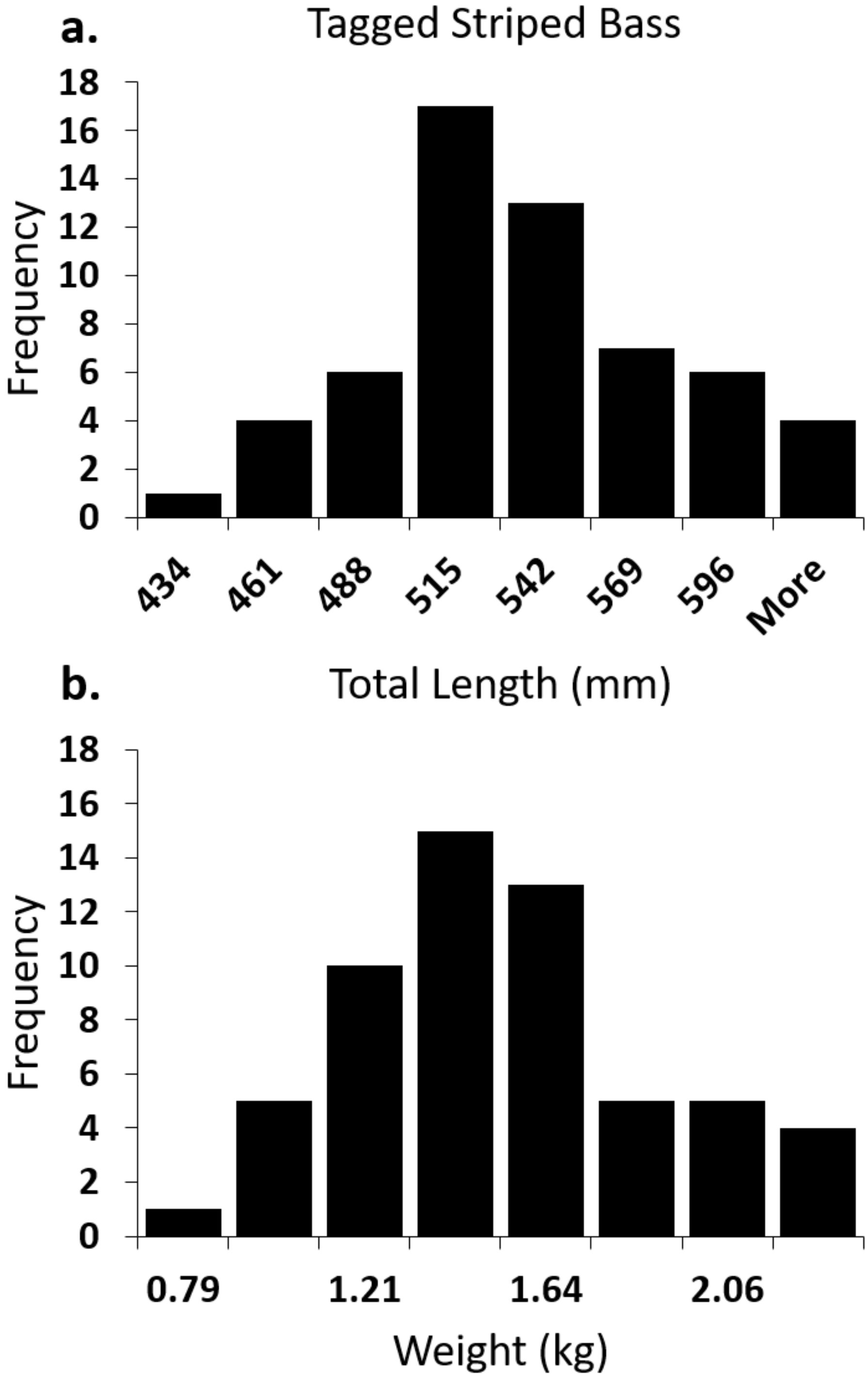


Figure A.1: Histograms illustrating (a) the length distribution of tagged striped bass and (b) the weight distribution of tagged striped bass.

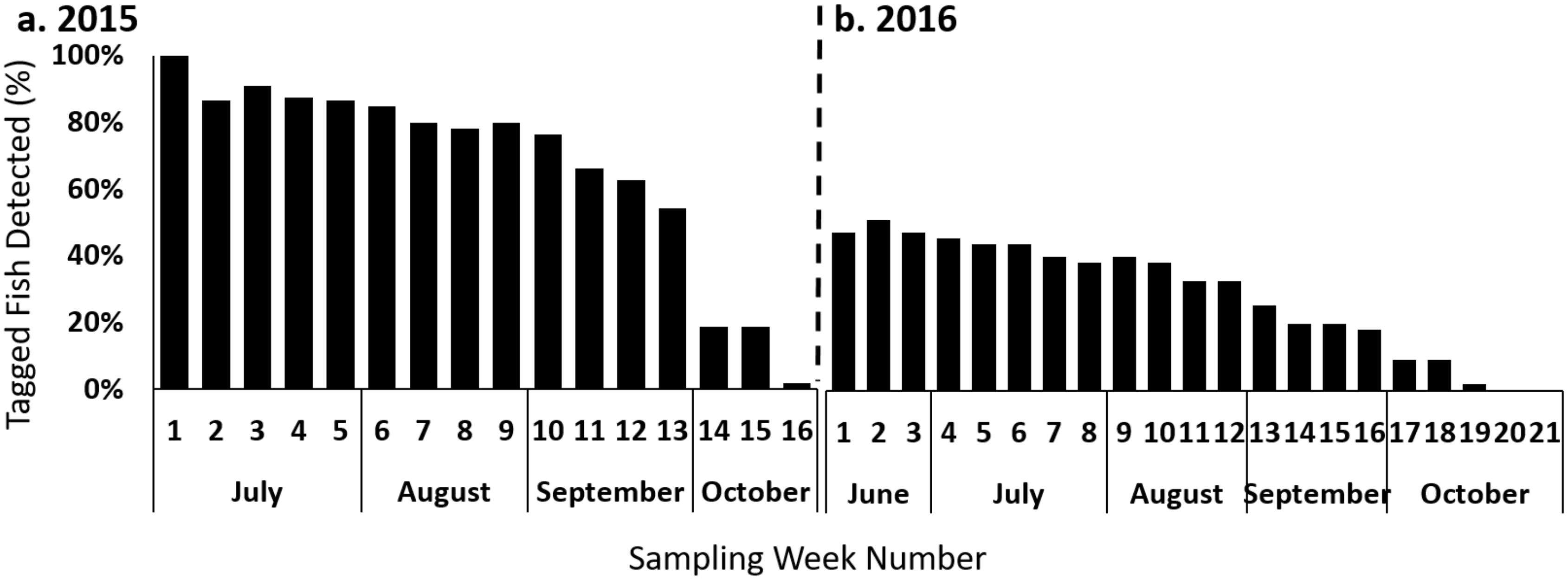


Figure A.2: Bar graph depicting the percentage of tagged fish detected on the y axis over the sampling week number on the x axis for (a) 2015 and (b) 2016.

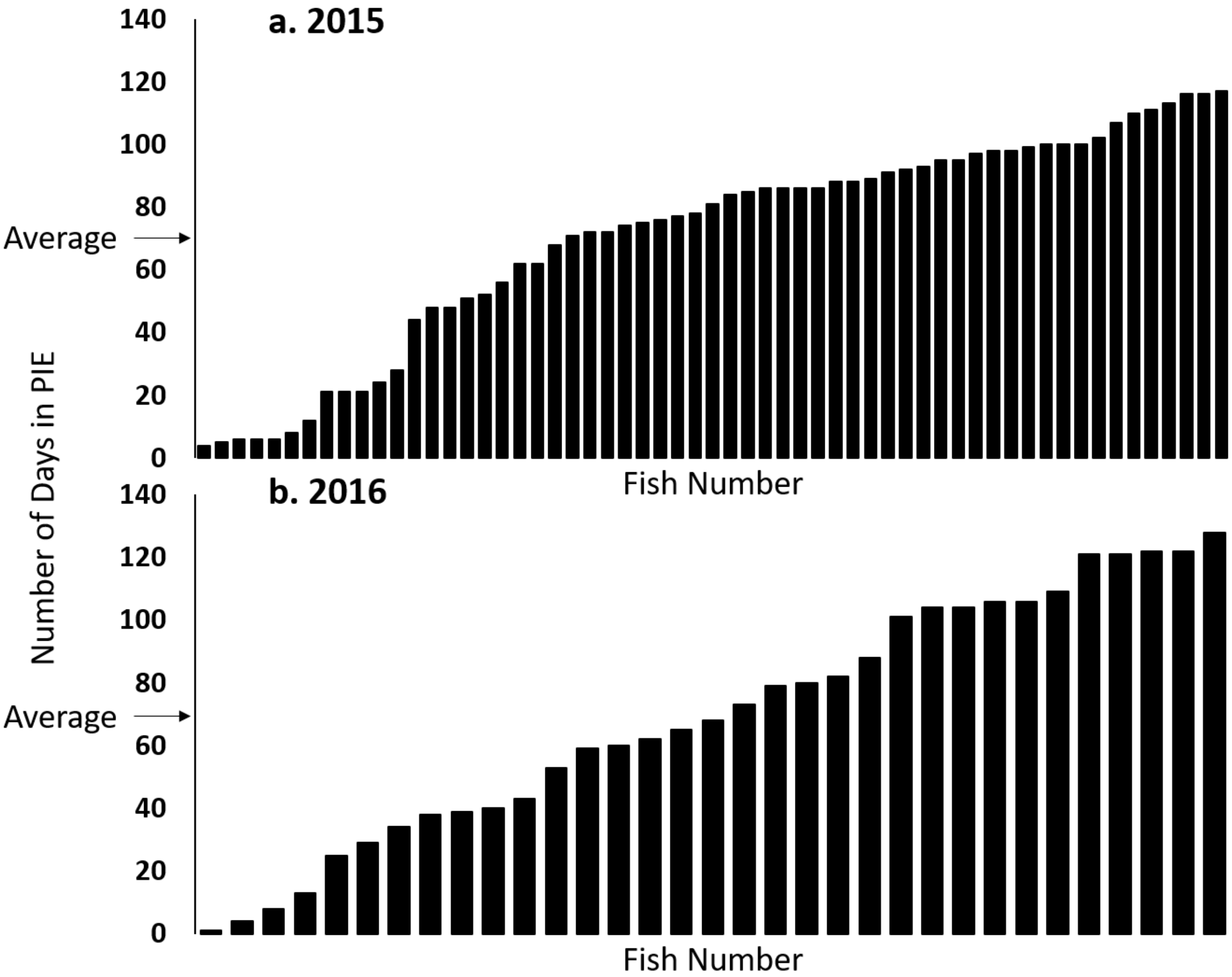
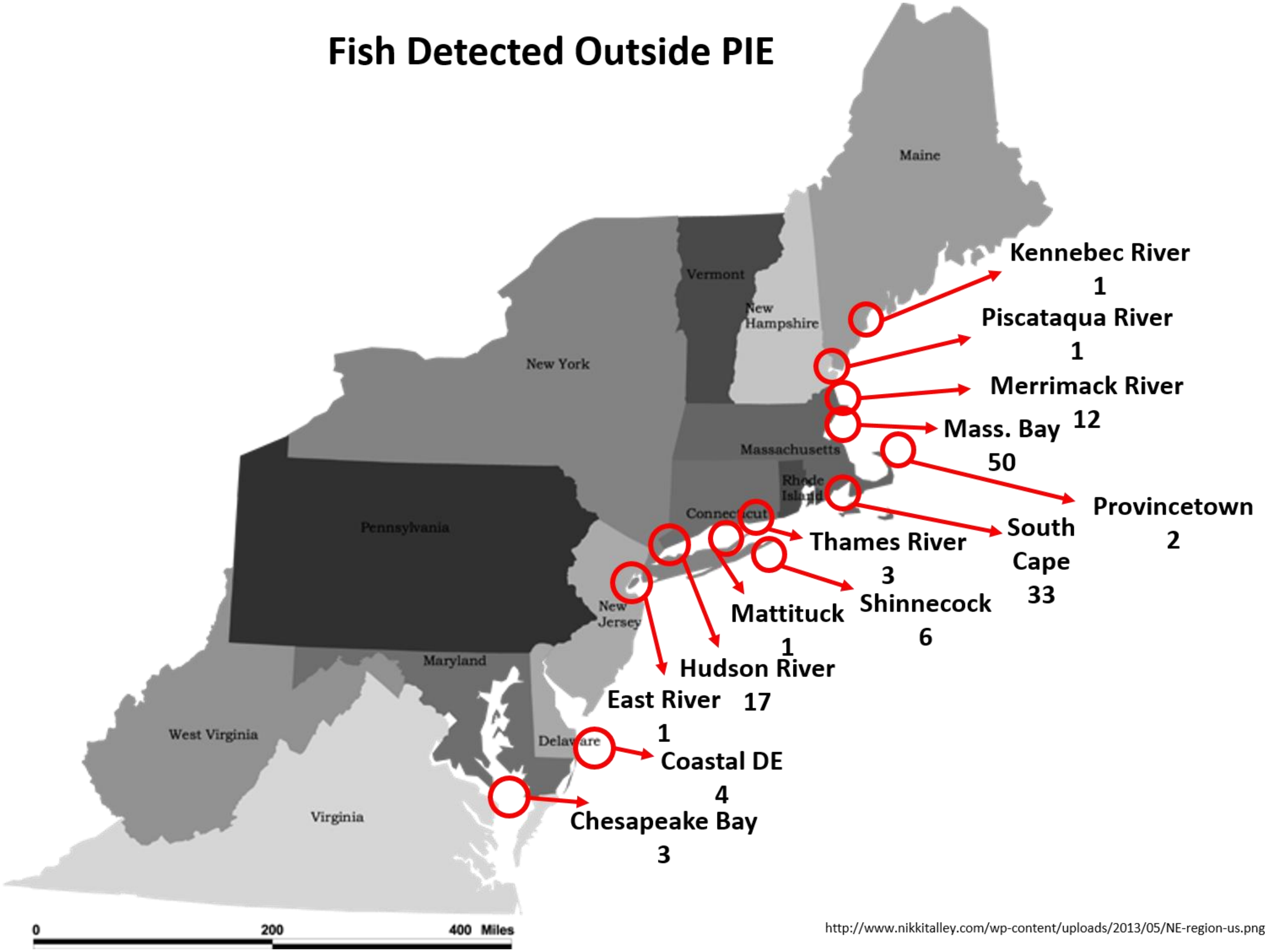


Figure A.3: Bar graph depicting on the y axis the number of days each individual fish spent in Plum Island total. Each bar represents a single fish.



Fish Detected Outside PIE

http://www.nikkitalley.com/wp-content/uploads/2013/05/NE-region-us.png

Figure A.4: Map showing the distribution of fish that were tagged in Plum Island in 2015 and their reported detections outside of Plum Island. The name indicates the general geographic area where fish were detected and the numbers indicate the number of unique individuals detected in this area.

Appendix B - Yearly Differences Between 2015 and 2016 in Number of Unique Individuals, Residence Time, and Number of Movements

Justification

In Chapter 1, I reviewed estuary-wide trends in number of tagged fish, residence time, and number of movements for striped bass predators in 2015. Here I review the same responses for 2016 and compare similarities and differences in trends across these two years (2015 vs 2016).

Questions

(1) How do the responses (a) number of unique individuals, (b) residence times, and (c) number of movements differ across individual locations within Plum Island in 2016?

(2) How do trends in number of unique individuals, residence times, and number of movements of tagged striped bass compare across 2015 and 2016?

Methods

We set up a 29 stationary receiver array (VR2W-69 kHz) and used the same 59 tagged striped bass (Vemco V13) from 2015 to track tagged striped bass in 2016. Of the 29 receiver locations, 26 remained the same as in 2015. Three were new additions to provide greater coverage of non-confluence locations across the estuary (receivers 27, 28, & 29).

For the metrics number of *unique individuals, residence time,* and *number of movements* a Chi-square analysis with 2000 Monte Carlo simulations (‘chisq.test’ function, ‘stats’ package, R) was performed to compare the observed measurements to an expected value based on an even distribution.

Residence time was tested against geomorphic types using a one-way ANOVA ('anova' function, 'stats' package, R). A one-way ANOVA was also used to test differences between individual confluences, individual non-confluences, individual exits, and parts of the confluence. Data were log transformed to meet assumptions of normality. A post-hoc Tukey test ('tukeyHSD' function, 'stats' package, R) was used to identify which geomorphic sites and regions were significantly different. A critical value of $P<0.05$ was used to determine statistical significance.

Results

Overview. Of the 59 fish tagged in 2015, 33 unique individuals returned in 2016. In both 2015 & 2016 those individuals stayed an average of 69 days. Most findings were consistent between 2015 and 2016 and these trends are reviewed below.

Unique Individuals. Looking at numbers of unique individuals across the estuary, tagged fish were present at all locations (No zeros for numbers; Fig. B.1a). As in 2015, in 2016 numbers of individuals were high at receivers 1, 3, 5, 6, 9, 13, 14, 17, 18, 20, 24 (Fig. B.1a), but receivers 4 and 26 had lower numbers in 2016 than in 2015. All three new receivers added in 2016 (27, 28, & 29) had high numbers of individuals. As in 2015, in 2016, numbers of individuals were low again at receivers 2, 10, 11, 12, 15, 16, 22, 23 (Fig. B.1a).

Based on the chi-square analysis, more fish than expected were present at some sites (receivers 1, 3, 5, 6, 7, 13, 18, 19, 20, 21, 24, 25, 27, 28, & 29; $P<0.001$; $\alpha = 0.05$; $\chi^2 = 97.10$; Fig. B.2a). Fewer individual striped bass than expected were detected at other locations (2, 4, 8, 9, 10, 11, 12, 14, 15, 16, 17, 22, 23, & 26; ($P<0.001$; $\alpha = 0.05$; $\chi^2 = 97.10$; Fig. B.2a). Compared to 2015, in 2016, receivers 21 & 25 had higher numbers of individuals and receivers 4, 14, 17, 22, 23, & 26 had lower numbers of individuals.

Residence Time. *Residence time* varied widely across receivers in both 2015 and 2016 (Fig. B.1b). In 2016, as in 2015, mean *residence time* for acoustically tagged striped bass was low at some sites (receivers 1, 2, 3, 6, 8, 10, 11, 15, 16, 20, 21, 22, 23, 24, 25, & 26) and high at other sites (receivers 4, 5, 7, 9, 12, 13, 14, & 17) (Fig. B.1b). According to the Chi-Square analysis, in 2016 higher *residence time* than expected occurred at some locations (receivers 5, 7, 9, 12, 14, 17, 18, 19, & 28; $\chi^2 = 13882.86$; Fig. B.2b) and lower *residence time* than expected was observed at all other locations (receivers 1, 2, 3, 4, 6, 8, 10, 11, 13, 15, 16, 20, 21, 22, 23, 24, 25, 26, 27, & 29; $\chi^2 = 13882.86$; Fig. B.2b). In 2016, receivers 4 & 13 had lower *residence time* than in 2015 and receivers 18 & 19 had higher *residence time* than in 2015.

Movements. In 2016, *numbers of movements* were low at receivers 1, 2, 4, 10, 11, 16, 17, 19, 20, 21, 22, 23, 24, 25, & 26 and high at others (receivers 5, 7, 9, 12, & 14; Fig. B.1c). According to the Chi-square analysis, in 2016, more movements were made than expected at certain locations (Receivers 5, 6, 7, 9, 12, 13, 14, & 28; $\chi^2 = 4277.27$; Fig. B.2c). Fewer movements were made than expected at all other locations (receivers 1, 2, 3, 4, 10, 11, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, 26, 27, & 29; $\chi^2 = 4277.27$; Fig. B.2c). In 2016, receivers 3 & 8 had higher movements than in 2015 and receivers 12 & 13 had lower movements than in 2015.

Geomorphic Site Types. In 2016, non-confluences and exits were the only geomorphic types that were significantly different (Fig. B.3a, $P<0.05$). In 2016, confluences and non-confluences were not significantly different; nor were confluences and exits (Fig. B.3a.). In contrast, in 2015 there were significant differences between confluences and exits as well as confluences and non-confluences. In 2016, individual confluence, non-confluence, and exits were not significantly different (Fig. B.3b, c, & d). In contrast, in 2015, significant differences occurred between individual confluences and individual non-confluence locations. In 2016, geomorphic site types and individual locations within geomorphic site types were more similar than in 2015.

Confluence Parts. In 2016, as in 2015, parts of a confluence were significantly different ($P<0.05$; Fig.B.4). In both years, the sweet spots had significantly higher residence time than the arm locations ($P<0.05$; Fig. 1.8). As in 2015, for 2016, these differences were especially apparent when compared to the confluence averages (Fig. B.5; Fig. 1.9). In 2016, Rowley was only significantly different from one of the arms ($P<0.05$; Fig. B.5). Grape Island was not significantly different between the arms and sweet spots, this was the same as in 2015.

Regional Trends. Finally, the regional differences remained the same between 2015 and 2016 with both the Rowley and Middle regions having significantly higher residence times than the Upper and Lower regions ($P<0.05$; Fig. B.6; Fig. 1.10).

Yearly Trends. Overall, many of the main conclusions drawn from 2015 remained the same in 2016. Fish were not distributed evenly across the estuary in 2016 according to any of the metrics used. This finding is the same as in 2015 although some of the specific receivers that were higher or lower than expected based on an even distribution differed between years. When we look at residence time by geomorphic type, exits were again significantly different from non-confluences, but 2016 showed no difference between confluences and non-confluences. This is likely due to our decision to add three new non-confluence receivers that provided a broader picture of non-confluences, including both high and low occupancy sites across the estuary. Also different from 2015 was that in 2016 we did not see any differences within each geomorphic type. There were no differences among separate confluences, non-confluences, or exits. The lack of trends in 2016 could be attributed to having fewer fish than in 2015. We did see differences between confluence parts in both 2015 and 2016 and we also saw the same regional trends in both years.

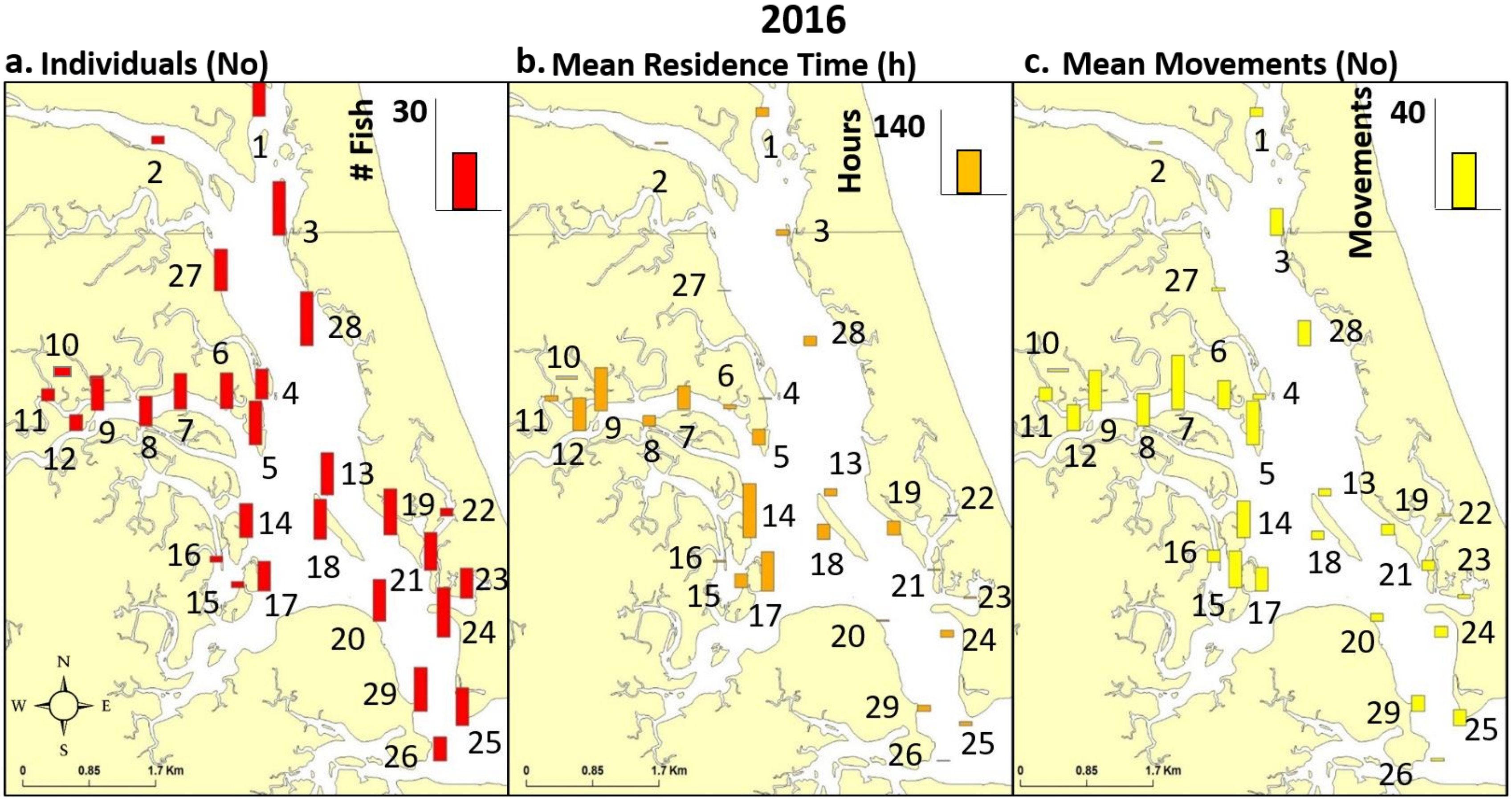


Figure B.5: The spatial distribution of (a) numbers of individuals, (b) average residence time, and (c) average number of movements in Plum Island Estuary, MA for 33 tagged striped bass at 29 receivers. Receiver numbers are indicated next to the associated bars. A scale bar is in the right top corner of each plot. Figures A.1 and A.2 are related.

