Quantifying the movements of Paddlefish *Polyodon spathula* in the lower Alabama River and Mobile-Tensaw River Delta

by

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Abstract

Paddlefish *Polyodon spathula* are mobile potamodromous fish that move among riverine, deltaic, and estuarine habitats in coastal drainages. Despite a reasonable amount of research having been conducted on Paddlefish life history and migrations, relatively little is known about their use of downstream deltaic or estuarine (low salinity) areas. To address this knowledge gap, I tagged and tracked Paddlefish in order to quantify their movements in the lower Alabama River and Mobile-Tensaw River Delta (MTRD), Alabama; identify distinct movement behaviors, assess interannual consistency in those behaviors, and evaluate associations between MTRD use and several environmental factors (i.e., temperature, salinity, gage height). From December 2024 through January 2026, 148 Paddlefish were tagged with acoustic-radio transmitters and monitored using both passive (N = 17 receivers in the Alabama River and 18 receivers throughout the MTRD) and active telemetry during 8 seasonal surveys of the lower Alabama River and MTRD. Movement metrics were analyzed with k-means clustering, and weekly MTRD use was modeled using generalized linear mixed models. Of the 148 tagged fish, 131 provided sufficient detections for inclusion in the data set (N=4,057,456 total detections), and 110 (83%) used the MTRD. Three distinct movement behaviors were identified in Year 1, two of those unique movements were also identified in Year 2. Among the 43 fish that could be classified in both years, 40% showed similar behaviors. MTRD use increased with upstream salinity and temperature but decreased with river stage. These results state extensive use of deltaic habitat during non-spawning periods and suggested that some individuals may repeat similar movement behaviors between years. Paddlefish conservation and management must

consider the importance of these downstream estuarine habitats due to their importance as a summer and fall refuge for this species.

Artificial Intelligence (AI) Use Disclosure Statement

In the preparation of this, the following Artificial Intelligence (AI) tools were used: ChatGPT. These tools were used primarily to troubleshoot errors associated with coding as well as check for grammatical errors in my code. I acknowledge full responsibility for the intellectual content of this work and have ensured that all AI-assisted sections have been reviewed and revised for accuracy and appropriate academic style. All AI-generated content was reviewed and validated for relevance, appropriateness, and accuracy before incorporation into the final document to maintain scholarly integrity of this research.

Digital Accessibility Disclosure

In the preparation of this thesis, the following digital accessibility tools were used to ensure this document complies with federal requirements: Microsoft Word Accessibility Checker. I acknowledge full responsibility for the intellectual content of this work and have made a good faith effort to comply with digital accessibility requirements in publishing, wherein the nature of the content does not significantly change in order to do so. Furthermore, all content has been reviewed and revised to meet these requirements prior to final publication.

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List of Abbreviations

AICc: .... Akaike's Information Criterion corrected

AR(1): .... first order autoregressive correlation structure

CART: .... Combined Acoustic - Radio Tag

CLD: .... Claiborne Lock and Dam

EFL: .... Eye-to-Fork Length

GLMM: .... Generalized Linear Mixed Model

GPS: .... Global Positioning System

IACUC: .... Institutional Animal Care and Use Committee

L&D: .... Lock and Dam

LAR: .... Lower Alabama River

MS-222: .... Tricaine Methanesulfonate

MTRD: .... Mobile-Tensaw River Delta

RKM: .... River Kilometer

SE: .... Standard Error

USACE: .... U.S. Army Corps of Engineers

Introduction

Fishes across the world can express a diversity of migratory strategies, including anadromy, where fish spend most of their lives in saltwater but move into freshwater areas to spawn, catadromy, where fish spend most of their lives in freshwater environments but migrate into saltwater areas to spawn, and potamodromy where fish complete all migrations within a freshwater system, with migrations undertaken to reach critical habitats at different life stages for spawning and feeding (Lucas and Baras 2008; Brönmark et al. 2014) . In fact, within North America at least 25% of fish species are considered to be migratory (Leggett 1977; Dean et al. 2022). Most research on migratory fishes has been focused on anadromous salmonids and sturgeons, while potamodromous fishes are less speciose, less prevalent, and less frequently studied (Thurow 2016). Species that exhibit potamodromous migration strategies extending into estuarine habitats represent an even less-studied aspect of riverine fish migration.

Despite the knowledge gap regarding movements by potamodromous fishes into estuarine areas, numerous examples exist of anadromous fishes using both habitats (Paradis et al. 2021, 2022; Greenheck et al. 2023). Within the sturgeons (*Acipenseridae)*, some species are potamodromous while others are anadromous, and these potamodromous sturgeons may provide some insights as to how riverine migratory species may be using estuarine environments. For example, in a recent study, Paradis et al. (2021, 2022) described the movements of Lake Sturgeon (*Acipenser fulvescens*), and Atlantic sturgeon (*Acipenser oxyrinchus*) in the St. Lawrence Estuary. Using a 35-year mark-recapture dataset, the investigators found that some Lake Sturgeon individuals, generally considered a potamodromous species, were recaptured in the estuary and even tended to display site fidelity. Despite some evidence for estuarine use by potamodromous migrators, additional research is clearly needed; particularly relative to understanding the effects habitat connectivity and fragmentation on these species.

The United States currently has 92,366 onstream dams (USACE 2020). These dams vary in form and function, early dams were built to retain water for irrigation, flood control, and to supply water to growing human population centers (Baxter 1977). In the 19^{th} century, as cities grew and demand for more commercial products and raw materials increased, damming rivers for navigation increased (Di Baldassarre et al. 2021). Dams create numerous ecological problems including habitat destruction, habitat fragmentation, altered flow regimes, sediment sequestration, and changes to natural nutrient cycling (Lydeard and Mayden 1995; Graf 1999; Mettee et al. 2005; Jelks et al. 2008; Kratina et al. 2023).

For potamodromous fishes, dams can disrupt movement by fragmenting the river–estuary continuum and limiting access to habitats used for spawning, feeding, refuge, and overwintering. Highly migratory fishes often move long distances among these habitats (McIntyre et al. 2015; Dean et al. 2022); however, barriers can delay or completely block movement between downstream estuarine areas and upstream riverine habitats (Larinier 2003; Meixler et al. 2009; Hoover et al. 2019; Huang and Li 2024). Although potamodromous fishes do not migrate among freshwater and marine environments like anadromous species, their movements may still depend on connectivity between rivers, deltas, and low-salinity estuarine habitats. Therefore, dams may limit a fish’s ability to reach important upstream and downstream habitats (Larinier

2003). Understanding estuary use by potamodromous fishes therefore requires consideration of how upstream barriers shape movement strategies throughout the system.

The Mobile River basin illustrates how river fragmentation can lead to declines of highly migratory fishes. It is one of the largest and most aquatically biodiverse drainages in North America (Elkins et al. 2019), encompassing roughly 114,000 km^2 of Alabama, Georgia, Mississippi, and Tennessee, including tributaries in the Blue Ridge Mountains to the east and the Mississippi Coastal Plain to the west (Boschung and Mayden 2004). Historically, the Mobile River system was home to several migratory fish species, including those with anadromous, potamodromous, and catadromous life histories (Hershey et al. 2024). After the construction of nearly 40 dams within the Mobile River basin, migratory fish abundance within the system declined sharply, such as Gulf Sturgeon and Alabama Sturgeon (Freeman et al. 2005; Hershey et al. 2024).

The Mobile-Tensaw River Delta (MTRD) is located 10 river kilometers (RKM) downstream of the Alabama and Tombigbee rivers confluence and provides an ideal study site to quantify potamodromous fish estuarine habitat use in the downstream extents of their range, as well as movements to and from their upstream spawning habitats (Figure 1). The MTRD encompasses >280 km^2 of wetland habitat, representing the nexus for the entire Mobile River Watershed (Stout 1982). In 1974, the MTRD was designated as a National Natural Landmark due to its integral role both ecologically and culturally (Stout 1982). The MTRD has been affected by numerous anthropogenic factors, including commercial logging (Aust et al. 2012), commercial fishing (Mettee et al. 2009; Rider et al. 2019), shipping channel dredging, damming of vital tributaries

(Mettee et al. 2005; Kuhajda and Rider 2016) and the urban expansion in Mobile, Alabama.

The Paddlefish *Polyodon spathula (*one of the more charismatic residents of this system)*,* provides a unique opportunity to examine how a potamodromous species might use different riverine and estuarine habitats throughout the year. As stated previously, the movements of salmonid and sturgeon species between riverine and marine systems have been studied in some detail. In contrast, few Paddlefish studies on this topic have been conducted. One study found individuals tagged over two years downstream in Mobile Bay migrated 30-56 km upstream into the MTRD, with some individuals moving up to 288 km to the tailrace of the lowermost lock and dam structure (Claiborne L&D), presumably to spawn (Mettee et al. 2009). The authors also reported fish caught and tagged further upstream, below the next upstream structure (Miller's Ferry L&D), and released in the moved downstream past Claiborne L&D and into the lower Alabama River, lower Tombigbee River, and MTRD (Mettee et al. 2009), demonstrating that such long-distance potamodromous movements into the estuarine MTRD can occur.

<u>Study Questions:</u>

While the previous work of Mettee et al. (2006) provides a foundation for future research, it also shows that relatively little is known about Paddlefish movements downstream throughout the Mobile-Tensaw River Delta estuary. A potential hypothesis that I propose is one that is similar to Clark's (1968) "Contingency Hypothesis." In his study, he found that different groups of Striped Bass *Morone saxatilis* were found in the same spatial range varied in the timing of their upstream spawning migration (Clark

1968). These Striped Bass inhabited the same area during the summer, fall, and winter when they functionally acted as a single population until their spring migratory movements. Smaller “contingents”, or groups, of this larger population were observed to routinely behave in predictable ways that differed from one another (Clark 1968). Here I propose addressing questions raised by these studies relative to their downstream estuarine use in an effort to better understand the population-level movements of Paddlefish throughout the lower areas of the Mobile River basin and Mobile-Tensaw River Delta. Knowing the mechanics of these movements will better allow managers to create strategies to better allow for the continued success of this species. Specifically, I plan to address the following questions:

1. Do multiple spawning contingents exist within Paddlefish that inhabit the MTRD throughout the summer, fall, and winter?
2. If so, do Paddlefish that form these potential spawning contingents remain within the same contingent between years, or do their migration strategies show plasticity year to year?
3. How do environmental conditions such as fluctuating temperature, discharge, and salinity levels affect the timing of the potential spawning contingent moving upstream?

My overall goal is to provide answers to questions related to not only the movement of Paddlefish into estuarine habitats, but also to speak to the broader use of estuaries by migratory fishes in general. Given that the commercial Paddlefish fishery in Alabama closed indefinitely in 2018 (Rider et al. 2019), my results will help to inform not only ongoing Paddlefish research and conservation but also inform any potential future

Paddlefish fishery management within the lower Alabama River, lower Tombigbee River, and Mobile-Tensaw River Delta. Understanding how and when these fish move between important habitats throughout the year would play large part in a future reestablishment of the fishery or even just for the overall conservation of Paddlefish.

Methods

Study Species:

Paddlefish *Polyodon spathula* is a potamodromous species whose migratory movements within mainstem rivers have been relatively well-studied (Lein and DeVries 1998; Stancill et al. 2002; Firehammer and Scarnecchia 2007; Tripp et al. 2019; Thomas et al. 2024). However, a relatively less studied aspect of Paddlefish migrations is the extent to which individuals toward the downstream end of their riverine environments migrate into estuarine and moderately saline areas such as bays and deltas (Mettee et al. 2006, 2009). Paddlefish have been observed migrating upstream from these estuarine habitats and concentrating in large schools below dams (Mettee et al. 2006, 2009), although the origin of these individuals and their contribution to spawning populations remains unclear.

Paddlefish tend to display long-distance migrations to reach suitable spawning habitats (Jennings and Zigler 2000; Miller and Scarnecchia 2008; Bettoli et al. 2009; Gerken and Paukert 2009; Tripp et al. 2019). During non-spawning periods, some Paddlefish tend to Paddlefish migrate to summer and overwintering habitats that consist of slow-moving backwaters and oxbows (Jennings and Zigler 2000; Paukert and Fisher 2000; Mettee et al. 2009). These non-spawning habitats can act as both nursery grounds for juvenile Paddlefish (Moen et al. 1992; Hoxmeier and DeVries 1997; Gerken and Paukert 2009; Mettee et al. 2009), and as important summer feeding grounds and overwintering habitat for adults (Firehammer and Scarnecchia 2006). In the spring, Paddlefish move out of these more lentic areas and move into mainstem flowing portions of the river. This upstream migration is triggered by abiotic cues such as rising temperature and pulses in discharge (Lein and DeVries 1998; Paukert and Fisher 2001; Firehammer and Scarnecchia 2006). Paddlefish move upstream in search of fast-flowing water over coarse gravel bars or bedrock substrate to spawn (Firehammer and Scarnecchia 2006; Jennings and Zigler 2009).

Paddlefish face anthropogenic threats throughout most of their range (Jennings and Zigler 2000; Jelks et al. 2008). For example, due to their need for long stretches of unimpeded river, dams have acted as barriers for spawning Paddlefish (Zigler et al. 2004; Jennings and Zigler 2009). Paddlefish in the U.S. face some of the same challenges that the only other species in their family, the Chinese Paddlefish *Psephurus gladius,* previously faced prior to its extinction (Stone 2008; Zhang et al. 2009; Scarnecchia 2023) due to overharvest and habitat destruction from a series of major dam construction projects on the Yangtze River in China (Zhang et al. 2009). In addition to habitat changes due to dam construction, fishing pressure may also influence Paddlefish populations; for example, Paddlefish in Alabama have been protected under multiple harvest moratoria over the past 30 years. The first was instituted in 1988 and remained in place until 2013. The fishery was reopened in a limited capacity from 2013 to 2018, but after reassessment in 2018, the fishery was once again indefinitely closed, as it currently remains (Rider et al 2019). Despite all of these challenges, Paddlefish populations continue to be sustained throughout much of their current range.

Study Area:

I defined my study area as from the tailrace of Miller's Ferry L&D (MFLD) at the upstream end, downstream to the I-10 causeway across Mobile Bay (Figure 1). The Lower Alabama River (LAR) flows uninterrupted roughly 117 km from Claiborne L&D (CLD) before reaching its confluence with the Tombigbee River, forming the Mobile River. This highly channelized section of river has few backwater habitats until it reaches the Mobile-Tensaw River Delta (MTRD). Paddlefish movement in this section of river has received some research attention over the last 20 years (Mettee et al. 2005, 2006, 2009; Simcox et al. 2015).

