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Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) in the Mobile Bay Estuary, Alabama: Documentation of Use Outside of Designated Critical Habitat

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ABSTRACT

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Gulf Sturgeon (GS) are an anadromous, federally threatened subspecies of Atlantic Sturgeon that feed primarily in estuarine and marine systems in the northern Gulf of Mexico from October to April. All extant natal river systems and adjacent estuarine and marine environments were designated as critical habitat for GS in 2003, excluding the Mobile River Watershed because of lack of data indicating an extant spawning population at the time of listing. Previous studies had identified that GS from river systems east of Mobile Bay use habitats within the Mississippi Sound, suggesting GS must at least traverse Alabama waters. Therefore, this study's objective was to quantify the use of the Mobile Bay Estuary by GS. GS were acoustically tagged in all extant natal river systems and detected by an array of receivers deployed in the Mobile Bay Estuary during 2016–21. A total of 210 adult and subadult GS from western ($n = 97$) and eastern ($n = 113$) river systems were detected in the Mobile Bay Estuary for up to 4 months, with 110 individuals detected from 2 to 6 years during the monitoring period. The sustained use of the Mobile Bay Estuary by GS from western and eastern river systems strongly indicates that Alabama's waters are suitable habitat despite extirpation of the natal spawning population in the Mobile River Estuary. Foraging in the Mobile Bay Estuary is probable because previous sediment and benthic macroinvertebrate sampling in this system indicated relatively low-percent sand content and high polychaete richness, which are characteristic of foraging habitats previously identified in the Pascagoula River delta. The Mobile Bay Estuary is not designated as critical habitat for GS; however, this study indicates nonanomalous use of this habitat by GS during the foraging period, so inclusion of this system under the critical habitat designation should be considered.

ADDITIONAL INDEX WORDS: *Acipenseridae, acoustic telemetry, movement ecology, network analyses.*

INTRODUCTION

Anadromous Gulf Sturgeon (GS; *Acipenser oxyrinchus desotoi*; Figure 1) are a subspecies of the Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) and are classified under the U.S. Endangered Species Act (ESA) as federally threatened across their range, which spans from the Pearl River, Louisiana, to the Suwannee River, Florida (USFWS and NOAA, 1991). The historic range of GS presumably extended from Texas to southern Florida, with spawning populations in all large coastal rivers from the Mississippi River to the Suwannee River (Sulak *et al.*, 2016). However, overfishing, damming of natal spawning rivers, and habitat degradation contributed to the overall decline in their abundance and the

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Figure 1. A photograph of a Gulf Sturgeon swimming in the Pascagoula River, Mississippi. Photo courtesy of Michael Andres.

presumed extirpation of spawning populations in the Mobile River system (*i.e*. the Tensaw, Mobile, and Alabama Rivers) in Alabama (Sulak *et al*., 2016; Wooley and Crateau, 1985). Therefore, GS were listed under the ESA in 1991 (USFWS and NOAA, 1991). At the time of listing, it was uncertain which rivers and adjacent estuarine and marine environments to include as critical habitat; therefore, critical habitat designation did not occur until 2003 (USFWS and NOAA, 2003). The critical habitat designation protected the seven natal rivers with extant spawning populations, as well as estuarine and marine environments adjacent to these rivers. However, it excluded the Mobile River system and Mobile Bay Estuary (*i.e*. Alabama waters in the jurisdiction of Baldwin and Mobile Counties and Mobile Bay proper) because of a lack of data indicating an extant spawning population at the time of listing (Mettee *et al*., 2005; USFWS and NOAA, 2003). The only recent observations of GS in the Mobile Bay Estuary had been from irregular captures (Mettee, O'Neil, and Pierson, 1996; Mettee *et al*., 2009), dead GS reports (M.J. Andres and A. Kaeser, *personal communication*), and limited acoustic detections (USFWS, 2015). The exclusion of the Mobile Bay Estuary and the Mobile River system created a gap in critical habitat coverage across the range of the species (Figure 2) and has resulted in the exclusion of these systems from recovery plans that have focused on the extant river populations and adjacent habitats (USFWS, 2022). The seven extant spawning river systems of GS can be generally categorized as western (*i.e*. natal to the Pearl and Pascagoula Rivers) or eastern (*i.e*. natal to the Escambia, Yellow and Blackwater, Choctawhatchee, Apalachicola, and Suwannee Rivers) based on their location relative to the Mobile Bay Estuary (Figure 2; Dugo *et al*., 2004). Each natal river system has a distinct genetic signature, and genetic relatedness is higher among geographically proximate rivers. As such, GS from western river systems exhibit more genetic similarity than they do with eastern river system GS, and vice versa.

As part of their anadromous life cycle, GS migrate from all natal rivers to estuarine and marine systems from October to April to opportunistically forage on benthic macroinvertebrates (*e.g*., polychaetes, callianassids, isopods, and amphipods; Carr, Tatman, and Chapman, 1996; Harris, Parkyn, and Murie, 2005; Mason and Clugston, 1993). In general, it is hypothesized that juvenile GS remain and feed within estuaries adjacent to their natal river system (Peterson *et al*., 2018), whereas subadult and adult GS migrate to nearshore and offshore environments with optimal feeding habitats (Ross *et al*., 2009; Vick, Peterson, and Slack, 2018). Previous studies have described GS from eastern river systems making westward migrations from their natal rivers to habitats between Pensacola Bay, Florida, and Gulf Shores, Alabama (east of Mobile Bay, Alabama; Parauka, Duncan, and Lang, 2011), as well as longer westward migrations (up to 250 km) to suitable foraging habitat at Mississippi barrier islands (Vick, Peterson, and Slack, 2018). In addition, Peterson *et al*. (2018) detected GS from western and eastern river systems near Gulfport, Mississippi. These previous studies have shown that GS from the eastern river systems migrate through the unprotected waters of Alabama to habitats west of the Mobile Bay Estuary. However, GS from the western river systems have been thought to typically stay in habitats west of the Mobile Bay Estuary, with few records of GS from western river systems having been captured or detected east of this system (Dugo *et al*., 2004; USFWS, 2015). Furthermore, there are low transition probabilities associated with GS from western river systems and higher transition probabilities associated with GS from eastern river systems, especially those from the Escambia and Yellow and Blackwater Rivers (Rudd *et al*., 2014), which supports movement patterns demonstrated by previous studies (Parauka, Duncan, and Lang, 2011; Peterson *et al.,* 2018; Vick, Peterson, and Slack, 2018).

The Mobile Bay Estuary likely represents a suitable foraging habitat for GS, because it has high river discharge and high faunal diversity generated by the convergence of turbid, mud-bottom habitats and clear, sand-bottom habitats along this

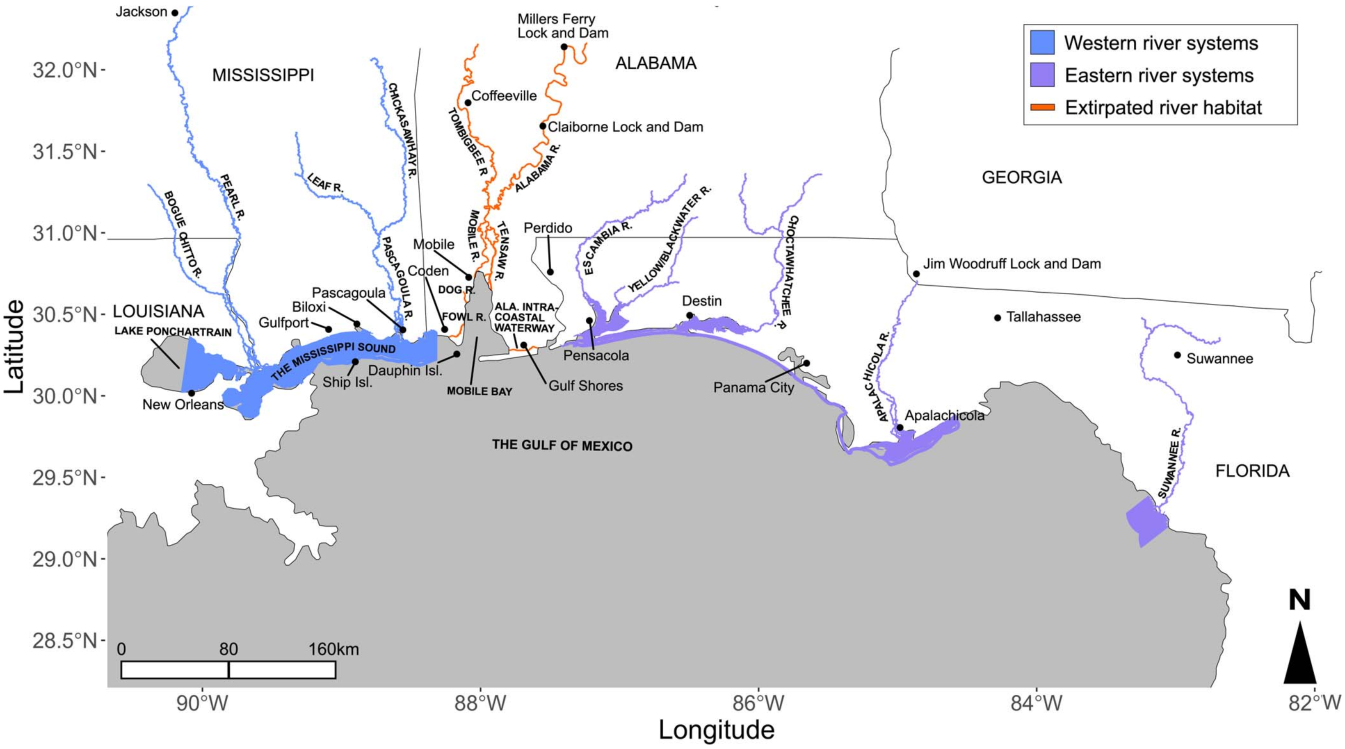

Figure 2. A map of the Gulf Sturgeon critical habitat designation (modified from USFWS and NOAA, 2003). The blue lines and polygons represent the western river systems (*i.e.* the Pearl and Pascagoula Rivers west of Mobile Bay) and the purple lines and polygons represent the eastern river systems (*i.e.* the Escambia, Yellow and Blackwater, Choctawhatchee, Apalachicola, and Suwannee Rivers east of Mobile Bay). The Mobile River system (in orange) is presumed to be extirpated habitat for Gulf Sturgeon (Sulak *et al.,* 2016).

geomorphological break (Shipp, 1977; Wilber, Peterson, and Slack, 2019). Previous studies have identified known GS prey items (*i.e.* polychaetes and amphipods) within the Mississippi Sound from Dauphin Island to Gulf Shores, Alabama, and in the mouths of the Tensaw, Mobile, and Alabama Rivers (Berkowitz *et al.*, 2020; Wilber, Peterson, and Slack, 2019). Furthermore, the Mobile Bay Estuary was noted as a potential overwinter feeding habitat for juvenile GS (Sulak *et al.*, 2016), and Parauka, Duncan, and Lang (2011) tracked 43 tagged adult GS to the mouth of Mobile Bay proper. However, no studies have investigated the frequency and duration that GS spend within the Mobile Bay Estuary and the lower portion of the Mobile River system.

The objective of this study was to document use of habitats outside of GS critical habitat designation in the Mobile Bay Estuary, Alabama, by western and eastern river system GS. The temporal period in which GS were detected within the Mobile Bay Estuary was documented to compare with their known overwintering period (Sulak *et al.*, 2016), and overall use of the system was inferred by calculating the number of years and duration that an individual was detected. GS passage into the Mobile Bay Estuary for individuals from both western and eastern river systems was documented to identify important pathways that GS use when entering and exiting this system. In addition, intrasystem connectivity was quantified using network analyses to understand movement pathways within the Mobile Bay Estuary and to compare use of the system by GS from western and eastern river systems. GS detections in the upper portion of the system were also documented and were coupled with confirmation that all individuals that entered the system exited in the same year to hypothesize whether individuals may be remaining within the Mobile River system, rather than returning to the system in which they were tagged, for spawning and summer residency. Finally, this study addressed Species Recovery Grant priority objectives outlined by the National Oceanic and Atmospheric Administration (NOAA) SE region to investigate passage within the Mobile River basin (NOAA, 2023), which has not been formally assessed because of its exclusion under critical habitat designation.

