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Using Side-Scan Sonar and *N*-Mixture Modeling to Estimate Atlantic Sturgeon Spawning Migration Abundance

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Abstract

Understanding the relationship between number of spawners and recruitment is essential for managing fish populations. Atlantic Sturgeon *Acipenser oxyrinchus* (ATS) are endangered anadromous fish inhabiting the rivers, estuaries, and marine environments along the Atlantic coast of North America. Atlantic Sturgeon are periodic life history strategists that exhibit both spring and fall spawning migrations. Traditional capture–mark–recapture techniques can be used to estimate spawning run abundance but are resource intensive and potentially stressful on migrating individuals. Noninvasive methods, such as side-scan sonar, can be a less stressful alternative to estimating abundance. We sampled the uppermost portion of the Savannah River, USA, over 50 occasions from August to November 2017 using side-scan sonar. Bayesian *N*-mixture modeling was used to estimate spawner abundance and covariate effects based on spatially and temporally replicated count data obtained from sonar recordings. We detected at least one ATS on each sampling occasion and estimated a maximum daily spawner abundance between 35 and 55 individuals (95% credible interval) within the sampled area during the 2017 fall spawning season. Maximum discharge significantly affected ATS detection, and site average maximum depth significantly affected ATS abundance. Our results suggest that side-scan sonar can be used as an alternative to traditional mark–recapture techniques for spawner abundance estimation. Routine sampling by using our methods will efficiently produce spawning run estimates and provide insight regarding the effects of environmental covariates on spawner abundance seasonally.

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Diadromous fishes are susceptible to numerous threats, including habitat fragmentation and alteration, exploitation, pollution, and climate change (Limburg and Waldman 2009). As periodic life history strategists (high fecundity, slow generation time, and low juvenile survivorship), sturgeons (Actinopterygii: Acipenseridae) are particularly vulnerable (Musick 1999; Winemiller 2005) and have suffered extirpations in many rivers around the world (Birstein 1993; Billard and Lecointre 2000; Lenhardt et al. 2006). Atlantic Sturgeon *Acipenser oxyrinchus* (ATS) inhabit rivers, estuaries, and marine environments along the Atlantic coast of North America from the Saint John's River, Florida, USA, to the St. John River, Canada (Smith and Clugston 1997; Dadswell 2006). Atlantic Sturgeon are separated into five distinct population segments (DPSs): Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (Hilton et al. 2016). The Gulf of Maine DPS is federally listed as threatened in the USA, while the other four DPSs are listed as endangered. Because ATS populations from each DPS mix in nearshore and offshore habitats outside of spawning seasons, population monitoring efforts in every river system where spawning occurs are necessary to make appropriate management decisions for protection of ATS rangewide.

Understanding the relationship between the number of spawners and recruitment is essential for managing fish populations; this requires routine standardized monitoring of spawning run size and juvenile abundance. Sturgeon spawning run sizes have been estimated in several rivers (Auer and Baker 2007; Peterson et al. 2008; Kahn et al. 2014, 2019; Comer 2017), but many rivers remain unassessed. Among those is the Savannah River, which forms the border between the states of Georgia and South Carolina, USA. Atlantic Sturgeon recruitment in the Savannah River has been estimated (Bahr and Peterson 2016), and the addition of seasonal standardized sampling of spawner abundance will contribute to our knowledge of the ATS population dynamics in this river. The Savannah River is a highly modified system containing five successive reservoirs and an industrialized harbor. Throughout their life span, ATS use the entire portion of the Savannah River between the estuary and the first barrier to upstream migration—the New Savannah Bluff Lock and Dam (NSBLD), located 300 fluvial kilometers upstream of the estuary (Figure 1). Juvenile, subadult, and adult ATS in the system are primarily threatened by habitat degradation but are also susceptible to boat strikes and dredging operations in the Savannah Harbor.

In the past, ATS run estimates have been generated by using traditional capture–mark–recapture methods (Peterson et al. 2008; Kahn et al. 2014). This approach requires capture via gill nets, which can be stressful on individuals, particularly during spawning runs and/or warm seasons

(Baker et al. 2008). Capture–mark–recapture approaches are also labor intensive and can become costly if large areas are to be sampled over long time periods. As an alternative, hydroacoustic tools (e.g., dual-frequency identification sonar [DIDSON] and side-scan sonar [SSS]) provide a noninvasive alternative for enumerating sturgeon populations. Fisheries researchers typically use split-beam sonar (Auer and Baker 2007; Crossman et al. 2011; Mora et al. 2018) or SSS (Thomas and Haas 2002; Flowers and Hightower 2013, 2015; Seesholtz et al. 2014; Hughes et al. 2018). Hydroacoustic data can be easily recorded in the field and then processed and analyzed in a lab setting, during which sturgeon can be enumerated and measured. Incorporation of hydroacoustic technologies for sturgeon abundance estimation can minimize cost and maximize efficiency of future population monitoring efforts.

Accounting for incomplete detection is crucial for estimating the abundance of any organism (Kéry and Schmidt 2008). Detection is a hierarchical process in that organisms need to be seen or captured given that they are present in the sampling area, but such an approach is only recent in abundance estimation models (Royle 2004). Binomial mixture or N -mixture models are a form of hierarchical regression used to estimate both abundance and detection probability under certain assumptions and constraints (Kéry 2018) based on spatially and temporally replicated data collected within a relatively short time period during which population closure is assumed (Kéry and Schaub 2011). Coupling N -mixture modeling with sturgeon enumeration data obtained from SSS recordings would prove to be a methodological advance in estimating sturgeon abundance while accounting for detection probability in a routine, efficient, and noninvasive manner.

In this study, we used SSS and Bayesian N -mixture modeling to (1) estimate the daily number of fall-run ATS located at putative spawning areas in the Savannah River during the extent of the spawning season and (2) identify covariates affecting ATS detection and abundance. To date, few studies have estimated the number of spawners, instead focusing on abundance of all individuals in the system. This is an important difference, as sturgeon exhibit periodic reproductive behavior and may be present in estuaries downriver but do not necessarily contribute to the spawning population each season. Thus, we present a novel approach for estimating spawning run abundance of ATS by using low-cost SSS technology.

