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Movements and outmigration of juvenile Atlantic Sturgeon (A*cipenser oxyrinchus oxyrinchus*) in Georgia

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Abstract

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is a federally endangered anadromous fish found along the east coast of North America. Many populations have not fully recovered despite two decades of federal protection, and major knowledge gaps remain, especially in the southern portion of the species' range. The seasonal movement patterns of river-resident juveniles (RRJs) are not well understood, and little is known about the transition from the RRJ life stage to the marine migratory juvenile (MMJ) life stage. During the summers of 2014-2016 we captured and acoustically tagged age 1 RRJ Atlantic Sturgeon in the Ogeechee, Altamaha, and Satilla Rivers in order to 1) describe and quantify seasonal movements of RRJ Atlantic Sturgeon to identify important estuarine nursery areas, and 2) examine temporal patterns in outmigration to better understand the critical transition from RRJ to MMJ in Georgia rivers.

Movements of 79 fish were monitored using an array of stationary receivers deployed below the heads of tide in each river system. During the summer months in each river, the fish congregated in upriver, freshwater reaches, but during the winter months they moved downriver and became more broadly distributed. Some fish (36.7%; n=29) migrated back up their natal river in the spring and remained there as age 2 RRJs. We confirmed the outmigration of 30.4% (n=24) of age 2 fish in December-March, based on detections outside their natal river. The results of this study support the assumption of closure of age 1 populations that underpins recent quantitative studies of Atlantic Sturgeon recruitment.

Introduction

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is a large anadromous fish that historically occurred along the east coast of North America from maritime Canada to northern Florida. Adults live in marine waters and periodically return to their natal rivers to spawn. Recent studies have documented important clinal variations in spawning times among northern and southern populations. In the New York Bight, spawning occurs in the spring (Bain 1997). In at some Chesapeake Bay rivers, populations spawn in both fall and spring (Balazik and Musick 2014), but others exhibit fall spawning only (Hagar et al. 2014; Smith et al. 2015). In southern rivers (i.e. the Altamaha River in GA), spawning only occurs in the fall (Ingram and Peterson 2016). Preferred spawning habitat is typically found in areas with strong currents and rocky substrate (Gilbert 1989). After hatching, larval sturgeon migrate downstream toward the estuary where they eventually settle as river-resident juveniles (RRJs) (Bain 1997; Kynard and Horgan 2002). River-resident juveniles remain in their natal estuary, typically residing in the mesohaline waters below the head of tide. Outmigration to marine waters marks the transition to the marine migratory juvenile (MMJ) life stage; this may happen as early as age 2 or as late as age 6 (Dovel and Berggren 1983; Bain 1997). As the MMJs grow and mature in the marine environment, they may return to natal or non-natal estuarine or riverine habitats for prolonged periods during the summer months (Dovel and Berggren 1983; Bain 1997; Altenritter et al. 2017; Wipplehauser et al. 2017).

During the early 20th century Atlantic Sturgeon populations collapsed from a combination of anthropogenic factors including commercial overharvest, pollution, and the damming of many Atlantic coast spawning rivers (Bemis and Kynard 1997; Smith and Clugston 1997; Atlantic Sturgeon Status Review Team [ASSRT] 1998; Secor 2002; ASSRT 2007). As a result, the commercial fishery was closed in United States waters in 1998, and the species was eventually listed as endangered in 2012. Under the listing, US populations were divided into five distinct population segments (DPS): Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic. All DPSs were listed as endangered except for the Gulf of Maine DPS, which was listed as threatened (ASSRT 2007; Federal Register 2012a, 2012b). Despite federal protections, Atlantic Sturgeon currently spawn in fewer than 20 rivers, compared to 35-38 historic spawning populations (ASSRT 2007). Recovery of many populations has been impeded by loss of spawning habitat due to dams and incidental bycatch in commercial fisheries (Collins et al. 2000; ASSRT 1998; ASSRT 2007). Within the South Atlantic DPS, many populations have shown little sign of recovery, and several may be extirpated (ASSRT 1998; ASSRT 2007; Fox et al. 2018a and b).

To aid species recovery, the National Marine Fisheries Service (NMFS) identified a number of key research needs including quantified status assessments for each population (ASSRT 2007). Unfortunately, the complex migratory life history of Atlantic Sturgeon precludes comprehensive population estimates, and because the adults only spawn intermittently, spawning run estimates are similarly lacking. Several researchers have argued that annual assessment of RRJs should be a focus of range-wide population assessments, because that life stage represents the only period in the species' life cycle when an entire cohort can be effectively sampled within a well-defined location, prior to any migration or mixing (Bain et al. 1999; Peterson et al. 2000; Schueller and Peterson 2010). By estimating abundance of age 1 cohorts, studies have quantified annual recruitment for populations including the Hudson River (Peterson et al. 2000) and the Delaware River (Hale et al. 2016). Within Georgia, the Ogeechee River is home to a relatively small Atlantic Sturgeon population that exhibits only intermittent recruitment of small age 1 cohorts (Farrae et al. 2009). The Altamaha River hosts the largest known population of Atlantic Sturgeon in the southeast (ASSRT 2007), and exhibits consistent annual recruitment of several hundred to several thousand individuals (Schueller and Peterson 2010). The Satilla River hosts a small remnant population with infrequent recruitment and low RRJ abundances (Fritts and Peterson 2011; Fritts et al. 2016). These studies used similar methods to conduct mark-recapture estimates of age 1 RRJs within estuarine nursery habitats during the summer months. A key assumption of these studies is that the age 1 cohort represented a closed population during the assessment period; however, this assumption has not been well tested. Regardless, these recruitment estimates represent one of the few quantitative measures of Atlantic Sturgeon recovery since the species was listed as endangered in 2012.

The identification of Atlantic Sturgeon nursery habitats within each spawning river has also been identified as a key research need by NMFS (ASSRT 2007). In 2016, NMFS designated critical habitat for the species to include all mainstem reaches from the river mouth to either the fall line or the lowermost barrier within each of these river systems (Federal Register 2017). Within these reaches, a characterization of suitable nursery habitat is needed to identify potential environmental stressors and anthropogenic threats (Atlantic States Marine Fisheries Commission 1998; ASSRT 2007). A complete understanding of nursery habitat is also necessary to accurately quantify annual recruitment, which requires sampling of the entire age 1 cohort. However, no studies have yet documented movement patterns of RRJ Atlantic Sturgeon within estuarine nursery habitats within the South Atlantic DPS. In addition, little is known about the timing and drivers of outmigration as RRJs transition to the MMJ life stage. Therefore, the objectives of this study were to 1) describe and quantify seasonal movements of RRJ Atlantic Sturgeon to identify important estuarine nursery areas, and 2) examine temporal patterns in outmigration to better understand the critical transition from RRJ to MMJ in three separate rivers in the South Atlantic DPS. The new information obtained by this study helps fill knowledge gaps that have been identified by NMFS, and has a broad application to range-wide Atlantic Sturgeon management.

Methods

Study Sites.—This study was conducted in three adjacent rivers along the Georgia coast: the Ogeechee, the Altamaha, and the Satilla Rivers (Fig. 1). The Ogeechee River is a blackwater river that flows from the edge of Georgia's Piedmont province to Ossabaw Sound, south of Savannah, GA; the head of tide is typically located at or near river kilometer (rkm) 61 (Sheldon and Alber 2005). During the summer months, low flows and hypoxic conditions can degrade estuarine habitats used by juvenile Atlantic Sturgeon (ASSRT 2007, Farrae et al. 2013). The Altamaha River flows from the Georgia Piedmont to Altamaha Sound near Darien, GA, approximately 60 km south of Ossabaw Sound; the head of tide typically occurs near rkm 54 during normal flow conditions (Sheldon and Alber 2005). The Satilla River is a blackwater river situated entirely within the coastal plain of Georgia. Its mouth is located approximately 40 km south of Altamaha Sound, and the head of tide is typically located at or near rkm 50 (Sheldon and Alber 2005). Hypoxic conditions (mean 3.20 mg/L) are common throughout the lower estuary during summer months (Fritts and Peterson 2011).

