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# Identifying Environmental Cues for Atlantic Sturgeon and Shortnose Sturgeon Spawning Migrations in the Savannah River

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**Abstract**

We investigated environmental cues for spawning migration behavior of Atlantic Sturgeon *Acipenser oxyrinchus* and Shortnose Sturgeon *A. brevirostrum* in the lower Savannah River, South Carolina and Georgia, from January 2013 to May 2018. Sturgeon were implanted with acoustic transmitters and detected on an array of 45 stationary receivers located every 5–10 km between Savannah Harbor and the upstream-most barrier to movement (301 fluvial kilometers). Throughout the study period, we observed six Atlantic Sturgeon attempting nine fall migrations ( $n = 918$  records), four Atlantic Sturgeon attempting eight spring migrations ( $n = 257$  records), and 15 Shortnose Sturgeon attempting 29 spring migrations ( $n = 3,542$  records). Cues for the initiation of migration and upriver movement were species-specific. We observed significance in the main effects of water temperature, 3-d lagged temperature, maximum discharge, and 3-d lagged discharge, as well as in the interaction effect of 3-d lagged temperature  $\times$  3-d lagged discharge. Water temperature was the primary predictor of sturgeon migrations, which can be used to determine spawning season, but discharge also played a significant role in predicting upriver movement, particularly when high flows began to diminish. Directed flow regulation (e.g., intermittent flood pulsing) during key temperature thresholds may better facilitate the upriver movement of sturgeons and aid in the conservation of these imperiled species.

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Quantitative understanding of reproductive ecology is critical for the conservation and management of imperiled fishes (Allendorf 1988; Jonsson et al. 1999). Diadromous fishes have complex reproductive strategies that often require long dispersal events to access a variety of marine and freshwater habitats. Moreover, many diadromous

fishes exhibit a “periodic” life history strategy of large body size and late maturation (Winemiller and Rose 1992). Accordingly, diadromous fishes are particularly vulnerable to numerous threats, including overfishing, habitat alteration, and migration barriers (Jonsson et al. 1999; Limburg and Waldman 2009), and are

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disproportionately imperiled relative to other guilds of fishes (Leidy and Moyle 1998; Jelks et al. 2008). Diadromous sturgeons (Acipenseridae) are no exception; nearly every species is considered imperiled somewhere in its native range (Pikitch et al. 2005). Although harvest moratoria have reduced the mortality of adult sturgeon (Bain et al. 2007), contemporary declines in most species are associated with reproduction—either degraded or inaccessible spawning habitat (Auer 1996a). Accordingly, range-wide quantification of environmental cues that initiate spawning migrations, as well as the location and size of spawning aggregations, will provide information that is essential to the conservation and recovery of sturgeons (Pollock et al. 2015).

Variation in behavior, age at maturity, and migration strategy exists among diadromous fish populations, and populations must be protected at a regional scale due to these differences. Atlantic Sturgeon (ATS) *Acipenser oxyrinchus* and Shortnose Sturgeon (SNS) *A. brevirostrum* are anadromous or amphidromous and inhabit estuarine or nearshore marine habitats before attempting riverine spawning migrations (Bemis and Kynard 1997). Atlantic Sturgeon attempt migrations every 1–5 years, and SNS attempt migrations every 1–4 years (Billard and Lecointre 2000). Females of both species migrate less frequently than males due to the high energetic cost of egg production. Male SNS reach maturity between ages 2 and 11, and female SNS attain maturity between ages 4 and 18 (Dadswell et al. 1984). Male ATS mature between ages 5 and 20, whereas female ATS reach maturity between ages 7 and 30 (Smith 1985). Age at maturation increases with latitude for both species (Bemis and Kynard 1997; Kynard 1997). Atlantic Sturgeon in the northern Atlantic Ocean are separated into five distinct population segments (DPSs): Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (Grunwald et al. 2008). The Gulf of Maine DPS is listed as threatened, while the others are listed as endangered. Shortnose Sturgeon have been considered endangered since the Endangered Species Preservation Act of 1966, and 19 DPSs were identified by the Shortnose Sturgeon Recovery Team in 1998. In 2010, the Shortnose Sturgeon Status Review Team recommended that SNS be managed as river-specific populations separated into five genetically distinct regional population clusters due to SNS movement and genetic overlap between rivers (Bahr and Peterson 2017).

Seasonal variation in ATS and SNS spawning migrations occurs regionally. Atlantic Sturgeon populations in northern latitudes tend to migrate during spring, while individuals in southern populations exhibit fall or dual annual spring and fall spawning migrations (Balazik and Musick 2015). Additionally, fall- and spring-run ATS individuals may constitute genetically distinct stocks on some rivers of the eastern USA (Balazik et al. 2017; Farrae

et al. 2017). Shortnose Sturgeon spawning migrations all occur between winter and spring, but variation exists in migration strategy and timing based on each population's latitudinal location. Within seasons, the timing and intensity of spawning migrations can be influenced by environmental factors, such as water temperature, river discharge, and photoperiod (Northcote 1984; Jonsson 1991). The associated migration strategy used by an individual sturgeon reflects energetic adaptations to environmental challenges, such as distance to the spawning grounds, river temperature, discharge, and physiological condition (Kynard 1997).

Although many studies have investigated riverine movement and spawning behavior of ATS and SNS (Balazik and Musick 2015; Smith et al. 2015; Ingram and Peterson 2016; Breece et al. 2018; Pendleton et al. 2018), we know of no prior study that has quantified spawning migration cues. Accordingly, the goal of this study was to identify the relationships between abiotic variables and spawning migrations of ATS and SNS in the Savannah River of Georgia and South Carolina. We sought to accomplish two objectives: (1) identify temperature and discharge cues associated with spawning migration initiation by ATS and SNS; and (2) within spawning migrations, identify the effects of temperature and discharge on spatial position (river kilometer [rkm]) in the river. Diadromous fishes in the Savannah River are threatened by migration barriers and altered flow regimes from impoundments as well as by estuarine habitat degradation due to the continued development of Savannah Harbor (Winger and Lasier 1994; Collins et al. 2002). The quantification of cues for sturgeon migrations in the Savannah River can provide inference for system-specific conservation and represents an important step toward understanding the reproductive ecology of these species throughout their range.

