ARTICLE

# Seasonal migration cues differ for dual-spawning Atlantic Sturgeon in the Great Pee Dee River

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## Abstract

**Objective:** We investigated environmental variables associated with spawning migration behavior for a dual-spawning population of endangered Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* in the Great Pee Dee River, South Carolina.

**Methods:** From 2016 to 2021, 147 Atlantic Sturgeon were captured, implanted with acoustic transmitters, and monitored using a stationary array of 40 receivers located every 5–20 km along a 302-km section of the Great Pee Dee River from the river mouth at Winyah Bay to the first movement barrier at Blewett Falls Dam, North Carolina.

**Result:** We observed 47 Atlantic Sturgeon attempting 74 spring migrations and 39 Atlantic Sturgeon attempting 76 fall migrations across 4 years of telemetry observations (2018–2021). Mixed-effects models indicated that discharge interacted with water temperature to affect both migration initiation and upriver movement, and these interactions differed between the spring and fall runs. Spring runs were cued by rising temperatures and high river discharge, whereas fall runs were cued by falling temperatures and low discharge. Within migrations, spring-run fish migrated further upriver when discharge was falling, and fall-run fish moved further upriver when discharge was rising. Overall, fall-run sturgeon migrated significantly further upriver than spring-run sturgeon.

**Conclusion:** Differences in migratory behavior between the two runs suggest potentially unique adaptations to ambient river conditions during the respective spawning seasons. Identifying the environmental factors that drive—and thereby limit—Atlantic Sturgeon migrations in the Great Pee Dee River informs regional recovery efforts and highlights the importance of studying and managing this species at the population level.

### KEYWORDS

diadromous, endangered species, flow, migratory contingents, phenology, temperature

# INTRODUCTION

An understanding of reproductive ecology is necessary to inform the conservation and management of imperiled fishes, especially those with diadromous life histories. Diadromous fishes are particularly vulnerable to exploitation and habitat loss because they require a diversity of well-connected marine and freshwater habitats to complete their life history and they tend to aggregate seasonally in areas where they are easily exploited (Limburg and Waldman 2009; Geist 2011). Accordingly, diadromous fishes are disproportionately imperiled relative to fishes with other life history strategies (Jelks et al. 2008; Limburg and Waldman 2009). Anadromous sturgeons (Acipenseridae) are of particular conservation concern, as large body size and late maturation have contributed to both intense exploitation and slow rates of recovery despite increased protections (Pikitch et al. 2005). Since diadromous fishes face a variety of threats at different stages of their life history, understanding the timing and drivers of life history events can help us to partition the effects of threats on the conservation and recovery of imperiled species.

The Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* is one of the largest and longest-lived anadromous fishes in North America, occurring along the Atlantic slope from Labrador, Canada, to Florida, USA. Atlantic Sturgeon exhibit a periodic life history strategy that increases their vulnerability to exploitation and habitat change, thus complicating conservation and recovery efforts (Winemiller 2005). Historical fisheries targeted Atlantic Sturgeon for their roe and resulted in the collapse of most populations by the late 19th century, although landings continued through the 20th century until a coastwide moratorium was enacted in 1998 (Atlantic States Marine Fisheries Commission [ASMFC] 1998). Atlantic Sturgeon were federally listed under the Endangered Species Act in 2012 across their range (NOAA 2012). As part of this listing, rivers in the United States were split into five distinct population segments (DPSs). The New York Bight, Chesapeake, Carolina, and South Atlantic DPSs were listed as endangered, and the Maine DPS was listed as threatened (NOAA 2012). Although adult mortality has largely been reduced as a result of harvest moratoria (Dadswell 2006; ASMFC 2017), recruitment remains a major challenge to recovery due to degraded or inaccessible spawning habitat (Auer 1996). A better understanding of spawning behavior is needed to effectively manage Atlantic Sturgeon locally and across their range.

Most historical documentation of Atlantic Sturgeon spawning behavior was obtained from fisheries-dependent data during periods of commercial exploitation (e.g., Smith 1985). Since the enactment of harvest moratoria, fisheries-independent data have shown Atlantic

**Impact statement**

Some populations of Atlantic Sturgeon have uniquely adapted to spawn in both spring and fall. Each seasonal spawning run is cued differently by the interplay between river temperature and flow. Because they are present in rivers for a longer period of time, dual-spawning sturgeon may be more susceptible to a wider range of threats.

Sturgeon spawning behaviors to be highly variable among river systems in terms of timing and periodicity. Atlantic Sturgeon appear to exhibit a subdivided metapopulation structure along the Atlantic coast, with high philopatry among spawning adults leading to genetically distinct populations among river systems (ASMFC 2017; White et al. 2021). Historical accounts suggest that spawning intervals range from 3 to 5 years for females and from 1 to 5 years for males (Smith 1985); however, recent studies suggest that spawning may be more frequent in some systems (Hager et al. 2020; Breece et al. 2021). Timing of spawning varies latitudinally, with upriver migrations beginning as early as March in southern climates and as late as July for more northerly populations (Dadswell 2006; Hilton et al. 2016). Age at maturity likewise varies, ranging from 4 years in southern systems to 27 years in northern systems (Scott and Crossman 1973; Van Eenennaam and Doroshov 1998; Peterson et al. 2008).

Atlantic Sturgeon in some rivers exhibit dual spring and fall spawning runs (Balazik et al. 2012; Hager et al. 2014; Smith et al. 2015) that can be genetically distinct from one another (Balazik et al. 2017; Farrae et al. 2017; White et al. 2021). This life history strategy is fairly unique, as dual spawning runs are rare in diadromous fishes outside of Salmonidae. Based on temperature optimization for juvenile growth, recent research suggests that dual spawning runs should be an optimal reproductive strategy at latitudes centering on the Chesapeake Bay, becoming less advantageous as latitude increases or decreases (Markin and Secor 2020). However, detection of dual spawning in Georgia suggests that this an open area of research (Ingram and Peterson 2016; Vine et al. 2019; Wirgin et al. 2023). Quantifying patterns of Atlantic Sturgeon spawning migrations in previously understudied rivers along the Atlantic coast will provide a more thorough understanding of the prevalence of dual spawning runs in this species and the consequences of this behavior for population regulation.

There is an increasing recognition that population-level variability in the migratory behavior of Atlantic Sturgeon may have regional management implications (Hilton

et al. 2016; ASMFC 2017). It is possible that spawning could provide a "portfolio effect" by diversifying reproductive opportunities and thereby stabilizing annual recruitment (Secor et al. 2020). On the other hand, this strategy also implies that adult sturgeon may be present in rivers for a longer duration than previously realized, exposing them to threats such as boat strikes and bycatch (Brown and Murphy 2010; Balazik et al. 2012). As such, an understanding of similarities and differences in timing, environmental cues, and behaviors of spring and fall migrations will be useful for conservation and management of this species. For example, Balazik and Musick (2015) found that fall-run Atlantic Sturgeon traveled much further upriver than spring-run fish in the James River, Virginia. Moreover, Vine et al. (2019) found that fall-run Atlantic Sturgeon initiated spawning in association with temperature, while spring-run spawning initiation was variable. System-specific studies of Atlantic Sturgeon spawning movements have focused primarily on the timing of spawning migrations (e.g., Collins et al. 2000; Ingram and Peterson 2016; Breece et al. 2021) and/or environmental conditions corresponding with spawning migrations (e.g., Balazik et al. 2012; Smith et al. 2015; Hager et al. 2020). Though such descriptive studies are fundamental to informing our knowledge of Atlantic Sturgeon spawning behavior across the species' range (Dadswell 2006; Balazik and Musick 2015), a better understanding of how environmental conditions cue spawning migrations is needed. Detailed knowledge of how the environment affects Atlantic Sturgeon movement can provide insight into the dynamic habitat needs of migrating sturgeon, thereby enabling managers to focus conservation efforts where they have the greatest impact (Secor et al. 2022). Although studies quantifying the drivers of spawning movements have the potential to increase the efficiency of Atlantic Sturgeon recovery efforts, such studies are relatively rare (but see Breece et al. 2018; Vine et al. 2019).

In this study, we used a robust acoustic telemetry data set to quantify movement patterns and spawning cues for adult Atlantic Sturgeon in the Great Pee Dee River (GPD) system of South Carolina, USA. Although the GPD is suspected to have the highest Atlantic Sturgeon abundance of any river in the Carolina DPS (Flowers and Hightower 2015), relatively little is known about how Atlantic Sturgeon use this system for reproduction. The main objective of this study was to investigate the effects of temperature and discharge on (1) spawning migration initiation and (2) spatial position (i.e., river kilometer [RKM]; where RKM 0 is the mouth of the river) for fall- and spring-run Atlantic Sturgeon. Identifying the run-specific environmental factors associated with sturgeon behavior can inform conservation efforts within this system as well as contribute to our understanding of the complex reproductive ecology of the Atlantic Sturgeon throughout its range.

