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No Place Like Home: An Investigation of Homing in Mummichog in a Restored Marsh

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Abstract

Homing, the ability of an organism to return to a specific location when displaced by ecologically significant distances, has been documented for several terrestrial and nektonic species. An ability to navigate the local environment is crucial for avoiding threats and competing for resources and reproductive partners. Homing could be especially important for organisms living in spatially and temporally heterogeneous environments. The homing capability of Mummichogs (*Fundulus heteroclitus*) across varying distances was examined within created marsh systems in Poplar Island, Maryland, during 2019 and 2021 using mark-recapture techniques involving movement of Mummichogs to distant creeks as well as releases into their capture creeks as controls. In July 2019, 25.7% of relocated fish returned to their capture creek (353 m distance) within 24 h, and 5.7% were recaptured at their collection site 3 months later. Similar results were found in 2021 when specimens were moved further from their original location. After roughly one week, 26.3% of tagged individuals were recaptured in their original location, 522 m from where they were released. These findings not only confirm previous studies showing site fidelity of Mummichogs but also indicate their ability to home over distances of at least 500 m. This study adds considerably to the growing body of literature examining population movement dynamics and habitat utilization and could have implications for restoration practices in estuaries and stock management in fisheries.

Keywords: homing; Fundulus; Mummichog; tagging study; site fidelity; restored marsh

Key Contribution: Site homing was investigated for a resident estuarine fish, *Fundulus heteroclitus*, in a restored marsh. Homing was found in distances of at least 500 m.

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1. Introduction

Understanding movement patterns of target nekton, including site fidelity, is crucial to understanding habitat connectivity. Several key concepts describe different aspects of local habitat utilization: home range, site fidelity, and homing. Gerking suggested that an animal's home range is "an area in which the animal normally travels" [1]. By Gerking's definition, home range refers to an area the animal forages in, but it can also include where its nest or burrow, spawning, or refuge sites are located. Site fidelity is staying in a spatially defined location, mathematically defined by Munger to exist if the observed area an animal utilizes is smaller than that of an area utilized if the movement was random [2]. Homing

behavior has been broadly defined as an "animal's ability to return to a spatially restricted location it previously occupied following displacement to an unfamiliar location" [1,3,4].

Initial work related to homing for fish was conducted with salmon and eels [5–8]. However, homing has been demonstrated in a variety of nektonic species, from rock pool specialists [9,10] and intertidal fishes [4,11,12] to coral reef fishes [13,14] and riverine fishes [15,16]. These studies indicate homing specificity among species may vary widely, ranging from only a few meters to two kilometers. One of the more abundant nekton species in marshes along the Atlantic and Gulf of Mexico coasts, grass shrimp (*Palaemonetes* spp.), exhibits high site fidelity but does not exhibit homing [17]. Garwood et al. showed that five of the dominant transient fish species in the United States (US) southeast Atlantic coastal salt marshes, pinfish (*Lagodon rhomboides)*, spot (*Leiostomus xanthurus*), silver perch (*Bairdiella chrysoura*), and the striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*), all exhibit high site fidelity during their seasonal residence in the estuary; but homing ability was not investigated [18]. Homing may be an effective strategy for a variety of ecosystem types and be particularly beneficial in spatially and temporally heterogeneous environments with local predictability.

The Mummichog (*Fundulus heteroclitus*) is a dominant coastal salt marsh resident ranging from northeastern US Florida to the southern Newfoundland coast of Canada [19]. *Fundulus heteroclitus* can be found in salty, brackish, and freshwater areas, and is adapted to survive wide ranges of temperature, salinity, oxygen, and even pollution levels [20–23]. Spawning takes place from midspring to late summer during spring tides to ensure egg deposition in refuge high marsh regions [24]. Deposited eggs incubate primarily in the air but require tidal immersion to hatch and can be delayed for weeks until the right environmental conditions are met [25]. *Fundulus heteroclitus* larvae are typically restricted to intertidal marsh pools and interior marsh surface as refuge [24,26,27].

Juvenile and adult *F. heteroclitus* utilize the marsh interior with the flood tide to feed on a variety of benthic and epibenthic invertebrates [28,29], followed by a retreat with the ebbing tide into shallow sublittoral habitats [30–32]. *Fundulus heteroclitus* tend to concentrate in the upper reaches of creeks [33]. Halpin also found that capture rates decline with increasing water depth, which is supported by findings that *F. heteroclitus* are typically restricted to depths <70 cm [33–35]. *Fundulus heteroclitus* experience increased growth rates when given access to the intertidal marsh surface compared to individuals denied access, suggesting occurrence in shallow water may be due to a combination of predation, refuge, and food source habitat [36].

Numerous studies have attempted to determine a seasonal home range for *F. heteroclitus*. Lotrich found a restricted home range of 36 m linear distance within a tidal creek in Delaware, US [37]. Teo and Able estimated the home range of *F. heteroclitus* to be up to 15 hectares within a restored salt marsh [38]. Sweeny et al. found a home range of ~650 linear meters in Plum Island Estuary (Massachusetts, US), while Butner and Brattstrom off Lido Beach in Long Island, New York (US), found little evidence to indicate existence of a home range [28,39]. *Fundulus heteroclitus*' home range may depend on the complexity of the environment, for example, an area's dendriticity, whether the system is open or closed, how much flooded marsh is accessible to *F. heteroclitus*, or even the size of the individual *F. heteroclitus*.

Fundulus heteroclitus display high site fidelity during spring and summer [38,40,41]. They forage and spawn throughout their home range in spring and summer, but *F. heteroclitus* show a strong seasonal tendency to return to a spatially restricted location. In fall, *F. heteroclitus* exhibit seasonal migratory patterns and travel up to 2000 m [42]. In temperate environments, *during winter, F. heteroclitus* burrow into sediment and reside in permanent upstream pools where sediment temperatures remain slightly warmer and sediment has higher organic content [37,43–45]. Autumnal cold temperature pulses are suspected to act as a signal for the dispersion of *F. heteroclitus*, aided by a decrease in abundance in predators in late autumn and winter [46,47].

Fundulus heteroclitus has been the focus of many laboratory experiments largely because it is abundant, physically tolerant of handling stress as an adult and as an egg, and easy to obtain. Atz expressed surprise at the number of laboratory studies on *F. heteroclitus* when its field biology is "practically unknown except as a bait fish" [48]. Likewise, Kneib notes that surprisingly little information exists on the role and impact of *F. heteroclitus* in its natural habitat [26]. New information increasingly points to *F. heteroclitus* having a dominant influence in coastal ecosystems along the North American east coast. The word 'mummichog' is a Native American word meaning "going in crowds" which relates to their abundance [49], and they have among the highest productivity values reported for fish [50,51]. They are a key species within the marsh community and a vital link for energy transfer between the marsh matrix and adjacent coastal waters. There is an anthropogenic importance connected with *F. heteroclitus* as well, since they can be used as a bioindicator and monitoring species due to its tolerance to a range of conditions [52,53].