## METHODS

*Study system and data collection.*—The Savannah River forms the border between South Carolina and Georgia in the southeastern United States (Figure 1). The upper Savannah River is impounded by five large reservoirs, but the lower 300 km remain undammed. There is little anthropogenic development along most of the Savannah River, with the exception of two nuclear power facilities: the Savannah River Site (Aiken County, South Carolina) and Plant Vogtle (Burke County, Georgia). Further downriver sits the Savannah Harbor, a highly industrialized estuary impacted by dredging, intense shipping practices, and urbanization. The seasonal distribution and intensity of river flow are highly modified by hydrologic regulation from five successive reservoirs, with the lowermost (J. Strom Thurmond Lake) providing the most direct impact. At rkm 300, the New Savannah Bluff Lock and

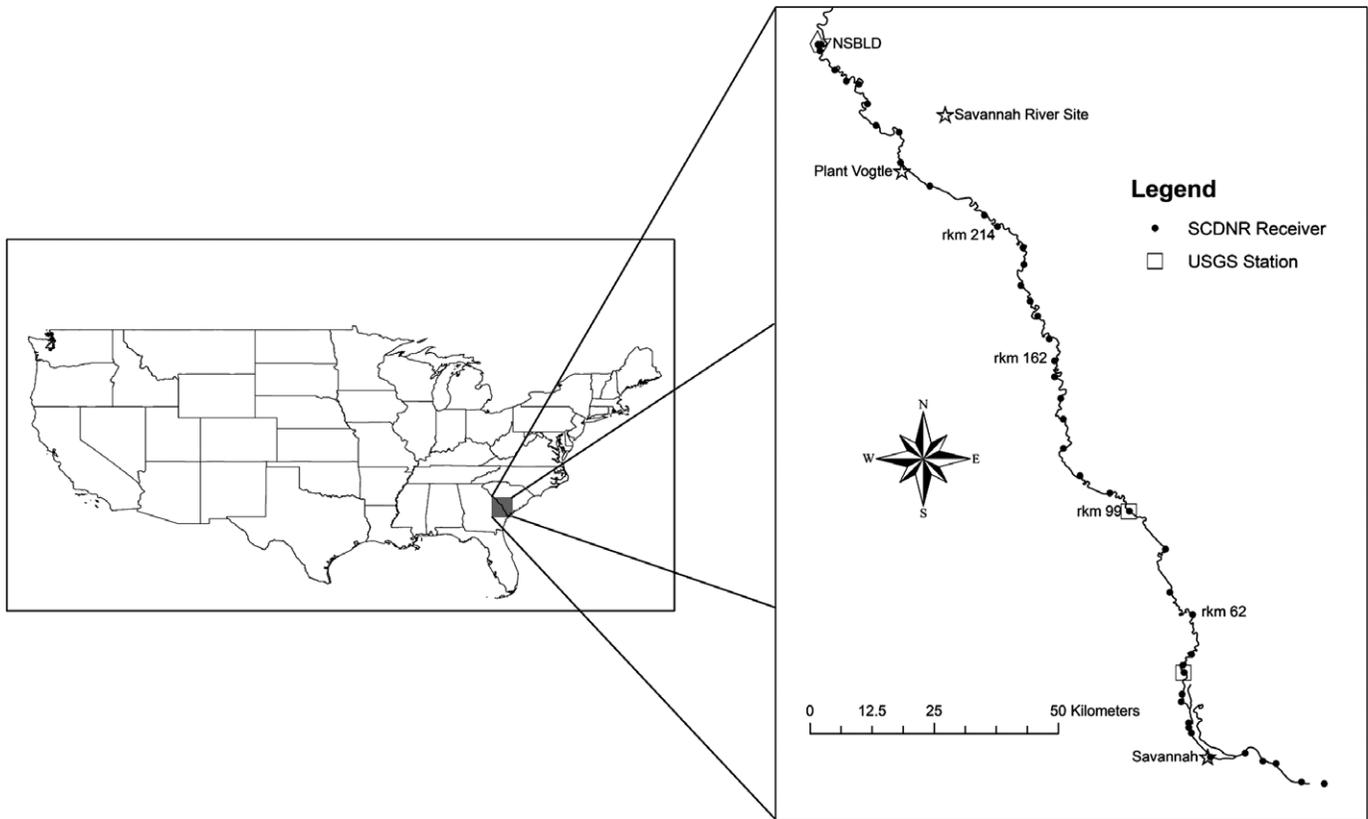


FIGURE 1. The Savannah River serves as the border between South Carolina and Georgia. The zoomed portion of the map reveals the South Carolina Department of Natural Resources (SCDNR) telemetry receiver array, U.S. Geological Survey (USGS) stations, and landmarks along the Savannah River (rkm = river kilometer; NSBLD = New Savannah Bluff Lock and Dam).

Dam (NSBLD) is the downstream-most barrier to diadromous fish movement and serves as the most likely spawning site of ATS and SNS in the Savannah River.

We monitored ATS and SNS movement up the Savannah River between January 2013 and May 2018. Sturgeon were captured by personnel representing agencies and universities from Georgia, South Carolina, Delaware, and New York (Table 1), and were surgically implanted with Vemco V9 (24 mm; 2.1 g), V13 (36 mm; 6 g), or V16 (54 mm; 8.1 g) 69-kHz acoustic transmitters via the protocol outlined by the National Marine Fisheries Service (Kahn and Mohead 2010). We obtained acoustic telemetry data from a stationary array of 45 Vemco VR2W 69-kHz receivers maintained by the South Carolina Department of Natural Resources' (SCDNR) Diadromous Fisheries Section (Figure 1). The receivers of interest begin at the NSBLD and are located approximately every 5–10 rkm down the main stem of the Savannah River, extending to Savannah Harbor. Data were retrieved at least twice annually, organized in Vemco User Environment (VUE) software, and screened for false detections.