## METHODS

### Study system

The GPD drains approximately 47,600 km$^2$ and is part of the Yadkin–Pee Dee River basin. Originating near Blowing Rock, North Carolina, the upper section of the GPD is impounded by seven reservoirs before continuing undammed for about 300 fluvial kilometers to its mouth at Winyah Bay in Georgetown, South Carolina (Figure 1). Atlantic Sturgeon have been documented as far upstream as the tailrace of Blewett Falls Dam, North Carolina, at RKM 302 (Figure 1). However, detection of Atlantic Sturgeon at Blewett Falls Dam was the result of a single incident in 2018 after the landfall of Hurricane Florence. Although dam operations affect hydrology and temperature in the GPD, the vast majority of Atlantic Sturgeon terminate their migrations much further downstream, where river conditions are in a more natural state. The GPD supported the largest commercial gill-net fishery for Atlantic Sturgeon in the Southeast from 1870 until 1985, when South Carolina enacted a harvest moratorium (Smith et al. 1984; NMFS 2007). Little is known about spawning movements in this river, but genetic evidence and collection of juvenile Atlantic Sturgeon suggest that recruitment is occurring in the GPD for both spring and fall runs (Post et al. 2014; White et al. 2021).

### Fish capture

Atlantic Sturgeon were captured beginning in 2016 by personnel from the South Carolina Department of Natural Resources (SCDNR) Diadromous Fishes Section. Sturgeon were captured via anchored gill nets that were 45.7 m long, with a stretched mesh size between 30.5 and 35.6 cm. Nets were set from February through mid-March and again in mid-September through October of each year in an effort to capture adult Atlantic Sturgeon from both the spring and fall spawning runs. Since telemetry data suggested that Winyah Bay is an important aggregation area for multiple Atlantic Sturgeon populations (Post et al. 2014), netting efforts focused on upriver locations in areas where fish of target size were expected to be attempting upriver migrations (Figure 1). The area near the confluence of the GPD and the Little Pee Dee River (~RKM 53) is one of these locations and is characterized by many river bends and small tributaries that help to create areas of backflow (Figure 1).
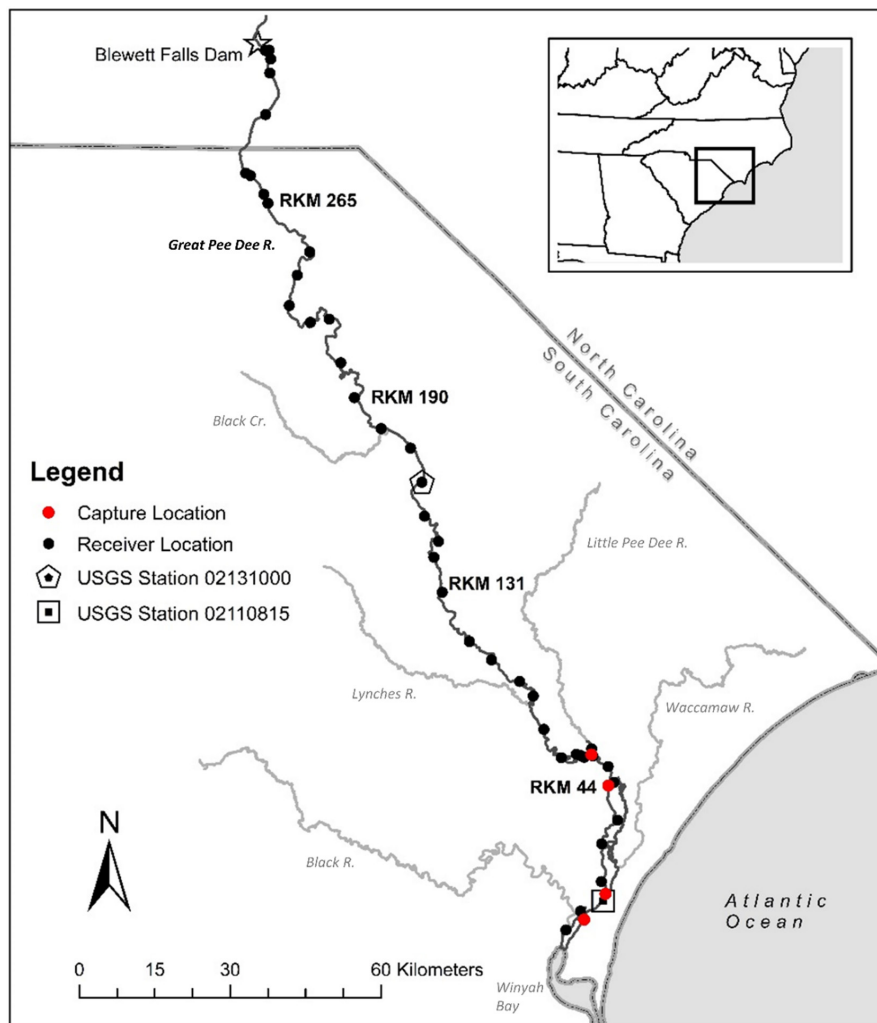
**FIGURE 1** The Great Pee Dee River of North Carolina and South Carolina, USA, including major sub-tributaries and the acoustic receiver array maintained by the South Carolina Department of Natural Resources. The map includes receiver locations; locations where Atlantic Sturgeon were captured and implanted with transmitters; U.S. Geological Survey (USGS) station 02131000, where discharge records were collected; USGS station 02110815, where temperature records were collected; and labels indicating the position of selected receivers (river kilometer [RKM]) relative to the mouth of the river at Winyah Bay in Georgetown, South Carolina.

Upon capture, Atlantic Sturgeon were placed in an onboard live well and were allowed to recover. All fish were measured (total length, fork length [FL], and girth) and weighed. Sex was also recorded if gametes were visible (running ripe males; visibly present eggs in females). Sturgeon that were of suitable size and condition to represent putatively spawning individuals (>1500 mm FL) were surgically implanted with Innovasea V16 69-kHz acoustic transmitters. These tags measure $68 \times 16$ mm, weigh 34 g, and have a battery life of up to 10 years. Other adult sturgeon larger than 1200 mm FL that were thought to be making spawning migrations were tagged opportunistically. In accordance with guidelines set forth by the National Marine Fisheries Service (NMFS)-issued Biological Opinion (NMFS Consultation Number SER-2009-5521), gravid females were not implanted with transmitters unless eggs were noticed after an initial incision was made.

## Telemetry

We monitored movements of spring- and fall-run Atlantic Sturgeon in the main-stem GPD from January 2018 to December 2021. Movement data were obtained via a stationary array of about 40 Innovasea VR2W 69-kHz receivers (Figure 1). Receivers were located approximately every 5–20 km from the mouth of the GPD in Winyah Bay upstream to the Blewett Falls Dam tailrace in North Carolina (Figure 1). Data were retrieved at least four times per year and were exported via Innovasea VUE software. Sturgeon that were captured and implanted

with transmitters by researchers in other river systems and that made movements up the GPD were also included in our analysis. Telemetry data collected from a sturgeon during the same year in which that individual was captured were excluded from that year's analysis to avoid potential negative impacts of capture on spawning behavior.

## Abiotic variables

Water temperature and discharge data were analyzed for their effect on sturgeon movement. We chose to obtain data from two U.S. Geological Survey (USGS) stations based on the availability of long-term data. Daily water temperature (°C) records were obtained from USGS station 02110815 near RKM 12, located roughly near the confluence of the GPD and the Waccamaw River. Daily discharge ($m^3$/s) records were obtained from USGS station 02131000 near RKM 190 because this is the downstream-most non-tidally influenced USGS station in the GPD for which discharge data were available. Because sturgeon are expected to respond to changes in discharge and temperature during spawning migrations (Forsythe et al. 2012; Vine et al. 2019; Moore et al. 2021), we chose to include metrics indexing the change in daily mean values of temperature and discharge over 24-h periods. Photoperiod, measured as day length in hours, was obtained from the Geosphere package in R version 3.5.4 (Hijmans 2021; R Core Team 2022). However, this variable was ultimately removed from analyses due to high collinearity with water temperature ($r = 0.84$).

