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ARTICLE

Occurrence of Atlantic Sturgeon in the St. Marys River, Georgia

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Abstract

The Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* is an anadromous species that historically has been found along the Atlantic coast of North America from maritime Canada to the St. Johns River, Florida. Decades of overharvest and habitat loss has resulted in range-wide population declines, and in 2012 the species was listed under the U.S. Endangered Species Act as five Distinct Population Segments (DPSs). The extirpation of several populations, including some in the South Atlantic DPS, was identified as an important consideration in the final determination to list this DPS as endangered. In the St. Marys River, Georgia, the second-most southern river within their historical range, Atlantic Sturgeon were thought to have been extirpated for several decades. The objectives of this study were to document the seasonal occurrence of Atlantic Sturgeon in the St. Marys River and to document any evidence of an extant population in the river. During the summers of 2013–2016, we set 533 nets and captured a total of 25 Atlantic Sturgeon, including several age-1, river-resident juveniles. Genetic analyses indicated that these juveniles were descendants of a remnant population that is distinct but more closely related to other populations within the South Atlantic DPS than those in more northern rivers. Using acoustic telemetry, we monitored the movements and habitat use of 14 individual sturgeon in the St. Marys River estuary. Acoustically tagged juveniles resided mainly within the St. Marys River main stem, but we did detect a number of adult migrants using Cumberland Sound on a seasonal basis. Our results indicate that Atlantic Sturgeon persist in the St. Marys River and that the estuary also provides seasonally important habitat for migrating adults from other populations.

The Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* is an anadromous fish that historically has been found in rivers and estuaries along the Atlantic coast of North America, from the Saint Lawrence River, Quebec, south to the St. Johns River, Florida. Throughout their range, Atlantic Sturgeon populations collapsed during the late 19th and early 20th centuries because of commercial overharvest, industrial development, pollution, and the construction of dams on many of its Atlantic coast spawning rivers (Bemis and Kynard 1997; Smith and Clugston 1997; NMFS 1998; Secor 2002; ASSRT 2007).

As a result of the major declines in Atlantic Sturgeon populations, federal management agencies in the United States

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implemented several protections during the late 20th century. The commercial Atlantic Sturgeon fishery was closed in all state waters in 1998, and the species was listed under the U.S. Endangered Species Act (ESA) in 2012. This listing designated five distinct population segments (DPSs) in U.S. waters: Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic. All DPS populations were listed as endangered except for the Gulf of Maine DPS, which was listed as threatened (ASSRT 2007; NOAA 2012a, 2012b).

Within the South Atlantic DPS, many Atlantic Sturgeon populations have shown few signs of recovery, and several may be extirpated (NMFS 1998; ASSRT 2007). Despite federal protections from harvest, recovery of many populations has been impeded by degraded habitats in spawning rivers, loss of spawning habitat due to dams, and incidental bycatch in commercial fisheries targeting other coastal (Wirgin et al. 2015) or estuarine species (NMFS 1998; Collins et al. 2000; ASSRT 2007; Wirgin et al. 2018). Although modern environmental regulations have helped reduce the pollution affecting many of these river systems, nonpoint sources continue to degrade water quality, particularly in estuarine habitats that are critically important to juvenile Atlantic Sturgeon (ASSRT 2007).

As an anadromous species, Atlantic Sturgeon adults typically reside in marine environments but migrate into their natal freshwater rivers to spawn (Vladykov and Greeley 1963). Recent studies have shown that the timing of spawning varies by latitude; northern populations spawn in the spring (Bain 1997) and at least some central and southern populations spawn only or primarily in the fall (Hager et al. 2014; Flowers and Hightower 2015; Ingram and Peterson 2016). Young, river-resident juveniles (RRJs) typically reside in estuarine habitats near the freshwater–saltwater interface for their first 2–4 years before transitioning to nearshore marine habitats as marine migratory juveniles (MMJs) (Bain 1997; Schueller and Peterson 2010). The presence of age-1 RRJs within a particular river system is widely recognized as strong evidence of an extant population, especially in rivers where adult spawners may be rare (Schueller and Peterson 2010; Bahr and Peterson 2016; Fox et al. 2018).

The St. Marys River in southeastern Georgia (Figure 1) is the second-most southern river in the Atlantic Sturgeon's range and historically hosted a spawning population (ASSRT 2007). During the 1980s and 1990s, the river supported a small commercial fishery for Atlantic Sturgeon (Weber et al. 1995). The population has not been well studied, and the most recent surveys suggest that the population may have been extirpated. Targeted sampling conducted by Fritts and Peterson (2011) documented the presence of MMJs, but not RRJs. Genetic analyses of tissue samples obtained from the MMJs captured in that study suggested that the fish originated within the South Atlantic DPS, but because a genetic baseline was never established for the St. Marys River, Fritts and Peterson (2011) were unable to determine whether the fish were native to the system or merely migrants from some other nearby population.

Establishing the extirpation of any fish population is difficult, but doing so for Atlantic Sturgeon populations is especially problematic because of their cryptic nature, complex migratory life history, late age at first reproduction, and protracted and intermittent spawning periodicity. To determine whether there is an extant population of Atlantic Sturgeon within the St. Marys River, the objectives of this study were to: (1) conduct an extensive survey to determine the presence or absence of RRJ Atlantic Sturgeon within the St. Marys River estuary, (2) quantify seasonal habitat use by resident and/or nonresident individuals, and (3) determine the genetic relationship of its population to others in the South Atlantic DPS. Because loss of individual populations is an important criterion for listing under the ESA, the results of this study will help clarify the current status of the St. Marys River population.

METHODS

Study site.— The St. Marys River forms much of the southeastern boundary between coastal Georgia and northeastern Florida (Figure 1). Its watershed encompasses approximately 3,366 km^2 and lies entirely within the coastal plain of Georgia. As a typical blackwater river in the southeastern United States, the St. Marys River is characterized by a tea-colored appearance and a relatively low but highly variable discharge (Dame et al. 2000; Blair et al. 2009). There are no major impoundments on the St. Marys River system, and a total of 274 river kilometers (rkm) of free-flowing habitats are accessible to sturgeons and other anadromous fishes. Point sources of pollution in the St. Marys River include several wastewater treatment facilities and a now-defunct paper mill. The river also collects nutrient-laden runoff from silvicultural sites and urban areas (GDNR–EPD 2002).

