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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 595-606

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2016.1243599

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Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8:595–606, 2016
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2016.1243599

ARTICLE

Annual Spawning Migrations of Adult Atlantic Sturgeon in the Altamaha River, Georgia

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Abstract

The Atlantic Sturgeon *Acipenser oxyrinchus* has declined throughout its range, and the species is now protected under the U.S. Endangered Species Act. Information on the timing and extent of spawning migrations is essential for the development and implementation of effective management and recovery strategies, yet this information is lacking for most populations. The objectives of this study were to document and identify temporal and spatial patterns in the seasonal movements and spawning migrations of Atlantic Sturgeon in the South Atlantic distinct population segment. A stationary array of acoustic receivers was used to monitor the movements of 45 adults in the Altamaha River system, Georgia, from April 2011 through March 2014. Telemetry data revealed that putative adult spawners exhibited two distinct patterns of upriver migration: a spring two-step migration and a fall one-step migration. During the spring two-step migration, the adults appeared to stage in the upper Altamaha during the spring and early summer, before migrating to suspected spawning habitats in the Ocmulgee and Oconee tributaries during the fall. During the fall one-step migration, fish entered the system in late summer and migrated directly upriver to suspected spawning habitats in the Ocmulgee and Oconee tributaries. Regardless of which pattern was used during the upstream migration, all fish returned downstream and left the system by early January. Although direct evidence of spawning has not yet been obtained, the telemetry and environmental data provide strong circumstantial evidence that Atlantic Sturgeon spawning in the Altamaha population occurs only during the fall months when water temperatures are less than 25°C. These findings further illustrate the clinal variation in the life history of Atlantic Sturgeon and highlight the need to manage the species as distinct population segments with regionally specific recovery goals.

The Atlantic Sturgeon *Acipenser oxyrinchus* (family: Acipenseridae) is a large, long-lived fish that is broadly distributed along the Atlantic coast of North America. Historically, spawning populations occurred in virtually all major rivers from Ungava Bay, Canada, to as far south as the St. Johns River, Florida (Vladykov and Greeley 1963; Dadswell 2006). In total, this historical range included approximately 38 individual rivers, 35 of which supported discrete spawning populations (ASSRT 2007).

A decline in Atlantic Sturgeon abundance throughout their range has resulted in harvest restrictions and federally mandated protection. All U.S. Atlantic Sturgeon fisheries were closed in 1998 and the species was listed under the U.S. Endangered Species Act in 2012. At present, spawning

Subject editor: Donald Noakes, Vancouver Island University, Nanaimo, British Columbia

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Received March 23, 2016; accepted September 25, 2016

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populations are supported in less than 20 rivers (ASSRT 2007). The healthiest populations are currently thought to reside in the Saint John and Saint Lawrence rivers, Canada (Dadswell 2006); the Hudson River, New York (Peterson et al. 2000; Kahnle et al. 2007); and the Altamaha River, Georgia (Schueller and Peterson 2010; Moyer et al. 2012). The paucity of quantified population assessments, however, makes river-specific comparisons difficult (ASSRT 2007).

Atlantic Sturgeon are anadromous, using riverine, estuarine, and marine habitats throughout their range. Although the majority of their life history is spent in marine and coastal waters, mature adults will return periodically every 1–5 years to freshwater rivers to spawn (Smith 1985). These migrations are important to optimizing reproductive success by partitioning resources at different life stages and preventing intraspecific competition (Smith et al. 1982; Bain 1997). Despite decades of research, many knowledge gaps remain regarding adult spawning migrations, particularly within the South Atlantic distinct population segment (SADPS).

Atlantic Sturgeon spawning sites have been identified in only a few river systems—mostly within northern rivers (ASSRT 2007). Within the southern portion of the range, however, spawning habitats of Atlantic Sturgeon have only been identified for the Edisto and Combahee rivers, South Carolina (Collins et al. 2000). Previous studies of spawning movements have shown that spawning occurs in the uppermost reaches of accessible river channels with moderate flows of 46–76 cm/s and depths of 11–27 m (Smith and Clugston 1997; Bain et al. 2000). The adhesive eggs are broadcast over hard-bottom substrates composed of gravel and cobble (Gilbert 1989; Smith and Clugston 1997; Sulak and Clugston 1998). Previous research, including both laboratory and field studies, suggest that water temperatures of 13–25°C are optimal for egg survival and hatching (Borodin 1925; Smith 1985; Kieffer and Kynard 1993; Hatin et al. 2002; Smith et al. 2015).

The timing of Atlantic Sturgeon spawning is highly variable at both the population and individual levels (Bemis and Kynard 1997). Most information regarding the timing of spawning has been obtained from populations at the northern end of the range, where spawning typically occurs from May to August (Bain 1997; Dadswell 2006). In rivers south of the Hudson, however, adults are often observed in riverine habitats during both spring and fall (Smith and Dingley 1984; McCord et al. 2007), and there is strong empirical evidence of fall spawning runs in Virginia (Balazik et al. 2012), South Carolina (Collins et al. 2000), and North Carolina (Smith et al. 2015).

In contrast to many of the other large river systems along the Atlantic coast, the Altamaha River system is a relatively pristine habitat for Atlantic Sturgeon (ASSRT 2007). Isolated rocky shoal habitats are abundant in the upper river above river kilometer (rkm) 160 and in both the Oconee and Ocmulgee tributaries (Litts and Kaeser 2016). Although both of these major tributaries are impounded in their upper reaches, the dams are located at or above the fall line. Consequently, migrating adults have access to virtually all historical spawning habitats dispersed over approximately 794 km of unimpounded riverine habitats (ASSRT 2007). As the largest and most undisturbed river system available to Atlantic Sturgeon within the SADPS, the Altamaha River provides a unique opportunity to better understand the spatial and temporal dynamics of the species' spawning migrations within the southern portion of its range. Consequently, the objectives of this study were to document and describe both the temporal and spatial aspects of the freshwater migrations of adult Atlantic Sturgeon in the Altamaha River system. Because the timing and locations of Atlantic Sturgeon spawning are largely unknown within the SADPS, the results of this research will be critical for future assessment of the spawning runs and habitat within the Altamaha River system.