Once formed, the Mobile River flows roughly 9.3 km south before reaching its confluence with the Tensaw River, marking the upper end of the MTRD, which contains 5 major rivers (Apalachee, Blakely, Middle, Mobile, and Tensaw rivers) along with many smaller rivers and backwaters. The Delta then flows roughly 72 km south until it reaches the head of Mobile Bay (Stout 1982). The lower reaches of the MTRD experience a single daily lunar tide cycle with seasonal salinity fluctuation and are considered to be estuarine (Stout 1982). The upper reaches of the Delta are mostly freshwater habitats (although with seasonal salinity intrusion) and are run-of-the-river with numerous sprawling backwaters and oxbows (Figure 1).

Fish Collection:

Paddlefish collection occurred in the uppermost sections of the LAR (in the tailrace below CLD; Figure 1) during December 2024 through January 2026, using large mesh multifilament (150-200 mm) gillnets. A total of 148 fish, 75 in Year 1 and 73 in Year 2, were collected and tagged with either Lotek Combined Acoustic Radio Tags

(CART) or Lotek acoustic tags. Once captured, Paddlefish were placed in a live well (see “Tag Implantation” section below), anesthetized, and both eye-to-fork length (EFL) and weight were measured (Carlander and Smith 1945). During surgery, Paddlefish were checked for sex by checking for presence of tubercles (Mettee et al. 2009; Miller and Scarnecchia 2011) as well as checking for the presence of eggs in female fish and developed testes in male fish at the incision site.

<u>Tag Implantation:</u>

I surgically implanted 95 fish with a combined acoustic and radio transmitter (LOTEK Wireless CART tag model MM-MM-16-50) that included a temperature sensor that recorded both the fish’s location and water temperatures that it experienced every 20 seconds. Tag lifespan was approximately 1500 days, which exceeded the duration of my study. The other 53 fish were tagged with acoustic LOTEK tags that had both temperature and pressure (depth) sensors during a concurrent study, but my equipment had the capability to record data for these tags as well. Tags were implanted in fish that were large enough so that they never exceeded 2% of the fish’s body weight (Cooke et al. 2010). Surgery was conducted on a V-shaped surgery board lined with closed-cell foam which was kept moist to prevent any damage to the fish’s skin. A 3-cm incision was made on the left ventral side of the fish’s belly (Hershey et al. 2022; Thomas et al. 2024) to implant the CART tag into the fish’s abdominal cavity. Because these tags also included a radio transmitter, a radio antenna extended ~250 mm from the posterior of the CART tag. Once the tag was implanted, 1-2 simple-interrupted, polydioxanone sutures were used to close the incision; they were secured with a surgeon’s knot, and 3M Vetbond was applied to each surgeon’s knot to close the incision. On the right side of the fish, in roughly the same location as the incision on the left side, a smaller incision was made to implant a small, uniquely-number-coded T-bar anchor tag to allow for external identification of the fish in the event of a recapture. All tools used for surgery were kept in a container filled with diluted chlorohexidine between surgeries to make sure that the tools were sterile and to avoid cross contamination. Prior to surgery, Paddlefish were held in a live well with a low concentration (100 ppm) of MS-222 to anesthetize the fish, and during surgery a small pump was used to provide a constant water flow over the gills of the fish. I only tagged Paddlefish 650 millimeters eye-to-fork length or greater given that Hoxmeier and DeVries (1997) found these to be sexually mature (Figure 2). Tags were set to transmit both an acoustic and radio signal every 20 seconds to maintain battery life throughout my study. All work was conducted under Auburn University IACUC Protocol Number 2022-5117 and IPROTO 202500000070 and Alabama state scientific collecting permits.

Passive Acoustic Telemetry:

I installed 17 LOTEK WHS 3250 acoustic receivers throughout the Alabama River and 16 of the same acoustic receivers across the MTRD (Figure 1, red circles). Receivers were deployed an average distance of 8.4 RKM between each other, and were attached with 6.35 mm stainless steel cable to a tree onshore and to a 36-kg anchor and were suspended in the water column with 2 buoys. Latitude and longitude were recorded for each receiver, and batteries were replaced and data were downloaded every 3-4 months.

Manual Tracking:

Once fish were tagged, I conducted quarterly manual tracking trips to collect additional fish location data, particularly for reaches between stationary acoustic receivers. I used a three-bar Yagi antenna and a LOTEK SRX 800 radio receiver with the gain set to 70 (to reduce interference without significantly reducing signal detection). I navigated downstream at a relatively slow speed (<12 kph), with the antenna placed at the bow of the boat, pointing towards the water. Every 30 seconds, the antenna was moved from the port to the starboard side of the boat to ensure that fish on both sides of the boat were detected. Once a fish was detected, I slowed the boat and searched for the fish on a finer scale. Once the maximum detection strength was achieved (70-115 signal strength), multiple detections were made, the individual was identified, and GPS coordinates were recorded. A LOTEK AcouTrack mobile acoustic tracking receiver was used to obtain tag temperature readings for the located fish. I also used a YSI Pro1030 meter to record temperature and salinity at the approximate location of the fish, with temperature and salinity being recorded at roughly 6.5m depth.

Salinity Monitoring:

To record changes in ambient salinity levels over time, I attached three HOBO MX800 Series Water Data Loggers to either existing acoustic receiver anchors or to newly deployed moorings at a depth of 3 m (Figure 1, yellow triangles). These three salinity/conductivity loggers recorded data every 15 minutes, and were distributed across the MTRD, with one deployed in upper Mobile River, one in the latitudinal central part of the Delta (between the lower confluence of the Middle River and the Tensaw River, and one in the lowermost Tensaw River, near its outflow into Mobile Bay (Figure

1). Data were downloaded from these salinity/conductivity loggers quarterly, roughly at the same time as the battery changes/data downloads for the stationary acoustic receivers.

Data Collection and Analysis

To evaluate Paddlefish movement patterns and habitat use in the LAR, Tombigbee River, and MTRD, I collected both fish location and environmental data. Fish location data included detections from the network of passive acoustic receivers deployed throughout the study area, as well as detections from my manual radio tracking surveys. Environmental data, specifically salinity and temperature, were collected using the fixed-location loggers at multiple points within the Delta as well as at precise fish locations observed during manual tracking events. All data analyses were conducted in RStudio and ArcGIS Pro. To answer the objectives, I proposed in the introduction, I used the following analytical methods.

Detections

Individual movement histories were summarized using the R package “actel” (Flávio and Baktoft 2020), and improbable detections flagged by the software were reviewed manually to determine whether they should be retained. Detections were removed if they represented unrealistic movements, including instances where an individual appeared to move past more than five receivers without being detected (this was selected to allow for potential non-detections of skipped receivers) , or if a fish was detected only once at a receiver to remove potential false detections.

Individual Movement Metrics

Individual movement metrics were calculated from validated detections after each acoustic receiver was assigned an RKM position. Using the confluence of the Alabama and Tombigbee rivers as a reference point (RKM=0), the distance between each receiver in my array was calculated by measuring shortest possible distance between receivers. If a receiver was upstream of the confluence, it was >0, downstream was <0. In the study, an event refers to an individual detection or multiple detections at a single receiver, whereas a step refers to the movement interval between 2 consecutive events for the same individual. Steps were calculated by ordering detections chronologically for each individual and subtracting the RKM of the previous detection from the RKM of the current detection. Positive step values indicated an upstream movement, negative steps indicated downstream movement, and the absolute value of each step represented the distance moved between consecutive detections. The average movement rate per day was calculated by dividing the total distance an individual moved by the number of days the individual was observed. The total range in RKM a fish moved between was calculated by subtracting the minimum RKM at which a fish was detected from the maximum RKM at which it was detected. Proportional use of the MTRD was determined by dividing the number of times an individual was detected in the MTRD by the total number of detections for the individual. The proportion of upstream and downstream movements were first calculated by determining the movement direction of an individual. This was done by subtracting the current receiver RKM where an individual was detected by the last receiver RKM at which it was detected. After this value was calculated, the proportion of downstream movement was calculated by dividing the number of downstream movements by the total number of movements for each individual and inversely, the number of upstream movements was calculated by dividing the total number of upstream movements for each individual by the total number of movements for an individual. And finally, the median step distance, which is defined as the typical distance moved between consecutive detections, was calculated by taking the median of the absolute change in RKM between consecutive detections.

Movement Behaviors Identified from Clustering (Objective 1).

Using individual movement metrics, I ran a k-means clustering analysis (e.g., Politikos et al. 2021) to identify groups of Paddlefish with similar movement behaviors between years. Clustering variables included an individual’s movement rate, the total range in RKM that a fish was detected between, proportional use of the MTRD, the proportion of downstream movements an individual made, and the median distance between movement steps an individual made. All clustering variables were standardized using z-score normalization before analysis. Clustering was conducted on a subset of Paddlefish that met minimum data requirements to reduce the influence of sparse detection histories on cluster assignment. For an individual to meet these criteria, they must have been observed across at least half of the annual study period, had at least 5 detection events, and made at least 5 movement steps between receivers. Year 1 detections spanned from December 1, 2024-December 1, 2025, and year 2 detections spanned from December 1, 2025-May 1, 2026. Because Year 2 represented a shorter monitoring period than Year 1, interannual comparisons were interpreted as comparisons of observed movement behavior across available monitoring periods rather than equivalent full-year movement cycles. Using a silhouette width analysis (Batool and Hennig 2021), which is a measure of how similar an individual is to its assigned cluster compared to the nearest alternative cluster, the number of clusters was determined by testing the number of clusters (*k*) that displayed the highest silhouette width (=s(i)), as follows;

$$s(i) = \frac{b(i) - a(i)}{max(a(i), b(i))}$$

where *a(i)* represents the average distance between individual fish *i* and all other individuals in its assigned cluster. *b(i)* represents the lowest average distance between individual fish *i* and fish in any other cluster. *max(a(i), b(i))* represents the maximum distance represented between *a(i)* and *b(i)* and is used to scale the value between -1 and 1. 1 representing perfect separation between clusters and -1 representing that an individual may be assigned to the wrong cluster.

Year to Year comparison (Objective 2).

To evaluate whether individual Paddlefish maintained similar movement behaviors between years, I compared cluster membership for fish that met clustering criteria in both Year 1 and Year 2. Fish that were assigned to a cluster in both years were used to assess whether individuals displayed a similar movement behavior year to year or displayed plasticity in their movement behavior. An alluvial diagram was used to visualize how these individuals either maintained or shifted their movement behaviors year to year.

Environmental Effects on Paddlefish Presence in the MTRD (Objective 3).

To evaluate how environmental conditions influenced Paddlefish presence in the MTRD, I modeled weekly MTRD use during the environmental modeling period.

Detections were first summarized at the daily level for each individual fish, where a fish-day was classified as MTRD use if the individual was detected at least once within the MTRD on that date. Daily records were then aggregated to the weekly level for each fish. For each fish-week, MTRD use was modeled as the number of detected days in which a fish was present in the MTRD out of the total number of days that fish was detected during that week. This response was modeled using a binomial response structure with the number of MTRD-use days and non-MTRD-use days specified as successes and failures, respectively.

Environmental covariates included salinity at the upstream logger, salinity at the downstream logger, mean MTRD water temperature, and river gage height. Because the response variable was summarized weekly, environmental covariates were also averaged by week prior to analysis. All environmental covariates were standardized using z-score normalization before model fitting to improve model convergence and allow comparison of relative effect sizes among variables.

I used generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function to evaluate relationships between environmental variables and weekly MTRD use. Fish identity was included as a random intercept to account for repeated observations of the same individuals through time. Because preliminary residual diagnostics indicated temporal autocorrelation in the daily MTRD-use model, I incorporated a first-order autoregressive [AR(1)] correlation structure into the weekly model, with week modeled as an ordered temporal factor within each fish. This structure accounted for the expectation that MTRD use by an individual fish in one week was likely related to its MTRD use in the previous week.

Candidate models representing different combinations of salinity, temperature, and gage height were fit and compared using Akaike's Information Criterion corrected for small sample size (AICc). Models with ΔAICc values less than 2 were considered competitive. The most parsimonious model was evaluated using convergence diagnostics, checks for multicollinearity, and simulated scaled residuals generated with the R package DHARMa.

Results

A total of 148 Paddlefish were tagged during the study period, of which 131 individuals met the criteria for inclusion in subsequent movement analyses (i.e., if they were detected more than twice during the study). This accounted for tagged individuals that may have shed tags, had malfunctioning tags, or any mortalities. Following the review process mentioned in the Methods Section, 4,057,456 valid detections remained and were used in subsequent analyses. After following the criteria for clustering analysis mentioned in the Methods Section, I was left with 70 of the 75 tagged individuals for Year 1 and 78 of the 148 tagged individuals for Year 2. After comparing Year 1 and Year 2 cluster membership tables for each individual and using individuals that were members of a cluster for both years, I was left with 43 individuals that met these criteria.

Year 1 Detections

For year 1 detections, the optimal silhouette width was determined to be 3 clusters with an overall average silhouette width of 0.43 (Figure 3). Cluster 1 contained 37 fish, had an average silhouette width of 0.44, and was considered to be MTRD resident fish. Cluster 2 contained 24 fish, had an average silhouette width of 0.34, and was considered to be transient fish. Cluster 3 contained 9 fish, had an average silhouette width of 0.64, and was considered to be AL River residents (Figure 4). The movement metrics used to define clusters showed clear separation among movement groups (Kruskal-Wallis; all $p<0.001$; Table 1 and 2). In addition, all possible comparisons of movement metrics across clusters were significant except for the difference in the median RKM distance between steps for clusters 2 and 3 ($p = 0.68$) (Table 2), the difference in movement rate per day between clusters 2 and 3 ($p = 0.49$) (Table 2), and the ranges in river kilometer between clusters 1 and 2 ($p= 0.68$).

Fish in Cluster 1 appeared to be relatively transient during December-March, but once they reached the MTRD in March, they generally remained there (Figure 5). Individuals in this cluster had the significantly highest movement rate, range, and MTRD use throughout the year, with an intermediate downstream movement throughout the year, and the significantly lowest median step distance (Table 2). Fish in Cluster 2 tended to be more transient, often oscillating to and from the MTRD and even upstream past CLD (Figure 5). Individuals in this cluster had a high movement range and median step distance, and an intermediate movement rate, MTRD use, and downstream steps (Table 2). Fish in Cluster 3 tended to be more sedentary when compared to the other 2 clusters (Figure 5). These fish never entered the MTRD and once they passed CLD, they did not move back downstream of this structure. Individuals in this cluster had the lowest movement rate, range, MTRD use, and downstream steps, but the highest median step distance (Table 2).