## Statistical analysis

Our analytical approach closely followed that of Vine et al. (2019), who quantified environmental cues for sturgeon migration movements in the Savannah River of South Carolina and Georgia. We used mixed-effects linear models to estimate the effects of our environmental variables on two complementary response variables describing (1) the timing of putative spawning migrations and (2) spatial position within putative spawning migrations. To calculate our response variables, we first summarized daily detections representing the upstream-most detection of each fish for each day; an individual's last known position was carried forward until its next detection. We then calculated a binary response variable indicating whether a fish was engaged in a putative spawning migration based on that individual's position (RKM) and movement direction (upstream) in the river. Sturgeon that were detected above RKM 44 were considered to be attempting

a putative spawning migration, as preliminary analysis indicated that (1) once sturgeon ascended past RKM 44, they did not return downstream without further upriver movement; and (2) sturgeon stayed below RKM 44 outside of the spawning seasons. Individuals upstream of RKM 44 were considered to be engaged in putative spawning migrations until the date on which they reached their upstream-most detection in the river. For the purpose of our analysis, individuals moving downstream after the date on which they reached their upstream-most detection were not considered to be engaged in a spawning migration. In addition, we calculated a continuous response variable indexing sturgeon movement within putative spawning migrations. This variable was simply the daily spatial position of sturgeon (RKM) given that they were engaged in a putative spawning migration.

We constructed a total of four mixed-effects models to estimate the effects of environmental variables on spawning initiation and spatial position within the river for each spawning run. Because we expected the effects of environmental variables on sturgeon movement to be season specific, data were split into two groups for analysis, reflecting each spawning run. Sturgeon that reached their upstream-most detection prior to June 15 were considered spring-run fish, and sturgeon that reached their upstream-most detection after this date were considered fall-run fish. The binary spawning indicator was modeled as a random binomial variable (generalized linear mixed model [GLMM]), and the continuous response variable indicating spatial position during putative spawning runs was modeled as a random normal variable (linear mixed model [LMM]). All models were run using the glmmTMB package (Brooks et al. 2017) in R. Random intercepts of individual identity and year were included in all four models. An offset term representing the migration indicator and the RKM of the most recent detection was used to account for temporal autocorrelation in spawning phenology. Each model contained four main effects indexing daily water temperature, daily discharge, 24-h change in daily water temperature, and 24-h change in daily discharge. Since telemetry data from the GPD suggested that Atlantic Sturgeon initiate spring migrations when temperatures are rising and initiate fall migrations when temperatures are declining (Post et al. 2014), we used maximum daily water temperature in models for spring-run fish and minimum daily water temperature in models for fall-run fish. Maximum daily discharge was included in all models. In addition, we allowed each discharge variable to interact with each temperature variable in all models. Incorporating the interaction effects allowed us to determine whether the effect of any one variable on migratory behavior was dependent on the value of another variable. Effects were considered significant if standardized parameter estimates with 95%

confidence intervals (CIs) did not overlap zero. Abiotic variables were screened for collinearity using pairwise Pearson correlations ($r < 0.70$) and were standardized to a mean of zero and a standard deviation (SD) of 1.0 prior to analyses. To ensure that model results were meaningful, we compared them against analogous intercept-only (null) models with the same error and random effect structure based on Akaike's information criterion (AIC). Models within 2 AIC units of one another (AIC difference [$\Delta$AIC] < 2) are considered equally plausible (Burnham and Anderson 2002).

## RESULTS

Water temperatures reflected typical seasonal variation, ranging from winter minima of approximately 7°C to summer maxima of approximately 30°C (Figure 2). A notable high-discharge event occurred in fall 2018 after the landfall of Hurricane Florence in North Carolina on September 14, 2018, with discharge peaking at a historic 3737 m$^3$/s. While smaller floods also occurred throughout the course of our study, discharge tended to vary seasonally, with higher flows in winter and lower flows throughout the summer and into the fall (Figure 2).

Tagging efforts resulted in the deployment of 147 acoustic transmitters in adult Atlantic Sturgeon from 2016 to 2021, including 12 females, 71 males, and 64 individuals of unknown sex. Ninety-two percent (135) of these fish were captured between RKM 44 and RKM 66. The remaining 12 fish were captured in the lower reaches of the river system, primarily as a result of opportunistic tagging while sampling for Shortnose Sturgeon *A. brevirostrum*. Tagged Atlantic Sturgeon had a mean FL $\pm$ SD of 164 $\pm$ 19 cm and a mean weight of 40.1 $\pm$ 12.1 kg. In total, 79 tagged sturgeon returned to the GPD in the years after tagging, including 8 females, 39 males, and 32 sturgeon of unknown sex, and made a total of 140 putative spawning migrations

(Table 1). An additional seven Atlantic Sturgeon tagged by other researchers outside of South Carolina made 11 putative spawning runs up the GPD; six of these fish were tagged off the coast of Delaware, and one fish was tagged in the James River, Virginia. Overall, 74 spring migrations and 76 fall migrations spanning 4 years (2018–2021) were included in the analysis.

Spring-run Atlantic Sturgeon initiated putative spawning migrations between late January and mid-February of each year at water temperatures between 8.8°C and 10.8°C and at river discharge levels between 541 and 799 m$^3$/s (Table 1). The spring run completely exited the river by the first week of May each year, when water temperatures had risen to between 20°C and 23°C and when discharge had fallen to 170–368 m$^3$/s (Table 1). The putative fall-run spawning migrations began as early as May, when water temperatures were still rising between 25°C and 30°C. Fall-run sturgeon had completely departed the river between late October and mid-November once water temperatures had fallen to between 14°C and 20°C (Table 1).

Spring and fall runs differed in the spatial extent of putative upstream spawning migrations (Figure 3). Of the 47 individuals attempting 74 spring migrations, sturgeon attained a mean upstream-most RKM $\pm$ 95% CI of 103 $\pm$ 12 (Table 1). In contrast, 39 sturgeon attempting 76 fall migrations attained a mean upstream-most RKM of 168 $\pm$ 9 (Table 1). The temporal duration of putative upriver spawning migrations was similar between runs: spring-run Atlantic Sturgeon spent on average 14 $\pm$ 2 days ($\pm$95% CI) making upriver migrations, while fall-run Atlantic Sturgeon spent on average 16 $\pm$ 3 days making upriver migrations across years (Table 1).

All mixed-effects models achieved adequate fit, with $\Delta$AIC much greater than 2 for each of the four models, relative to the null model (Table A.1). Results from our GLMMs indicated that the main effects of temperature and 24-h change in temperature significantly influenced the probability of migration for both spring- and fall-run
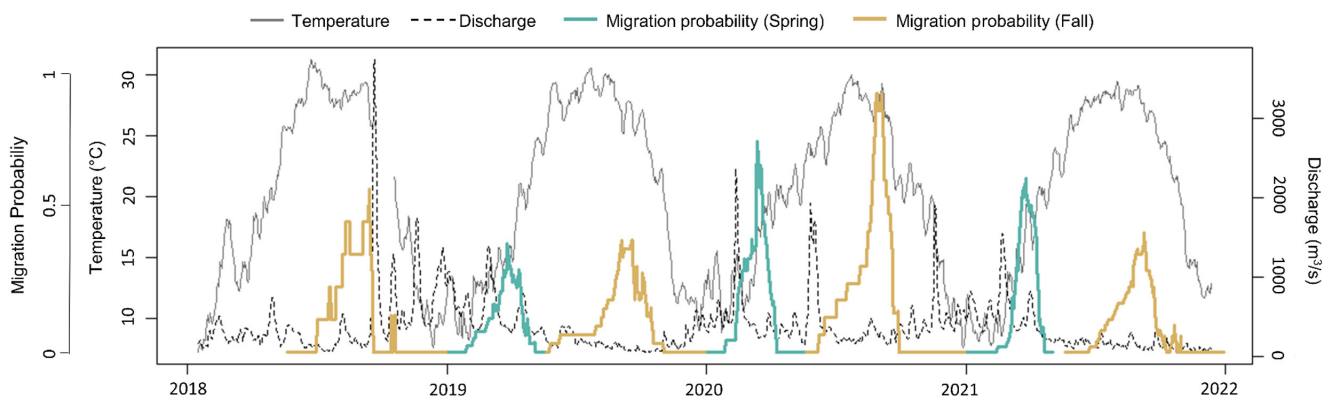


**FIGURE 2** Water temperature (°C) and discharge (m$^3$/s) in the Great Pee Dee River and the migration probability (mean migration indicator value) of Atlantic Sturgeon from January 2018 to December 2021.