We were interested the effects of two key mechanisms on sturgeon movement: temperature and discharge. We

first obtained daily water temperature ( $^{\circ}\text{C}$ ) and discharge ( $\text{m}^3/\text{s}$ ) records from two U.S. Geological Survey (USGS) stations located near rkm 42 and rkm 95, respectively (Figure 1). We chose both stations based on the availability of long-term data. For the entire duration of the study period, discharge data contained only 13 d of missing observations, and water temperature data contained only 40 d of missing observations. Other USGS stations monitor water temperature and discharge along the Savannah River, although data were insufficient for the entire study period. We did not want to incorporate discharge and temperature data from other stations because they would be inherently correlated with the data from the stations we chose for the analysis.

*Statistical analyses.*—We calculated metrics indexing daily and lagged effects of temperature and discharge. These include maximum and minimum daily temperature and maximum daily discharge. Because daily effects may not always be indicative of factors influencing fish behavior (Forsythe et al. 2012), we also calculated 1-d and 3-d lagged changes in temperature and discharge. The 1-d and 3-d measures were highly correlated with one another ( $r = 0.73$  and  $0.86$ , respectively); thus, we chose to only

TABLE 1. Yearly temperature ( $^{\circ}\text{C}$ ) and discharge ( $\text{m}^3/\text{s}$ ) statistics for the Savannah River over the duration of the study period (2013–2018); 2018 statistics do not represent an entire year and only incorporate data from January to May.

Statistic	2013	2014	2015	2016	2017	2018
Mean temperature	19.49	18.53	20.38	20.94	21.67	14.79
Maximum temperature	27.5	29.5	30.1	30.8	30.8	20.6
Minimum temperature	9.4	5.4	7.6	7.4	9.2	5.2
Mean discharge	328.8	310.9	288.1	355.3	187.8	192
Maximum discharge	1,642.4	1,081.7	778.7	1,574.4	402.1	266.2
Minimum discharge	124	139.3	146.1	140.5	137.1	154.9

use 3-d lagged temperature and discharge, as the effects of variation in discharge and temperature would be more prominent over a 3-d period.

We modeled two complementary response variables indexing putative spawning migration behavior by ATS and SNS. First, we modeled the probability that an individual sturgeon would be engaging in upriver movement toward spawning grounds on a given day. Effects on this binary variable represent conditions that cue the initiation of upstream migration. To do so, we first identified every individual's location based on the most upstream detection each day. We then calculated a binary variable indexing whether each individual was engaging in a putative spawning migration based on its movement direction (upstream) and position (rkm) in the river. Atlantic Sturgeon that were detected above rkm 99 were considered to be attempting a spawning migration, while rkm 62 served as the migration threshold for SNS. These rkm locations were selected because (1) once ATS and SNS individuals crossed the associated threshold, no individual of either species returned to downstream locations without further upriver movement; and (2) individuals remained below their associated threshold during periods outside of the spawning season. We used the migration indicator to represent a point in time at which an individual exhibited upstream movement toward spawning habitat; individuals moving downstream above their associated rkm threshold were not considered to be engaging in a spawning run. It is important to clarify that we are not estimating the effects of temperature and discharge on the act of spawning—rather, we are estimating the effects on movement patterns of *putative* spawning migrations.

As a complement to whether or not an individual had initiated a putative spawning run, we also modeled the spatial location of individuals within the Savannah River given that they were on a putative spawning run. This variable was simply the rkm of the upstream-most receiver detecting an individual on each day of a spawning run. This information allowed us to assess movement dynamics in relation to temperature and discharge within spawning runs.

We used mixed-effects linear models to estimate effects of temperature and discharge on the putative spawning migration of ATS and SNS. The binary variable indexing whether a species was on a spawning run was modeled as a random binomial variable (generalized linear mixed model [GLMM]), and daily rkm during putative spawning runs was modeled as a random normal variable (linear mixed model [LMM]). Observational units in all models were daily observations of individual sturgeon. All models had the same error structure. We included random intercepts of individual identity to account for repeated measures on individuals. Likewise, we also included random intercepts of year to account for the nested effects of temperature and discharge experiencing similar conditions in similar years. Finally, we included the migration indicator and rkm of the most recent detection as an offset to account for temporal autocorrelation in spawning phenology for our GLMM and LMM, respectively. To avoid problems associated with calculating  $P$ -values for mixed-effects models, we interpreted variable significance as standardized parameter estimates with 95% confidence intervals not bounding zero. All models were fitted using the lme4 package in R version 3.3.4 (Bates et al. 2015).

Each model contained four main effects: daily temperature, daily discharge, 3-d lagged temperature, and 3-d lagged discharge. We were also interested in the interactions between these variables. Specifically, we were interested in how the levels of discharge set the context for the effects of temperature (or vice versa). Accordingly, we allowed each discharge variable to interact with each temperature variable in each model. For example, a 3-d increase in discharge may trigger a movement event but only under certain temperature conditions. We expected the effects to be species- and season-specific (e.g., fall-run ATS are likely respond to decreasing temperatures, while spring-run ATS are likely to do the opposite). Accordingly, we split data into three groups for separate analyses: fall-run ATS (May–November), spring-run ATS (February–May), and spring-run SNS (December–April). We included minimum daily temperature in the model for fall-migrating ATS because we expected decreasing summer temperatures to cue migration (Smith et al. 2015), while

we used maximum daily temperature for SNS and spring-migrating ATS because we expect an increase in winter temperatures to cue migration (Peterson and Bednarski 2013). We used maximum daily discharge and 3-d change in discharge in all models. All variables were screened for collinearity ( $r \leq 0.70$ ; variance inflation factor  $\leq 3.0$ ) and were standardized to a mean of zero and an SD of zero prior to analyses.

## RESULTS

Savannah River water temperature and discharge varied throughout the duration of the study period (Table 1). High-discharge events occurred in the years 2013 and 2016, reaching maximum flows of 1,642 and 1,574 m<sup>3</sup>/s, respectively. After 2016, maximum discharge never exceeded 402 m<sup>3</sup>/s, and the lowest yearly average of 188 m<sup>3</sup>/s occurred in 2017. Water temperature followed typical seasonal variation, reaching minima of 5°C in the winter and maxima of 30°C in the summer (Figure 2). The coldest water temperatures occurred in 2014 (5.4°C) and 2018 (5.2°C), whereas the warmest temperatures occurred consecutively in 2016 (30.1°C) and 2017 (30.2°C). Maximum water temperatures consistently increased from 2013 to 2017.