Year 2 Detections

For year 2 detections, the optimal silhouette width was determined to be 2 clusters, with an overall average silhouette width of 0.46 (Figure 6). Cluster 1 contained 58 fish, had an average silhouette width of 0.47, and were considered AL River resident fish. Cluster 2 contained 20 fish, had an average silhouette width of 0.45, and were considered MTRD resident fish (Figure 7). Because the detections for Year 2 only contained 2 clusters, a Kruskal-Wallis Test was not needed, and a pairwise Wilcoxon rank-sum test was used to determine that all comparisons between each cluster and movement metric were significant except for the median distance between steps ($p = 0.093$) (Table 3).

Fish in Cluster 1 appeared to remain in the LAR throughout the year, although in early April, most individuals made a sudden downstream movement to the MTRD before immediately heading back upstream (Figure 8). Individuals in this cluster had significantly highest movement rate, range, and downstream steps, and significantly lowest MTRD use (Table 3). Fish in Cluster 2 almost exclusively used the MTRD throughout the year (Figure 8). Individuals in this cluster had significantly the highest MTRD use, but the significantly lowest movement rate, range, and downstream steps (Table 3).

Comparing Contingent Membership

When comparing cluster membership from Year 1 to Year 2, I had a subset of 43 fish that met the criteria for inclusion in the interannual cluster analyses. Of these 43 fish that were able to be classified in a cluster in both years, during Year 1, 26 were “MTRD Residents”, 11 were “Transient Fish”, and 6 were “AL River Residents.” In Year 2, 16 of the original “MTRD Resident” continued to display this movement behavior. 10 original “MTRD Resident” fish transitioned to becoming “AL River Residents.” Of the original “AL River Residents”, only 1 fish continued to display this movement behavior, while 5 “AL River Residents” transitioned to “MTRD Residents” from Year 1 to Year 2. Of the 11 “Transient Fish” in Year 1, 3 individuals transitioned into “MTRD Residents”, and 8 “Transient Fish” individuals transitioned into “AL River Residents.” (Figure 9).

Mobile-Tensaw River Delta Environmental Effects

Throughout the study period, 110 of 131 Paddlefish (83%) with valid movements were detected in the MTRD at least once (Figure 10). Generalized linear mixed models were used to evaluate how weekly MTRD detections were associated with environmental conditions, including salinity, temperature, and river gage height. During the environmental modeling period which occurred from 06/01/2025 – 04/15/2026, salinity at the upstream logger ranged from 0.00 to 1.15 ppt, while salinity at the downstream logger ranged from 0.00 to 11.71 ppt. Mean MTRD temperature ranged from 10.66 to 32.01°C, and gage height ranged from -0.234 to 1.765 m.

Weekly MTRD use was modeled as a binomial response, with fish identity included as a random intercept to account for repeated observations of individuals. Candidate models were compared using AICc. Of the 16 candidate models evaluated, three had ΔAICc values < 2 and were considered competitive. The top-ranked model included upstream salinity, mean MTRD temperature, and gage height. The second-ranked model included upstream salinity and mean MTRD temperature, while the third-ranked model included all four covariates. Because downstream salinity appeared only in the third-ranked competitive model and was absent from the top-ranked model, support for downstream salinity was weaker than support for upstream salinity, temperature, and gage height. To test whether temporal autocorrelation was an issue within my dataset, I used scaled DHARMa residuals that were ordered by date within each fish. Lag-1 autocorrelation was calculated separately for each fish. The mean lag-1 autocorrelation across all fish tested was -0.0528, indicating near-zero temporal autocorrelation in the model residuals. In the top-ranked model, MTRD use was positively associated with both salinity at the upstream logger ($\beta = 3.42 \pm 0.82$ SE, $p < 0.001$) and with mean MTRD temperature ($\beta = 6.89 \pm 0.84$ SE, $p < 0.001$), and negatively associated with gage height ($\beta = -0.63 \pm 0.324$, $p = 0.05$).

Manual Tracking

Manual tracking provided additional information on Paddlefish locations and experienced environmental conditions throughout the study area. Although these additional detections were not included in the acoustic telemetry clustering model due to low detection probabilities, they still provide important insight into Paddlefish location information. Tracking events that took place in the LAR during spring 2025 and Winter 2026 and in the MTRD during Winter 2025 and Spring 2025 were not included given that no fish were detected.

During Winter 2025, 12 unique individuals were detected in the LAR. Fish 44500 was detected just downstream of CLD on 2025-02-13, then subsequently detected roughly 52.5 RKM downstream the next day (Figure 11). Individuals detected in this area and season experienced an average water temperature of 13.55 C and an average salinity level of 0.1 ppt. In Summer 2025, 1 individual was detected in the LAR. This individual experienced a water temperature of 37.04 C and a salinity of 0.06 ppt (Figure

12). In the MTRD during Summer 2025, 22 unique individuals were detected. Fish 16400 was detected in the lower Tensaw River, but then later in the day moved roughly 15 RKM and was detected in the Mobile River (Figure 13). Individuals in this area experienced an average water temperature of 31.48 C and an average salinity of 0.11 ppt. In the LAR, during Fall 2025, 7 unique individuals were detected and experienced an average water temperature of 18.70 C and an average salinity of 0.10 ppt (Figure 14). In the MTRD during Fall 2025, 22 unique individuals were detected. Fish 17650 was detected in the lower Tensaw River on 2025-11-04, and then again in the same place on 2025-11-24 (Figure 15). Individuals in this area experienced an average water temperature of 21.35 C and an average salinity of 0.10 ppt. in the MTRD during Winter 2026, 6 unique individuals were detected. These individuals experienced an average water temperature of 13.98 C and an average salinity level of 1.57 ppt (Figure 16). In the LAR during Spring 2026, 13 unique individuals were detected. These individuals experienced an average water temperature of 16.86 C and an average salinity of 0.11 ppt (Figure 17). In the MTRD during Spring 2026, 1 individual was detected. This individual experienced a water temperature of 20.60 C and a salinity of 0.10 ppt (Figure 18). In the LAR during Summer 2026, 1 individual was detected. This individual experienced a water temperature of 26.00 C and a salinity of 0.10 ppt (Figure 19). In the MTRD during Summer 2026, 17 unique individuals were detected. These individuals experienced an average water temperature of 28.12 C and an average salinity of 0.10 ppt (Figure 20).

Discussion

Here I evaluated broad-scale movement patterns of Paddlefish tagged below CLD, year-to-year consistency in movement strategies, use of the MTRD, and environmental factors associated with presence in the MTRD. Paddlefish in this study did not exhibit a single movement pattern but, fish tended to display several different movement behaviors. Most tagged Paddlefish (83%) used the MTRD at some point during the study. While some individuals moved repeatedly between the river and delta, others remained primarily within the Alabama River. Similar patterns of river and delta use were observed by Mettee et al. (2006) although they reported that a large number of their tagged Paddlefish were Alabama River resident fish, which was not what I observed in year 1 of my study, but similar patterns were observed for year 2 of my study (12% in year 1 and 74% in year 2). When movement strategies were compared between years, many year 1 MTRD resident fish continued to use the MTRD in year 2, whereas transient and Alabama River resident fish showed greater shifts in movement strategy. Statistical modelling incorporating environmental conditions as predictive factors suggested that Paddlefish presence in the MTRD was associated with upstream salinity, mean water temperature, and river stage. These environmental variables are highly correlated to seasonal conditions, thereby reflecting the broader seasonal and hydrologic conditions that coincide with Paddlefish occupation of the MTRD rather than directly driving habitat use.

Throughout the study, Paddlefish used both deltaic and riverine habitats throughout the year, using them at different rates from year to year. From May 2025 - December 2025, around 87% of the tagged Paddlefish were detected in the MTRD for extended periods of time. This pattern may be related to the abundance of foraging locations in backwater and oxbow habitats that characterize the MTRD (Hoxmeier and DeVries 1997; Burr and Warren 2014; Scarnecchia et al. 2019). The remaining Paddlefish remained in Claiborne Lake, and a small proportion remained in the LAR. Of the Paddlefish that remained in the LAR during summer and fall of 2025, more were detected in the reservoir formed upstream of CLD than in the stretch of river between CLD and the confluence of the Tombigbee and Alabama rivers. The reservoir formed by CLD (Claiborne Lake) is a much more lentic system when compared with the stretch of river below CLD, and it offers more backwater habitats for those fish that did not move downstream into the MTRD during summer and fall.

Relative to my first objective, which was to identify potential spawning contingents and describe broad movement patterns, I identified three distinct movement patterns during year 1: MTRD Residents, Transient Fish, and Alabama River Residents. Individuals classified as MTRD Residents were tagged directly below Claiborne Lock and Dam during the spawning season, similar to most other tagged individuals that year. An additional seven individuals were tagged approximately 50 RKM downstream of CLD. Of these seven fish, three were classified as Transient Fish, two as MTRD Residents, and two as Alabama River Residents. MTRD Residents moved repeatedly between the Claiborne Lock and Dam area and the MTRD during January 2025 through May 2025 before moving downstream and remaining primarily within the MTRD until the following spawning season in late 2025. During December 2025, most individuals (75%) in this cluster returned upstream toward Claiborne Lock and Dam, suggesting a repeated seasonal movement pattern that may have been associated with spawning.

This behavior is consistent with previous studies documenting some spawning site fidelity in Paddlefish (Lein and DeVries 1998; Stancill et al. 2002; Firehammer and Scarnecchia 2007). Therefore, individuals in this group could represent a spawning contingent, in which fish use the same general spawning area during consecutive spawning seasons and then migrate downstream to occupy more suitable non-spawning habitats during summer and winter (Clark 1968; Secor 1999).

Paddlefish in the second identified movement pattern, "Transient Fish", were characterized by making sporadic long-distance (> 200 RKM) movements throughout the year. Individuals displaying this behavior remained below CLD until late February 2025 when most of them (63%) passed CLD going upstream during an inundation period, inhabiting Claiborne Lake until March 2025. These Transient Fish made a series of downstream movements into the MTRD during April 2025 and May 2025. During July 2025, these fish all made a sudden upstream movement and passed CLD. These individuals then moved back downstream during August and September 2025 to the MTRD, where they remained until moving back to CLD at the same time as the year 1 MTRD Residents in November - December 2025. Mettee et al. (2006) documented transient individuals in their report but did not report any sudden upstream movement in the late summer as I observed. Because individuals in this cluster were able to pass Claiborne Lock and Dam during this period, and because this movement coincided with elevated gage height, this late-summer movement may have been associated with a discharge-related cue. Similar associations between increased flow, water level, and upstream Paddlefish movements have been reported in other systems (Jennings and

Zigler 2009; Lallaman 2012; Pracheil et al. 2014) although primarily during the spawning perid

Individuals in the third identified movement behavior during year 1, “AL River Residents”, were characterized by little to no downstream movement past CLD. These fish remained in or near the CLD tailrace until April 2025, after which they passed CLD going upstream during an inundation period, remaining in Claiborne Lake throughout the rest of the year. Mettee et al. (2006) observed similar resident movement behavior in the Alabama River, although resident fish made up a larger proportion of their observations than was observed here. In year 1 of my study, Alabama River Residents included the fewest individuals of the three movement-behavior groups. One possible explanation for this difference is that most fish sampled by Mettee et al. (2006) were collected in the Miller’s Ferry Lock and Dam tailrace, the next upstream dam from CLD, many of which remained further upstream, between CLD and Miller’s Ferry Lock and Dam. In contrast, relatively few Paddlefish tagged below CLD in my study remained in Claiborne Lake after passing the dam but rather they moved back downstream of CLD. This difference could lend support for the possibility that Paddlefish associated with different spawning areas in the Alabama River represent distinct movement contingents. Fish that spawn in Miller’s Ferry Lock and Dam tailrace may make greater use of Claiborne Lake and the Alabama River, whereas fish spawning below Claiborne Lock and Dam may be more likely to use the MTRD during non-spawning periods. This pattern is consistent with the general concept of migratory contingents, in which groups within a population exhibit distinct but repeated patterns of habitat use and movement (Clark 1968; Secor 1999). To confirm the consistency of the movement of these fish would require additional tagging and tracking of fish in the Millers Ferry Lock and Dam tailrace.

In Year 2, only two distinct movement behaviors were observed: “Alabama River Residents” and “MTRD Residents.” Individuals classified as Alabama River Residents made up the majority of fish detected during this period (74%) and they generally remained in or near the Claiborne Lock and Dam tailrace until April 2026. Between March and April 2025, many individuals made brief downstream movements into the MTRD before quickly returning upstream and passing Claiborne Lock and Dam toward the end of April 2026. Because the second year of detections only included approximately five months of data, interpretation of this movement behavior requires some caution. Although this group was found to be statistically distinct from MTRD Residents, some individuals displayed movements that were similar to the Transient Fish observed in Year 1. Specifically, several fish moved downstream into the MTRD before making rapid upstream movements back toward Claiborne Lock and Dam and into Claiborne Lake. Therefore, it is possible that this Year 2 Alabama River Resident group included individuals that may have been classified as Transient Fish if detections had continued across a full annual cycle.

The second movement behavior observed in Year 2, “MTRD Residents,” was characterized by continued use of the MTRD throughout most of the second year. Most individuals in this group remained in the MTRD until February 2026, when they moved slightly upstream to approximately RKM 50, or about halfway to CLD. Later that month, these fish returned downstream to the MTRD, where they remained for the rest of the study period. This pattern could be consistent with non-annual spawning, which has been documented in Paddlefish populations in this and other systems (Lein and DeVries 1998; Scarnecchia et al. 2007; Tripp et al. 2019; Johnston et al. 2023). However, movement-group membership alone cannot determine whether these individuals spawned. Their continued use of the MTRD may reflect differences in reproductive condition, the timing or extent of spawning movements, or other unmeasured factors. Therefore, these observations are best interpreted as evidence of predominant MTRD use during the study period rather than direct evidence that individuals delayed or skipped spawning.

Relative to my second objective, 43 Paddlefish had sufficient detections to be assigned to a movement-behavior group in both Year 1 and Year 2 and were compared to evaluate whether individuals maintained similar movement strategies between years. Of these individuals, 40% retained their original cluster (movement) membership from Year 1 to Year 2, suggesting that some Paddlefish exhibited repeated movement behavior across years, while others shifted movement strategies. This pattern is consistent with the concept of migratory contingents, in which individuals within a population may exhibit distinct seasonal movement patterns, but also suggests that these strategies may not be fixed for all individuals (Secor et al. 2020; Chapman et al. 2012). Annual shifts in movement behavior could be influenced by several factors, including reproductive condition, spawning periodicity, energetic costs associated with migration, or variation in environmental conditions among years (Firehammer and Scarnecchia 2007; Scarnecchia et al. 2007; Tripp et al. 2019). Similar flexibility in migratory behavior has been described in partially migratory fishes, where individuals within the same population may differ in whether, when, or how far they migrate among seasons or years (Chapman et al. 2012; Brönmark et al. 2014). Additionally, because Year 2 only represented approximately five months of detections, some individuals classified as Alabama River Residents or MTRD Residents might have exhibited additional movements later in the year if monitoring had continued across a complete annual cycle.