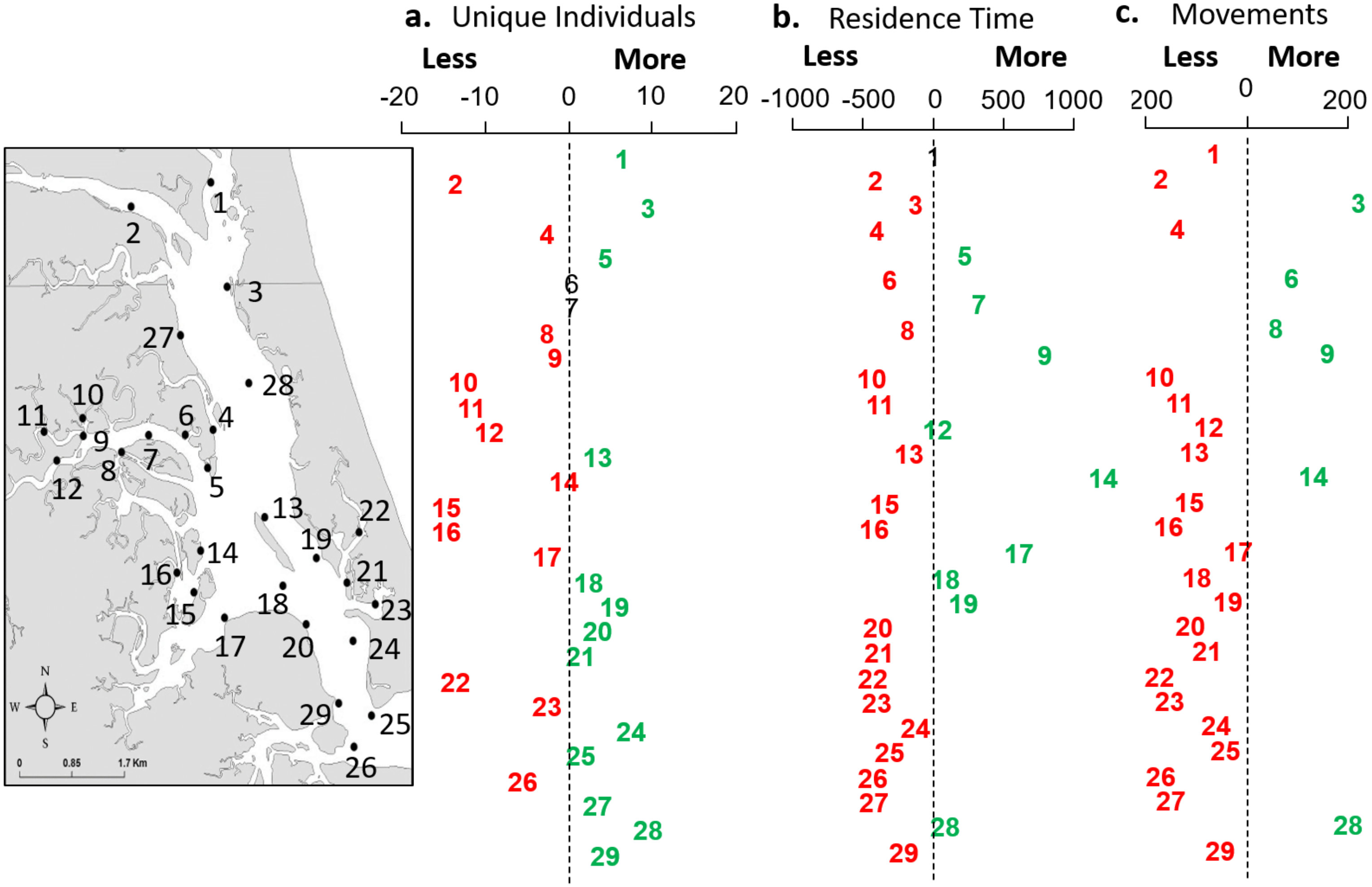


Figure B.6: Results of a Chi-square analysis that identified (a) which receivers saw more individuals than expected and which receivers saw less individuals than expected. The expected is based on an even distribution (i.e. the same amount of individuals at all receivers). (b) At which receivers fish spent more or less time than expected based on an even distribution, and (c) at which receivers fish moved more or less than expected based on an even distribution.

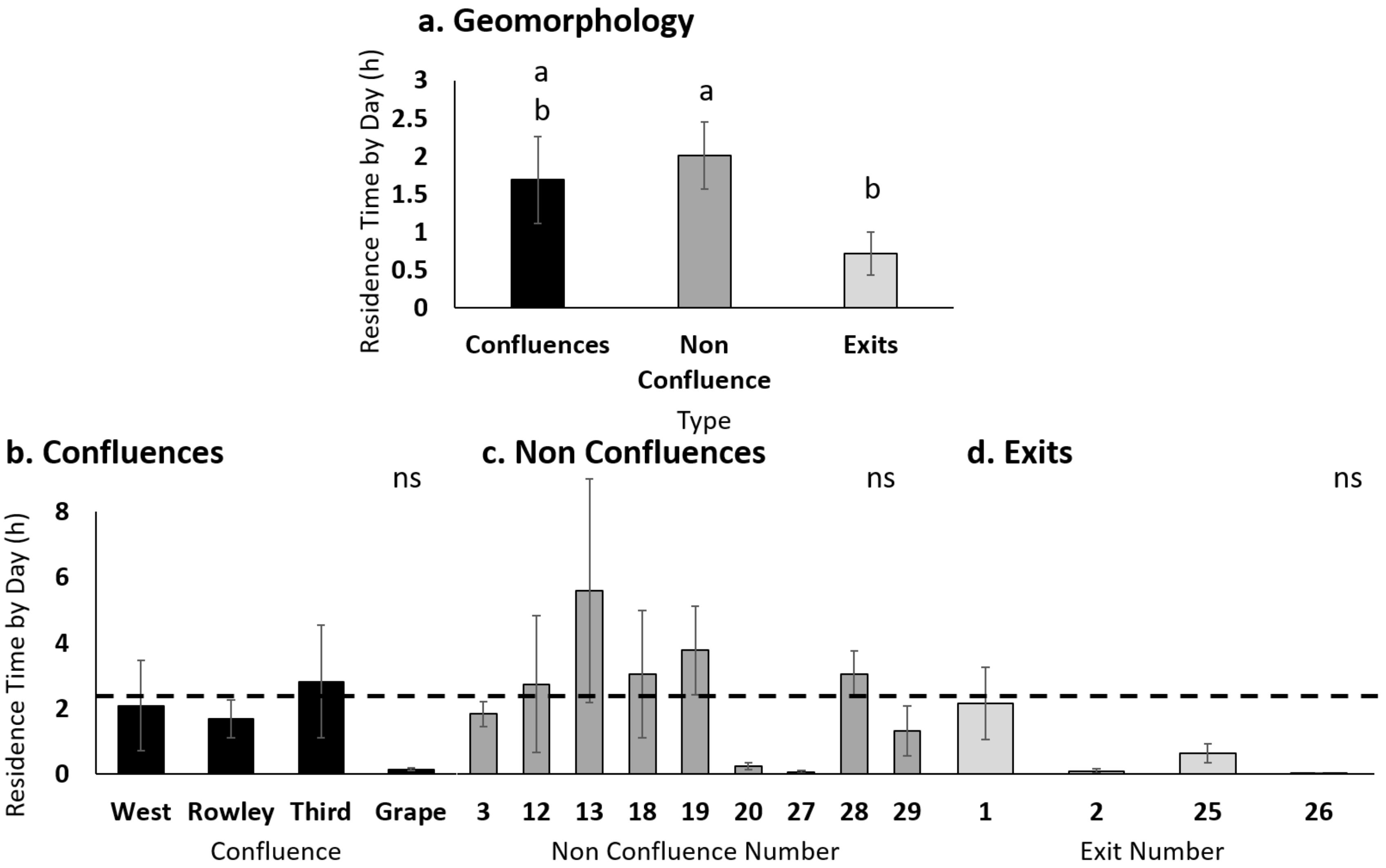


Figure B.7: Bar graphs depicting mean and standard error (a) geomorphology types (confluences, non-confluences, and exits), mean and standard error of (b) confluences, (c) non-confluences, and (d) exits. The dotted line is the estuary mean. Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

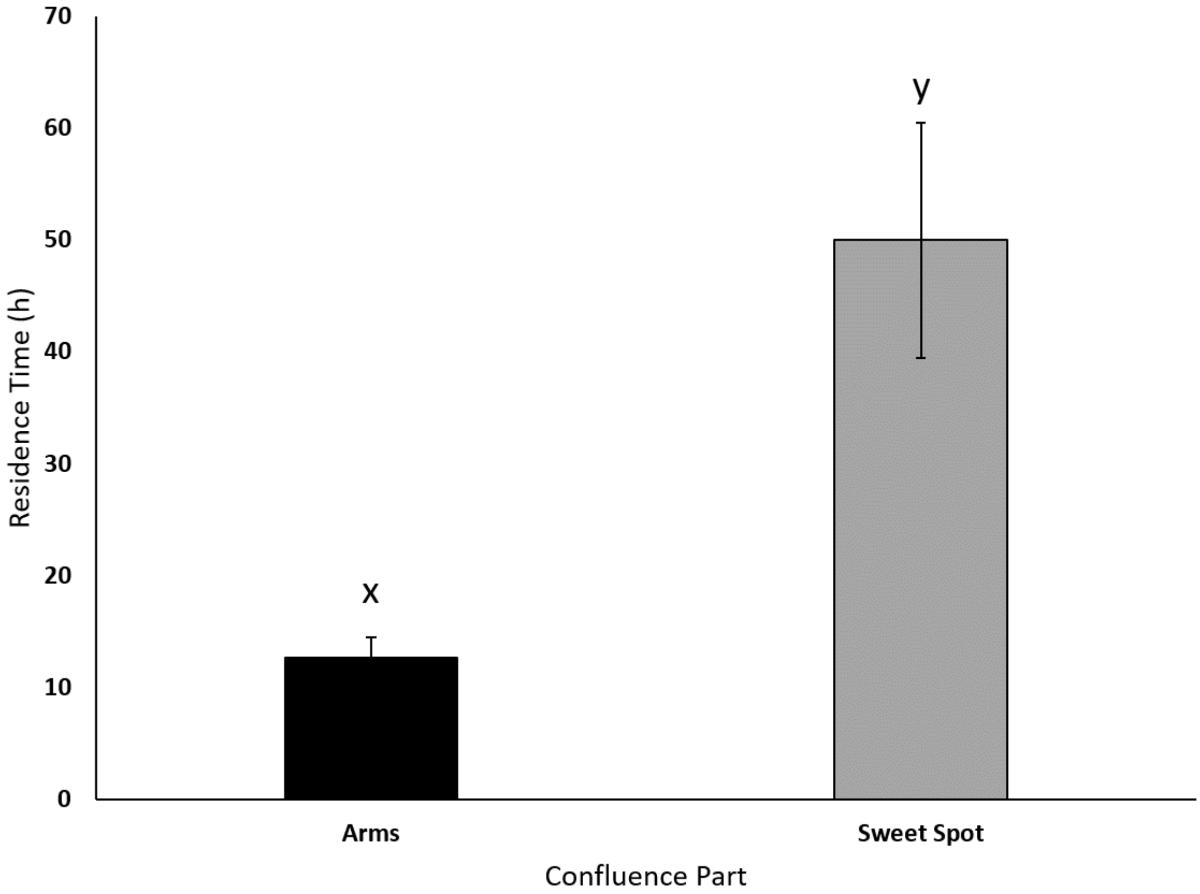


Figure B.8: Bar graph depicting residence time (mean +/- 1 SE) for confluence parts in 2016. Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

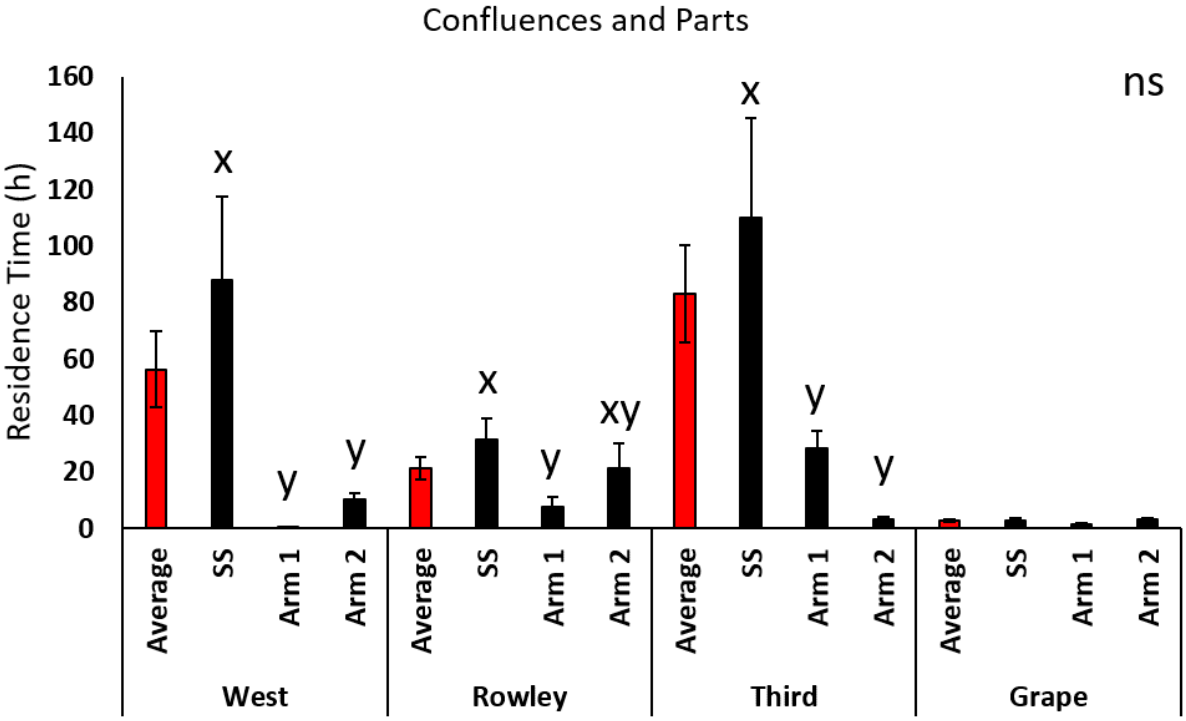


Figure B.9: Bar graphs depicting the differences among the confluences, their overall averages, and their corresponding parts ("arms" and "sweet spot"). Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

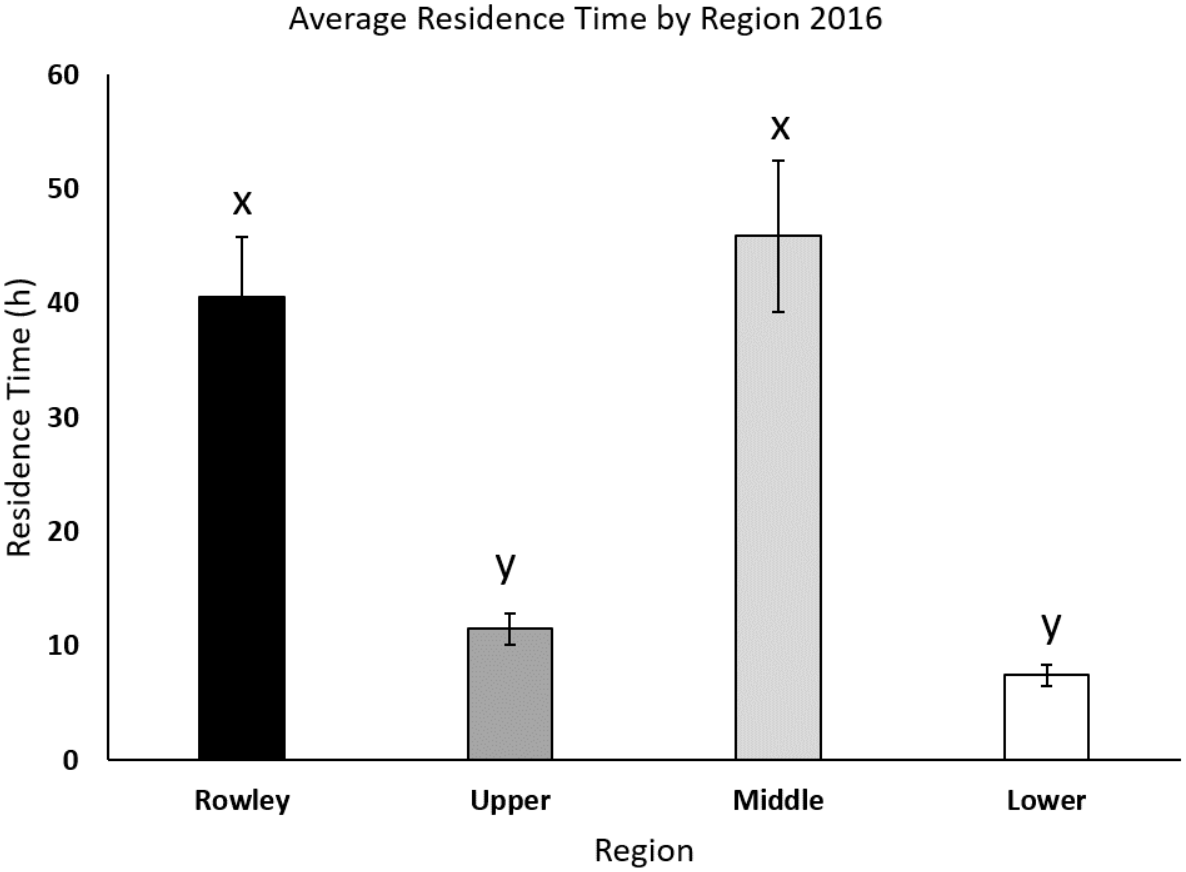


Figure B.10: Bar graph depicting the differences in residence time between regions in 2016. Letters indicate the results of Tukey post hoc comparisons. *P*<0.05 was used to determine significance.

Appendix C - Yearly Differences Between 2015 and 2016 in Distributional Groups and Geomorphic Types and Regions

Justification

In Chapter 2, I reviewed estuary-wide distributional groups for 2015 and assessed if these distributional groups differed across geomorphic types and regions for striped bass predators. Here I repeat this analysis for 2016. Then, I compare similarities and differences in trends across these two years (2015 vs 2016).

Questions

(1) In 2016, which distributional groups used PIE? In 2016, how many fish were in each group?

(2) Were trends in distributional groups the same across years?

(3) In 2016, how did distributional groups affect use of geomorphic site types and regions?

(4) Were these relationships among distributional groups, geomorphic site types, and regions the same across both years (2015 vs 2016)?

Methods

Tagged fish and stationary arrays. In 2016 we again used a 29 stationary receiver array (VR2W-69 kHz) and the same 59 tagged striped bass (Vemco V13) from 2015 (Taylor 2017; Chapter 1). Out of the 29 locations in 2016, 26 of them were the same ones used in 2015. The three additions provided greater spatial coverage of non-confluence locations (receivers 27, 28, & 29).

Cluster Analyses. To identify distribution groups in 2016 we again performed the same statistical analyses as described for 2015 (Taylor 2017, Chapter 2).

Relationship between geomorphic site and distributional groups. In 2016, these groups were again tested to see if geomorphic type and distributional group affected residence time using two 2-way ANOVAs ('anova' function, 'stats' package, R) as described for 2015 (Taylor 2017, Chapter 2).

Results

Types of distributional groups. In 2016, as in 2015, the cluster analyses [spatial (one cluster; Fig. C.1) and temporal spatial (four clusters; Fig. C.2)] identified five seasonal resident distributional groups and one group of Short-Timers for striped bass in PIE. These clusters were distinct based on Jaccards mean values >0.6.

In 2016, we had only four fish (of 33 total) classified as Short-Timers (staying in PIE <30 days) that were excluded from future analyses (Fig. C.3). Eight fish clustered in the first Rowley River distributional group (Fig. C.1; Fig. C.3). Seven fish clustered into the Exploratory 1 group and seven fish clustered into the Exploratory 2 group (Fig. C.2; Fig. C.3). Five fish clustered into the Extreme Fidelity distribution group (Fig. C.2: Fig. C.3). Two fish clustered into the Plum Island Sound distributional group (Fig. C.2; Fig. C.3).

Exploratory 1 Distributional Group. The 2016 Exploratory 1 distributional group was characterized by low seasonal residence in PIE (average: 46.71 days SE: 5.51; Fig. C.4a), visited a high *number of receivers* (average: 12.71, SE: 1.38; Fig. C.4b), had low *numbers of movements* (average: 61.86, SE: 10.46; Fig. C.4c), had a low but variable *highest proportion of time spent at a single receiver* (average: 0.49, SE: 0.05; Fig. C.4d), and had a low *coefficient of variation of residence time* (average: 2.97, SE: 0.19; Fig. C.4e).

Exploratory 2 Distributional Group. The 2016 Exploratory 2 distributional group was characterized by average seasonal residence in PIE (average: 83.71 days SE: 6.04; Fig. C.4a), visited a high *number of receivers* (average: 18.71, SE: 1.25; Fig. C.4b), had an average *numbers of movements* (average: 148.57, SE: 25.94; Fig. C.4c), had a low *highest proportion of time spent at a single receiver* (average: 0.41, SE: 0.05; Fig. C.4d), and had a low *coefficient of variation of residence time* (average: 2.56, SE: 0.26; Fig. C.4e).

Extreme Fidelity Distributional Group. The 2016 Extreme Fidelity distributional group was characterized by average seasonal residence in PIE (average: 94.20 days SE: 14.22; Fig. C.4a), visited a low *number of receivers* (average: 8.40, SE: 0.81; Fig. C.4b), had low *numbers of movements* (average: 29.40, SE: 11.72; Fig. C.4c), had a high *highest proportion of time spent at a single receiver* (average: 0.72, SE: 0.09; Fig. C.4d), and had a high *coefficient of variation of residence time* (average: 4.00, SE: 0.40; Fig. C.4e).

Rowley River Distributional Group. The 2016 Rowley River distributional group was characterized by an average seasonal residence in PIE (average: 80 days SE: 13.8; Fig. C.4a), visited a *high number of receivers* (average: 16.13, SE: 1.99; Fig. C.4b), had very high but variable *numbers of movements* (average: 257.00, SE: 77.73; Fig. C.4c), had a high but variable *highest proportion of time spent at a single receiver* (average: 0.55, SE: 0.07; Fig. C.4d), and had a low *coefficient of variation of residence time* (average: 3.22, SE: 0.32; Fig. C.4e).

Plum Island Sound Distributional Group. The 2016 Plum Island Sound distributional group was characterized by high seasonal residence in PIE (average: 118.50 days SE: 9.50; Fig. C.4a), visited a high *number of receivers* (average: 20.50, SE: 0.50; Fig. C.4b), had high *numbers of movements* (average: 285.50, SE: 56.50; Fig. C.4c), had a high but variable *highest proportion of time spent at a single receiver* (average: 0.76, SE: 0.09; Fig. C.4d), and had a high *coefficient of variation of residence time* (average: 4.15, SE: 0.47; Fig. C.4e).

Distributional group metrics for 2016. In 2015, distributional groups were based on 59 fish and in 2016 they were based on 33 fish**.** For the metric *Total Days* the only groups significantly different from each other were the Exploratory 1 and Plum Island Sound distribution groups ($P<0.05$; Fig. C.4a). For the metric *Total Receivers Visited*, the Exploratory 2 distribution group visited significantly more receivers than the Extreme Fidelity group ($P<0.05$; Fig. C.4b). For the metric *Total Movements*, the Rowley River, Exploratory 2, and Plum Island Sound distribution groups had significantly more movements than the Extreme Fidelity distribution group ($P<0.05$; Fig. C.4c). For the metrics *Highest Proportion of Time Spent* and *Coefficient of Variation*, there were no statistical differences among the distribution groups (Fig. C.4d; Fig. 2.4e). The split between the Exploratory groups is new to the 2016 fish, but the differences are mainly that the Exploratory 1 group spends less time in the estuary overall, and the Exploratory 2 group exhibits entire-estuary usage and low residences times.

Differences in distributional group metrics between 2015 and 2016. In 2015, for the metric *Total Days*, the Exploratory group spent less time in Plum Island than all three other groups. In 2016, the Exploratory 1 group was only different from the Plum Island Sound group in this metric. For the metric *Total Receivers Visited*, in 2015, the Extreme Fidelity group also visited significantly less receivers than the Rowley and Plum Island Sound group, but not the

Exploratory. So, the trend of the Extreme Fidelity group visiting less receivers remains the same, but exactly which groups it differs from (2015: Rowley and Plum Island Sound groups, 2016: Exploratory 2 group) has changed. For the metric *Total Movements*, in 2015, we also saw that the Extreme Fidelity group had significantly less movements than the Rowley and Plum Island Sound Groups, but in 2016 the Extreme Fidelity group also had less movements than the Exploratory 2 group. In 2015 we did have significant differences for both metrics, *Highest Proportion of Time Spent* and *Coefficient of Variation*, but both metrics showed the same trends. In 2015, the Extreme Fidelity group had a higher *Highest Proportion of Time Spent* and *Coefficient of Variation*, but in 2016 there were no significant differences.

Geomorphic Drivers of Distributions in 2016. In 2016, the only significant difference was between distributional group usage of confluences ($P<0.05$; Fig. C.5). Variation in groups usage of exits or non-confluences was not significantly different. The Plum Island Sound group used confluences significantly more than the Exploratory 1 group. The other three distributional groups were not significantly different from each other.

Differences in Geomorphic Drivers of Distributions between 2015 and 2016. As in 2015, the only significant difference was the use of confluences between the groups. Different from 2015, in 2016, the Plum Island Sound distribution group used confluences significantly more than the Exploratory 1 group ($P<0.05$; Fig. C.5). In 2015, the Rowley distribution group had significantly higher confluence usage, but in 2016 it did not. In 2015, there were also no significant differences in non-confluence or exit usage across distributional groups.