Sturgeon Sampling.—Sampling in each of the three river systems was conducted below the heads of tide in each system from May through July, 2014-2016. In the Ogeechee River, netting occurred between rkm 20-55, in the Altamaha between rkm 10-30, and in the Satilla between rkm 25-55. Atlantic Sturgeon were captured with anchored gill and trammel nets designed to capture juveniles as described by several previous studies (Fox et al. 2018a and b; Bahr and Peterson 2016; Schueller and Peterson 2010). Gill nets 91.4 m long and 3.1 m deep, were composed of monofilament mesh panels of 7.6-,10.2-, and 15.3-cm (stretch measure). Trammel nets were of similar dimensions and material and were composed of one 7.6-cm inner panel and three 30.5-cm outer panels. Nets were deployed within the main channels at slack tides and were soaked for 30- to 90-min periods. As nets were retrieved, entangled Atlantic Sturgeon were removed and placed in floating net pens tethered to the research vessel. Once all nets had been recovered, each fish was measured to the nearest mm FL and inspected for tags. If no tag was present, a passive integrated transponder (PIT) tag was injected under the 4th dorsal scute. In each year of the study, up to 14 age 1 RRJs were randomly selected from each river for surgical implantation of an acoustic transmitter (age was estimated based on length, after Schueller and Peterson 2010, and a random subsample of pectoral fin ray sections were collected to validate ages). Surgical methods used for transmitter implantation were similar to those described by Boone et al. (2013). Captured fish were placed into lateral recumbency on a v-shaped surgical board, and a small pump maintained a gentle stream of fresh river water flowing over the gills. A sterile scalpel was then used to make a 1-cm incision along the midline of the ventrum for insertion of a 69kHz Vemco V7-4x acoustic transmitter (Vemco, Bedford, Nova Scotia, Canada). The manufacturer estimated the battery life of these transmitters to be 426 days. The incision was closed using a 2/0 absorbable monocryl suture (Monoswift™ L943) in a single interrupted pattern. Once the incision was closed, the fish was allowed to fully recover in a net pen before being returned to the river at its original capture site.

Acoustic Telemetry.— To monitor fish movement, we deployed a total of 42 stationary acoustic receivers (Vemco VR2W) throughout the three individual study rivers. Nine receivers were deployed in the Ogeechee River array, 24 in the Altamaha River array, and nine in the Satilla River array (Fig. 1). The Ogeechee River array extended from rkm 14.7-64.0. The Altamaha array extended from rkm 3.2-43.4. In the Satilla River, the array extended from rkm 10.2-50.2. Within each array, submerged receivers were mounted in an upright position, typically 2-3 m below the surface, and were attached to channel markers and trees using stainless steel cable or aluminum u-channel. Range testing at receivers revealed a maximum tag detection radius of approximately 800 m. Receivers were deployed for 38 consecutive months (~167 weeks), from 4 May 2014 through 10 July 2017. Data were downloaded from receivers at approximately 3-4 month intervals.

Raw telemetry data were checked to ensure that fish detection locations made sense (e.g., an individual was not in 2 places at the same time, and that transit times between receiver stations were reasonable); single detections were included in analysis. Data were then transformed into "detection days," defined as one detection per individual per receiver per day. Based on these detection days we then calculated the median rkm position of each fish on a daily, weekly, and monthly basis. We also calculated the minimum, 25th percentile, 75th percentile, and maximum rkm positions of all fish within each river for each month of the study.

Water Quality Monitoring.—Data on water temperature were obtained from a variety of sources located as close to the study sites as possible. Ogeechee River temperature data were obtained from a monitoring station operated by the Phinizy Center for Water Sciences at river kilometer (rkm) 50. Altamaha River temperature data were from a University of Georgia monitoring station located at rkm 23 (Di Iorio 2017). Satilla River temperature data from May 2014 through October 2014 were obtained from USGS streamgage 02228000 located at approximately rkm 140; data for the remainder of the study came from streamgage 02226500 located at approximately rkm 250. Additional measurements of water temperature, salinity, and dissolved oxygen were obtained from a portable YSI Pro2030 multiprobe (YSI, Inc., Yellow Springs, OH) while nets were soaked at each sampling site.

Statistical Analysis.—We used a single-factor ANOVA to assess differences (among rivers) in the proportion of fish that outmigrated as age 2 MMJs, as well as the proportion of fish that remained as age 2 RRJs. A single-factor ANOVA was also used to determine whether the pooled rate of outmigration (for all rivers) differed by study year; a Tukey's HSD test was used to determine which year(s) were different. We used a 2-sample T-test, assuming equal variances, to determine if there was a difference between the length (FL at tagging) of fish that outmigrated as age 2 MMJs vs. those that remained as age 2 RRJs, for pooled data from all rivers and then within each river. Prior to each analysis, we tested for normality and homogeneity of variance using a Shapiro-Wilk test. Results for all analyses were considered significant at α = 0.05.

Results

Sturgeon Sampling.—Netting was conducted in the Ogeechee, Altamaha, and Satilla Rivers between May and August 2014-2016. Over the three years of the study, we set a total 1570 nets, for a total of 1186 hours of sampling effort (Table 1). Across all three rivers, we captured 990 Atlantic Sturgeon, 606 of which were RRJ (Table 1; Fig. 2). In the Ogeechee River, we captured 264 Atlantic Sturgeon; annual catch varied from 66-104 individuals (RRJ catch range: 48-71). The total catch of Atlantic Sturgeon in the Altamaha River was 540 individuals; total annual catch varied from 72-353 (RRJ catch: 32-220). We captured a total of 186 Atlantic Sturgeon in the Satilla River; annual catch varied from 37-81 (RRJ catch: 18-58).

Transmitters were surgically implanted into 92 age 1 RRJ Atlantic Sturgeon: 25 in the Ogeechee River, 35 in the Altamaha River, and 32 in the Satilla River (Tables 2 and 3). Four of the tagged fish (4.3%) were never detected, and eight fish (8.7%) were last detected ≤7 days after tagging; these individuals were removed from all subsequent analyses (see Supplementary Table S.1). The remaining 79 tagged juveniles comprised 17 individuals in the Ogeechee River, 32 in the Altamaha River, and 30 in the Satilla River. A total of 349,087 detections of these fish were recorded on our receiver arrays or obtained from similar arrays deployed by other researchers working in nearby areas. Overall, the mean number of detections per fish was 4419 (range: 16-80,325) and the mean number of days these individuals were tracked (days between tagging date and last detection) was 298 (range 20-432). One tagged sturgeon in the Satilla River had considerably more detections (n=80,325) than any other fish; that individual did disappear from the array for periods of time, and its overall behavior was not dissimilar from other tagged fish, so it was included in our analyses. The mean number of days each fish was tracked was similar across all three rivers: 306 days (range: 20-415) in the Ogeechee River, 294 days in the Altamaha River (range: 21-432), and 298 days in the Satilla River (range: 63-431).

Movement Patterns.—Over the course of the study, transmittered RRJs were detected on every receiver in each of the three river arrays. Telemetry data indicated a similar pattern of juvenile habitat use in all three rivers: during the summer months the fish congregated in upriver reaches, but during the winter months they moved downriver and became more broadly distributed (Figs. 3-5).