In this study of site fidelity and homing behavior, *F. heteroclitus* was chosen because it is a key, often dominant, resident tidal marsh species; it is abundant along the US Atlantic coast, including the restored marshes of Poplar Island (Figure 1), and its population dynamics can significantly influence coastal marsh ecosystems. However, significant gaps remain in our understanding of their movements, population dynamics, and how these relate to the overall function of US Atlantic coast estuaries. Population movement dynamics are critical to our understanding of ecosystem function, including trophic transfer, genetic shifts, and population connectivity. A fuller understanding of site fidelity and homing will improve our understanding of population dynamics, restoration practices, and ecosystem management. The hypothesis for this study was to examine whether the marsh resident *Fundulus heteroclitus* exhibits site-specific homing behavior.

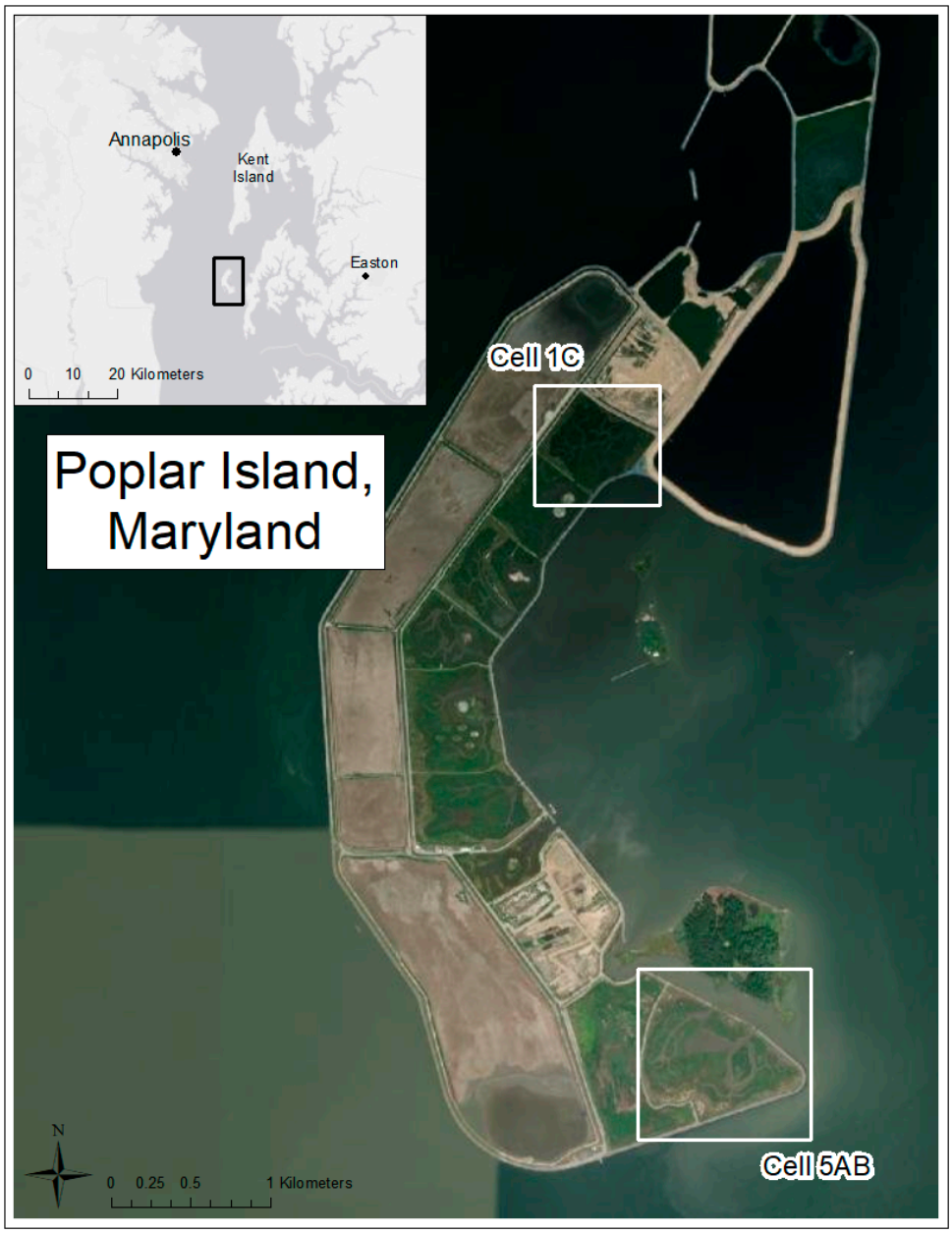


Figure 1. Poplar Island, Maryland, 38°46′01″ N 76°22′54″ W, with boxes around the two study sites: Cell 1C on the north side of the island and Cell 5AB on the south side of the island. The brown area on the west side of the island is the unfinished upper marsh. New additions are being added to the island's north side.

2. Materials and Methods

2.1. Study Site

Poplar Island, Maryland, US (Chesapeake Bay) (Figure 1), is a large-scale island restoration project composed of clean dredged material placed to re-establish Poplar Island to its 1847 footprint [54]. As of 1996, the island had eroded to less than four acres due to hydrodynamic influences, as have numerous islands in Chesapeake Bay [55]. When completed, Poplar Island will be 1715 acres in size and include 776 wetland acres, 829 upland acres, and 110 acres of open-water embayment habitat. The restored wetlands of Poplar Island are subdivided into "cells" and then "subcells" containing restored low and high marsh, marsh channels, and ponds, all with inlet access to the Chesapeake Bay (Figure 1). Dikes separate each cell and subcell, with cells connected by channels between subcells.

The upland cells of Poplar Island are predominantly positioned on the western side of the island facing the heaviest wave action, while the wetland cells align on the eastern portion of the restoration, creating a sheltered harbor area.

Two subcell salt marsh systems in separate wetland cells were used in this study: subcells 1C (contained within Cell 1) (Figure 2) and 5AB (contained within Cell 5) (Figure 3). Initial work was conducted in subcell 1C (planted in 2011, 16.18 hectares in size) during 2019, and the study expanded during 2021 to include subcell 5AB (planted in 2018, 33.59 hectares in size). Each subcell has defined constructed channels and low and high salt marsh subhabitats. Environmental parameters across subcells were homogenous [54]. Monotypic plantings of low marsh, smooth cordgrass (*Sporobolus alterniflorus*) and high marsh, salt hay (*Spartina patens*) were established across the restored cells, and the sediment for each wetland restored cell was homogenous across the cell and comprised of silt-clay.