METHODS

GS were captured by multiple research groups in all natal river systems from April to October at times when surface water temperatures were less than 30°C using anchored or drifting gill nets (both monofilament and multifilament nets were used with mesh sizes ranging from 2.5- to 12.5-cm bar). All captured GS were measured by the research groups for total length (TL; in millimeters), fork length (FL; in millimeters), and weight (in kilograms); most had a fin clip taken from the left pelvic fin for genetic sequencing. Upon capture, all GS were scanned for a passive integrated transponder (PIT) tag, and unmarked individuals were tagged subdermally below the dorsal fin with a unique PIT tag. These PIT tags were used to associate captured GS to their GS identifier (ID) within the Gulf Sturgeon Database, which is a shared database accessible for researchers to enter and retrieve GS capture and detection data. Depending on the river system and fish size, GS in a healthy condition were surgically implanted with InnovaSea 69-kHz coded acoustic transmitters following standard procedures (Kahn and Mohead, 2010; USFWS, 1993). The tagging effort varied between research groups targeting GS from the eastern and those targeting GS from the western population units, with more adult GS tagged in eastern population unit systems and a variable tagging effort in western population unit systems (Appendix A). All capture data and tagging information were uploaded by researchers to the Gulf Sturgeon Database, which was used to access the list of acoustic transmitters deployed in GS from all river systems.

Acoustic Receiver Array

Telemetered GS within the Mobile Bay Estuary were detected within a network of autonomous acoustic receivers (*i.e.* array) maintained during 2016–21 (Figure 3). The array was designed to monitor fish movement into the major tidal rivers in the Mobile Bay Estuary and Mississippi Sound systems and to gate major egress positions from Mobile Bay proper (Mobile Bay Inlet and the connection between Mobile Bay proper and eastern Mississippi Sound; see Nelson, Hightower, and Powers, 2021; Nelson and Powers, 2020). The acoustic receivers were downloaded and cleaned, and the batteries were replaced at least twice a year with limited data interruptions. These types of arrays support multiple research objectives, ranging from individual animals to whole communities (Ellis *et al*., 2019). The array was delineated into receiver zones using bay geomorphology and bottom and surface salinity data acquired from Alabama's Real-Time Coastal Observing System (ARCOS) database (https://arcos.disl.org) for analysis (Figure 3).

Telemetry Data Organization

Detections (date- and time-stamped detection of unique transmitter IDs) of GS were imported and organized in R (R Core Team, 2021) before analyses. False detections (spurious detections caused by the collision of multiple transmitters) were removed by calculating the amount of time between detections for a single fish and removing instances where the time between detections was less than the minimal interval for the acoustic tag. All receivers were assumed to have a detection range of at least 300 m with 100% detection efficiency, which had been previously tested for this same acoustic array in previous studies (Nelson, Hightower, and Powers, 2021; Nelson and Powers, 2020). Previous studies found that GS were detected in marine foraging areas from October to April (Ross *et al*., 2009), and GS in this study were detected in the Mobile Bay Estuary between 15 October and 16 June. Therefore, the monitoring year was defined as 1 October to 31 September to capture the entire winter period for GS, and the year was assigned as the respective calendar year in September. Entry and exit detections of GS within the Mobile Bay Estuary were confirmed using the previous and subsequent detection, respectively, from acoustic telemetry data (*i.e.* detections associated with natal river and estuarine monitoring) using the Gulf Sturgeon Database. For individuals that entered and exited the array multiple times within a year, each event (*i.e.* entry instance) was considered unique unless entry instances were within 6 hours of each other. The number of days that an individual GS was detected within the array was the sum of the number of unique days in which a GS was detected at least twice on any receiver within the array.

GS Capture Data Organization

GS capture data for all detected individuals were acquired from the Gulf Sturgeon Database and were organized in R (R Core Team, 2021) before analysis. To account for growth of an individual from the time of initial capture to the time of detection, an age-length model (Andres *et al*., 2018) was applied to FL measurements taken at the time of capture to calculate estimated age at capture (A_c) using Equation (1):

$$A_c = -\frac{1}{0.123} \times \ln\left(1 - \frac{\text{FL}}{209.8}\right) - 0.52. \qquad (1)$$

Then, the difference in capture year and detection year were added to A_c to obtain a detection age estimate (A_e) and calculate size at detection, or corrected fork length (FL_c), using Equation (2):

$$\text{FL}_c = 209.8 - 209.8 \times \exp(-0.06396 - 0.123 \times A_e), \qquad (2)$$

which is an equivalent equation to Equation (1). GS of less than 890-mm FL_c (<4.2 years) were categorized as juveniles, 890- to 1250-mm FL_c (4.2–7 years) were categorized as subadult, and more than 1250-mm FL_c (>7 years) were categorized as adults (Parauka, Duncan, and Lang, 2011; Sulak *et al*., 2016; Vick *et al*., 2018). These calculations accounted for growth of juvenile and subadult GS into the next size class (*i.e.* subadult and adult, respectively) to accurately assess use of the Mobile Bay Estuary by individuals of various sizes.

Individual GS were assigned to a distinct natal river system using the best available data, either based on genetic analysis (from fin-clip samples) or based on the individual's capture river at the time of transmitter deployment. All GS from Pensacola Bay rivers (*i.e.* Escambia and Yellow and Blackwater Rivers) were pooled, because they all exit Pensacola Bay to enter marine habitats and they do not exhibit the same degree of genetic differentiation that is seen among some other river systems (B.R. Kreiser *et al*., unpublished data). Therefore, individuals from the Escambia and Yellow and Blackwater Rivers are hereafter considered to be from the Pensacola Bay river system. Genetic sample processing was variable among river systems in that samples were analyzed for 91 of the GS that were initially captured in the Pascagoula River ($n = 96$ total), whereas one or no samples were analyzed for individuals initially captured in the Pensacola Bay river system ($n = 65$ total), Choctawhatchee River ($n = 43$ total), or Pearl River ($n = 6$ total). However, the inclusion of available genetic assignment data altered the total number of GS assigned to each river system, with a 133.33% increase in individuals assigned to the Pearl River system (Appendix B).

The total number of active tags (*i.e.* tags that were deployed in all systems and had the potential to be detected) was

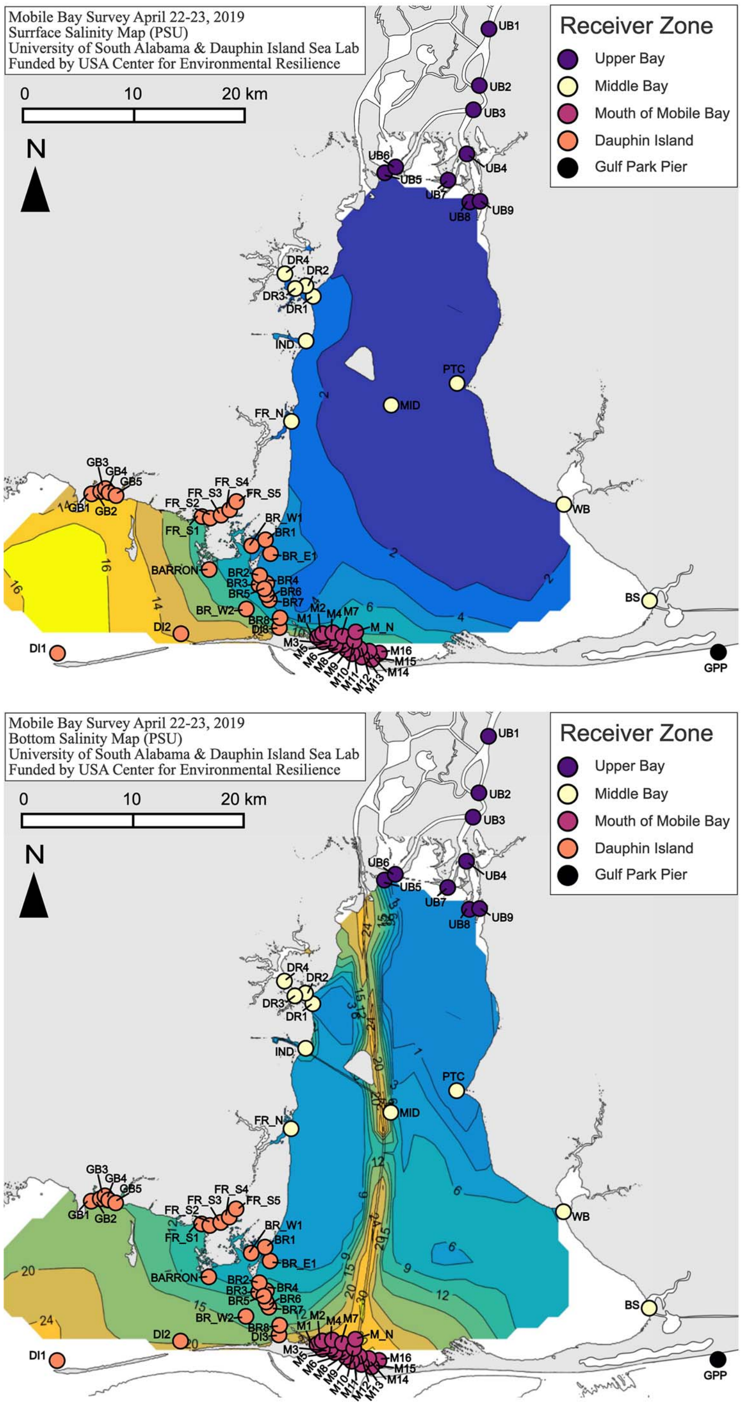

Figure 3. The network of autonomous receivers (*i.e.* array) maintained within the Mobile Bay Estuary during 2016–21. The acoustic receivers were delineated into different zones based on geographical location and from surface salinity (top) and bottom salinity (bottom) data acquired from Alabama's Real-Time Coastal Observing System (https://arcos.disl.org).

obtained from the Gulf Sturgeon Database for each natal river system (Appendix A). All tags had an estimated tag expiration, which was calculated by adding the estimated tag longevity to the tag deployment date. Each tag was determined to be active for a given monitoring year if it was deployed and did not expire between October 1 and June 30 of each year. FL_c was calculated for each tagged GS within the active tag pool using Equations (1) and (2). Juvenile GS (<890-mm FL_c) were removed from the active tag pool, because they are hypothesized to remain within estuaries adjacent to their natal river system during the overwinter period and because no juvenile GS were detected during this study (Peterson *et al*., 2018).

Spatial Network Graphs

Spatially projected networks were created to understand the use of the Mobile Bay Estuary for GS using the R package igraph (Csardi and Npeusz, 2006). The spatial networks were composed of nodes (*i.e*. receivers) and edges (movement of an individual GS between receivers assuming the shortest, direct path was taken). GS were treated as unique between years and entry instances (see the preceding definition), and networks were only created when at least 50 detections occurred. All networks included loops (*i.e*. a node connection to itself), because the loops provide indication of a GS staying within a given area. The receivers in the mouth of Mobile Bay (M1–M16 and M_N), along the Dauphin Island bridge (BR1–BR8, BR_E1, BR_W1, and BR_W2), in the upper bay (UB1–UB9), in Dog River (DR1–DR4), and in the southern portion of Fowl River (FR_S1–FR_S5; Figure 3) were pooled into a single node for data visualization and to understand use of the Mobile Bay Estuary on a coarser scale. Degree (*i.e*. the number of edges connecting to a node; Minor and Urban, 2008) was calculated per individual for each node (either an individual receiver or receiver groups). Network diameter (*i.e*. the greatest distance between any pair of nodes; Urban and Keitt, 2001) was calculated for each spatial network graph per individual GS. The calculated diameters were compared among river systems for each GS in each monitoring year using a Kruskal–Wallis test with an α of 0.05, which assumes data independence and random sampling of observations within the dataset. If significant differences were found, a pairwise Wilcoxon test with Bonferroni corrections and an α of 0.05 was used to identify the significant differences among river systems for all monitoring years. The spatial network graphs were created by pooling all GS for all monitoring years and entry instances for each river system (*i.e*. Pearl River, Pascagoula River, Pensacola Bay river system, and Choctawhatchee River). The size of each node was based on the median degree calculations for the individual network objects. Each edge was weighted by the frequency of movement of GS between two nodes multiplied by a weighting factor, w_p. The w_p accounted for varying number of total individuals detected in each river system (Appendix B) using Equation (3), in which n is the number of GS detected in each river system and N is the total number of GS detected in all river systems:

$$w_p = 1 - \frac{n}{N}. \tag{3}$$

Community Detection Analyses

Bipartite network graphs were calculated for each year of the monitoring period to validate the *a priori* assumption that individual GS within a river system would show similar use within the Mobile Bay Estuary. In addition, these would help validate *a priori* receiver zone groupings. The community algorithms identify heavily connected groups of nodes (*i.e*. communities) using different metrics (see Yang, Algesheimer, and Tessone, 2016, for further definitions of available community detection algorithms). The number of nodes within the network was small (<1000), so three community algorithms were chosen (infomap, multilevel, and walk trap), because they were shown to outperform and have higher accuracy than other community algorithms when the network size was small (Yang, Algesheimer, and Tessone, 2016). The best community detection algorithm was selected based on the highest modularity scores. Modularity is a measure of network quality after it has been divided into communities by taking the number of intracommunity edge and vertex connections and subtracting a null community network. The null community network is defined as a network with the same number of communities but random edge and vertex connections (Finn *et al*., 2014; Newman and Girvan, 2004).