Although distinct movement patterns were evident within each year, these behaviors did not appear to represent fixed, long-term strategies at the individual level. Many Paddlefish shifted between MTRD-oriented and Alabama River-oriented behaviors across years, while others repeated similar patterns, indicating that movement behavior in this population was flexible. Therefore, the groups identified in this study are better interpreted as annually expressed movement contingents rather than stable subpopulations composed of individuals that consistently follow the same movement strategy throughout their lives. Such flexibility may allow individuals to adjust their use of riverine and estuarine habitats in response to changing reproductive condition, energetic demands, habitat quality, and opportunities for passage among habitats (Secor 1999; Chapman et al. 2012). The movement pattern expressed by an individual each year may therefore depend not only on its previous behavior, but also on the environmental conditions that influence habitat connectivity and suitability throughout the system. Such flexibility highlights the importance for mitigating fish passage at these barriers that impede free movement between these mostly separate river reaches. This behavioral flexibility provides an important context for interpreting the environmental associations examined under my third objective.

Relative to my third objective, my measured environmental factors were both associated with Paddlefish presence in the MTRD, suggesting that use of the delta may be influenced by both riverine and estuarine conditions. Paddlefish presence in the MTRD was most strongly associated with upstream salinity, mean water temperature, and river stage. Although downstream MTRD salinity was considered as a potential predictor, it was not retained in the most parsimonious model, suggesting that salinity farther downstream in the MTRD was less useful for explaining Paddlefish presence than upstream salinity, temperature, and river stage during the study period.

Although downstream salinity was not retained in the top model, detections at the most downstream Tensaw River receiver are still biologically interesting. This receiver, located near the downstream salinity logger and just upstream of Mobile Bay, was the second most frequented receiver in the MTRD receiver array, detecting 70% of the tagged Paddlefish and recording 852,664 total detections. This number of detections suggest that Paddlefish may tolerate at least intermittent exposure to the salinity conditions that occur in the lower Tensaw River. However, because downstream salinity was not retained in the most parsimonious model, these detections should be interpreted as evidence of habitat use near a more estuarine portion of the MTRD rather than evidence that downstream salinity was associated with Paddlefish presence.

Paddlefish were more likely to be detected in the MTRD as upstream salinity increased. One possible explanation is that upstream salinity increased during summer and fall, when Paddlefish were more likely to occupy the MTRD, due to reduced freshwater inflow from the Alabama and Tombigbee rivers and increased estuarine influence within the MTRD (Norris et al. 2010; Balder et al. 2026). Mean water temperature was also positively associated with Paddlefish presence in the MTRD. Paddlefish were more likely to be detected in the delta as temperatures increased, which corresponds with the period when many individuals migrate back down river after spawning. This pattern is consistent with previous observations of Paddlefish using backwater or low-flow habitats after spawning and during warmer portions of the year, potentially as areas for foraging or refuge during non-spawning periods (Scarnecchia et al. 2011). In contrast, Paddlefish were less likely to be detected in the MTRD as river stage increased. This relationship suggests that higher river stage may be associated with upstream movement or reduced delta occupancy, particularly during winter and spring when seasonal rainfall can increase river stage and discharge. This pattern is consistent with previous studies showing that increased flow or water level can cue upstream movements by Paddlefish, especially during the spawning season (Lein and DeVries 1998; Schwinghamer et al. 2018; Tripp et al. 2019).

These results indicate that Paddlefish use of the MTRD was strongly associated with flow-related conditions throughout much of the year, rather than only during periods commonly associated with large-scale spawning and post-spawning movements. Hydrology likely influences Paddlefish movement throughout the system by affecting habitat conditions, river–estuary connectivity, and opportunities for passage among habitats. In fragmented and regulated systems such as the LAR, however, dams and altered flow regimes may modify the timing and magnitude of the hydrologic cues under which these movements historically occurred. These findings therefore highlight the importance of maintaining or restoring connectivity among riverine and estuarine habitats, particularly during periods when low-flow conditions may restrict upstream or downstream passage.

Manual tracking data provided additional and more precise spatial information for Paddlefish that was complementary to passive acoustic array detections. These additional fine-scale detections supported general trends that I observed with the passive acoustic array while also giving exact environmental conditions experienced by an individual at a particular location. In the spring, I tended to detect fish more often in the upper LAR, around CLD which coincides with fish making spawning migrations. In summer, I tended to detect more Paddlefish in the MTRD than in the LAR, which coincides with Paddlefish summer movement patterns in this system as well as in other systems (Southall and Hubert 1984; Zigler et al. 2004; Tripp et al. 2019). During fall, Paddlefish were detected in both the MTRD as well as the LAR. Most Paddlefish that were detected during this season were male, both in the MTRD as well as later in the fall in the LAR. An interesting observation was a large congregation of Paddlefish detected in the lower Tensaw River in summer and fall 2025. This could potentially be a congregation of males that formed, then subsequently moved upstream to prepare for spawning as a loose school, which has been observed in other systems, albeit rarely (Jennings and Zigler 2009). Interestingly, the following summer (2026), I detected a large sized congregation in the same location on the lower Tensaw River. Meyer (1960) observed a similar phenomenon and surmised that it was a feeding congregation. In the winter, most fish were detected throughout the LAR and lower MTRD similar to observations by Mettee et al. (2006, 2009) found that Paddlefish overwintered in the lower MTRD and even occurred in Mobile Bay. It is possible that Paddlefish are choosing to overwinter in Mobile Bay due to increased discharge during this season allows for more extended downstream movements into the bay (i.e., movements of fresher, low salinity water out into to Mobile Bay), as well as abundant foraging resources (Borom 1979).

Another notable observation was the detection of two Paddlefish in the lower MTRD during winter 2025 at locations where measured salinity was 4.50 ppt. This is biologically interesting because limited salinity tolerance information is available for Paddlefish, with one study suggesting that juvenile Paddlefish begin avoiding salinity near 4 ppt (Virgil 1999). Although these observations certainly do not quantify salinity tolerance, they suggest that adult Paddlefish in the Mobile Basin may tolerate at least short-term exposure to salinity levels near or above those previously reported to elicit avoidance behavior by juveniles. This finding highlights the need for additional research on salinity tolerance and estuarine habitat use by Paddlefish in coastal river systems.

Conclusions

Paddlefish in this system exhibited diverse and flexible movement patterns across the LAR, and MTRD. Paddlefish in this system did not follow any single dominant movement strategy, but instead, some fish repeatedly used the MTRD, some made long-distance transient movements between riverine and estuarine habitats, and others simply remained in the Alabama River primarily. Year-to-year comparisons in these observed movement behaviors showed that while just under half of these tagged individuals expressed the same movement behaviors between years, most did not shift movement behaviors between years. This indicates that there is variation as to whether year-to-years movement behaviors are fixed versus flexible. Environmental modeling suggested that MTRD use for Paddlefish was associated with upstream salinity, mean weekly water temperature, and river stage, highlighting the importance of both riverine and estuarine conditions in shaping Paddlefish distribution throughout the system although these factors could be coincident with the timing of Paddlefish spawning and post spawning movement. Together, these findings indicate that the MTRD represents important Paddlefish habitat in this coastal river system and should be considered as important movement destinations as well as critically important habitat alongside upstream riverine habitats when evaluating Paddlefish ecology, conservation, and management in the lower Mobile River Basin.

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Tables

Table 1. Kruskal-Wallis test results comparing movement metrics among k-means clusters for Year 1 detections. Significant p-values indicate that at least two clusters differed from another for that metric.

Year 1 Kruskal–Wallis tests comparing movement metrics among clusters					
Statistic	Movement rate (rkm/day)	River-kilometer range	Proportion of delta detections	Proportion of downstream steps	Median step size (rkm)
χ^2	25.79	23.85	48.85	49.32	51.50
df	2	2	2	2	2
P-value	<0.001	<0.001	<0.001	<0.001	<0.001

Table 2. Overall movement metrics during year 1 for Paddlefish in the lower Alabama River separated into three distinct clusters based on movement rate per day, range in RKM, proportion of time spent in the MTRD, proportion of downstream steps, and the average median step length between detections. Unique superscripts (*a, b, and c)* represent statistical differences in movement metrics, see Appendix 1 and 2.

Year 1 Paddlefish Movement Clusters						
		Movement metrics				
Cluster	**N fish**	**Movement rate (rkm/day)**	**Rkm range (rkm)**	**Delta events**	**Downstream steps**	**Median step (rkm)**
1	37	2.67 ± 1.03^{a}	226.66 ± 44.79^{a}	0.75 ± 0.15^{a}	0.54 ± 0.03^{a}	2.31 ± 0.93^{a}
2	24	1.62 ± 0.55^{b}	231.51 ± 46.54^{a}	0.33 ± 0.18^{b}	0.64 ± 0.06^{b}	9.79 ± 3.77^{b}
3	9	1.44 ± 0.38^{b}	74.16 ± 19.98^{b}	0.00 ± 0.00^{c}	0.48 ± 0.04^{c}	9.07 ± 3.39^{b}

Table 3. Overall movement metrics during year 2 for Paddlefish in the lower Alabama River separated into two distinct clusters based on movement rate per day, range in RKM, proportion of time spent in the MTRD, proportion of downstream steps, and the average median step length between detections. Unique superscripts (*a and b)* represent statistical differences in movement metrics, see Appendix 3.

Year 2 Paddlefish Movement Clusters						
		Movement metrics				
Cluster	**N fish**	**Movement rate (rkm/day)**	**Rkm range (rkm)**	**Delta events**	**Downstream steps**	**Median step (rkm)**
1	58	3.81 ± 1.76^{a}	169.01 ± 40.34^{a}	0.21 ± 0.17^{a}	0.62 ± 0.10^{a}	8.07 ± 3.67^{a}
2	20	0.91 ± 0.53^{b}	32.77 ± 11.63^{b}	0.85 ± 0.37^{b}	0.44 ± 0.06^{b}	10.51 ± 5.39^{a}

Table 4. AICc table for GLMM evaluating factors associated with MTRD use by Paddlefish in the study area. Factors represented are the model number from the overall model selection, upstream MTRD salinity, downstream delta salinity, gage height for the MTRD, mean temperature in the MTRD between the upstream and downstream temperature loggers, the number of estimated parameters in the model K, the mean log likelihood of how well the model fits the data, AICc scores, the difference between AICc scores, and the weight of each model.

Model-selection Results for MTRD Use

	Environmental covariates included				Model fit				
Model	**Upstream salinity**	**Downstream salinity**	**Temperature**	**Gage height**	**K**	**Log likelihood**	**AICc**	**ΔAICc**	**AICc weight**
1	X		X	X	7	−934.81	1,883.68	0.00	0.509
2	X		X		6	−936.69	1,885.43	1.75	0.213
3	X	X	X	X	8	−934.75	1,885.56	1.88	0.199

Figures

Figure 1. Map of the study area, indicating the two dams (green diamonds), locations of acoustic receivers (red circles), and salinity loggers (yellow triangles).

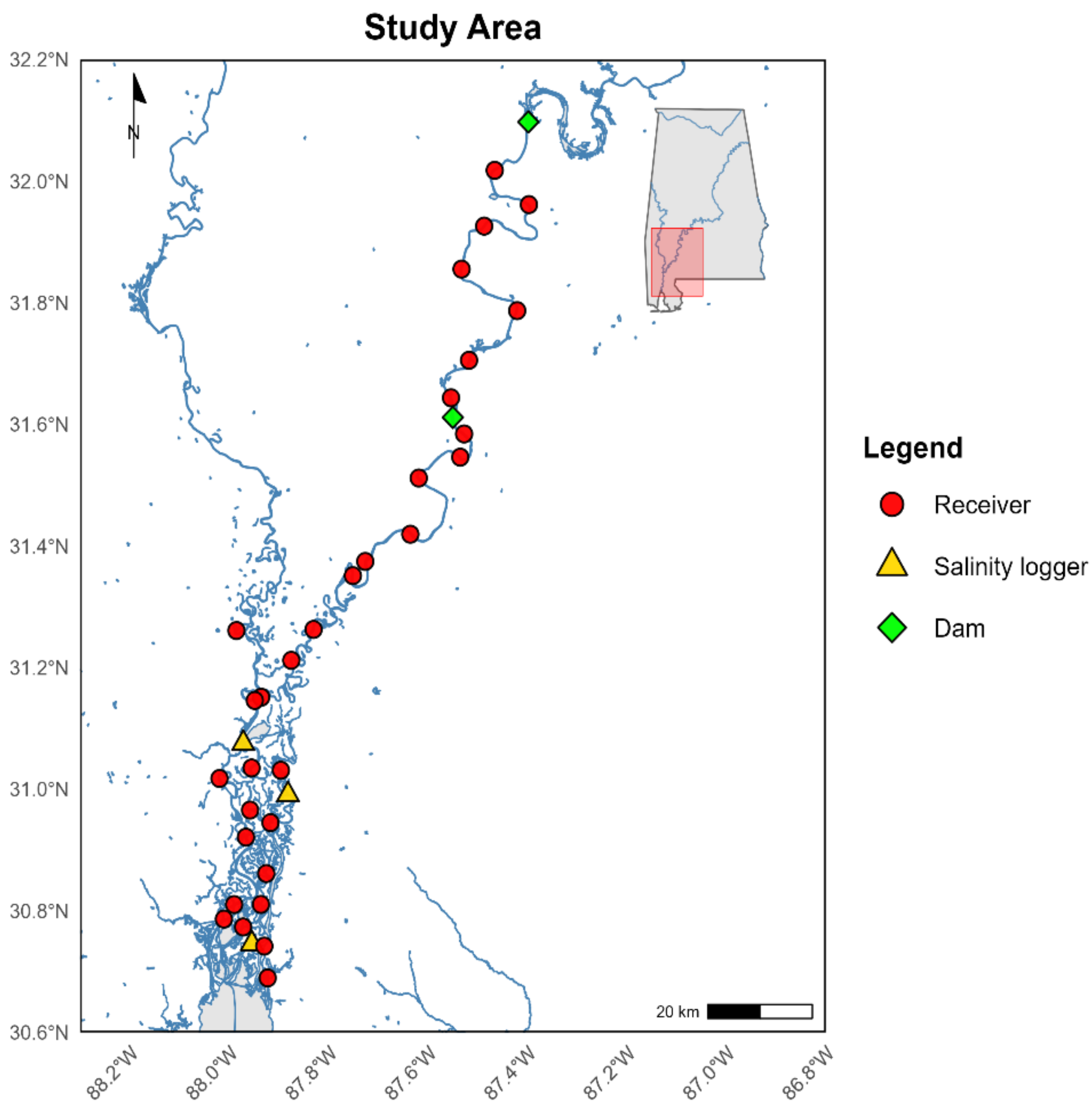


Figure 2. Length and weight distributions of all tagged Paddlefish throughout the study. Boxes represent the interquartile range, while the dark line in the box is the median, the whiskers are observations within 1.5 times the interquartile range, and individual data points are potential outliers.