METHODS

Study site.—The Altamaha River system, located entirely within Georgia, is formed by the confluence of the Oconee and Ocmulgee rivers (Figure 1). The main stem flows across the Atlantic coastal plain in a southeasterly direction for 207 km to the coast where it empties into the Atlantic Ocean near Darien, Georgia. Mid-channel depths average 2–3 m, with a maximum of 18 m in Altamaha Sound (Heidt and Gilbert 1978). The lower Altamaha estuary is characterized by a tidally flooded salt marsh that gradually gives way upstream to a cypress swamp. The location of the fresh–saltwater interface varies depending on flow but typically occurs between rkm 35 and 50 during normal flows (Rogers and Weber 1995). Tidal range averages 2 m, and tidal influence can persist as far upstream as rkm 60 (Sheldon and Alber 2002). Most of the Altamaha River's total discharge is contributed by the Ocmulgee (40%) and Oconee (36%) tributaries (Rogers and Weber 1995). Isolated rocky shoal habitats are found above rkm 80 in the Altamaha main stem and throughout the lower reaches of both major tributaries (Flournoy et al. 1992). Although both tributaries are impounded above the fall line, the biological effects of these dams are considered to be moderate (Dynesius and Nilsson 1994).

Fish sampling.—All methods for the capture and handling of Atlantic Sturgeon in this project were authorized under National Marine Fisheries Permit 16482 and by the University of Georgia's Institutional Animal Care and Use Committee (AUP A2013 01-012-R1). Adult Atlantic Sturgeon were captured from April to June of 2011–2013 with drift gill nets deployed in the lower portion of Altamaha Sound. These nets were constructed of multifilament meshes measuring 30.5, 35.6, and 40.6 cm (stretch measure) and were 91.44 m long and 3.05 m deep. Nets were deployed during the last 30 min of running tides and soaked continuously until the end of the subsequent slack tide—typically a period of about 1 h. Nets were tended continuously so that entangled fish could be removed immediately while the nets continued to fish. Upon capture, Atlantic Sturgeon were immediately transferred to a floating net pen (1 × 3 × 1 m)

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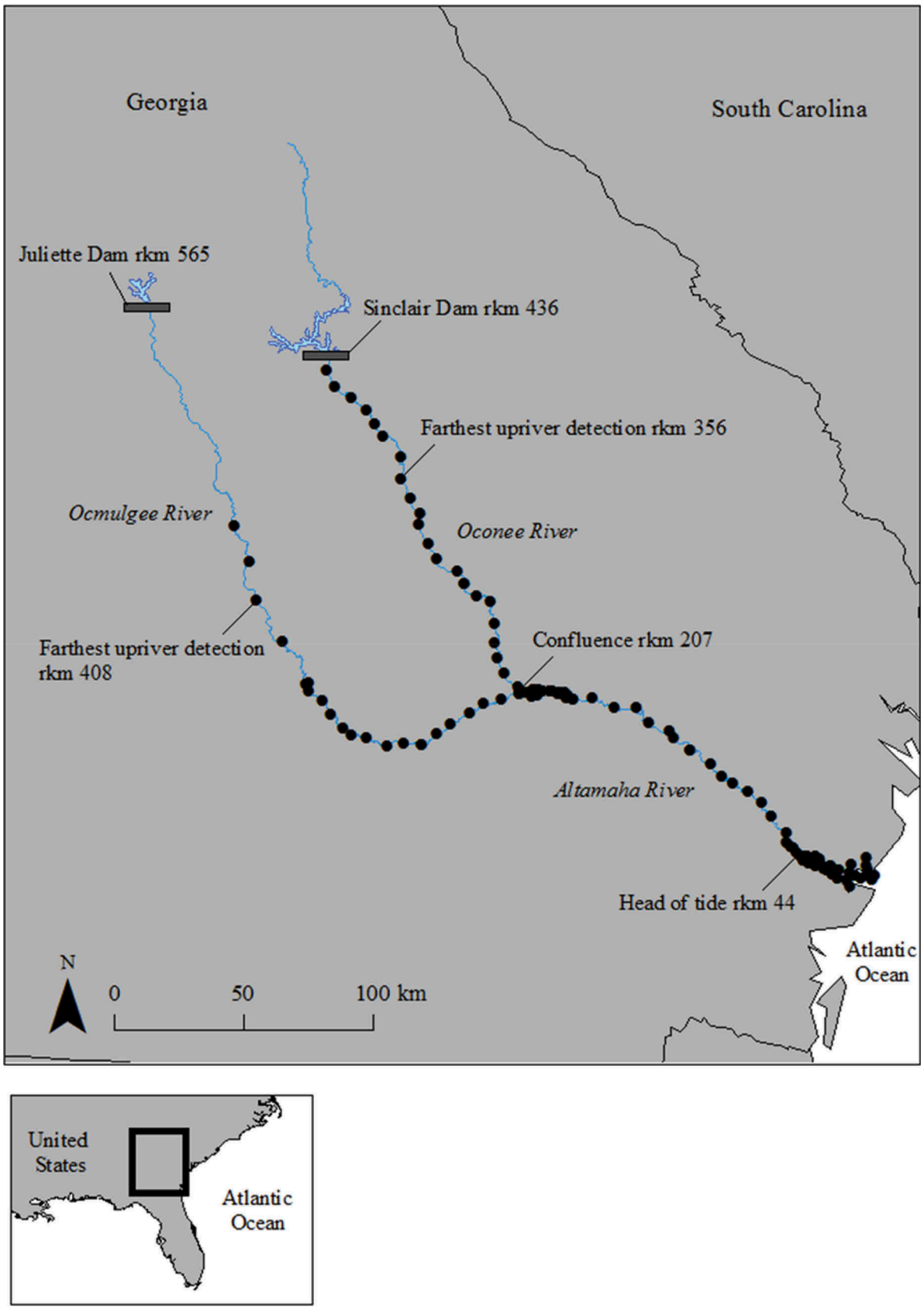