Outmigration.—Of the 79 RRJs included in the analysis, 24 individuals (30.4%) were detected at least once on an acoustic receiver outside of their natal river (Table 3), providing confirmation that these individuals had outmigrated from their natal river as MMJs. These fish were detected by receiver arrays in other study rivers or by other researchers' receiver arrays in coastal Georgia and South Carolina. A greater proportion of transmittered juveniles outmigrated from the Altamaha River (50.0%; n=16) than from the Ogeechee (11.8%; n=2) or Satilla Rivers (20.0%; n=6), but the difference was not significant when compared among all years of the study (p=0.782, F=0.256, df=2; tests for normality and homogeneity of variance of data showed that both assumptions were met). In the Ogeechee River, one fish (100%) tagged in 2014 was a confirmed outmigrant, 0 fish tagged in 2015 outmigrated, and 1 fish (12.5%) tagged in 2016 outmigrated. In the Altamaha River, five fish (62.5%) tagged in 2014 were confirmed outmigrants, 2 fish (18.2%) tagged in 2015 outmigrated, and nine fish (69.2%) tagged in 2016 outmigrated. In the Satilla River, four fish (57.1%) tagged in 2014 were confirmed outmigrants, one fish (9.1%) tagged in 2015 outmigrated, and two fish (16.7%) tagged in 2016 outmigrated. The overall rate of outmigration for all rivers was significantly different among study years (p=0.039, F=5.812, df=2). In 2014, tagged juveniles outmigrated at a higher rate than 2015 (p=0.035), but there were no significant differences between 2014 and 2016 (p=0.165) or between 2015 and 2016 (p=0.472).

As tagged juvenile sturgeon outmigrated from their natal river, some individuals (n=7; 29.2% of confirmed outmigrants) were able to pass undetected by the acoustic receiver(s) located at or near the river mouth. In the Ogeechee River, the single confirmed MMJ in the Ogeechee River was detected by the lowermost receivers as it left that system. Four Altamaha River fish (12.5% of confirmed MMJs there) and three Satilla River fish (10% of confirmed MMJs) were able to exit the system without being detected near the river mouth. All fish that outmigrated were last detected in their natal river during the winter months; nine fish outmigrated in December, and January-March each had 5 fish that outmigrated. No outmigration was observed between April and November in any river system in any year of the study.

When tagged fish from all study rivers were pooled, those that transitioned to MMJs at age 2 were significantly larger (p=0.011, t=2.366, df=48) at the time of tagging (361.8 mm FL ±45.80 mm, Std. Dev) than those that remained as age 2 RRJs (336.6 mm ± 34.0 mm) (Table 6). However, within each study site, only the Ogeechee River had significantly larger tagged fish that outmigrated, compared to those that remained as age 2 RRJs (p=0.004, t=2.228, df=10). There was no significant difference in length between tagged fish that outmigrated and those that did not in either the Altamaha (p=0.09, t=2.080, df=21) or the Satilla Rivers (p=0.06, t=2.120, df=16).

Twenty-nine of the 79 transmittered juveniles (36.7%) remained in their natal rivers as RRJs until at least summer of the year after they were tagged. A greater proportion of fish remained as RRJs in the Ogeechee River (58.8%; n=10) than in the Altamaha (21.9%; n=7) or Satilla (40%; n=12), but these differences were not significant (p=0.628, F=0.504, df=2). Twenty-six tagged fish (32.9%) were confirmed neither as outmigrants nor as RRJs the summer after tagging. Nine of these individuals were last detected near the mouth of their natal river between December and March, and an additional nine were last detected in their natal river in December-March.

Discussion

Movement Patterns.—In all three years of this study, RRJs exhibited a similar pattern of seasonal habitat use; in the warmest months of the year (May-July), RRJ distribution was concentrated upriver, while in the coldest months (Dec-Feb), RRJs were more widely distributed throughout the lower reaches of the estuary. In the Altamaha River (Fig. 4), fish did not move as far upriver as in the Ogeechee (Fig. 3) and Satilla Rivers (Fig. 5); this may be attributed to the fact that the Altamaha is much larger than the others, both in terms of available habitat (in the form of multiple, braided distributary channels), and in terms of flow. The greater freshwater input in the Altamaha River estuary pushes the salt wedge farther downstream, creating more freshwater estuarine habitat below the head of tide than in the Ogeechee and Satilla Rivers. Previous studies have shown that habitat selection by RRJ Atlantic Sturgeon is likely associated with several water quality parameters including temperature, salinity, dissolved oxygen (DO), and flow (Secor and Gunderson 1997; Bain et al. 2000; ASSRT 2007; Niklitschek and Secor 2010; Allen et al. 2014; Moberg and DeLucia 2016). It is interesting to note that water quality data collected at net sites suggests that southern sturgeon may be tolerant of relatively low DO conditions - in the Satilla River, the mean DO at net sites was 3.33 mg/L (SD 0.65), and healthy sturgeon were captured (and released in good condition) in DO as low as 2.03 mg/L.

Suitable nursery habitat for RRJ Atlantic Sturgeon in Georgia appears to reach a yearly minimum in the summer. During winter months RRJs were broadly distributed throughout the lower estuaries of each river in this study, but in the June and July, when water temperatures frequently exceeded 30 °C, most RRJs inhabited upriver reaches with observed salinities of 0-10 ppt (Fig. 6). A similar seasonal pattern of distribution was described for RRJs in the Hudson River, NY: from April-October, RRJs demonstrated preferences for water temperatures of 24-28 °C, and salinities of 0-5 ppt, but during the winter RRJs moved downstream into river reaches where salinities reached 18 ppt (Bain et al. 2000). Niklitsheck and Secor (2005) found that suitable habitat for juvenile sturgeon in the Chesapeake Bay also reached a yearly minimum in the summer, due to elevated temperatures, high salinity, and low DO. The upriver reaches occupied by sturgeon in the summer represent important refugia within the designated critical habitat for the species (Federal Register 2017), and may warrant additional protections, at least during summer months. Further studies are necessary to determine whether degraded summer refugia habitat may explain the lack of sturgeon recovery in some rivers, especially within the South Atlantic DPS.

Outmigration.—This study is the first to document the timing and patterns of outmigration by telemetered Atlantic Sturgeon in the South Atlantic DPS. Across all three rivers in this study, 30.4% of tagged Atlantic Sturgeon were detected outside of their natal river after completing their transition to the MMJ stage during the winter after tagging (Table 4). Given that Ingram and Peterson (2016) found that spawning occurs from October-December in the Altamaha River, the results of this study suggest that RRJs began their initial transition to MMJs during the winter and early spring months immediately after reaching age 2. In all three study rivers, age 1 RRJs dispersed downstream in their natal estuary during the winter. The final natal river detections of fish that outmigrated occurred in December-March, indicating that those fish continued their downstream movement into the ocean, transitioning into age 2 MMJs. We observed that 36.7% of fish in this study moved back upriver as age 2 RRJs in the spring, as water temperatures increased.

The observed proportion of fish that were confirmed as age 2 MMJs in this study should be viewed as conservative. The life stage of approximately 32.9% of fish in this study was not definitively known at age 2 – they were not detected within or outside of their natal river, and therefore could not be confirmed as RRJs or MMJs. Some of these individuals may have died, experienced transmitter failure, or remained in their natal river without being detected, but at least some of these fish likely outmigrated. Nine fish (34.6% of those with unknown fates) were last detected in their natal river at a receiver close to the mouth between December and March, the time period in which all confirmed MMJs outmigrated. These individuals almost certainly outmigrated without being detected outside of their natal river; this is not unlikely given the sparse and inshore-biased distribution of acoustic receiver stations along the coast of the southeastern U.S. An additional nine fish with unknown fates were last detected in their natal river between December and March, but not by a receiver near the mouth - these fish also likely outmigrated without being detected outside of their natal river. Several confirmed MMJs were able to bypass receivers near the mouth of their natal river as they outmigrated, due to the spatial and physical complexities of each estuary. Assuming all 18 of these fish are classified as "putative outmigrants," the total proportion of tagged fish in this study that definitely or probably outmigrated at age 2 was 53.2% (n=42).