Over the study period, we detected six ATS attempting nine fall migrations, four ATS attempting eight spring migrations, and 15 SNS attempting 29 spring migrations (Table 2). Six ATS and six SNS traveled 300 rkm to the NSBLD. Five SNS and two ATS reached locations between rkm 186 and rkm 214; four SNS and one ATS reached only locations between rkm 144 and rkm 162. We present data only regarding ATS and SNS migrations and cannot assume spawning success during any portion of the study period.

Spring-run SNS began their migrations between December and February at water temperatures between 11°C and 15°C and at river discharge levels from 127 to 776 m<sup>3</sup>/s. Migrations began as water temperatures dropped to the winter low, leveled, and began to increase. Spring-run ATS initiated migration between February and March at water temperatures between 16°C and 18°C and at river discharge levels between 194 and 340 m<sup>3</sup>/s. Spring-run ATS typically entered the system and immediately began upriver migrations when water temperatures began to exceed 15°C. Fall-run ATS initiated migration between May and August at water temperatures from 24°C to 29°C and at river discharge levels from 144 to 223 m<sup>3</sup>/s. Individuals initiated migrations as summer high water temperatures leveled and began to decline (Figure 2).

The GLMMs indicated that water temperature significantly affected the probability of migration for SNS ( $n = 3,542$  records) and fall-run ATS ( $n = 918$  records) but not for spring-run ATS ( $n = 257$  records), whereas 3-d lagged temperature was a significant predictor for only

spring-run SNS. Discharge and 3-d lagged discharge were also significant predictors of migration for spring-run SNS, while neither was a significant predictor for spring- or fall-run ATS. We observed no significant interaction effects for any sturgeon population, and we found no main effects that were significant in predicting spring-run ATS migrations (Table 3; Figures 3, 4).

Results of LMMs indicated that within putative spawning migrations, water temperature and 3-d lagged temperature each had a significant main effect on the daily maximum rkm of detection for spring-run SNS. Interestingly, we observed a significant interaction effect of 3-d lagged discharge and 3-d lagged temperature on the daily maximum rkm of spring-run ATS. This was the only significant effect observed in any model for spring-run ATS. No main effects or interaction effects were found to be significant predictors of the maximum rkm of detection for fall-run ATS during putative spawning migrations (Table 4; Figure 5).

## DISCUSSION

We observed patterns of putative spawning migrations by ATS and SNS in the Savannah River that were affected primarily by shifts in water temperature and secondarily by discharge. However, cues for migration initiation and spatial position within putative spawning runs were species-specific. The significant main effect of temperature on both migration movement and maximum rkm of detection was negative for SNS, while the effect of 3-d lagged temperature was positive. The significant main effect of temperature on the migration movement of fall-run ATS was positive, while the 3-d lagged effect of temperature, although negative, was not significant in predicting migration movement. Discharge had a significant negative effect on the probability of migration for SNS, while the 3-d lagged effect of discharge was positive. This suggests that high levels of discharge may inhibit SNS upriver movement, but decreasing flows promote upriver movement. Moreover, inferences on spring- and fall-run ATS are limited by low sample size. Of course, observed movement patterns do not demonstrate successful spawning, although suitable spawning habitat exists in locations where both species were observed congregating, and young-of-the-year ATS and SNS were detected in the lower Savannah River during the study period, indicating successful reproduction (Bahr and Peterson 2016, 2017).

Our results are comparable to those of other studies focused on the migratory behavior of sturgeon species. Migration analysis of White Sturgeon *A. transmontanus* in the Kootenai River, British Columbia, revealed that neither temperature nor discharge was significant for influencing the onset of migrations by males; however, the onset of migrations by females was primarily affected by water