RESULTS

A total of 210 GS were detected within the Mobile Bay Estuary for all monitoring years (2016–21) from all western ($n =$ 97) and eastern ($n = 113$) river systems, except for the Apalachicola and Suwannee river systems. Genetic sample processing was variable among river systems because of funding constraints, except for the Pascagoula River system (Appendix C). Most GS that were detected from western river systems were natal to the Pascagoula River ($n = 83$), which represented 10.9 to 37% of the active tag pool (Figure 4; Appendix C). The Pearl River system had the fewest number of individuals detected ($n =$ 14) and the lowest proportion of tags detected in the Mobile Bay Estuary, which ranged from 2.2 to 15.6% of the active tag pool. GS from Pensacola Bay river system also had numerous unique individuals detected ($n = 67$) that represented 6.1 to 47.7% of the active tag pool. The Choctawhatchee River system ($n = 31$) had fewer individuals detected than the Pascagoula and Pensacola Bay river systems and represented 2.2 to 32.5% of the active tag pool. Most GS detected were adults ($n = 187$; >1250-mm FL_c), and of the subadults detected ($n = 33$; 890- to 1250-mm FL_c), all but one were from western river systems (Appendix D). Of the subadults detected, only one was from the eastern river systems, in which it was genetically assigned to the Choctawhatchee River but had been originally tagged in the Pascagoula River. Ten fish throughout the study were initially classified as subadults but grew into the adult size class throughout the monitoring period. Nearly half of the total unique individual GS within the Mobile Bay Estuary were detected for only a single year ($n = 100$), whereas the remaining 110 fish were detected for 2 to 6 years of the study (Figure 5). Only one fish (ID 65; genetically assigned to the Pearl River system) was detected all 6 years of the study.

Detection Period and Fish Passage

The detection period for GS within the Mobile Bay Estuary was from October to late May or early June for all years (Figure 6) and is consistent with previous studies that have defined overwinter feeding periods for GS from both western and eastern river systems (Ross *et al*., 2009; Sulak *et al*., 2016; Vick *et al*., 2018). No GS were detected within the Mobile Bay Estuary between mid-June and October. Presumed entry (first detection) and exit (last detection) for an individual were similar for individuals within the western and eastern river

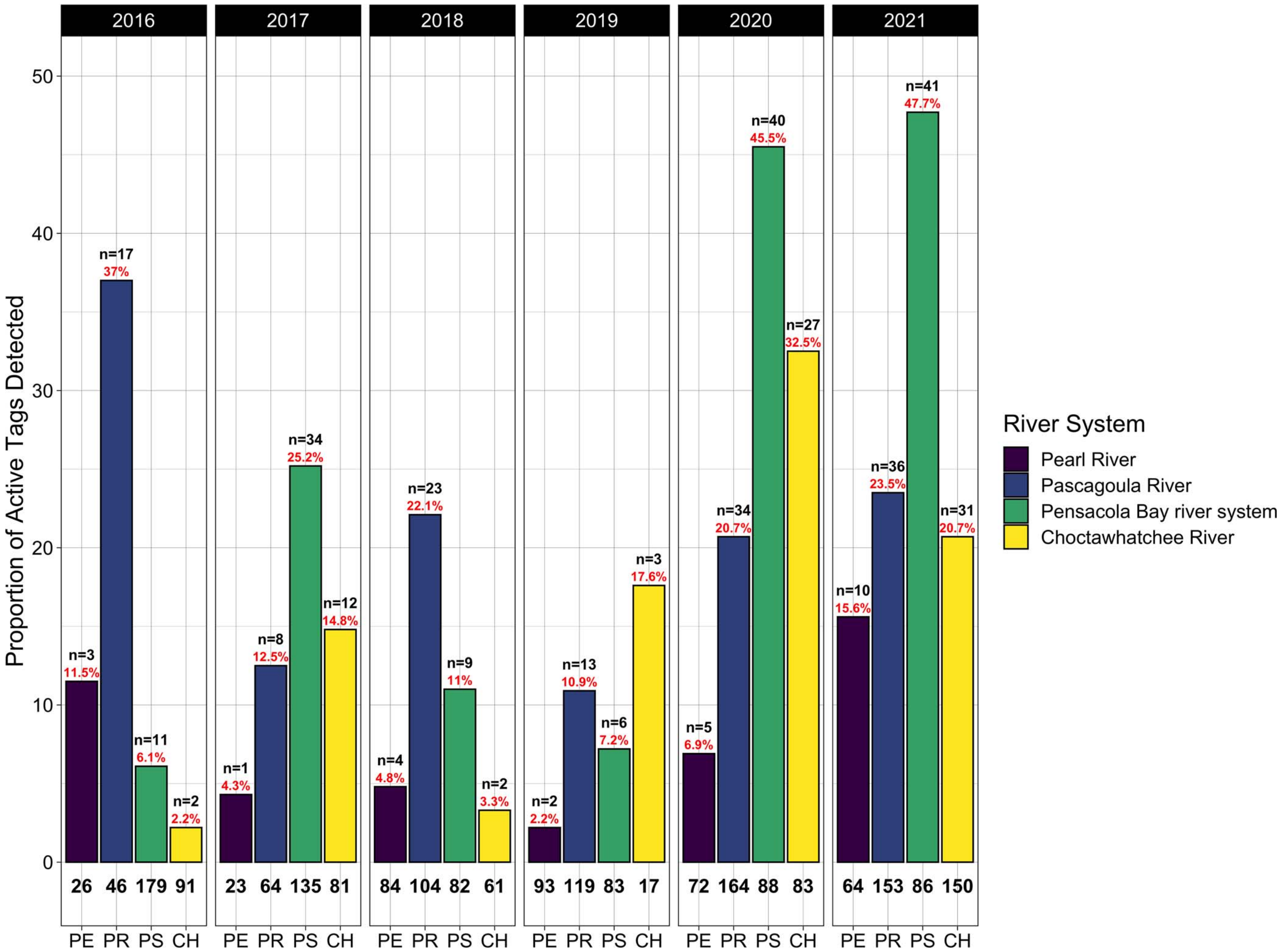

Figure 4. A bar plot of the proportion of detected Gulf Sturgeon based on the number of active acoustic transmitters deployed in subadult and adult Gulf Sturgeon (>890-mm corrected fork length) during 2016–21 in the Mobile Bay Estuary. The number of active tags was acquired from the Gulf Sturgeon Database for each river system. Each color represents the assigned river system for the individual. The numbers (in black) show the number of fish detected from each river system and the percentages (in red) show the proportion of active acoustic transmitters detected. The numbers below each bar show the total number of active acoustic transmitters deployed in Gulf Sturgeon within each river system.

systems (Figure 7). Western system GS were detected along Dauphin Island and the mouth of Mobile Bay proper, and eastern river system GS were detected near Gulf Shores, Alabama, and the mouth of Mobile Bay proper (Figures 3 and 7). There was no evidence of GS use of Fowl River to move between the eastern Mississippi Sound and Mobile Bay proper (despite receivers maintained throughout Fowl River during the monitoring period) or through the Alabama Intracoastal Waterway that connects Mobile Bay proper to Perdido Bay. However, only a single receiver was deployed during 2016–18 in the mouth of the Alabama Intracoastal Waterway, so it remains unknown whether GS used this channel during 2019–21. Most GS entered and exited the Mobile Bay Estuary once per year; however, 15 fish entered and exited in two unique events and a single fish (ID 202) entered and exited the array four unique times in a single year. The total number of days detected within the Mobile Bay Estuary also varied by individual and by year, with some individuals detected consecutively for only 1 day and others detected for up to 4 months (Appendix E). Moreover, in the 2017 and 2020 monitoring years, a greater number of GS were detected over a longer period, whereas in the 2018 and 2021 monitoring years, GS were detected for a shorter period. Most GS were confirmed to have left the Mobile Bay Estuary using detection data from external arrays that were deployed concurrent with the monitoring period of this study; however, in 38 of 785 total entry and exit instances, individual GS were missing either entry or exit detections from external arrays deployed west and east of the Mobile Bay Estuary.

Spatial Network Analyses

Spatial network analyses showed variable use of the Mobile Bay Estuary by GS from the four river systems that were

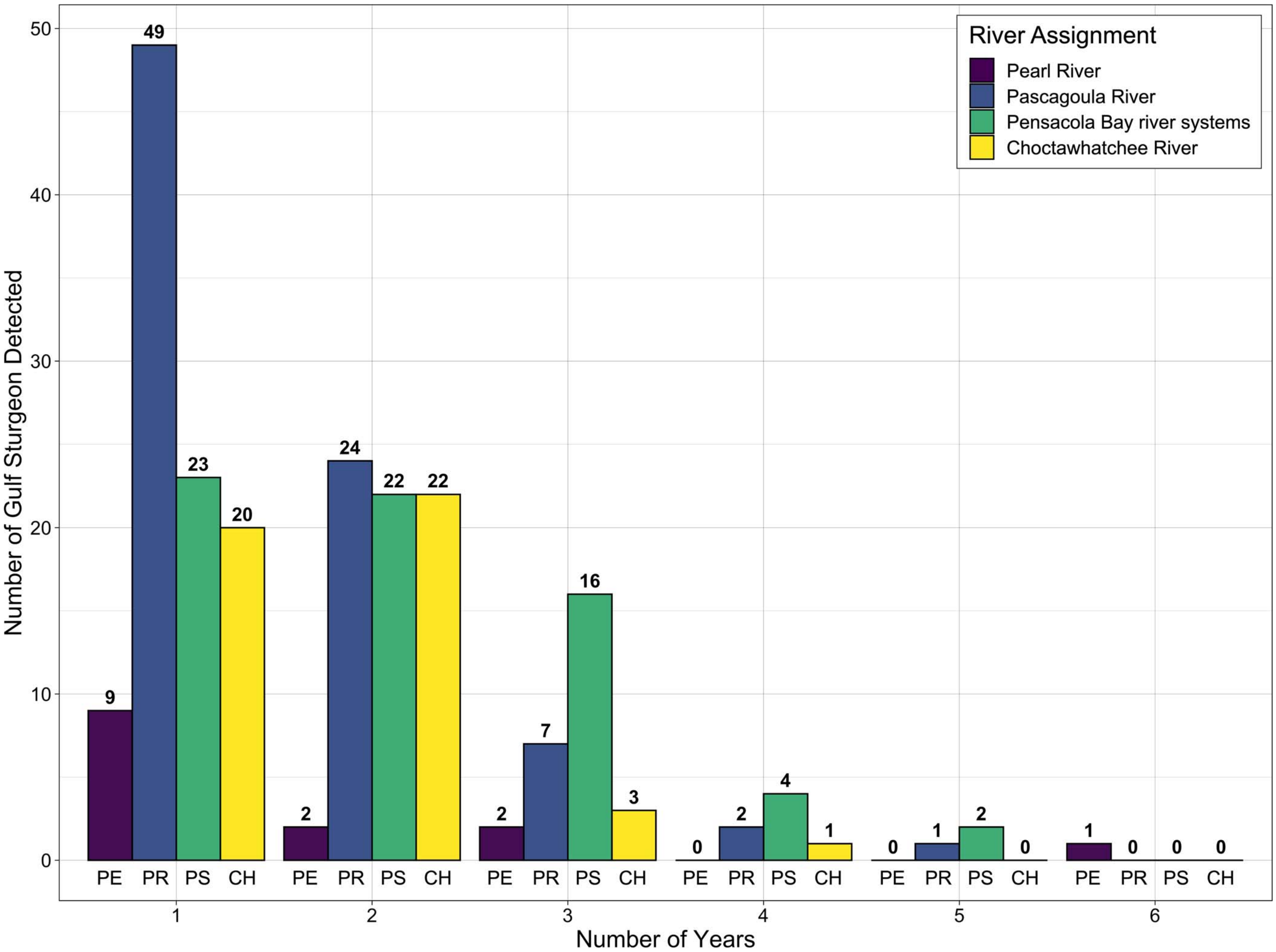

Figure 5. A bar plot of the number of years an individual Gulf Sturgeon was detected in the Mobile Bay Estuary during 2016–21. Each color represents the assigned river system for an individual, and the numbers (in black) show the number of fish detected from each river system.

detected (Figure 8; Appendices F and G). The network diameter was significantly different between GS from western and eastern river systems; GS from the Pascagoula River system had a significantly higher diameter than GS from eastern river systems, and GS from the Pearl River system had a significantly higher diameter than GS from the Pensacola Bay river system (Appendix F). Eastern river system GS had a generally high node degree associated with the mouth of Mobile Bay proper, Dauphin Island Bay, and Middle Bay receiver zones (Appendix G). Western river system GS had a lower node degree associated with the mouth of Mobile Bay proper compared with GS from the eastern river systems, but it was similarly high within Dauphin Island Bay and Middle Bay receiver zones (Appendix G). Movement between the mouth of Mobile Bay proper and receivers deployed along the Dauphin Island bridge occurred frequently for detected GS (Figure 8). In addition, individuals from the Pascagoula, Pensacola Bay, and Choctawhatchee river systems moved between the mouth of Mobile Bay proper to a receiver near the Middle Bay Lighthouse (MID), presumably along the Mobile Ship Channel and near the Industrial Canal (Figures 3 and 8). GS from all four river systems were detected in the upper bay receiver zone near the mouths of the Alabama, Mobile, and Tensaw Rivers, but overall detections in this receiver zone were low for all GS except those from the Pascagoula River system (Figures 3 and 8; Appendix H).