Little is known about the mortality of RRJ Atlantic Sturgeon. Of the 79 fish included in our analysis, 69 (87.3%) were still being detected six months after being tagged, and 21 (26.6%) were still being detected at least one year after tagging. Because tagged fish are only detected when they come within range of a receiver, it is not possible to ascertain whether an individual's lack of detections indicate mortality. Based on recaptures of transmittered fish in this and other studies from our research group (Fox et al. 2019; Ingram and Peterson 2016), surgical incisions healed completely within one month of capture. Of the 92 total fish tagged across three years in this study, 15 (16.3%) were last detected less than one month after being tagged. The disappearances of these fish from our array could have been the result of tagging mortality, natural mortality, or tag failure.

Ontogenetic shifts in habitat use are well-documented for many species, including Atlantic Sturgeon; these patterns are not well-understood within the RRJ stage of development. Results of this study revealed that tagged fish that outmigrated as MMJs at age 2 were significantly larger (when tagged at age 1) than fish that remained as age 2 RRJs. In laboratory experiments, Niklitschek and Secor (2009a and b) found that age 1 juveniles are more tolerant of salinity than age 0 juveniles, suggesting a link between body size and salinity tolerance; however, this relationship has not been evaluated in older juveniles. The outmigration of larger juveniles in this study suggests that salinity tolerance may be a function of body size. However, further studies are needed to better understand how differences in juvenile growth affect the complex interactions of temperature, salinity, and seasonal habitat preferences of RRJs within South Atlantic DPS river systems. It should also be noted that we selected age 1 RRJs for acoustic tagging based on the length-frequency analysis of Schueller and Peterson (2010) in the Altamaha River. Length-frequency analyses for the Ogeechee and Satilla River sturgeon catches from this study suggest that age 1 fish in those rivers may be slightly smaller than those in the Altamaha River (Fig. 2). Therefore, it is possible that some of the larger RRJs that we tagged in those rivers may have been age 2; fin ray sections were not taken from telemetered fish.

Interestingly, outmigrating MMJs showed no consistent pattern of directional movement after leaving their natal estuaries. Some fish appeared to use the Atlantic Intracoastal Waterway to travel to an adjacent river, while others moved directly offshore. Several MMJs even returned to their natal river after spending time in other river systems. A few age 2 MMJs tagged in this study were detected in South Carolina rivers >300 km away. Although the dispersal of MMJ appeared to be without discernable pattern, further studies with larger sample sizes could help managers understand broader patterns of habitat connectivity among different populations. As Atlantic Sturgeon populations continue to recover, these dispersal patterns may become increasingly important to identifying and protecting MMJ habitats during their critical transition to marine environments. Future studies may be able to use transmitters with extended battery life to discern longer-term patterns of MMJ movements.

A number of recent studies have quantified Atlantic Sturgeon recruitment by estimating RRJ cohort sizes using capture-mark-recapture models (Schueller and Peterson 2010; Bahr and Peterson 2016; Fritts et al. 2016; Hale et al. 2016). Many of these studies used Huggins closed-capture models, which assume population closure (Huggins 1989). The results of this study indicated that age 1 RRJ populations were in fact closed during the summer. Recruitment estimation requires intensive mark-recapture sampling of age 1 RRJ cohorts within their nursery habitats during the summer months. Results from this study showed that no age 1 RRJs left their natal estuary until winter - a strong indicator that the age 1 cohorts are, in fact, closed to emigration during the summer months. Our telemetry data also showed that up to 50% of tagged sturgeon left their natal river as MMJs before the summer of age 2. These results support the findings of Schueller and Peterson (2010) that mark-recapture estimates of RRJs older than age 1 may substantially underestimate the number of fish in those cohorts. Consequently, we suggest that mark-recapture estimates of age 1 RRJ cohorts remains the best available method for assessing annual recruitment of Atlantic Sturgeon – at least within the southern portion of the range. Similar studies of juvenile movements and outmigration are needed in other parts of the range to account for clinal variations in ecology of the species.

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Table 1: Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) sampling effort, catch, and catch per unit efford (CPUE) in the Ogeechee, Altamaha, and Satilla Rivers, GA, USA 2014-2016. Fish with a fork length <500 mm were considered to be river-resident juveniles (RRJs).

River	Year	Net sets	Net hours (h)	Total catch	RRJ catch	Total CPUE (fish h^{-1})	RRJ CPUE (RRJs h^{-1})
Ogeechee	2014	197	137	66	48	0.482	0.350
	2015	263	175	104	71	0.594	0.406
	2016	241	156	94	53	0.603	0.340
Altamaha	2014	88	85	115	64	1.353	0.753
	2015	49	43	72	32	1.674	0.744
	2016	160	155	353	220	2.277	1.419
Satilla	2014	159	97	37	18	0.381	0.186
	2015	185	176	68	58	0.386	0.330
	2016	228	166	81	42	0.488	0.253

Table 2: Number of acoustically tagged age 1 river-resident juvenile (RRJ) Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*), and the number subsequently detected in the Ogeechee, Altamaha, and Satilla Rivers, GA, USA 2014-2016.

	No. RRJs tagged (detected)			
River	2014	2015	2016	Total
Ogeechee	2 (1)	11 (8)	12 (8)	25 (17)
Altamaha	10 (8)	11 (11)	14 (13)	35 (32)
Satilla	8 (7)	11 (11)	13 (12)	32 (30)
Total	*20 (16)*	*33 (30)*	*39 (33)*	*92 (79)*

Table 3: Status of acoustically tagged Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) tagged in the Ogeechee, Altamaha, and Satilla Rivers, GA, USA (n=79). RRJ = river-resident juvenile; MMJ = marine migratory juvenile.

River	n Confirmed age 2 RRJ (%)	n Confirmed age 2 MMJ (%)	Unknown status (%)	Outmigration detection
Ogeechee	10 (58.8)	2 (11.8)	5 (29.4)	100.0%
Altamaha	7 (21.9)	16 (50.0)	9 (28.1)	75.0%
Satilla	12 (40.0)	6 (20.0)	12 (40.0)	50.0%
Total	*29 (36.7)*	*24 (30.4)*	*26 (32.9)*	*70.1%*

Table 4: Mean fork lengths (FL) of acoustically tagged Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Ogeechee, Altamaha, and Satilla Rivers, GA, USA 2014-2016. Lengths are from time of tagging as age 1 river-resident juveniles during the summer months.

	Remained in natal river				Outmigrated from natal river			
River	n	Mean FL (mm)	Std. dev. (mm)	Range (mm)	n	Mean FL (mm)	Std. dev. (mm)	Range (mm)
Ogeechee	10	329.3	23.6	309-379	2	409.5	24.4	371-448
Altamaha	7	321.4	24.4	300-365	16	342.3	27.3	294-403
Satilla	12	351.6	41.5	290-446	6	398.2	55.7	310-459
Total	*29*	*336.6*	*34.0*	*290-3446*	*24*	*361.8*	*45.8*	*294-459*

Figure Captions

Figure 1: Maps of study sites in the Ogeechee (A), Altamaha (B), and Satilla (C) Rivers, GA, USA. Black dots represent acoustic receiver stations. When possible, heads of tide and water quality data collection station sites are noted. River kilometer (rkm) location of several receiver stations is included for reference.