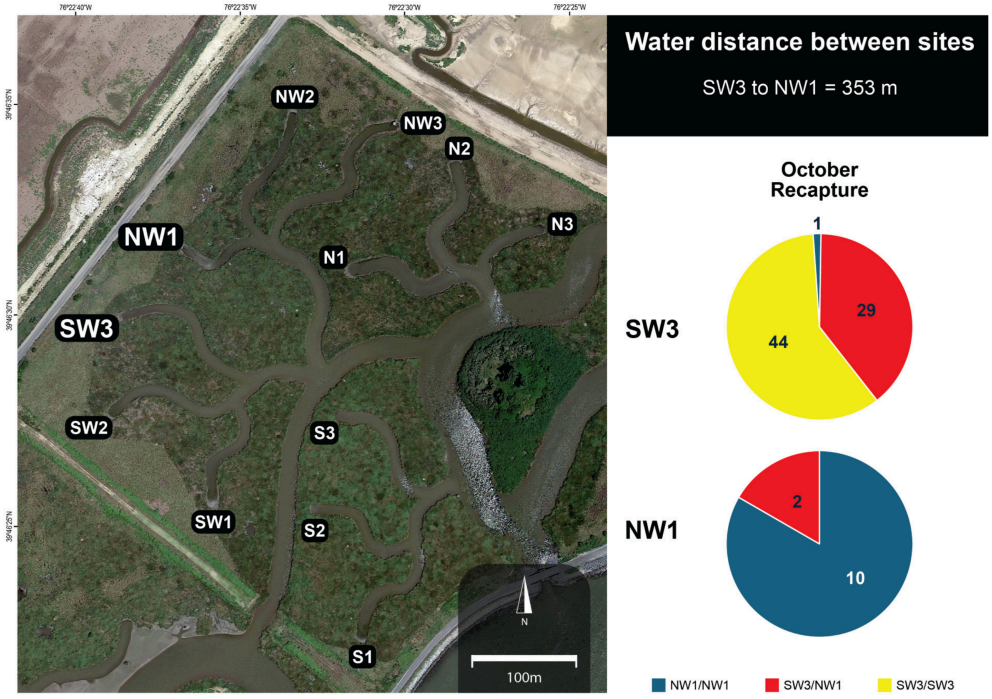


Figure 2. Cell 1C with all nine sites labeled (Table 2 for intermediate site recaptures). SW3 and NW1 were the two tagging sites. The first graph (SW3) displays 44 SW3/SW3 (yellow, 8.7%), 29 SW3/NW1 (red, 5.7%), and 1 NW1/NW1 (blue, 0.2%). The second graph (NW1) displays 10 NW1/NW1 (blue, 2.0%), and 2 SW3/SW3 (red, 0.4%).

Subcell 1C, located on the northern portion of Poplar Island, was used in the initial tagging effort. An inlet with two 1.8-m × 1.8-m culverts connects subcell 1C to Poplar Harbor on the eastern side of Poplar Island. The inlet opens internally into a channel that encircles an island and is connected to two main creeks, each subdividing into three subcreeks, which further subdivide, providing water access to the interior marsh habitat (Figure 2). We selected two sites for the initial tagging effort: one in the northern creek (NW1) and one in the southern creek (SW3) (Figure 2). Along with the tagging sites in subcell 1C, 10 nontagging recaptures sites were sampled to observe dispersion of fish (SW2, SW1, S1, S2, S3, NW2, NW3, N1, N2, and N3).

Because of disturbance in cell 1C, we used subcell 5AB, located on the southern end of the island, in the subsequent tagging effort during 2021 to further confirm and delineate *F. heteroclitus* site fidelity and movement. Subcell 5AB includes two joined subcell areas (5A and 5B) with a more variable landscape than subcell 1C. The eastern side of subcell 5AB

contains an island surrounded by a wide channel moat, while the western side contains a lagoon. Two 6.2 m-wide inlets (no culvert), one on the eastern and one on the western portion of the north subcell 5AB dike adjacent to Coach's Island, create access to an external channel and into Chesapeake Bay. The western side (containing the lagoon) was the portion of subcell 5AB in which the 2021 tagging study occurred. The inlet channel for the western portion of subcell 5AB splits into two subchannels, one into the lagoon and the other into marsh habitats (Figure 3). Two tagging sites were established on subcreeks located on the western portion of the marsh subchannel on northern (Site A) and southern (Site B) subcreeks, while a third tagging site (Site C) was located on a northern portion of a subcreek that accessed the eastern portion of the marsh subchannel near the lagoon (Figure 3). Along with the tagging sites in subcell 5AB, five nontagging recapture sites were sampled (Inlet, Dead End, SW, SS, and A/B confluence). The subchannel separating sites A and B from site C was >1.5 m deep at mean low tide, deeper than the usual occurrence of *F. heteroclitus* [32,35].