**TABLE 1** Atlantic Sturgeon migration statistics by year and season in the Great Pee Dee River, South Carolina, including the number of detected individuals attempting migration ($N$); the mean river kilometer of upstream-most detection for each individual ($RKM_{max}$), with 95% confidence interval (CI); the date on which the first individual exceeded the migration threshold per season (onset date); the date on which all individuals exited the system (departure date); the temperature (Temp; °C) and discharge (m³/s) upon migration and departure; and the duration of individual migration (days with 95% CIs).

| Year | Season | $N$ | $RKM_{max}$ (±95% CI) | Onset date | Temp at onset | Discharge at onset | Departure date | Temp at departure | Discharge at departure | Duration (±95% CI) |
|---|---|---|---|---|---|---|---|---|---|---|
| 2018 | Fall | 8 | 109±41 | Jul 2, 2018 | 30.2 | 125 | Oct 31, 2018 | 15.6 | 583 | 10±9 |
| 2019 | Spring | 10 | 101±19 | Jan 29, 2019 | 8.8 | 799 | Apr 30, 2019 | 22 | 323 | 17±3 |
| | Fall | 19 | 162±25 | May 26, 2019 | 28 | 159 | Nov 13, 2019 | 14.4 | 143 | 14±5 |
| 2020 | Spring | 20 | 105±19 | Jan 28, 2020 | 10.8 | 549 | Apr 30, 2020 | 20.9 | 268 | 12±3 |
| | Fall | 17 | 184±20 | Jun 8, 2020 | 24.8 | 564 | Nov 1, 2020 | 20.1 | 385 | 19±8 |
| 2021 | Spring | 44 | 103±13 | Feb 14, 2021 | 9.2 | 541 | May 4, 2021 | 23.4 | 178 | 13±2 |
| | Fall | 32 | 179±17 | Jun 24, 2021 | 27.5 | 166 | Nov 6, 2021 | 15.5 | 153 | 17±6 |
| All years | Spring | 74 | 103±12 | May 26–Jul 2 | 9.6 | 630 | Oct 31–Nov 13 | 22.1 | 256 | 14±2 |
| | Fall | 76 | 168±9 | Jan 28–Feb 14 | 27.6 | 253 | Apr 30–May 4 | 16.4 | 316 | 16±3 |

Atlantic Sturgeon in the GPD (Figure 4; Table A.2). Temperature positively affected migration probability for both runs, whereas the 24-h change in temperature positively affected migration probability for spring-run Atlantic Sturgeon and negatively affected migration probability for fall-run individuals (Figure 4; Table A.2). Discharge had a significant main effect on migration probability for fall-run Atlantic Sturgeon but not for spring-run sturgeon. The LMMs indicated that the main effect of temperature significantly affected spatial position within spawning migrations for spring-run Atlantic Sturgeon. For fall-run Atlantic Sturgeon, discharge and the 24-h change in temperature significantly affected spatial position within spawning migrations (Figure 4; Table A.2).

Significant interaction effects were observed in three of the four models, indicating that the effects of some variables depended on the effects of others. Temperature and discharge had a significant interaction effect on migration probability for both spring and fall runs, and discharge and 24-h change in temperature had a significant interaction effect on migration probability for the spring run. Temperature and 24-h change in discharge had a significant interaction effect on spatial position for the spring run, whereas no significant interaction effect on spatial position was observed for the fall run (Figure 4; Table A.2). Temperature positively affected migration probability for fall-run Atlantic Sturgeon across all levels of discharge, although increasing levels of discharge decreased the strength of this relationship (Figure 5C). Interaction effects in other models resulted in a reversal of the direction of the relationship between main effects and the response (Figure 5A,B,D). For spring-run Atlantic Sturgeon, temperature negatively affected migration probability at lower levels of discharge but positively affected migration probability at higher levels of discharge (Figure 5A). In the same model, the 24-h change in temperature had a weak negative effect on migration probability when discharge was high, but the 24-h change in temperature had an increasingly positive effect on migration probability as discharge declined (Figure 5B). Temperature positively affected spatial position for spring-run fish when the 24-h change in discharge was negative, whereas temperature negatively affected spatial position when the 24-h change in discharge was positive (Figure 5D).

## DISCUSSION

By using an extensive acoustic telemetry data set and a suite of environmental variables that were hypothesized to affect movement, we were able to describe and identify environmental factors associated with putative upriver spawning movements of Atlantic Sturgeon in the GPD.
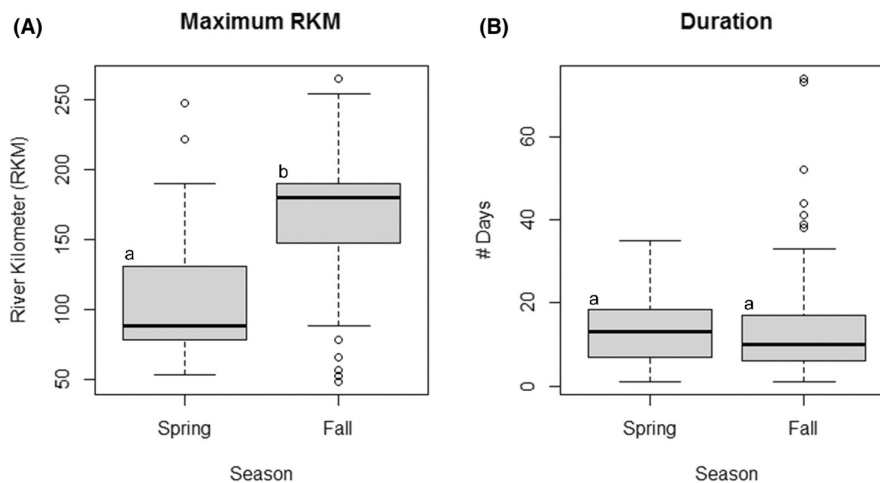
**FIGURE 3** Box plots comparing distributions of (A) the upstream-most detection location (maximum river kilometer [RKM]) and (B) the duration of migration (number of days) for spring- and fall-run Atlantic Sturgeon in the Great Pee Dee River. Plots show medians (lines within boxes), quartiles (box ends), 95th percentiles (whiskers), and outliers (dots). Lowercase letters indicate significant differences in mean values between runs as determined by a two-sample $t$-test ($\alpha = 0.05$).

Our observation of two separate and distinct spawning runs provides baseline knowledge on the migratory behavior of Atlantic Sturgeon in this system. We found that the effects of the environmental variables associated with migration initiation and spatial position were run specific, reflecting differences in ambient river conditions during respective spawning seasons and potentially unique adaptations between the two genetically distinct groups. Identification of significant interactions between environmental variables associated with Atlantic Sturgeon movement offers further insight into the complex and interdependent factors affecting dual-run Atlantic Sturgeon migration.

Spring-run Atlantic Sturgeon engaged in putative spawning migrations from late January to early May, when river discharge declined following winter highs and when water temperature began rising. Accordingly, temperature and the 24-h change in temperature were positively associated with migration probability for spring-run fish. Temperature also had a significant positive effect on movement within spawning migrations, indicating that warming temperatures not only cued migration but also contributed to greater upriver movement given that an individual sturgeon had initiated a spawning run. However, the presence of significant interaction effects indicated that discharge mediated the effect of temperature in cueing migration. Temperature had the greatest effect on migration probability when discharge levels were high, indicating that higher temperature and elevated flow most strongly cued spring spawning migrations. Conversely, temperature was negatively related to migration probability at lower flows, reflecting a tendency of Atlantic Sturgeon to emigrate once flows dropped and temperatures continued to rise. Curiously, we observed a positive relationship between the 24-h change in temperature and migration probability at low and mean flows but a weak negative relationship at higher flows. We might expect increases in daily temperature to initiate migration when flows are highest earlier in the spawning season, but the weak effect of the 24-h change in temperature at high flows ultimately suggests that raw temperature was more important than the change in temperature in cuing migration. For the spatial position of spring-run Atlantic Sturgeon, temperature had a strong positive effect on upriver movement when flows were decreasing and a much weaker effect on upriver movement when flows were rising. This "masking" effect of rising discharge on the effect of temperature indicated that although temperature was most strongly associated with upriver movement for spring-run Atlantic Sturgeon, the greatest upriver movement occurred when higher temperatures coincided with declining flows. It is possible that rising flows represented unnecessary energetic costs to spring-migrating Atlantic Sturgeon, thus resulting in a selection for periods of dropping flows to migrate upriver when temperatures were optimal.