Sturgeon sampling.— All sampling was conducted below the head of tide (located at approximately rkm 60) in the St. Marys River estuary from May to July, 2013–2016. Sturgeon were captured with anchored gill and trammel nets, which have been proven effective for catching juvenile sturgeon in Georgia (Schueller and Peterson 2010; Bahr and Peterson 2016; Fox et al. 2018). Gill nets, 91.4 m in length and 3.1 m deep, were composed of panels of 7.6-, 10.2-, and 15.3-cm monofilament mesh (stretch measure). Trammel nets were of similar dimensions and material and were composed of one 7.6-cm inner panel and two 30.5-cm outer panels. Nets were deployed within the channel between rkm 0 and rkm 45 (Figure 1) and were soaked for approximately 30- to 90-min periods around the slack tides. As nets were retrieved, entangled sturgeon were quickly removed and placed in a floating net-

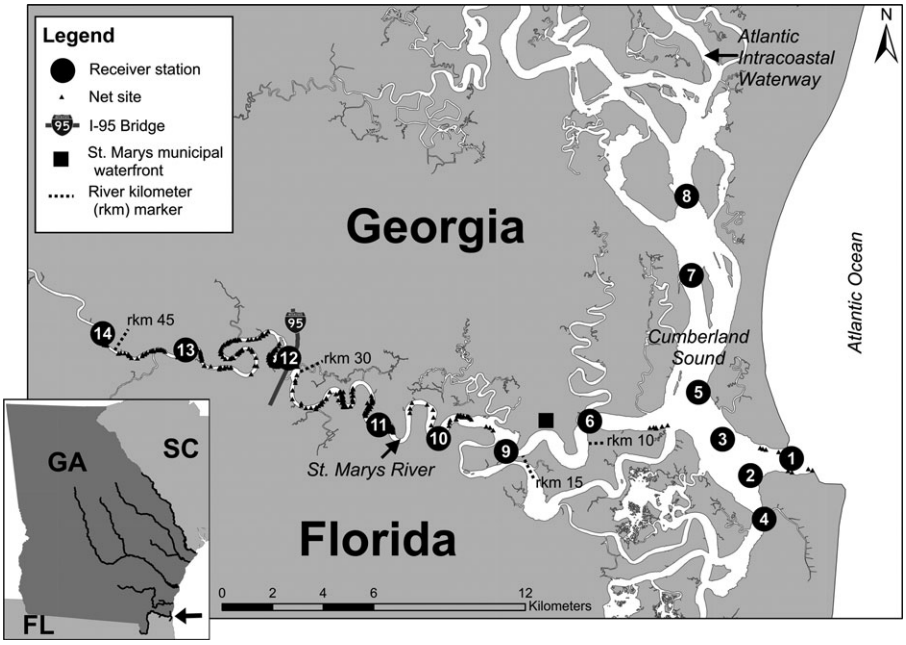

FIGURE 1. Study site in the St. Marys River, Georgia. Numbered black circles indicate the locations of acoustic receiver stations. Black triangles represent the locations of net sets, 2013–2016. The black square indicates the location of the city of St. Marys municipal waterfront.

pen tethered to the research vessel. Once all nets had been recovered, each captured sturgeon was measured to the nearest millimeter TL and inspected for tags. If no tag was present, a PIT tag was injected under the 4th dorsal scute, and a small tissue sample was taken from the dorsal fin and stored in 95% ethanol for subsequent genetic analysis. Water temperature, salinity, and dissolved oxygen were obtained at sampling sites each time nets were set using a YSI Pro2030 multiprobe (YSI, Yellow Springs, Ohio). The first eight juvenile sturgeon captured each year were fitted with acoustic transmitters that were surgically implanted into the body cavity. Surgical methods used for this procedure were similar to those described by Boone et al. (2013). Captured fish were removed from the floating net-pen and placed into lateral recumbency on a V-shaped surgical board; 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 69 kHz Vemco acoustic transmitter (Vemco, Bedford, Nova Scotia). In 2013, we deployed V16-4x transmitters (weighing 19 g), and in 2014–2015, we deployed V7-4x transmitters (weighing 1.9 g). Regardless of model, transmitter weights were always <2% of the weight of the RRJs that were tagged. The surgical 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 returned to the river at its original capture site. Fish life stage was inferred from age, which was estimated based on TL as established in several previous studies (Peterson et al. 2000; Schueller and Peterson 2010; Bahr and Peterson 2016). Captured juveniles measuring <550 mm TL were considered age-1 RRJs, those that were 550–700 mm TL were considered age-2 RRJs, and those measuring 700–1,200 mm TL were considered MMJs.

Acoustic telemetry.— A passive array of 15 stationary acoustic receivers (Vemco VR-2W) was distributed throughout the lower St. Marys River system, including connecting waters of the Intracoastal Waterway and Cumberland Sound (Figure 1). Range testing of receivers revealed a tag detection radius of approximately 400 m. Within the array, receivers 1–4 collectively formed a "leaky" acoustic gate (i.e., nonoverlapping acoustic detection radii) at the south entrance to Cumberland Sound, through which the fish had to pass as they moved between the sound and the Atlantic Ocean. Receivers 7–8 formed a similar gate at the north end of Cumberland Sound. Receiver 5 was used to detect the presence of tagged individuals within the interior portion of Cumberland Sound. Receiver 6 formed the third and final gate between Cumberland Sound and the main stem of the St. Marys River, while receivers 9–14 monitored the movements of tagged fish in the river reach upstream from the Cumberland Sound. The submerged receivers were mounted in an upright position, typically 2–3 m below the surface, and were attached to floating navigational buoys, channel markers, and other stationary structures using stainless steel cable or aluminum U-channel. Receivers were monitored over 25 consecutive months (~139 weeks), from May 23, 2014, to December 7, 2016. Data were downloaded from receivers at approximately 3-month intervals throughout

the duration of the study, except when environmental conditions precluded safe access to the receivers. To quantify the occurrence of sturgeon, we transformed the raw telemetry detection data into "detection days"—defined as one detection per individual per receiver per day—for analysis. Year-round water temperature data were obtained from U.S. Geological Survey stream gauge 02231254 located at the I-95 highway bridge (rkm 31).