Community Detection Analyses

Heavily connected groups of nodes (*i.e.* communities) were best identified using the multilevel community detection algorithm, which had the highest modularity values for every monitoring year except 2019, in which the modularity value was 0.01 lower than the infomap algorithm (Figure 9; Appendix I). The next best algorithm was the infomap, followed by the walk trap (Appendix I). The multilevel algorithm identified five communities in 2016 and 2021 and seven communities for all other monitoring years (modularity score range of 0.41–0.70).

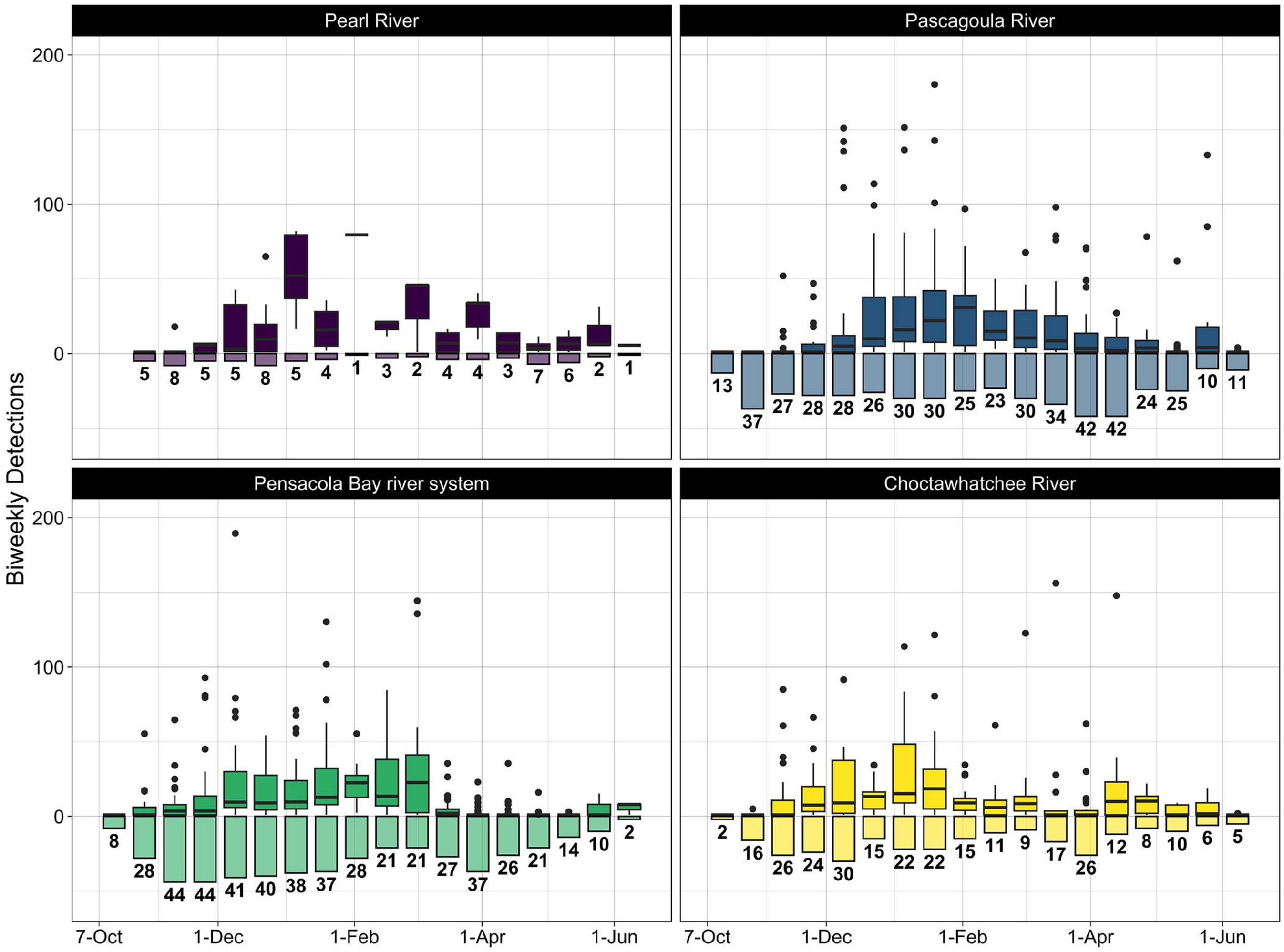

Figure 6. The positive y-axis is a boxplot of the mean number of biweekly detections for an individual Gulf Sturgeon detected in the Mobile Bay Estuary, and each panel and color represents the natal river system assignment for an individual. The boxes are the first and third quartiles, the horizontal line is the median, and the vertical lines are the minimum and maximum values for the data, with the outliers represented by points. The negative y-axis is a bar plot of the number of individual Gulf Sturgeon detected biweekly for each river system.

The multilevel algorithms did not identify unique communities of GS based on *a priori* grouping by river system; however, *a priori* receiver zones clustered into unique communities in some years (Figures 3 and 9). The upper bay receivers clustered together in two overlapping communities in 2016 (communities C and B in Figure 9), in a single community in 2018 (community G, with 1 GS), and in two communities in 2019 (communities A and C). Receivers deployed in the mouth of Mobile Bay proper formed a unique community in 2018 (community A, with 2 GS) and were generally clustered closely together in all other years. In 2018, some Middle Bay receivers formed another unique community (community F, with 1 GS), and in 2019, the Dog River receivers (DR1–DR4) grouped into a single community (community E). However, the Middle Bay receivers did not typically cluster together or group into a single community, nor did the Dauphin Island bridge receivers.

DISCUSSION

This study documented that GS from western and eastern river systems have consistent and extensive use of the Mobile Bay Estuary, which has not been documented previously. Before this study, recent observations of GS in the Mobile Bay Estuary were from irregular captures (Mettee, O'Neil, and Pierson, 1996; Mettee *et al*., 2009), dead GS reports (M.J. Andres and A. Kaeser, *personal communication*), and limited acoustic detections (USFWS, 2015) within this system. This study found adult and a few large subadult GS from five of the seven natal river systems (*i.e.* the Pearl, Pascagoula, Escambia, Yellow and Blackwater, and Choctawhatchee Rivers) to cooccur in overwinter habitats within the Mobile Bay Estuary. GS detected in this study traveled long distances (~40–200 km, assuming the shortest path between receivers was taken) to overwinter habitats, which is consistent with previous literature (Parauka, Duncan, and Lang, 2011; Peterson *et al*., 2018;

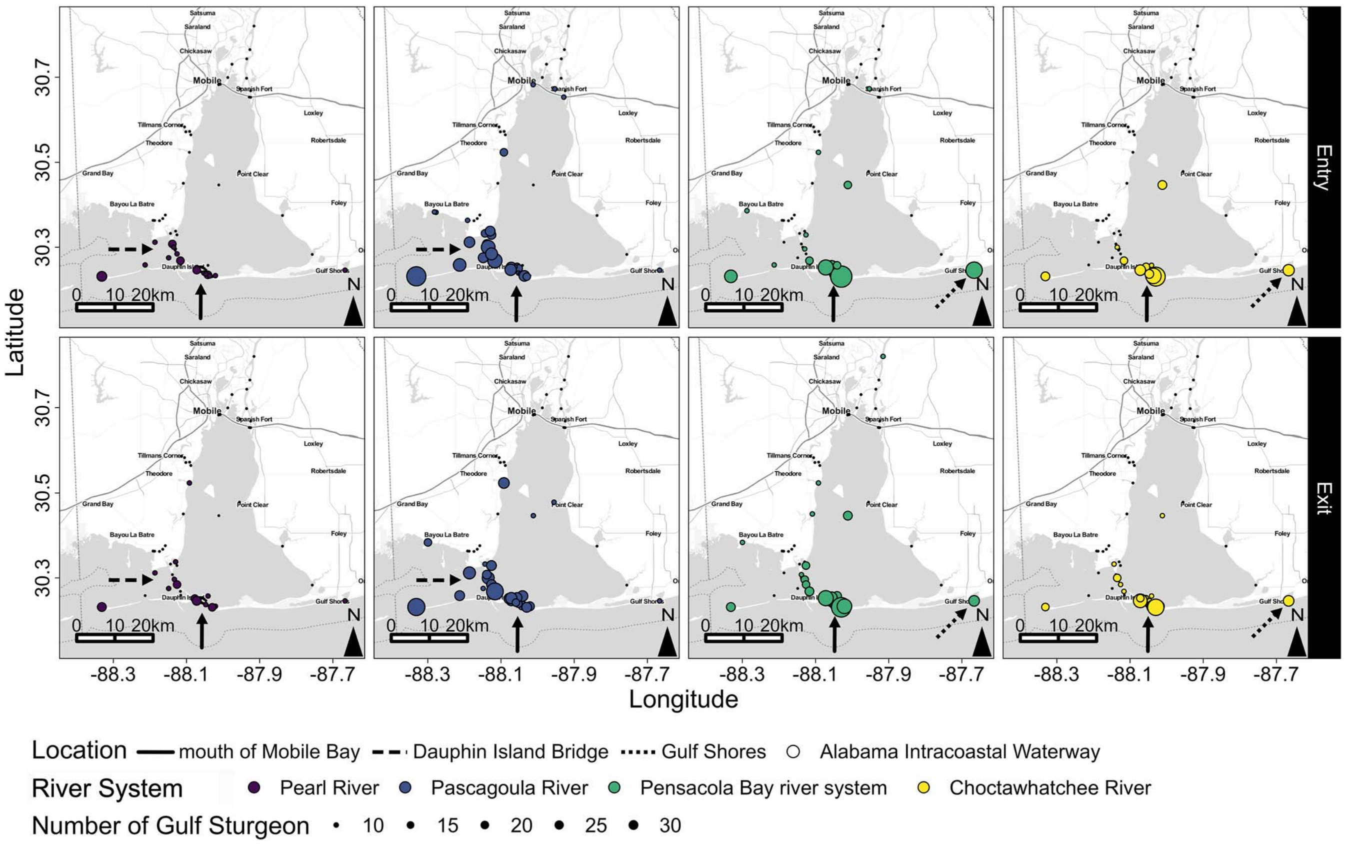

Figure 7. Entry and exit receivers for Gulf Sturgeon detected in the Mobile Bay Estuary. The colors and columns show each river system. The circle and arrows identify potential fish passage into Mobile Bay proper. The size of each point represents the number of Gulf Sturgeon detected at an individual receiver.