Fall-run Atlantic Sturgeon engaged in putative spawning migrations from May to early November, when temperatures were falling and when river discharge was lowest. The significant negative effects of discharge and the 24-h change in temperature on migration probability reflected the role of low discharge and falling temperatures in cueing migration for the fall run. Temperature had a positive overall effect on migration probability, likely reflecting the emigration of Atlantic Sturgeon as temperatures cooled later in the fall. Furthermore, temperature had the strongest effect on migration probability when discharge was lowest, further emphasizing the
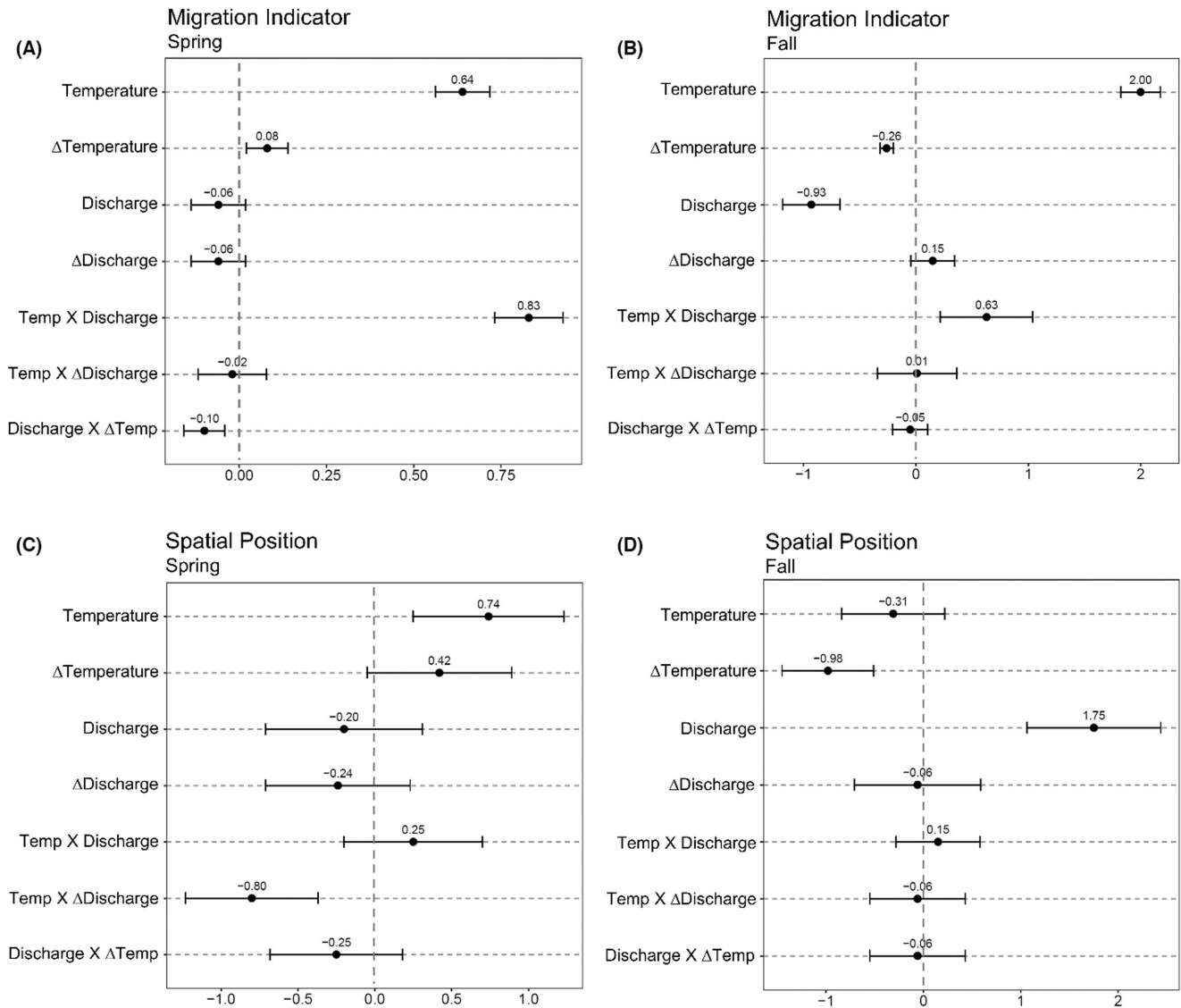
**FIGURE 4** Generalized linear mixed model estimates (with 95% confidence intervals) estimating the effects of temperature (Temp), discharge, 24-h change in temperature (ΔTemperature), 24-h change in discharge (ΔDischarge), and interaction terms on (A), (B) migration probability and (C), (D) spatial position (river kilometer) of spring- and fall-run Atlantic Sturgeon engaged in putative spawning migrations in the Great Pee Dee River. Note that the x-axes are scaled differently to allow for symmetrical paneling. Parameter estimates, standard errors, and null model comparisons are presented in Table A.2.

intersection of higher temperatures and lower flows in cueing fall migration. Within spawning migrations, discharge had a positive effect on upriver movement and the 24-h change in temperature had a negative effect on upriver movement, suggesting that Atlantic Sturgeon moved further upstream during periods of falling temperature and elevated discharge. Our finding that discharge was a significant main effect for fall migratory behavior but not for spring migratory behavior might be attributable to differences in habitat use between the two runs. Fall-run Atlantic Sturgeon migrated further upstream on average than spring-run Atlantic Sturgeon; therefore, flows may play a greater role in affecting the ability of fall-run sturgeon to navigate shallower

upstream habitats. The tendency of fall-run Atlantic Sturgeon to move upriver in response to elevated discharge stands in contrast to the behavior of spring-run Atlantic Sturgeon, for which rising discharge mitigated the effect of temperature on upriver movement. This difference in the effect of discharge on spatial position among runs may be attributed to the hydrological regime of the GPD: higher flows observed during the spring migration may facilitate upriver movement throughout the season, resulting in the selection for periods of falling flows and, therefore, lesser energetic costs to move upriver. Lower flows observed during fall migrations may actually impede upriver movement, especially in the upstream reaches occupied by fall-run Atlantic Sturgeon,
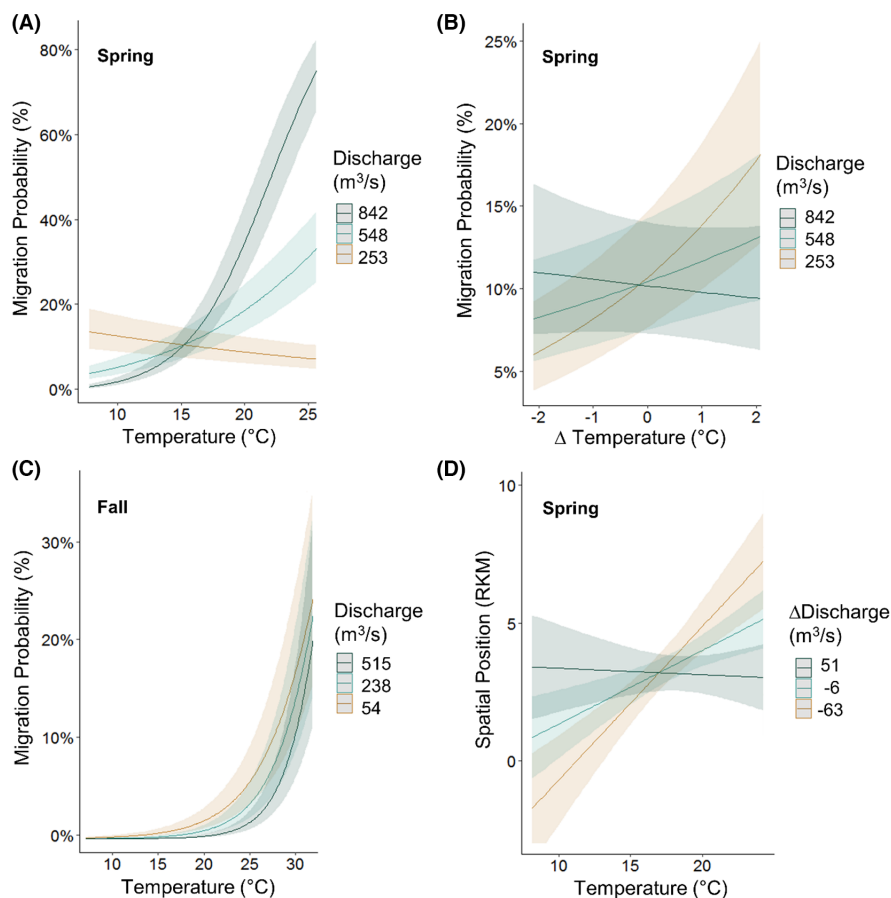
**FIGURE 5** Marginal effects of significant interaction terms on the predicted values of (A)–(C) migration probability or (D) spatial position (river kilometer [RKM]) of spring- or fall-run Atlantic Sturgeon for each model. Parameter estimates for all models are provided in Figure 4 and the Appendix. For each pair of significant interaction terms, model predictions (with 95% confidence intervals) are shown for the independent variable at three levels of the interacting variable: the mean value (orange), the mean plus one standard deviation (green), and the mean minus one standard deviation (red). Note the difference in *y*-axis ranges.

resulting in a selection for periods of higher flows, when upriver movement was possible. Dissolved oxygen is also relatively low in the fall season, and timing the migration with higher flows may increase recruitment success (Greene et al. 2009).