Genetic analysis.— The genetic profile of the juvenile Atlantic Sturgeon collected from the St. Marys River was compared with that of juvenile specimens (<524 mm TL) from four other rivers in the South Atlantic DPS: the Savannah, Ogeechee, Altamaha, and Satilla rivers. Genotypes of a subset of specimens from these rivers were previously characterized in Savoy et al. (2017). Specimens from the earlier Savoy et al. (2017) study were supplemented with additional collections from the Ogeechee (n = 112 collected in 2015 and 2016), Altamaha (n = 137 collected in 2014–2016), and Satilla (n = 68 collected in 2015 and 2016) rivers. In total, genotypes were compared among 589 specimens from the South Atlantic DPS in this study. Regardless of collection date, all fin clips from specimens used for this analysis were collected in the field, immediately preserved in 95% ethanol, and stored at ambient temperatures until processing.

Isolations of DNA were conducted using standard phenol–chloroform extractions followed by ethanol precipitations. Concentrations of DNA were determined with a Nanodrop spectrophotometer (NanoDrop Technologies, Wilmington, Delaware) and were adjusted to 50 ng/μL for standardization of subsequent procedures. Genotypes were determined at 11 informative microsatellite loci: *LS19*, *LS39*, *LS54*, *LS68* (May et al. 1997), *Aox23*, *AoxD45* (King et al. 2001), *Aox44*, *AoxD165*, *AoxD170*, *AoxD188*, and *AoxD241* (Henderson-Arzapalo and King 2002). Polymerase chain reactions were performed exactly as described in Savoy et al. (2017), and separations of microsatellite alleles from collections new to this study and those from earlier collections were performed on a Beckman Coulter CEQ 8000 capillary-based DNA sequencer in the New York University School of Medicine Molecular Facility Core using the FRAG 1 program (Beckman Coulter, Brea, California). All runs on the sequencer included the CEQ DNA Size Standard-400 (Beckman Coulter) along with internal positive controls.

Composite microsatellite allelic profiles were compiled for each individual and genotype frequencies for each population collection. These were evaluated for Hardy–Weinberg and linkage disequilibrium in GENEPOP (version 1.2) (Raymond and Rousset 1995) using the default parameters and a Bonferroni correction. Genetic diversity of the St. Marys River sturgeon collection was compared with other populations in the South Atlantic DPS using GenAlEx (Peakall and Smouse 2006, 2012) and GenoDive (version 2.0b23) (Meirmans and Van Tienderen 2004) to calculate the number of alleles per locus (N_A), effective number of alleles (A_E), observed heterozygosity (H_o), and expected heterozygosity (H_e). Evaluation of population structuring among all collections in the South Atlantic DPS was determined using F_{ST} calculated in GenAlEx. The index F_{ST} is not a highly informative measure of genetic differentiation for highly variable markers like microsatellites because the maximum F_{ST} value of 1.0 usually cannot be obtained even if collections have nonoverlapping sets of alleles (Hedrick 1999). Therefore, we also calculated F'_{ST} using GenoDive, which is a true measure of allelic differentiation between populations; F'_{ST} scales F_{ST} values based on observed allelic diversity so that F'_{ST} always equals 1 when no alleles are shared. Genetic relationships among 12 coastwide collections of Atlantic Sturgeon juveniles and adults were visualized in an unweighted pair-group method with arithmetic averages (UPGMA) tree constructed in POPTREE2 software (Takezaki et al. 2010) using the F_{ST} measure of genetic distance. Data for collections outside of the South Atlantic DPS in the UPGMA tree were from Savoy et al. (2017). Finally, STRUCTURE version 2.3.4 (Pritchard et al. 2000) was used to determine the number of genetic clusters in the South Atlantic DPS using the admixture model that used sampling locations as a prior with allelic frequencies correlated. Burn-in lengths of 10,000 and run lengths of 100,000 were used, and 10 replicates were done for each run of

TABLE 1. Annual sampling effort and catch of Atlantic Sturgeon in the lower St. Marys River, Georgia, during the summers of 2013–2016. Total catch, total number of unique individuals, and number of unique age-1 and age-2 river-resident juveniles (RRJs) are also reported for each year.

	Effort		Catch			
Year	Number of sets	Soak time (h)	Total catch	Unique individuals captured	Age-1 RRJs	Age-2 RRJs
2013	178	192	1	1	0	0
2014	85	102	10	9	8	0
2015	122	105	9	6	0	5
2016	148	159	5	4	0	0
Total	533	558	25	20	9	8

TABLE 2. Acoustic telemetry data for Atlantic Sturgeon tagged in the St. Marys River, Georgia, 2013–2016. Fish tagged in this study were either river-resident juveniles (RRJs) or marine migratory juveniles (MMJs). Life stage and age classification was based on length (Schueller and Peterson 2010). St. Marys River detections of each fish are separated by year (X = detected, 0 = not detected). Fish ATS-01 was never detected in the St. Marys River, but was subsequently detected by a receiver array in the Altamaha River, Georgia (A. G. Fox and D. L. Peterson, unpublished data,). Fish ATS-04 was never detected. NA = not available.

Fish identification	TL (mm)	Age (years)	Tagging year	Year(s) detected		
				2014	2015	2016
RRJs						
ATS-02	336	1	2014	X	X	0
ATS-03	376	1	2014	X	X	0
ATS-04	325	1	2014	0	0	0
ATS-05	393	1	2014	X	X	0
ATS-07	374	1	2014	X	X	0
ATS-08	374	1	2014	X	X	0
ATS-09	405	1	2014	X	X	0
ATS-10	684	2	2015	NA	X	X
ATS-11	655	2	2015	NA	X	X
ATS-13	576	2	2015	NA	X	X
ATS-14	651	2	2015	NA	X	X
MMJs						
ATS-01	1,093	NA	2013	0	0	0
ATS-06	932	NA	2014	X	X	0
ATS-12	735	NA	2015	NA	X	X

K = 1–5. The best K was determined from values of lnP(D) by using STRUCTURE HARVESTER (Earl and vonHoldt 2012).

RESULTS

Sturgeon Sampling

From April 12, 2013, to July 7, 2016, we deployed a total of 533 nets for a total of 557 h of soak time, which yielded a total of 25 Atlantic Sturgeon (20 unique individuals), all either RRJs or MMJs (Table 1). Length-frequency analysis of all Atlantic Sturgeon captured in 2014 indicted that eight age-1 RRJs were captured in that year. In 2015, the same analysis indicated that no age-1 fish were present in the catch, but that five individuals were age-2 RRJs. One of these individuals was initially captured as an age-1 RRJ in 2014. Water quality conditions during the summer sampling period varied from 24°C to 30°C, from 0.1‰ to 26.5‰ salinity, and from 2.97 to 5.53 mg/L dissolved oxygen. The RRJs were exclusively captured in 24.5–27.6°C water having salinities of 0.1–13.1‰ and dissolved oxygen concentrations of 2.97–5.53 mg/L.