Rogillio *et al.*, 2007; Ross *et al.*, 2009; Vick, Peterson, and Slack, 2018). This study also indicated frequent occurrences of western river system GS making eastward migrations during the overwinter period, which previously had been sporadic (Dugo *et al.*, 2004; USFWS, 2015). Subadult and adult GS exclusively feed in marine environments, because they must consume sufficient prey items to regain weight loss during riverine fasting, maintain positive growth, and have sufficient energy for spawning (Fox, Hightower, and Parauka, 2002; Gu *et al.*, 2001; USFWS and NOAA, 2003). The Mobile Bay Estuary has sediment characteristics similar to previously identified foraging habitats in the Mississippi Sound that have been found to be used by both western and eastern river system GS (Berkowitz *et al.*, 2020; Ross *et al.*, 2009; Vick, Peterson, and Slack, 2018; Vick *et al.*, 2018; Wilber, Peterson, and Slack, 2019). In addition, sediment and benthic macroinvertebrate sampling in the Mobile Bay Estuary identified GS prey items within this system (Berkowitz *et al.*, 2020). Therefore, the nonanomalous occurrence of up to 47.7% of tagged GS detected in the Mobile Bay Estuary (Figure 4) indicates this system is used by GS as foraging habitat. Use of the Mobile Bay Estuary as foraging habitat is furthermore supported as GS were detected annually, with half of the detected GS returning to this system for between 2 and 6 years of the monitoring period for up to 4 months (Figure 5; Appendix E).

Overall use within the Mobile Bay Estuary was variable by river system and individual (Figure 8; Appendices E–H). GS from the eastern river system had low degree values associated with the mouth of Mobile Bay receiver zone and significantly lower network diameter (relative to the western river system), indicating that GS remained within the mouth of Mobile Bay and that some did not venture farther into Mobile Bay proper. Conversely, western population GS appeared to spend more time roaming within the Mobile Bay Estuary and Mobile Bay proper (for up to 4 months), because western river system GS had generally higher degree values (especially within the Middle Bay receiver zone) and had significantly higher diameter (Figure 8; Appendix F). Differences in use within the Mobile Bay Estuary are likely related to osmoregulatory stress associated with adapting to saltwater tolerance during the overwinter period. Previous studies have found that nearshore habitats west of the Mobile Bay Estuary are largely controlled by freshwater export pathways, whereas higher salinity occurs in nearshore habitats east of the Mobile Bay Estuary (Cambazoglu *et al.*, 2017; Hollenbeck, Portnoy, and Gold, 2019). Therefore, GS from western systems may be able to traverse the Mobile Bay Estuary more so than those from

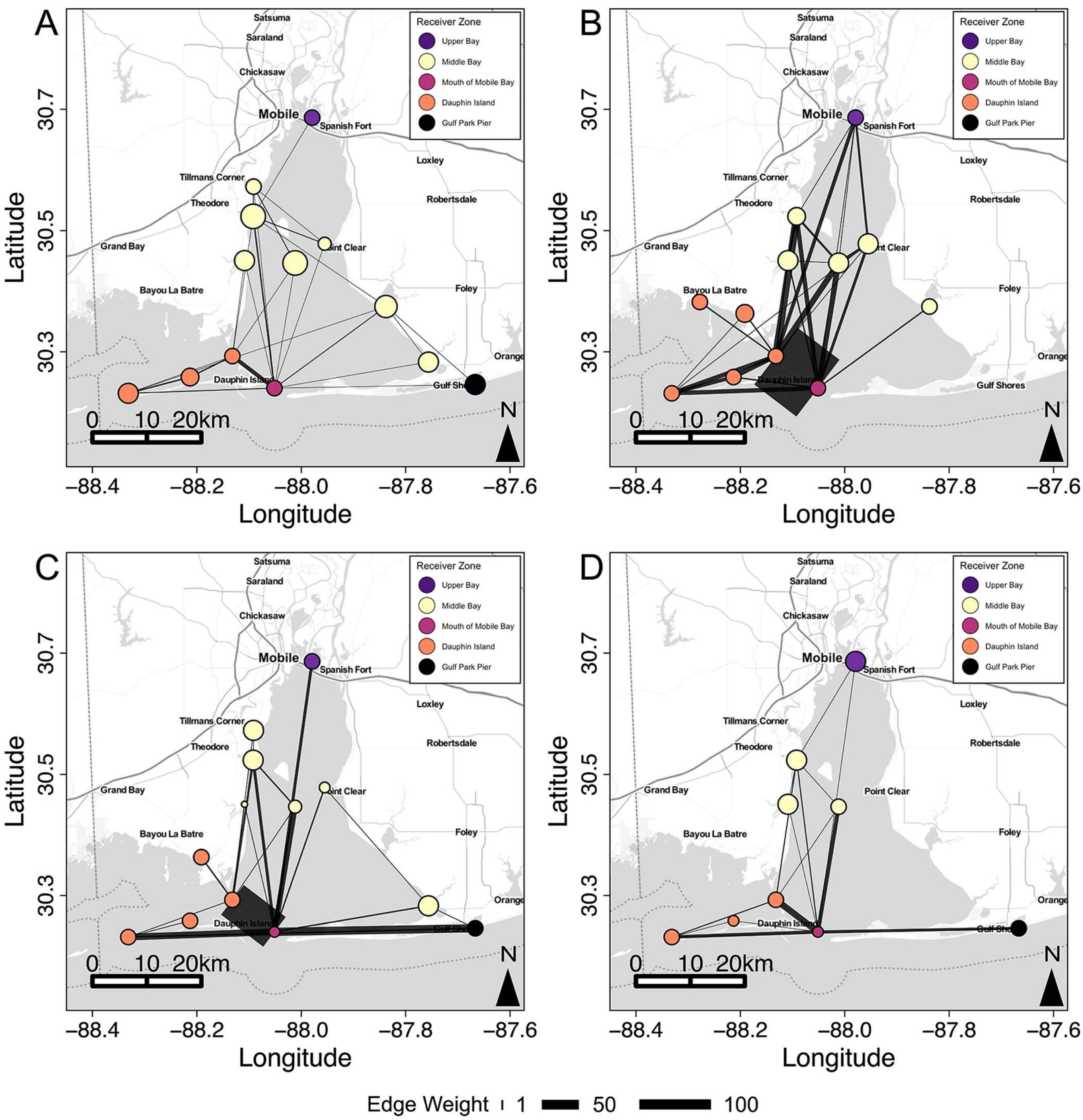

Figure 8. Spatial network analyses pooled for all years of the monitoring study (2016–21) for all Gulf Sturgeon from the (A) Pearl River, (B) Pascagoula River, (C) Pensacola Bay river system, and (D) Choctawhatchee River with more than 50 detections. The nodes (circles) represent receivers, and the edges (lines) represent movements between receivers. The receivers in the mouth of Mobile Bay proper (M1–M16 and M_N), along the Dauphin Island bridge (BR1–BR8, BR_E1, BR_W1, and BR_W2), in the upper bay (UB1–UB9), in Dog River (DR1–DR4), and in the southern portion of Fowl River (FR_S1–FR_S5; Figure 3) were pooled into a single node for data visualization on a coarser scale. The size of each node represents the median degree (*i.e.* the number of edges connecting to a node; Minor and Urban, 2008) calculated for an individual Gulf Sturgeon within each river population, and the edges represent connections (weighted by the frequency of connections multiplied by a weighting factor, w_p) between nodes.

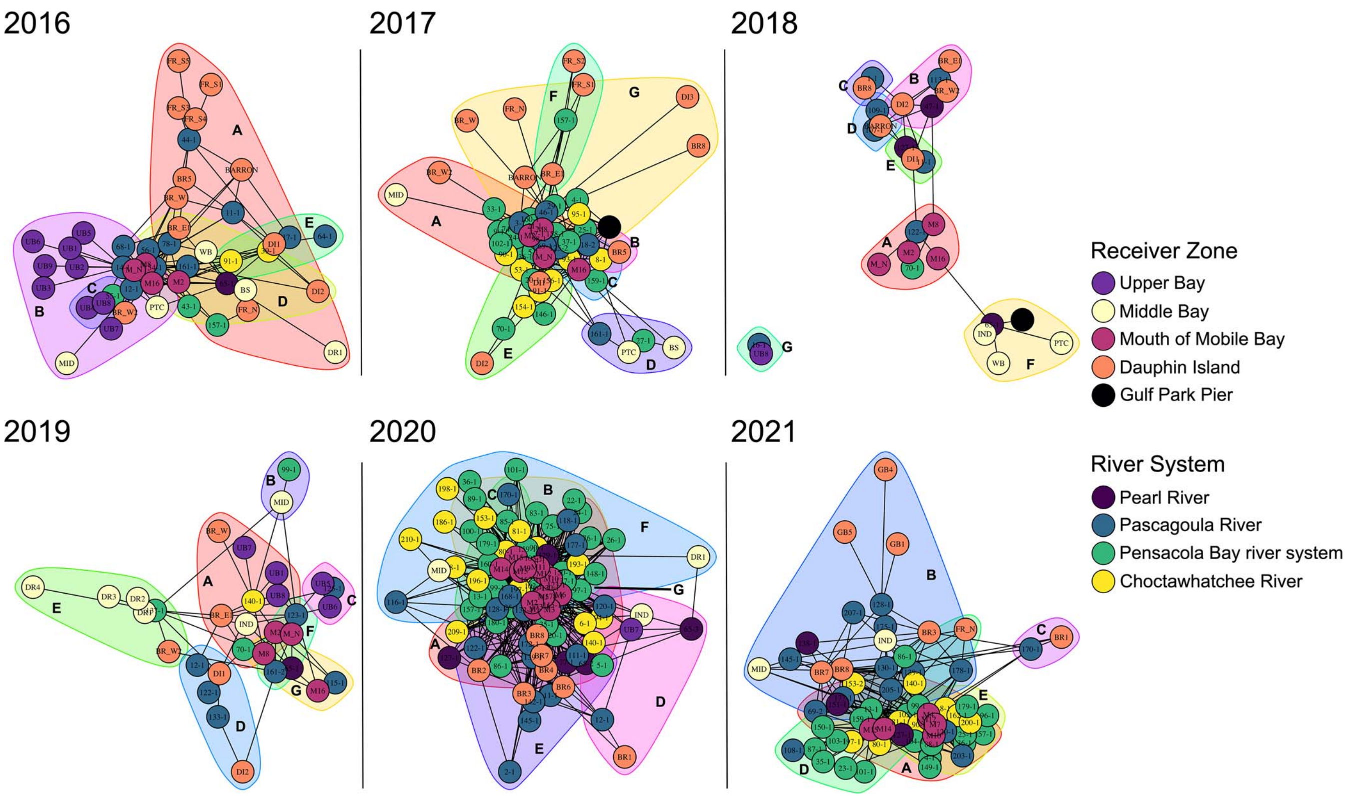

Figure 9. A bipartite graph of receivers and Gulf Sturgeon communities by the multilevel community algorithm. The node color represents either a receiver zone (which has an alphabetic label and corresponds to Figure 3) or a river system (which has a numeric label, the unique individual ID followed by the number of entry instances within a given year). The letters within each polygon represent an individual community identified by the multilevel algorithm.

eastern systems, because they have not yet undergone complete osmoregulatory adaptation to more saline environments compared with eastern system GS. Despite differences among river systems, these differences were not strong enough to parse out in the community detection algorithms that indicated little distinct clustering of individuals and receivers within the Mobile Bay Estuary (Figure 9). The Mobile Bay Estuary likely does not represent important habitat for juvenile GS or for individuals from the Apalachicola or Suwannee River populations that were not detected within this system, despite active tags in adult fish during the monitoring period (Appendix A).

There were consistent themes across years regarding movement pathways associated with the Mobile River Estuary for GS. GS entry and exit into the Mobile Bay Estuary coincided with the direction of movement from assigned natal rivers. Western river system GS entered and exited the array within the Dauphin Island receiver zone (Figure 7) and had frequent movement (*i.e.* thicker edge weights) along Dauphin Island (DI1–DI3; Figures 3 and 8), suggesting these individuals made alongshore or nearshore migrations within the eastern Mississippi Sound. GS from the eastern river system had higher detections near Gulf Shores, Alabama (Figure 7), and appeared to make alongshore movements between Gulf Shores, the mouth of Mobile Bay proper, and the west end of Dauphin Island, Alabama (*i.e.* DI1; Figures 3 and 8). Entry and exit of GS from both river systems associated with the mouth of Mobile Bay proper (Figure 7) and frequent movement between the mouth of Mobile Bay proper and the MID receiver deployed along the Mobile Ship Channel (assuming a direct path was taken by GS; Figure 8) support use of this channel for fish passage into and out of Mobile Bay proper. Shipping and navigation channels have been used as potential migration pathways by western and eastern river system GS (Fox, Hightower, and Parauka, 2002; Peterson *et al.*, 2018) and were selected by Lake Sturgeon, *Acipenser fulvescens,* as migration pathways in the Great Lakes system because they provide greater depths and higher flow (Hondorp *et al.*, 2017) and would provide increased salinity in coastal systems. These channels, again, may be used by GS that have already undergone the physiological stress of adapting to increased salinity for movement in and out of the Mobile Bay system. It is somewhat surprising that no GS were found to use the Alabama Intracoastal Waterway in migration from Perdido Bay to Mobile Bay (Figures 2 and 7), which has been previously noted as a pathway used by manatees (R. Carmichael, *personal communication*). In addition, movements *via* intercoastal waterway have been suggested for Choctawhatchee River GS between Choctawhatchee and Escambia Bays (Fox, Hightower, and Parauka, 2002). Fowl River, which connects the eastern

Mississippi Sound to Mobile Bay, was also not used as passage for GS into the system, and Dog River was little traversed by GS, aside from receivers near the mouth of that system (despite receiver coverage up into Dog River; Figures 7 and 8). These systems are not used as fish passage by other species monitored by this array (*i.e. Sciaenops ocellatus* and *Paralichthyes lethostigma*), because these habitats are relatively shallow and presumed to represent overall poor habitat (T.R. Nelson and D. Kiene, *personal communication*).