FIGURE 1. Map of the Altamaha River watershed, Georgia with inset showing relative location within the USA. Unique receiver station locations are represented by filled circles. Dams delineate the upper boundary of habitat accessible to Atlantic Sturgeon in the Ocmulgee and Oconee River tributaries. Maximum upstream detections of Atlantic Sturgeon in both tributaries and other relevant river kilometer (rkm) locations are indicated.

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TABLE 1. Data associated with 42 adult Atlantic Sturgeon caught and tagged with sonic transmitters in the Altamaha River, Georgia, April 1, 2011 to March 31, 2014. Putative spawning migrations indicating spring two-step migration (S), fall one-step migration (F), or no observed migration (N), migration being defined as directed upstream movements of more than 160 km during a single year of the study.

Identifier	Release date	Fork length (mm)	Total length (mm)	Valid detections	Putative spawning migration pattern		
					Year 1	Year 2	Year 3
ATS-1	Apr 21, 2011	1,584	1,792	27,275	S	S	S
ATS-2	Apr 22, 2011	1,630	1,850	28,806	F	S	S
ATS-3	Apr 25, 2011	1,520	1,690	7,465	F	F	N
ATS-4	Apr 25, 2011	1,430	1,585	8,968	F	N	N
ATS-5	Apr 26, 2011	1,720	1,955	18,191	N	S	N
ATS-6	Apr 29, 2011	1,494	1,610	24,268	S	N	S
ATS-7	Apr 29, 2011	1,590	1,825	7,990	N	N	S
ATS-8	Apr 29, 2011	1,535	1,660	12,471	N	F	F
ATS-9	May 3, 2011	1,755	1,980	72	N	N	N
ATS-10	May 3, 2011	1,680	1,880	16	N	N	N
ATS-11	May 4, 2011	1,440	1,600	22,343	F	F	F
ATS-12	May 4, 2011	1,600	1,795	131	N	N	N
ATS-13	May 4, 2011	2,030	2,310	15,085	F	N	N
ATS-14	May 9, 2011	1,490	1,700	16,197	S	S	S
ATS-15	May 9, 2011	1,900	2,160	3,489	N	N	N
ATS-16	May 10, 2011	1,710	2,010	72	N	N	N
ATS-17	Apr 21, 2012	1,600	1,790	5,122		F	F
ATS-18	May 14, 2012	1,710	2,040	5,703		N	F
ATS-19	May 17, 2012	1,930	2,220	998		N	N
ATS-20	May 17, 2012	1,460	1,640	1		N	N
ATS-21	May 18, 2012	1,880	2,120	12,853		N	N
ATS-22	May 21, 2012	1,660	1,870	186		N	N
ATS-23	May 23, 2012	1,950	2,240	1		N	N
ATS-24	May 25, 2012	1,940	2,220	60,276		F	N
ATS-25	May 31, 2012	2,000	2,130	120,420		F	N
ATS-26	Jun 11, 2012	1,640	1,940	3,158		F	N
ATS-27	Jun 15, 2012	1,650	1,870	1,323		N	N
ATS-28	Apr 25, 2013	1,460	1,650	2,277			F
ATS-29	Apr 30, 2013	1,255	1,442	62,226			S
ATS-30	Apr 30, 2013	1,495	1,680	5,415			F
ATS-31	Apr 30, 2013	1,450	1,580	1,449			F
ATS-32	May 1, 2013	1,500	1,692	30			N
ATS-33	May 1, 2013	1,595	1,790	1			N
ATS-34	May 1, 2013	1,310	1,466	2,636			N
ATS-35	May 7, 2013	1,480	1,660	8,513			F
ATS-36	May 7, 2013	1,640	1,840	208			N
ATS-37	May 7, 2013	1,420	1,600	9,235			S
ATS-38	May 7, 2013	1,670	1,860	12,487			F
ATS-39	May 8, 2013	1,430	1,620	2,065			F
ATS-40	May 8, 2013	1,450	1,570	2,451			F
ATS-41	May 8, 2013	1,440	1,640	3,932			F
ATS-42	May 8, 2013	1,390	1,520	9			N