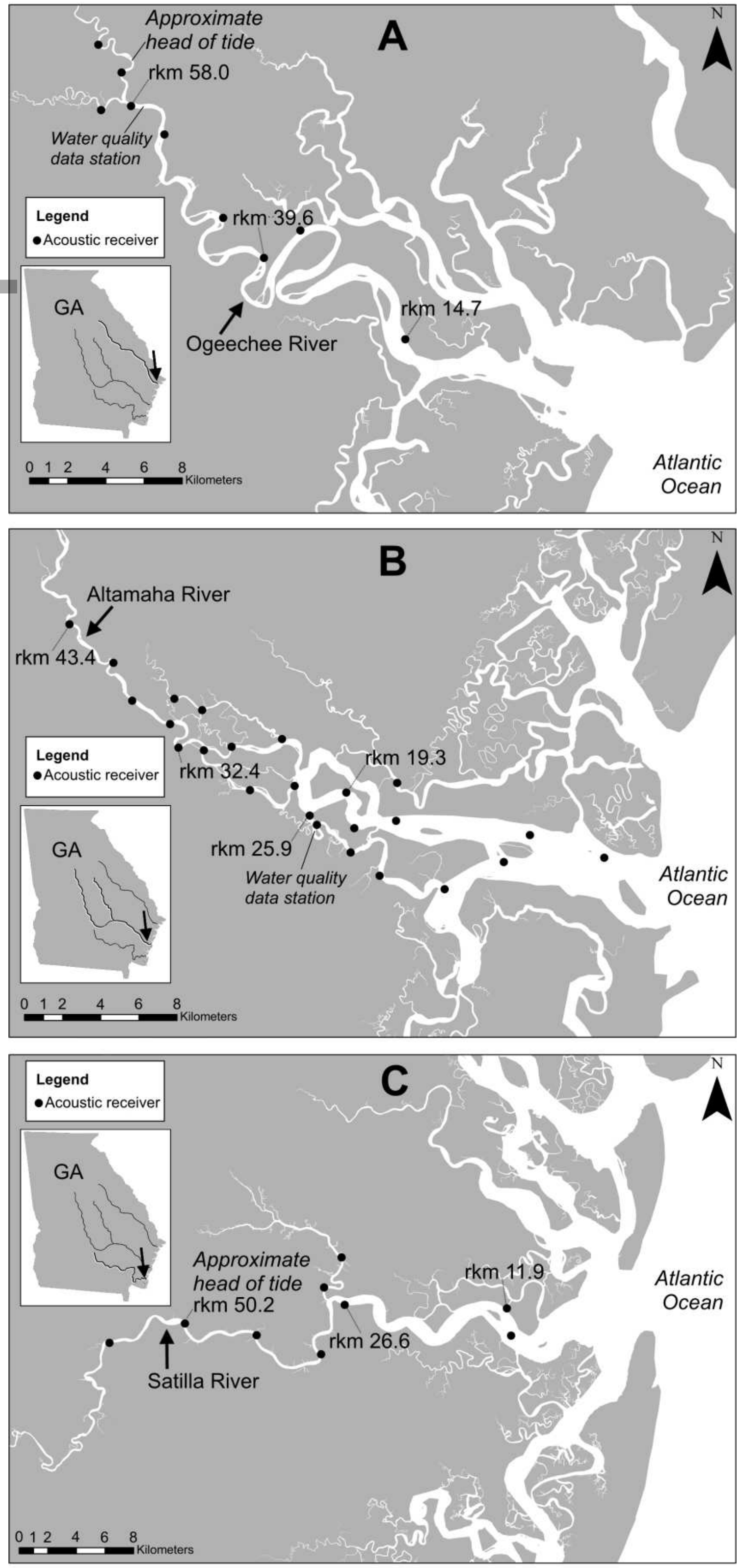
Figure 2: Length-frequency histograms for Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) captured in the Ogeechee, Altamaha, and Satilla Rivers, GA, USA in 2014-2016.

Figure 3: Habitat use by age 1 juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) tagged in the Ogeechee River, GA, USA. Boxplot ends represent 25th and 75th percentiles of all tag detections. Line within box is median river kilometer (rkm) position of all fish. Error bars [whiskers] represent minimum and maximum rkm detections. The number over each box indicates the number of individuals detected that month. Dots along the main Y-axis represent the rkm positions of receivers in the acoustic array. The blue line indicates water temperature.

Figure 4: Habitat use by age 1 juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) tagged in the Altamaha River, GA, USA. Boxplot ends represent 25th and 75th percentiles of all tag detections. Line within box is median river kilometer (rkm) position of all fish. Error bars [whiskers] represent minimum and maximum rkm detections. The number over each box indicates the number of individuals detected that month. Dots along the main Y-axis represent the rkm positions of receivers in the acoustic array. The blue line indicates water temperature.

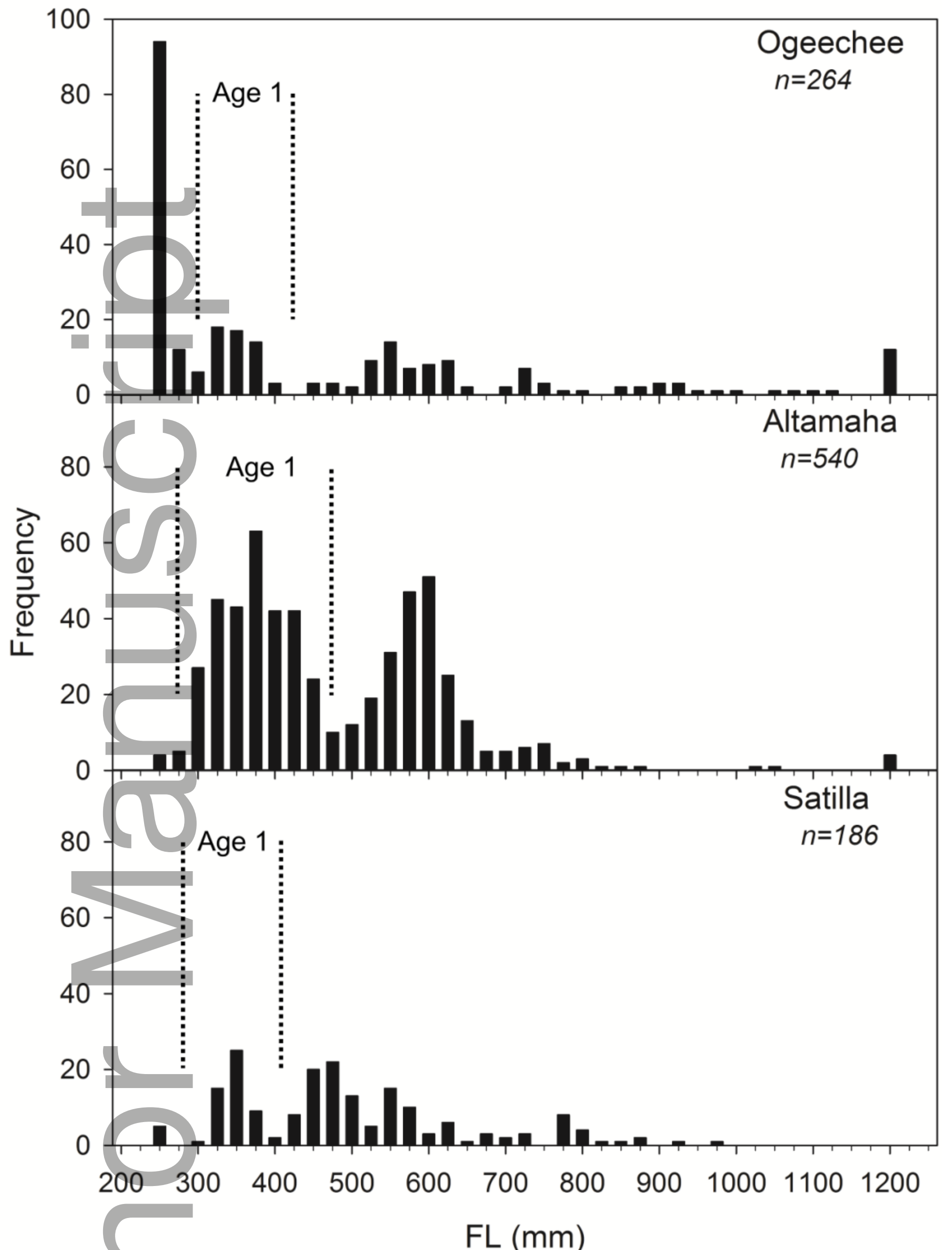
Figure 5: Habitat use by age 1 juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) tagged in the Satilla River, GA, USA. Boxplot ends represent 25th and 75th percentiles of all tag detections. Line within box is median river kilometer (rkm) position of all fish. Error bars [whiskers] represent minimum and maximum rkm detections. The number over each box indicates the number of individuals detected that month. Dots along the main Y-axis represent the rkm positions of receivers in the acoustic array. The blue line indicates water temperature.