METHODS

Study area.—The NSBLD, located at river kilometer (rkm) 301 (where rkm 0 is the mouth of the Savannah River), serves as the first barrier for ATS migrations in the Savannah River. Putative spawning habitat (W. C. Post, unpublished data) is located just below the NSBLD

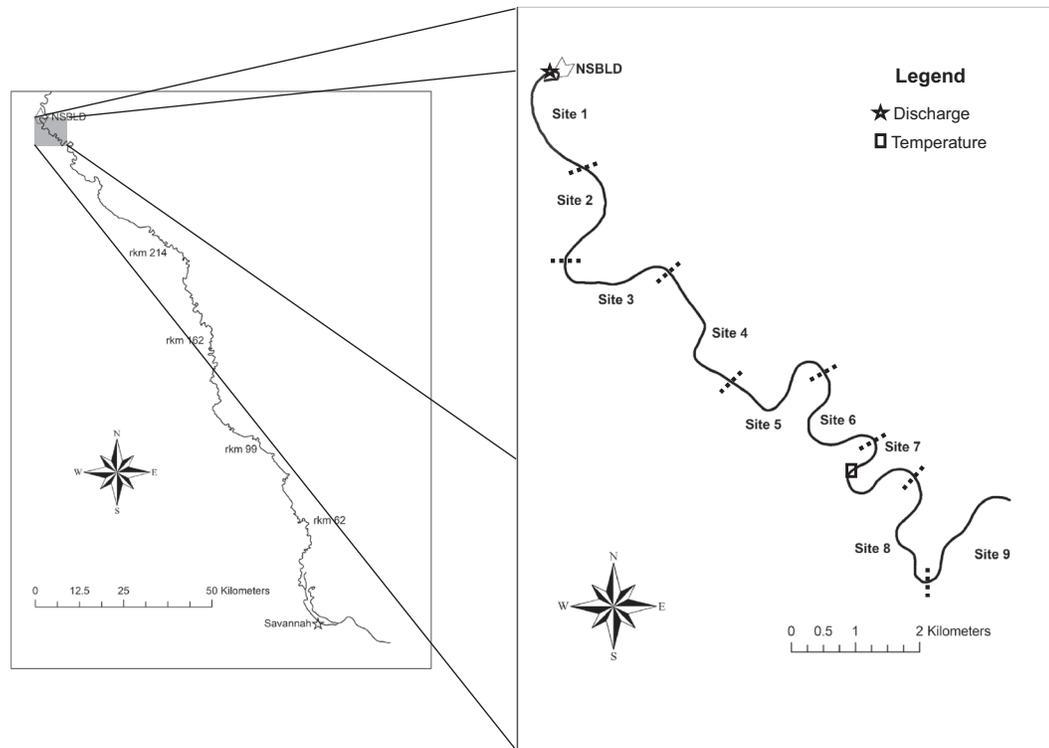


FIGURE 1. Map of the lower 301 river kilometers (rkm) in the Savannah River, zoomed in to the uppermost undammed portion of the river (rkm 281–301). We designated nine 2-km sites and sampled two passes over 50 occasions (NSBLD = New Savannah Bluff Lock and Dam).

within the uppermost portion of the river (Figure 1). We focused our sampling effort for ATS in the uppermost 20-km section of the river (rkm 281–301). Our decision to focus sampling efforts in the uppermost 20 km of the river was based on acoustic telemetry, which suggested that when ATS attempt spawning migrations they typically traverse the entire length of the river to the first barrier at the NSBLD (Vine et al. 2019). Existing literature for the Savannah River suggests that Shortnose Sturgeon *A. brevirostrum* (SNS) spawning may occur anywhere between rkm 113 and rkm 283 (Hall et al. 1991; Collins and Smith 1993). However, telemetry evidence suggests that SNS do not use the sampled portion of the river during the months in which we sampled (Vine et al. 2019), as they are present in upriver locations only between December and May. Therefore, we are confident that any sturgeon detected were indeed ATS that had moved to the study area to spawn, given the opportunity. Our sampling area contained a variety of microhabitats, including hard substrates such as gravel bars, rocks, rip-rap, tree roots, and bedrock, which are presumed to serve as suitable spawning substrate (Smith 1985; Smith and Clugston 1997; Collins et al. 2000).

Field sampling.—We sampled nine consecutive sites of approximately 2 km in length throughout the presumed

spawning habitat on 50 occasions from August to November 2017. Reach lengths of 2 km were found to be appropriate by Flowers and Hightower (2013) based on the behavior of ATS in their study systems during that period. Although we did not follow Flowers and Hightower (2013) in exploring potential differences in site length, a concurrent telemetry study (Vine et al. 2019) suggested that this site length was appropriate. Site lengths below 2 fluvial kilometers were not justifiable based on telemetry data and would likely have inflated the sample size and violated assumptions of closure during observation periods. Likewise, increasing the site length would likely have coarsened the detection data to an unfavorable resolution.

Each occasion amounted to sampling all nine sites twice consecutively (2 passes) in a single day, during which population closure at each site was assumed. Side-scan sonar sampling on each occasion took approximately 6–7 h, and the time between passes on each site was typically between 1 and 3 h. On our first 17 occasions, each pass was sampled only in the downstream direction. On occasions 18–50, the first pass was sampled in the downstream direction and the second pass was sampled in the upstream direction. The driver of the vessel attempted to stay on the same path during every pass and occasion and was directed to stay in or as close to

the river channel as possible. Boat speed remained between 5.6 and 9.6 km/h for the duration of the sampling period.

We used the Humminbird Helix 12 CHIRP-Mega-SI-GPS-G2N mounted to a stock transducer for sonar recording. We chose this unit based on the habitat located within the uppermost portion of the Savannah River. We sampled portions of the Savannah River that were too shallow to be safely scanned with tow-behind SSS units, and many areas contained high amounts of snags in the form of cypress roots or root balls, downed trees, and rocks. Water depth rarely exceeded 10 m, so the Humminbird SSS unit was able to efficiently and effectively produce quality SSS recordings.

During sonar recording, we set the ping rate to automatic per the recommendation of the Humminbird SSS manual. This produced faster ping rates and higher quality recordings than would have been obtained if the ping rate had been manually set to the lowest level. We recorded data onto a 16-GB SD (i.e., Secure Digital) card and transferred the data to an external hard drive each day. Sonar frequency remained at 1.2 MHz for the entire sampling duration. We set the SSS to scan 30.5 m on either side of the vessel during data collection. This sampling width was chosen to sample a majority of the river area to either side of the boat. Width of the river in the sampled area rarely exceeded 80 m.