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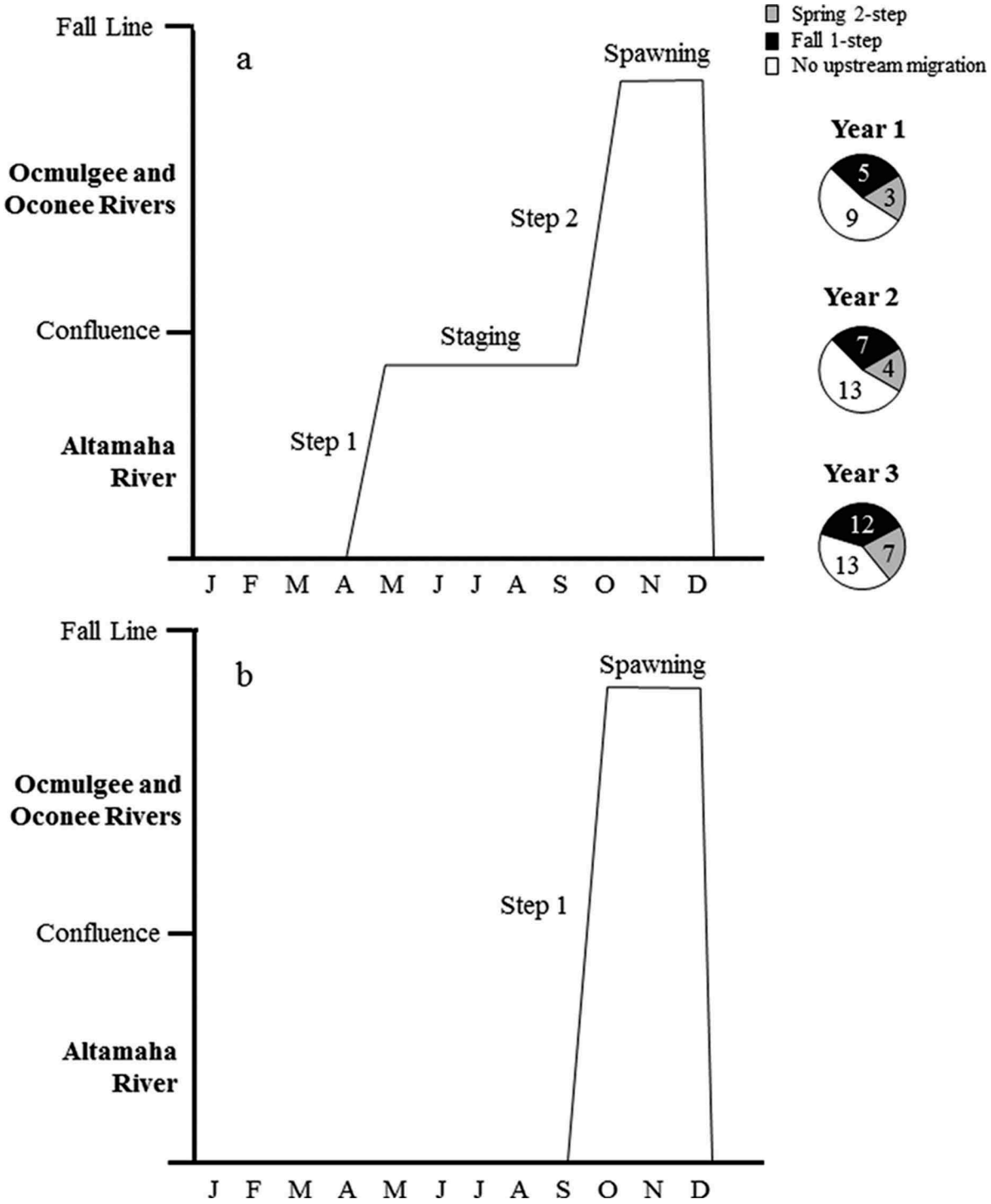


FIGURE 2. General representation of putative **(a)** spring two-step and **(b)** fall one-step spawning migrations of Atlantic Sturgeon in the Altamaha River system, Georgia. Pie charts show prevalence of each migration strategy documented using acoustic telemetry from study year 1 (April 1, 2011 to January 31, 2012), year 2 (April 1, 2012 to January 31, 2013), and year 3 (April 1, 2013 to January 31, 2014).

stationed near the vessel where they were allowed to recover until netting activities had been completed. After all nets had been retrieved, the captured fish were examined for internal and external tags. If none were found, a passive integrated transponder tag was inserted into the body musculature beneath the fourth dorsal scute. Measurements of total length, fork length,

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and weight were recorded. Coded VEMCO (Halifax, Nova Scotia) acoustic transmitters (V16-6 H; 69 khz; tag delay 30–90 s; estimated battery life = 1,633 d) were then surgically implanted into each individual fish using the surgical methods described by Moser et al. (2000) and Boone et al. (2013). Following surgeries, the fish were returned to the net pen and monitored for 5–10 min until they had fully recovered before being released at their original capture site.

Passive acoustic telemetry.—To monitor movements of acoustically tagged fish, a station array consisting of 112 acoustic receivers (VEMCO VR2W) with omnidirectional hydrophones was deployed over a total of 670 km throughout the Altamaha River system (Figure 1). Receivers were placed at sites approximately 10 km apart, except at the confluence of the Ocmulgee and Oconee rivers and in Altamaha Sound, where they were placed at 2–3-km intervals to provide finer resolution of fish movements in these areas. The submerged receivers were attached to anchored buoys and deployed so that they were suspended approximately 1 m from the river bottom in an upright position. To ensure efficient retrieval of the receivers, anchors were tethered with 32-mm stainless steel cable to the nearest structure. Within riverine habitat, receivers were positioned in the main channel and tethered to trees on the adjacent bank. In open water habitats, such as Altamaha Sound, receivers were tethered to channel markers or pilings. Range testing at receivers revealed an average tag detection radius of approximately 400 m (range = 200–800 m). Although detection range is known to vary depending on water depth, sea state, bottom substrates, and the degree of receiver biofouling (Heupel et al. 2008), we observed similar detections ranges at all sites evaluated, regardless of habitat type. Because the channel widths of the Altamaha, Oconee, and Ocmulgee rivers average only 160 m, 89 m, and 77 m, respectively, the minimum detection range of the receivers was more than sufficient to ensure bank-to-bank coverage of the river channel throughout the entire study reach. Once deployed, the receivers were downloaded at least every 3 months throughout the study, except when environmental conditions made the river unnavigable.