Figure 6: Observed salinity ranges in the Ogeechee, Altamaha, and Satilla Rivers, GA, USA during June and July 2015-2016. Shaded area represents the range (minimum to maximum) of recorded salinities (on the Y-axis) at each receiver station (plotted by river kilometer on the X-axis). Median monthly positions of age 1 Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) for each month are indicated with vertical lines.



583

584 **Figure 1**



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586 **Figure 2**

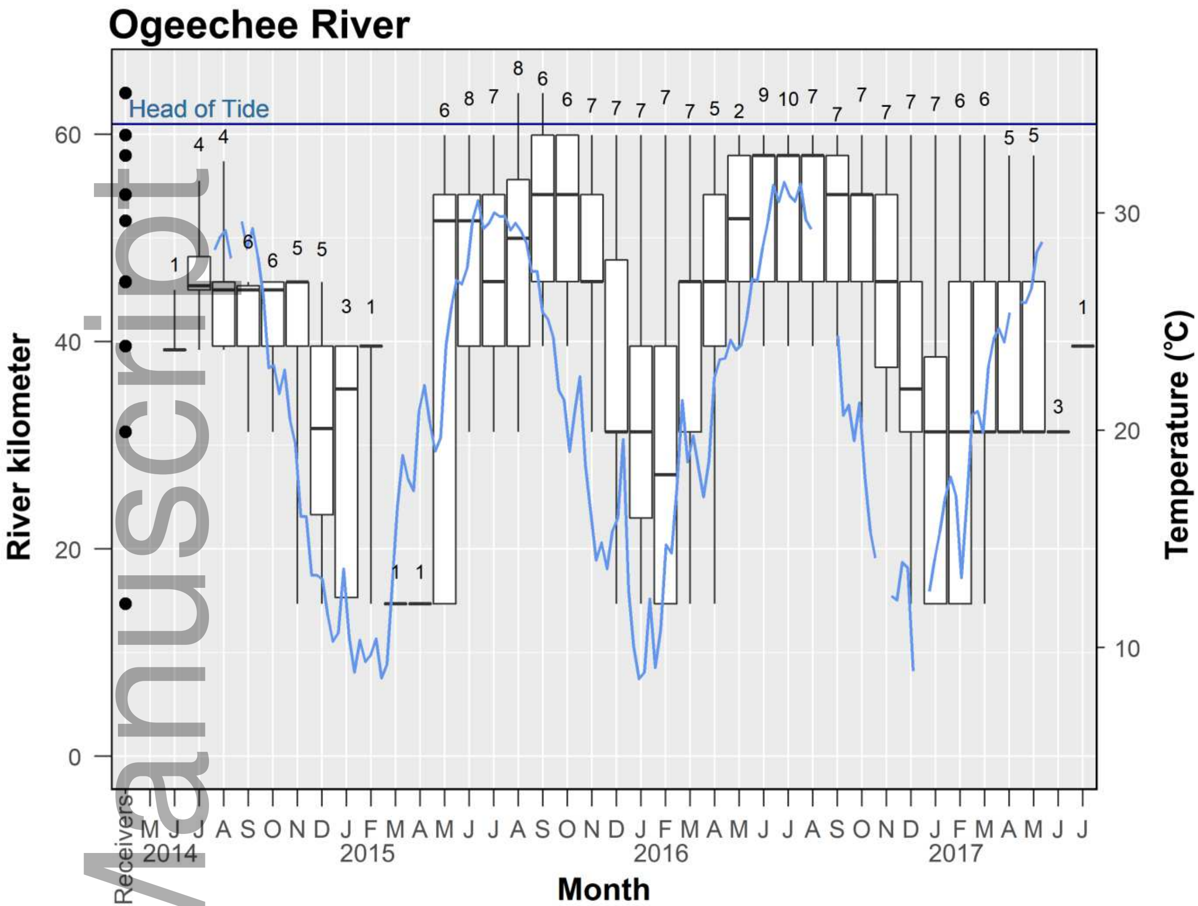

Ogeechee River
Head of Tide
River kilometer
Temperature (°C)
Month
Receivers
0
20
40
60
10
20
30
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
2014
2015
2016
2017

Figure 3.

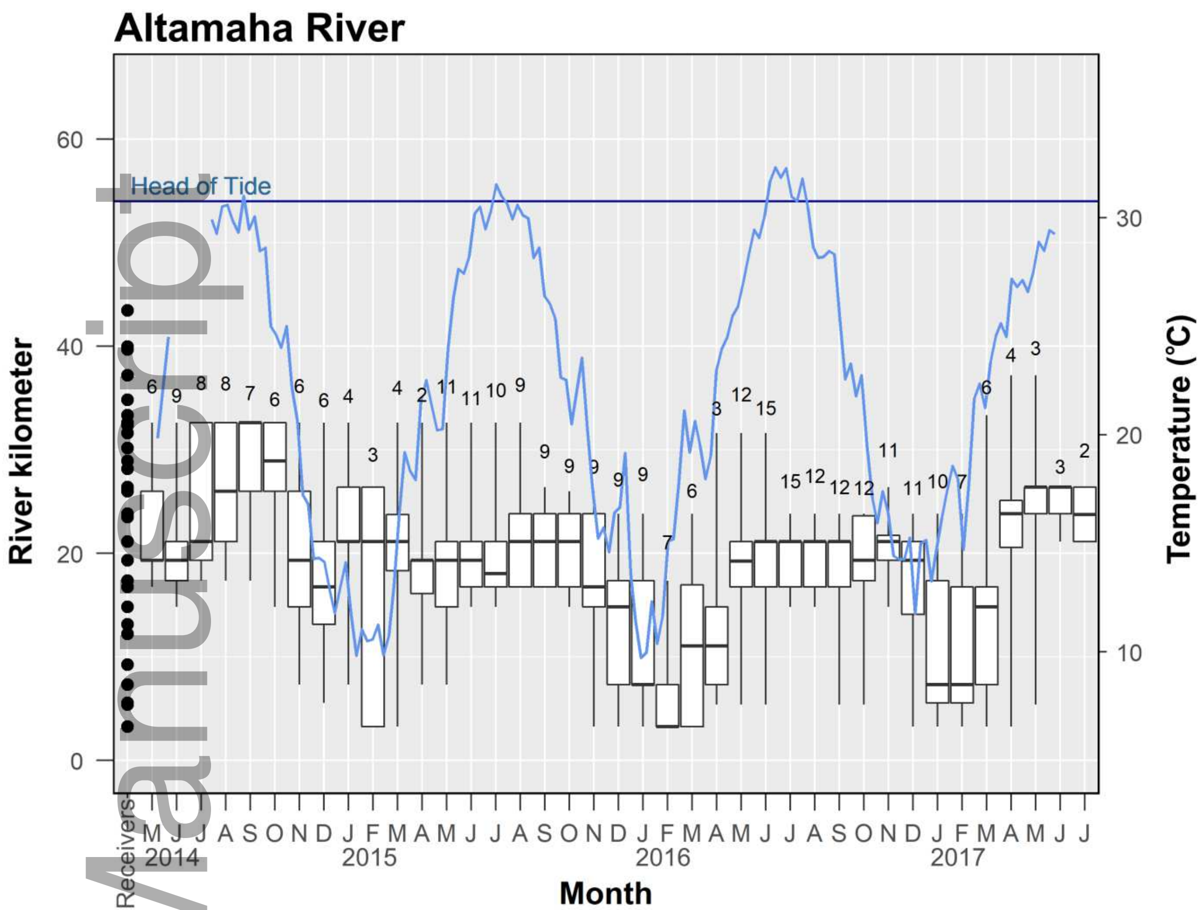

Altamaha River
Head of Tide
River kilometer
Temperature (°C)
Month
Receivers
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
2014
2015
2016
2017
0
20
40
60
10
20
30

Figure 4.