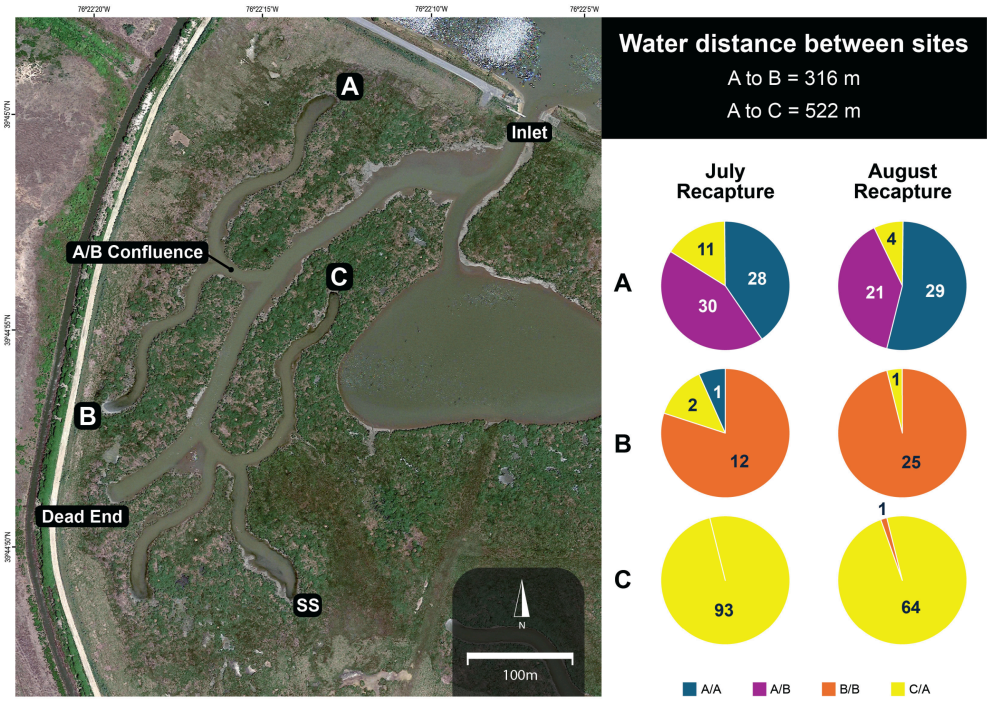


Figure 3. Cell 5AB with all 8 sites (Table 3 for intermediate site recaptures). Sites A, B, and C were the three tagging sites. The first graph (Site A July) displays 28 A/A (blue 9.3%), 30 A/B (pink 10.0%), and 11 C/A (yellow 3.1%). The second graph (Site A August) displays 29 A/A (blue 9.6%), 21 A/B (pink 7.0%), and 4 C/A (yellow 1.1%). The third graph (Site B July) displays 12 B/B (orange 3.9%), 1 A/A (blue 0.3%), and 2 C/A (yellow 0.5%). The fourth graph (Site B August) displays 25 B/B (orange 8.2%) and 1 C/A (yellow 0.3%). The fifth graph (Site C July) displays 93 C/A (yellow 26.3%). The sixth graph (Site C August) displays 64 C/A (yellow 18.1%) and 1 A/B (pink 0.3%).

2.2. Field Methods

2.2.1. Tagging

Tagging was conducted using Visible Implant Elastomer (VIE) tags purchased from Northwest Marine Technology in Anacortes WA, USA. VIE is a well-tested animal tagging method in laboratory and field studies [56–59]. The method involves inserting a small amount of colored elastomer either manually or via an air-driven injection system and is known to have a low tagging mortality and is visible for over 6 months [60–64]. Tagging handling time was ~10 s for the injection.

2.2.2. Collection

During July 2019 and 2021, *F. heteroclitus* were collected on site using minnow traps (40 cm length, 17 cm diameter with a 3 cm opening and a 1 cm mesh size; bait with 65 g of dog food held within 1 mm mesh nylon bags) and kept in aerated buckets as remaining traps were collected, then transferred into chilled aerated coolers in preparation for tagging. *Fundulus heteroclitus* were then transferred as necessary to small holding containers to be tagged. We tagged fish on the left side near the dorsal fin. The *F. heteroclitus* were then placed in a chilled holding container to ensure tag retention and to verify fish did not show signs of stress. Successfully tagged fish were measured to the nearest millimeter (mm) for standard length (SL) and gender determined (during 2021 only). Total handling time for tagging and measurement was ~30 s, and mortality related to the tagging effort was rare (<0.36% (10 individuals) over all tagging efforts). All fish captured were tagged, with the largest tagged individual being 82 mm and the smallest 12 mm. Once ~300 fish had been tagged, they were transported to their designated release locations.

The 2019 recapture involved two recapture efforts; one occurred 24 h after initial release during July, and the second during October 2019. During 2019, recapture efforts within each collection site used four minnow traps, one set at the head of the creek and three down the sides of the creek bank spaced about 10 m apart, which were fished for ~20 h, set during a late afternoon high tide and collected during low tide the next day. During the 2021 recapture efforts, four separate field collections occurred: during July (24 h and one week after release), August (one month after release), and September (two months after release). During 2021, eight minnow traps were placed at each collection site with one set at the head of the creek and the remaining seven set ~5 m apart along alternating side banks of the creek (total linear length of the area fished was ~35 m). Minnow traps were fished for ~1.5–3 h during the low tide cycle [35]. During 2019 and 2021, minnow trap set and retrieval water depths and soak times were recorded. Site environmental data (salinity, temperature, dissolved oxygen, Secchi depth) were recorded during trap sets. The samples were processed by hand on site. Fish SL was measured to the nearest mm, and tagged individuals were held in a holding bucket until completion of site collection events to avoid repeated recapture of any tagged individuals. A random subset of ~20 non-tagged *F. heteroclitus* was also measured. All non-tagged individuals were immediately released back to the collection site.

2.3. Statistics

Statistical tests were performed to assess environmental, site, and *F. heteroclitus* biotic characteristics that might be influential in the observed collection patterns. Student's *t*-tests and analysis of variance (ANOVA) were used to assess mean depth variability of 2019 and 2021 collection sites, respectively. For the 2019 and 2021 collections, Kolmogorov–Smirnov tests were performed to assess differences in size class distributions of tagged and recaptured *F. heteroclitus*. ANOVA was used to assess significant differences in mean size between each treatment group, with a Tukey–Kramer post hoc test to determine which pairwise comparisons significantly differed ($p < 0.05$). Chi-square tests were performed on 2021 *F. heteroclitus* data to determine the significance of gender related to return rate, and linear regression analysis was used to determine the relationship between *F. heteroclitus* SL and return distance traveled. The 2019 analyses used untransformed data, as the data did not differ significantly from a normal distribution. 2021 analyses were conducted on $\log_{10}$-transformed data.

3. Results

Consistent with the design of the restoration efforts, the sites did not significantly differ from one another in the environmental parameters measured (Table 1). The depth of each creek is nearly identical. Trap depths in 2019 and 2021 showed no significant difference within the same cell (combined mean = 40.6 cm, t crit = 1.943, $p > 0.05$; combined mean = 43.21 cm, F = 1.104, $p > 0.05$, respectively; Table 1 for individual creek means). Likewise, the water temperature of each site was within 2 degrees of one another across each month for both years, and the salinity at each site ranged from 13.9–14.8 ppt in 2019 and from 10.0–11 ppt in 2021 (Table 1).

Table 1. Average water depth in centimeters across all traps at each site, water temperature °C, salinity ‰, DO mg/L and DO % for each site both during tagging and recapture events. "X" denotes no measurement recorded for that site. The DO meter was malfunctioning in October 2019 and therefore no measurements were taken. The avg. depth measurements for 7th July were lost and denoted as 'X' as well. All 3 sites for 2021 were measured within a few minutes of each other on 7 July 2021 to ensure no tidal or time effects.