Data processing.—At the conclusion of each field season, all telemetry data were carefully reviewed to identify and remove any spurious detections that were obvious based on the spatial and temporal chronology of individual fish movements. Simultaneous detections of a single transmitter at two geographically separate locations, for example, were removed. Mean daily locations of each transmittered fish were determined by calculating mean river kilometer, based on all telemetry detections during each 24-h period after the fish was released. From these mean daily values, mean weekly river-kilometer values for individual fish were then calculated to construct box plots of weekly river distributions for every fish that made significant (>160 km) upstream movements. When mean weekly river-kilometer values were unavailable because of limited fish movement, the last known position of the fish was used for that particular week. To simplify data processing, study year was defined by the beginning date of the project, rather than calendar year. Thus, study year 1 was defined as April 1, 2011 to March 31, 2012; study year 2 as April 1, 2012 to March 31, 2013; and study year 3 as April 1, 2013 to March 31, 2014.

Mean weekly temperature for the Altamaha River was obtained from the Georgia Coastal Ecosystems Long Term Ecological Research hydrographic monitoring station at rkm 20 near Darien, Georgia.

RESULTS

Over the 3 years of the study, 45 adult Atlantic Sturgeon were captured and tagged with acoustic transmitters. The size range of the tagged fish was 1,255 to 2,030 mm FL, with a mean of 1,618 mm (SD, 178). Forty-two of the fish (93%) were detected by stationary receivers within the study area after their release, and 26 of these (58%) made putative spawning migrations within the Altamaha River during at least one year of the study (Table 1). The other 19 individuals either left the study area or never migrated more than 160 km upstream. Of the 26 fish that made putative spawning migrations within the Altamaha system, valid detections varied from 1,449 to 120,420, yielding a combined total of 493,788 individual detections over the course of the study.

Although each individual migration was unique, most fish adhered to one of two common movement patterns with regard to the timing and duration of their upriver migration: (1) an early migration initiated in spring or early summer that occurred in two discrete steps (Figure 2a), or (2) a late migration in late summer or early fall that occurred in only one continuous step (Figure 2b). The early two-step migrants typically entered the river from April to May but remained at mid-river sites for several weeks or months during the summer before resuming their upstream migration in the fall. The late-year one-step migrations, however, were typically initiated in August or September and were generally nonstop. Seven of the eight fish (88%) that made upriver migrations in multiple years used the same migration pattern; however, one individual exhibited different patterns in different years. Regardless of which migration pattern was used during upstream migration, all fish exhibited a rapid and continuous downstream migration in December and early January.

Over the 3 years of the study, the percentage of adult spawners that used the two-step pattern was remarkably consistent: year 1 = 3 of 8 fish (38%), year 2 = 4 of 11 (36%), and year 3 = 7 of 19 (37%). The first step of these two-step migrations was typically characterized by a rapid upstream movement to mid-river sites located above the head of tide (rkm 44). Once there, the fish exhibited little movement (<1 km/d) throughout the summer, even as water temperatures exceeded 30°C (Figure 3). Specific locations of these over-summering sites were variable, although several sites were used repeatedly by

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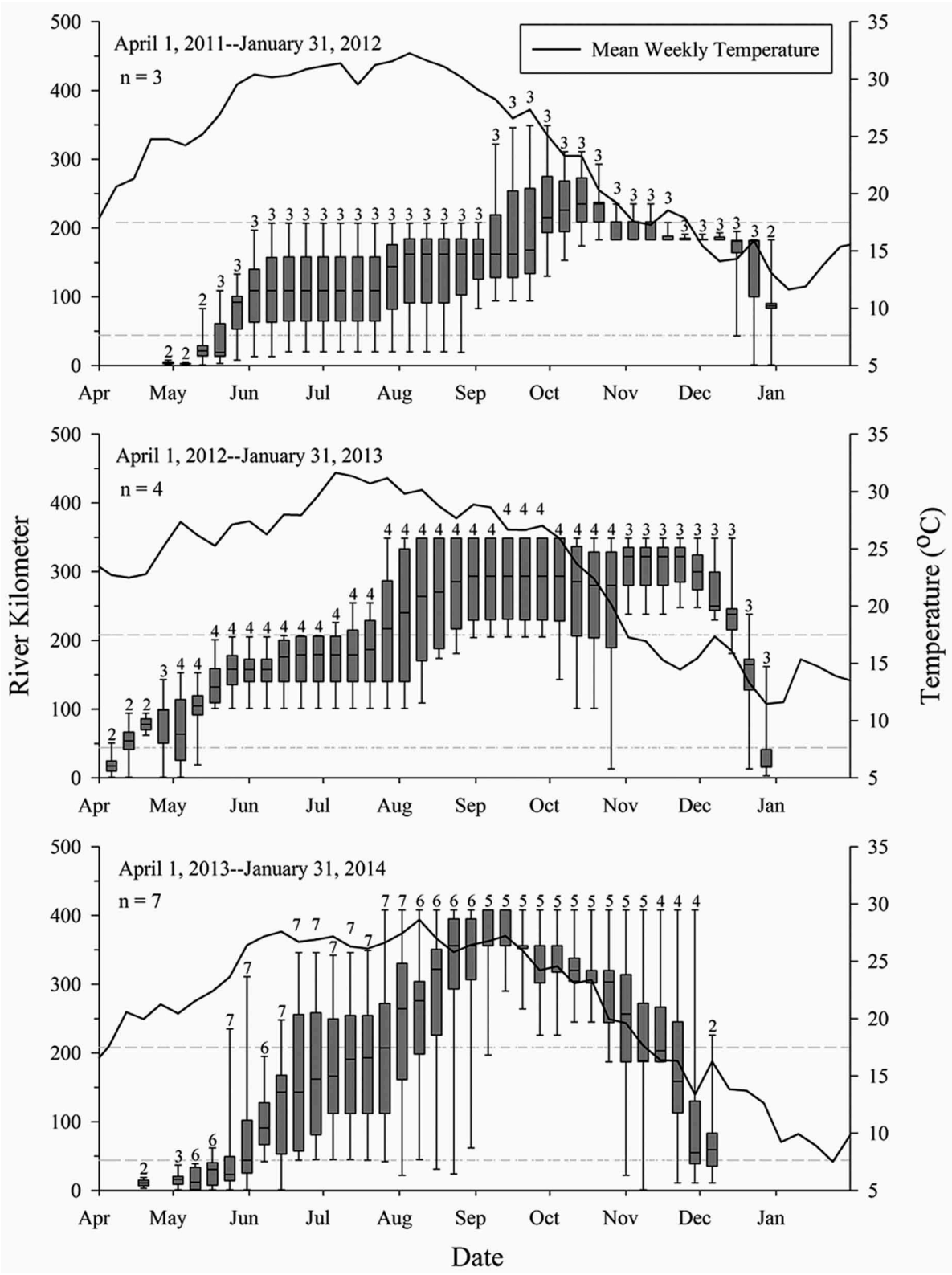