Sonar file analysis.—We imported SSS files into SonarTRX Pro version 17.1 software and analyzed them visually for ATS detection. Objects that were considered to be sturgeon (based on shape, size, and cross-referenced comparisons to other occasions) in each recording were enumerated. Examination of available run estimate data obtained via gill nets (25.4–45.7-cm stretch mesh) in the southeastern USA suggests ATS lengths of at least 1.2 m TL (Collins et al. 2000; Peterson et al. 2008; Kahn et al. 2014; Ingram and Peterson 2016); therefore, only fish measured to be greater than or equal to this length were considered ATS. We also observed shadows created by marks in the sonar and looked for determining features of ATS (i.e., heterocercal tail, dorsal fin), but when estimating length for each sturgeon we measured the actual mark created by the sonar rather than the shadow produced by the mark (Flowers and Hightower 2013, 2015). We were very conservative when enumerating sturgeon detections, and we only counted individuals that were confidently identified as sturgeon because N -mixture models can account for only false negatives (i.e., missing individuals given presence) but not false positives (i.e., recording individuals despite absence).

Statistical methods.—We used N -mixture modeling to estimate daily ATS spawner abundance and determine covariates that were significant in ATS detection and abundance. N -mixture models are hierarchical regression

models composed of an ecological process to characterize spatiotemporal variation in abundance and an observation process that links the true latent state (i.e., abundance) to observed data by accounting for imperfect detection (Royle 2004). In our application, the ecological process modeled variation in ATS abundance over space (i.e., sites) and time (i.e., occasions) using a zero-inflated Poisson model with covariates, and the observation process quantified our ability to detect ATS by using a binomial model.

This approach comes with a few assumptions and caveats. Our model provides inference for the daily abundance estimates, not the total number of individuals for the entire season. Thus, the model assumes closure between passes within the same day rather than over the entire study period. We evaluated this assumption by using telemetry data (Vine et al. 2019) from one transmitted ATS that was detected in the study area during our sampling period (August 17–November 9, 2017). We had four stationary receivers in the study area located at rkm 285, 293, 299, and 300. Ninety-six percent of the time, if the individual was detected at a receiver on a given day, it was never detected at another receiver on the same day. This reveals that the individual exhibited little movement within the study area during the amount of time between our sampling passes on each occasion. The individual was detected in our study area on September 25 and 26; October 3, 7, 16, 17, 27, and 28; and November 11. We sampled on six of those nine occasions. Accordingly, we are confident in our assumption of within-day closure and our choice of 2-km site delineations.

The ecological process was modeled based on the premise that ATS abundance varies by site and occasion, and this variation can be partly explained by spatial and temporal covariates. True but imperfectly observed abundance at site i and occasion t ($N_{i,t}$) was modeled to follow a zero-inflated Poisson distribution due to the prevalence of zeroes (68% of observations) in the data:

$$Q_{i,t} \sim \text{Bernoulli}(\Omega_i), \quad (1)$$

$$\log_{10}(\lambda_{i,t}) = \alpha_0 + \alpha_1 \cdot \text{temperature}_t + \alpha_2 \cdot \text{discharge}_t + \alpha_3 \cdot \text{depth}_t, \quad (2)$$

$$N_{i,t} \sim \text{Poisson}(Q_{i,t} \cdot \lambda_{i,t}), \quad (3)$$

where $Q_{i,t}$ is a binary variable that takes on a value of 1 (suitable habitat) and 0 (unsuitable habitat) for site i and occasion t based on a Bernoulli probability Ω_i (equation 1). This probability is indexed by site i because ATS abundance was spatially aggregated, with some sites recording

a higher frequency of zeroes than others. Abundance for site i and occasion t ($\lambda_{i,t}$) was modeled as a linear function with an intercept (α_0) and three covariates with corresponding slopes (α_1 , α_2 , and α_3 ; equation 2). Covariates tested were minimum water temperature ($^{\circ}\text{C}$) on occasion t , maximum discharge (m^3/s) on occasion t , and site average maximum depth (m) at site i (Table 1). Water temperature data were obtained from a temperature logger maintained by Phinizy Swamp Nature Center, and river discharge data were obtained from U.S. Geological Survey station 02197000 (Figure 1). To calculate site average maximum depth, we exported maximum depth measurements from sonar recordings in SonarTRX on the occasion in which the highest discharge rates occurred and averaged across each site. We \log_{10} transformed maximum discharge and then scaled and centered all covariates to a mean of 0 and an SD of 1. Finally, ATS abundance at site i and occasion t was modeled as a product of $Q_{i,t}$ and $\lambda_{i,t}$ (equation 3), indicating that abundance will follow a Poisson distribution only if $Q_{i,t}$ is equal to 1 (i.e., suitable habitat). Daily ATS abundance in the entire study area (i.e., spawner abundance) was estimated by summing local abundance across nine sites on each occasion (i.e., $N_{i,t}$).

We considered more complex structures in the ecological model but settled on the model described above. First, we included random site and site \times occasion (i.e., overdispersion) effects (equation 2). Although models with additional random effects appeared to converge based on \hat{r} -values (Gelman and Hill 2006), abundance estimates were excessively high with small detection probabilities, which are characteristic symptoms of parameter unidentifiability when the N -mixture model uses negative binomial or overdispersed Poisson distributions (Kéry 2018). Second, because over 50 occasions (days) of sampling took place for a relatively short period (4 months), ATS abundance at each site was potentially dependent on the previous site abundance (i.e., temporal autocorrelation). However, we did not detect signs that residuals of abundance estimates were temporally autocorrelated based on the Breusch–Godfrey test (Lagrange multiplier statistic = 3.66, $\text{df} = 1$, $P = 0.06$).

Because not all ATS individuals present at a given site were detected with sonar technology, the observation model was specified such that a subset of ATS individuals

present were recorded on any site i and occasion t based on a binomial process:

$$y_{i,t} \sim \text{Binomial}(N_{i,t}, p_t), \tag{4}$$

$$\text{logit}(p_t) = \beta_0 + \beta_1 \cdot \text{discharge}, \tag{5}$$

where $y_{i,t}$ was the observed number of ATS (i.e., data) at site i and occasion t ; and p_t was the detection probability of ATS, which varied by occasion. The detection probability was modeled as a function of maximum discharge on the logit scale due to the possibility of behavioral differences in ATS during high-discharge conditions. We assessed whether detection probability differed by pass direction (i.e., upstream versus downstream) by letting β_0 vary by direction in preliminary analyses, and we confirmed that detection probability did not differ significantly between the upstream direction (posterior mean = 0.27; 95% credible interval [CI] = 0.18–0.37) and the downstream direction (posterior mean = 0.30; 95% CI = 0.05–0.40) based on the overlapping 95% CI values between the two. Thus, pass direction was removed from the observation model. We did not expect that river depth would influence detection probability given the range capability of the sonar unit relative to the width (≤ 80 m) and depth (≤ 12 m) of the study area.