Dates	Sites	Avg. Depth cm	Water Temp. °C	Salinity ‰	Do mg/L	DO %
28 October 2019	S1	45	19.6	14.4	X	X
30 October 2019	S2	50.8	18.6	14.7	X	X
29 October 2019	S3	35.2	18.6	14.8	X	X
28 October 2019	SW1	32.8	19.4	14	X	X
30 October 2019	SW2	42.8	18.4	14.7	X	X
29 October 2019	SW3	33.5	18.7	14.5	X	X
28 October 2019	NW1	37	19.5	13.9	X	X
30 October 2019	NW2	40.5	18.3	14.6	X	X
29 October 2019	NW3	40.5	19	14.5	X	X
28 October 2019	N1	43.8	20	14.2	X	X
30 October 2019	N2	45.2	18.3	14.7	X	X
29 October 2019	N3	41	18.8	14.6	X	X
7 July 2021	Site A	X	30.3	10.6	14.3	200
7 July 2021	Site B	X	29.6	10.6	12.9	179
7 July 2021	Site C	X	29.6	10.5	11.1	157
16 July 2021	Site A	42.5	32.4	10.8	11.7	170
16 July 2021	Site B	36.9	31.6	11	13.5	195
17 July 2021	Site C	42.5	34.6	10.8	12.6	190
9 August 2021	Site A	41.4	27	10.2	13.7	180
9 August 2021	Site B	41.9	26.6	10.1	11	145
10 August 2021	Site C	44.2	28.4	10.1	9.4	130
13 September 2021	Site A	37.6	26.1	10.4	19	247
12 September 2021	Site B	34.5	25.3	10.2	17.5	226
11 September 2021	Site C	38.1	26.3	10.1	17.9	232

During July 2019, 1514 fish were marked and released in subcell 1C (Figure 2). (Note: the following transplant identifications will all follow the convention of "original capture site/release site".) For NW1/NW1, a total of 506 *F. heteroclitus*, tagged blue (mean

length = 45.9 mm, n = 506, SD = 10.33), were captured from NW1 and released back to NW1. For SW3/NW1, a total of 504 *F. heteroclitus*, tagged red (mean length = 45.4 mm, n = 504, SD = 10.07) were captured from SW3, translocated, and released into NW1. For SW3/SW3, a total of 506 *F. heteroclitus*, tagged yellow (mean length = 47.3 mm, n = 506, SD = 8.94), were captured from SW3 and released back to SW3. Recapture proceeded with the translocated treatment SW3/NW1 before SW3/SW3 to observe potential short-term (<24 h) movement from site NW1 to site SW3. A total of 130 SW3/NW1 tagged individuals (25.7%) were recollected at site SW3 within 24 h of translocation to NW1, a distance of 353 m away via creek movement (Figure 2). During the more encompassing October 2019 recapture efforts, collections confirmed July site fidelity and homing patterns. At site NW1, 10 blue-tagged NW1/NW1 individuals (2.0%) and 2 red-tagged SW3/NW1 individuals (0.4%) were recaptured. At site SW3, 1 blue-tagged NW1/NW1 individual (0.2%), 29 red-tagged SW3/NW1 individuals (5.7%, 353 m of movement via creek from translocation site), and 44 yellow-tagged SW3/SW3 individuals (8.7%) were recaptured (Figure 2 and Table 2). Few tagged individuals were collected at the non-tagging supplemental collection sites during October 2019, suggesting targeted movement direction.

Table 2. Recaptures for Cell 1C in October 2019. NW1 and SW3 were the two tagging sites. NW1/NW1 (blue), SW3/SW3 (yellow), SW3/NW1 (red).

Sites	NW1/NW1	SW3/SW3	SW3/NW1
NW1	10	0	2
NW2	0	0	0
NW3	0	0	0
SW1	0	0	0
SW2	0	0	1
SW3	1	44	29
S1	0	1	0
S2	0	0	0
S3	0	0	1

During July 2021, a total of 1255 *F. heteroclitus* were tagged and released in subcell 5AB at sites A, B, and C (Figure 3). As in 2019, tagging was conducted during 2021 to observe potential short-term (<24 h) movement between sites. A total of 300 A/B *F. heteroclitus* tagged pink individuals (mean = 35.0 mm, n = 300, SD = 13.95) were collected from site A and translocated to site B. A total of 300 A/A *F. heteroclitus*, tagged blue (mean length = 33.2 mm, n = 300, SD = 11.70), were collected from site A and released back to site A. 302 B/B *F. heteroclitus*, tagged orange (mean length = 29.0 mm, n = 302, SD = 9.12) were collected from site B and released back to site B. Finally, a total of 353 C/A *F. heteroclitus*, tagged yellow (mean length = 39.4 mm, n = 353, SD = 12.87), were collected at site C and translocated to site A. Similar to return movements observed during July 2019, over 3 days there were overlapping movement patterns during July 2021. A total of 17 pink-tagged A/B individuals were recaptured at site A within 24 h of release at site B, 316 m via creek movement, and 5 yellow-tagged C/A individuals were recaptured at site C within 24 h of release at site A, a distance of 522 m traveled via creek movement.

During July 2021, 8 days after tagging, recapture efforts were conducted across the western portion of subcell 5AB. At site A, 28 blue-tagged A/A individuals (9.3%), 30 pink tagged A/B individuals (10%, 316 m traveled), and 11 yellow-tagged C/A individuals (3.1%) were recaptured. At site B, 10 orange tagged B/B individuals (3.9%), 2 yellow-tagged C/A individuals (0.5%), and 1 blue-tagged A/A individual (0.3%) were recaptured. At site C, 93 yellow-tagged C/A individuals (26.3%, 522 m traveled) were recaptured.

During the recapture event conducted in August 2021, similar results as during July 2021 were observed. At site A, 29 blue-tagged A/A individuals (9.6%), 21 pink-tagged A/B individuals (7%), and 4 yellow-tagged C/A individuals (1.1%) were recaptured. At site B, 25 orange-tagged B/B individuals (8.2%) and 1 yellow-tagged C/A individual (0.28%) were recaptured. In C, 64 yellow-tagged C/A individuals (18.1%) and 1 pink-tagged A/B individual (0.3%) were recaptured (Figure 3 and Table 3).

Table 3. Recaptures for Cell 5AB in July, August, and September 2021. Sites A, B, and C were the three tagging sites. The nomenclature for catch-and-release sites follows the pattern of "site originally collected/sit released to after marking". Figure 3 for locations of other sites with respect to the tagging sites. A/B Confluence is between sites A and B, and the "X" denotes it was not sampled during the month of July.

	A/A	**A/A**	**A/A**	**B/B**	**B/B**	**B/B**	**A/B**	**A/B**	**A/B**	**C/A**	**C/A**	**C/A**
Sites	July	August	September	July	August	September	July	August	September	July	August	September
A	28	29	19	0	0	3	30	21	27	11	4	5
B	1	0	0	12	25	22	0	0	0	2	1	2
C	0	0	0	0	0	1	0	1	0	93	64	38
SS	0	0	0	0	1	0	0	0	0	0	1	0
SW	0	0	0	0	0	0	0	0	0	0	1	0
Dead End	0	0	0	0	0	1	0	0	0	0	0	0
Inlet	0	0	0	0	0	0	0	0	0	0	0	0
A/B Confluence	X	0	2	X	0	4	X	0	2	X	0	1

Similar results to previous recapture events were observed within subcell 5AB during September 2021, although fall movement of *F. heteroclitus* [42,46] may have begun to occur. At site A, 19 blue-tagged A/A individuals (6.3%), 27 pink-tagged A/B individuals (9.0%), 5 yellow-tagged C/A individuals (1.4%) and 3 orange-tagged B/B individuals (1.0%) were recaptured. At site B, 22 orange-tagged B/B individuals (7.3%) and 2 yellow-tagged C/A individuals (0.5%) were recaptured. At site C, 38 yellow-tagged C/A individuals (10.7%) and 1 orange-tagged B/B individual (0.3%) were recaptured (Figure 4). During the recapture events in July, August, and September 2021, only 4-tagged individuals were collected at subcell 5AB supplemental sites: inlet, dead end, SW, or SS, while at the A/B confluence, blue, orange, yellow, and pink individuals were collected, suggesting the potential mixing of *F. heteroclitus* subpopulations among sites was possible, but not observed.