Over the 4 years of the study a total of 14 Atlantic Sturgeon were successfully tagged with acoustic transmitters (Table 2). In 2013, one MMJ was tagged with an acoustic transmitter. In 2014, seven age-1 RRJs and one MMJ were acoustically tagged. In 2015, four age-2 RRJs and one MMJ

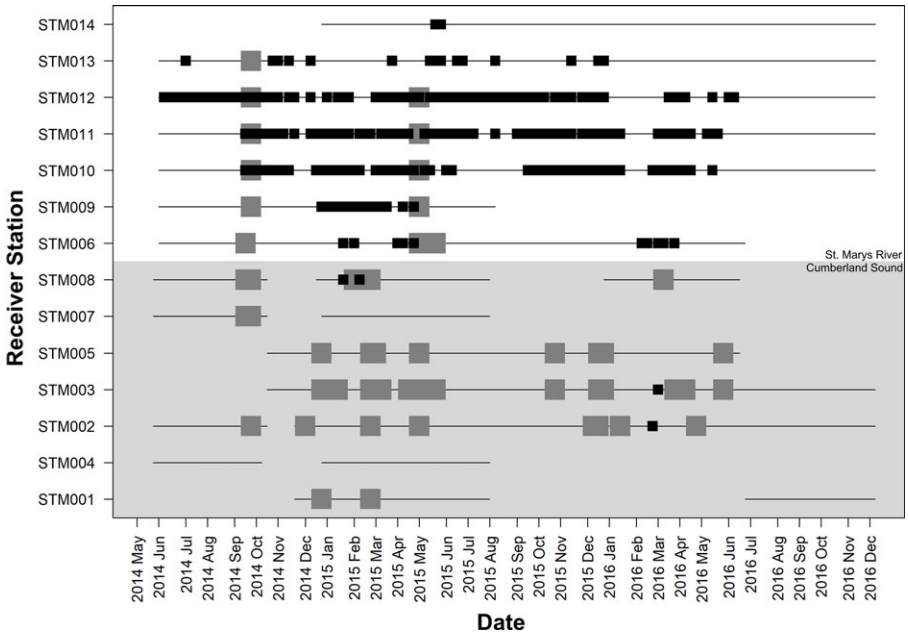

FIGURE 2. Weekly receiver coverage (thick black line) and Atlantic Sturgeon detections in the St. Marys River estuary from June 2014 to December 2016. Natal sturgeon (black square) were tagged in the St. Marys River during this study; migrant sturgeon (gray square) were originally tagged in other river systems. Receivers (on the y-axis) are arranged by river kilometer from the river mouth. The shaded background indicates detections and coverage within Cumberland Sound, and white background indicates St. Marys River main stem.

had transmitters implanted in them. All tagged fish were released in excellent condition, and 85.7% (n = 12) were detected at least twice by our receiver array.

Acoustic Telemetry

During the entirety of this study, the stationary acoustic array recorded a total of 46,548 transmitter detections of Atlantic Sturgeon (Figure 2). Of these, 45,062 detections were from fish tagged as part of this study (Table 2); the remaining 1,486 detections were from 20 individual Atlantic Sturgeon tagged by researchers working in other Atlantic coast river systems (Table 3). Eight of these individuals were tagged in other Georgia rivers, three in South Carolina, six in North Carolina, one in Virginia, and two in Delaware.

Although the array was serviced by field crews at regular intervals throughout the entire study, several receivers either failed or were lost during the intervening periods, causing gaps in receiver coverage during various periods throughout the study (Figure 2). Over the course of the entire study, mean weekly coverage at each receiver station was 74% (range, 40–100 The array was active for a total of 1,413 receiver-weeks: 754 receiver-weeks during the "warm season" (May–October) and 659 receiver-weeks during the "cool season" (November–April).

Acoustically tagged Atlantic Sturgeon were detected at all receiver stations within the St. Marys River main stem and all but one (receiver 4) in Cumberland Sound (Figure 2). Of the 11 RRJs and 3 MMJs tagged in this study, most remained entirely within the river main stem; only three were ever detected below the river gate receiver (receiver 6). One individual that was tagged in 2013 (before the array was fully in place) left the study area and was later detected by the authors' receiver array in the nearby Altamaha River (69 km north). The other two individuals were last detected by gate receivers at the south entrance to Cumberland Sound in November and March.

TABLE 3. Acoustic telemetry data for migrant Atlantic Sturgeon detected in the St. Marys River, Georgia, 2013–2016. Fish were originally tagged by researchers in other rivers; original tagging location, year, and TL at tagging are provided, when available. The distinct population segment (DPS) of origin for each fish is based on genetic analyses provided by the U.S. Geological Survey Leetown Science Center, which maintains a comprehensive genetic database for all known populations of Atlantic Sturgeon. Life stage (MMJ = marine migratory juvenile, A = adult or subadult) refers to life stage at the time of detection by this study. NA = not available.

Tagging information				Detection information	
Location	Year	TL (mm)	DPS of origin	Year(s) detected	Life stage
Satilla River, Georgia[a]	2014	532	South Atlantic	2015	MMJ
Satilla River, Georgia[a]	2015	369	South Atlantic	2016	MMJ
Altamaha River, Georgia[a]	2012	2,040	South Atlantic	2014	A
Altamaha River, Georgia[a]	2012	1,870	South Atlantic	2015–2016	A
Altamaha River, Georgia[a]	2013	1,650	South Atlantic	2016	A
Altamaha River, Georgia[a]	2013	1,580	South Atlantic	2014	A
Altamaha River, Georgia[a]	2013	1,840	South Atlantic	2015	A
Ogeechee River, Georgia[a]	2014	623	South Atlantic	2015	MMJ
Savannah River, Georgia[b]	2013	1,030	South Atlantic	2015	A
Santee River, South Carolina[b]	2014	922	South Atlantic	2015	A
G. Pee Dee River, South Carolina[b]	2013	1,353	South Atlantic	2016	A
Cape Fear River, North Carolina[c]	2012	NA	NA	2015	A
Cape Fear River, North Carolina[c]	2013	NA	South Atlantic	2015	A
Cape Fear River, North Carolina[c]	2013	NA	South Atlantic	2014	A
Cape Fear River, North Carolina[c]	2013	NA	South Atlantic	2015	A
Cape Fear River, North Carolina[c]	2013	NA	South Atlantic	2015	A
Cape Fear River, North Carolina[c]	2013	NA	South Atlantic	2015	A
James River, Virginia[d]	2014	1,970	NA	2015–2016	A
Coastal Delaware[e]	2011	NA	South Atlantic and/or Carolina	2015	A
Coastal Delaware[e]	2013	NA	South Atlantic	2015	A