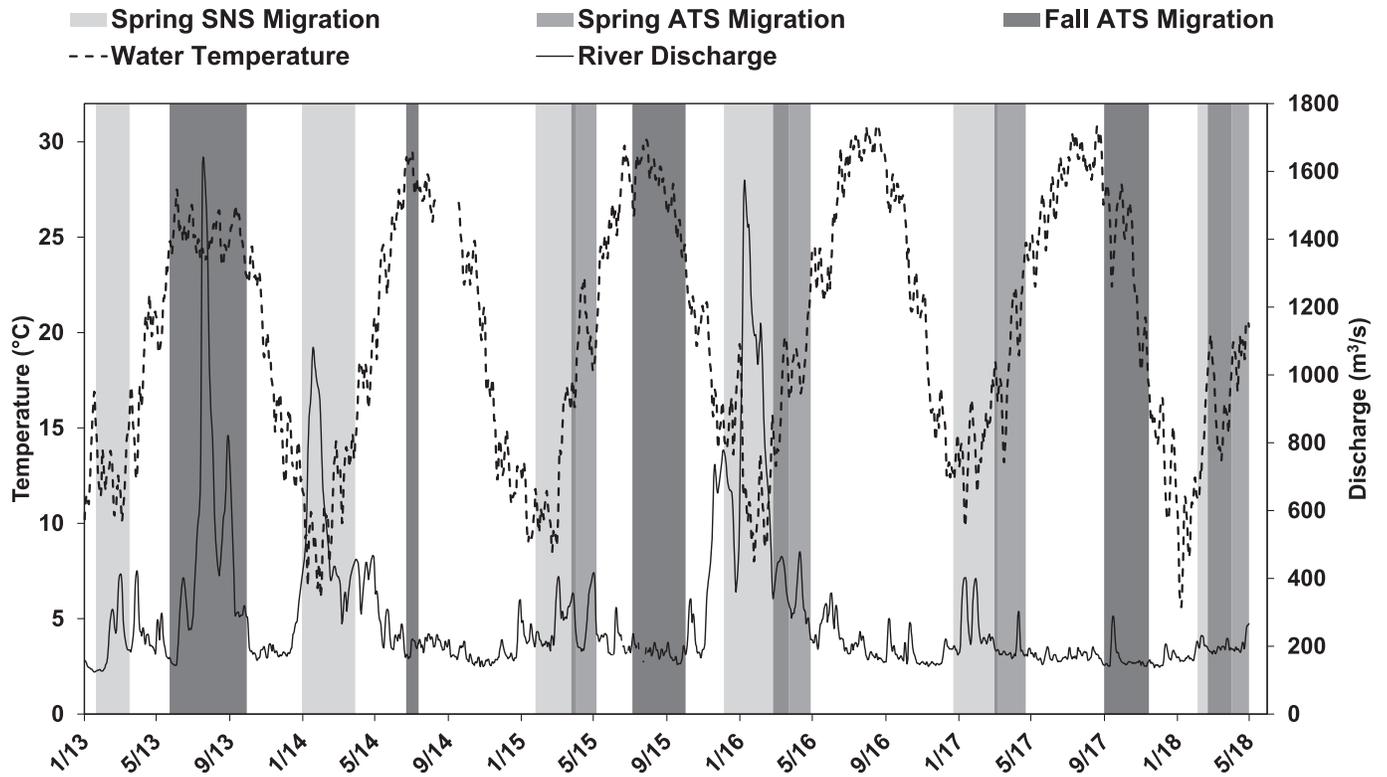


FIGURE 2. Savannah River water temperature and river discharge from January 2013 to May 2018, overlain with observed Atlantic Sturgeon (ATS) and Shortnose Sturgeon (SNS) spawning migration periods.

TABLE 2. Shortnose Sturgeon (SNS) and Atlantic Sturgeon (ATS) migration statistics per year and season, including the total number of detected sturgeon attempting a migration ( $N_m$ ), date of first migration (Onset), date of final departure (Dep.), temperature ( $^{\circ}\text{C}$ ) and discharge ( $\text{m}^3/\text{s}$ ) upon migration onset ( $t_o$ ,  $d_o$ ), and temperature and discharge upon departure ( $t_d$ ,  $d_d$ ).

Year	Season	Species	$N_m$	Onset	$t_o$	$d_o$	Dep.	$t_d$	$d_d$
2013	Spring	SNS	3	Jan 20, 2013	14.9	127	Mar 17, 2013	15.6	190
		ATS	0						
2014	Fall	ATS	4	May 23, 2013	24.7	167	Sep 29, 2013	23	286
		SNS	6	Dec 30, 2013	12.3	391	Mar 29, 2014	14.4	453
2015	Spring	ATS	0						
		ATS	1	Jun 22, 2014	29.1	172	Jul 13, 2014	27.3	207
2016	Fall	SNS	6	Jan 24, 2015	11.8	209	Apr 1, 2015	16.7	255
		ATS	1	Mar 25, 2015	16.3	337	May 6, 2015	20	235
2017	Spring	ATS	2	Jul 5, 2015	27.5	223	Oct 2, 2015	24.1	175
		SNS	5	Dec 5, 2015	14.9	776	Mar 22, 2016	17.1	326
2018	Fall	ATS	2	Feb 25, 2016	15.2	340	Apr 28, 2016	22.6	219
		ATS	0						
2017	Spring	SNS	6	Dec 22, 2016	12.7	196	Mar 5, 2017	17	188
		ATS	1	Mar 1, 2017	18.2	195	Apr 22, 2016	24.7	176
2018	Fall	ATS	2	Aug 31, 2017	27	144	Nov 14, 2017	17.2	156
		SNS	3	Feb 3, 2018	11.3	214	Apr 1, 2018	18	191
2018	Spring	ATS	4	Feb 20, 2018	17.8	194			
		ATS	0						

TABLE 3. Generalized linear mixed model estimates ( $\pm$ SE) for spring-run Shortnose Sturgeon (SNS), spring-run Atlantic Sturgeon (ATS), and fall-run ATS in the Savannah River. Results estimate the main effects of temperature (Temp), discharge, 3-d lagged temperature ( $\Delta$ Temp), and 3-d lagged discharge ( $\Delta$ Discharge) and four interaction terms on the probability of migration for each sturgeon attempting migration. Estimates in bold italics were significant predictors of migration as determined by the 95% confidence intervals.

Effect	Spring SNS	Spring ATS	Fall ATS
Temp	<b><i>-2.16 <math>\pm</math> 0.21</i></b>	0.21 $\pm$ 0.22	<b><i>3.16 <math>\pm</math> 0.69</i></b>
Discharge	<b><i>0.50 <math>\pm</math> 0.16</i></b>	0.03 $\pm$ 0.27	0.86 $\pm$ 0.75
$\Delta$ Temp	<b><i>0.38 <math>\pm</math> 0.08</i></b>	-0.33 $\pm$ 0.19	-0.24 $\pm$ 0.19
$\Delta$ Discharge	<b><i>-0.34 <math>\pm</math> 0.20</i></b>	-0.17 $\pm$ 0.22	0.37 $\pm$ 0.43
Temp $\times$ Discharge	0.26 $\pm$ 0.11	0.30 $\pm$ 0.28	2.02 $\pm$ 1.32
Temp $\times$ $\Delta$ Discharge	-0.19 $\pm$ 0.17	-0.12 $\pm$ 0.26	0.70 $\pm$ 0.66
Discharge $\times$ $\Delta$ Temp	-0.04 $\pm$ 0.05	0.05 $\pm$ 0.27	0.04 $\pm$ 0.33
$\Delta$ Temp $\times$ $\Delta$ Discharge	0.01 $\pm$ 0.05	0.18 $\pm$ 0.21	0.03 $\pm$ 0.22