Small and varied sample sizes for the returns made the results from the Kolmogorov–Smirnov tests difficult to interpret (Table 4). ANOVA examining mean size difference among recapture groups were not significant during 2019 ($F = 0.325$, $df = 2$, $p = 0.724$) but differed significantly among recapture groups for each recapture event during 2021 (July 2021 $F = 7.038$, $df = 3$, $p < 0.05$, August 2021 $F = 6.096$, $df = 3$, $p < 0.05$, September $F = 5.570$, $df = 3$, $p < 0.05$). The size difference and observed movement patterns suggest that *F. heteroclitus* sub populations within 5AB had limited mixing and high site fidelity. When examined further, the analysis between each recapture group typically indicated non-significant relations except for comparisons with the C/A group in 2021 which had larger sizes (Table 5). This suggests that the size classes of *F. heteroclitus* at site C tended to be significantly larger than sites A and B. Regression analysis did indicate a weak significant relationship with size and distance traveled (Figure 5). There was no significant difference in return rates based on gender (Table 6).

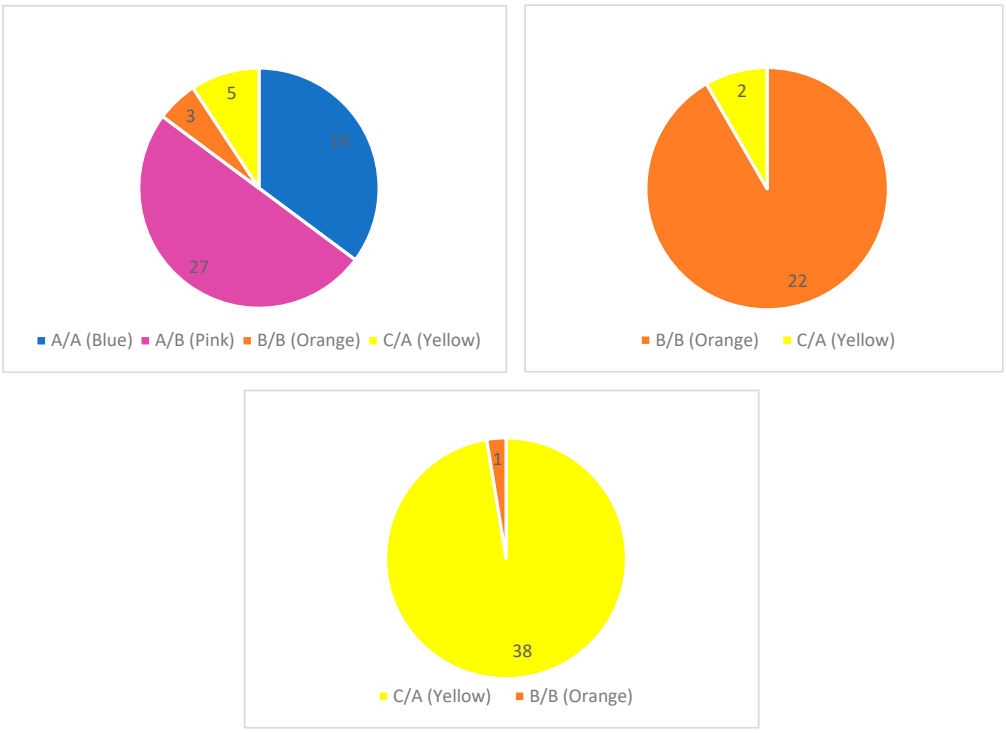


Figure 4. Recaptures for each tagging site in September 2021. Graph 1 (Site A September) contains 19 A/A (blue 6.3%), 27 A/B (pink 9%), 3 B/B (orange 1%), and 5 C/A (yellow 1.4%). The second graph (Site B September) contains 22 B/B (orange 7.3%), and 2 C/A (yellow 0.5%). The third graph (Site C September) contains 38 C/A (yellow 10.7%) and 1 B/B (orange 0.3%).

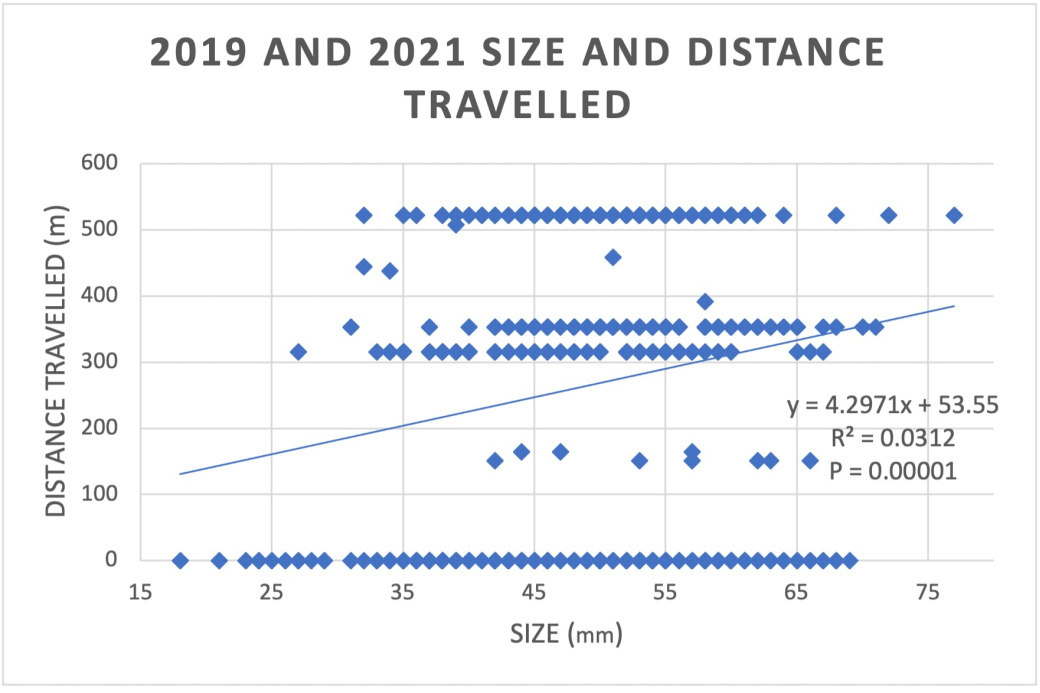


Figure 5. Relationship between individual size and distance traveled, with the regression line, equation, and *p*-value displayed. Note the difference in recapture numbers around the 30 mm mark when comparing 0 m traveled (marked, returned to original capture sites) to >500 m traveled.