Of the 785 total entry and exit events, 38 were missing data from external arrays deployed concurrent with the monitoring period of this study. One large subadult GS from the Pascagoula River population (ID 14, 1174-mm FL_c) was not found to exit Mobile Bay, and its last known detection was on 27 May 2016 on a receiver located across from Sizemore Creek in the Alabama River (river kilometer [rkm] 64). This area is a spring-fed creek that is about 4 to 5°C cooler than the main stem of the Alabama River (Kuhajda and Rider, 2016) and is about 8.5 rkm south of the Claiborne Lock and Dam. The estimated tag death for this individual was not until 2025, so tag death is unlikely. There were 16 instances in which GS were not detected from April to October in natal rivers but were detected in later years, indicating that these individuals did not die or shed their tags but their summer whereabouts were unknown. Three of the nine fish were detected on receivers in the upper bay during the same year that they lacked detections on external arrays, again supporting that these individuals may have overwintered in unmonitored river habitats within the Mobile River system (Appendix H). However, without detection histories, it is impossible to confirm whether the individuals lacking summer holding detections occupied habitats within the Mobile River system or other unmonitored riverine, estuarine, or marine environments throughout the northern Gulf of Mexico. Regardless, when taken with the consistent findings of GS during the 6 years of the study period, GS should at minimum be considered reliable winter residents of this system.

CONCLUSIONS

The presumed decline of GS across their historic range, including the Mobile River Watershed, can be attributed to heavy habitat alteration, damming of the main stem and large tributaries, and fishing of these systems from the late 1800s to the early 1900s. The Mobile River system would likely have had the largest amount of available river habitat for GS before the construction of dams (Sulak *et al*., 2016) and presumably had a large historic spawning population of GS. There are 17 active dams on the Alabama, Tombigbee, and Black Warrior Rivers (Sulak *et al*., 2016) that limit available riverine habitat for GS to areas below the Claiborne (Alabama River; rkm 220) and Coffeeville (Tombigbee River; rkm 227) dams (Freeman *et al*., 2003; USFWS, 2022). These available riverine habitats and the Mobile Bay Estuary have undergone maintenance dredging since 1826, which can indirectly affect GS (among other species) *via* the disruption of benthic infauna (*i.e*. GS prey source), increased saltwater intrusion through the dredged channel (Yuan and Zhu, 2015), and alteration of the hydrography of riverine habitat (*i.e*. vertical gradient, sinuosity, and deep holes used for GS holding or staging; Randall *et al*., 2013; Sulak *et al*., 2016). Dredging can also directly affect GS, with a report in 2004 of two GS killed by a hopper dredge near the mouth of Mobile Bay proper (Kuhajda and Rider, 2016). Lastly, GS landings were recorded to be historically most prominent in Florida and Alabama (NOAA and USFWS, 1991), which contributed to their decline in these systems. Previous observations and salvage reports of GS have demonstrated that GS were using this system prior this study and likely in greater numbers than what was previous suspected during critical habitat designation within the Mobile River Watershed. This study provides further evidence that GS are consistent seasonal residents of this system and should be considered part of the transient ichthyofauna associated with the Mobile Bay Estuary.

According to the ESA, critical habitat is defined as specific areas within or outside of the geographical area occupied by the species that are essential for conservation of the species using available scientific data (U.S. Congress, 1973, 16 U.S.C. § 1531(3)), but the specifics as to what makes a habitat critical is a complicated process that factors many variables into its consideration (Van Horne, 1983). Overall, a habitat is deemed critical if it is needed to ensure long-term species persistence (Martin *et al*., 2017). However, critical habitat designation can be a contentious and laborious process, notably when these habitats coincide with areas of economic importance, which is the case in the Mobile Bay Estuary. It is and has been an active shipping port since the early 1800s and supports commercially and recreationally important fisheries. However, the ESA states that critical habitat can be revised when appropriate based on available scientific data (U.S. Congress, 1973, 16 U.S.C. § 1531(4)), which at the time of critical habitat designation for GS was unavailable for the Mobile Bay Estuary and for the Mobile River system (USFWS and NOAA, 2003). GS are slow to recolonize previously inhabited areas after population decline (USFWS, 2022), so use (or lack thereof) of the Mobile River system and the Mobile Bay Estuary more than 30 years ago may not be representative of contemporary use.

The Mobile Bay array was not designed to assess GS use of this system, so interpretation of the overall importance of the Mobile Bay Estuary and the suspected use of the Mobile River system cannot be fully derived from this study alone. However, this study demonstrated that the Mobile Bay Estuary represents important GS habitat. In addition, this study highlights the importance and utility of autonomous receiver arrays and data sharing from such arrays among collaborators to elucidate important information regarding fish habitat use. Western and eastern river system GS were confirmed to extensively using the Mobile Bay Estuary, and resource managers should be aware when permitting dredging operations within this system, because they may affect GS with in this system, especially from October to April. This study also strongly suggests that individual GS from extant river populations are making or attempting to make upriver migrations in the Mobile River system, possibly for spawning, because individuals were detected in the upper bay receiver zone and detections were lacking during the summer residency period. The Mobile Bay Estuary and Mobile River system have been largely ignored by GS conservation efforts because of a paucity of data at the time of critical habitat designation, but this study shows that these areas warrant further investigation. Managers should consider continued monitoring of this system through gating of entry and exit into Mobile Bay proper (*i.e.* along the Dauphin Island bridge and in the mouth of Mobile Bay), in addition to along Dauphin Island and Gulf Shores, Alabama, to further understand movement associated with the Mobile Bay Estuary. In addition, increased receiver effort within Mobile Bay proper, in particular associated with the eastern portion of Mobile Bay proper, and in the lower Mobile River system should be included as an extension to the existing Mobile Bay array to further understand GS use throughout this system.

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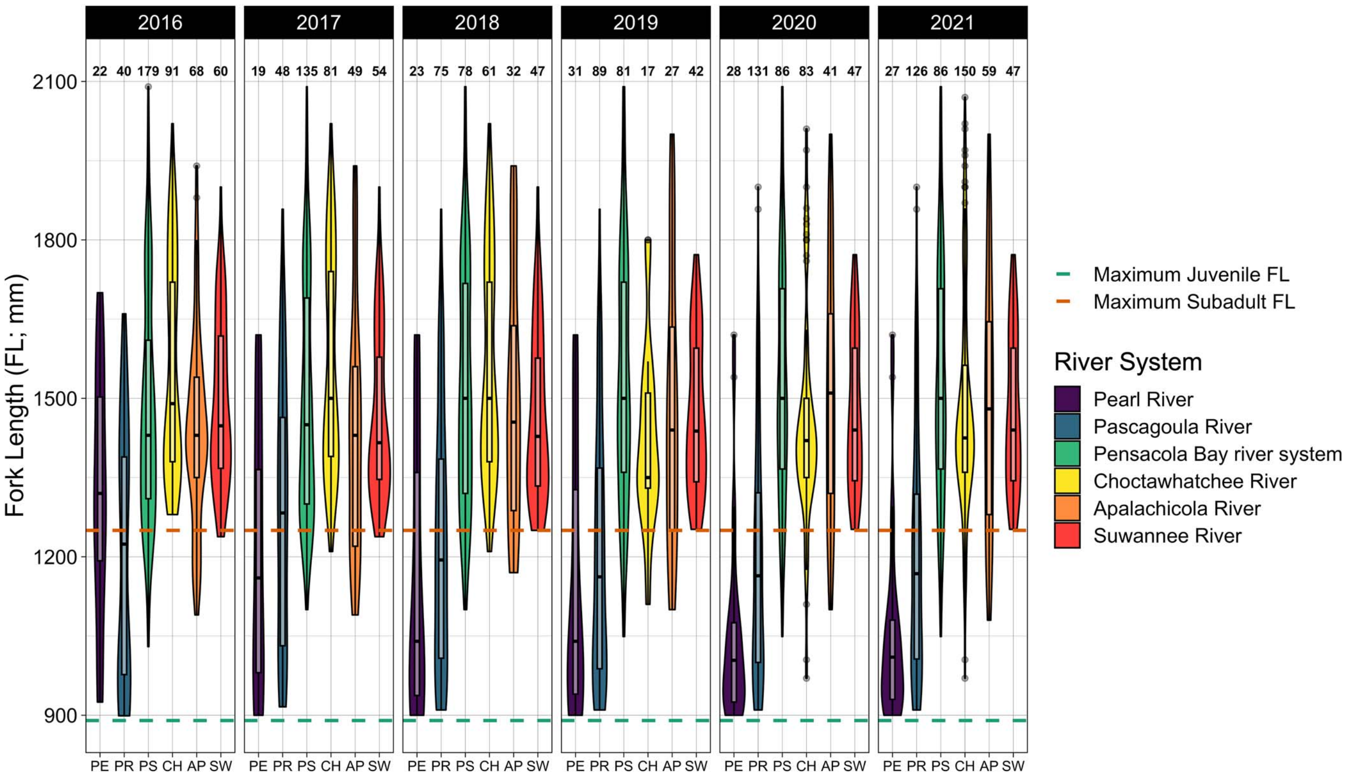
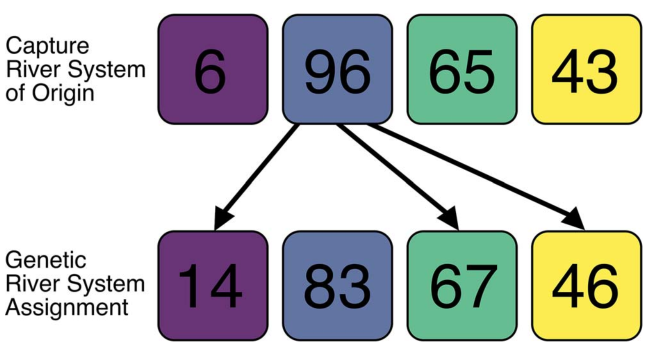
APPENDIX A

A violin plot of FL_c for all active acoustic transmitters deployed in subadult and adult GS (>890-mm FL_c) that were recorded in the Gulf Sturgeon Database. The inset boxplots show the first and third quartiles, the horizontal line is the median, and the vertical lines are the minimum and maximum values for the data. Each color represents the capture river at the time of transmitter deployment, and the numbers above each plot show the total number of active tags for each river system. The orange horizontal dashed line is the maximum FL for subadult GS (890- to 1250-mm FL_c), and the green horizontal dashed line is the maximum FL for juvenile GS (<890-mm FL_c).