Models were fit in a Bayesian framework using the jagsUI package in R version 3.5.1 (Kellner 2019). We used three independent Markov chain–Monte Carlo chains, and posterior parameter estimates were summarized by taking every 10th sample from 10,000 iterations after discarding 5,000 burn-in iterations. Diffuse priors were used throughout the model, including $\Omega_i \sim \text{Uniform}(0, 1)$, $\alpha_0 \sim \text{Uniform}(0, 5)$, $\alpha_1 \sim \text{Normal}(0, 1,000)$, $\alpha_2 \sim \text{Normal}(0, 1,000)$, $\alpha_3 \sim \text{Normal}(0, 1,000)$, $\sigma \sim \text{Uniform}(0, 3)$, and $\delta \sim \text{Uniform}(0, 3)$. Convergence was assumed for \hat{r} -values less than 1.1 (Gelman and Hill 2006). We used the deviance information criterion (DIC) and the widely applicable information criterion (WAIC) to aid in model selection (Spiegelhalter et al. 2002; Watanabe 2013). Model fit was assessed visually by plotting predicted versus observed ATS counts across samples. Predicted count for site i and occasion t was derived as a binomial product ($N_{i,t} \times p_t$;

TABLE 1. Covariates used in the models, with number of observations (N), mean, SD, and range. Temperature, discharge, and depth represent minimum daily temperature, maximum daily discharge, and site average maximum depth, respectively. Temperature and discharge varied temporally for each occasion, whereas we considered site average maximum depth as constant for each site.

Covariate	Level	Units	N	Mean	SD	Minimum	Maximum
Temperature	Occasion	$^{\circ}\text{C}$	50	24.1	2.08	19.7	27.2
Discharge	Occasion	m^3/s	50	133.39	16.84	106	205
Depth	Site	m	9	3.78	0.43	3.1	4.1

equation 4). Pearson's product-moment correlation was used to assess the association between predicted and observed counts.

RESULTS

We detected ATS on each sampling occasion and recorded 803 total detections throughout the study period (Figure 2). Maximum discharge ranged between 121 and 195 m³/s; minimum water temperature ranged between 19.7°C and 27.2°C. Average maximum depth at each site was between 3.2 and 4.1 m (Table 1). Site 4 (see Figure 1) contained the greatest number of detections ($n = 505$). The peak 50 ATS detections occurred on September 8, 2018, when temperature was 25°C and discharge was 125 m³/s. All sampling occasions containing 30 or more ATS detections occurred at minimum temperatures between 25°C and 26°C and a maximum discharge between 120 and 149 m³/s.

Our global model contained minimum water temperature, average maximum depth, and maximum discharge as covariates affecting abundance and included maximum discharge as a covariate affecting detection (Table 2). The global model produced the highest DIC and WAIC values (2,145.46 and 1,562, respectively). Minimum temperature and maximum discharge were not significant predictors of ATS abundance (i.e., the 95% CI overlapped with a value of zero) and were removed, which resulted in a model having smaller DIC and WAIC values (2,097.33 and 1,551.4, respectively). Our final model contained maximum discharge as a covariate affecting ATS detection and average maximum depth as a site covariate affecting ATS abundance (Table 2). Habitat suitability (Ω) for each site ranged between 0.10 and 1.00 (95% CI; Table 3). The highest ATS abundance (95% CI = 35–55) was estimated on September 29, 2018, when minimum temperature was 26°C and maximum discharge was 121 m³/s. Lowest abundance estimates (95% CI = 5–24) occurred on our final two sampling occasions (November 7 and 9, 2017) at minimum temperatures between 15.2°C and 23.8°C and at a maximum discharge between 121 and 133 m³/s (Figures 3, 4).

We observed a significant negative effect of discharge on ATS detection (Figure 3). Our final model predicted that the mean probability of detecting ATS by using SSS in the Savannah River was 0.35 (95% CI = 0.29–0.42) at an average log discharge level of 133 m³/s. Observed daily count was highly correlated with predicted daily abundance (Pearson's product-moment correlation coefficient = 0.80, $P < 0.001$), but their bi-plot revealed that our detection model functioned such that a low observed count resulted, due mainly to low detection probability associated with high discharge, and detection was high on days with a high observed count (Figure 4). Thus, the range of predicted

abundance among occasions (8–44 fish) shrank relative to variation in the observation count (3–44; Figure 5).

DISCUSSION

We used SSS and N -mixture modeling to estimate ATS spawner abundance and determine covariates that were significant in abundance and detection in the Savannah River. Our methods are novel in that we were able to produce a range of abundance estimates for ATS on each sampling occasion. Previous studies using sonar to estimate sturgeon abundance have focused on enumerating all individuals within the system (Flowers and Hightower 2015; Hughes et al. 2018), whereas our methods are meant to estimate only adults within the uppermost reach of the Savannah River expected to be contributing to spawning (*sensu* Mora et al. 2018; Kahn et al. 2019). We repeatedly sampled putative spawning grounds on each occasion over the entire fall run to identify key times in which spawner abundance increased. This approach will enable managers to estimate the abundance of sturgeon species by using noninvasive acoustic sampling.

Depth was a significant site-level covariate of ATS abundance; more ATS were present in deeper sites. High counts in deeper habitats below putative spawning grounds may be representative of male aggregations awaiting the arrival of ripe females. It is hypothesized that in the James River, Virginia, males aggregate between 2 and 10 km below spawning habitat for similar reasons (Hilton et al. 2016). These deep areas may provide cooler water conditions and appear to contain higher amounts of large, hard objects (i.e., cypress stumps, large woody debris, and rip-rap). These structures could provide flow variation and create eddies, which can lessen energy consumption by males while waiting for the arrival of females and suitable spawning conditions. Research suggests that ATS in the South Atlantic and Carolina DPSs use rocks, rubble, and limestone for spawning (Smith 1985; Collins et al. 2000). The putative spawning location for ATS in the Savannah River is between 9 and 10 m deep and contains both large rip-rap near the bank and a rocky-cobble sandbar. Although we have no evidence of spawning (i.e., eggs or larval fish), ATS clearly used the deeper portions of the upper Savannah River. Further investigation of ATS microhabitat use during all phases of the spawning run is necessary for fully understanding this relationship.