Region. Regional differences in 2016 were also very similar to 2015. As in 2015, the only significant differences were in the Rowley and Middle regions ($P<0.05$; Fig. C.6). The

Rowley distribution group used the Rowley region significantly more than the other four groups. The Plum Island Sound distribution group used the Middle region significantly more than the other four groups. As in 2015, in 2016, no significant differences existed between distributional groups using the Upper or Lower regions.

Yearly Trends. We again saw strong evidence for fish clustering into distributional groups based on the same characteristics used in 2015. One of the differences was the split in the Exploratory group, but when we look at the two new Exploratory groups, we see that the features of the original are still there. As groups, the other three still behaved similarly to the way they did in 2015. The Rowley distribution group still used the Rowley River for the majority of its time, the Extreme Fidelity distribution group still spent the majority of its time at a single receiver location, and the Plum Island Sound distribution group spends the majority of its time at receivers within the Sound. The similarities also held up in our geomorphic type and regional comparisons where confluences were the only type with significant differences among the distributional groups (in both 2015 and 2016). But it differed in 2016 with the Plum Island Sound group using confluences the most in 2016 and the Rowley group using confluences the most in 2015. Regionally, the same regions had significant differences among distribution groups in 2015 and 2016 (Rowley and Middle regions). In the Rowley region, the Rowley distribution group again had the highest residence time, but in the Middle region, only the Plum Island Sound distribution group had a significantly higher residence time (in 2015, the Extreme Fidelity group also had significantly higher residence time).

For all comparisons, the reduced number of fish in 2016 as well as the additional coverage of non-confluences in 2016 likely contributed to year-to-year differences in distributional groups as much as the annual variability in abiotic and biotic conditions.

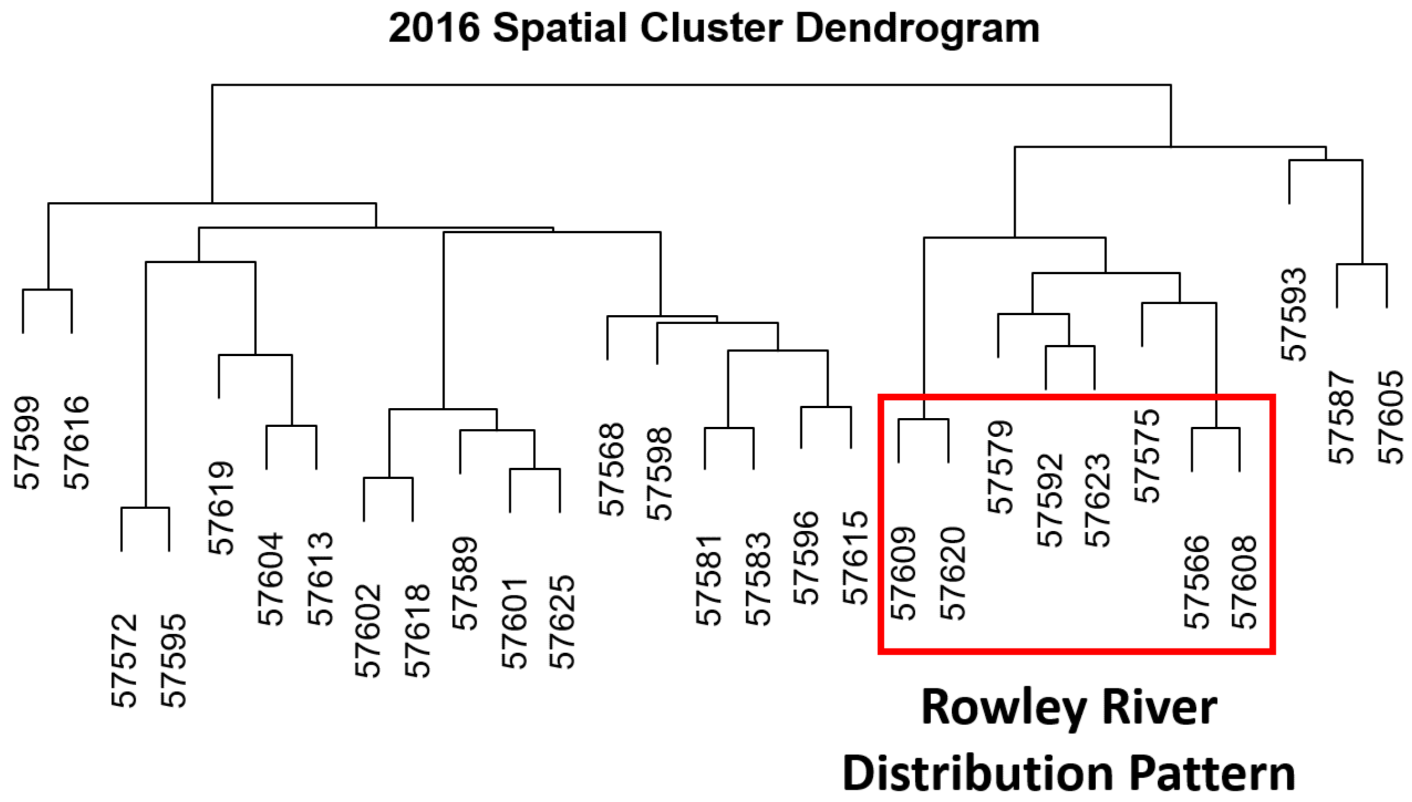


Figure C.1: Spatial cluster dendrogram for 2016 data based on proportion of time spent at each receiver. The red box indicates fish within the Rowley River Distribution Group. Each number indicates an individual fish.

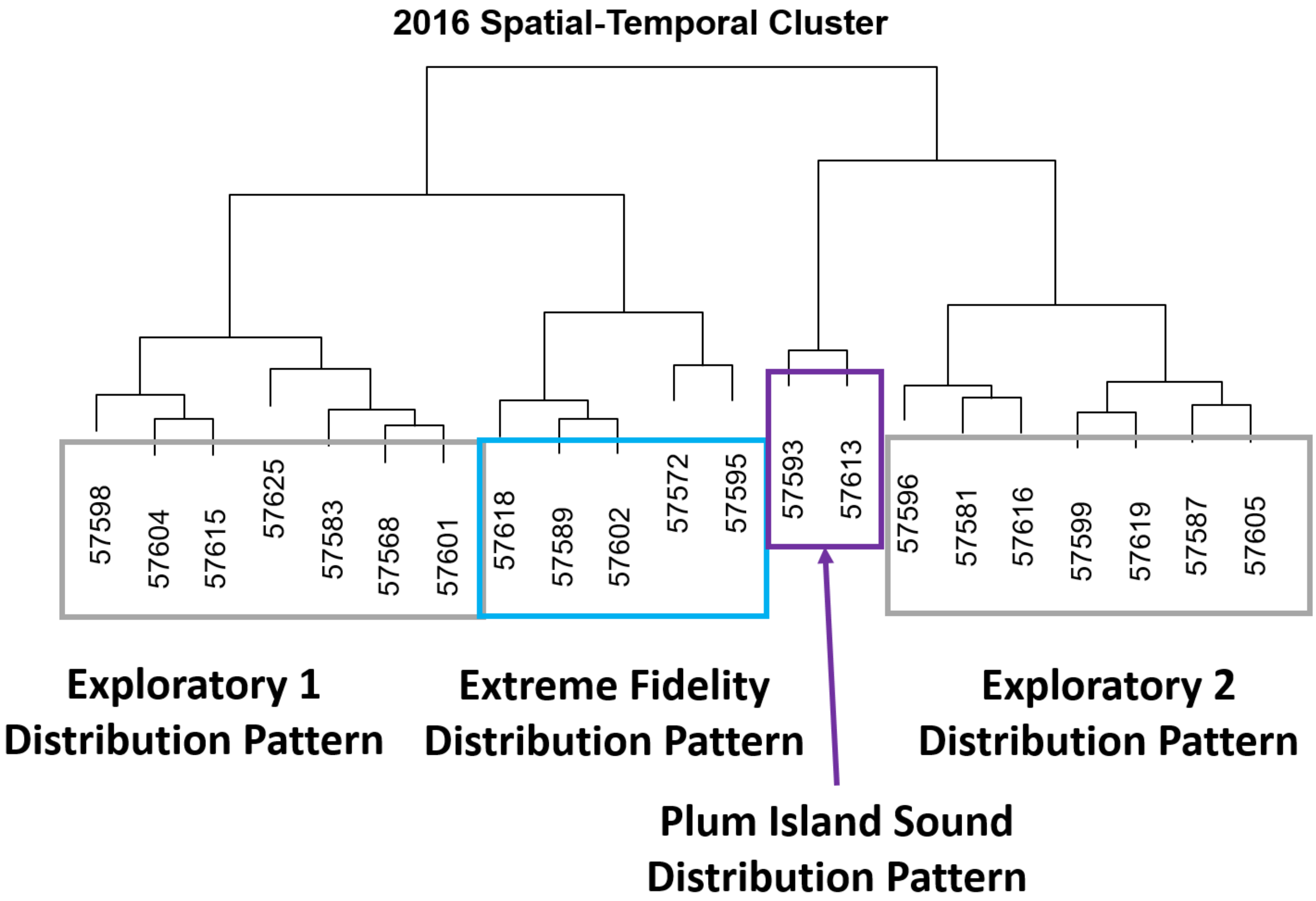

2016 Spatial-Temporal Cluster
57598
57604
57615
57625
57583
57568
57601
57618
57589
57602
57572
57595
57593
57613
57596
57581
57616
57599
57619
57587
57605
Exploratory 1 Distribution Pattern
Extreme Fidelity Distribution Pattern
Exploratory 2 Distribution Pattern
Plum Island Sound Distribution Pattern

Figure C.2: Temporal-spatial cluster dendrogram for 2016 using the *total number of days* in PIE, total *number of receivers visited, total movements, highest proportion of time spent at a single receiver*, and *coefficient of variation of residence time*. Each number indicates an individual fish. The Rowley River Distribution Group (spatial cluster 1) is excluded.

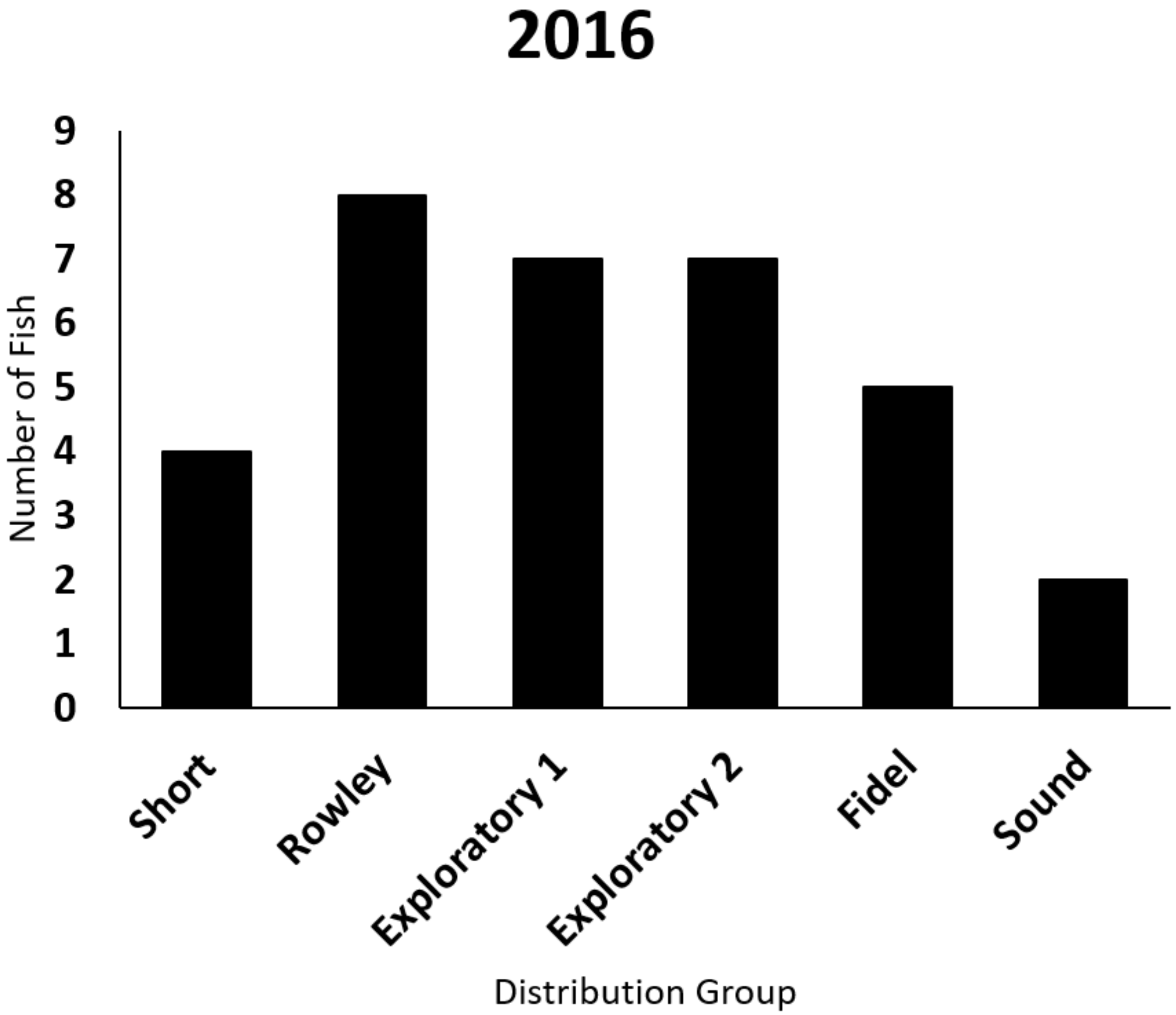


Figure C.3: Bar graphs illustrating for 2016 the number of tagged fish in each distribution group. Short-timers were excluded from subsequent analysis.

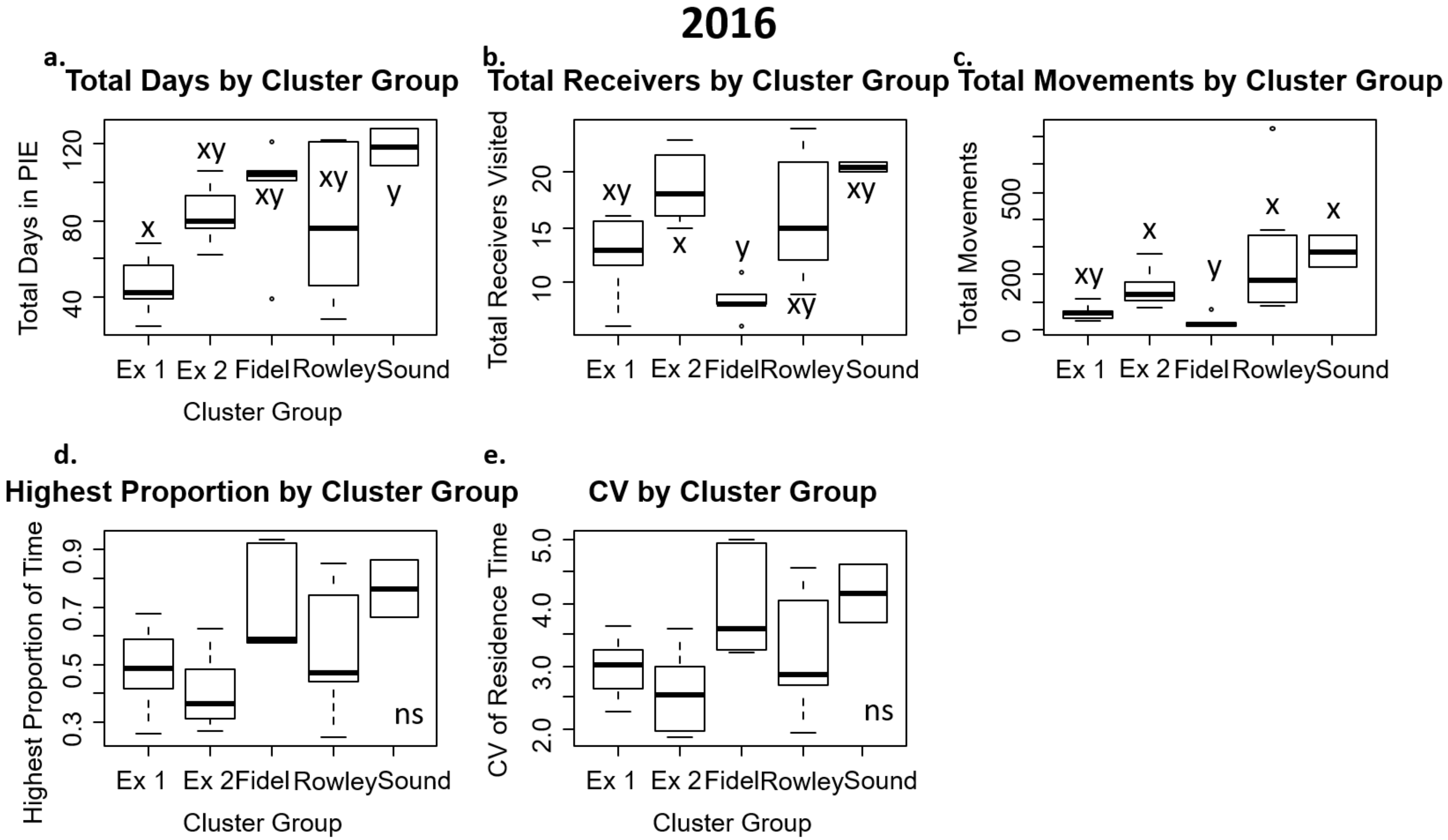


Figure C.4: For the five 2016 cluster groups (X Axis), shown are the box plots (Y axis) of (a) *total days in PIE,* (b) *total receivers visited,* (c) *total number of movements,* (d) *highest proportion of time at a single receiver,* and (e) *coefficient of variation of residence time*. Letters indicate statistical differences

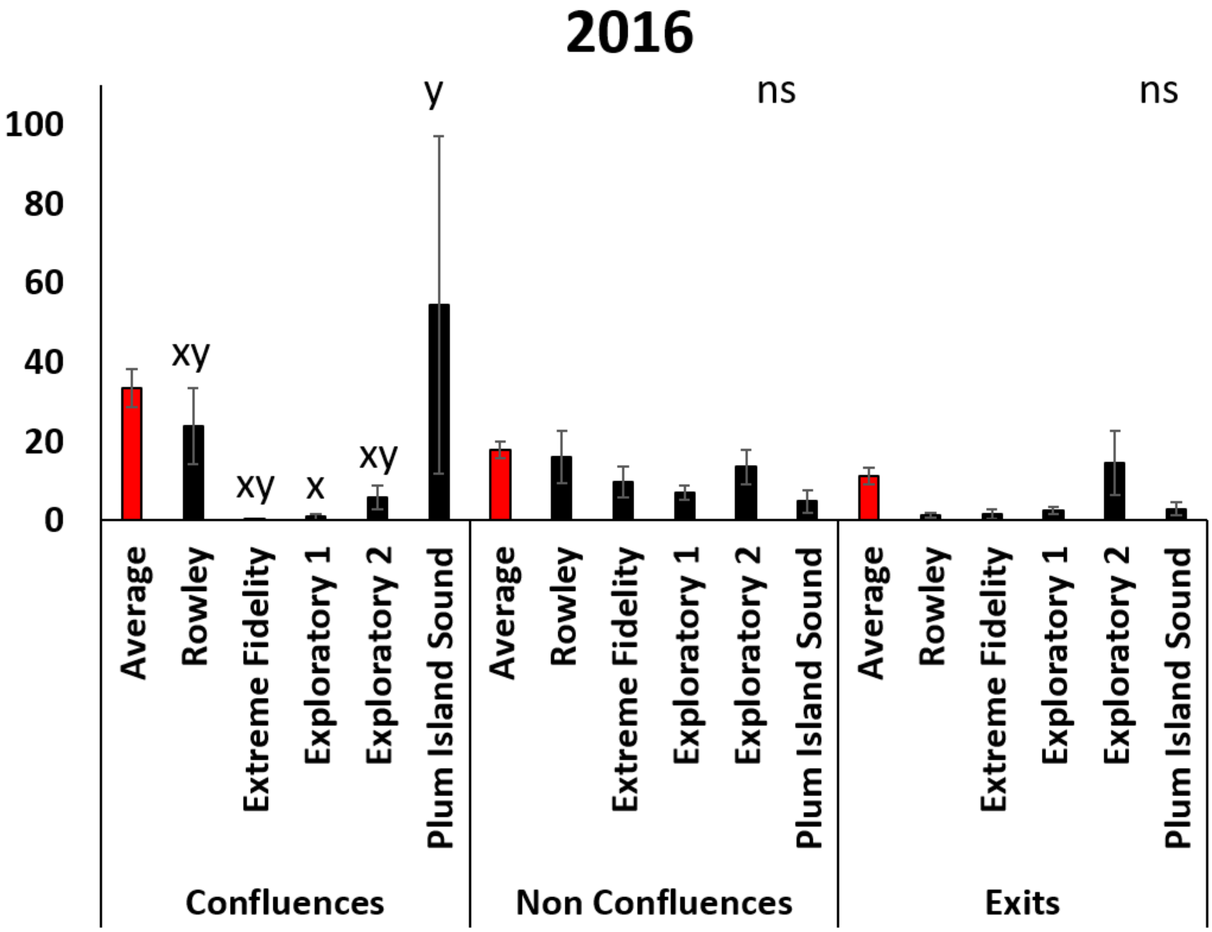


Figure C.5: Bar graphs depicting for 2016 the average residence time (h) (Y axis) for each distribution group (X axis) by geomorphic type (confluence, nonconfluence, exit). Letters indicate statistical differences.

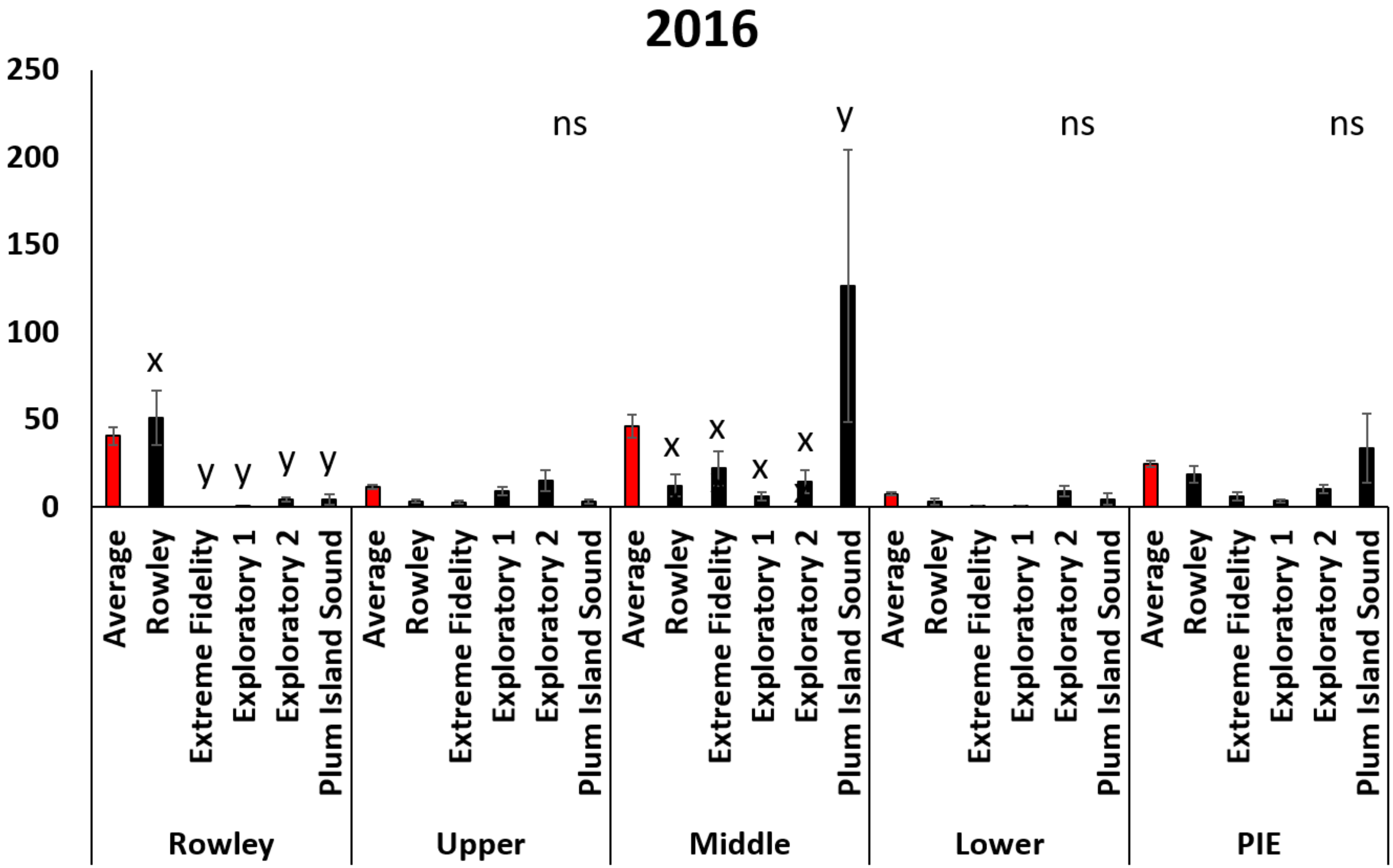


Figure C.6: Bar graphs depicting for 2016 the average residence time (h) (Y axis) for each distribution group (X axis) by region. Letters indicate statistical differences.

Appendix D - Trajectories

Do fish behave the same over two years?

Trajectories were created using detection data for individual fish mapped relative to receiver locations. Lines indicate movements from one receiver to another. Different colored dots on top of one another along the y axis indicate detections through time. Fish shown are only those that were tagged in 2015 observed in 2015, then returned in 2016. Also noted are the clusters for the distributional groups (See Chapter 2 and Appendix B) and total days in Plum Island.