[a]Fish tagged by the authors in a previous study.
[b]W. Post, 2018, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, South Carolina 29422-2559, personal communication.
[c]M. Loeffler, 2018, North Carolina Division of Marine Fisheries, 3441 Arendell Street, Morehead City, North Carolina 28557, personal communication.
[d]M. Balazik, 2018, Center for Environmental Studies, Virginia Commonwealth University, 1000 West Cary Street, Richmond, Virginia 23284, personal communication.
[e]D. Fox, 2018, Department of Agriculture and Natural Resources, College of Agriculture and Related Sciences, Delaware State University, Agriculture Annex Room 123, 1200 North DuPont Highway, Dover, Delaware 19901, personal communication.

All migrant Atlantic Sturgeon (n = 20) detected during this study were detected by at least one of the Cumberland Sound gates during the time that they used the St. Marys River estuary. Ninety-five percent of individuals (n = 19) were first detected by gate receivers at either the north or south entrances to Cumberland Sound. Despite potential gaps in coverage between receivers within each gate, only one individual apparently went undetected by gate receivers, as it was first detected by an interior receiver. Interestingly, the three MMJ migrants (originally tagged by the authors in other Georgia rivers) were all first detected at the north gate in Cumberland Sound. Of the remaining 17 migrants (all adults or subadults), 16 were first detected by the Cumberland Sound south gate. The Cumberland Sound gate receivers also recorded the final detection for 85% of the migrant individuals (n = 17). Few to no migrant sturgeon were detected between June and November (Figure 3).

Spatial and temporal analyses showed that age-1 and age-2 RRJ Atlantic Sturgeon tagged during this study exhibited a distinct pattern of seasonal habitat use within the lower St. Marys River (Figure 4). During summer months, RRJs congregated in a relatively upriver reach, but during the cool season they moved downriver and became more broadly distributed. During the warm season, juveniles were detected exclusively within the St. Marys River, and migrant individuals were mainly detected in Cumberland Sound (Figure 5A). In the summers of 2014–2016, both RRJs (both age 1 and 2) and MMJs tended to congregate in upstream reaches of the study area from rkm 25 to rkm 35, where water salinity was relatively low. During the cool season, juveniles were detected mainly within the St. Marys River, but RRJs and MMJs became increasingly dispersed throughout downstream habitats near the river mouth and Cumberland Sound. Migrant individuals detected in the cool season exclusively used Cumberland Sound (Figure 5B). Two of 14 (14.3%) fish tagged in this study eventually left the St. Marys River and were subsequently detected by acoustic receivers in the Altamaha and Ogeechee rivers (Fox and Peterson 2018).

Genetic Analysis

We addressed the genetic uniqueness of the collection of RRJ Atlantic Sturgeon from the St. Marys River by comparing them with a much larger sample of RRJs collected over 2–5 years from four other rivers within the South Atlantic DPS (Table 4). That analysis showed that there was no consistent pattern of Hardy–Weinberg disequilibrium after Bonferroni correction at any of the 11 loci surveyed in this study; therefore, all loci were retained for subsequent statistical analyses. However, four loci (*LS 39*, *LS 68*, *Aox 44*, and *AoxD 188*) did exhibit Hardy–Weinberg disequilibrium in the Ogeechee River collection. Similarly, there was no consistent pattern of linkage disequilibrium between any pair of loci. Levels of genetic diversity at all indices were comparable among collections with the exception of the St. Marys River collection, which exhibited a smaller mean number of alleles and allelic richness than did the other collections but showed similar levels of expected and observed heterozygosity (Table 5).

We found significant genetic differentiation among all pairwise comparison of collections from all five rivers using two different statistical measures, F_{ST} and F'_{ST} values (Table 6). For example, F'_{ST} values between sturgeon from the St. Marys River and the other four rivers in the South Atlantic DPS (F'_{ST} = 0.205–0.369) were far greater than all pairwise F'_{ST} comparisons among the other four rivers

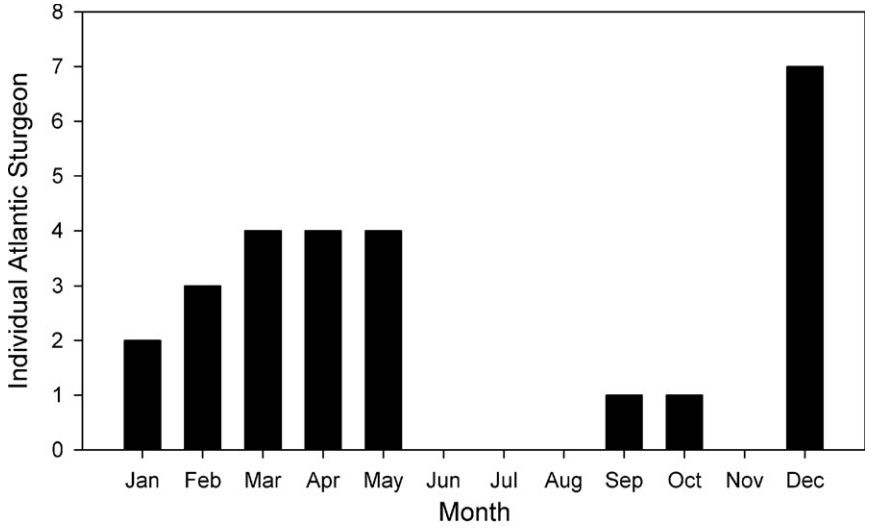

FIGURE 3. Seasonal detections of nonnatal Atlantic Sturgeon in the St. Marys River and estuary from May 2014 to December 2016. Black bars represent the total number of unique individuals detected by the acoustic array for each month of the study across all years of the study. Although our receiver array actually had more coverage during warm months (May–October), nearly all migrant sturgeon detections occurred during cool months (November–April).