Discharge had a significant negative effect on ATS detection using SSS as a sampling gear (Table 2; Figure 3). Dam release in mid-September increased discharge and limited our ability to detect ATS by using SSS. High-discharge conditions may cause ATS to seek shelter in locations near the river bottom or near large structures in the river, making them more difficult to detect using SSS. Additionally, boat speed inevitably increases while

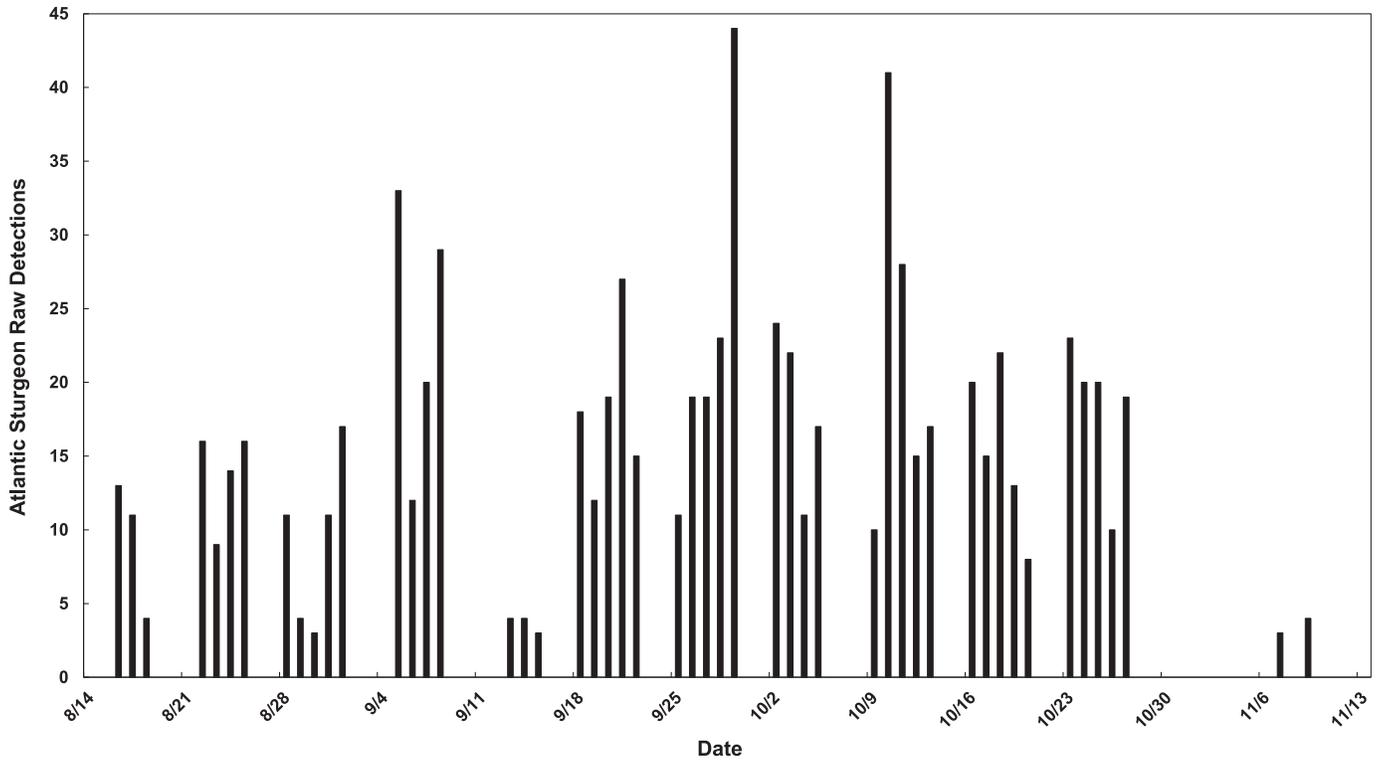


FIGURE 2. Atlantic Sturgeon (ATS) raw detections in the Savannah River for the duration of the study period in 2017. We detected at least one ATS on every sampling occasion. The maximum number of detections ($n=44$) occurred on September 29, and the minimum number of detections ($n=4$) occurred on August 30, September 15, and November 7.

TABLE 2. *N*-mixture model parameter estimates (\pm SD) presented with 95% credible intervals (CIs). Global model results are shown as well as reduced model results after removing covariates that were not significant predictors of Atlantic Sturgeon (ATS) abundance (*A*) or detection (*D*). We chose our final model based on the lowest deviance information criterion (DIC) and widely applicable information criterion (WAIC) values. Results suggest that site average maximum depth was a significant predictor of ATS abundance and that discharge significantly affected our ability to detect ATS.

Model DIC	Model WAIC	Covariate	Estimate	95% CI	
				Lower	Upper
2,097.33	1,551.4	Depth (<i>A</i>)	0.79 ± 0.06	0.67	0.91
		Discharge (<i>D</i>)	-0.49 ± 0.08	-0.65	-0.35
2,145.46	1,562	Temperature (<i>A</i>)	0 ± 0.05	-0.09	0.1
		Discharge (<i>A</i>)	0.32 ± 0.23	-0.12	0.76
		Depth (<i>A</i>)	0.79 ± 0.06	0.67	0.91
		Discharge (<i>D</i>)	-0.86 ± 0.27	-1.35	-0.33

sampling in the downstream direction in high-discharge conditions, which may also increase the probability of not detecting sturgeon. Although we found no significant effect of sampling direction on detection, SSS images were slightly less clear when sampling in the upstream direction (i.e., from propeller wash); this could limit our ability to distinguish ATS from other objects in sonar recordings. Discharge can be highly variable during the summer and fall months, due not only to high precipitation but also to

dam release for hydropower and flood control. Hurricanes may play a role in detecting ATS in rivers where hurricane mitigation release occurs; this took place in our study as a response to potential (but unrealized) effects of Hurricane Irma. Although high precipitation and discharge events occur and are naturally uncontrollable, understanding the effects of discharge on detection by SSS will be an important consideration for designing acoustic protocols with which to monitor sturgeon populations.

TABLE 3. Estimated habitat suitability (\pm SD; presented with 95% credible intervals [CIs]) for Atlantic Sturgeon at each site in the uppermost portion of the Savannah River below the New Savannah Bluff Lock and Dam. Sites 1–9 are consecutive (2 km each) and are assumed to hold individuals contributing to the spawning population (i.e., spawner abundance).