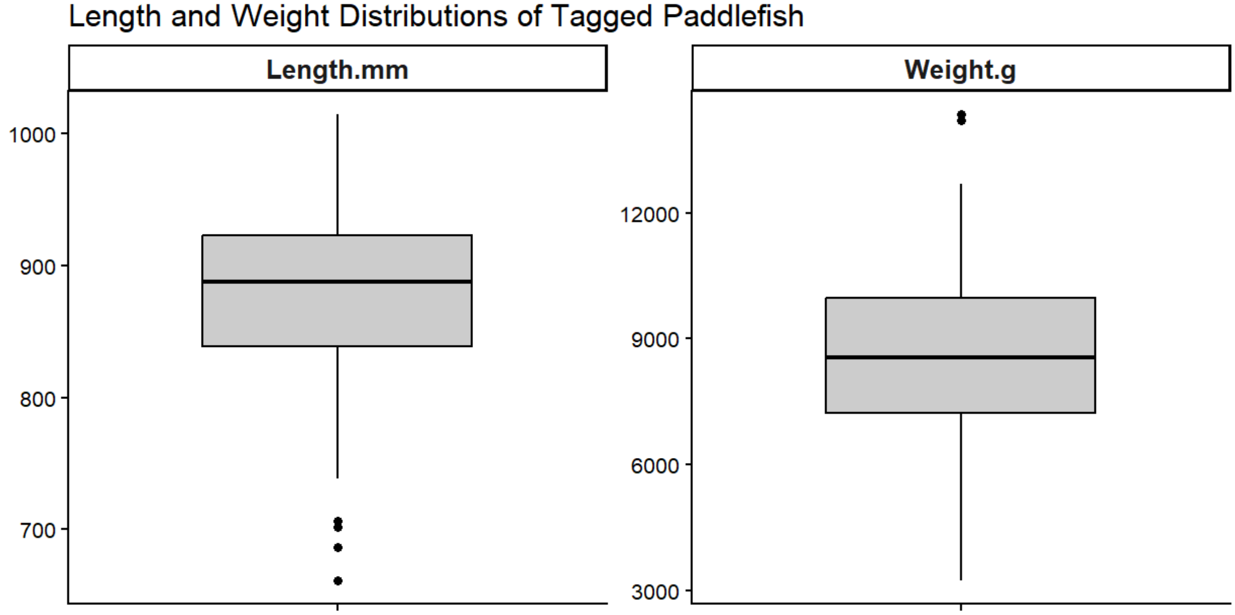


Figure 3. Average silhouette width for year 1 individuals as a function of the number of clusters (k). A sensitivity analysis was run using the z-normalized movement metrics to determine the optimal number of clusters (k) with which to run a k-means clustering analysis. The number of clusters with the highest average silhouette width was chosen.

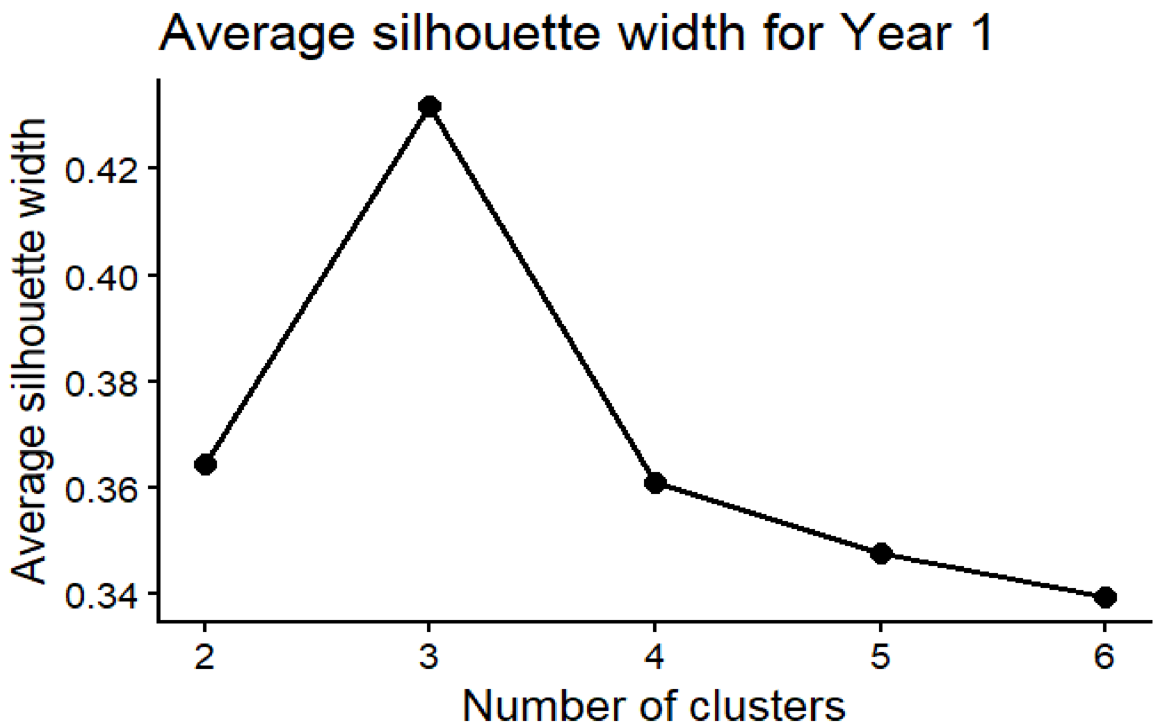


Figure 4. Silhouette width for each individual Paddlefish detected in Year 1, ordered in decreasing width within each cluster. Cluster 1 represents “MTRD Resident Fish”, Cluster 2 represents “Transient Fish”, and Cluster 3 represents “Alabama River Resident Fish.” The dotted horizontal line represents the average model silhouette width, 0.43.

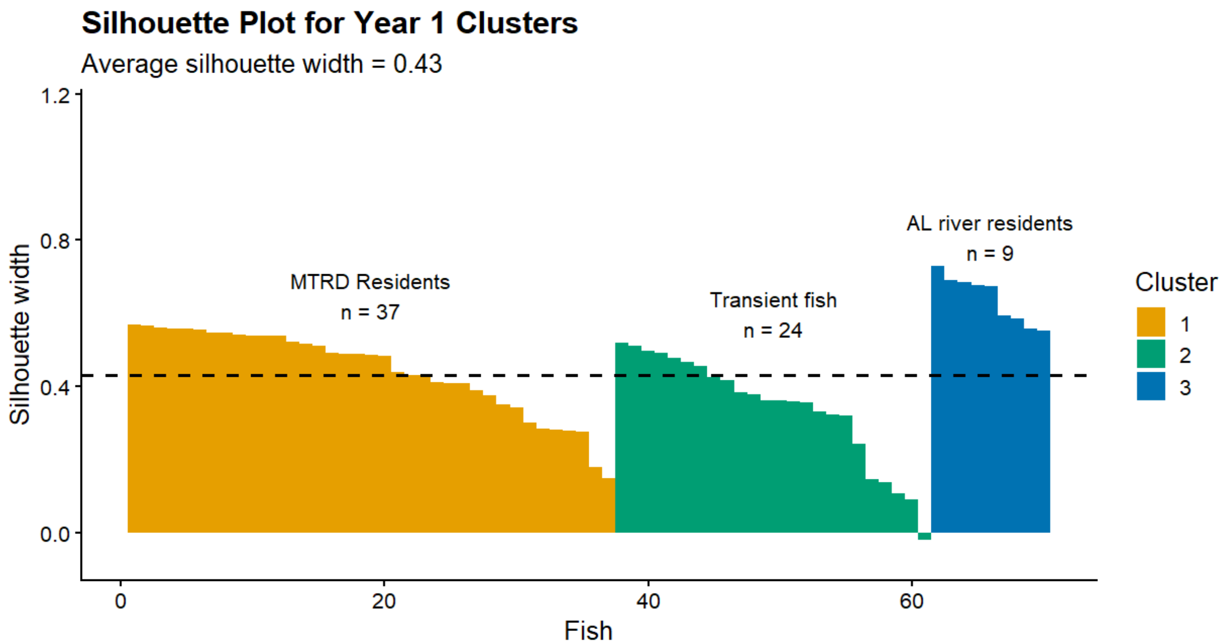


Figure 5. Year 1 cluster movements for the three different identified clusters. Cluster 1 represents “MTRD Resident Fish.” Cluster 2 represents “Transient Fish.” Cluster 3 represents “Alabama River Resident Fish.” Each bold line represents the median location of individuals per date with the shadow above the line representing the upper quantile and the shadow below the line representing the lower quantile. The highest dotted horizontal line represents Claiborne Lock and Dam. The lower dotted horizontal represents the beginning of the Mobile-Tensaw River Delta.

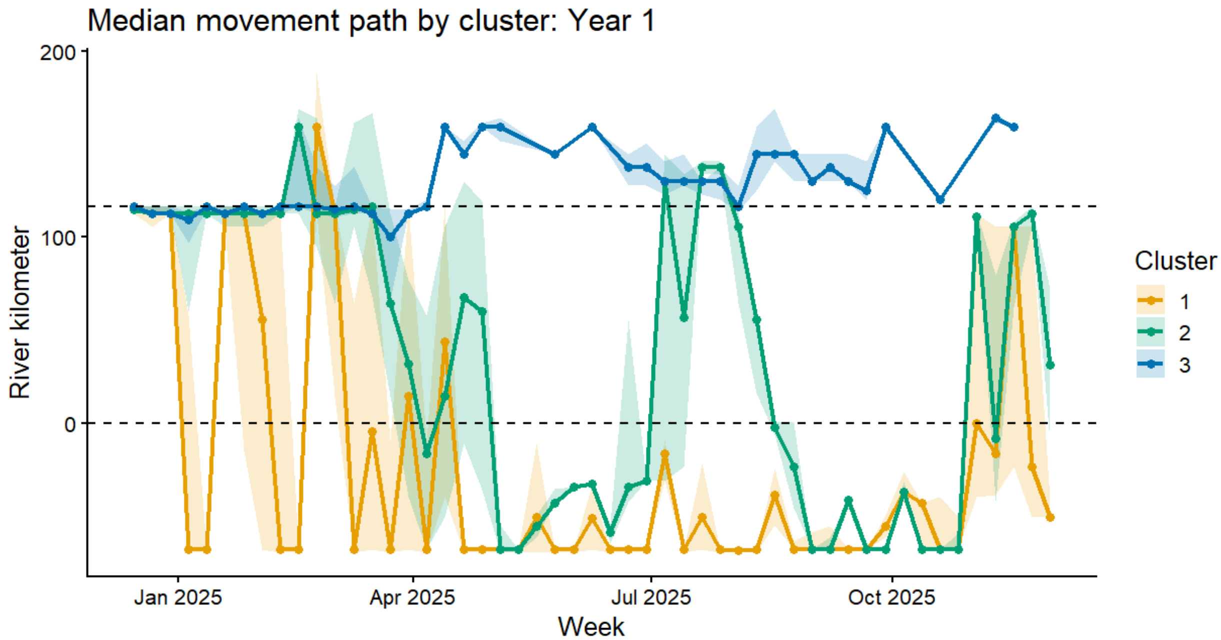


Figure 6. Average silhouette width for year 2 individuals as a function of the number of clusters (k). A sensitivity analysis was run using the z-normalized movement metrics to determine the optimal number of clusters (k) with which to run a k-means clustering analysis. The number of clusters with the highest average silhouette width was chosen.

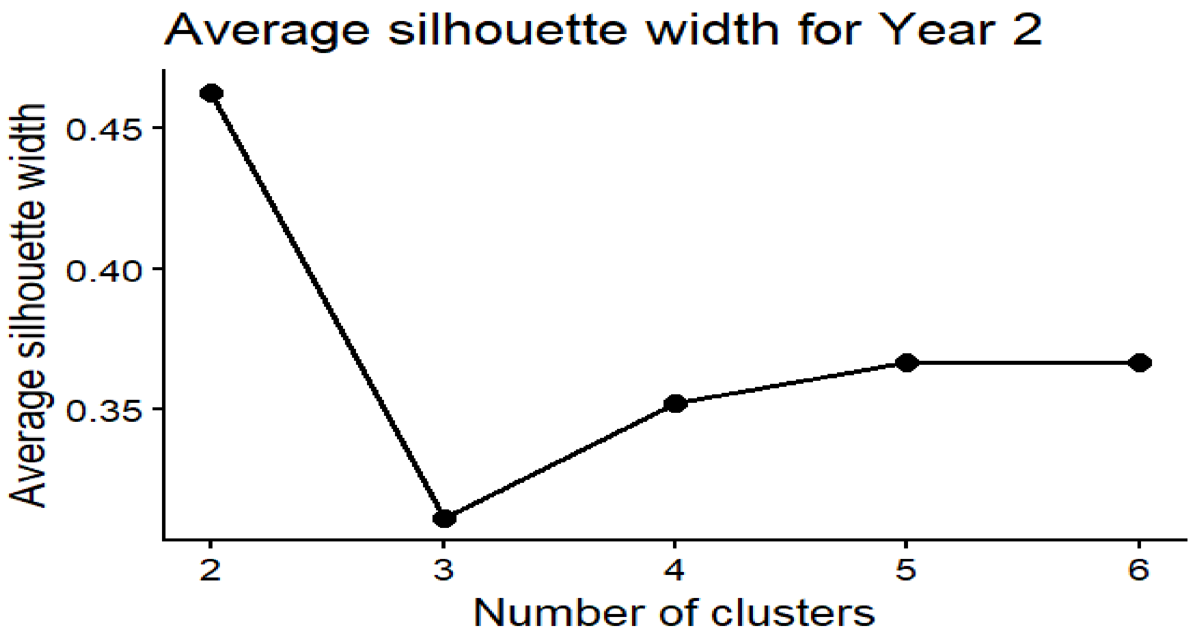


Figure 7. Silhouette width for each individual Paddlefish detected in Year 2, ordered in decreasing width within each cluster Cluster 1 represents “Alabama River Resident Fish,” and Cluster 2 represents “MTRD Resident Fish.” The dotted horizontal line represents the average model silhouette width, 0.46.