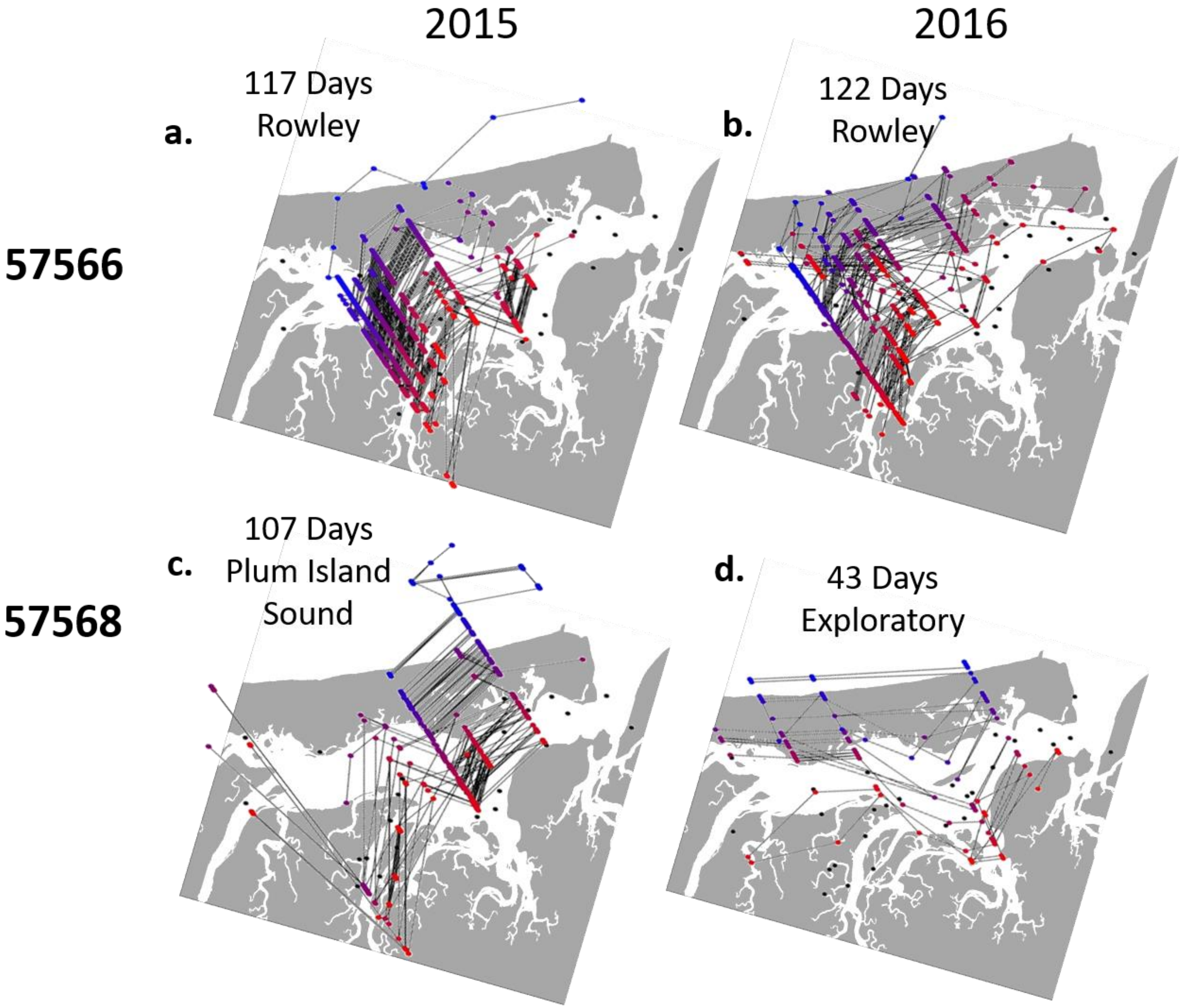

2015
2016
57566
a.
117 Days
Rowley
b.
122 Days
Rowley
57568
c.
107 Days
Plum Island
Sound
d.
43 Days
Exploratory

Figure D.1: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

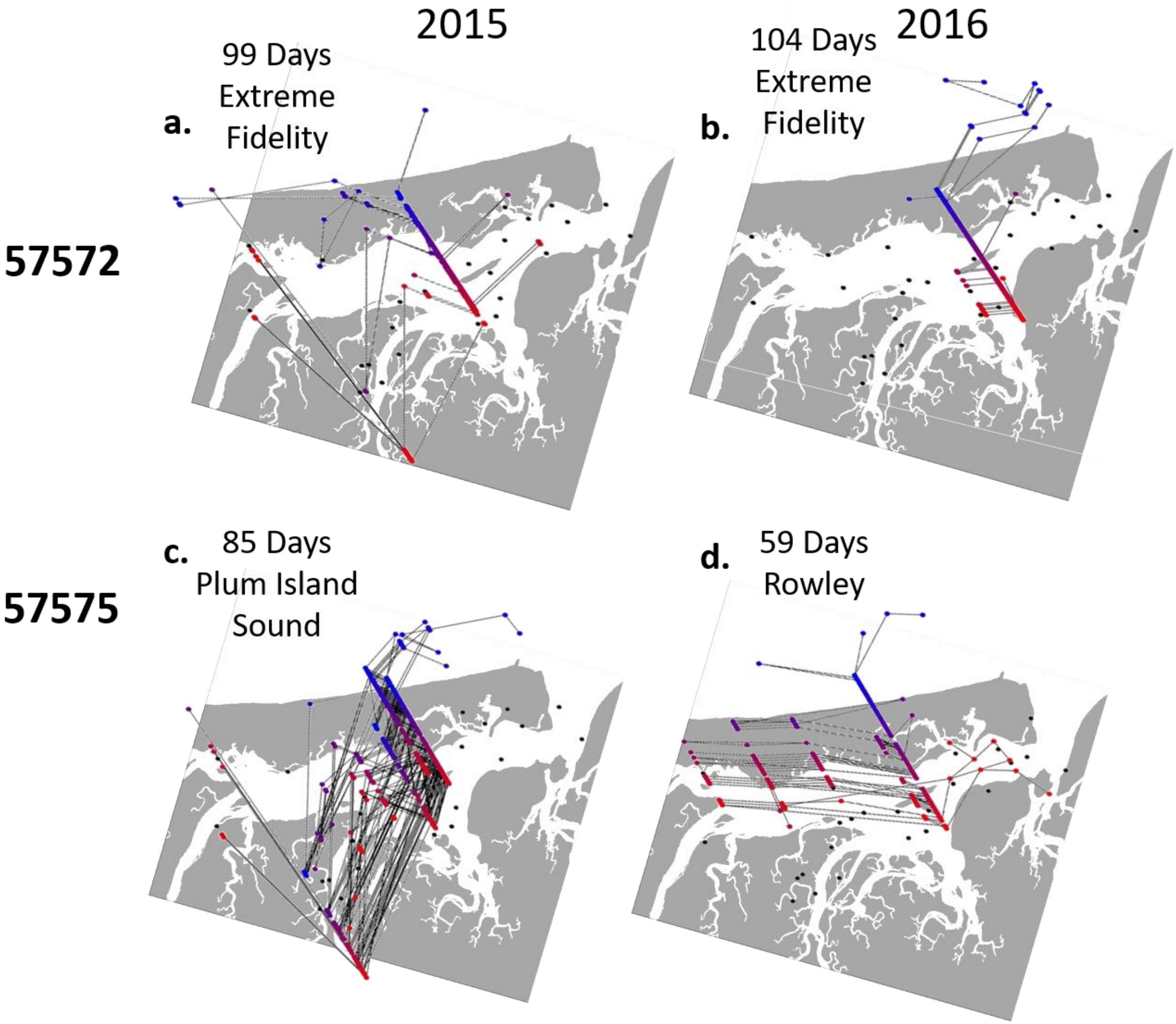

2015
2016
57572
57575
a.
99 Days
Extreme
Fidelity
b.
104 Days
Extreme
Fidelity
c.
85 Days
Plum Island
Sound
d.
59 Days
Rowley

Figure D.2: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

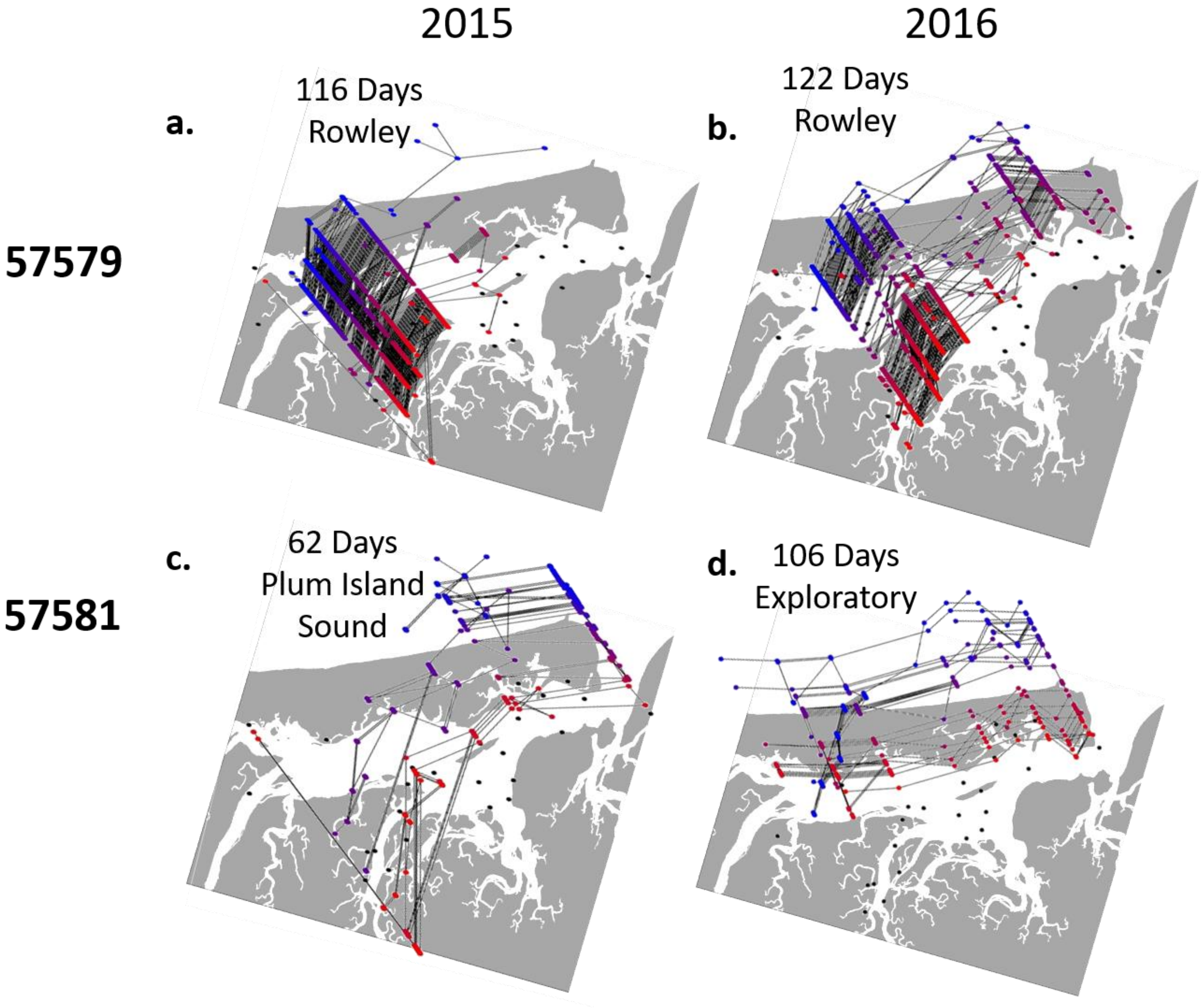

2015
2016
57579
57581
a.
116 Days
Rowley
b.
122 Days
Rowley
c.
62 Days
Plum Island
Sound
d.
106 Days
Exploratory

Figure D.3: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

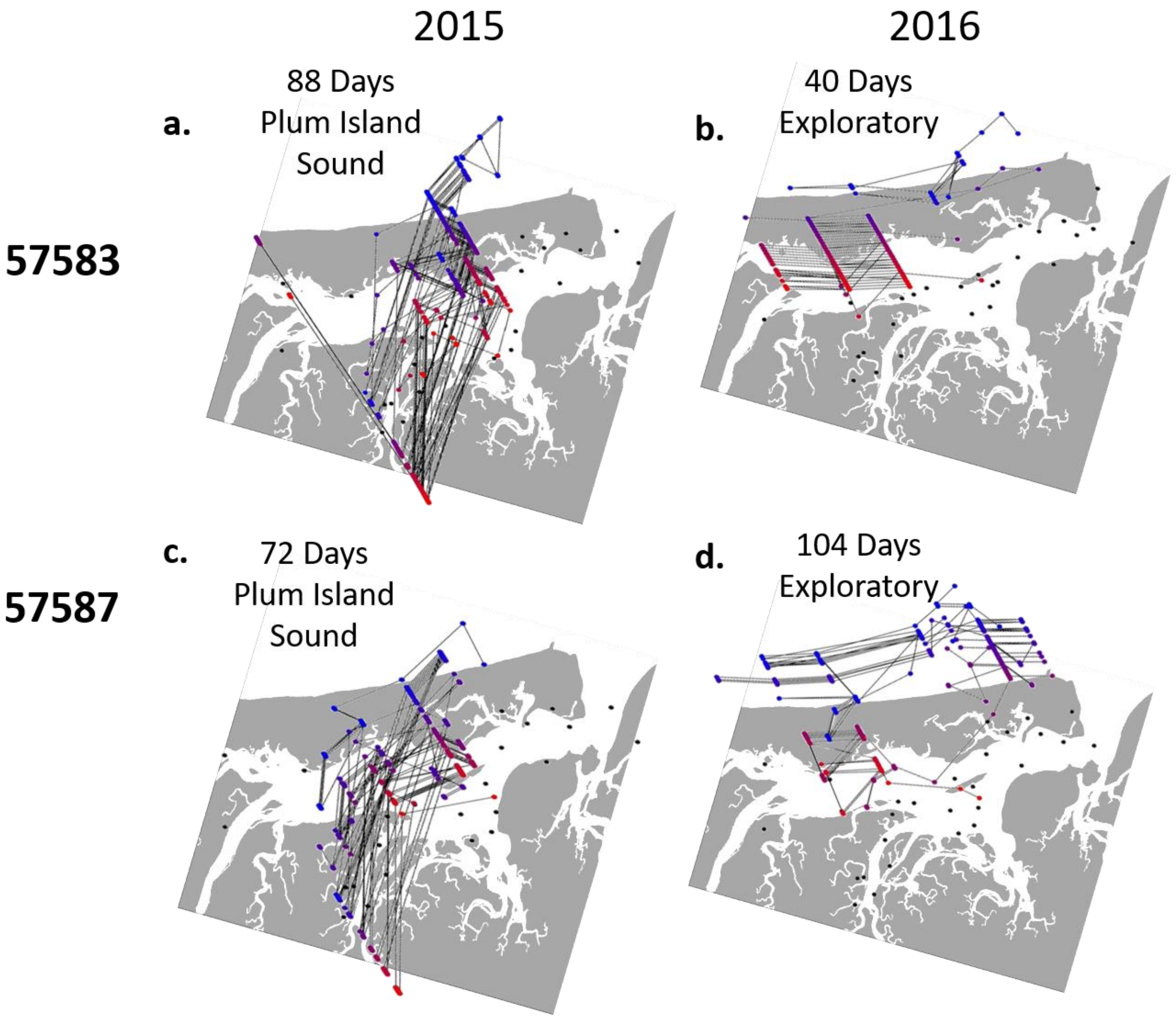

2015
2016
a.
88 Days
Plum Island
Sound
b.
40 Days
Exploratory
57583
c.
72 Days
Plum Island
Sound
d.
104 Days
Exploratory
57587

Figure D.4: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

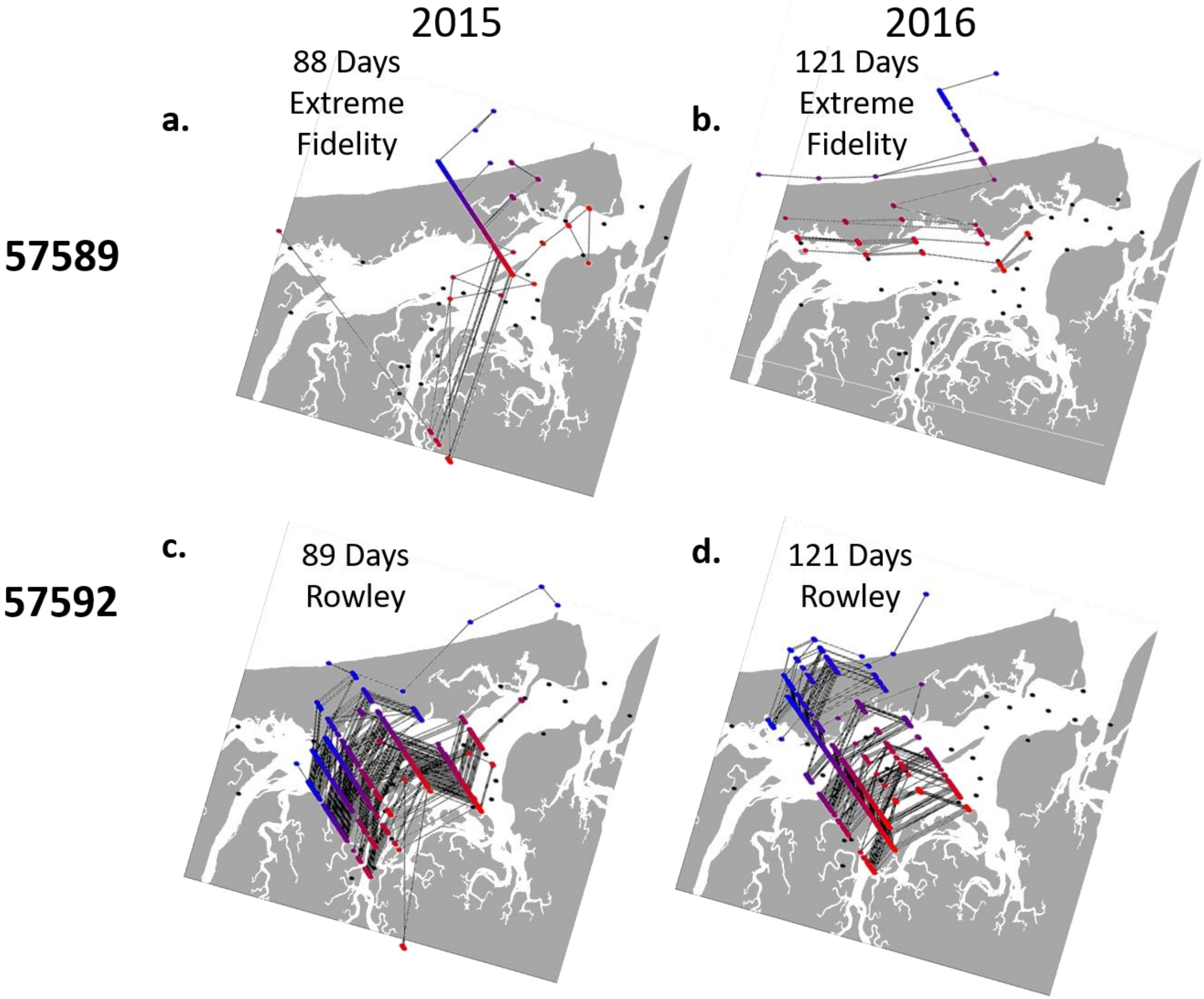

2015
2016
57589
a.
88 Days
Extreme
Fidelity
b.
121 Days
Extreme
Fidelity
57592
c.
89 Days
Rowley
d.
121 Days
Rowley

Figure D.5: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

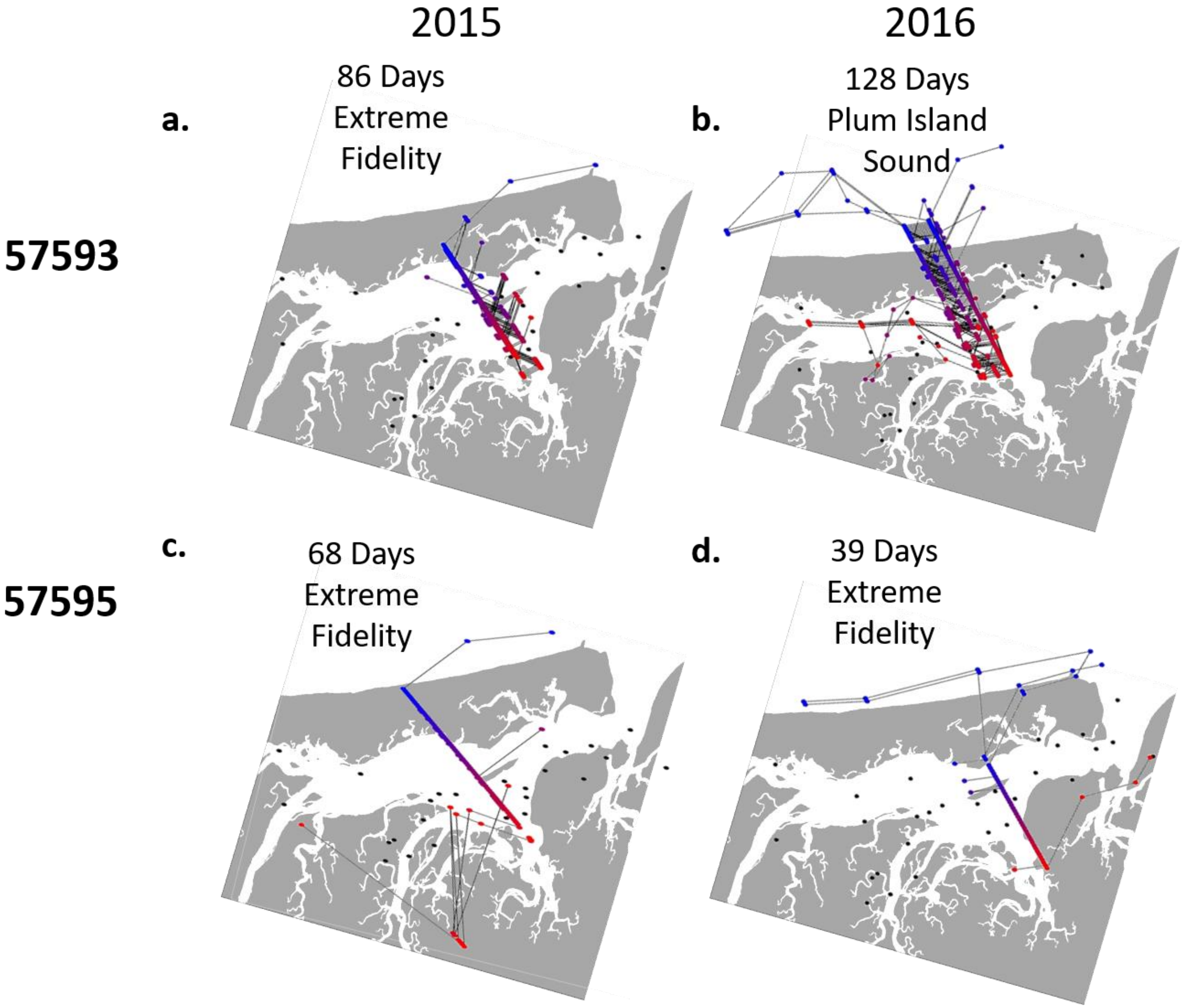

2015
2016
57593
a.
86 Days
Extreme
Fidelity
b.
128 Days
Plum Island
Sound
57595
c.
68 Days
Extreme
Fidelity
d.
39 Days
Extreme
Fidelity

Figure D.6: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

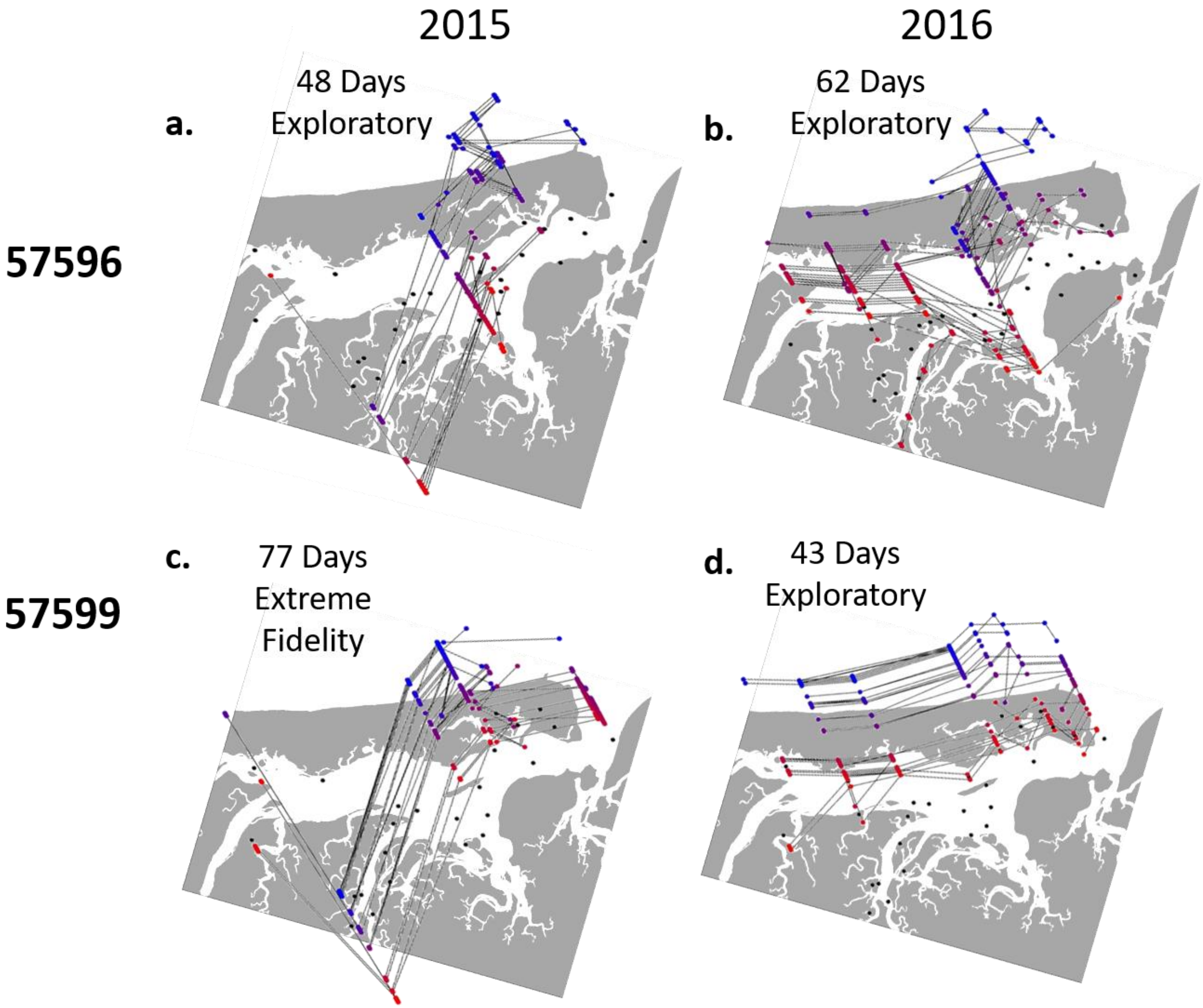

2015
2016
57596
a.
48 Days
Exploratory
b.
62 Days
Exploratory
57599
c.
77 Days
Extreme
Fidelity
d.
43 Days
Exploratory