Site	Estimate	95% CI	
		Lower	Upper
1	0.75 \pm 0.06	0.62	0.86
2	0.82 \pm 0.12	0.54	0.99
3	0.32 \pm 0.07	0.2	0.47
4	0.95 \pm 0.03	0.87	1.00
5	0.49 \pm 0.07	0.35	0.63
6	0.92 \pm 0.07	0.75	1.00
7	0.20 \pm 0.06	0.1	0.32
8	0.23 \pm 0.06	0.12	0.37
9	0.62 \pm 0.10	0.42	0.82

It is important to place our results in the proper context: we present daily abundance estimates of fall-migrating ATS in the Savannah River between August and November 2017. Our models do not estimate the entire number of ATS in the Savannah River; many mature individuals, especially females, only attempt spawning migrations every few years. Likewise, we have no way of knowing which individuals, if any, released gametes while in the putative spawning habitat. It is possible that our

lower cutoff of 1.2 m excluded some smaller reproductive males from analyses. However, we would rather present conservative estimates based on known life history information with high certainty than risk misclassifying a potential spawner and inflating abundance estimates. These problems are not unique to SSS surveys; traditional capture–mark–recapture abundance estimates would have similar problems identifying spawning behaviors without visual observation of the spawning act, and they experience length bias associated with gill-net mesh size.

Another important context is that our abundance estimates are from a single season (fall) for a species that is known to exhibit dual migrations. Spring ATS migrations also occur in the Savannah River (Vine et al. 2019), but we are currently unaware whether they incorporate individuals from genetically distinct subpopulations. There is evidence of genetically distinct populations of spring- and fall-migrating ATS in the Edisto River, South Carolina (Farrae et al. 2017), and the James River, Virginia (Balazik et al. 2017). In future abundance estimates, it will be crucial to include ATS in both seasons to quantify the entirety of the ATS spawning population. Continued sampling efforts will increase our understanding of the true spawning stock as well as the effects associated with environmental covariates on spawner abundance and detection during each season and year.

Limitations of *N*-mixture models should also be acknowledged. Despite their appealing promise that

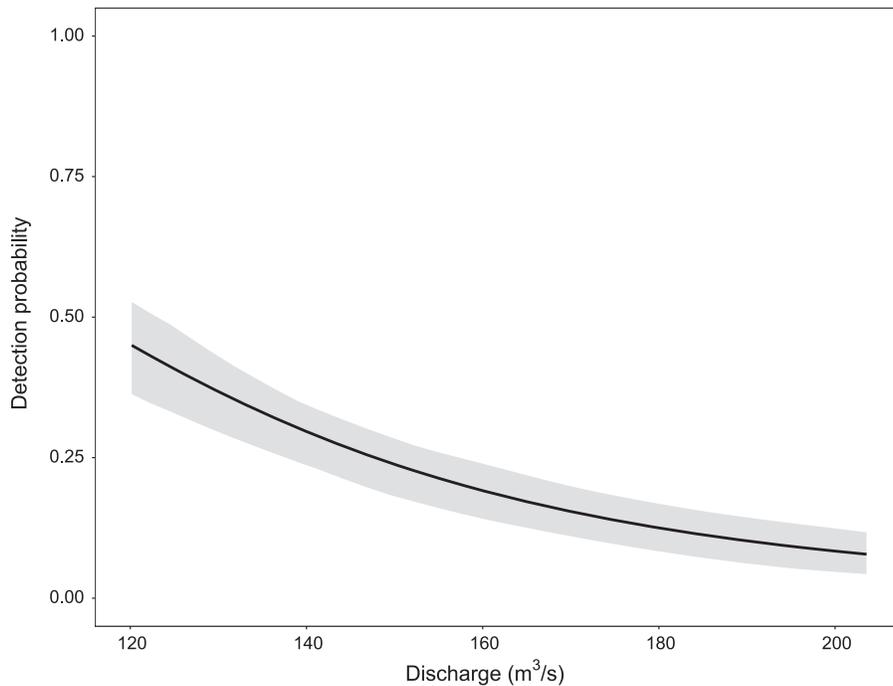


FIGURE 3. Estimated effect of Savannah River discharge on our ability to detect Atlantic Sturgeon by using side-scan sonar as a sampling gear (gray-shaded area = 95% credible interval). Periods of high discharge were estimated to have a significant negative effect on detection probability.