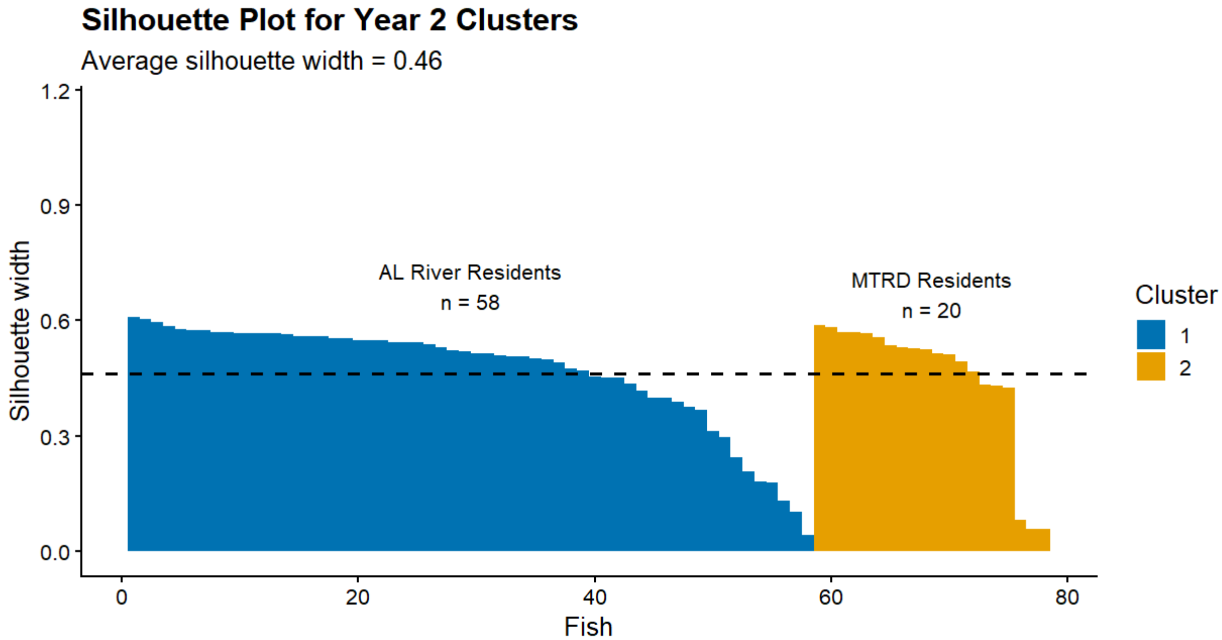


Figure 8. Year 2 cluster movements for the two different identified clusters. Cluster 1 represents “Alabama River Resident Fish.” Cluster 2 represents “MTRD Resident Fish.” Each bold line represents the median location of individuals per date with the shadow above the line representing the upper quantile and the shadow below the line representing the lower quantile. The highest dotted horizontal line represents Claiborne Lock and Dam. The lower dotted horizontal represents the beginning of the Mobile-Tensaw River Delta.

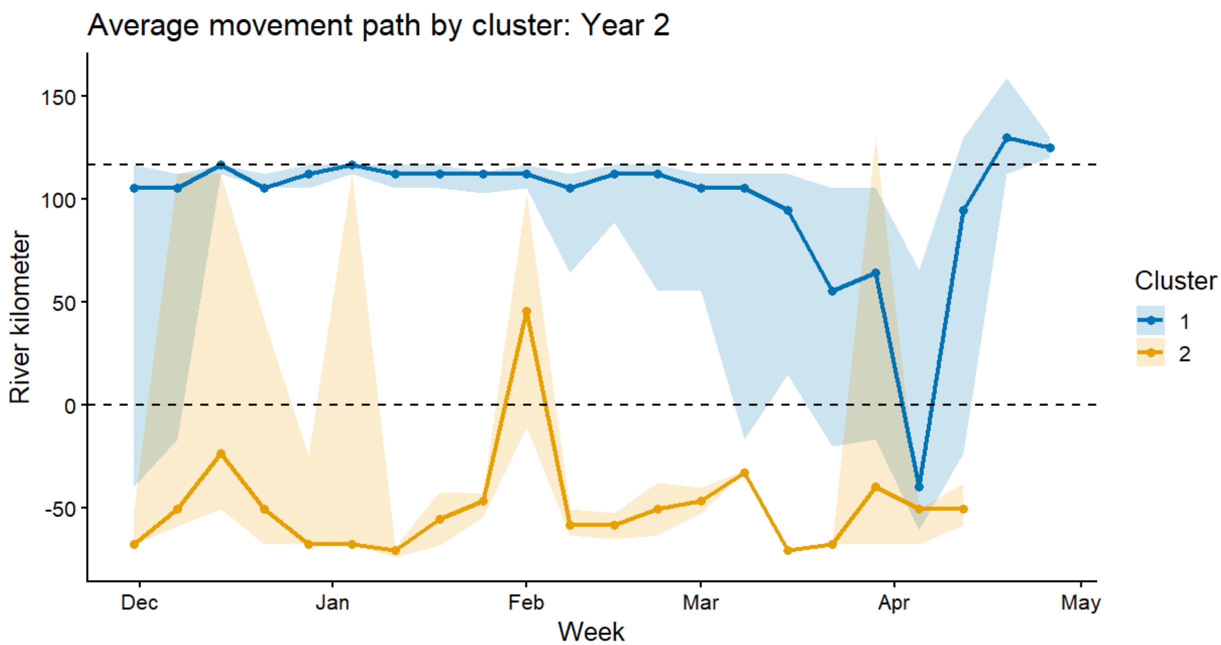


Figure 9. Alluvial diagram displaying how cluster membership shifted or stayed the same from Year 1 to Year 2. 61.5% of Year 1 “MTRD Residents” maintained their movement behavior in Year 2. 38.5% of Year 1 “MTRD Residents” shifted to “AL River Residents” in Year 2. 27.3% of Year 1 “Transient Fish” shifted to “MTRD Residents” in Year 2. 72.7% of Year 1 “Transient Fish” shifted to “AL River Residents” in Year 2. 83.3% of Year 1 “AL River Residents” shifted to “MTRD Residents” in Year 2. 16.7% of “AL River Residents” maintained their movement behavior in Year 2.

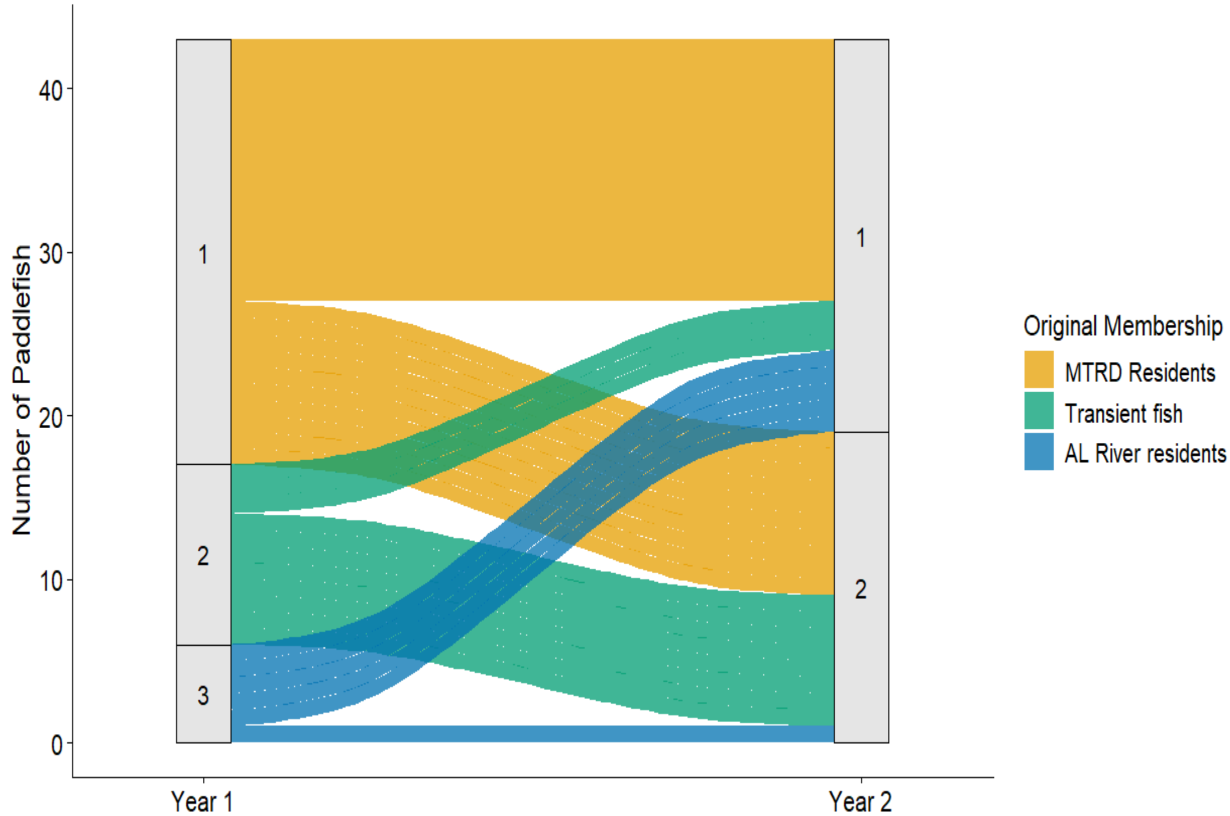


Figure 10. The percentage of Paddlefish with active tags located in particular areas of the lower Alabama River and Mobile-Tensaw River Delta from December 2024-May 2026. Each color represents a distinct river section in which a fish was located.

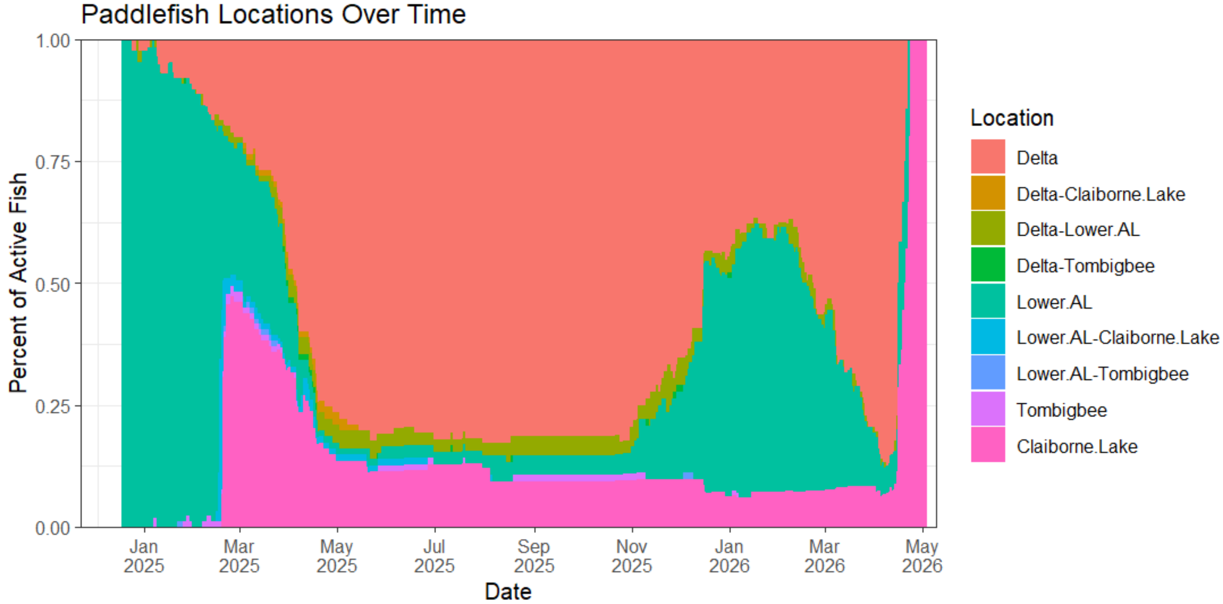


Figure 11. Individual locations of Paddlefish tracked via manual receiver in the Lower Alabama River during Winter 2025.

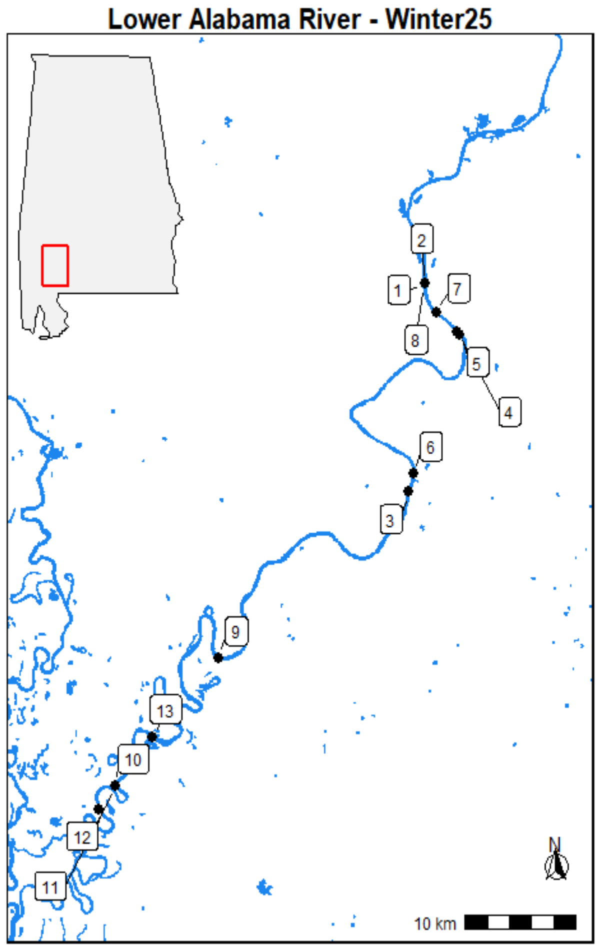


Figure 12. Individual locations of Paddlefish tracked via manual receiver in the Lower Alabama River during Summer 2025.