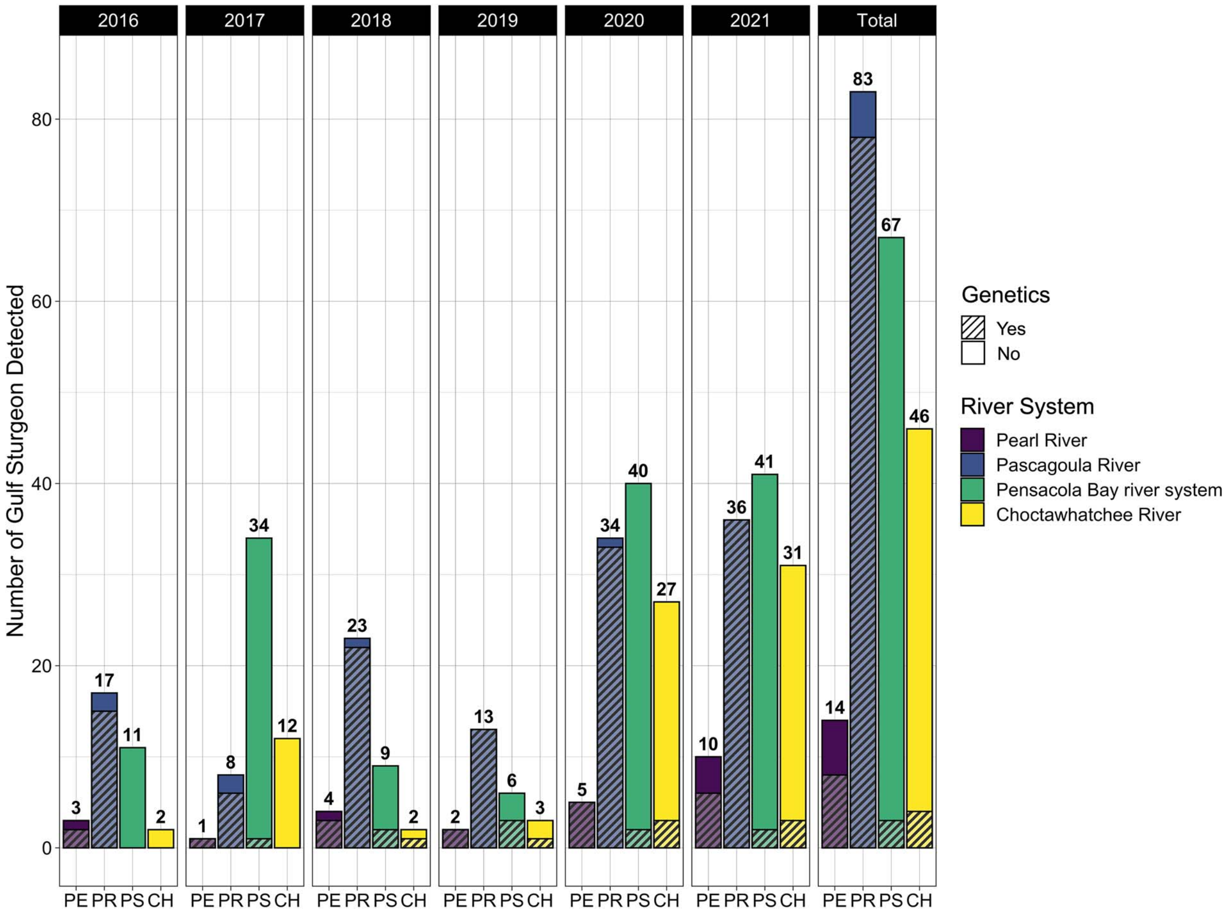
APPENDIX B

A schematic outlining the differences in the total number of GS assigned to each river system using capture river system of origin data *vs*. genetic river system assignment data. The colors represent the four river systems detected within the Mobile Bay Estuary: the Pearl River (purple), Pascagoula River (blue), Pensacola Bay river system (green), and Choctawhatchee River (yellow). The numbers in each box show the total number of GS assigned to each river system based on capture (top) and genetic (bottom) data. The arrows show individuals that were assigned to a different river system based on genetic assignment data.



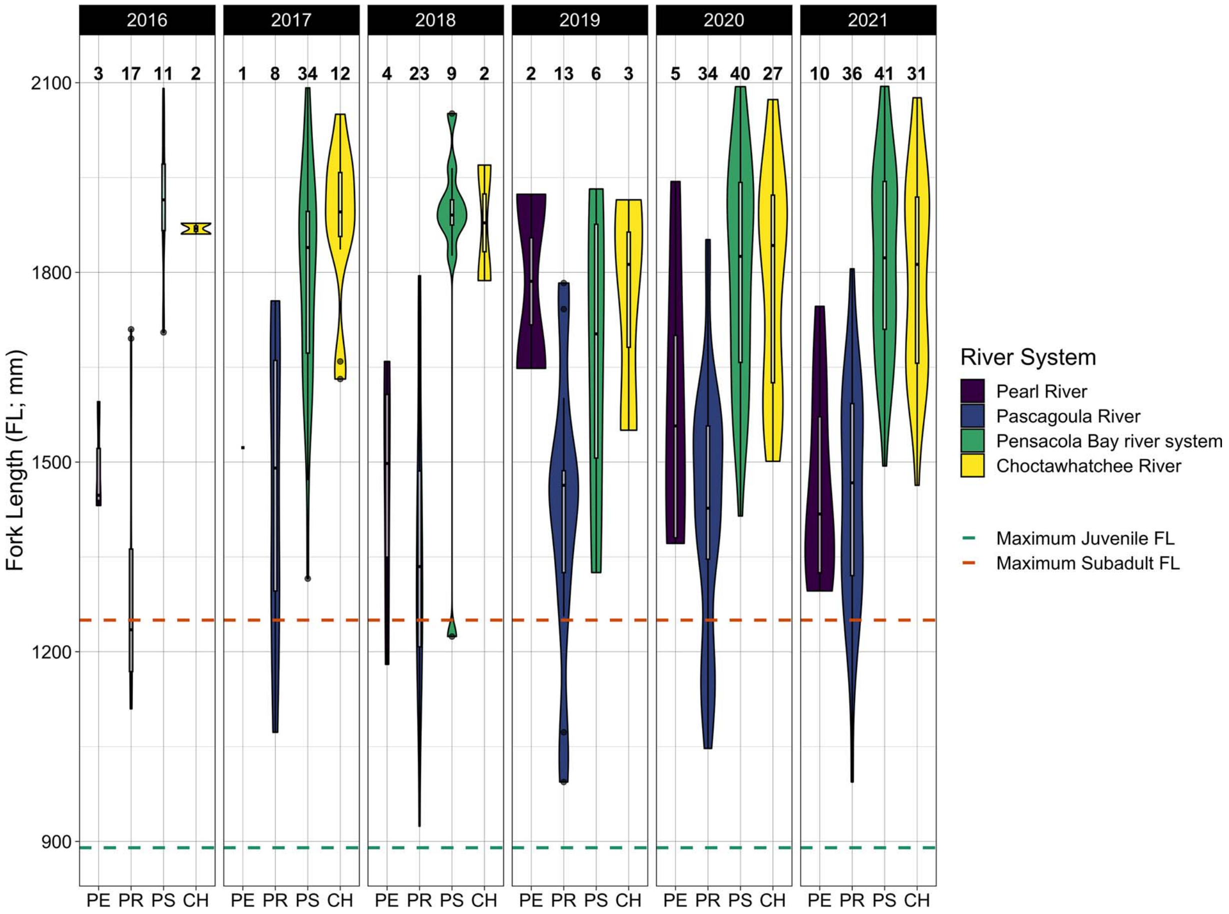
APPENDIX C

A bar plot of the number of GS detected during 2016–21 in the Mobile Bay Estuary and for all years combined. Each color represents the assigned river system for an individual, which was determined either by genetic analysis (striped pattern) or by capture river at the time of transmitter deployment (solid pattern). The numbers above each bar (in black) show the number of GS detected from each river system.



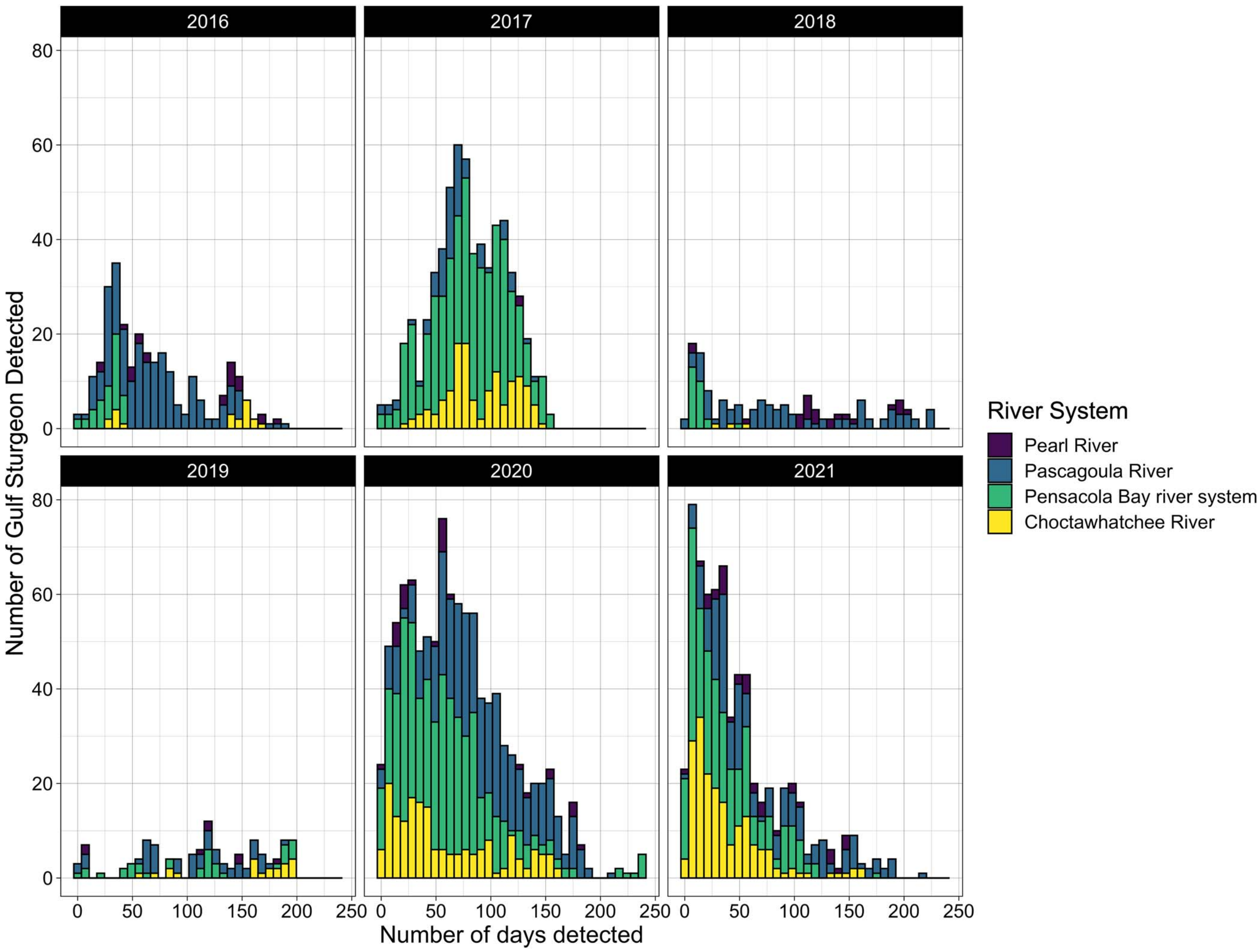
APPENDIX D

A violin plot of FL_c of GS detected in the Mobile Bay Estuary. The inset boxplots show the first and third quartiles, the horizontal line is the median, and the vertical lines are the minimum and maximum values for the data. Each color represents the assigned river system for an individual GS, and the numbers above each plot represent the number of individual fish detected. The orange horizontal dashed line is the maximum FL for subadult GS (890- to 1250-mm FL_c), and the green horizontal dashed line is the maximum FL for juvenile GS (<890-mm FL_c).