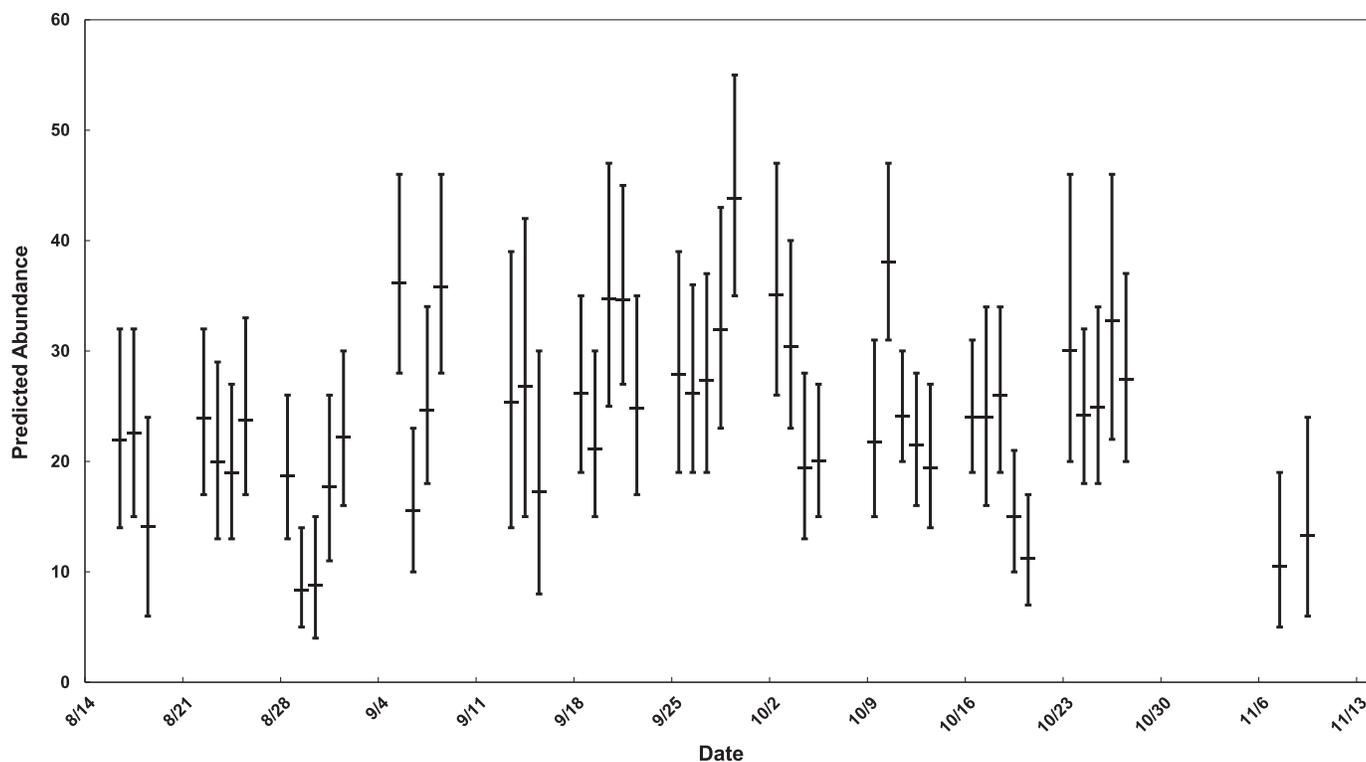


FIGURE 4. Model posterior mean estimates ($\pm 95\%$ credible interval) plotted over time. Estimates represent Atlantic Sturgeon spawner abundance in our sampled area on each occasion.

unbiased estimates of abundance (N) and detection probability (p) can be obtained separately without marking individuals, different combinations of N and p can fit a given data set equally well, and available model diagnostics may not be able to determine the correct combination of true parameters (Barker et al. 2018; Kéry 2018). Given that discharge alone is not likely to explain temporal variation in detection probability perfectly, combined with the contextual constraints discussed above, the abundance estimates reported in this study should be interpreted with caution. However, as long as data are collected in accordance with a standardized sampling protocol and are analyzed consistently (e.g., consistent interpretation of sonar files for sturgeon identification; the same covariates and distribution assumptions in analysis), such abundance estimates can serve at least as a reliable index of abundance (Barker et al. 2018)—that is, annual sampling effort based on our approach should reveal a temporal population trend of adult ATS in a given river.

Estimation of run size, year-1 recruitment (i.e., number of individuals that successfully reach age 1), and the environmental factors associated with their variation is vital to understanding ATS population dynamics in the South Atlantic DPS. Adult ATS spring-run estimates via capture-mark-recapture methods in the nearby Altamaha

River, Georgia, were reported in 2004 (mean = 324; 95% CI = 143–667) and 2005 (mean = 386; 95% CI = 216–787; Peterson et al. 2008), and year-1 estimates for that time were reported as 483 (95% CI = 368–643) and 1,345 (95% CI = 1,077–1,697), respectively (Schueller and Peterson 2010). The Altamaha River is home to the most abundant ATS populations in the South Atlantic DPS, while the Savannah River is considered to have the second-largest population (Schueller and Peterson 2010). Year-1 ATS estimates in the Savannah River between 2013 and 2015 obtained via gill nets and capture-mark-recapture methods range from 402 to 852 (Bahr and Peterson 2016). No adult run estimates are available for the Savannah River during that time. Our models suggest a maximum abundance between 35 and 55 ATS in the uppermost portion of the Savannah River in fall 2017. Our ATS spawner estimates are much lower than adult run estimates in the Altamaha River, although our data represent only the fall-migrating portion of the spawner population in the Savannah River. Implementation of capture-mark-recapture techniques for recruitment estimation of juveniles paired with SSS sampling methods for adult spawner abundance estimation will greatly contribute to our understanding of the ATS population dynamics in the Savannah River as well as increase our understanding of the environmental factors that are significant in predicting

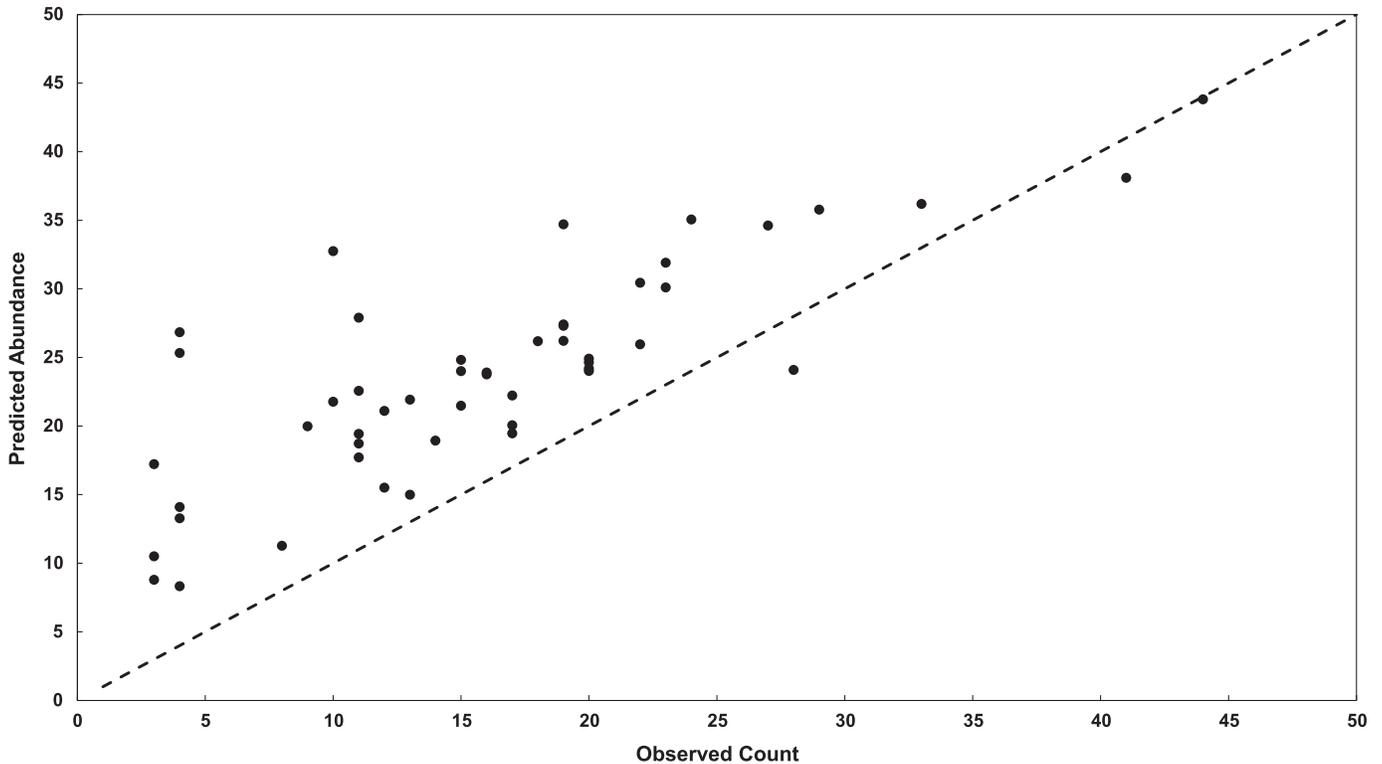


FIGURE 5. Model-predicted abundance of Atlantic Sturgeon spawners plotted against raw detections on each occasion. Detections for each occasion include double-counted individuals due to the two-pass sampling design. Higher abundance estimates are conservative because underpredictions occur at high observed counts. The dashed line represents 1:1 predicted abundance : observed detection.

variation in spawner abundance and recruitment in the South Atlantic DPS annually.