Table 4. Kolmogorov–Smirnov distribution test for recaptures in each season (critical value: >84), and NS denotes not significant.

Dates	Treatment	Dmax	D× n1×n2	Significance
October 2019	SW3/NW1 × SW3/SW3	0.11	140.36	$p < 0.05$
October 2019	NW1/NW1 × SW3/NW1	0.28	81.2	NS
October 2019	NW1/NW1 × SW3/SW3	0.18	78	NS
July 2021	A/A × A/B	0.23	196	$p < 0.05$
July 2021	A/A × B/B	0.33	112	$p < 0.05$
July 2021	A/A × C/A	0.52	1348	$p < 0.05$
July 2021	A/B × B/B	0.18	66	NS
July 2021	A/B × C/A	0.44	1215	$p < 0.05$
July 2021	B/B × C/A	0.34	381	$p < 0.05$
August 2021	A/A × A/B	0.22	135	$p < 0.05$
August 2021	A/A × B/B	0.25	181	$p < 0.05$
August 2021	A/A × C/A	0.55	1019	$p < 0.05$
August 2021	A/B × B/B	0.09	47	NS
August 2021	A/B × C/A	0.35	472	$p < 0.05$
August 2021	B/B × C/A	0.32	518	$p < 0.05$
September 2021	A/A × A/B	0.25	176	$p < 0.05$
September 2021	A/A × B/B	0.13	55	NS
September 2021	A/A × C/A	0.55	399	$p < 0.05$
September 2021	A/B × B/B	0.17	99	$p < 0.05$
September 2021	A/B × C/A	0.33	337	$p < 0.05$
September 2021	B/B × C/A	0.45	374	$p < 0.05$

Table 5. Tukey post hoc test for mean size of July, August, and September 2021 recaptures (critical value: >3.36), and NS denotes not significant.

July Treatments	Abs Mean Diff.	N 1	N 2	SE	Q	Significance
A/A × A/B	2.338	28	30	1.448	1.615	NS
A/A × B/B	3.071	28	12	1.901	1.616	NS
A/A × C/A	6.937	28	93	1.188	5.841	$p < 0.05$
A/B × B/B	0.733	30	12	1.882	0.390	NS
A/B × C/A	4.599	30	93	1.157	3.976	$p < 0.05$
B/B × C/A	3.866	12	93	1.690	2.287	NS
August Treatments	**Abs Mean Diff.**	**N 1**	**N 2**	**SE**	**Q**	**Significance**
A/A × A/B	2.007	29	21	1.534	1.308	NS
A/A × B/B	2.443	29	25	1.461	1.672	NS
A/A × C/A	6.639	29	64	1.198	5.540	$p < 0.05$
A/B × B/B	0.436	21	25	1.585	0.275	NS
A/B × C/A	4.632	21	64	1.346	3.441	$p < 0.05$
B/B × C/A	4.196	25	64	1.263	3.324	NS

Table 5. *Cont.*

September Treatments	Abs Mean Diff.	N 1	N 2	SE	Q	Significance
A/A × A/B	0.628	19	27	1.571	0.400	NS
A/A × B/B	0.459	19	22	1.643	0.280	NS
A/A × C/A	6.526	19	38	1.474	4.427	$p < 0.05$
A/B × B/B	0.168	27	22	1.507	0.112	NS
A/B × C/A	5.899	27	38	1.320	4.466	$p < 0.05$
B/B × C/A	6.067	22	38	1.406	4.316	$p < 0.05$

Table 6. Chi-square results analyzing sex ratios. The critical value used is >3.84. Only A/B July and September were significant, denoted by the * symbol; all other results were nonsignificant, and the degrees of freedom were 1. Only 2021 recaptures were sexed.

Dates	July	August	September
Treatments	χ^2	χ^2	χ^2
A/A	0.092	1.38	0.11
B/B	0.176	0.61	0.24
A/B	6.69 *	12.32 *	1.51
C/A	0.094	1.27	3.46

4. Discussion

The results of this study further confirm site fidelity in *F. heteroclitus* and show that this fish also displays homing behavior [40]. While there is substantial evidence for homing in birds, mammals, and certain fish (salmon, eels, etc.) [5,6,13,65], there is sparse evidence for homing in estuarine fishes, particularly key estuarine species such as *F. heteroclitus*. Data from this study demonstrate substantial returns of tagged, translocated *F. heteroclitus* to their original capture location within 24 h, and prolonged residence times (months) within the same original marsh sites.

During 2019, *F. heteroclitus* site fidelity was confirmed within the restored salt marsh habitat complex of subcell 1C, as indicated by recaptures of individuals marked and released to their capture location. In 2019, F. heteroclitus homing was also observed within subcell 1C, with substantial numbers of tagged, translocated individuals returning (25.7%) from the release site to the original collection sites within 24 h. Neap tides occurred during the July 2019 recapture for SW3/NW1 tagged individuals, and tidal inundation was observed to only penetrate a few meters into the marsh fringe. The most direct path for return was via marsh creek, not over the low and high marsh between the sites; each individual that returned was required to travel ~353 m as measured by channel distance. This site fidelity and homing pattern persisted three months later, albeit catches were lower, with 5.7% being recaptured at site SW3. During the October 2019 collections, there was little evidence of tagged *F. heteroclitus* movement outside original collection locations to non-tagging locations. Only 3 tagged fish were collected at non-tagging sites.

Similar site fidelity was observed during 2021, subcell 5AB, as demonstrated by catches of individuals marked and released at their capture site over the 2 months of sampling. Tagged individuals were routinely caught through spring and summer in their collection sites and were rarely caught at other nearby sites, even though tidal flow was noted to allow for sub-population mixing. In the October recapture event, some fall movement was seen in the confluence site (Table 3), suggesting that *F. heteroclitus* fall movement may begin in October in this area [35,36]. The homing behaviors for *F. heteroclitus* observed during 2019 in subcell 1C also occurred during 2021 in subcell 5AB with a more robust

sampling design. Two different distances for homing were examined: a similar distance as during 2019 (316 m A/B) and a longer distance (522 m C/A) with a deep channel (>1.5 m deep at low tide) separating sites C and A. *F. heteroclitus* prefer water depths shallower than 70 cm [32,35], so a distance with a deep channel crossing was assessed to determine whether longer distances and a depth impediment would act as a barrier to homing. During the July 2021 tagging/recapture work, within 24 h. of release, 16 fish translocated from site C to A had returned to their original capture area (522 m). During the ~2-month recollection period for subcell 5AB, 76 tagged A/A individuals (caught, marked, and released at site A) were recaptured at site A, with only 1 tagged A/A individual collected at site B. A total of 59 tagged B/B individuals were collected at site B, and only 3 tagged B/B individuals were collected at site A. *F. heteroclitus* had intentional movement, and even relatively deep channel crossings did not prevent them from returning to their capture location, with 93 tagged C/A individuals (26.3% of the total individuals tagged) recaptured at site C only one week after tagging and relocation to site A. During this ~2-month recollection period for subcell 5AB, a total of 195 yellow-tagged C/A individuals were recaptured at site C, with only 2 tagged of a different color (pink and orange) recaptured at that location. Field observations indicated that individuals not only returned to the same creek but also returned to the upper reaches of the creek where they were originally caught, supporting Halpin's finding that *F. heteroclitus* tend to concentrate in the upper reaches of creeks [33].