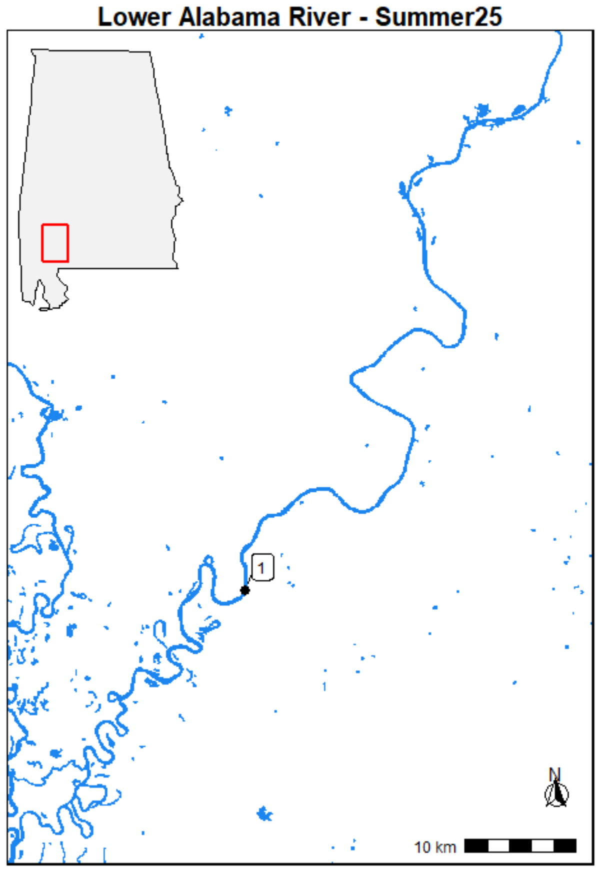


Figure 13. Individual locations of Paddlefish tracked via manual receiver in the Mobile-Tensaw River Delta during Summer 2025.

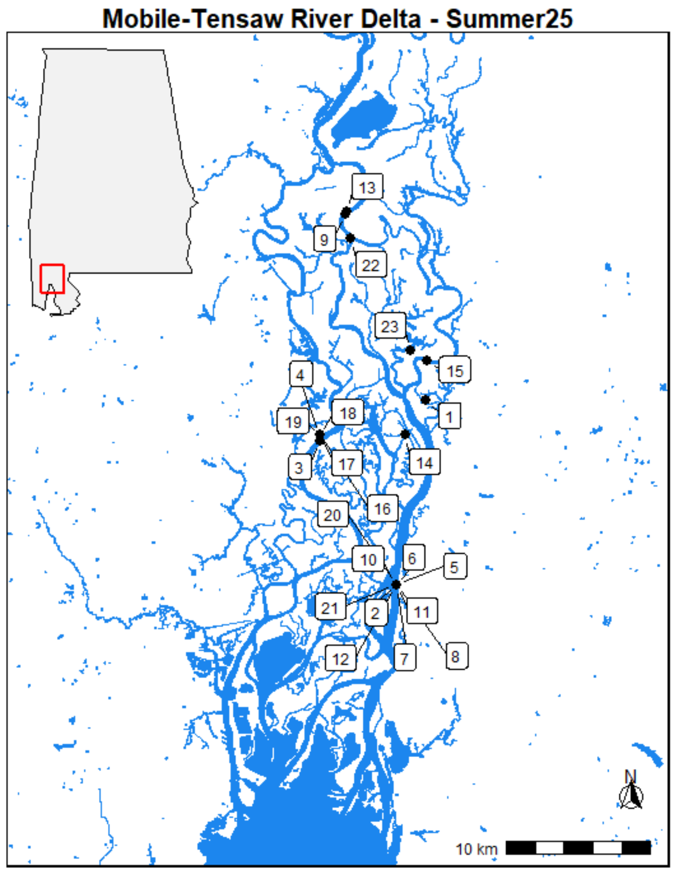


Figure 14. Individual locations of Paddlefish tracked via manual receiver in the Lower Alabama River during Fall 2025.

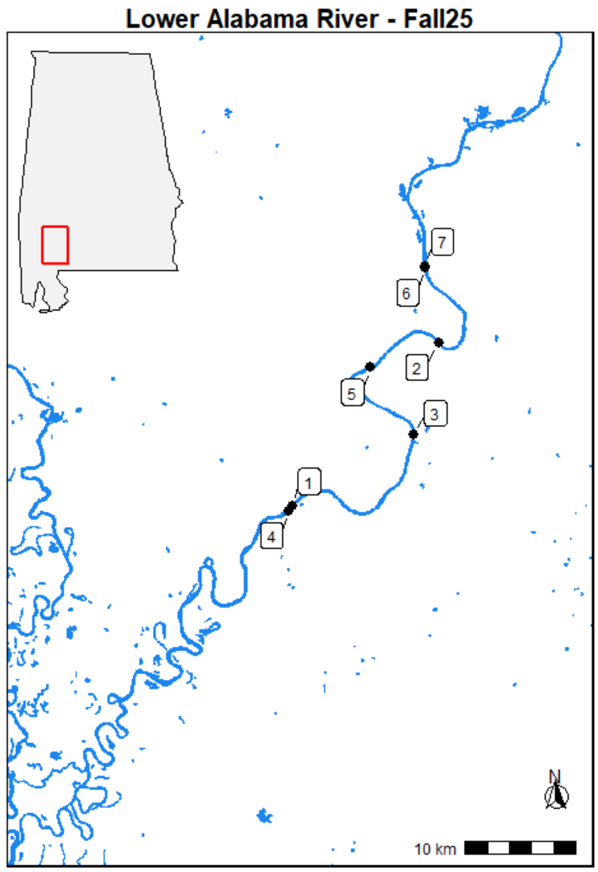


Figure 15. Individual locations of Paddlefish tracked via manual receiver in the Mobile-Tensaw River Delta during Fall 2025.

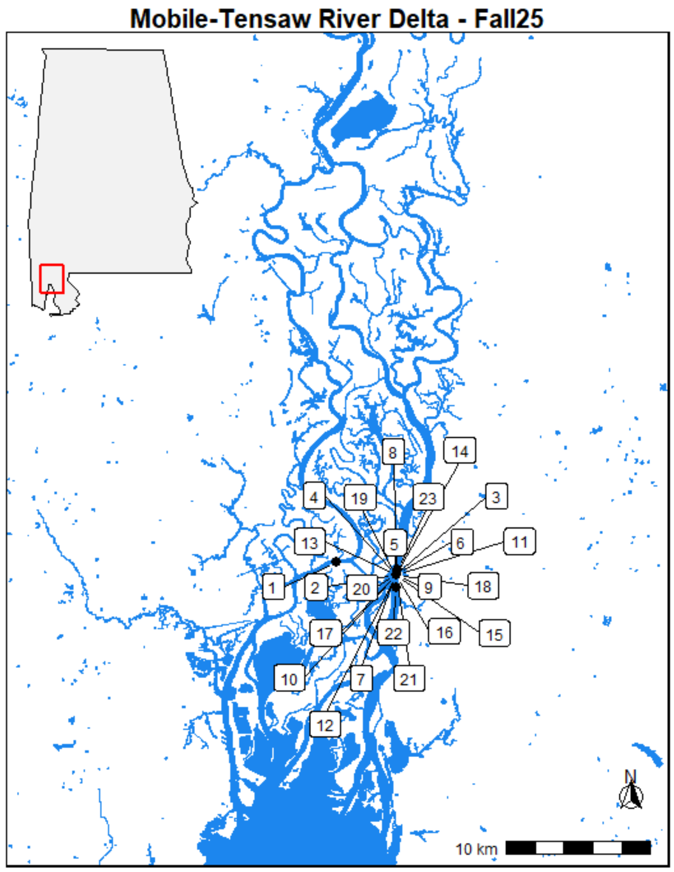


Figure 16. Individual locations of Paddlefish tracked via manual receiver in the Mobile-Tensaw River Delta during Winter 2026.

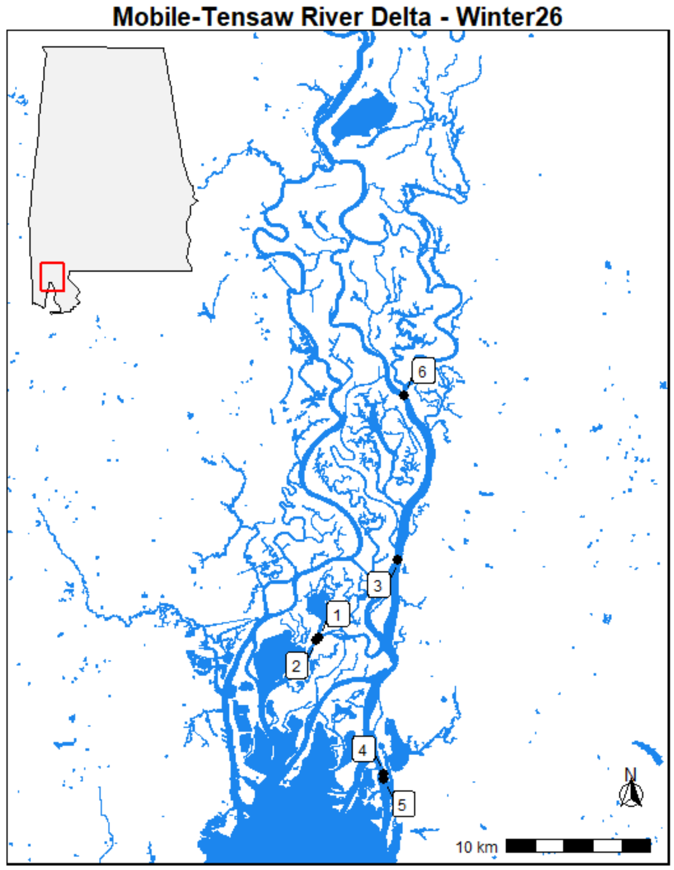


Figure 17. Individual locations of Paddlefish tracked via manual receiver in the Lower Alabama River during Spring 2026.

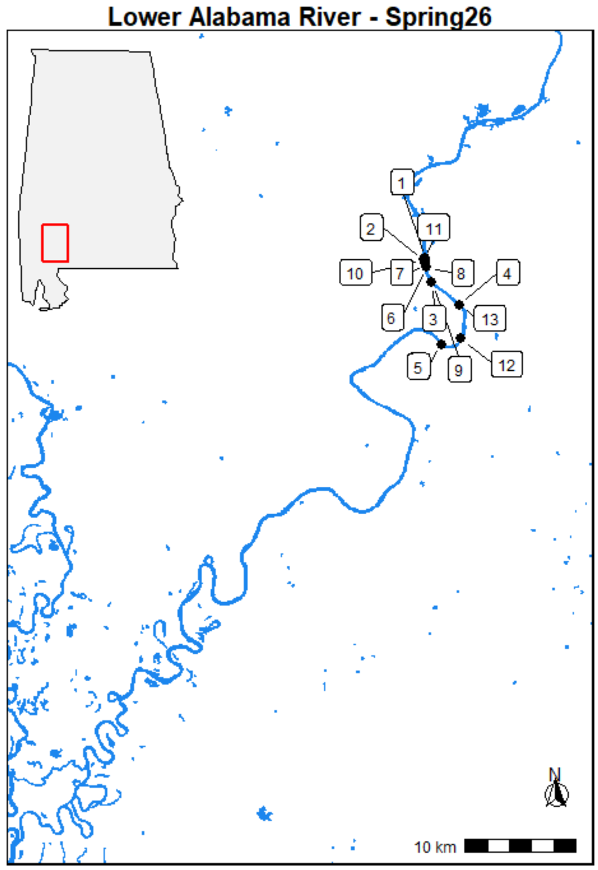


Figure 18. Individual locations of Paddlefish tracked via manual receiver in the Mobile-Tensaw River Delta during Spring 2026.

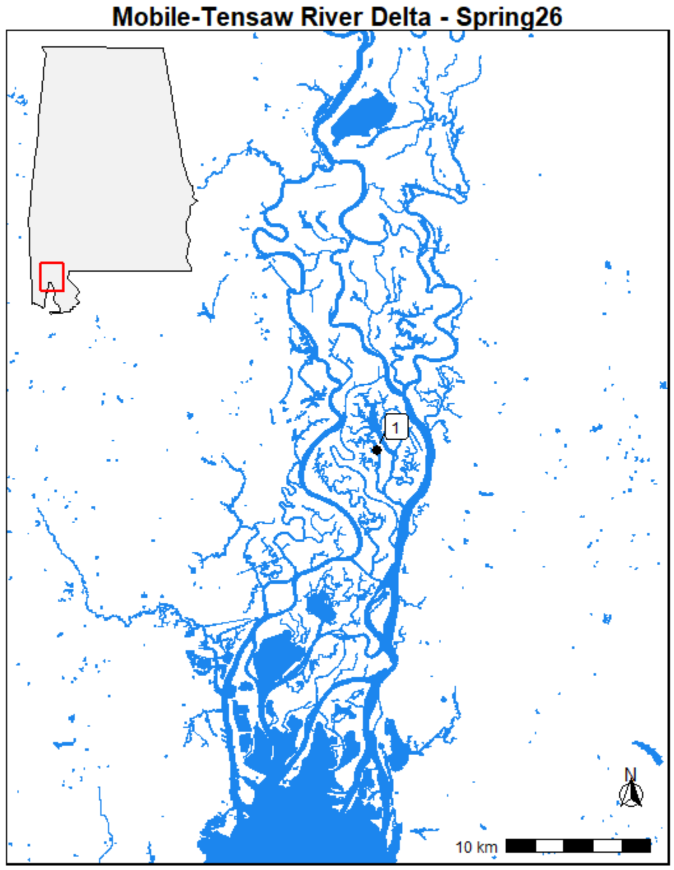


Figure 19. Individual locations of Paddlefish tracked via manual receiver in the Lower Alabama River during Summer 2026.