Figure D.7: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

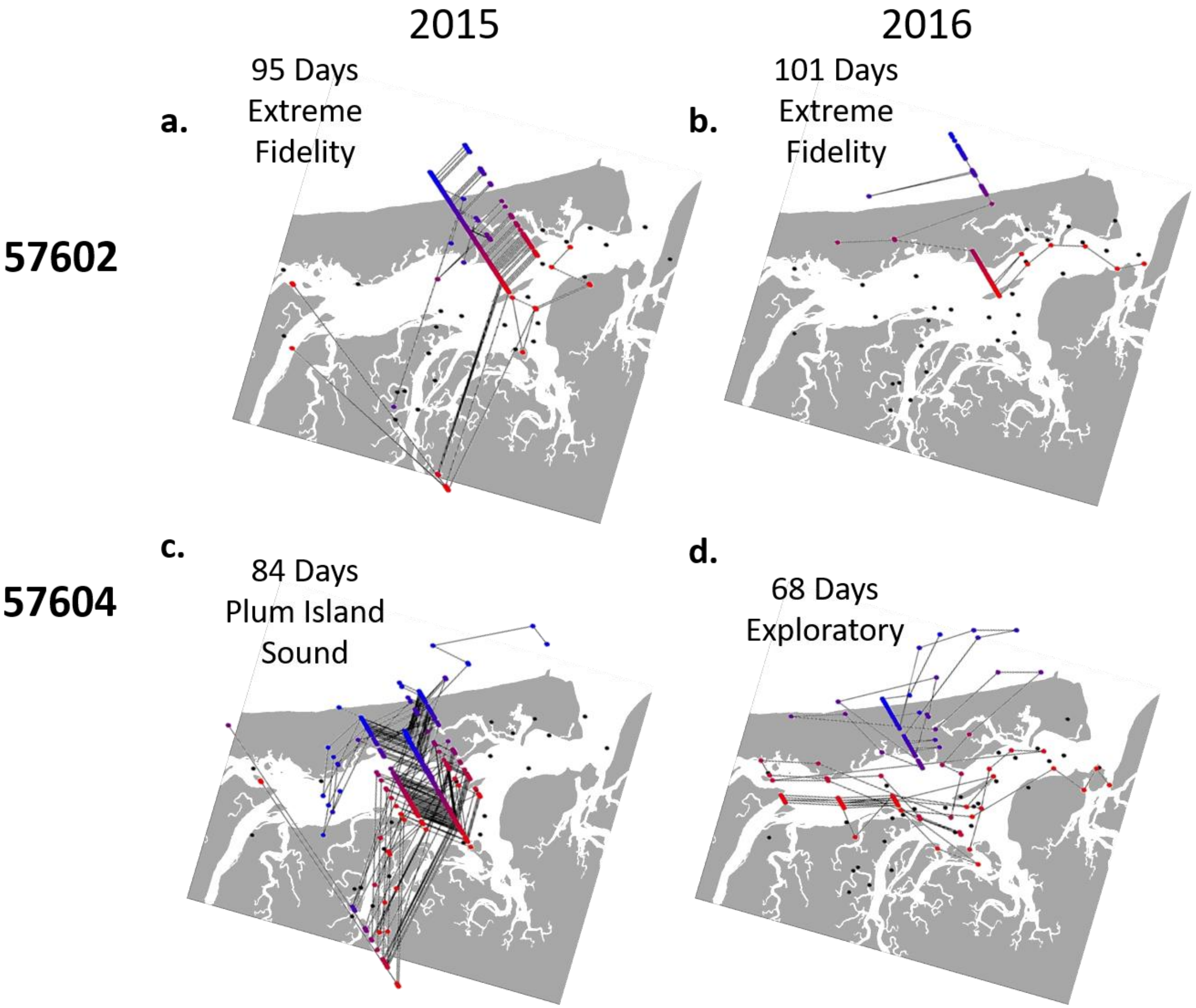

2015
2016
a.
95 Days
Extreme
Fidelity
b.
101 Days
Extreme
Fidelity
57602
c.
84 Days
Plum Island
Sound
d.
68 Days
Exploratory
57604

Figure D.8: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

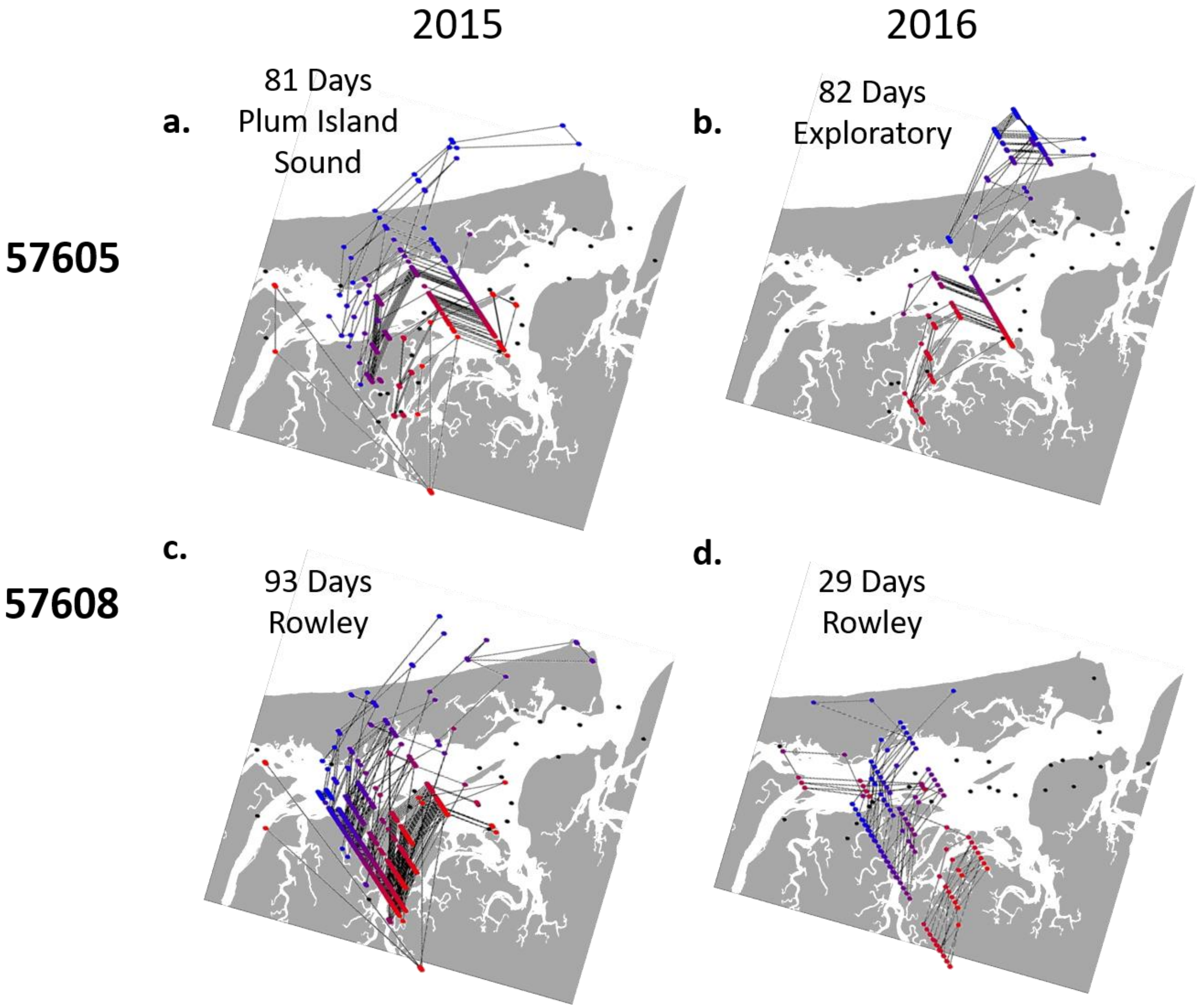

2015
2016
57605
57608
a.
81 Days
Plum Island
Sound
b.
82 Days
Exploratory
c.
93 Days
Rowley
d.
29 Days
Rowley

Figure D.9: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

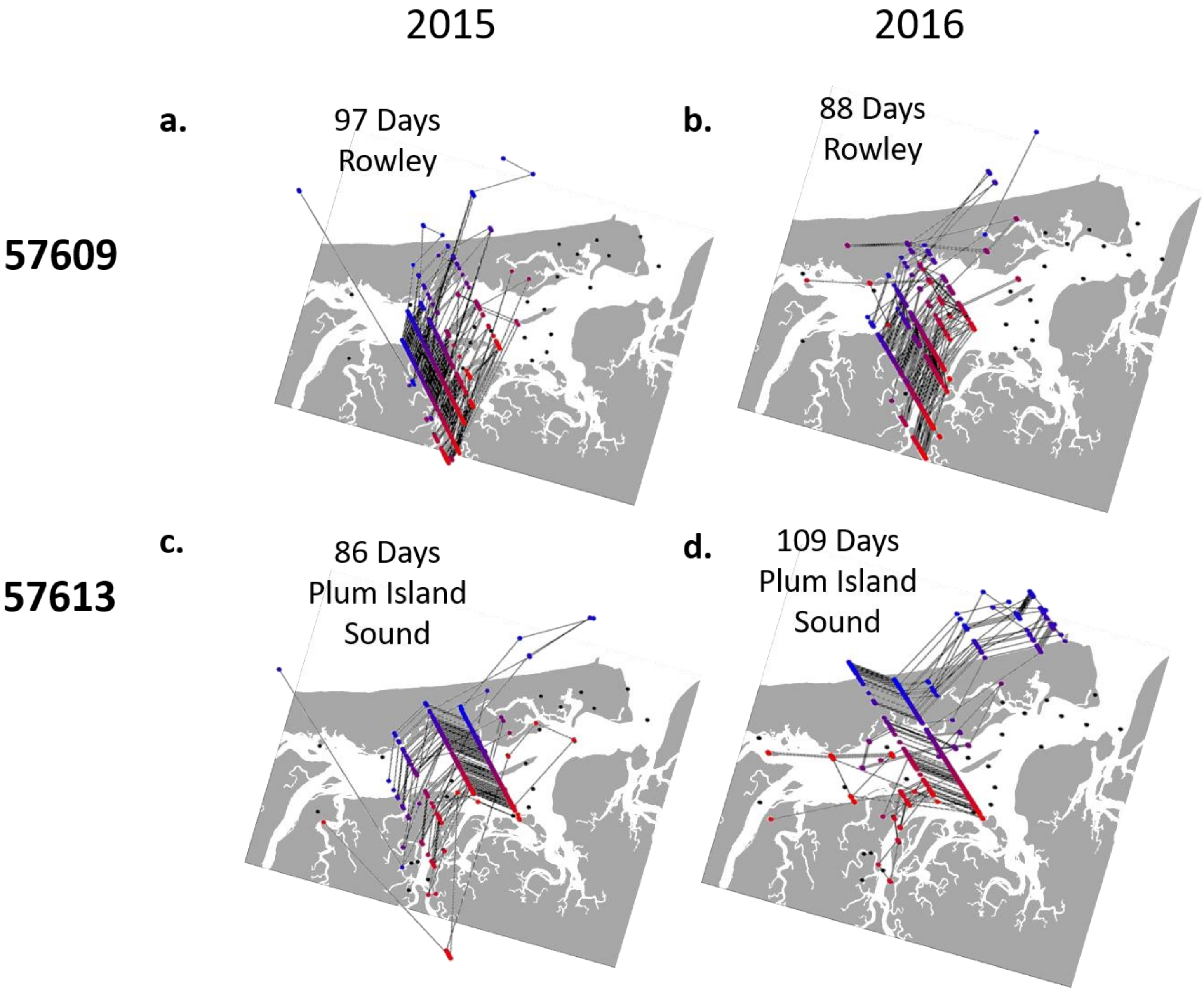

2015
2016
57609
57613
a.
97 Days
Rowley
b.
88 Days
Rowley
c.
86 Days
Plum Island
Sound
d.
109 Days
Plum Island
Sound

Figure D.10: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

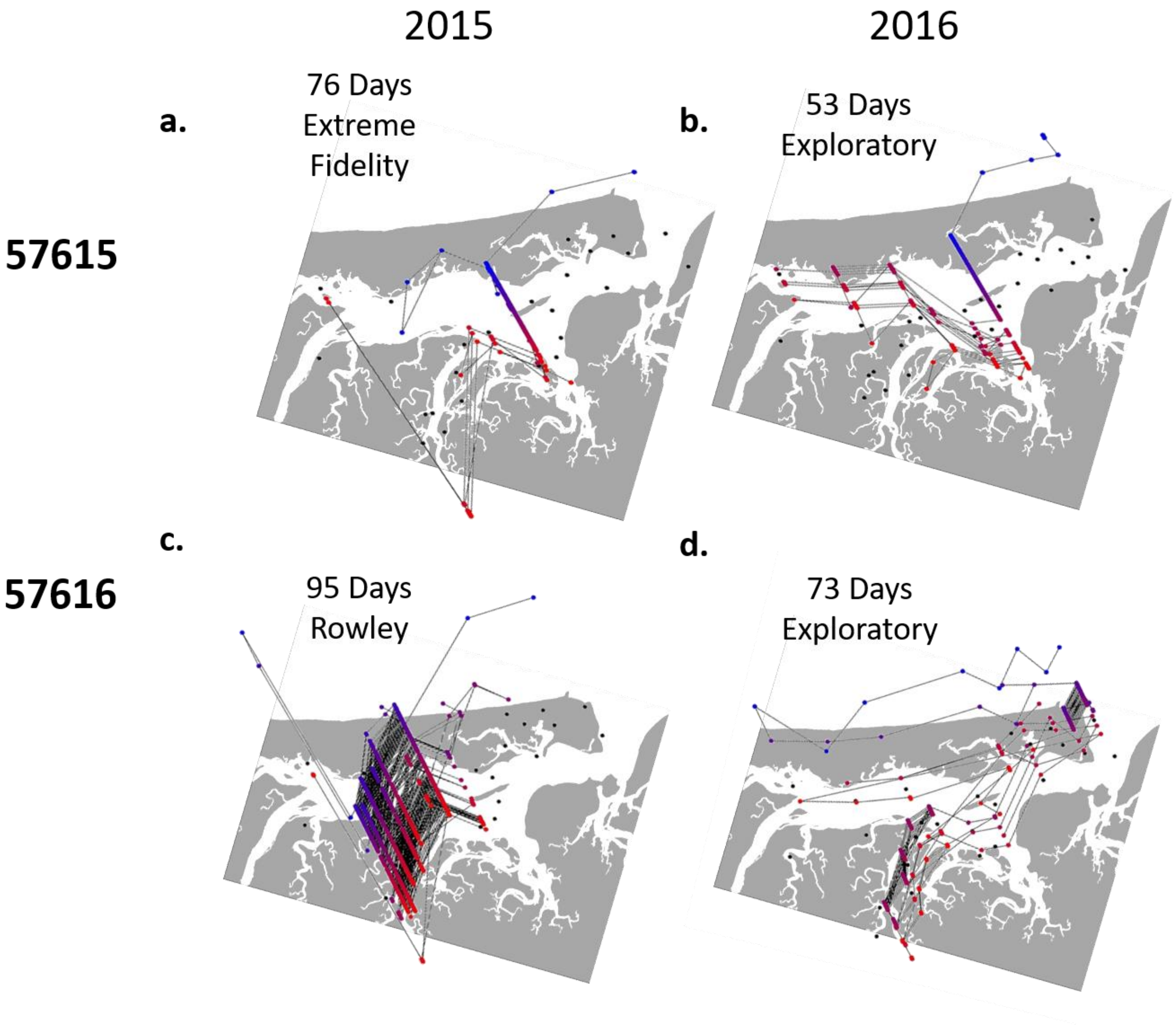

2015
2016
a.
76 Days
Extreme
Fidelity
b.
53 Days
Exploratory
57615
c.
57616
95 Days
Rowley
d.
73 Days
Exploratory

Figure D.11: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

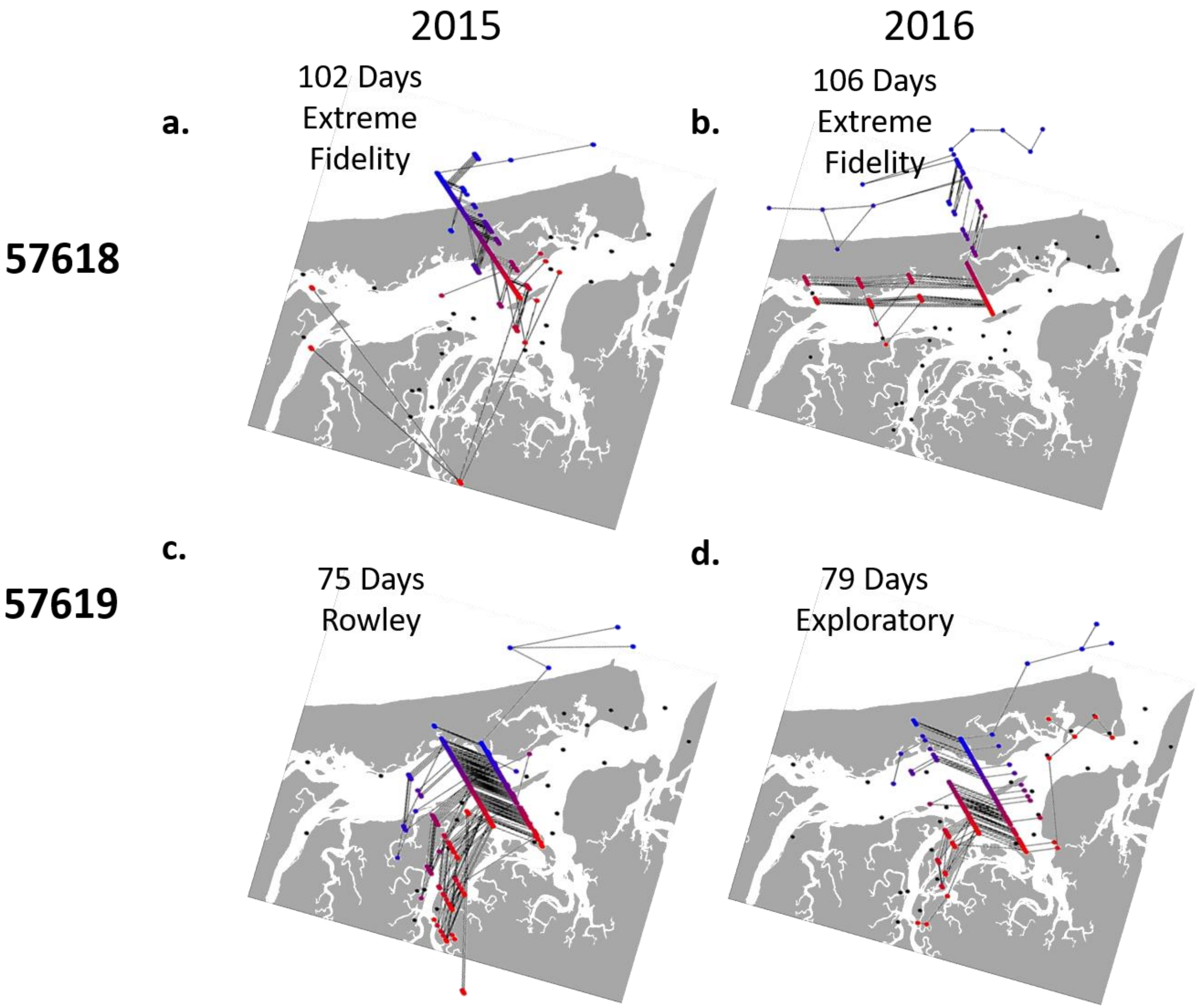

2015
2016
a.
102 Days
Extreme
Fidelity
b.
106 Days
Extreme
Fidelity
57618
c.
75 Days
Rowley
d.
79 Days
Exploratory
57619

Figure D.12: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

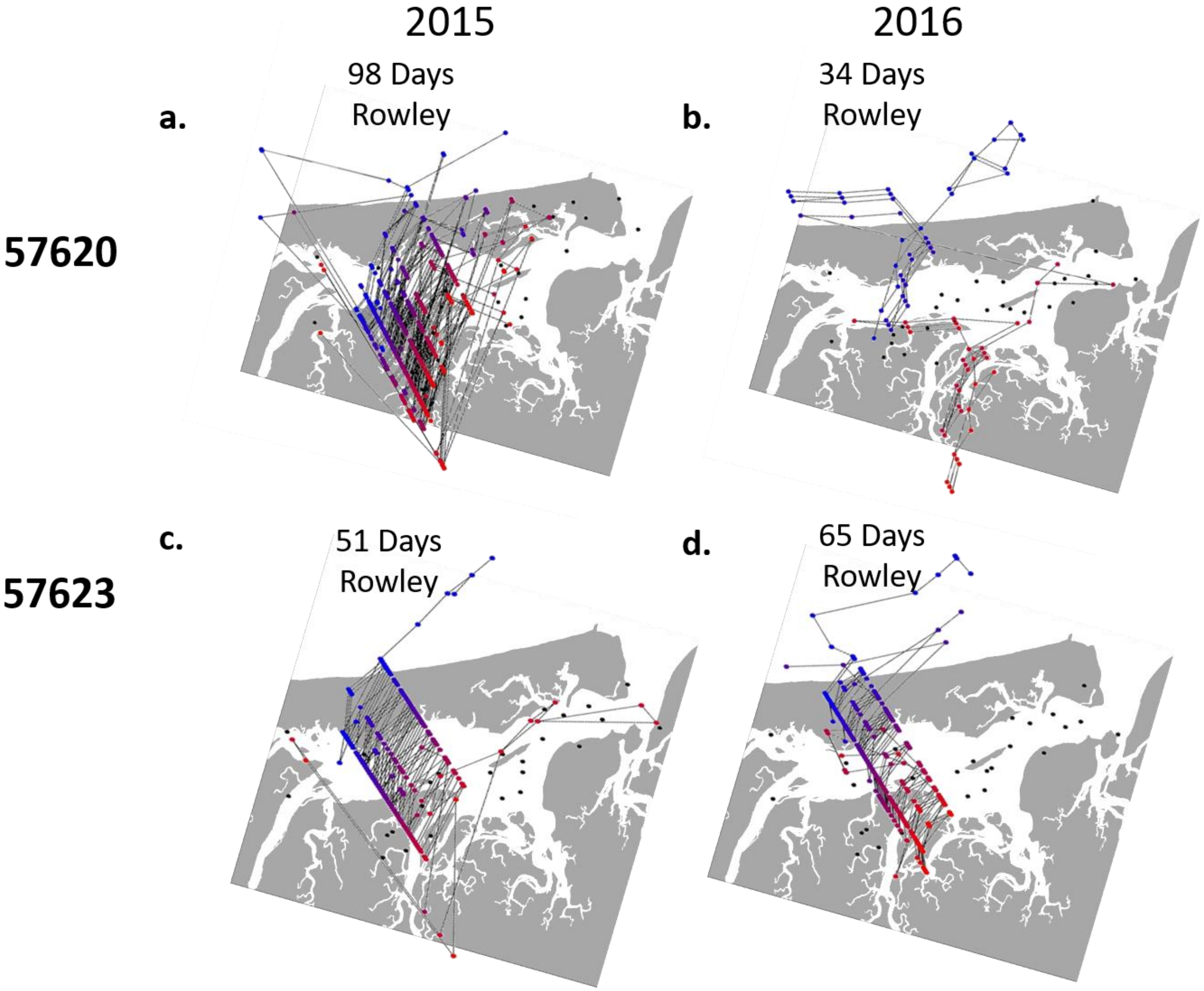

2015
2016
57620
57623
a.
98 Days
Rowley
b.
34 Days
Rowley
c.
51 Days
Rowley
d.
65 Days
Rowley

Figure D.13: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

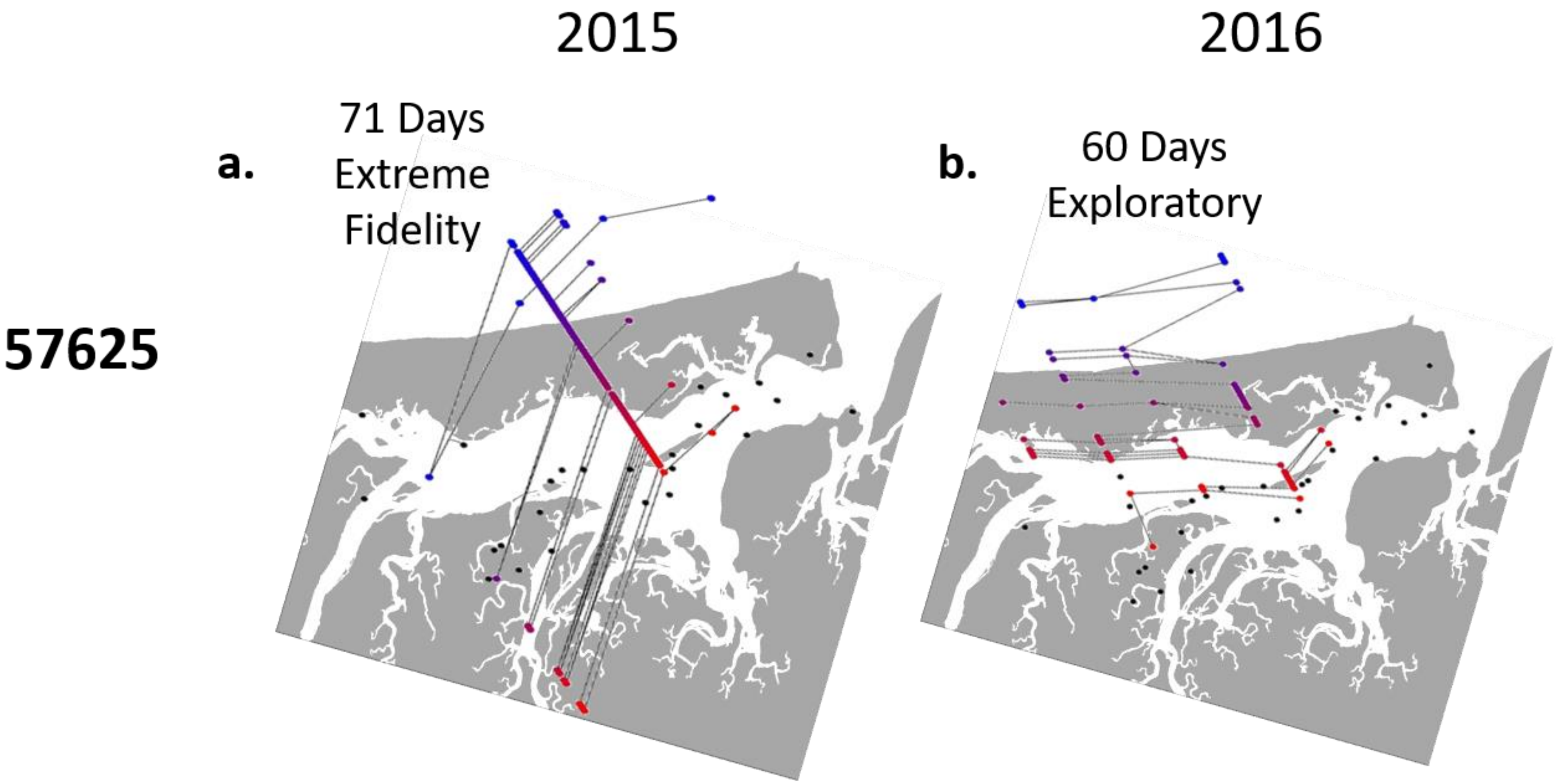


Figure D.14: Trajectories for two different fish, y axis, over two different years, x axis. Included is the total number of days spent in PIE for each fish during each year and the distribution group that fish was categorized under.