Our results are comparable to those of other studies investigating the migratory behavior of sturgeons. Using an analytical framework similar to the one used in this study, Vine et al. (2019) found that migrations of fall-run Atlantic Sturgeon in the Savannah River of Georgia and South Carolina were affected solely by temperature, and no significant environmental effects were identified for spring-run Atlantic Sturgeon. Although the results of Vine et al. (2019) corroborate our finding that temperature was most closely associated with migration probability for fall-run Atlantic Sturgeon in the GPD, our ability to identify additional factors associated with Atlantic Sturgeon migratory behavior is more likely a result of greater sample size than a reflection of relationships specific to our study system. Studies of other sturgeon species highlight a dominant role of temperature for

initiating migrations. Timing of river entrance by Gulf Sturgeon *A. oxyrinchus desotoi* in the Choctawhatchee and Suwanee rivers of Georgia and Florida is suspected to be determined primarily by temperature (Foster and Clugston 1997; Fox et al. 2000). In a study of spawning movements of Lake Sturgeon *A. fulvescens* in the Black River, Michigan, Forsythe et al. (2012) found that water temperature significantly affected the initiation of spawning migrations and the arrival of fish at spawning sites. Another study in the Osage River, Missouri, indicated that temperature significantly affected the upriver movement of Lake Sturgeon (Moore et al. 2021). Although Forsythe et al. (2012) and Moore et al. (2021) reported additional effects of discharge on Lake Sturgeon migratory behavior and Chapman and Carr (1995) identified a strong correlation between high discharge and initiation of migration for Gulf Sturgeon in the Suwanee River, the effect of discharge on the migratory behavior of sturgeons appears to depend upon the occurrence of optimal migration temperatures. Laboratory tests have found that the critical swim speeds of juvenile Atlantic

Sturgeon are lower than those reported for other sturgeon species (Wilkens et al. 2015), emphasizing a need for more research to understand how discharge affects the ability of Atlantic Sturgeon to complete upriver migrations. The role of temperature in influencing migrations is relatively well understood, but the effects of discharge on migratory behavior of sturgeons appear to be highly varied and system specific. Forsythe et al. (2012) reported a negative effect of higher river discharge on the upriver movement of Lake Sturgeon; this effect was attributed to an increased physiological cost of migrating at higher flows. In contrast, rising discharge was associated with increased upriver movement of Lake Sturgeon in some Osage River tributaries, potentially due to higher flows facilitating movement above anadromous barriers (Moore et al. 2021).

By introducing interaction terms into models, our analyses provided a more nuanced understanding of the effect of discharge on Atlantic Sturgeon migratory behavior and uncovered important differences in the response to discharge between the spring and fall runs of Atlantic Sturgeon. Although discharge on its own was not significantly associated with migratory behavior for spring-run Atlantic Sturgeon in the GPD, discharge significantly interacted with temperature variables in both models. We found that temperature had the strongest effect on spring migration probability when flows were highest and that temperature had the strongest effect on upriver movement when flows were dropping, indicating that higher flows helped cue migration for spring-run Atlantic Sturgeon, but most upriver movement occurred when flows were decreasing. Discharge is typically high in the spring, and a selection for upriver movement during periods of declining flows might conserve energy. Very little migration occurred for spring-run Atlantic Sturgeon under any amount of discharge when temperatures were below 15°C. Additionally, temperatures rose faster in the absence of new high-discharge events. Together, these results emphasize that temperature ultimately "sets the stage" for the effect of discharge on the spring run. For fall-run Atlantic Sturgeon, we observed an opposite role of discharge in influencing fall migrations: lower flows cued migration, and most upriver movement occurred when flows were elevated. Naturally lower flows observed during the fall may have restricted navigability of the river channel by Atlantic Sturgeon in the GPD, thereby influencing fish to move upriver during periods of elevated discharge. Although our results indicate that discharge affects upriver movement of Atlantic Sturgeon in the GPD, the spatial grain of our analysis was large (5–10 km between receivers), and finer-scale data may be needed to more precisely determine the effect of flow conditions on sturgeon movement.

The migrations observed in this study do not provide direct evidence of Atlantic Sturgeon spawning, but the correspondence between water temperature and the timing and extent of migrations indicated that these movements likely reflected attempted spawning migrations. Our results showed that the spring run initiated migrations when water temperatures were between 8°C and 11°C, and spring-run sturgeon completely exited the river once temperatures rose to 21–23°C. The fall run initiated migrations at higher temperatures (25–30°C) and mostly departed the river once temperatures fell to 14–16°C (20°C in fall 2020). Although the optimal temperature range for reproduction is not well understood and appears to vary across the species' range, spawning temperatures ranging from 13°C to 26°C have been reported in rivers from Georgia to Canada (Smith 1985; Dadswell 2006; Whippelhauser et al. 2017). In the nearby Edisto River, South Carolina, Atlantic Sturgeon in spawning condition were collected as early as March, when temperatures were 13.6°C, and again in September and October, when temperatures were 17–18°C (Collins et al. 2000). The Edisto River is unique in that it is entirely unimpounded and experiences a relatively unaltered flow and thermal regime. Water temperatures that were expected to be conducive to spawning success were thus mostly contained within observed migration seasons.

Timing of Atlantic Sturgeon spawning movements varies clinally along the East Coast (Hilton et al. 2016). Spring and summer spawning migrations are well documented north of the Chesapeake Bay (Bain 1997; Caron et al. 2002; Whippelhauser et al. 2017; Breece et al. 2021), and fall spawning migrations are known to occur in systems from Georgia to Virginia (Balazik et al. 2012; Hager et al. 2014; Smith et al. 2015; Ingram and Peterson 2016). Telemetry data indicate that dual spawning (both spring and fall) occurs in several systems within the South Atlantic DPS (Collins et al. 2000; McCord et al. 2007; Vine et al. 2019) and the Carolina DPS (Balazik et al. 2012; Balazik and Musick 2015). Furthermore, genetic studies have discovered genetically distinct spring and fall spawning runs in river systems including the Edisto, Savannah, James, and Ogeechee rivers and the GPD (Balazik et al. 2017; Farrae et al. 2017; White et al. 2021). Our observation of two separate and distinct annual spawning migrations of Atlantic Sturgeon in the GPD adds to the growing list of rivers with dual spawning migrations and supports the hypothesis that dual spawning may be more widespread than previously thought (Balazik and Musick 2015). Ingram and Peterson (2016) notably did not observe dual spawning in the Altamaha River, Georgia, and more data are needed to understand the prevalence of dual spawning across the range of Atlantic Sturgeon. Documentation of separate spring and fall spawning runs

in more rivers will also be important for understanding evolutionary relationships among populations (White et al. 2021). Our finding that fall-run Atlantic Sturgeon moved further upstream on average than spring-run Atlantic Sturgeon corroborates the pattern observed in the James River by Balazik and Musick (2015). Differences in habitat use among runs may help to explain why dual spawning has historically been poorly documented, and these differences also suggest that vulnerability to threats such as habitat degradation differs among runs.

A greater understanding of the factors initiating and promoting upriver movement of sturgeons has important implications for species recovery efforts. We found that temperature and discharge significantly affected putative upriver spawning migrations of both spring- and fall-run Atlantic Sturgeon in the GPD. These findings suggest that shifts in weather patterns as a result of climate change may influence migratory behavior in our study area. Although our analyses are correlative and not predictive, the data presented here can be used to develop predictive models forecasting the effect of climate change on the timing of spawning migrations (e.g., Breece et al. 2013). Our study also highlights the importance of considering interactions between environmental variables when estimating how they affect sturgeon movement. Temperature was the dominant factor constraining putative spawning migrations in the GPD, but discharge mediated the effect of temperature in the majority of models. Differences in the environmental factors that support—and thereby limit—migrations among runs highlight the importance of studying and managing Atlantic Sturgeon at the population level. The tendency for fall-run fish to move upriver when flows were rising and for spring-run fish to move upriver when flows were dropping suggests that flow pulses may facilitate migration, although more research is needed to better understand the fine-scale movements of Atlantic Sturgeon in response to discharge. Many rivers supporting sturgeon populations are dammed, including the GPD, and directed management of river flows during periods of optimal migration temperatures might help to ensure that the sturgeon reach suitable spawning habitat (e.g., U.S. Fish and Wildlife Service 2008; Vine et al. 2019). Ultimately, the spatial grain of our analysis was large (receivers were spaced 5–20 km apart), and future studies investigating fine-scale movements will be needed to better understand riverine habitat use and residency (e.g., Breece et al. 2018).

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## CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT
Data used in this work can be requested to the South Carolina Department of Natural Resources Marine Resources Research Institute.

## ETHICS STATEMENT
All netting procedures adhered to strict guidelines provided by the NMFS-issued Biological Opinion (NMFS Consultation Number SER-2009-5521).

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## REFERENCES
Atlantic States Marine Fisheries Commission. (1998). *Amendment 1 to the interstate fishery management plan for Atlantic Sturgeon.* (Fishery Management Report 31). Atlantic States Marine Fisheries Commission. http://www.asmfc.org/uploads/file/sturgeonAmendment1.pdf

Atlantic States Marine Fisheries Commission. (2017). *Atlantic Sturgeon benchmark stock assessment and peer review report.* Atlantic States Marine Fisheries Commission. http://www.asmfc.org/species/atlantic-sturgeon.