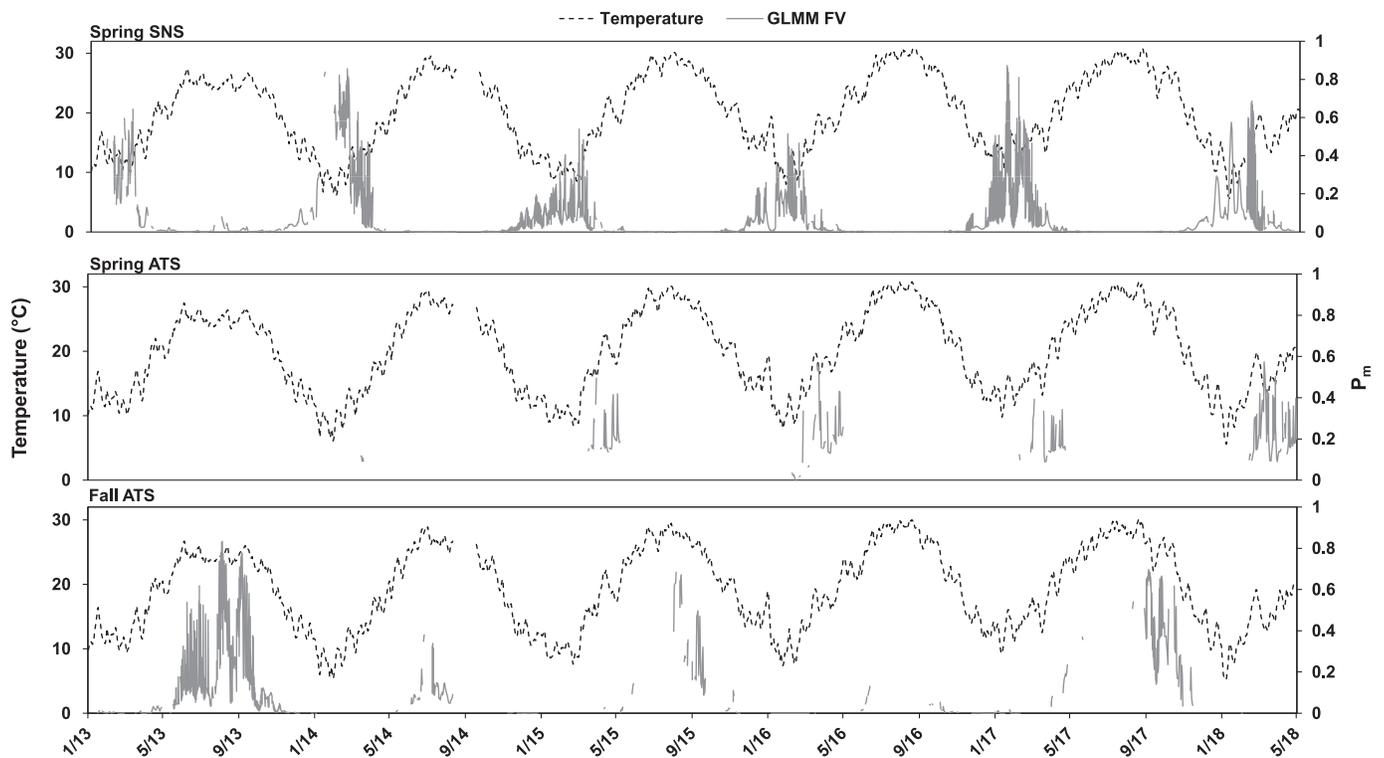


FIGURE 3. Generalized linear mixed model (GLMM) results for spring-run Shortnose Sturgeon (SNS), spring-run Atlantic Sturgeon (ATS), and fall-run ATS plotted against Savannah River water temperature over time. Model fitted values (GLMM FV) provide a probability of migration ( $P_m$ ) for each population. The  $P_m$  begins to increase as water temperatures reach near winter lows, level out, and begin to increase.

temperature and secondarily by river stage (Paragamian and Kruse 2001). Because our data set unfortunately does not contain sex information, we are unable to draw such a comparison. In Black Lake, Michigan, effects of water temperature and discharge significantly impacted the migrations of Lake Sturgeon *A. fulvescens* as well as their timing of arrival at spawning sites (Forsythe et al. 2012). Chinese Sturgeon *A. sinensis* in the Yangtze River exhibited variation in timing of upstream migration, which was likely

attributable to variation in water temperature and river discharge, although temperature was suggested as the primary cue (Wang et al. 2012). Research on Gulf Sturgeon *A. oxyrinchus desotoi* in the Choctawhatchee and Suwanee rivers of Alabama and Florida suggested that water temperature initiated migration, while flow patterns had no effect on migration behavior (Foster and Clugston 1997; Fox et al. 2000). However, previous research on Gulf Sturgeon in the Suwanee River indicated that migratory activity was highly