Appendix E - Site Fidelity

Site fidelity. Site fidelity has been defined as "the tendency to return to a previously occupied location" (Switzer 1993) but specific "rules" governing what specific criteria define type and degree of site fidelity are rare or nonexistent. Site fidelity can have three different components (Fig. E.1): site size, residence time, and rate of return. Relative to site size, many different potential sizes exist from small to large. For the component of residence, animals could stay within an area and never leave (long residence), or animals could stay for a little while and eventually leave, or animals could stay for an extremely brief period and leave almost right away (brief residence). Finally, relative to the component of return frequency, an animal that never or rarely leaves would have a low return rate, animals that leave frequently could return frequently (high return rate) as well as an array of intermediate conditions. Combining these three components three categories of site fidelity (Fig. E.1). The first sedentary category includes animals that stay within a small area and never leave. The second mixed category includes animals that stay in sites of varying sizes for intermediate amounts of time and left then return. And finally, the third category, which we called migrating, includes animals that had a much larger site, left almost immediately, but still returned. All three of these behavior categories are examples of site fidelity, but vary across the major components.

Literature. The literature on site fidelity is rapidly increasing and diverse in perspective. When we searched the literature review for peer-reviewed Web of Science papers with the phrase "Site fidelity" in the title, fish as the topic, and 2013-2017 as the time range, 29 papers were identified (Tab. E.1). These 29 papers, 93%(27) that empirically testing site fidelity (Tab. E.1), examine a range of different issues in different ways. For example, the size of the site fish use varies across studies from the entire bay area (e.g. Haulsee et al. 2016) to the particular holdfast that a seahorse attaches itself to (e.g. Harasti et al. 2014), but only 10% (3) studies acknowledge site size as a component of site fidelity (Tab. E.1). In PIE, we saw site fidelity at the receiver, region, or estuary scale. The size of the site does not necessarily need to be the same, but the scale at which site fidelity is being determined needs to be quantified

The other two components of site fidelity are residence time and return rate, but not not all researchers measure these responses in the same way. In the literature we reviewed, (83%; 24) included some measure of residence, 41% (12) measured returns, and 28% (8) measured both (Tab. E.1).

Most of the studies (83%; 24) included some measure of residence (Tab. E.1). Of those studies, some (25%; 6) consider at least one repeated detection (e.g. resighted, recaught, or redetected) to indicate residence (e.g. Ward et al. 2013; Rueger et al. 2014; Malard et al. 2016; Tab. E.1). Others define residence as days a fish was detected in the study site (33%; 8; e.g. Wolfe and Lowe 2015; Ferguson et al. 2013, 2016; Gardiner and Jones 2016; Tab. E.1) or the percentage of the population that stayed within an area (21%; 5; e.g. Gould et al. 2014; Rueger et al. 2014; Zemeckis et al. 2014; Tab. E.1). So, even though these studies are measuring the same concept of residence, they are not all measuring it with the same metrics.

Out of the 29 site fidelity studies, only 41% (12) measured returns (Tab. E.1). As for residence, there were multiple metrics used to describe returns. Of the studies that measured returns, some studies (58%; 7) performed a translocation experiment (e.g. Ward et al. 2013; Gould et al. 2014; Knope et al. 2017; Tab. E.1). Some studies consider one detection or return to be the minimum to be considered site fidel (17%; 2; Teesdale et al. 2015; Haulsee et al. 2016; Tab. E.1). While others measure return as a proportion of the population (67%; 8; e.g. Zemeckis et al. 2014; Binder et al. 2016; Knope et al. 2017; Tab. E.1). So again, metrics are not all comparable.

Site Fidelity in PIE - Residence. If we consider residence in PIE as fish spending more time at some sites over others, we saw three site sizes of site fidelity based on residence. At the estuary scale, if we look at a graph of the percent of fish that were detected anywhere in the estuary on a weekly basis, we saw an average of 67% of our fish weekly (Fig. E.2). So, for residence at an estuary site scale, two thirds of striped bass were site fidel to PIE for an average of 66 days (study length). At a regional site size (or scale), we can look at one of the fish that belonged to the Rowley River distribution group (Fig. E.3). This fish shows a near exclusive usage of the Rowley River region, but hardly any usage of areas in Plum Island outside of that area. So, at a regional site size, we again have evidence for regional fidelity. Finally, at a receiver site size, we can look at one of the fish that belonged to the Extreme Fidelity distribution group (Fig. E.4). This fish shows usage of only one receiver for almost the entire time it is in the estuary. So, we have some more evidence for fidelity at a site scale.

Site Fidelity in PIE - Returns. For 2016, 56% (33) of our original 59 tagged fish returned to Plum Island to feed in the second summer with an average of 30% of the fish seen weekly (Fig. E.5). So, at an estuary site size, site fidelity existed based on returns over two years. For the within estuary regional site size (e.g., Rowley River distribution group), individual fish can leave the region but consistently returns (Fig. E.6). So at least at two scales (or site sizes), estuary and within-estuary region, we observed site fidelity based on return rate

Site Fidelity Thresholds. Not only did we see different scales of site fidelity, we also saw different examples of thresholds that could be used to determine site fidelity. One example of a potential threshold is determining only fish that spent greater than 75% of their time at a single receiver (Fig. E.7; Fig. E.8). This would denote fish that spend a significant majority of their time at one location. We could also choose a lowest threshold if we only include fish that spent greater than 50% of their time at a single location (Fig. E.9; Fig. E.10). Finally, the lowest threshold we could determine site fidelity by is using any fish that spends above average time at any receiver in the estuary (4%). Being the loosest threshold, this includes all the remaining tagged fish (Fig. E.11; Fig. E.12).

Summary. "Site fidelity" is a useful ecological concept and widely used by researchers. Definitions are evolving, i.e., "movements through an area that are significantly more tortuous or confined than expected at random, indicating utilization of the area" (Wolfe and Lowe 2015). However, the development of more focused, rigorous, and standard definitions of all three components of site fidelity is needed before the potential for this concept to explain distribution can be realized. At many of our receivers, tagged fish either stayed at the site, returned frequently, or both. Knowing these fish show long term utilization of a Massachusetts estuary can support fisheries stock assessments, survival estimates, and help us understand the migration pattern of this important Atlantic coastal stock (Crossin et al. 2017).

Literature Cited

Atkins, S., et al. (2016). "Net loss of endangered humpback dolphins: integrating residency, site fidelity, and bycatch in shark nets." Marine Ecology Progress Series 555: 249-260.

Binder, T. R., et al. (2016). "Spawning site fidelity of wild and hatchery lake trout (*Salvelinus namaycush*) in northern Lake Huron." Canadian Journal of Fisheries and Aquatic Sciences 73(1): 18-34.

Bellwood, D. R., et al. (2016). "Site fidelity and homing in juvenile rabbitfishes (Siganidae)." Coral Reefs 35(4): 1151-1155.

Brame, A.B., et al. (2014) Site fidelity and condition metrics suggest sequential habitat use by juvenile common snook. Mar Ecol Prog Ser 509:255-269.

Breve, N. W. P., et al. (2014). "Explicit site fidelity of European catfish (*Silurus glanis*, L., 1758) to man- made habitat in the River Meuse, Netherlands." Journal of Applied Ichthyology 30(3): 472-478.

Crossin, G. T., et al. (2017). "Acoustic telemetry and fisheries management." Ecological Applications 27(4): 1031-1049.

Ferguson, A. M., et al. (2013). "A Herbivore Knows Its Patch: Luderick, *Girella tricuspidata*, Exhibit Strong Site Fidelity on Shallow Subtidal Reefs in a Temperate Marine Park." PLoS ONE 8(5).

Ferguson, A. M., et al. (2016). "Herbivore abundance, site fidelity and grazing rates on temperate reefs inside and outside marine reserves." Journal of Experimental Marine Biology and Ecology 478: 96-105.

Gannon, R., et al. (2015). "Fine-scale movements, site fidelity and habitat use of an estuarine dependent sparid." Environmental Biology of Fishes 98(6): 1599-1608.

Gardiner, N. M. and G. P. Jones (2016). Habitat specialisation, site fidelity and sociality predict homing success in coral reef cardinalfish. Marine Ecology Progress Series 558: 81-96.

Gould, A. L., et al. (2014). "Host preference, site fidelity, and homing behavior of the symbiotically luminous cardinalfish, *Siphamia tubifer* (Perciformes: Apogonidae)." Marine Biology 161(12): 2897-2907.

Harasti, D., et al. (2014). Ontogenetic and sex-based differences in habitat preferences and site fidelity of White's seahorse *Hippocampus whitei.* Journal of Fish Biology 85(5): 1413-1428.

Harasti, D., et al. (2015). "Movements, Home Range and Site Fidelity of Snapper (*Chrysophrys auratus*) within a Temperate Marine Protected Area." PLoS ONE 10(11).

Haulsee, D. E., et al. (2016). Implantation and Recovery of Long-Term Archival Transceivers in a Migratory Shark with High Site Fidelity. PLoS ONE 11(2).

Knope, M. L., et al. (2017). "Site fidelity and homing behaviour of intertidal sculpins revisited." Journal of Fish Biology 90(1): 341-355.

Malard, L. A., et al. (2016). "Site fidelity, size, and morphology may differ by tidal position for an intertidal fish, *Bathygobius cocosensis* (Perciformes-Gobiidae), in Eastern Australia." PeerJ 4.

Marsh, p. C., et al. (2013). "Diel cover use and local site fidelity of a large southwestern cyprinid, *bonytail Gila elegans*, in a lower Colorado river backwater." Western North American Naturalist 73(2): 211-218.

Neat, F., et al. (2015). "Site fidelity, survival and conservation options for the threatened flapper skate (*Dipturus cf. intermedia*)." Aquatic Conservation-Marine and Freshwater Ecosystems 25(1): 6-20.

Poulakis, G. R., et al. (2016). "Long-term site fidelity of endangered smalltooth sawfish (*Pristis pectinata*) from different mothers." Fishery Bulletin 114(4): 461-475.

Reubens, J. T., et al. (2013). "Residency, site fidelity and habitat use of Atlantic cod (*Gadus morhua*) at an offshore wind farm using acoustic telemetry." Marine Environmental Research 90: 128-135.

Rueger, T., et al. (2014). "Relationships between pair formation, site fidelity and sex in a coral reef cardinalfish." Behavioural Processes 107: 119-126.

Shapiera, M., et al. (2014). "Season and site fidelity determine home range of dispersing and resident juvenile Greenland cod *Gadus ogac* in a Newfoundland fjord." Marine Ecology Progress Series 503: 235-246.

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7: 533-555.

Teesdale, G. N., et al. (2015). "Patterns of home ranging, site fidelity, and seasonal spawning migration of barred sand bass caught within the Palos Verdes Shelf Superfund Site." Marine Ecology Progress Series 539: 255-269.

Twardek, W. M., et al. (2017). "Potential consequences of angling on nest-site fidelity in largemouth bass." Environmental Biology of Fishes 100(5): 611-616.

Vianna, G. M. S., et al. (2013). "Environmental Influences on Patterns of Vertical Movement and Site Fidelity of Grey Reef Sharks (*Carcharhinus amblyrhynchos*) at Aggregation Sites." PLoS ONE 8(4).

Vinagre, C., et al. (2016). "Can stable isotopes be used to infer site fidelity of nekton in open coastal areas?" Ecological Indicators 71: 175-180.

Ward, A. J. W., et al. (2013). "Site fidelity and localised homing behaviour in three-spined sticklebacks (*Gasterosteus aculeatus*)." Behaviour 150(14): 1689-1708.

White, G. E. and C. Brown (2013). "Site fidelity and homing behaviour in intertidal fishes." Marine Biology 160(6): 1365-1372.

Wolfe, B. W. and C. G. Lowe (2015). "Movement patterns, habitat use and site fidelity of the white croaker (*Genyonemus lineatus*) in the Palos Verdes Superfund Site, Los Angeles, California." Marine Environmental Research 109: 69-80.

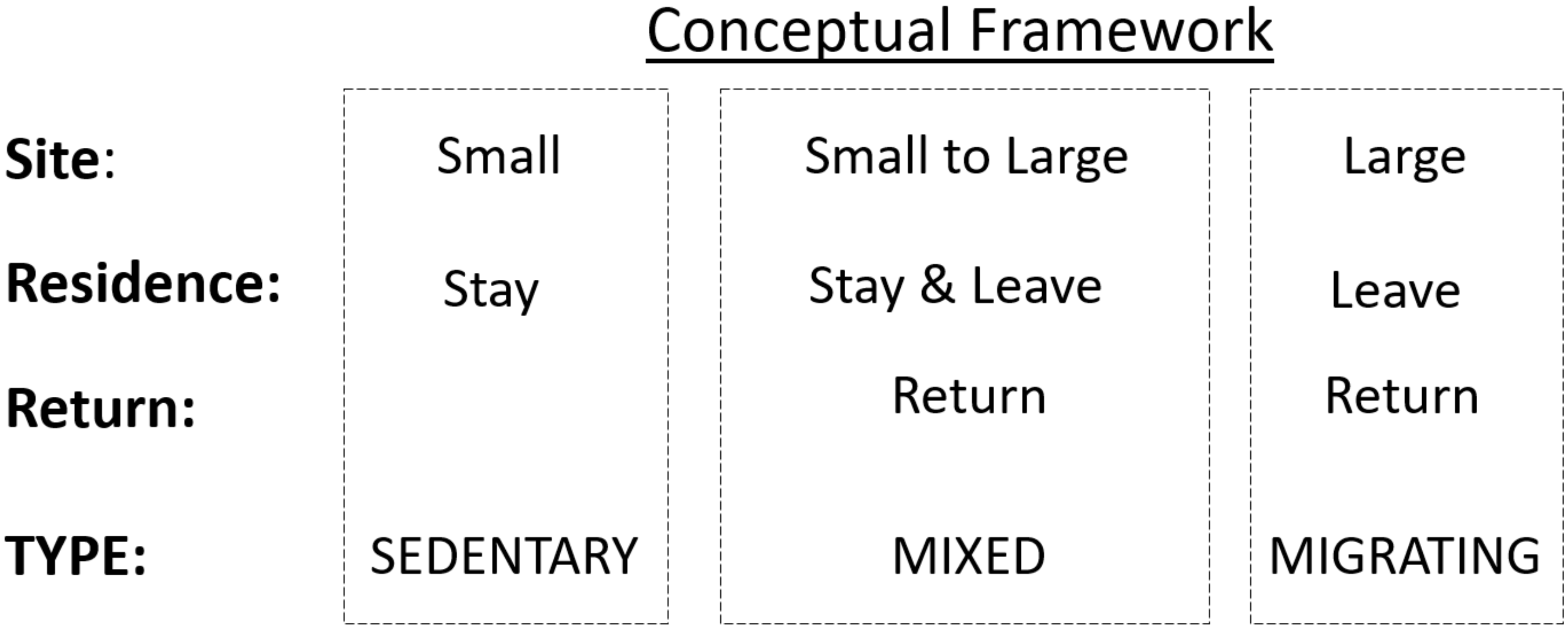
Zemeckis, D. R., et al. (2014). "Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: implications for population structure and rebuilding." Ices Journal of Marine Science 71(6): 1356-1365.

Table E.1: Summary of the literature review on site fidelity studies.

No.	Citation		Focus			Site Fidelity			Metrics		Residence Units					Return Units			
	Year	Author	System	Fish	Life Stage	Empirical Test?	Acknowledged Scale?	Modeled?	Residence	Return	# Detection	% Population	# Days	Residency Index	Other	Translocation	# Detections	% Population	Other
1	2017	Twardek et al.	FW - Lake	Fresh.	Breeding					X									X
2	2017	Knope et al.	Coast	Marine	General	X			X	X	X					X		X	
3	2016	Vinagre et al.	Coast	Multiple	General														
4	2016	Poulakis et al.	Estuary	Marine	General	X			X				X						
5	2016	Malard et al.	Coast	Marine	General	X		X	X		X								
6	2016	Haulsee et al.	Estuary	Marine	General	X				X							X		
7	2016	Gardiner and Jones	Coast	Marine	General	X	X		X				X						
8	2016	Ferguson et al.	Coast	Marine	General	X			X				X						
9	2016	Binder et al.	FW - Lake	Fresh.	Breeding	X		X	X	X								X	
10	2016	Bellwood et al.	Coast	Marine	General	X				X						X		X	
11	2016	Atkins et al.	Coast	Marine	General	X			X		X								
12	2015	Wolfe and Lowe	Coast	Marine	General	X			X	X			X						X
13	2015	Teesdale et al.	Coast	Marine	Breeding	X			X	X		X					X		
14	2015	Neat et al.	Coast	Marine	General	X		X	X		X								
15	2015	Harasti et al.	Coast	Marine	General	X	X		X					X					
16	2015	Gannon et al.	Estuary	Marine	General	X			X						X				
17	2014	Zemeckis et al.	Coast	Marine	Breeding	X			X	X			X					X	
18	2014	Shapiera et al.	Estuary	Marine	General	X			X			X				X			
19	2014	Rueger et al.	Coral Reef	Marine	General	X			X	X		X				X		X	
20	2014	Harasti et al.	Coast	Marine	General	X	X		X				X						
21	2014	Gould et al.	Island	Marine	General	X			X	X		X				X		X	
22	2014	Breve et al.	FW - River	Fresh.	General	X			X		X								

Table E.1 (cont.)

No.	Citation		Focus			Site Fidelity			Metrics		Residence Units					Return Units			
	Year	Author	System	Fish	Life Stage	Empirical Test?	Acknowledged Scale?	Modeled?	Residence	Return	# Detection	% Population	# Days	Residency Index	Other	Translocation	# Detections	% Population	Other
23	2014	McIvor et al.	Estuary	Marine	General				X										
24	2013	White and Brown	Coast	Marine	General	X			X	X		X				X		X	
25	2013	Ward et al.	Estuary	Marine	General	X				X						X		X	
26	2013	Vianna et al.	Coral Reef	Marine	General	X			X				X						
27	2013	Reubens et al.	Coast	Marine	General	X			X					X					
28	2013	Marsh et al.	FW - River	Fresh.	General	X			X		X								
29	2013	Ferguson et al.	Coral Reef	Marine	General	X			X				X						
		Taylor et al.	**Estuary**	**Anadr.**	**Feeding**	**X**	**X**		**X**	**X**	**X**	**X**	**X**	**X**			**X**	**X**	
Total						27	3	3	24	12	6	5	8	2	1	0	2	8	2



Conceptual Framework

Site:	Small	Small to Large	Large
Residence:	Stay	Stay & Leave	Leave
Return:		Return	Return
TYPE:	SEDENTARY	MIXED	MIGRATING

Figure E.1: Conceptual framework for examining site fidelity and its potential categorizations.

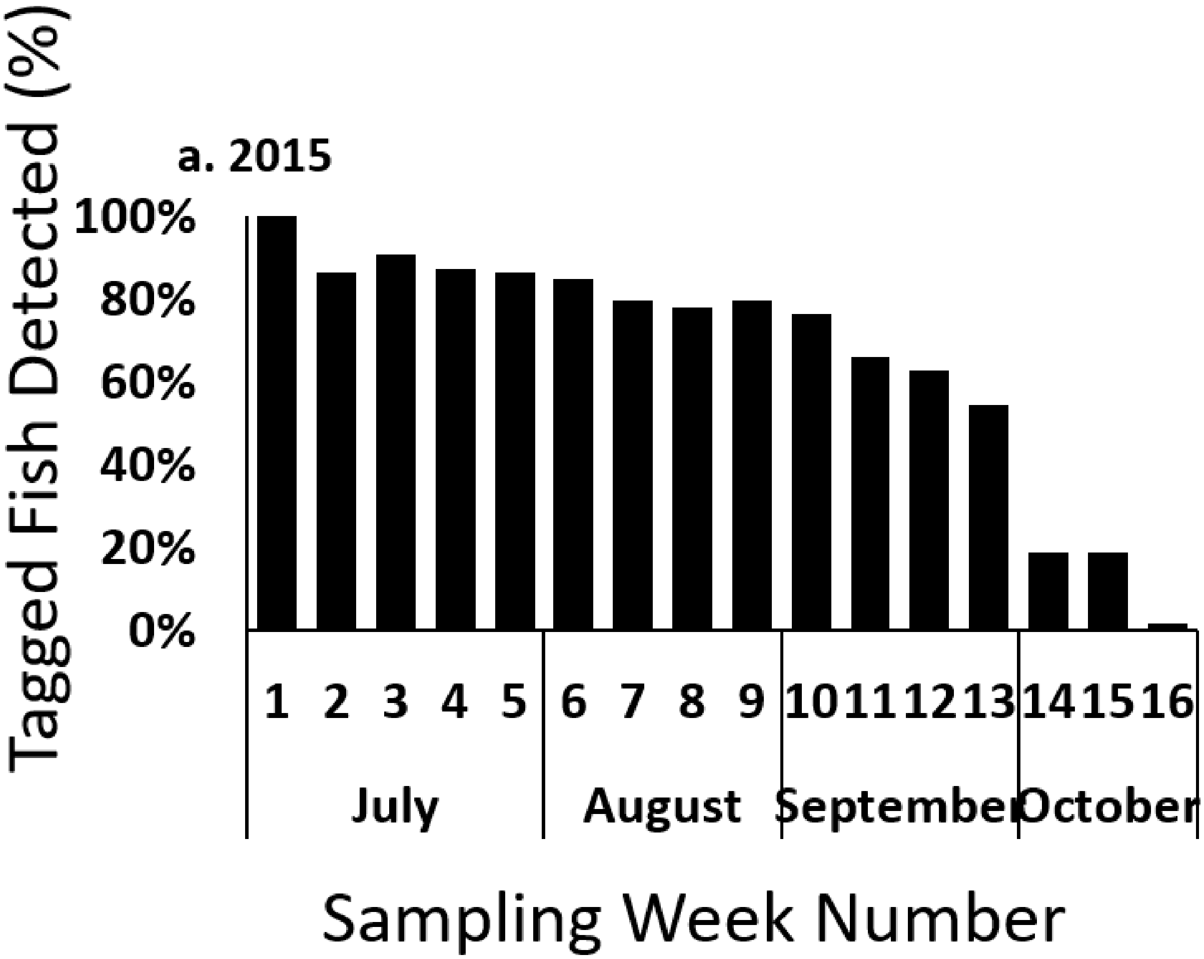


Figure E.2: Bar graph depicting the percentage of tagged fish detected on the y axis over the sampling week number on the x axis.