FIGURE 3. Box plots of mean weekly locations of Atlantic Sturgeon that made spring two-step migrations in the Altamaha River system, Georgia, where the box ends = 25th and 75th percentiles of ultrasonic tag detections, the line within box = median, error bars (whiskers) = minimum and maximum river kilometer (rkm) detections, and the number above the error bar = number of individual fish represented. Dashed lines denote head of tide at rkm 44 and the confluence at rkm 207. Mean weekly water temperature is from LTER GCE-7 mooring in the lower Altamaha River.

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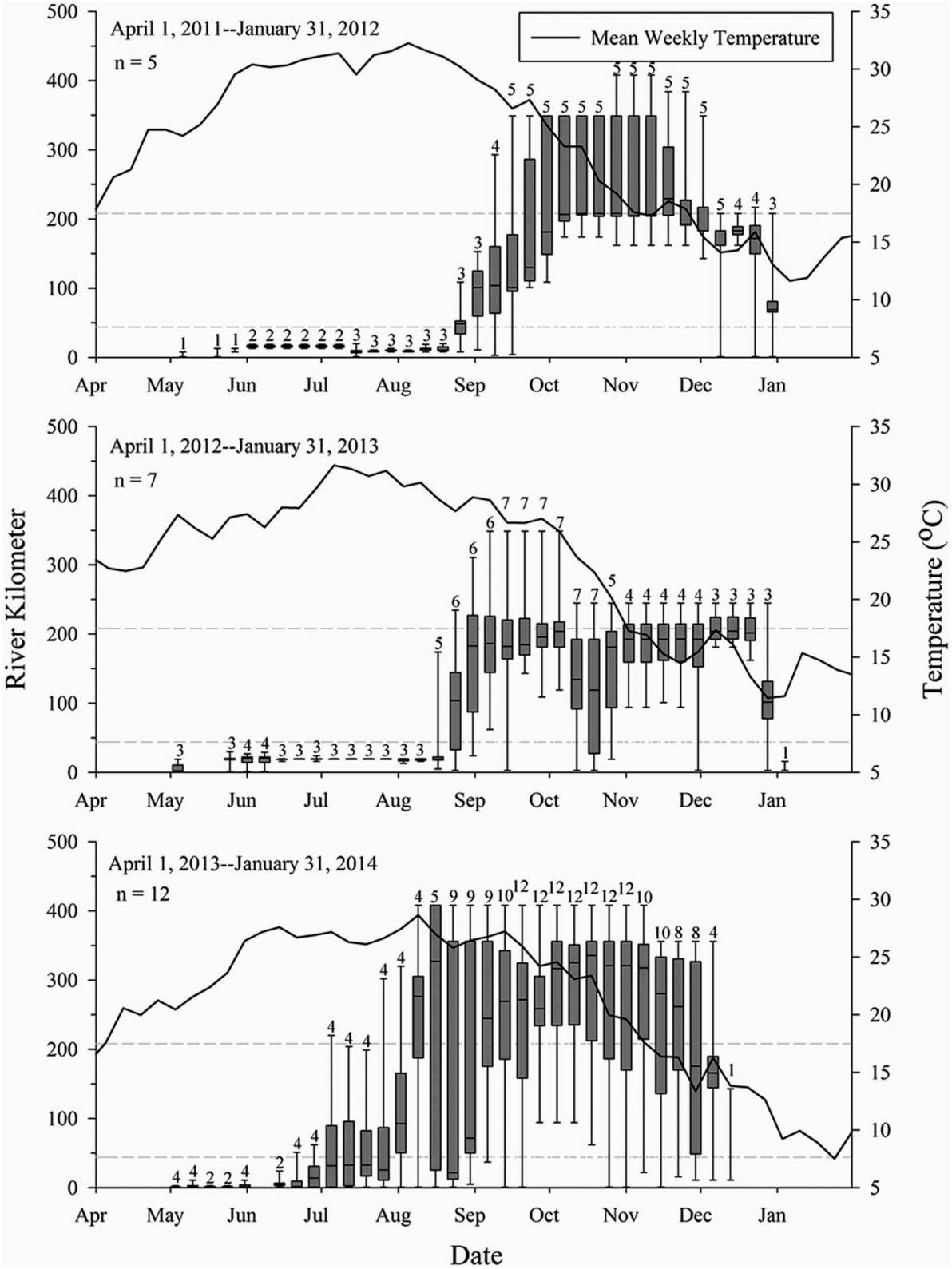


FIGURE 4. Box plots of mean weekly locations of Atlantic Sturgeon that made fall one-step migrations in the Altamaha River system, Georgia, as explained in Figure 3.