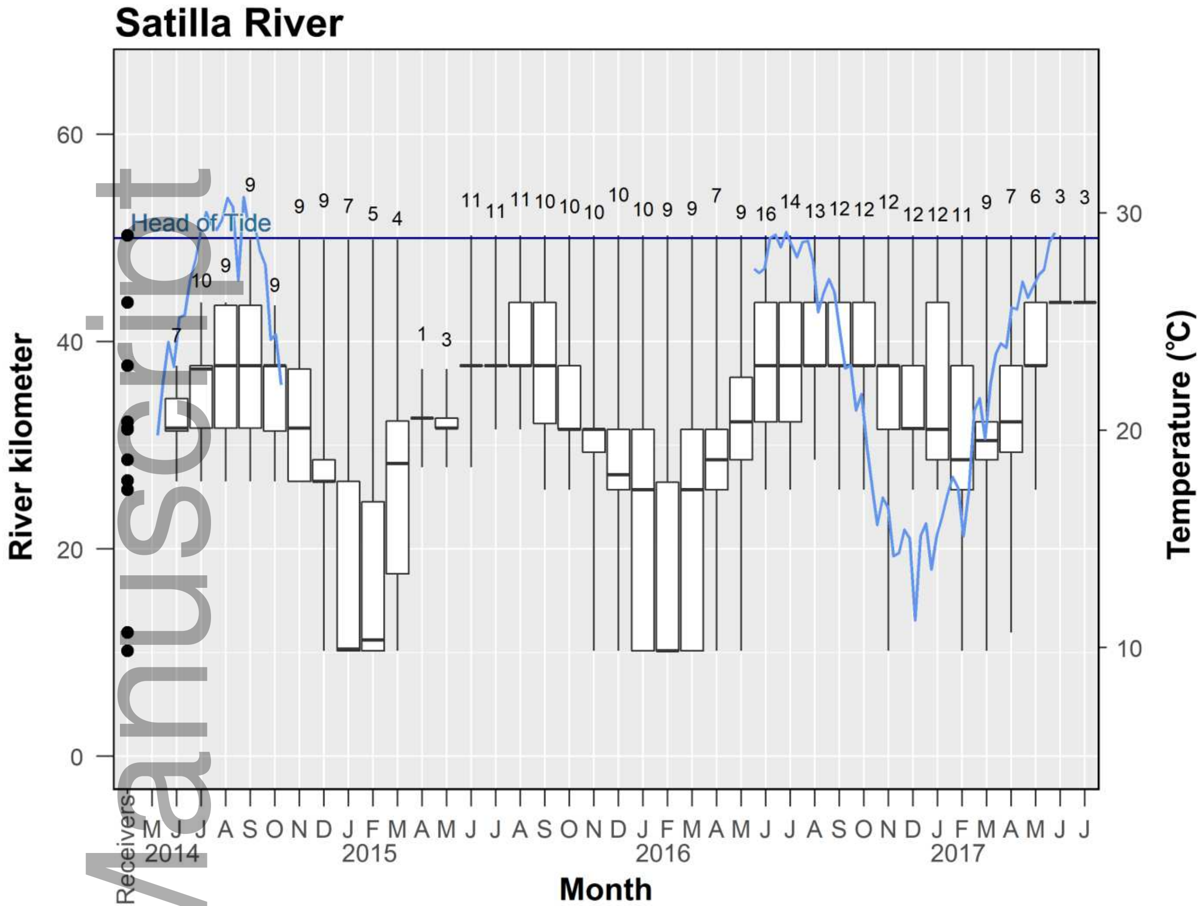
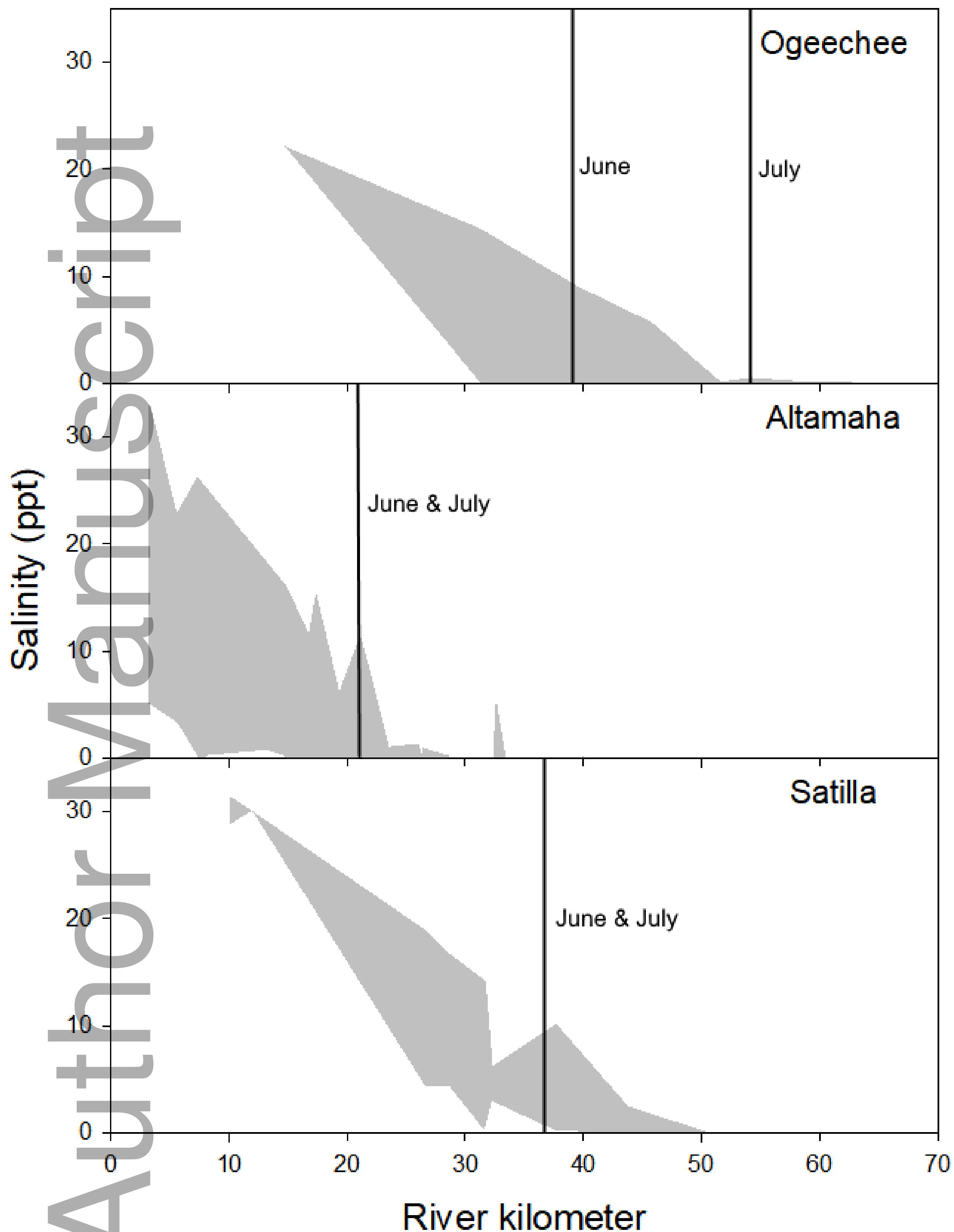

Satilla River
Head of Tide
River kilometer
Temperature (°C)
Receivers
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
2014
2015
2016
2017
Month

Figure 5.