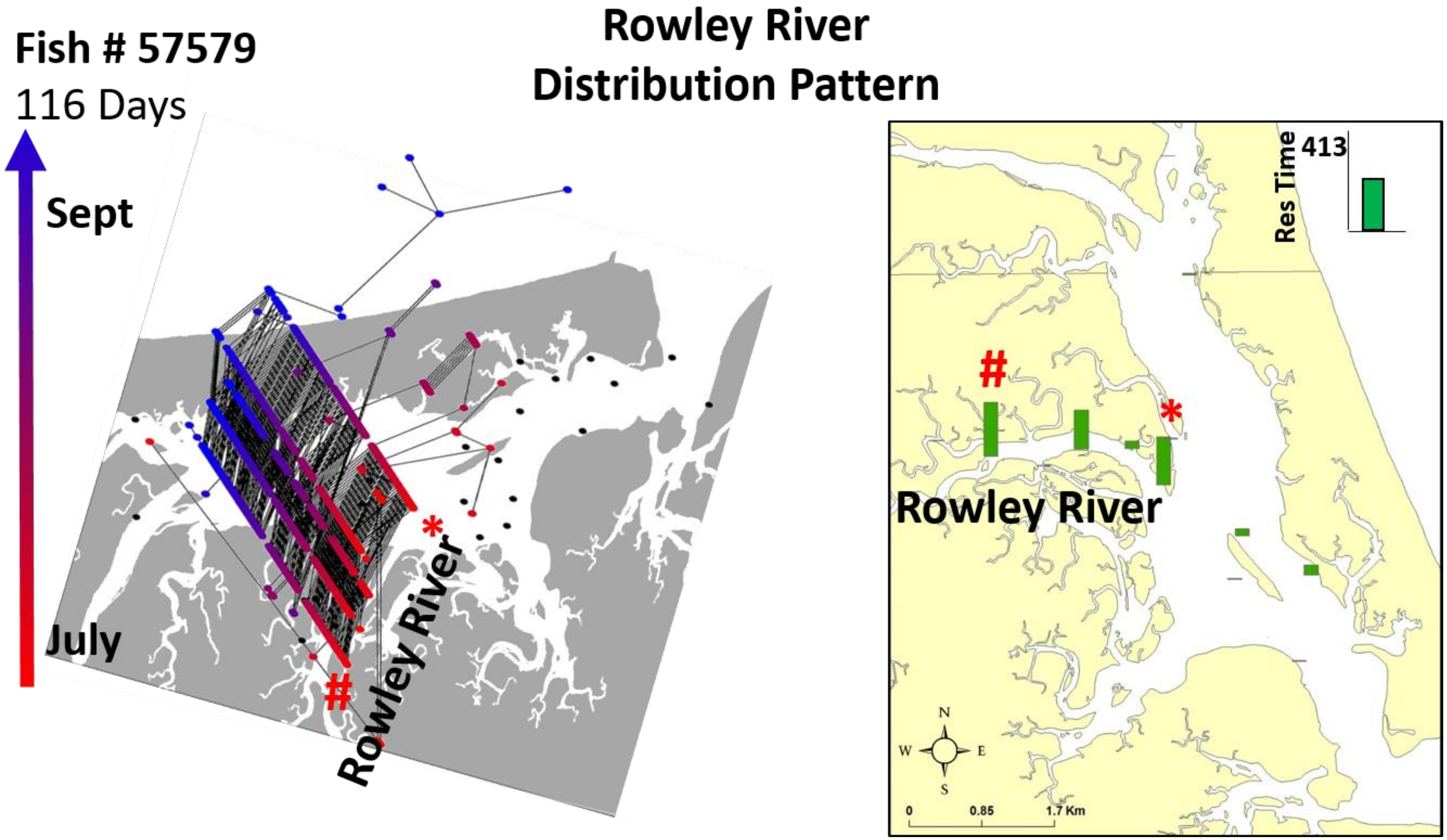


Figure E.3: An example of a fish from the Rowley River distribution group showing a trajectory displaying detections and movements among receivers over the entire study period and a map of the average residence time that this fish spends at each receiver location. The red symbols denote the same locations.

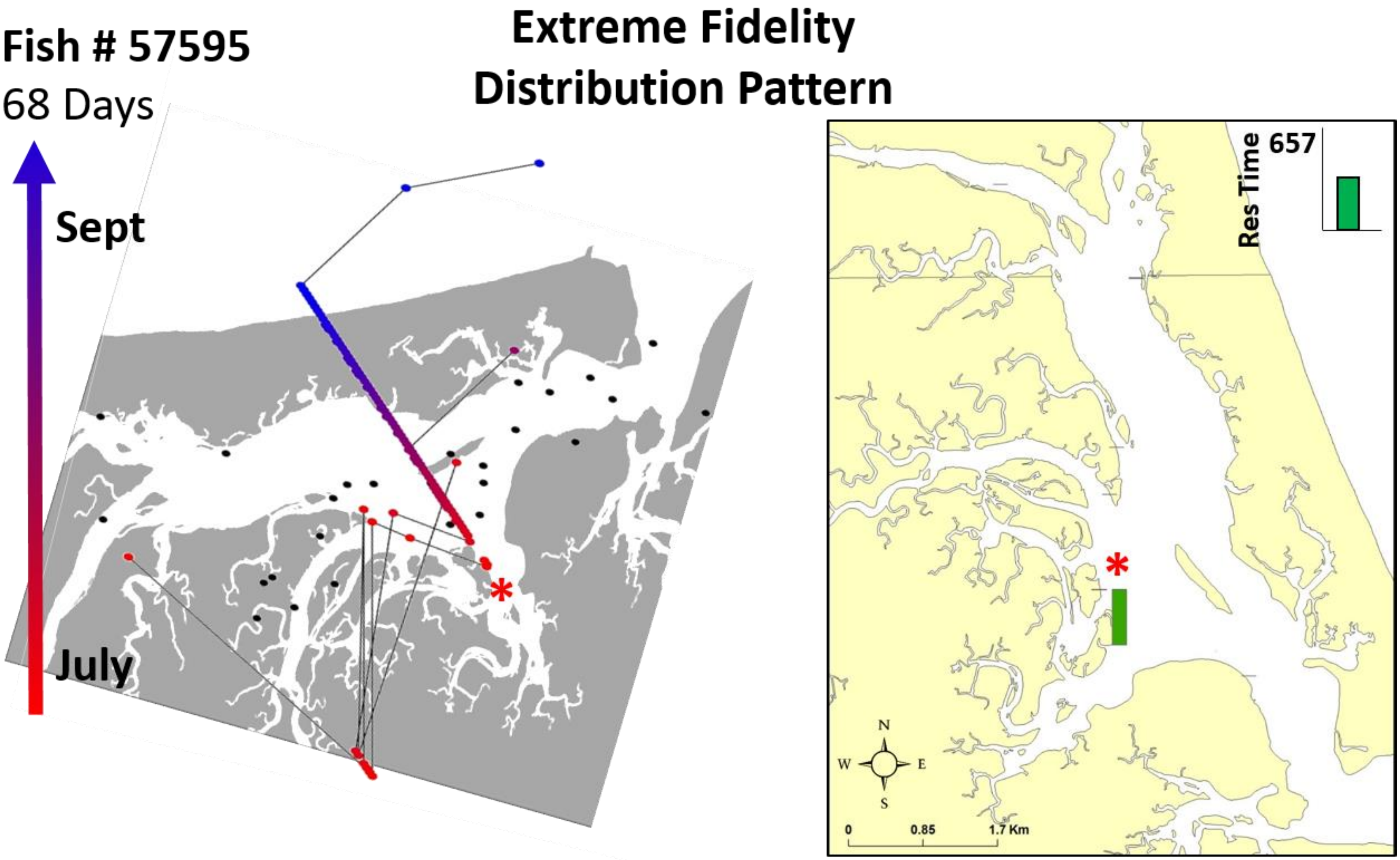


Figure E.4: An example of a fish from the Extreme Fidelity distribution group showing a trajectory displaying detections and movements among receivers over the entire study period and a map of the average residence time that this fish spends at each receiver location. The red symbols denote the same locations.

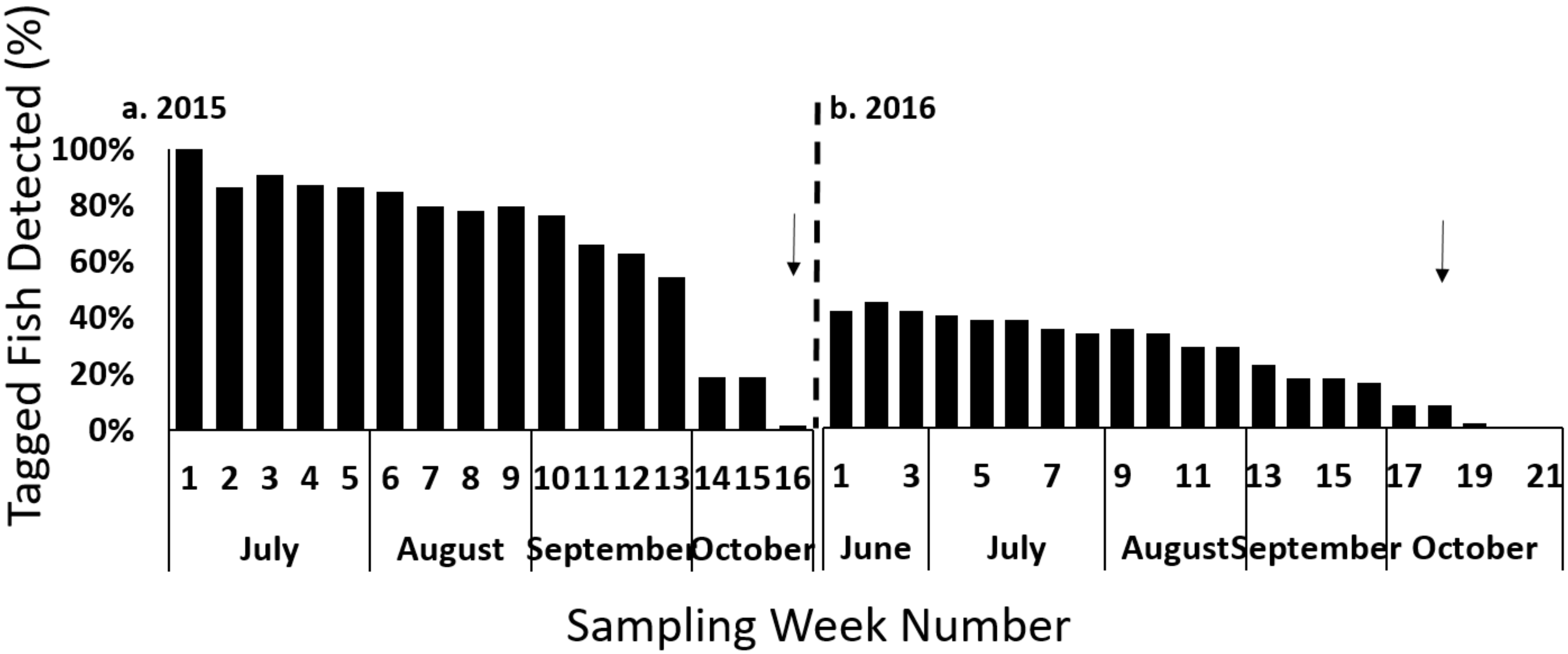


Figure E.5: Bar graph depicting the percentage of tagged fish detected on the y axis over the sampling week number on the x axis for (a) 2015 and (b) 2016. Arrows indicate for each year when fish all left the estuary.

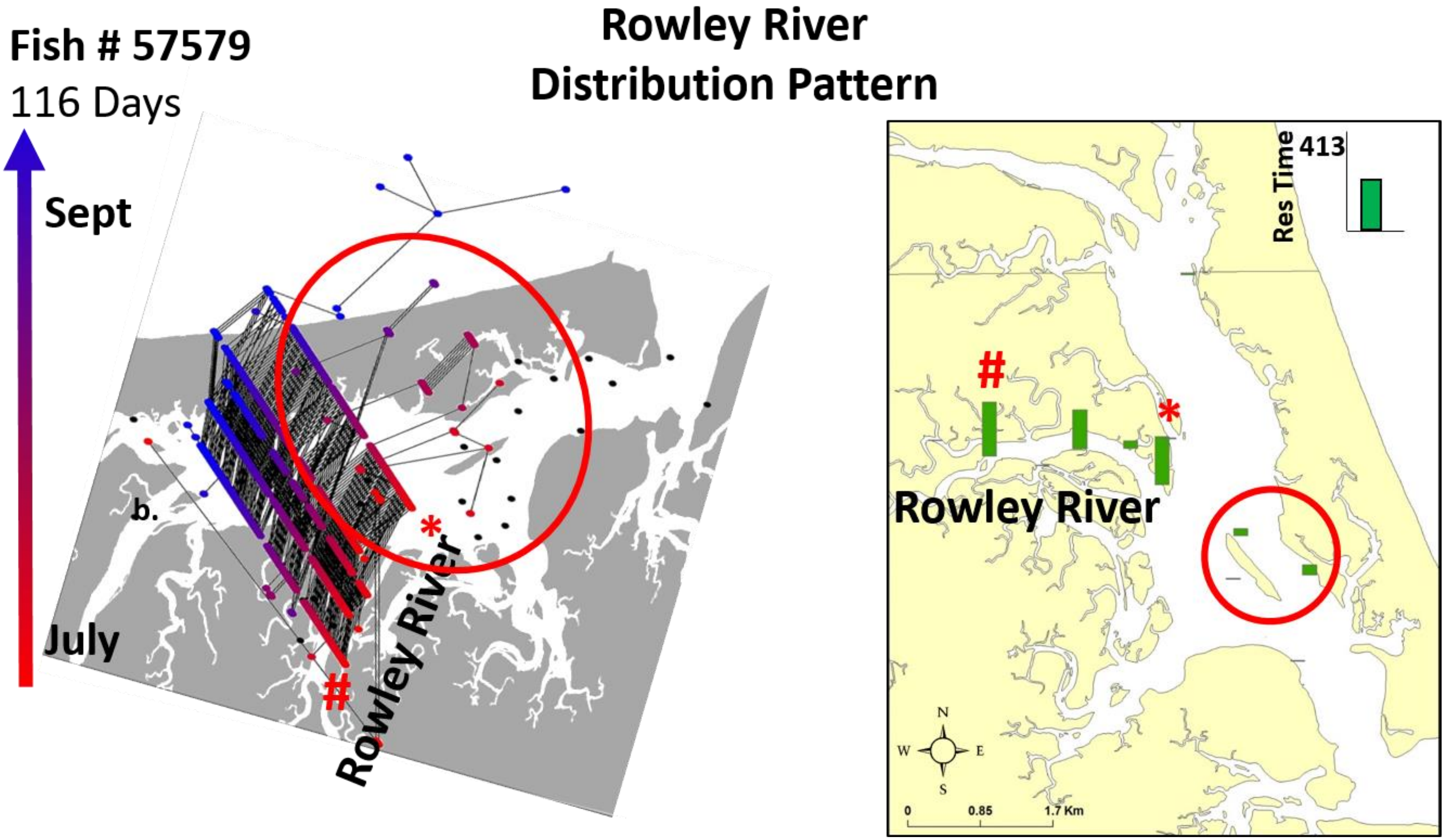


Figure E.6: An example of a fish from the Rowley River distribution group showing a trajectory displaying detections and movements among receivers over the entire study period and a map of the average residence time that this fish spends at each receiver location. The red symbols denote the same locations. Circles denote areas specifically referenced in the text.

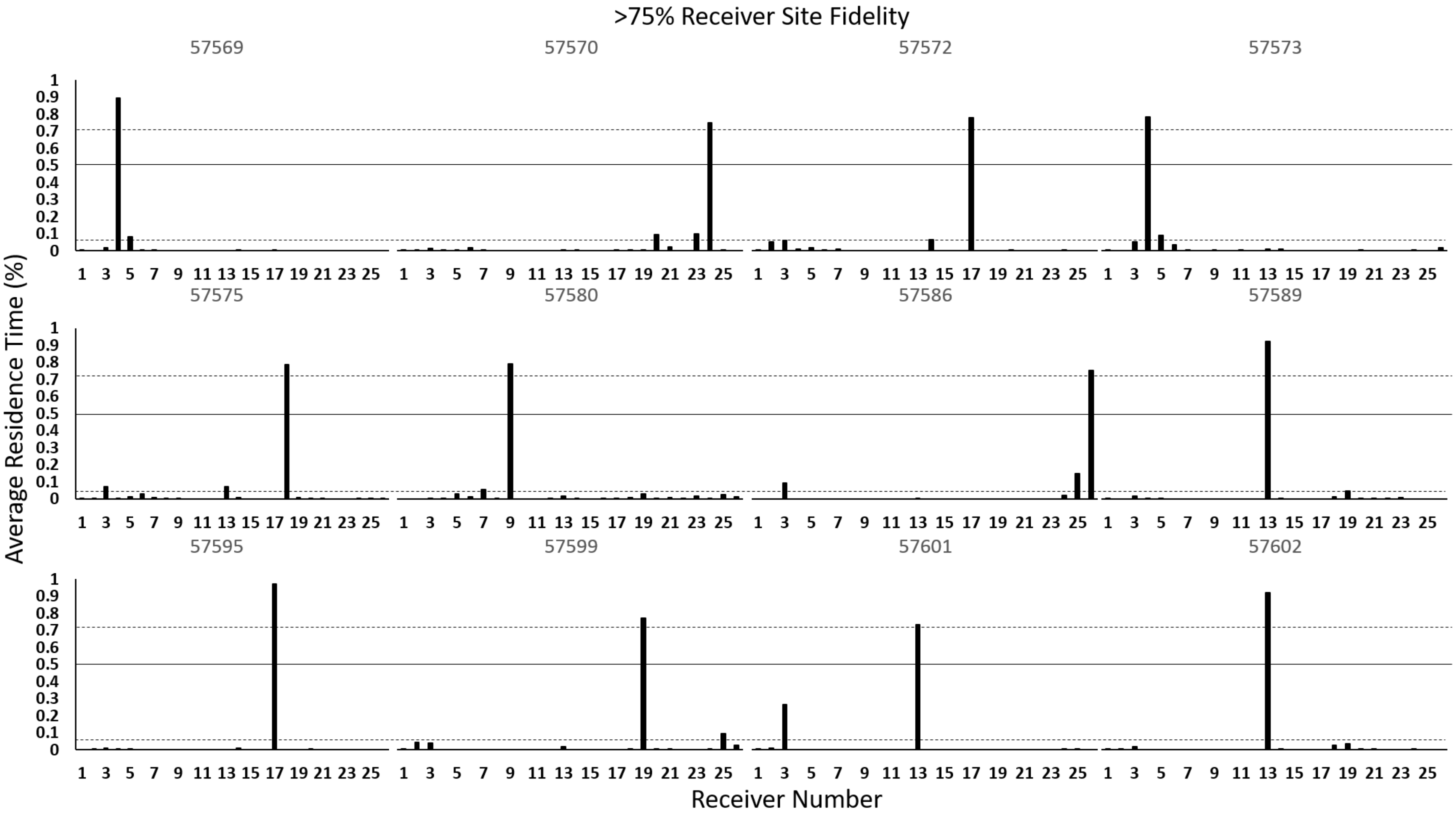


Figure E.7: Bar plots depicting the proportion of time spent at each receiver. Each plot is a different unique individual fish. The dashed lines indicate the three different site fidelity thresholds (75%, 50%, and 4%). These fish all exceed the 75% threshold.

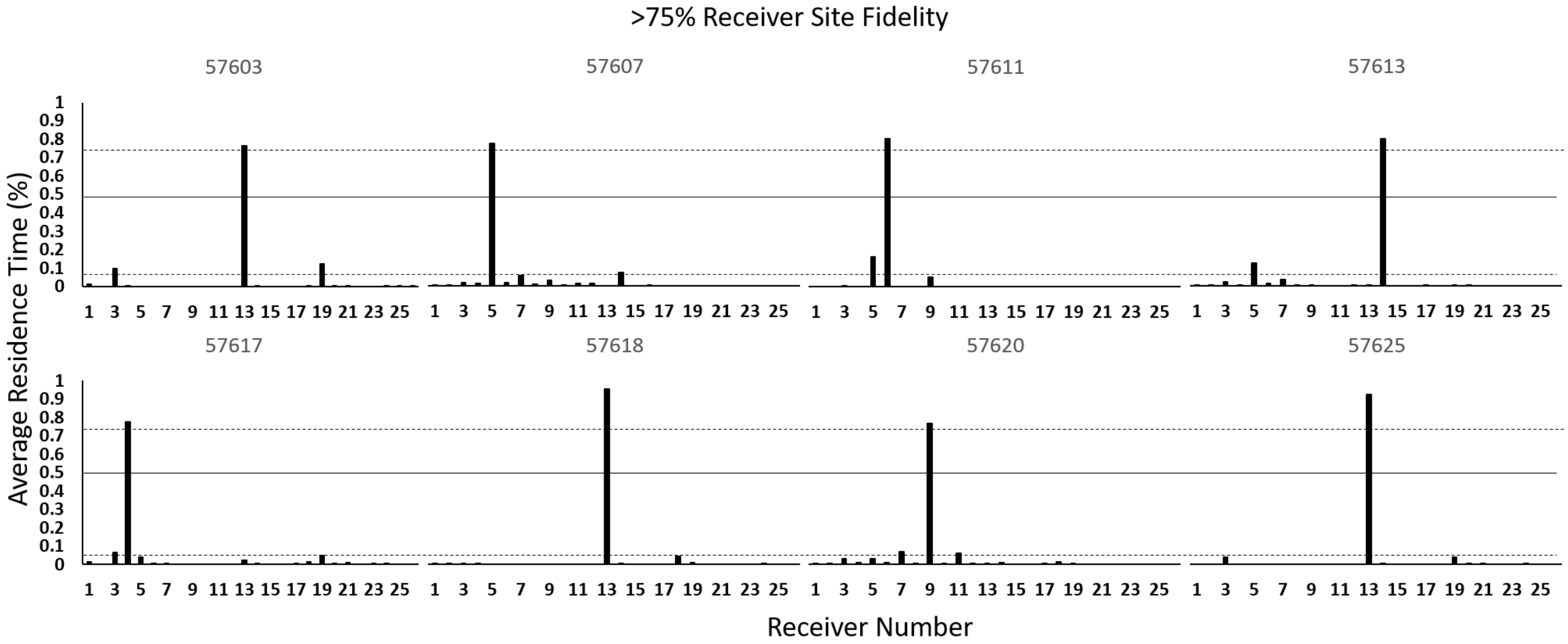


Figure E.8: Bar plots depicting the proportion of time spent at each receiver. Each plot is a different unique individual fish. The dashed lines indicate the three different site fidelity thresholds (75%, 50%, and 4%). These fish all exceed the 75% threshold.

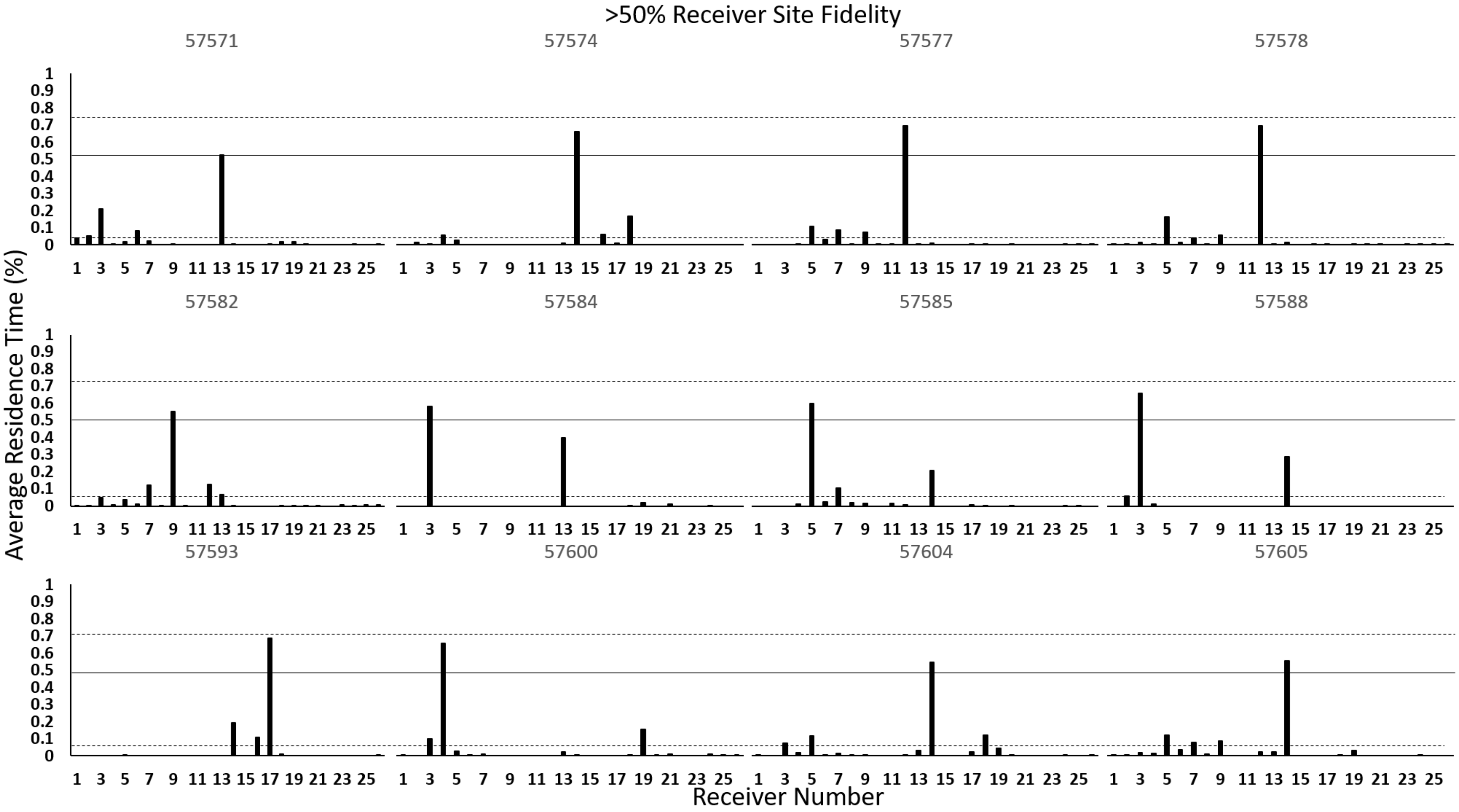


Figure E.9: Bar plots depicting the proportion of time spent at each receiver. Each plot is a different unique individual fish. The dashed lines indicate the three different site fidelity thresholds (75%, 50%, and 4%). These fish all exceed the 50% threshold.