One difficulty in mark-recapture studies is recapturing tagged individuals, especially in natural or open environments. The method of marking an organism can have a large impact on the expected return, but can be greatly limited by the type of organism, life stage of the organism, and resources. The recapture rates observed in this study were generally within the range observed in other studies. A study of movement and site fidelity in *Palaemon* successfully tagged 422 shrimp, and in the following 48 days were able to recapture 11% of the tagged shrimp [17]. Similarly, a study of Mummichogs in a habitat similar to this study, a restored marsh, managed to recapture 10.3% of their 14,784 fish that were tagged [38]. In a more open system, 1538 eels were tagged in the North Sea and were only able to recapture 77 eels (5%) [8]. In addition to movement patterns and site fidelity, predation and natural mortality, movement out of the system or navigational error, and trap avoidance can all have an impact on an individual's chances of being recaptured.

There were no significant patterns of gender influencing return or distance traveled. The sex ratios for recaptures did not significantly differ from initial capture sex ratios or among those translocated versus those returned to the original site of collection. This potentially eliminates breeding grounds as being the prime explanation for homing to a restricted area during the 2–3-month time period examined.

The SW3/SW3 distribution from 2019 had a significantly larger size class compared to NW1/NW1 and SW3/NW1 ($p < 0.05$). For 2021, the B/B size class was the smallest, with the smallest second bimodal peak compared to the other 2021 treatments. The C/A and A/B treatments in 2021 had large proportions of individuals corresponding to the second bimodal peak, which may have been a factor in the ability of the translocated individuals to return to the original collection sites, consistent with Kneib's findings that larger *F. heteroclitus* are more able to travel farther within salt marsh habitat [26]. These size distributions show that multiple cohorts of *F. heteroclitus* were tagged and recaptured throughout the study, with each annual cohort displaying homing. This indicated that the homing ability is present within young of the year as well as older *F. heteroclitus* cohorts.

The effect of size on return rate and distance traveled is less clear. There was a weak significant positive relationship between size and distance traveled for returning individuals. There was a low recapture rate of individuals sized 30–35 mm SL traveling distances greater than 500 m, and a higher recapture rate for 30–35 mm SL sized fish returning ~350 m.

Out of 768 tagged individuals smaller than 35 mm SL during July, 37 were recaptured. Only 1 fish <35 mm SL traveled over 500 m, and 2 individuals traveled ~480 m. The smallest translocated C/A tagged *F. heteroclitus* that returned to the original collection site across 522 m and a deep channel was 35 mm SL, with 10 of the 93 yellow tagged C/A translocated *F. heteroclitus* recaptured at site C during July <40 mm SL, and 4 individuals of the 63 recaptured during August at site C <40 mm SL. Also, during July 2021, the 11 tagged C/A translocated individuals that remained at site A had a mean size of ~39 mm SL, with 7 of the 11 < 40 mm SL and 2 < 30 mm SL. No translocated tagged A/B individuals were recaptured at their release location (site B) after the initial 24 h. The 4 recaptured tagged A/B individuals still in site B 24 h. after release had an average of ~23 mm SL, while the 17 tagged A/B individuals recaptured in site A 24 h. after translocation to site B had an average size of ~49 mm SL. 17 mm SL was the smallest tagged A/B individual, and the smallest tagged *F. heteroclitus* A/B individual recaptured at site A in July was 27 mm SL. The 30 mm–35 mm SL size range is within the known size range of transition for maturity of *F. heteroclitus* from juvenile to sub-adult. *F. heteroclitus* fully begins to utilize the marsh at ~15–20 mm TL [26]. Males reach sexual maturity at 32 mm TL (26 mm SL), while females reach sexual maturity at 38 mm TL (30 mm SL) [66]. A more targeted study of size and gender effects on both site fidelity and homing behavior is needed to discern these influences and how they change over time.

Cues used by *F. heteroclitus* for homing seem uncertain. Environmentally, all sites are relatively homogenous for the variables measured. The restored marshes within Poplar Island are relatively young, with subcell 1C planted in 2011 and subcell 5AB planted in 2018; as a result, the salt marsh sites have had little time to mature and develop site-specific differences among cells, subcells, or among sites within a subcell. Concurrent with tagging events, Secchi depth observations from Meyer [54] indicated that low visibility (mean Secchi depth of 22 cm) predominated the water columns of the Poplar Island wetland subcells and across study sites, typical of historic water column visibility measurements [54]. Recorded parameters of temperature, salinity, dissolved oxygen, and water depth also did not significantly differ among subcell sites sampled during 2019 and 2021. The use of chemical cues, as used by eels and salmonid fishes, might provide insight into the ability to return to specific sites within such a homologous system [5,6]. However, the homogenous nature of the dredged sediment dispersed throughout each of the restored Poplar Island wetland cells suggests that recent changes in sites relative to micro developments such as methanogenic decomposition, microalgal accumulation, or infaunal development might be the most likely directional cues for *F. heteroclitus* navigation.

There are many potential reasons as to why a resident estuarine fish has a homing ability, from the need to navigate a dynamic and changing landscape across both spatially and temporally heterogeneous environments, to the need to utilize an expansive marsh complex and then successfully return back to a safe or known home range. However, these findings have implications for rates of recolonization after a disturbance or degradation of habitat. Homing behavior and site fidelity for *F. heteroclitus* may impact responses to localized disturbances as well as rates of colonization for disturbed or restored/created marsh areas. However, this importance is not exclusive to *F. heteroclitus*. Other resident fishes face similar challenges and might also navigate landscapes to specific home ranges. Transient species may navigate landscapes in similar fashion daily, from forays into intertidal zones where the need to return with the falling tide is paramount to survival, to navigating the interlocking dendritic channels that many wetlands contain. A more involved study might include assessment of what *F. heteroclitus* key on for site return after translocation, and whether homing is present in other salt marsh species. Evidence of other estuarine species

exhibiting the homing capability could have significant implications for stock management, habitat protection efforts, and restoration efforts across coastal and oceanic environments.

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