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different fish throughout the study. Regardless of which specific oversummering sites were used, the median of mean weekly detections always occurred between the head of tide and confluence (Figure 3). The second step of these spring migrations occurred in late August or early September as the fish left their oversummering sites and moved upstream to sites above the confluence in either the Ocmulgee or Oconee tributaries. These movements were rapid and direct and always occurred as water temperatures began to decline from summer highs.

In contrast to the two-step migration pattern exhibited by spring migrants, the majority of migrating fish used a fall one-step pattern: year 1 = 5 of 8 (62%), year 2 = 7 of 11 (64%), and year 3 = 12 of 19 (64%; Figure 4). These fall migrations were characterized by a long (>200 km), single-step migration from the estuary upstream to tributary reaches above the confluence. These migrations typically were also initiated in late August or early September as the mean weekly water temperature began to decline from summer maxima (Figure 4). Although these one-step migrants typically mixed with the two-step migrants as they moved upriver, movement patterns of one-step fish were distinctly different in that they lacked any staging or resting period. Once the fall one-step migrants reached their presumed spawning areas above the confluence, the median of their mean weekly locations were virtually identical to those of the two-step migrants throughout the remainder of their stay in freshwater.

Regardless of migration pattern, all adult migrants remained near or above the confluence throughout the fall before returning back downriver between late November and early January as water temperatures approached their annual minimums (Figures 3, 4). In years 1 and 2 of the study, the last detection in Altamaha Sound occurred on January 4. In year 3, the last detection occurred on December 15. Downstream migrations were typically rapid and direct, occurring over only a few weeks (e.g., one fish travelled 330 km in only 8 d before exiting the system).

Summary data of seasonal movements indicated that the tagged fish were present in the Altamaha system from April to December in each year of the study (Figures 3, 4). Seven (16.7%) individuals left the study area within a few days of being tagged and did not return to the Altamaha. Of the 26 fish (42%) that made significant upstream migrations (>160 km), 8 migrated upstream in at least 2 years of the study and 4 migrated upstream in all 3 years (Table 1). The extent of these upstream migrations varied among individuals and study years. Although some individuals were detected upriver in multiple years, there was no evidence of site fidelity. A few of the upriver sites, however, were visited by several fish in every year of the study. This was particularly true for the reach extending from the confluence to rkm 350 in the Ocmulgee River. The number of fish entering the Oconee and Ocmulgee tributaries was also variable among years. More migrations penetrated the Ocmuglee River (42%) than the Oconee River (24%), while some penetrated both tributaries (18%) or remained in the main stem (16%). Of the fish that made multiple migrations, six out of eight (75%) used different rivers in different years. Although no fish were detected in the Oconee River in year 1 and only one fish was detected there in year 2, 15 individuals were detected there in year 3. The maximum extent of these upriver migrations was documented at rkm 408 on the Ocmulgee River and rkm 356 on the Oconee River (Figure 1). In total, these migrations covered 557 of the 794 km (70%) of the free-flowing habitats within the Altamaha system.

After leaving the Altamaha River, 36% (15/42) of the tagged Atlantic Sturgeon were detected on receiver arrays in other river systems, including the Ogeechee and Satilla rivers in Georgia (authors' unpublished data); the Savannah, Cooper, Sampit, and Waccamaw rivers in South Carolina (William Post, South Carolina Department of Natural Resources, personal communication); and the Nassau River in Florida (Eric Reyier, Kennedy Space Center Ecological Program, personal communication). These coastal movements required a minimum linear distance travelled of 80 km (Ogeechee River) to 350 km (Winyah Bay in South Carolina). Although the timing and duration of detections in these systems were variable, movements within these river systems were limited to non-spawning habitats within the estuaries and lower-river reaches.

DISCUSSION

Although the telemetry data obtained in our study do not provide direct evidence of Atlantic Sturgeon spawning, the timing and extent of adult movements in relation to the seasonal temperature regime provide strong circumstantial evidence that these movements were, in fact, spawning migrations. Previous habitat surveys on the Altamaha system have documented an abundance of suitable spawning substrates throughout both the Ocmulgee and Oconee tributaries (Litts and Kaeser 2016), and telemetry data revealed that these tributaries represented the upstream terminus for 32 of the 38 (84%) adult migrations that were identified in this study.

Our results showed that the timing of upstream migrations placed adult Atlantic Sturgeon over hard substrates in the upper Altamaha system in early to mid-October, just as water temperatures dropped below 25°C. Although the optimal temperature range for early life stages has not been established empirically, aquaculture studies have reported successful incubation of eggs at temperatures of 15–20°C (Dean 1895; Smith et al. 1980; Chapman and Carr 1995), with high mortality at water temperatures ≥25°C (Chapman and Carr 1995). In the Hudson River, ripe broodstock are typically captured at water temperatures of 23°C, albeit during spring months (Mohler 2003). Recent estimates of water temperatures at fall capture sites have been reported in Virginia (20–23°C; Balazik et al. 2012) and North Carolina (24.3–25.3°C; Smith et al. 2015); although these temperatures are near the upper end of the optimal range for early life stages, they compare favorably with the putative spawning migrations observed in our study.

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Putative spawning migrations described in this study adhered to one of two distinct patterns: a spring two-step or a fall one-step. Although dual migration patterns have been described previously for other sturgeon species (Bemis and Kynard 1997)—and more recently for Atlantic Sturgeon (Balazik and Musick 2015)—the results of our study are unique in that we documented the use of two distinct migration patterns that synchronized the arrival of adult fish at presumed spawning grounds in early fall.