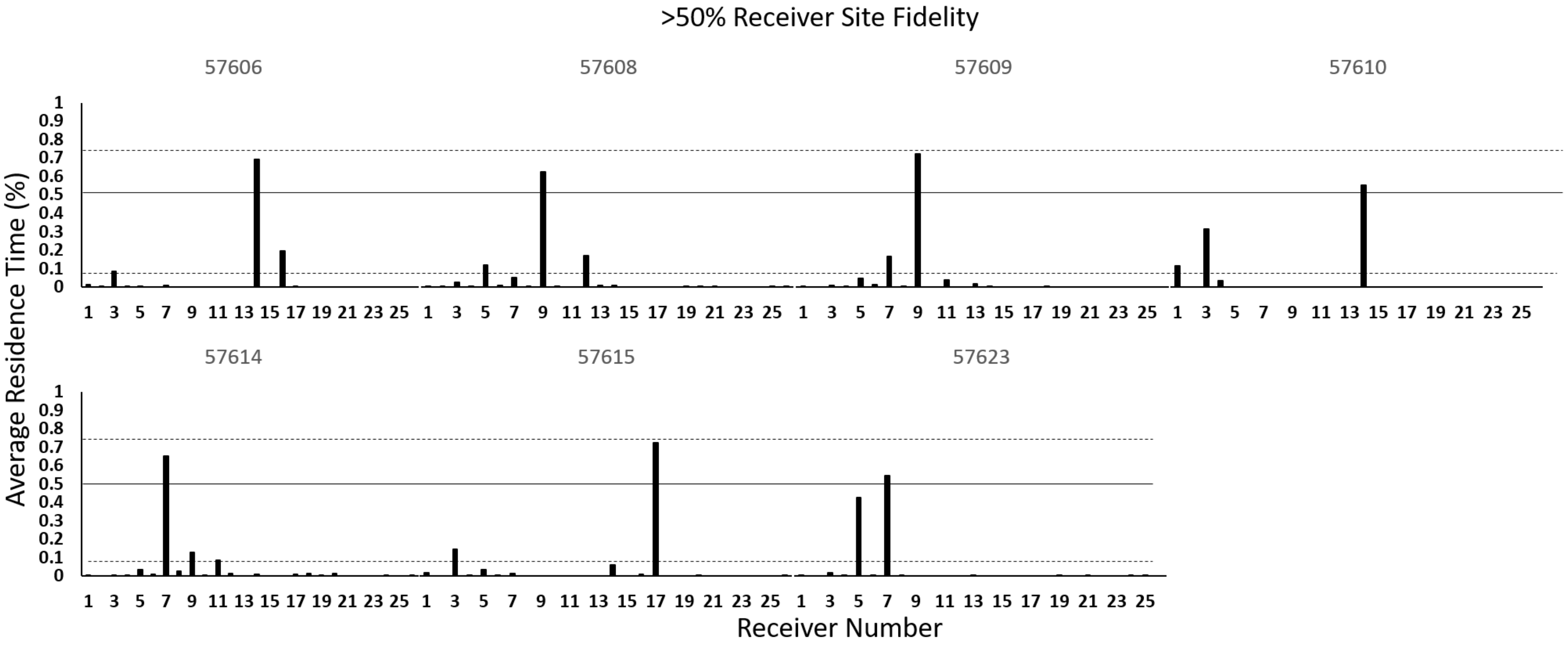


Figure E.10: Bar plots depicting the proportion of time spent at each receiver. Each plot is a different unique individual fish. The dashed lines indicate the three different site fidelity thresholds (75%, 50%, and 4%). These fish all exceed the 50% threshold.

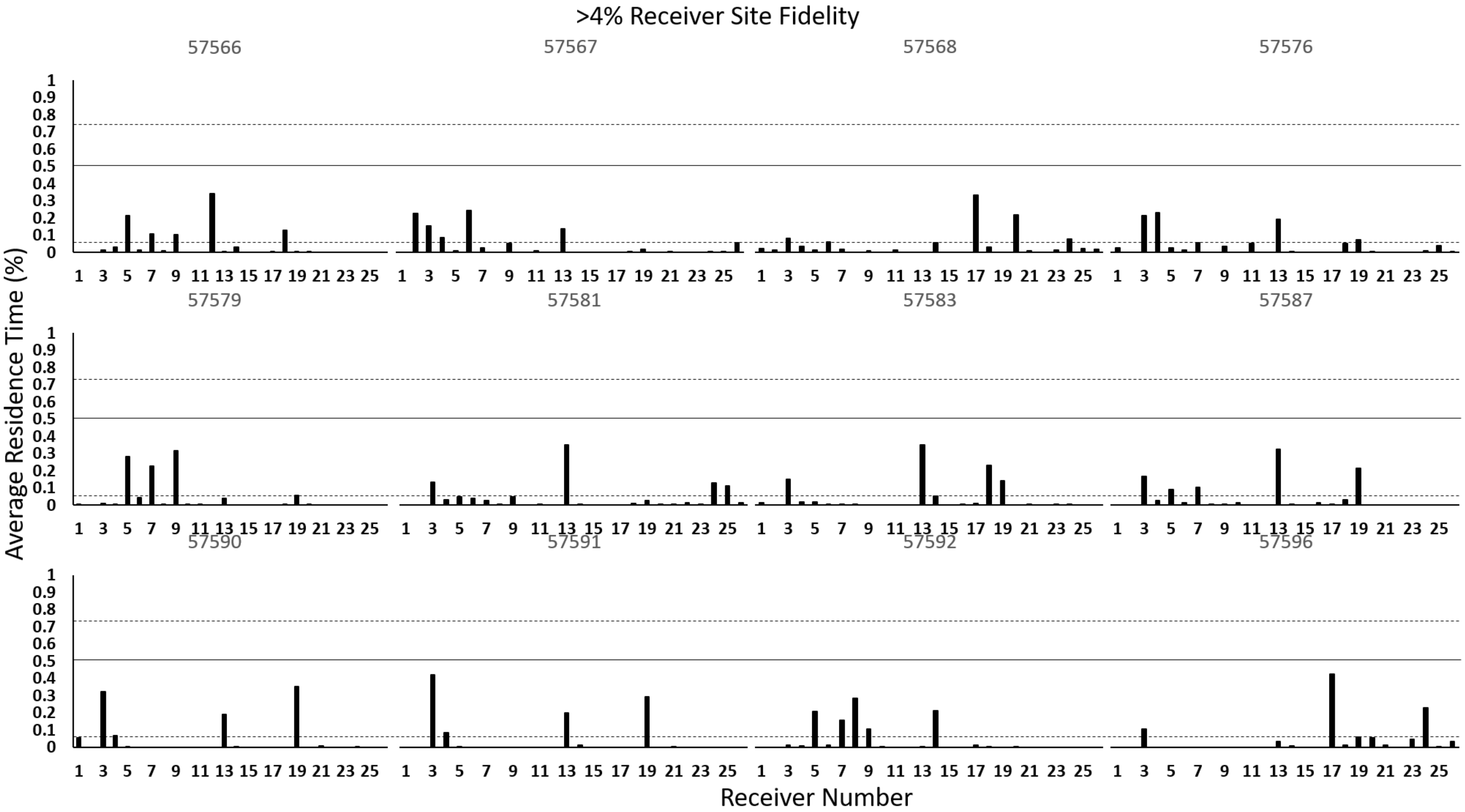


Figure E.11: Bar plots depicting the proportion of time spent at each receiver. Each plot is a different unique individual fish. The dashed lines indicate the three different site fidelity thresholds (75%, 50%, and 4%). These fish all only exceed the 4% threshold.

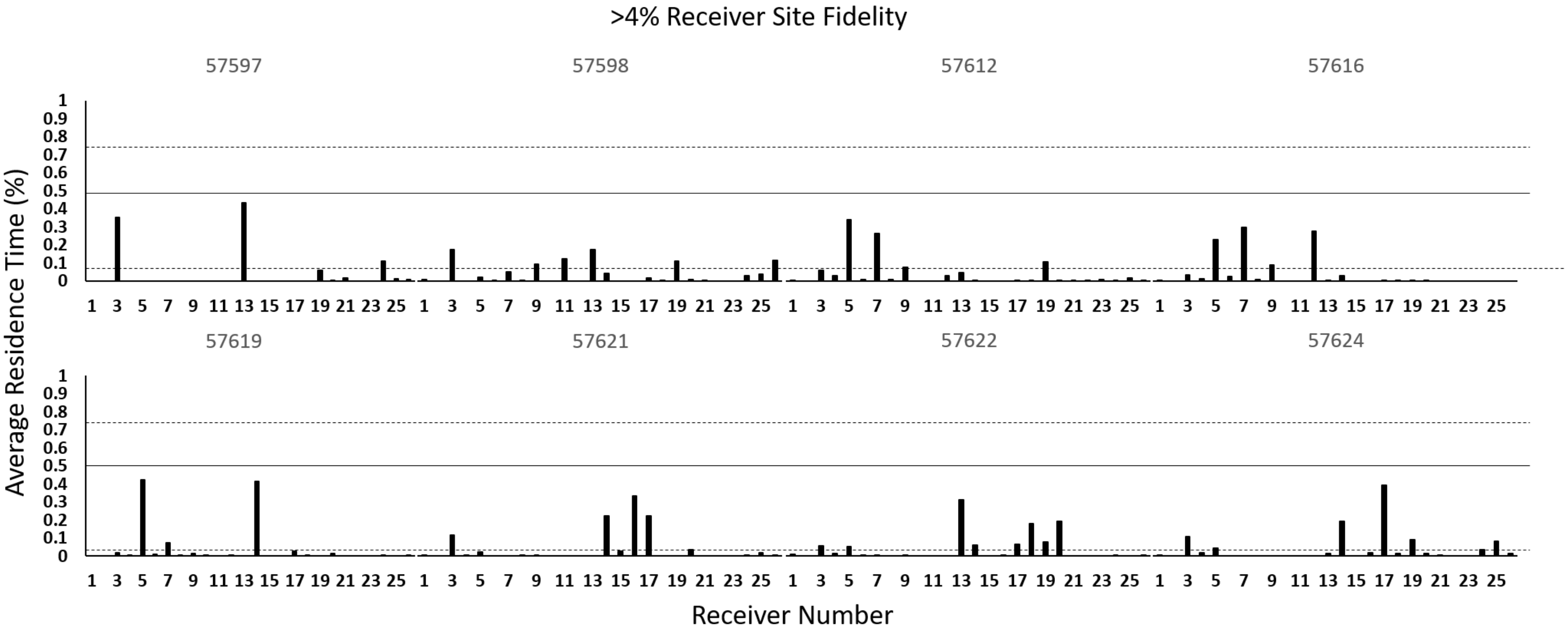


Figure E.12: Bar plots depicting the proportion of time spent at each receiver. Each plot is a different unique individual fish. The dashed lines indicate the three different site fidelity thresholds (75%, 50%, and 4%). These fish all only exceed the 4% threshold.

Appendix F - Prey

Question

What was the prey species composition across the estuary and how did that change over time?

Methods

Prey Collection. Prey samples were collected monthly via quarter-circle bag seine hauls from July-September at fifteen locations throughout the estuary in 2015 and 2016 (Fig. F.1). The seine net used was 15.2 m in length and 1.2 m in height with a mesh size of 4.8 mm and a 1.8 x 1.8 m bag. Two seine hauls were performed going against the direction of the tide. These hauls were combined for analysis. Prey was identified and quantified on location with a subsample of each species brought back to the lab for biomass measurement.

Sampling Locations. Sampling locations were picked based on several factors, but each location also included a stationary receiver. In 2015 there was no stationary receiver at the location called Pavilion Beach, but in 2016 one was placed there. Prey were collected at four different confluences (Rowley River, West Creek, Third Creek, and Grape Island). Prey were also collected at different confluence parts (arms and sweet spots). The arm was defined as a stream draining into the confluence area. The sweet spot was defined as the area within which the arms mix together. Each confluence had two sampled arms and one sampled sweet spot for a total of three sampled locations per confluence (twelve confluence locations total). In addition to the confluence locations, we sampled three non-confluences for comparison. These were sites called Horseshoe, Pavilion Beach, and Middle Ground.

Data Analysis. Pie charts were created to reflect prey composition. The size of each pie chart reflected overall prey abundance at that specific location. Abundance was dominated by three main prey items, *Fundulus heteroclitus* (Mummichog), *Menidia menidia* (Silversides), and *Crangon Septemspinosa* (Sand Shrimp). Although other species were collected, they were not collected in enough abundance for analysis.

Results

2015 Monthly Variation. In July, all sites differed in prey composition by number. *Crangon* dominated the more southern sites. The northern and central sites had more fish prey (Mummichog and Silversides; Fig. F.2a). Biomass increased at all locations in August (Fig. F.2b) when *Crangon* was less common than earlier in the summer. In August, more fish prey species occurred throughout PIE and Silversides were more common than Mummichogs. In September, prey total abundance diminished (Fig. F.2c) and the estuary prey community was again dominated by fish prey (i.e. a balance of Mummichog and Silversides).

2016 Monthly Trends. In 2016, prey was more variable in abundance than in 2015. In July 2016, as in 2015 *Crangon* dominated the South end of the estuary (Fig. F.3a) whereas Mummichogs were most common throughout the rest of the estuary. In August, we didn’t see a major surge in abundance as we did in 2015, but the abundances were overall higher than they were in 2015 (Fig. F.3b). We did not see the *Crangon* domination of the South end of the estuary (as we saw in 2015), but instead it was mostly Mummichogs with some Silverside presence. In September, we saw no decrease in overall prey abundance as we did in 2015, but as in 2015, the two dominant fish species (Mummichog and Silversides) were present in similar proportions (Fig. F.3c).

Yearly Comparison. The two years shared many trends in biodiversity across the estuary. In both years, *Crangon* was most common at sites in the southern end of the estuary in July. Fish prey dominated August and September. A major difference across years was the overall prey abundance. We found significantly more prey species in 2016 than 2015. This may be attributed exclusively to more Mummichog abundance in 2016 as most of the trends in composition in 2016 are based on more Mummichogs than all other species.

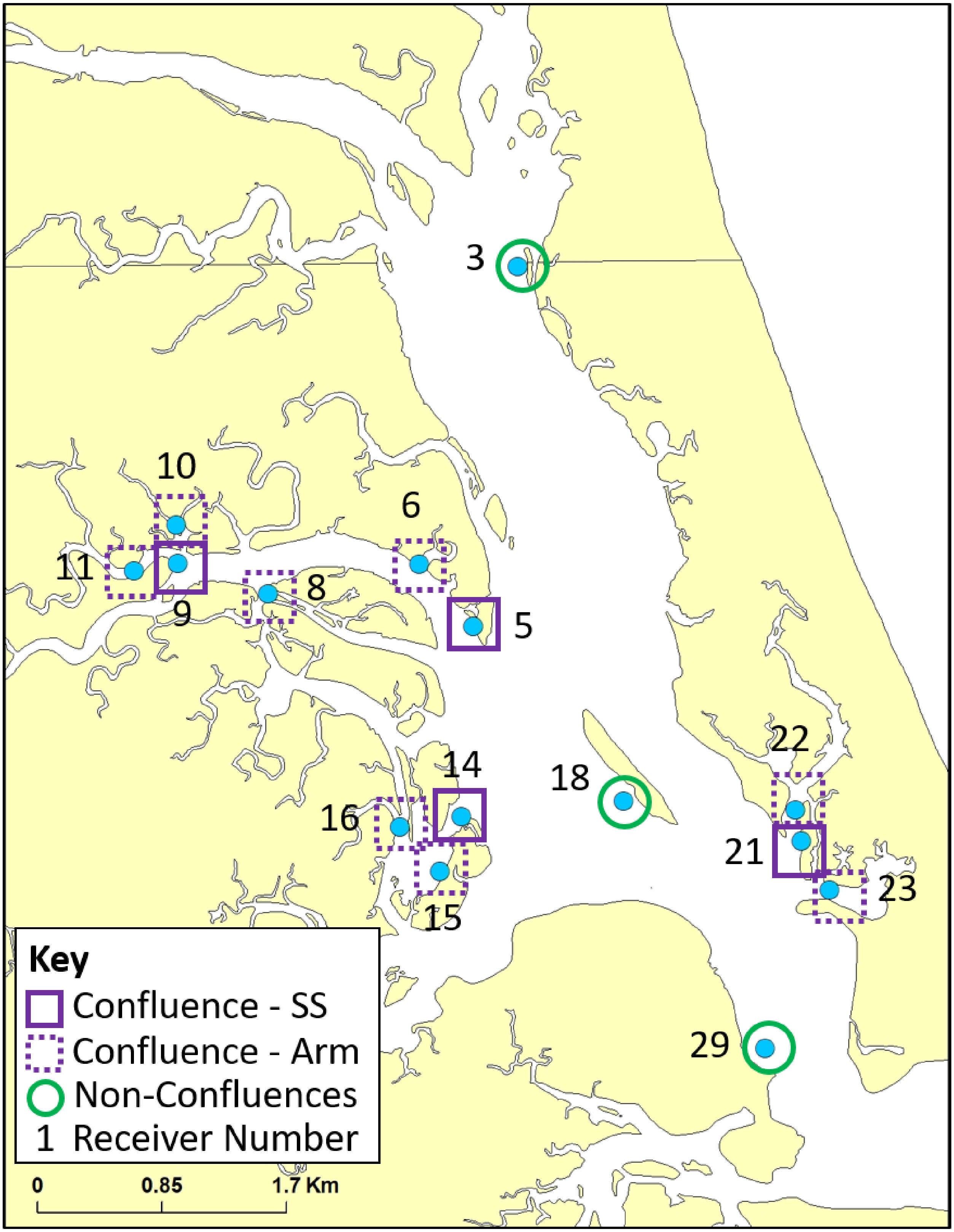

3
10
6
11
9
8
5
14
18
22
16
21
23
15
29
Key
Confluence - SS
Confluence - Arm
Non-Confluences
1 Receiver Number
0
0.85
1.7 Km

Figure F.1: Map showing the prey sampling locations. Shapes indicate geomorphic type and dashed or solid lines indicate confluence part. The numbers are the associated stationary receivers for each location.

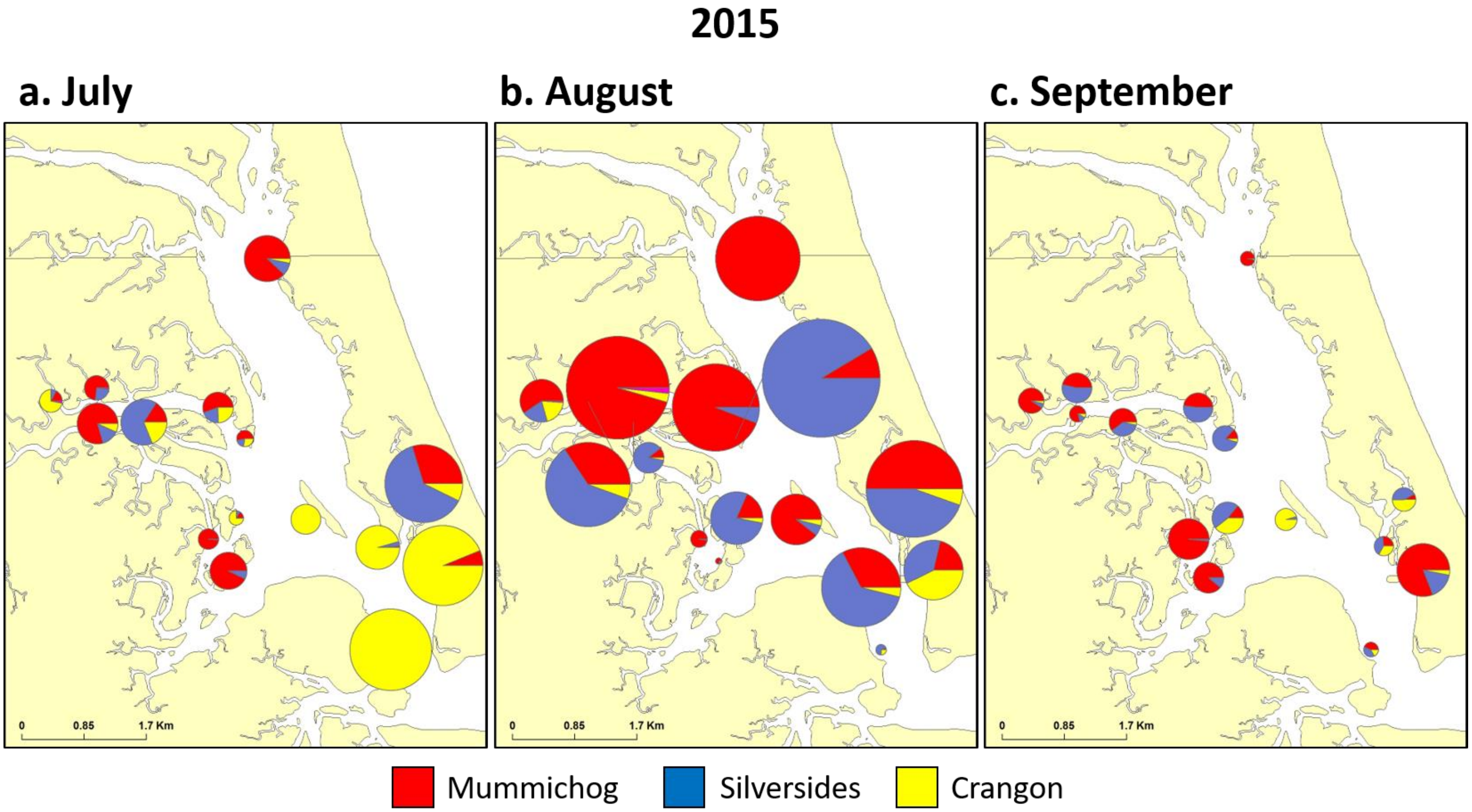


Figure F.2: Pie charts are located at each 2015 prey sampling location with colors indicating prey type and the size of the pie chart indicating overall prey species abundances. Each map shows sampling data from one month (a) July, (b) August, and (c) September.

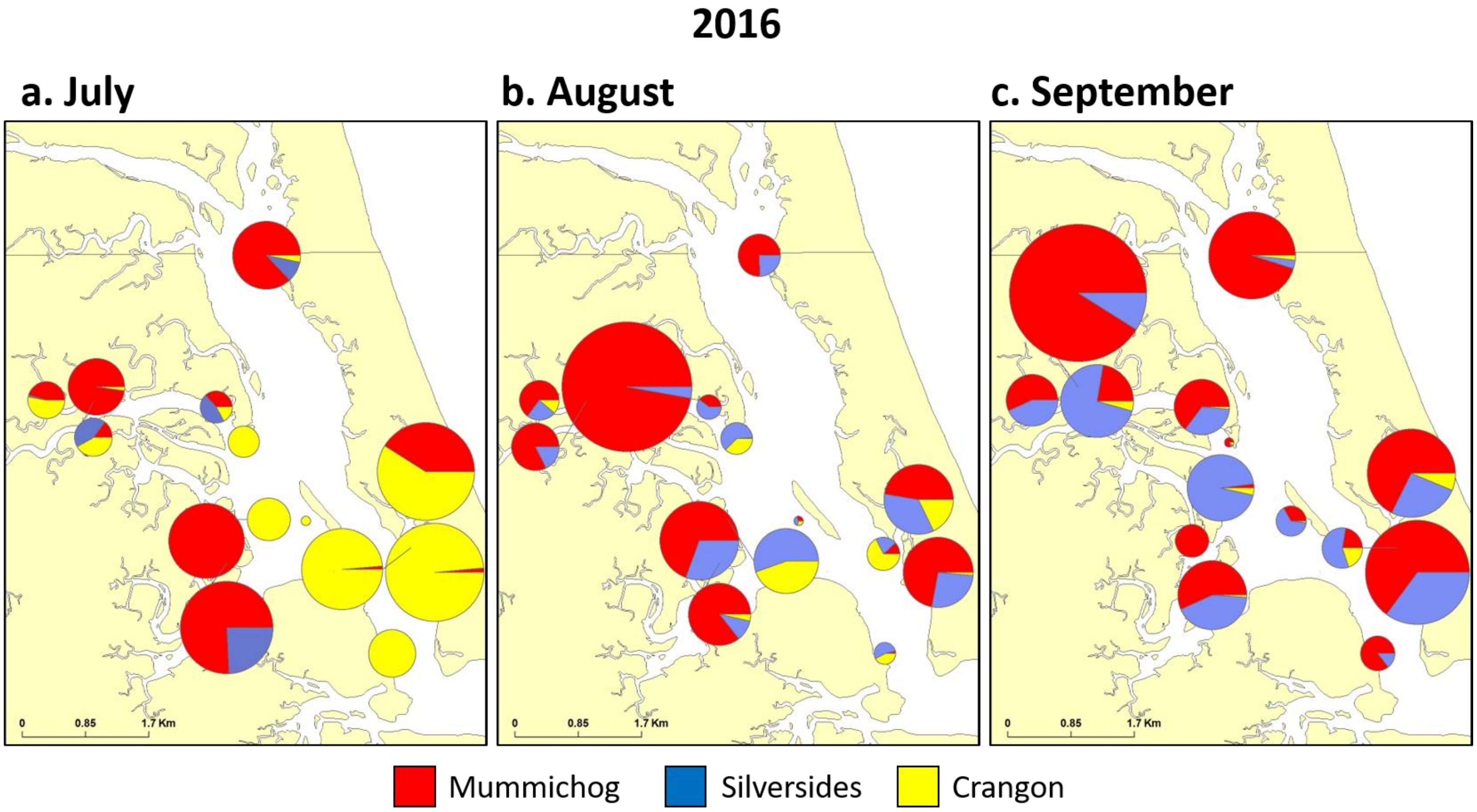


Figure F.3: Pie charts are located at each 2016 prey sampling location with colors indicating prey type and the size of the pie chart indicating overall prey species abundances. Each map shows sampling data from one month (a) July, (b) August, and (c) September.