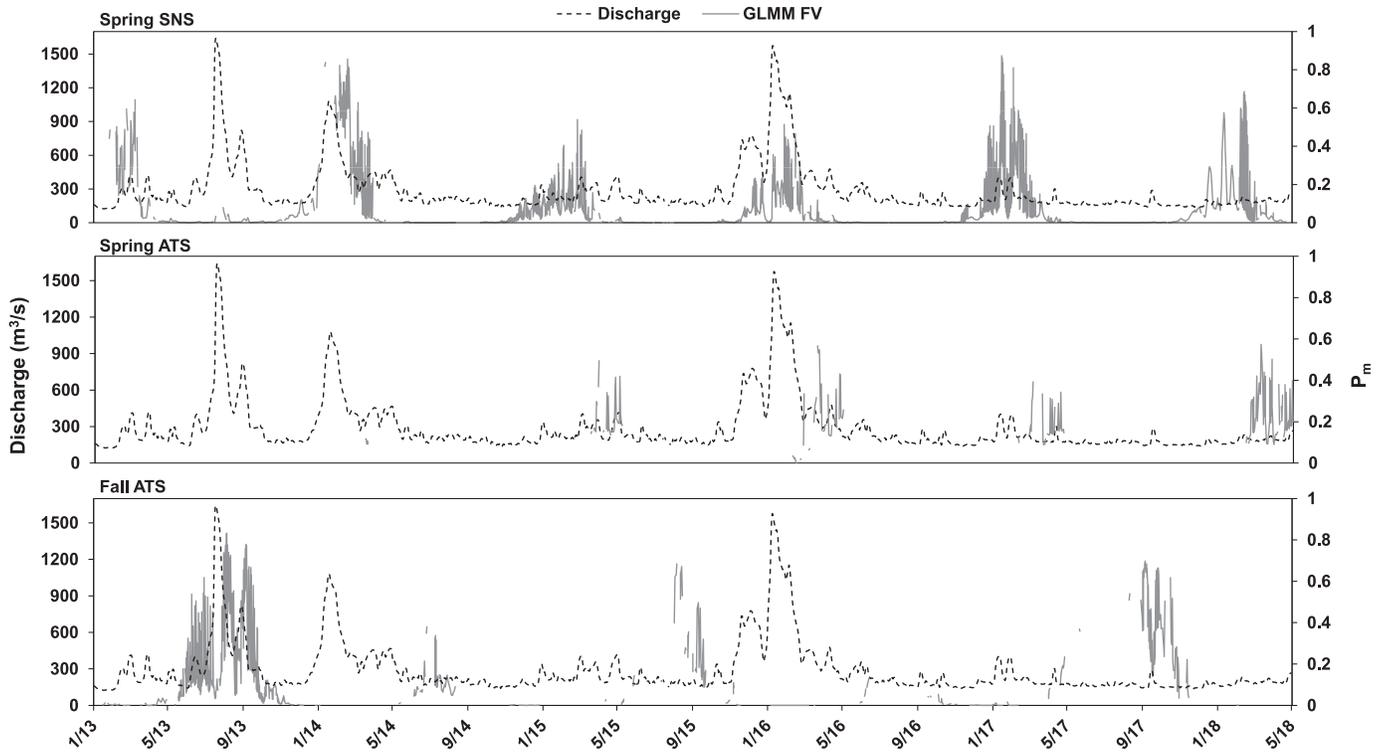


FIGURE 4. Generalized linear mixed model (GLMM) results for spring-run Shortnose Sturgeon (SNS), spring-run Atlantic Sturgeon (ATS), and fall-run ATS plotted against Savannah River discharge over time. Model fitted values (GLMM FV) provide a probability of migration ( $P_m$ ) for each population. During years in which discharge varied during temperatures that were conducive to spawning migrations (e.g., 2014 and 2016), higher migration probabilities occurred as discharge diminished.

TABLE 4. Linear mixed model estimates ( $\pm$ SE) for spring-run Shortnose Sturgeon (SNS), spring-run Atlantic Sturgeon (ATS), and fall-run ATS in the Savannah River. Results estimate the main effects of temperature (Temp), discharge, 3-d lagged temperature ( $\Delta$ Temp), and 3-d lagged discharge ( $\Delta$ Discharge) and four interaction terms on the upstream-most daily detection (river kilometer) of each sturgeon during putative spawning migrations. Estimates in bold italics were significant predictors as determined by the 95% confidence intervals.

Effect	Spring SNS	Spring ATS	Fall ATS
Temp	<b><i>-13.04 ± 2.67</i></b>	-5.71 ± 3.93	9.19 ± 4.74
Discharge	1.19 ± 3.15	3.97 ± 4.54	5.14 ± 4.96
$\Delta$ Temp	<b><i>7.30 ± 2.32</i></b>	-0.97 ± 3.62	2.15 ± 3.09
$\Delta$ Discharge	0.91 ± 2.67	-3.77 ± 3.64	2.03 ± 3.92
Temp × Discharge	1.93 ± 2.89	7.45 ± 4.25	4.10 ± 6.56
Temp × $\Delta$ Discharge	0.10 ± 2.95	0.10 ± 4.46	2.50 ± 5.54
Discharge × $\Delta$ Temp	-2.15 ± 1.87	0.91 ± 3.60	2.71 ± 4.12
$\Delta$ Temp × $\Delta$ Discharge	-1.59 ± 1.73	<b><i>8.40 ± 3.41</i></b>	-4.72 ± 3.99

correlated with increases in river discharge (Chapman and Carr 1995). Forsythe et al. (2012) found a decrease in the number of Lake Sturgeon individuals attempting migrations during periods of high discharge. This was attributed to an increased physiological cost of migration at high flows as well as a lower probability of egg fertilization and deposition on spawning substrate during high-flow conditions (LaHaye et al. 1992; Auer 1996b; Paragamian and Wakkinen 2002). Overall, sturgeon exhibit a variety of migratory

behaviors in response to changes in temperature and discharge, and the primary factors contributing to migration behavior, as well as the associated effects, can be different in each study and river system.

Many species exhibit variation in the timing and seasonality of spawning movement and behavior (Flitcroft et al. 2016). Our data suggest two separate spawning migrations (spring and fall) for ATS in the Savannah River. It is widely accepted that fall-spawning populations of ATS exist in the