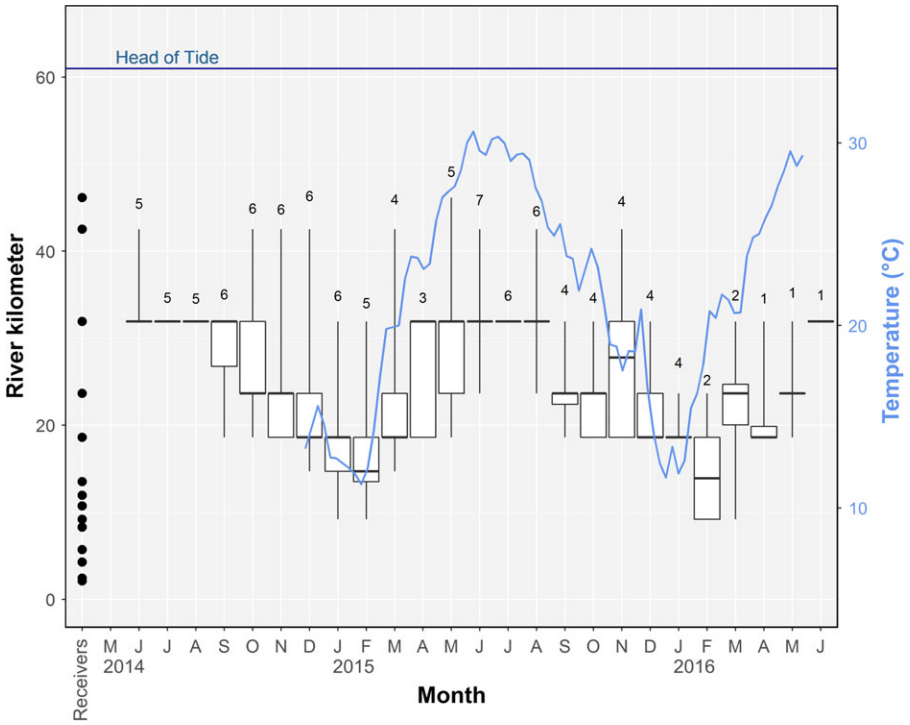

FIGURE 4. Habitat use by river-resident juvenile Atlantic Sturgeon (ages 1 and 2) tagged in the St. Marys River. Boxplot ends represent the 25th and 75th percentiles of all tag detections. The thick line within the box is median river kilometer position of all fish. Error bars (whiskers) represent minimum and maximum river kilometer detections. The number over each box indicates the number of individuals detected that month. Dots along the main *y*-axis represent the river kilometer positions of receivers in the acoustic array. The blue line indicates water temperature along the secondary *y*-axis. Data are from May 4, 2014, to June 17, 2016.

TABLE 4. Collections of juvenile Atlantic Sturgeon (≤524 mm TL) from four rivers in the South Atlantic Distinct Population Segment that were compared with that from the St. Marys River for genetic differentiation. Collections with asterisks (*) were previously characterized in Savoy et al. (2017); *n* = number collected.

Population	*n*	Collection date	TL range (mm)	Mean TL (mm)
Savannah River	50	May–Jun 2013*	316–447	391
	50	May 2014*	274–479	370
Ogeechee River	26	Jun 2007–Aug 2009*	199–520	286
	45	Jul–Aug 2014*	227–310	260
	65	May–Jul 2015	165–442	332
	47	May–Jul 2016	210–520	341
Altamaha River	49	Jun–Jul 2005*	319–404	379
	40	Jul–Aug 2011*	327–481	386
	55	May–Jun 2014	281–487	372
	18	May–Jun 2015	277–358	337
	64	May–Jul 2016	275–417	383
Satilla River	41	Jun–Jul 2015	228–428	382
	27	May–Jun 2016	229–524	437

(F'_{ST} = 0.046–0.141). Comparison of F'_{ST} values were greatest between sturgeon from the St. Marys and the Ogeechee rivers (F'_{ST} = 0.369) and smallest between collections from the Savannah and the Altamaha rivers (F'_{ST} = 0.046). Furthermore, STRUCTURE analysis best supported the presence of five distinct genetic clusters of Atlantic Sturgeon within the South Atlantic DPS (Table 7). We also developed a UPGMA tree based on genetic distance (F_{ST}) (Figure 6) to explore the genetic relationships between the St. Marys River juvenile collection and 11 other collections of juvenile and adult Atlantic Sturgeon that almost spanned the species' entire coastwide distribution. Two major groupings of populations were depicted, one included all northern and central Atlantic coast populations extending from the Saint John River to the James River and the second included all southern Atlantic coast populations from Albemarle Sound to the St. Marys River. However, the St. Marys River collection was highly differentiated from other collections within the South Atlantic DPS as it was located outside the clade that contained adjacent populations.

DISCUSSION

Population Status

The age-1 RRJs captured during the 2014 field season represent the first documented evidence of successful