Auer, N. A. (1996). Importance of habitat and migration to sturgeons with emphasis on Lake Sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 152–160. https://doi.org/10.1139/f95-276

Bain, M. B. (1997). Atlantic and Shortnose sturgeons of the Hudson River: Common and divergent life history attributes. *Environmental Biology of Fishes*, *48*, 347–358. https://doi.org/10.1023/A:1007325814893

Balazik, M. T., Farrae, D. J., Darden, T. L., & Garman, G. C. (2017). Genetic differentiation of spring-spawning and fall-spawning male Atlantic Sturgeon in the James River, Virginia. *PLOS ONE*, *12*(7), Article e0179661. https://doi.org/10.1371/journal.pone.0179661

Balazik, M. T., & Musick, J. A. (2015). Dual annual spawning races in Atlantic Sturgeon. *PLOS ONE*, *10*(5), Article e0128234. https://doi.org/10.1371/journal.pone.0128234

Balazik, M. T., Reine, K. J., Spells, A. J., Fredrickson, C. A., Fine, M. L., Garman, G. C., & McIninch, S. P. (2012). The potential for vessel interactions with adult Atlantic Sturgeon in the James River, Virginia. *North American Journal of Fisheries Management*, *32*(6), 1062–1069. https://doi.org/10.1080/02755 947.2012.716016

Breece, M. W., Fox, D. A., & Oliver, M. J. (2018). Environmental drivers of adult Atlantic Sturgeon movement and residency in the Delaware Bay. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *10*(2), 269–280. https://doi.org/10.1002/mcf2.10025

Breece, M. W., Higgs, A. L., & Fox, D. A. (2021). Spawning intervals, timing, and riverine habitat use of adult Atlantic Sturgeon in the Hudson River. *Transactions of the American Fisheries Society*, *150*(4), 528–537. https://doi.org/10.1002/tafs.10304

Breece, M. W., Oliver, M. J., Cimino, M. A., & Fox, D. A. (2013). Shifting distributions of adult Atlantic Sturgeon amidst post-industrialization and future impacts in the Delaware River: A maximum entropy approach. *PLOS ONE*, *8*(11), Article e81321. https://doi.org/10.1371/journal.pone.0081321

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*, 378–400. https://doi.org/10.32614/RJ-2017-066

Brown, J. J., & Murphy, G. W. (2010). Atlantic Sturgeon vessel-strike mortalities in the Delaware Estuary. *Fisheries*, *35*(2), 72–83. https://doi.org/10.1577/1548-8446-35.2.72

Burnham, K. P., & Anderson, D. R. (Eds.). (2002). *Model selection and multimodel inference: A practical-theoretic approach* (2nd ed.). Springer. https://doi.org/10.1007/b97636

Caron, F., Hatin, D., & Fortin, R. (2002). Biological characteristics of adult Atlantic Sturgeon in the St Lawrence River estuary and the effectiveness of management rules. *Journal of Applied Ichthyology*, *18*(4–6), 580–585. https://doi.org/10.1046/j.1439-0426.2002.00416.x

Chapman, F. A., & Carr, S. H. (1995). Implications of early life stages in the natural history of the Gulf of Mexico Sturgeon, *Acipenser oxyrinchus des otoi*. *Environmental Biology of Fishes*, *43*, 407–413. https://doi.org/10.1007/BF00001178

Collins, M. R., Smith, T. I. J., Post, W. C., & Pashuk, O. (2000). Habitat utilization and biological characteristics of adult Atlantic Sturgeon in two South Carolina rivers. *Transactions of the American Fisheries Society*, *129*(4), 982–988. https://doi.org/10.1577/1548-8659(2000)129<0982:HUABCO>2.3.CO;2

Dadswell, M. J. (2006). A review of the status of Atlantic Sturgeon in Canada, with comparisons to populations in the United States and Europe. *Fisheries*, *31*(5), 218–229. https://doi.org/10.1577/1548-8446(2006)31[218:AROTSO]2.0.CO;2

Farrae, D. J., Post, W. C., & Darden, T. L. (2017). Genetic characterization of Atlantic Sturgeon, *Acipenser oxyrinchus oxyrinchus*, in the Edisto River, South Carolina and identification of genetically discrete fall and spring spawning. *Conservation Genetics*, *18*, 813–823. https://doi.org/10.1007/s10592-017-0929-7

Flowers, H. J., & Hightower, J. E. (2015). Estimating sturgeon abundance in the Carolinas using side-scan sonar. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *7*(1), 1–9. https://doi.org/10.1080/19425 120.2014.982334

Forsythe, P. S., Scribner, K. T., Crossman, J. A., Ragavendran, A., Baker, E. A., Davis, C., & Smith, K. K. (2012). Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in Lake Sturgeon *Acipenser fulvescens*. *Journal of Fish Biology*, *81*(1), 35–53. https://doi.org/10.1111/j.1095-8649.2012.03308.x

Foster, A. M., & Clugston, J. P. (1997). Seasonal migration of Gulf Sturgeon in the Suwannee River, Florida. *Transactions of the American Fisheries Society*, *126*(2), 302–308. https://doi.org/10.1577/1548-8659(1997)126<0302:SMOGSI>2.3.CO;2

Fox, D. A., Hightower, J. E., & Parauka, F. M. (2000). Gulf Sturgeon spawning migration and habitat in the Choctawhatchee River system, Alabama–Florida. *Transactions of the American Fisheries Society*, *129*(3), 811–826. https://doi.org/10.1577/1548-8659(2000)129<0811:GSSMAH>2.3.CO;2

Geist, J. (2011). Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators*, *11*(6), 1507–1516. https://doi.org/10.1016/j.ecolind.2011.04.002

Greene, K. E., Zimmerman, J. L., Laney, R. W., & Thomas-Blate, J. C. (2009). *Atlantic Coast diadromous fish habitat: A review of utilization, threats, recommendations for conservation, and research needs* (Habitat Management Series No. 9). Atlantic States Marine Fisheries Commission. https://tethys.pnnl.gov/sites/default/files/publications/Greene_et_al_2009.pdf

Hager, C. H., Kahn, J., Watterson, J. C., Russo, J., & Hartman, K. (2014). Evidence of Atlantic Sturgeon spawning in the York River system. *Transactions of the American Fisheries Society*, *143*(5), 1217–1219. https://doi.org/10.1080/00028487.2014.925971

Hager, C. H., Watterson, J. C., & Kahn, J. E. (2020). Spawning drivers and frequency of endangered Atlantic Sturgeon in the York River system. *Transactions of the American Fisheries Society*, *149*(4), 474–485. https://doi.org/10.1002/tafs.10241

Hijmans, R. J. (2021). *geosphere: Spherical trigonometry* (R Package Version 1.5-14) [Computer software]. https://cran.r-project.org/package=geosphere

Hilton, E. J., Kynard, B., Balazik, M. T., Horodysky, A., & Dillman, C. B. (2016). Review of the biology, fisheries, and conservation status of the Atlantic Sturgeon, (*Acipenser oxyrinchus*, *oxyrhinchus* Mitchell, 1815). *Journal of Applied Ichthyology*, *32*(supp 1), 30–66. https://doi.org/10.1111/jai.13242

Ingram, E. C., & Peterson, D. L. (2016). Annual spawning migration of adult Atlantic Sturgeon in the Altamaha River, Georgia. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *8*(1), 595–606. https://doi.org/10.1080/19425 120.2016.1243599

Jelks, H. L., Walsh, S. J., Burkhead, N. M., Contreras- Balderas, S., Diaz-Pardo, E., Hendrickson, D. A., Lyons, J., Mandrak, N. E., McCormick, F., Nelson, J. S., Platania, S. P., Porter, B. A., Renaud, C. B., Schmitter-Soto, J. J., Taylor, E. B., & Warren, M. L., Jr. (2008). Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, *33*(8), 372–407. https://doi.org/10.1577/1548-8446-33.8.372

Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *Bioscience*, *59*(11), 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Markin, E. L., & Secor, D. H. (2020). Growth of juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in response to dual-season spawning and latitudinal thermal regimes. *U.S. National Marine Fisheries Service Fishery Bulletin*, *118*(1), 74–87. https://doi.org/10.7755/FB.118.1.7

McCord, J. W., Collins, M. R., Post, W. C., & Smith, T. I. J. (2007). Attempts to develop an index of abundance for age-1 Atlantic Sturgeon in South Carolina, USA. In J. Munro, D. Hatin, J. E. Hightower, K. A. McKown, K. J. Sulak, A. W. Kahnle, & F. Caron (Eds.), *Anadromous sturgeons: habitats, threats, and management* (Symposium 56, pp. 397–403). American Fisheries Society.