The migration patterns we documented indicate that there is only one spawning population of Atlantic Sturgeon in the Altamaha River represented by two patterns of movement, contrary to the previously hypothesized population structure. The observed fall synchronization of the two migration patterns may help to explain the persistent confusion regarding the timing and frequency of Atlantic Sturgeon spawning within the SADPS (e.g., Smith et al. 1984; Smith 1985; Collins et al. 2000). Recent authors have suggested that many populations (including those in Georgia) may have sympatric but distinct spring and fall races of Atlantic Sturgeon (Balazik and Musick 2015); however, we found no evidence to support that hypothesis in the Altamaha River. Instead, our results suggest that the presence of Atlantic Sturgeon in the lower reaches of the Altamaha River during the spring months is not indicative of a separate spring spawning race, but merely the first step of a two-step migration pattern that is used by approximately one-third of the adult population. However, because we only sampled adults during the late spring, we could have missed a hypothetical run of early spring spawners. Consequently, the possible coexistence of separate spring and fall spawning runs remains unresolved; however, previous length-at-age analyses of river-resident juveniles in the Altamaha River (Peterson et al. 2008; Schueller and Peterson 2010), Ogeechee River (Farrae et al. 2009), Satilla River (Fritts et al. 2016), and Savannah River (Bahr and Peterson 2015) have found no evidence of bimodal distributions within the juvenile cohorts of Atlantic Sturgeon in these rivers, as would be expected if separate spawns occurred in both spring and fall. Instead, our results showed that although many adults entered their natal rivers in spring, they did not immediately migrate upriver to potential spawning habitat, but rather appeared to stage in freshwater as they awaited cooler, more favorable water temperatures in the fall before resuming their upstream migrations. Regardless, the results of this study should help define the sampling parameters for future assessments of spawning runs within the Altamaha and other SADPS rivers—a critical need for quantitatively evaluating species recovery.

An important finding from the 38 putative spawning migrations documented over study years 1–3, was that adult Atlantic Sturgeon consistently used at least 70% of the free-flowing habitats available to them within the Altamaha system, including likely spawning habitats in both major tributaries. The Ocmulgee River was used extensively in all 3 years of the study (61% of putative spawners) while the Oconee River was used in 2 years (42% of putative spawners). Movements in the Oconee River were more sporadic and dispersed, some individuals moving upstream as far as rkm 356 (149 rkm above the confluence) and only 80 rkm below the Sinclair Dam. In contrast, movements of adults in the Ocmulgee River were less variable and largely restricted to the lowermost 150 km, though one individual moved upstream as far as rkm 408 (201 km above the confluence). Follow-up observations from concurrent research conducted in fall of 2015 documented several likely spawning adults at rkm 544–546 on the Ocmulgee, a site located approximately 140 rkm upstream of the uppermost detection obtained from the stationary receivers (Peterson, personal communication). Although these observations were merely anecdotal, they further illustrate how spawning site selection can vary widely in response to annual variations in environmental conditions.

From a management standpoint, annual variation in the migrations of adult Atlantic Sturgeon underscores the importance of maintaining all historical migratory pathways in recovery efforts for the species. Because the Altamaha River is undammed below the fall line, migrating adults have unrestricted access to all historical spawning sites, including approximately 587 km of free-flowing habitats in the Ocmulgee and Oconee tributaries. The results of our study should provide the framework for future studies of spawning dynamics and factors affecting survival during early life stages by providing detailed information regarding both the temporal and spatial extent of adult Atlantic Sturgeon migrations within the Altamaha system. This information is urgently needed to better understand how specific environmental variables (e.g., flow) influence spawning success and subsequent year-class formation within the SADPS. Once spawning is confirmed, subsequent evaluations of spawning habitats should also help delineate critical habitats in the Altamaha River and elsewhere—a key step in species recovery under the U.S. Endangered Species Act.

Understanding clinal variation in Atlantic Sturgeon ecology has important management implications for species recovery. Previous studies indicate that spawning in northern rivers occurs in early summer as temperatures increase from their winter lows (Dovel and Berggren 1983; Van Eenennaam et al. 1996; Bain 1997). For river systems south of the Hudson River, Balazik and Musick (2015) suggest that Atlantic Sturgeon spawning runs are likely comprised of distinct spring and fall races that constitute a dual-spawning strategy. In this study, however, telemetry data revealed that putative spawning migrations in the Altamaha occur only during the fall as water temperatures decline from their summer highs. These contrasts in study results further illustrate the extent of clinal variation in the life history of Atlantic Sturgeon. More importantly, however, they underscore the need to manage the species as distinct population segments with regionally specific recovery goals. Within the SADPS, future research is needed to document spawning events and early life stages and, subsequently, to identify the specific

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characteristics of spawning sites by incorporating the spatial and temporal information from this study with modern habitat mapping techniques. Future studies are also needed to better understand how clinal variation in Atlantic Sturgeon ecology affects population dynamics and, hence, the regionally specific factors limiting species recovery.

ACKNOWLEDGMENTS

Funding for this project was provided by the National Marine Fisheries Service. We thank Bill Post (South Carolina Department of Natural Resources) for his role in securing and administering project funding. We appreciate the field assistance we received from Ryan Harrell, Jason Garritt, Brandon Boehm, Alex Cummins, Derek Bahr, and Samantha Bahr. We also thank Michael Bednarski and David Higginbotham for their assistance with data analyses and field logistics. The contributions of Wade Sheldon and Adam Sapp were vital to the collection and analyses of annual temperature data.

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