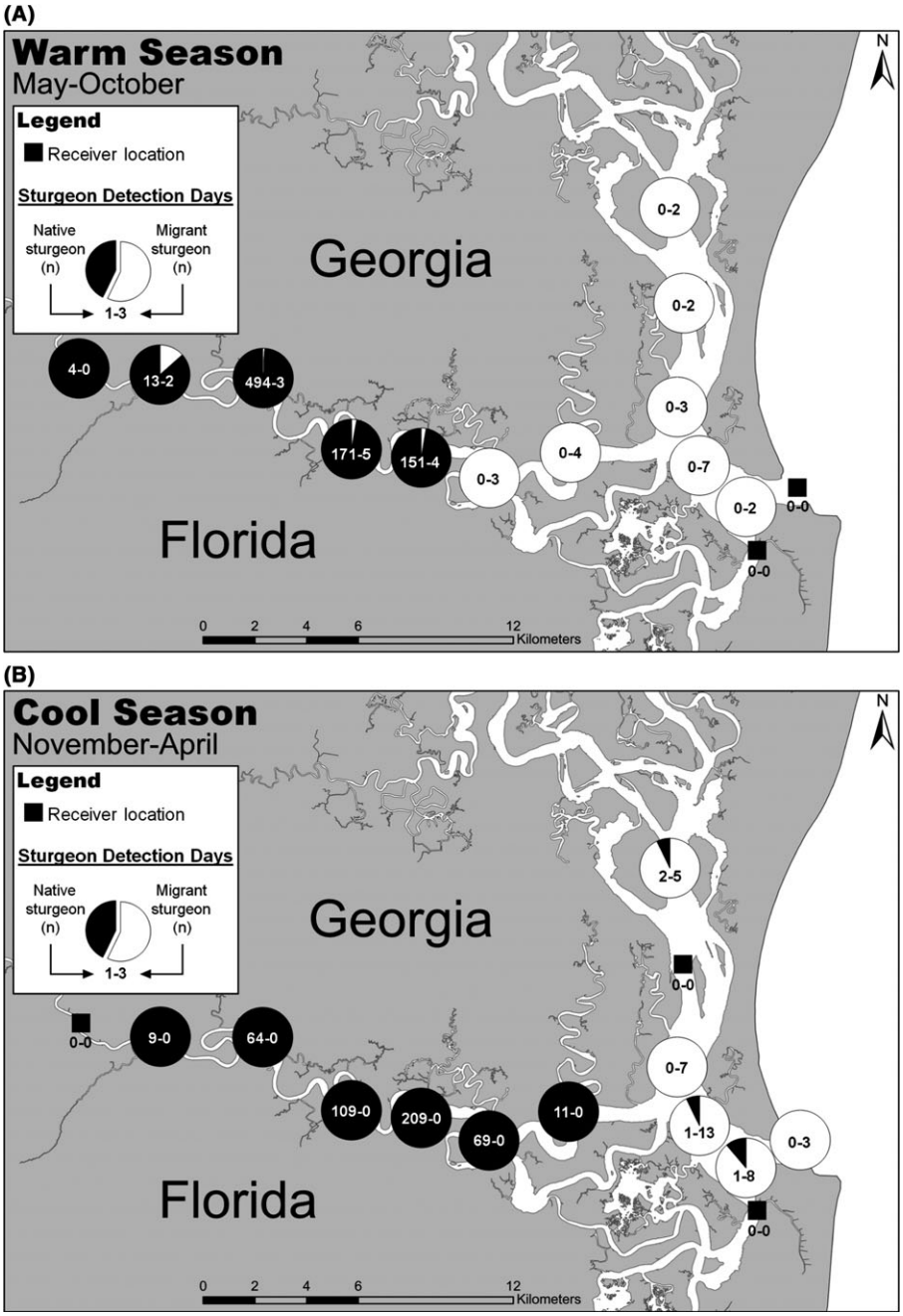

FIGURE 5. Seasonal trends in occupancy of Atlantic Sturgeon in the St. Marys River estuary, Georgia, 2014–2016, during **(A)** the warm season (May–October) and **(B)** the cool season (November–April). Each receiver is represented by a pie chart illustrating the proportions of native and migrant Atlantic Sturgeon detection days (one detection per fish per receiver per day, totaled across the three study years) at that site. Native sturgeon (black circle) were captured within the St. Marys River during this study; migrant sturgeon (white circle) were originally captured and tagged in other river systems or coastal areas. Receivers with no sturgeon detections are represented by a black square. Numerals within each pie chart indicate the total number of native and migrant detection days for that particular receiver location.

Atlantic Sturgeon reproduction within the St. Marys River. Despite much uncertainty regarding the status of this population, the results of our 2014 sampling provide strong evidence that the St. Marys River population has not been extirpated, as was previously suggested (ASSRT 2007; Fritts and Peterson 2011). However, the lack of consistent annual recruitment in the St. Marys River indicates that the population has likely persisted at only remnant status

and, as such, is likely precariously close to extirpation. Although historical data are not available for the St. Marys River, other South Atlantic DPS rivers with more robust populations (e.g., the Savannah and Altamaha rivers) typically produce annual cohorts of hundreds or thousands of fish (Schueller and Peterson 2010; Bahr and Peterson 2016). Genetic analyses of tissue samples obtained from juvenile sturgeon captured in this study suggest that the age-1 RRJs captured in 2014 and the age-2 RRJs captured in 2015 were closely related. One of the age-2 RRJs captured in 2015 was originally captured as an age-1 RRJ in 2014. Combined with the genetic evidence, we suspect that all of the RRJs we captured during this study were produced by a single successful spawning event in 2013.

Habitat Use

Receiver coverage throughout the St. Marys River main stem was consistent throughout most of the study (Figure 2) with the notable exception of receiver 9, located at rkm 14.1. Although this receiver was lost in August 2015, it was not a gate receiver, so its absence had no effect on the array's ability to detect tagged fish entering or leaving the St. Marys River main stem. The receiver array in Cumberland Sound, however, did experience several receiver failures that created operational gaps in the array, particularly within the northern and interior portions of Cumberland Sound. Despite these operational gaps the gate receivers performed well throughout the study. Of the 14 acoustically tagged Atlantic Sturgeon that we tracked during our study only one (7.1%) of these evaded detection by the gate receiver located between the main stem and Cumberland Sound. Likewise, the gate receivers at the north and south entrances of Cumberland Sound detected 19 of the 20 (95%) migrant Atlantic Sturgeon as they entered the St. Marys River system; the only other individual was detected by both interior and gate receivers as it moved through the system. Although it is possible that a small number of acoustically tagged migrants could have gone completely undetected during the operational gaps in the receiver array, the consistent detection of migrants documented at multiple interior and gate receivers suggests that this was not likely. Likewise, gaps in receiver coverage did not appear to bias seasonal comparisons of habitat use by natal and migratory Atlantic Sturgeon. Although there were more nonoperational receivers during the cool season (659 receiver-weeks during the cool season versus 754 receiver-weeks in the warm season), we detected most migrant Atlantic Sturgeon during the cool season.

Seasonal movements and habitat use of juvenile Atlantic Sturgeon documented in this study (Figure 4) were quite similar to those documented in other South Atlantic rivers (Fox and Peterson 2018). The acoustically tagged RRJs were detected exclusively within the St. Marys River main stem, mostly upstream from the St. Marys municipal waterfront. During the summer months, RRJs clustered farther upriver, probably to escape the combined effects of high temperatures and salinities typical in the lower river during this period (Niklitschek and Secor 2005). In cooler months, however, most of these juveniles moved downstream, becoming much more widely dispersed throughout the lower river and upper estuary. The number of RRJs detected by the array consistently declined through the winter months, suggesting that the transition to the MMJ life stage typically occurred during this seasonal period of cooler water temperatures. In other Georgia rivers, some RRJs out-migrate after moving downstream during the winter at age 2, while others return to upriver nursery areas as age-2 RRJs (Fox and Peterson 2018). In the St. Marys River in the summer, both age-1 and age-2 RRJs occupied the same 15-rkm reach directly upstream from the I-95 bridge (Figure 1).