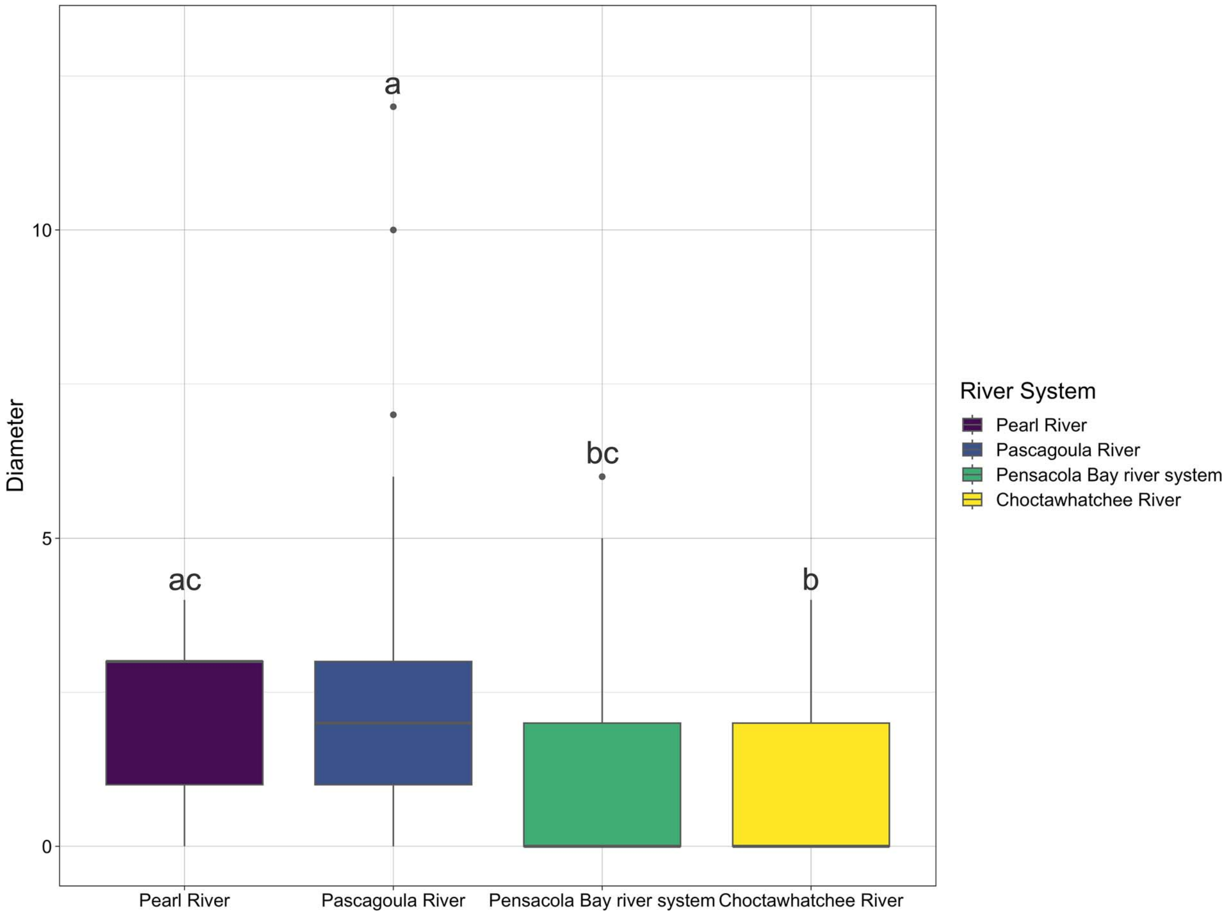
APPENDIX E

A histogram of the number of days (binned per week) that an individual GS was detected within the Mobile Bay Estuary for all years of the monitoring period (2016–21). The colors represent the assigned river system for an individual GS.



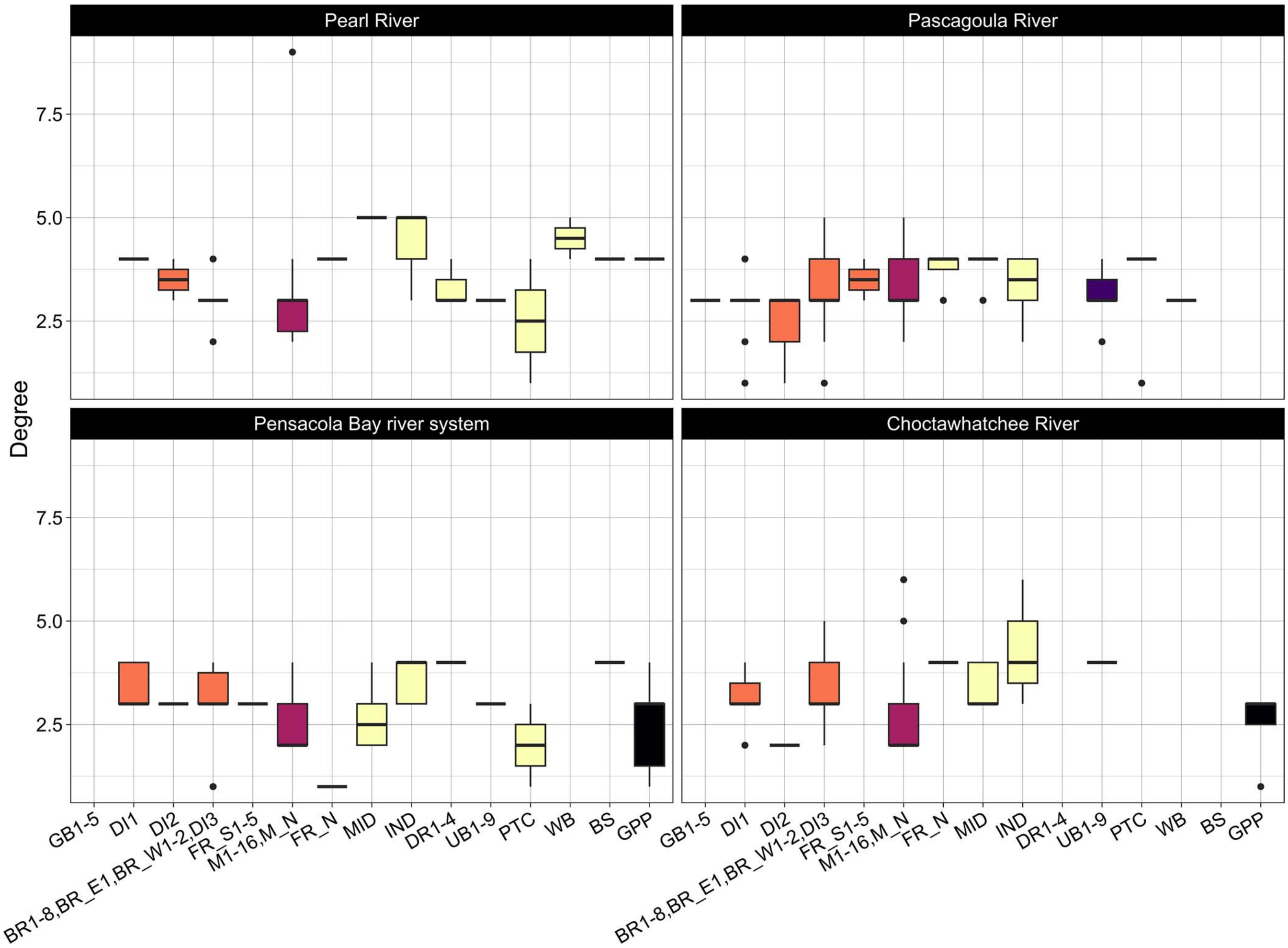
APPENDIX F

A boxplot of the network diameter (*i.e.* the greatest distance between any pair of nodes; Urban and Keitt, 2001) for each of the river systems (represented by each of the colors). The boxes are the first and third quartiles, the horizontal line is the median, and the vertical lines are the minimum and maximum values for the data, with the outliers represented by points. The letters above each plot show the significant difference between river populations based on pairwise Wilcoxon tests with Bonferroni corrections.



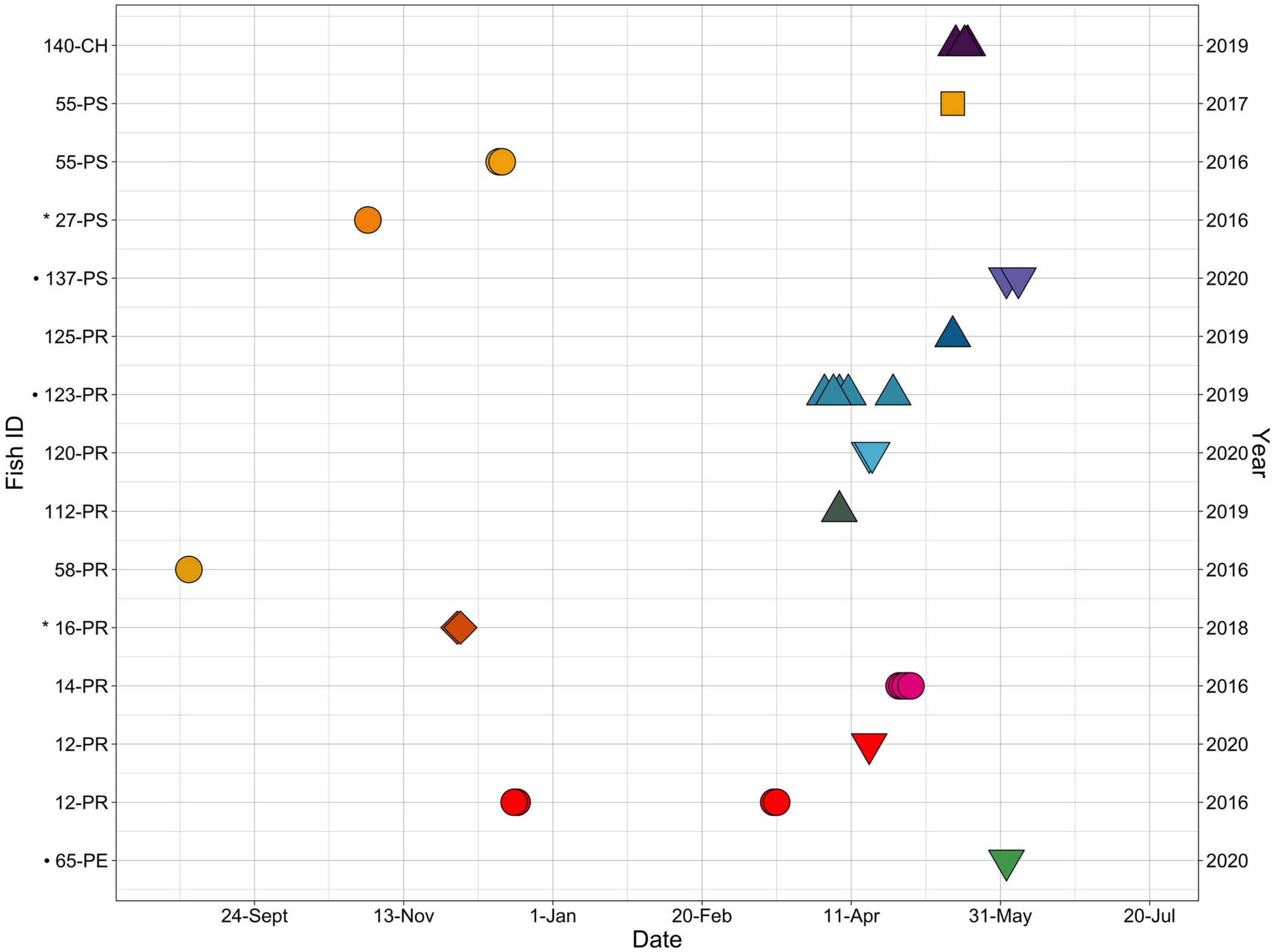
APPENDIX G

A boxplot of network degree (*i.e*. the number of edges connecting to a node; Minor and Urban, 2008) calculated for each node within the network (*i.e*. an individual receiver or a group of receivers) for each GS and monitoring year for the Pearl River, the Pascagoula River, the Pensacola Bay river system, and the Choctawhatchee River populations. The boxes are the first and third quartiles, the horizontal line is the median, and the vertical lines are the minimum and maximum values for the data, with the outliers represented by points. Each color corresponds to a given receiver zone, and the receiver groupings are listed on the x-axis (Figure 3).



APPENDIX H

A plot of GS detections in the upper bay receiver zone (Figure 3) at the mouths of the Tensaw, Mobile, and Alabama Rivers. Each color represents a unique GS, each shape represents an individual detection year, and each point represents a unique day that the individual was detected. The fish ID followed by the river population are on the left y-axis, and the detection year is on the right y-axis. The four river populations are abbreviated as Pearl River (PE), Pascagoula River (PR), Pensacola Bay river system (PS), and Choctawhatchee River (CH). GS IDs with a dot show individuals that were not detected exiting or entering the array during the same year as upper bay detections but had detections in later years. Those with an asterisk are individuals that did not have entry or exit detections and were not detected in later years.



APPENDIX I

Table I1. *Modularity scores and number of communities identified by each of the three community detection algorithms for each year of the monitoring period (2016–21).*

Monitoring Year	Community Detection Algorithm	No. Communities	Modularity Score
2016	Multilevel	5	0.480
	Infomap	8	0.420
	Walk trap	9	0.410
2017	Multilevel	7	0.490
	Infomap	8	0.410
	Walk trap	8	0.410
2018	Multilevel	7	0.700
	Infomap	7	0.700
	Walk trap	8	0.690
2019	Multilevel	7	0.630
	Infomap	7	0.640
	Walk trap	10	0.620
2020	Multilevel	7	0.410
	Infomap	10	0.280
	Walk trap	6	0.032
2021	Multilevel	5	0.490
	Infomap	10	0.440
	Walk trap	10	0.300