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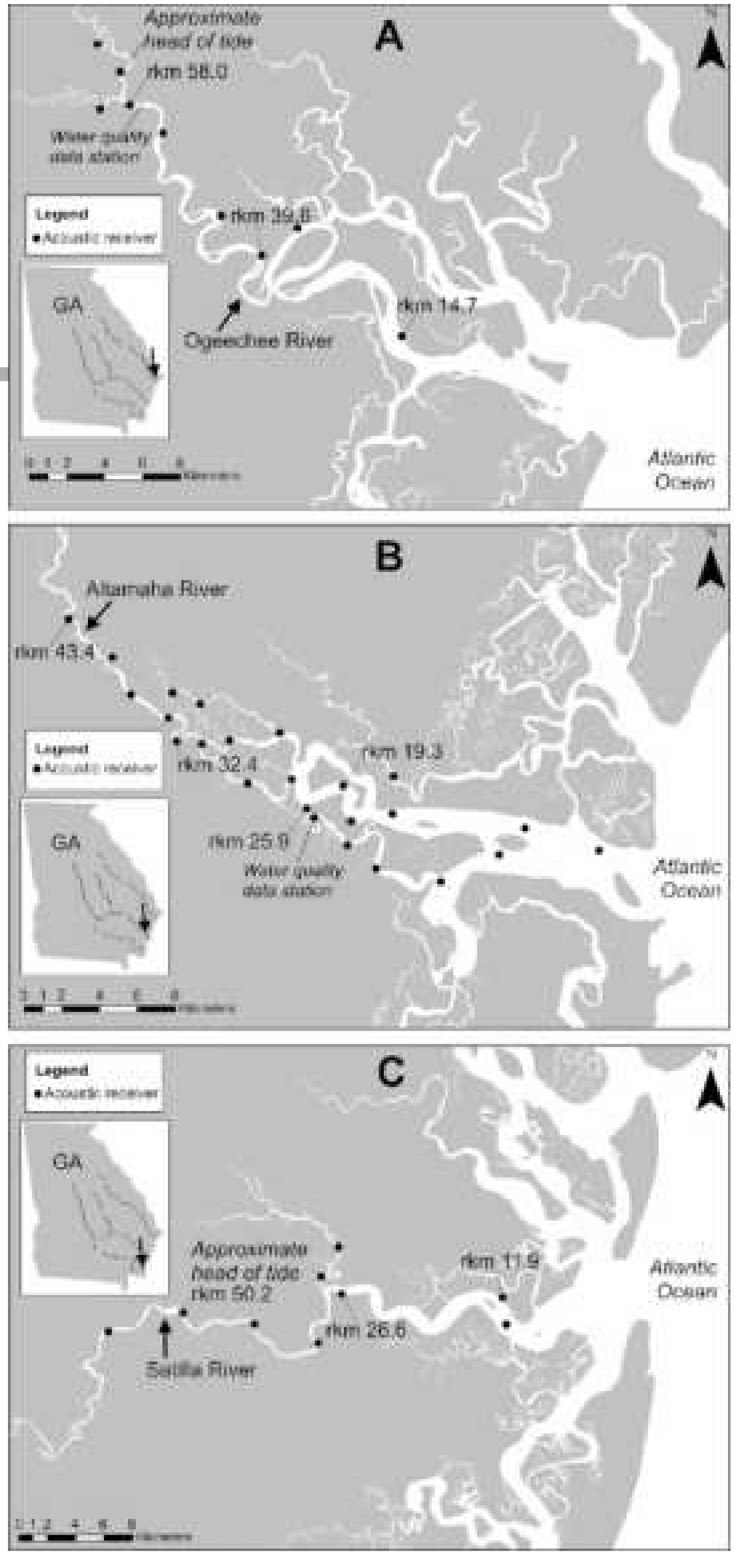
601 **Figure 4.**



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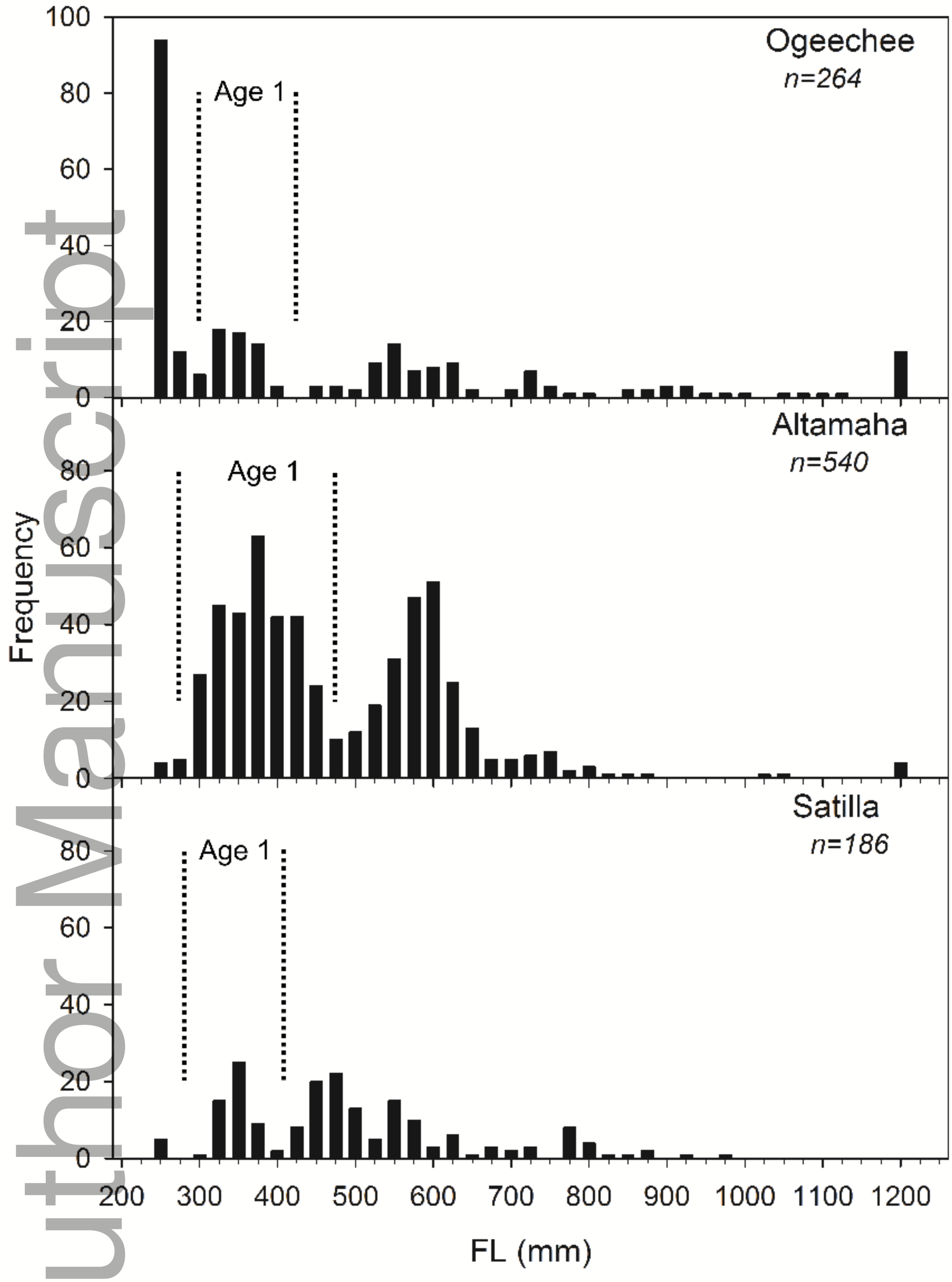

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