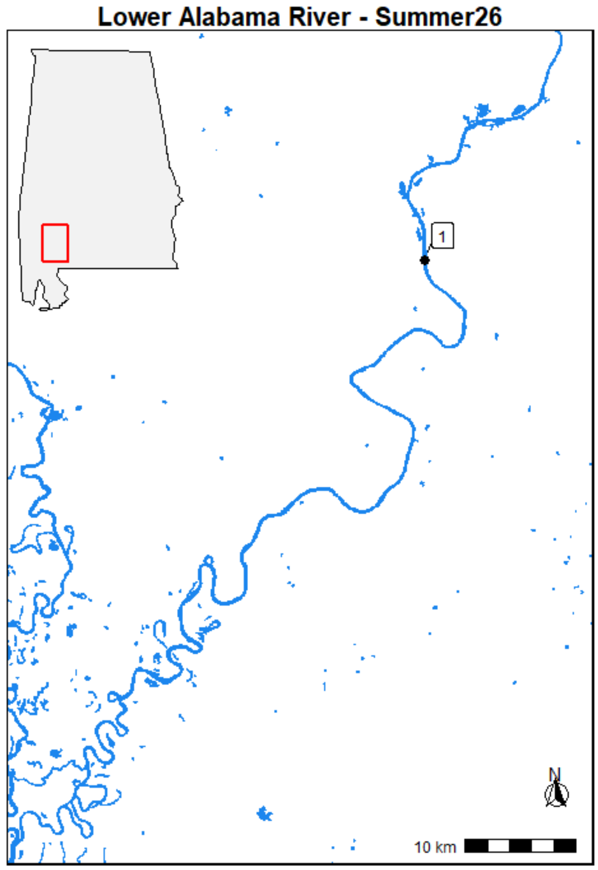
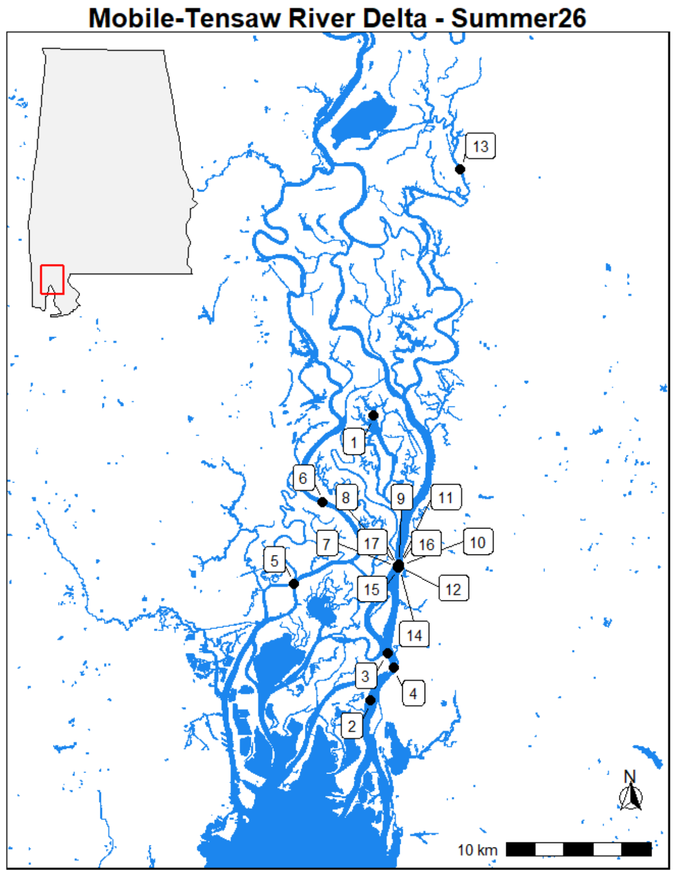


Figure 20. Individual locations of Paddlefish tracked via manual receiver in the Mobile-Tensaw River Delta during Summer 2026.



Appendices

Appendix 1
Pairwise Wilcoxon comparisons among k-means clusters for Year 1 detections.

Year 1 pairwise Wilcoxon comparisons among k-means clusters					
Statistic	**Movement rate (rkm/day)**	**River-kilometer range**	**Proportion of delta detections**	**Proportion of downstream steps**	**Median step size (rkm)**
Cluster 1 vs Cluster 2					
W	742.00	472.00	836.50	32.50	13.50
Adjusted p	<0.001	0.679	<0.001	<0.001	<0.001
Significance	****	ns	****	****	****
Cluster 1 vs Cluster 3					
W	297.00	333.00	333.00	315.00	9.00
Adjusted p	<0.001	<0.001	<0.001	<0.001	<0.001
Significance	***	****	****	****	****
Cluster 2 vs Cluster 3					
W	126.00	216.00	216.00	216.00	119.00
Adjusted p	0.486	<0.001	<0.001	<0.001	0.676
Significance	ns	****	****	****	ns

Appendix 2
Pairwise Wilcoxon comparisons among k-means clusters for Year 2 detections.

Year 2 pairwise Wilcoxon comparisons among k-means clusters

Statistic	Movement rate (rkm/day)	River-kilometer range	Proportion of delta detections	Proportion of downstream steps	Median step size (rkm)
Cluster 1 vs Cluster 2					
W	1137.00	1157.00	163.50	1133.00	434.00
Adjusted p	<0.001	<0.001	<0.001	<0.001	0.093
Significance	****	****	****	****	ns

Appendix 3.
Winter 2025 manual tracking data for individual paddlefish tracked in the Lower Alabama River along with the temperature, salinity, and latitude/longitude at their collection site.

Lower Alabama River Winter 2025 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	16950	2025-02-13	13.80	0.10	31.61239	−87.55102
2	17500	2025-02-13	13.80	0.10	31.61239	−87.55102
3	17600	2025-02-13	13.40	0.10	31.45711	−87.56696
4	32000	2025-02-13	13.50	0.10	31.57677	−87.52005
5	44000	2025-02-13	13.60	0.10	31.57492	−87.51751
6	44500	2025-02-13	13.60	0.10	31.47085	−87.56196
7	52800	2025-02-13	13.90	0.10	31.59109	−87.54005
8	72700	2025-02-13	13.80	0.10	31.61239	−87.55102
9	16750	2025-02-14	13.50	0.10	31.33306	−87.74759
10	17000	2025-02-14	13.30	0.10	31.23801	−87.84565
11	17850	2025-02-14	13.30	0.10	31.23801	−87.84565
12	18800	2025-02-14	13.30	0.10	31.22050	−87.86143
13	44500	2025-02-14	13.30	0.10	31.27421	−87.81062

Appendix 4.
Summer 2025 manual tracking data for the Lower Alabama River along with the temperature, salinity, and latitude/longitude at the fish's collection site.

Lower Alabama River Summer 2025 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	17750	2025-07-07	37.04	0.06	31.34284	−87.72250

Appendix 5.
Summer 2025 manual tracking data for the Mobile-Tensaw River Delta along with the temperature, salinity, and latitude/longitude at their collection site.

Mobile-Tensaw River Delta Summer 2025 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	16050	2025-07-17	31.10	0.08	30.92040	−87.89621
2	16150	2025-07-17	31.40	0.13	30.80574	−87.91775
3	16350	2025-07-17	31.50	0.09	30.89510	−87.97310
4	16400	2025-07-17	31.50	0.09	30.89892	−87.97310
5	16400	2025-07-17	31.40	0.13	30.80574	−87.91775
6	16600	2025-07-17	31.40	0.13	30.80574	−87.91775
7	16700	2025-07-17	31.40	0.13	30.80574	−87.91775
8	16800	2025-07-17	31.40	0.13	30.80574	−87.91775
9	16950	2025-07-17	31.20	0.08	31.03659	−87.95414
10	17050	2025-07-17	31.40	0.13	30.80574	−87.91775
11	17100	2025-07-17	31.40	0.13	30.80574	−87.91775
12	17250	2025-07-17	31.40	0.13	30.80574	−87.91775
13	17400	2025-07-17	31.20	0.08	31.03815	−87.95328
14	17550	2025-07-17	31.60	0.09	30.89892	−87.91098
15	18000	2025-07-17	31.10	0.08	30.94522	−87.89488
16	18100	2025-07-17	31.50	0.09	30.89892	−87.97310
17	44900	2025-07-17	31.50	0.09	30.89892	−87.97310
18	45000	2025-07-17	31.50	0.09	30.89892	−87.97310
19	52300	2025-07-17	31.50	0.09	30.89892	−87.97310
20	73300	2025-07-17	31.40	0.13	30.80574	−87.91775
21	74800	2025-07-17	31.40	0.13	30.80574	−87.91775
22	16450	2025-08-19	32.60	0.08	31.02105	−87.95050
23	17650	2025-08-19	32.20	0.08	30.95173	−87.90772

Appendix 6.
Fall 2025 manual tracking data for the Lower Alabama River along with the temperature, salinity, and latitude/longitude at their collection site.

Lower Alabama River Fall 2025 Manual Tracking Detections

Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	16150	2025-11-20	19.20	0.10	31.41399	−87.67774
2	16450	2025-11-20	18.50	0.10	31.54624	−87.53794
3	16750	2025-11-20	18.70	0.10	31.47194	−87.56234
4	17750	2025-11-20	19.20	0.10	31.40995	−87.68076
5	17800	2025-11-20	18.50	0.10	31.52652	−87.60348
6	43900	2025-11-20	18.40	0.10	31.60814	−87.55070
7	72900	2025-11-20	18.40	0.10	31.60904	−87.55063

Appendix 7.
Fall 2025 manual tracking data for the Mobile-Tensaw River Delta along with the temperature, salinity, and latitude/longitude at their collection site.

Mobile-Tensaw River Delta Fall 2025 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	17350	2025-11-03	20.70	0.10	30.81992	−87.96098
2	16250	2025-11-04	21.50	0.10	30.81202	−87.91780
3	16400	2025-11-04	21.50	0.10	30.81202	−87.91780
4	16500	2025-11-04	21.50	0.10	30.81202	−87.91780
5	16850	2025-11-04	21.50	0.10	30.81202	−87.91780
6	17000	2025-11-04	21.50	0.10	30.81202	−87.91780
7	17150	2025-11-04	21.50	0.10	30.81202	−87.91780
8	17200	2025-11-04	21.50	0.10	30.81202	−87.91780
9	17250	2025-11-04	21.50	0.10	30.81202	−87.91780
10	17450	2025-11-04	21.50	0.10	30.81202	−87.91780
11	17550	2025-11-04	21.50	0.10	30.81202	−87.91780
12	17650	2025-11-04	21.50	0.10	30.81202	−87.91780
13	17750	2025-11-04	21.50	0.10	30.81202	−87.91780
14	17950	2025-11-04	21.50	0.10	30.81202	−87.91780
15	18000	2025-11-04	21.50	0.10	30.81202	−87.91780
16	43600	2025-11-04	21.50	0.10	30.81202	−87.91780
17	52300	2025-11-04	21.50	0.10	30.81202	−87.91780
18	52700	2025-11-04	21.50	0.10	30.81202	−87.91780
19	73500	2025-11-04	21.50	0.10	30.81202	−87.91780
20	74800	2025-11-04	21.50	0.10	30.81202	−87.91780
21	16050	2025-11-24	20.60	0.10	30.81158	−87.91780
22	17650	2025-11-24	20.60	0.10	30.80385	−87.91783
23	17700	2025-11-24	20.60	0.10	30.81492	−87.91625

Appendix 8.
Winter 2026 manual tracking data for the Mobile-Tensaw River Delta along with the temperature, salinity, and latitude/longitude at their collection site.

Mobile-Tensaw River Delta Winter 2026 Manual Tracking Detections

Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	16950	2026-02-24	14.30	4.50	30.77157	−87.97388
2	17650	2026-02-24	14.30	4.50	30.77010	−87.97556
3	18600	2026-02-24	14.10	0.10	30.81974	−87.91634
4	43600	2026-02-24	13.70	0.10	30.68699	−87.92703
5	43800	2026-02-24	13.80	0.10	30.68364	−87.92650
6	53000	2026-02-24	13.70	0.10	30.92244	−87.91198

Appendix 9.
Spring 2026 manual tracking data for the Lower Alabama River along with the temperature, salinity, and latitude/longitude at their collection site.

Lower Alabama River Spring 2026 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	16450	2026-03-09	16.80	0.10	31.61370	−87.55079
2	17750	2026-03-09	16.80	0.10	31.61284	−87.55232
3	18200	2026-03-09	16.90	0.10	31.59389	−87.54486
4	18550	2026-03-09	16.90	0.10	31.57583	−87.51775
5	19000	2026-03-09	17.10	0.20	31.54350	−87.53459
6	19050	2026-03-09	16.80	0.10	31.60639	−87.54974
7	41	2026-03-09	16.80	0.10	31.60930	−87.55039
8	46	2026-03-09	16.80	0.10	31.60654	−87.54986
9	52	2026-03-09	16.80	0.10	31.59386	−87.54444
10	52700	2026-03-09	16.80	0.10	31.61260	−87.55209
11	70	2026-03-09	16.80	0.10	31.61222	−87.55069
12	72800	2026-03-09	17.00	0.10	31.54820	−87.51643
13	74700	2026-03-09	16.90	0.10	31.57563	−87.51783

Appendix 10.
Spring 2026 manual tracking data for the Mobile-Tensaw River Delta along with the temperature, salinity, and latitude/longitude at the fish's collection site.

Mobile-Tensaw River Delta Spring 2026 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	74300	2026-03-26	20.60	0.10	30.88780	−87.93159

Appendix 11.
Summer 2026 manual tracking data for the Lower Alabama River along with the temperature, salinity, and latitude/longitude at the fish's collection site.

Lower Alabama River Summer 2026 Manual Tracking Detections

Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	18050	2026-06-01	26.00	0.10	31.61215	−87.55100

Appendix 12.
Summer 2026 manual tracking data for the Mobile-Tensaw River Delta along with the temperature, salinity, and latitude/longitude at their collection site.

Mobile-Tensaw River Delta Summer 2026 Manual Tracking Detections						
Point	Fish ID	Date	Temperature (°C)	Salinity (ppt)	Latitude	Longitude
1	74300	2026-05-27	25.20	0.10	30.91136	−87.93400
2	19150	2026-05-28	24.40	0.10	30.73460	−87.93600
3	44900	2026-05-28	24.40	0.10	30.76400	−87.92390
4	74800	2026-05-28	24.40	0.10	30.75487	−87.91937
5	18100	2026-06-02	25.90	0.10	30.80700	−87.99197
6	69	2026-06-02	25.90	0.10	30.85797	−87.97105
7	16150	2026-06-11	30.00	0.10	30.81731	−87.91647
8	16250	2026-06-11	30.00	0.10	30.81840	−87.91625
9	16600	2026-06-11	30.00	0.10	30.81845	−87.91601
10	16700	2026-06-11	30.00	0.10	30.81849	−87.91578
11	17050	2026-06-11	30.00	0.10	30.81913	−87.91568
12	18250	2026-06-11	30.00	0.10	30.81834	−87.91571
13	18700	2026-06-11	27.90	0.10	31.06427	−87.87101
14	18900	2026-06-11	30.00	0.10	30.81779	−87.91592
15	50	2026-06-11	30.00	0.10	30.81710	−87.91599
16	52200	2026-06-11	30.00	0.10	30.81889	−87.91576
17	53000	2026-06-11	30.00	0.10	30.81743	−87.91607