Throughout this study, we detected a total of 20 migrant Atlantic Sturgeon within the lower St. Marys River and Cumberland Sound (Figure 2). The number and seasonal pattern of these detections suggest that the St. Marys River estuary may be an important seasonal habitat for the species as a whole, particularly for nonspawning, migratory life stages. Most migrant individuals ($n = 17$) were detected only in Cumberland Sound (Figure 5A, B) and only a few ($n = 3$) ever entered the lower reaches of the St. Marys River main stem. Interestingly, no migrant Atlantic Sturgeon were detected during the warmest months of the year. Most migrants were never detected in the river reaches used by RRJs, denoting a distinct difference in habitat use by migratory and RRJ life stages. Although Hilton et al. (2016) reported that Atlantic Sturgeon are rarely observed in nonnatal rivers in the more northerly portions of their range, this study provides evidence that nonnatal sturgeon regularly use the St. Marys River. A similar pattern of seasonal habitat use by migrant adults has also been documented in the St. Johns River (Fox et al. 2018); nonnatal Atlantic Sturgeon appear to commonly use estuaries within the South Atlantic DPS, particularly during the winter months.

TABLE 5. Indices of microsatellite allelic diversity in collections of juvenile Atlantic Sturgeon from five rivers in the South Atlantic Distinct Population Segment. Collection population, number of specimens (n), number of alleles (N_A), effective number of alleles (A_E), observed heterozygosity (H_o), and expected heterozygosity (H_e).

Population	n	N_A	A_E	H_o	H_e
Savannah	100	9.727	4.921	0.673	0.691
Ogeechee	182	10.273	5.449	0.646	0.687
Altamaha	226	9.364	5.051	0.684	0.689
Satilla	68	9.273	5.139	0.707	0.718
St. Marys	12	3.818	2.769	0.748	0.589

TABLE 6. Pairwise comparisons of genetic differentiation among collections of juvenile Atlantic Sturgeon from five rivers in the South Atlantic Distinct Population Segment. The F_{ST} values are shown above the diagonal break and the F'_{ST} values are depicted below the diagonal. An asterisk (*) indicates statistical significance ($P < 0.05$) following standard Bonferroni correction ($P < 0.005$).

Population	Savannah	Ogeechee	Altamaha	Satilla	St. Marys
Savannah		0.032*	0.014*	0.023*	0.091*
Ogeechee	0.103*		0.044*	0.025*	0.124*
Altamaha	0.046*	0.141*		0.020*	0.071*
Satilla	0.078*	0.084*	0.065*		0.096*
St. Marys	0.265*	0.360*	0.205*	0.292*	

TABLE 7. Results of STRUCTURE analysis ($K = 5$). Results are based on microsatellite DNA analysis at 11 loci in five collections of juvenile Atlantic Sturgeon from the South Atlantic Distinct Population Segment.

K	Replicates	Mean LnP(K)	SD LnP(K)
1	10	−22,186.8	1.3744
2	10	−20,750.6	5.3380
3	10	−20,475.5	35.019
4	10	−20,318.3	78.349
5	10	−20,221.3	83.514

The results of this study show that the St. Marys River remains an important riverine and estuarine habitat for both natal and migrant Atlantic Sturgeon. More importantly, however, our findings demonstrate that remnant Atlantic Sturgeon populations can survive and remain undetected for several years or even decades after a major population decline. The persistence of the St. Marys sturgeon population has important ramifications for populations in other river systems where the species is currently thought to be extirpated. During 4 years of directed sampling conducted in this study and 3 years of sampling previously by Fritts and Peterson (2011), recruitment (i.e., age-1 juveniles) was detected in only 1 year. Consequently, we emphasize the need for long-term studies with directed sampling for RRJs to definitively determine the status of Atlantic Sturgeon, particularly for rivers where historical populations are thought to be extirpated.

Genetic Analysis

Our evaluation of the genetic relationships among the St. Marys River RRJs captured in this study and those from other populations in the South Atlantic DPS and coastwide indicate that the St. Marys River collection likely represents descendants of a remnant population that is distinct, but is more closely related to other populations within the South Atlantic DPS than those in more northern rivers. Future studies are needed to increase the number of St. Marys River RRJ samples collected over several years to better define the demographic parameters as well as genetic structure of the St. Marys River Atlantic Sturgeon population.

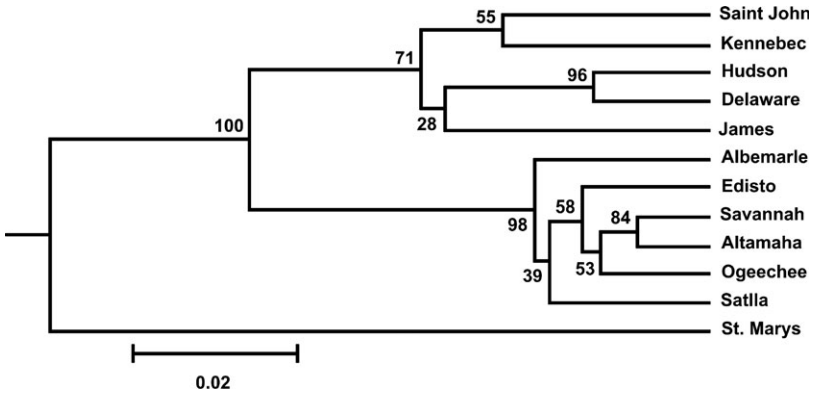

FIGURE 6. A UPGMA tree developed in the program POPTREE2 based on microsatellite data at 11 loci depicting genetic relationships among collections of juvenile (<524 mm TL) and adult (>1,300 mm TL) Atlantic Sturgeon from 12 rivers along the Atlantic coast of North America. Bootstrap values (10,000 replicates) are provided at the branching points of the tree. The reported bootstrap value is the percentage of bootstrap replicates in which the node showed up. Microsatellite data for collections outside of the South Atlantic DPS are those reported in Savoy et al. (2017).

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