Moore, M. J., Paukert, C. P., Brooke, B. L., & Moore, T. L. (2021). Lake Sturgeon seasonal movements in regulated and unregulated Missouri River tributaries. *Ecohydrology*, *15*(1), Article e2362. https://doi.org/10.1002/eco.2362

National Marine Fisheries Service. (2007). Status review of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*). Atlantic Sturgeon Status Review Team. https://repository.library.noaa.gov/view/noaa/16197

National Oceanic and Atmospheric Administration. (2012). Endangered and threatened wildlife and plants; threatened and endangered status for distinct population segments of Atlantic sturgeon in the northeast region, final rule. *Federal Register*, *77*(24), 5880–5912. https://www.federalregister.gov/d/2012-1946

Peterson, D. L., Schueller, P., DeVries, R., Fleming, J., Grunwald, C., & Wirgin, I. (2008). Annual run size and genetic characteristics of Atlantic Sturgeon in the Altamaha River, Georgia. *Transactions of the American Fisheries Society*, *137*(2), 393–401. https://doi.org/10.1577/T06-231.1

Pikitch, E. K., Doukakis, P., Lauck, L., Chakrabarty, P., & Erickson, D. L. (2005). Status, trends, and management of sturgeon and paddlefish fisheries. *Fish and Fisheries*, *6*(3), 233–265. https://doi.org/10.1111/j.1467-2979.2005.00190.x

Post, W. C., Darden, T., Peterson, D. L., Loeffler, M., & Collier, C. (2014). *Research and management of endangered and threatened species in the southeast: Riverine movements of Shortnose and Atlantic sturgeon* (Final Report Project NA10NMF4720036). South Carolina Department of Natural Resources.

R Core Team. (2022). *A language and environment for statistical computing*. R Foundation for Statistical Computing.

Scott, W. B., & Crossman, E. J. (1973). *Freshwater fishes of Canada* (Bulletin 184). Fisheries Research Board of Canada. https://publications.gc.ca/site/eng/9.870340/publication.html

Secor, D. H., O'Brien, M. H. P., Coleman, N., Horne, A., Park, I., Kazyak, D. C., Bruce, D. G., & Stence, C. (2022). Atlantic Sturgeon status and movement ecology in an extremely small spawning habitat: The Nanticoke River-Marshyhope Creek, Chesapeake Bay. *Reviews in Fisheries Science & Aquaculture*, *30*(2), 195–214. https://doi.org/10.1080/23308249.2021.1924617

Secor, D. H., O'Brien, M. H. P., Gahagan, B. I., Fox, D. A., Higgs, A. L., & Best, J. E. (2020). Multiple spawning run contingents and population consequences in migratory Striped Bass *Morone saxatilis*. *PLOS ONE*, *15*(11), Article e0242797. https://doi.org/10.1371/journal.pone.0242797

Smith, J. A., Flowers, H. J., & Hightower, J. E. (2015). Fall spawning of Atlantic Sturgeon in the Roanoke River, North Carolina. *Transactions of the American Fisheries Society*, *144*(1), 48–54. https://doi.org/10.1080/00028487.2014.965344

Smith, T. I. J. (1985). The fishery, biology, and management of Atlantic Sturgeon, *Acipenser oxyrinchus*, in North America. *Environmental Biology of Fishes*, *14*, 61–72. https://doi.org/10.1007/BF00001577

Smith, T. I. J., Marchette, D. E., & Ulrich, G. F. (1984). The Atlantic Sturgeon fishery in South Carolina. *North American Journal of Fisheries Management*, *4*(2), 164–176. https://doi.org/10.1577/1548-8659(1984)4<164:TASFIS>2.0.CO;2

U.S. Fish and Wildlife Service. (2008). *Biological opinion on the U.S. Army Corps of Engineers, Mobile District, revised interim operating plan for Jim Woodruff Dam and the associated releases to the Apalachicola River*. U.S. Fish and Wildlife Service.

Van Eenennaam, J. P., & Doroshov, S. I. (1998). Effects of age and body size on gonadal development of Atlantic Sturgeon. *Journal of Fish Biology*, *53*(3), 624–637. https://doi.org/10.1111/j.1095-8649.1998.tb01006.x

Vine, J. R., Holbrook, S. C., Post, W. C., & Peoples, B. K. (2019). Identifying environmental cues for Atlantic Sturgeon and Shortnose Sturgeon spawning migrations in the Savannah River. *Transactions of the American Fisheries Society*, *148*(3), 671–681. https://doi.org/10.1002/tafs.10163

Whippelhauser, G. S., Sulikowski, J., Zydlewski, G. B., Altenritter, M. A., Kieffer, M., & Kinnison, M. T. (2017). Movements of Atlantic Sturgeon of the Gulf of Maine inside and outside of the geographically defined distinct population segment. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *9*(1), 93–107. https://doi.org/10.1080/19425120.2016.1271845

White, S. L., Kazyak, D. C., Darden, T. L., Farrae, D. J., Lubinski, B. A., Johnson, R. L., Eackles, M. S., Balazik, M. T., Brundage, H. M., III, Fox, A. G., Fox, D. A., Hager, C. H., Kahn, J. E., & Wirgin, I. I. (2021). Establishing a microsatellite genetic baseline for north American Atlantic Sturgeon (*Acipenser o. oxyrhinchus*) and range-wide analysis of population genetics. *Conservation Genetics*, *22*, 977–992. https://doi.org/10.1007/s10592-021-01390-x

Wilkens, J. L., Katzenmeyer, A. W., Hahn, N. M., Hoover, J. J., & Suedel, B. C. (2015). Laboratory test of suspended sediment effects on short-term survival and swimming performance of juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*, Mitchill, 1815). *Journal of Applied Ichthyology*, *31*(6), 984–990. https://doi.org/10.1111/jai.12875

Winemiller, K. O. (2005). Life history strategies, population regulation, and their implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(4), 872–885. https://doi.org/10.1139/f05-040

Wirgin, I., Fox, A. G., Maceda, L., & Waldman, J. (2023). Two distinct life history strategies of Atlantic Sturgeon in the Ogeechee River, Georgia. *Diversity*, *15*(3), Article 325. https://doi.org/10.3390/d15030325

# APPENDIX: ADDITIONAL DATA

**TABLE A.1** Akaike's information criterion (AIC) values for mixed-effects models predicting environmental effects on migration initiation (binomial) or spatial position in the river (continuous; river kilometer) for spring- and fall-run Atlantic Sturgeon in the Great Pee Dee River from 2018 to 2021. Fully parameterized models (Figure 5) were compared to null models with the same random error structure but with only a single fixed intercept. The AIC difference (ΔAIC) represents the difference in AIC between the parameterized model and the null model. Models with ΔAIC values less than 2 are considered equally plausible (Burnham and Anderson 2002).

| Season | Variable | Parameterized model AIC | Null model AIC | ΔAIC |
|---|---|---|---|---|
| Fall | Migration indicator | 6404 | 9263 | 2859 |
| Fall | Spatial position in river | 7642 | 12,956 | 5314 |
| Spring | Migration indicator | 14,003 | 17,237 | 3234 |
| Spring | Spatial position in river | 17,273 | 23,490 | 6217 |

**TABLE A.2** Results of mixed-effects regression models (regression coefficients and standard errors [SE]) predicting environmental effects on migration initiation (binomial) or spatial position in the river (continuous; river kilometer) for spring- and fall-run Atlantic Sturgeon in the Great Pee Dee River from 2018 to 2021 (ΔTemperature = 24-h change in temperature; ΔDischarge = 24-h change in discharge). Estimates shown in bold are statistically significant at the 95% confidence level.

| | Migration indicator | | | | Spatial position in river | | | |
| | Spring | | Fall | | Spring | | Fall | |
| Variable | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
|---|---|---|---|---|---|---|---|---|
| Temperature | **0.64** | **0.04** | **2.00** | **0.09** | **0.74** | **0.25** | −0.31 | 0.27 |
| ΔTemperature | **0.08** | **0.03** | **−0.26** | **0.03** | 0.42 | 0.24 | **−0.98** | **0.24** |
| Discharge | −0.06 | 0.04 | **−0.93** | **0.13** | −0.20 | 0.26 | **1.75** | **0.35** |
| ΔDischarge | −0.06 | 0.04 | 0.15 | 0.10 | −0.24 | 0.24 | −0.06 | 0.33 |
| Temperature × Discharge | **0.83** | **0.05** | **0.63** | **0.21** | 0.25 | 0.23 | 0.15 | 0.22 |
| Temperature × ΔDischarge | −0.02 | 0.05 | 0.01 | 0.18 | **−0.80** | **0.22** | −0.06 | 0.25 |
| ΔTemperature × Discharge | **−0.10** | **0.03** | −0.05 | 0.08 | −0.25 | 0.22 | −0.06 | 0.25 |