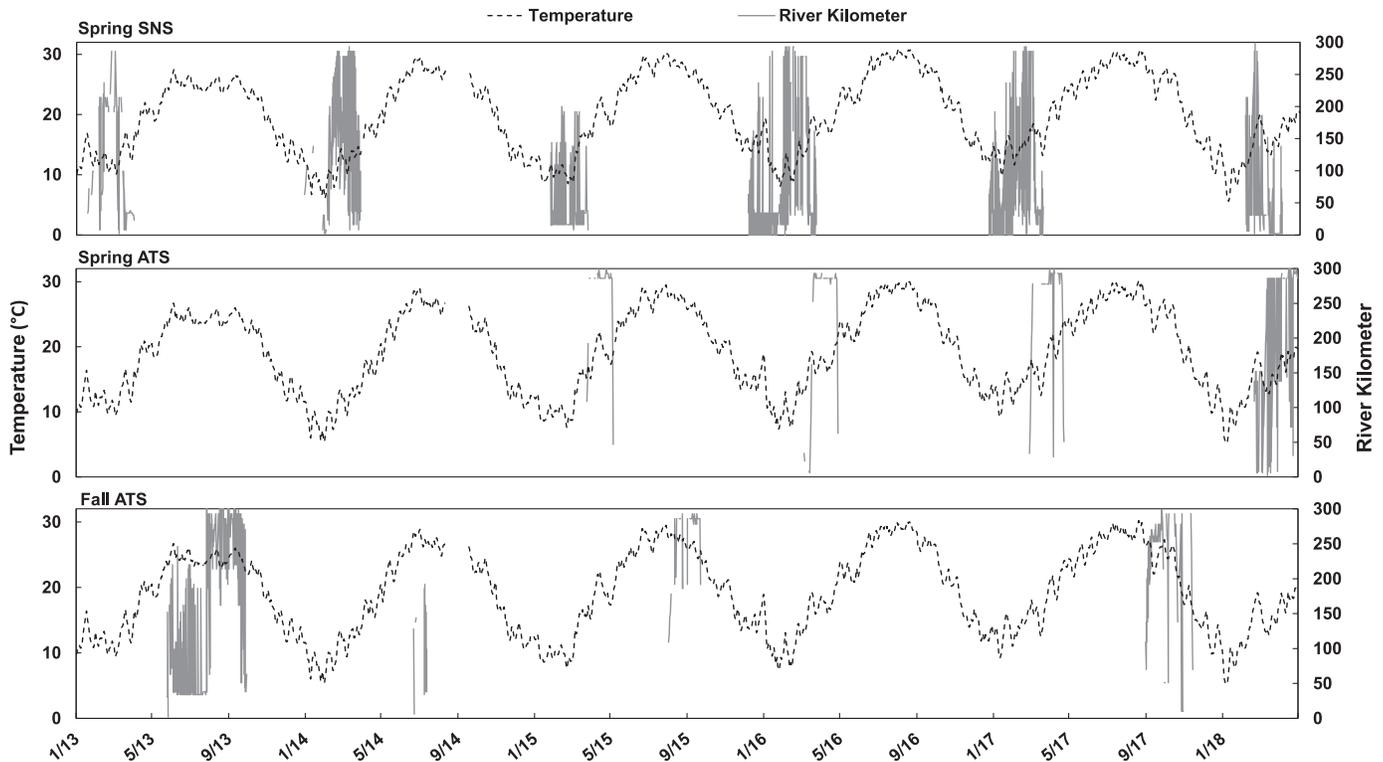


FIGURE 5. Savannah River temperature and maximum river kilometer of detection for spring-run Shortnose Sturgeon (SNS), spring-run Atlantic Sturgeon (ATS), and fall-run ATS over time. Data presented were used for linear mixed modeling and represent detections specifically obtained after the initiation of spawning migrations.

southern extent of the species' range (Balazik et al. 2012; Ingram and Peterson 2016), while dual-spawning populations have been described in systems north of the Savannah River (Collins et al. 2000; Balazik and Musick 2015). Genetically distinct populations of spring- and fall-migrating ATS exist in the Edisto River, South Carolina, and the James River, Virginia (Balazik et al. 2017; Farrae et al. 2017). In the Altamaha River (south of the Savannah River), ATS exhibit two migration strategies: a two-step migration in the spring; and a single, one-step migration in the fall (Ingram and Peterson 2016). However, both strategies result in individuals occupying putative spawning grounds during the fall, and all individuals are believed to be part of a single spawning population (Ingram and Peterson 2016). We did not observe spring-run ATS attempting a two-step migration pattern in the Savannah River. All ATS that attempted spring migrations either returned to down-river locations or exited the system before the fall migration occurred, and all spring- and fall-run ATS exhibited a single, one-step migration. Given the presence of separate spring- and fall-run populations of ATS in the Savannah River, further genetic analyses are necessary to determine whether these populations are indeed distinct.

Diadromous fishes can exhibit a wide variety of migration strategies (Northcote 1984). Spring-run SNS in the

Savannah River exhibited a long, one-step migration—roughly 160–270 km in length—to access putative spawning grounds. At higher latitudes, SNS in the Merrimack and Delaware rivers must only attempt a short (<30-km), single-step migration to reach suitable spawning habitat (Kieffer and Kynard 1993; O'Herron et al. 1993). Some individuals in the Connecticut River exhibited a two-step migration in which the primary movement took place during the late fall (Buckley and Kynard 1985). Individuals remained at these locations, closer to spawning sites, in preparation for the spawning event that occurred in the following spring. We did not observe any two-step migrations in the Savannah River, only long, single-step migrations—a finding that is consistent with historical documentation in the Savannah River (Hall et al. 1991) and in the Altamaha River (Ingram and Peterson 2018).

Rivers and their biota rely on a natural flow regime of floods and pulses (Junk et al. 1989). Dams and the associated hydrological alterations remove these naturally occurring processes, alter water temperatures, and modify the timing and intensity of hydrologic events downstream (Olden and Naiman 2010). The effect of dams on water temperature is variable and depends mainly on the mode of operation and mechanism of water release (McManamay 2014). River water temperature can be directly impacted by dam release

of water differing in temperature from that naturally occurring in the river (e.g., epilimnetic versus hypolimnetic release), or it can be indirectly impacted by the associated alterations in hydrology, which influence the processes controlling the distribution and retention of heat within the river channel. Research suggests that dams homogenize flow across hydroclimatic regions (Poff et al. 2007), reduce flood peaks, increase minimum flows, and alter the timing of peak and low flows (Magilligan and Nislow 2005; Fitzhugh and Vogel 2011). Hydroelectric facilities produce a variety of flow pulses (Young et al. 2011), all of which affect the naturally occurring biota downriver. Depending on the species and index of spawning, both water temperature and river discharge were important cues for imperiled sturgeons in the Savannah River. Directed management of river flows (e.g., intermittent flood pulsing) implemented during times when temperatures encourage migration behavior could help to ensure quality conditions for these endangered fishes to reach suitable spawning habitat.

Greater understanding of the temperature and flow conditions that initiate and promote upriver movement by sturgeons will continue to aid in the conservation of these species. Primarily utilizing water temperature to predict the timing of spring- and fall-run sturgeon migrations in the Savannah River, fish managers and reservoir managers can work together to ensure that the needs of humans and aquatic organisms are met. Increased numbers of adult fish that gain access to spawning habitat, as well as water temperature and discharge conditions favorable for hatching and survival of eggs, will improve the recruitment of sturgeons in the Savannah River and contribute to population restoration. We encourage similar research in natural and impounded river systems containing sturgeon to parse out the relative effects of hydrological variability on these imperiled fishes.

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