Management Implications

The benefits of using SSS to estimate sturgeon spawner abundance are clear: this approach is noninvasive and is not stressful to individuals. Such characteristics are critical, as sturgeons make long migrations in near-summer-high water temperatures. Migrating sturgeon can be sensitive to handling under reproductive conditions, and as managers we must minimize handling procedures that may stress individuals or interrupt spawning. Furthermore, the SSS equipment used in this study was inexpensive and required minimal labor in comparison with traditional capture–mark–recapture methods. Although sonar file analysis was time consuming (e.g., at least a 15-min analysis per 2-km site/pass), sonar recordings can be stored, cataloged, and reviewed by multiple observers in a laboratory setting to ensure accurate counts. Sonar recordings not only contain abundance information but can also be georeferenced and further analyzed for habitat information. There are clearly many benefits to using SSS as a sampling gear for sturgeon abundance estimation,

and there remains much to learn about integrating these sampling practices in rivers around the world.

Sampling strategy is extremely important when designing SSS surveys to estimate ATS spawner abundance. We separated putative spawning habitat into 2-km sections and sampled each site in both upstream and downstream directions twice (i.e., two passes) over 50 occasions. Sampling only during times when high ATS abundance is expected would optimize efficiency and decrease the number of occasions necessary to estimate spawner abundance. In rivers where ATS spawning behavior is well understood, sampling could occur on a minimal number of occasions within known aggregation areas to efficiently produce accurate spawner abundance estimates. Additionally, we sampled each site only twice on each occasion. In doing so, we revealed portions of the river that had a high probability of ATS occupancy (Table 3). In future sampling efforts, optimal allocations of sampling effort might involve limiting our sampling to these locations but instead increasing the number of repeat visits to characterize detection probability more confidently, although one must feel comfortable assuming population closure during the time between each pass.

Sampling direction did not affect our ability to detect ATS. This is important because sampling in both directions can reduce the time between passes for each site, improving the accuracy of calculating detection probability. Detection probability also decreased with increased discharge; SSS sampling in the Savannah River was most reliable during low-discharge conditions, and future sampling will be planned accordingly. Before designing large-scale SSS sampling protocols, managers should understand how these two variables and other potential key variables affect the detection of sturgeon. For example, some rivers may have such high discharge and/or substrate complexity that SSS sampling is not feasible. Likewise, propeller wash may interact with other sampling factors (engine size, type of SSS unit, and environmental factors) to increase efficiency in one sampling direction versus another. Our study represents a first step toward parsing out these factors.

Our estimates are likely conservative because they represent only larger individuals due to our 1.2-m length cutoff for ATS detections. Atlantic Sturgeon length estimates obtained from multi-beam DIDSON recordings were underestimated, possibly due to difficulty in detecting the snout and the long dorsal lobe at the end of the heterocercal tail (Hightower et al. 2013). It is also very important to consider that our estimates represent a single fall-run season. Spawning periodicity for ATS is between 1 and 5 years, so to produce more accurate spawning population estimates using our approach one must continue fall and spring sampling annually, especially during times when high ATS abundance is expected within putative spawning habitat. Future sampling efforts should also include egg and larval fish sampling techniques (i.e., D-nets, egg mats, and ichthyoplankton trawls) to confirm that spawning has occurred in the sampling area.

This work represents a first step toward developing standard protocols for estimating the number of spawning sturgeon in rivers. Coupling this approach (or modified versions of it) with traditional abundance estimation approaches outside of the spawning season will help to better calibrate the accuracy of SSS counts and *N*-mixture modeling. Conducting sonar-based approaches in conjunction with a robust telemetry program will also help to validate their accuracy as well as provide important insight into the influence of reproductive periodicity on estimates (Mora et al. 2018). Furthermore, accurate spawner abundance estimates paired with year-1 abundance estimates will greatly increase our understanding of ATS population dynamics. We urge similar sampling approaches in other river systems containing spawning sturgeon populations, as each system will encompass specific sampling challenges and the detection probability in each system will potentially vary.

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REFERENCES

- Auer, N. A., and E. A. Baker. 2007. Assessment of Lake Sturgeon spawning stocks using fixed-location, split-beam sonar technology. *Journal of Applied Ichthyology* 23:113–121.
- Bahr, D. L., and D. L. Peterson. 2016. Recruitment of juvenile Atlantic Sturgeon in the Savannah River, Georgia. *Transactions of the American Fisheries Society* 145:1171–1178.
- Baker, D. W., S. J. Peake, and J. D. Kieffer. 2008. The effect of capture, handling, and tagging on hematological variables in wild adult Lake Sturgeon. *North American Journal of Fisheries Management* 28:296–300.
- Balazik, M. T., D. J. Farrae, T. L. Darden, and G. C. Garman. 2017. Genetic differentiation of spring-spawning and fall-spawning male Atlantic Sturgeon in the James River, Virginia. *PLoS (Public Library of Science) ONE [online serial]* 12(7):e0179661.
- Barker, R. J., M. R. Schofield, W. A. Link, and J. R. Sauer. 2018. On the reliability of *N*-mixture models for count data. *Biometrics* 74:369–377.
- Billard, R., and G. Lecointre. 2000. Biology and conservation of sturgeon and Paddlefish. *Reviews in Fish Biology and Fisheries* 10:355–392.
- Birstein, V. J. 1993. Sturgeons and Paddlefishes: threatened fishes in need of conservation. *Conservation Biology* 7:773–787.
- Collins, M. R., and T. I. J. Smith. 1993. Characteristics of the adult segment of the Savannah River population of Shortnose Sturgeon. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 47:485–491.
- Collins, M. R., T. I. J. Smith, W. C. Post, and O. Pashuk. 2000. Habitat utilization and biological characteristics of adult Atlantic Sturgeon in two South Carolina rivers. *Transactions of the American Fisheries Society* 129:982–988.
- Comer, A. M. 2017. Adult Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) habitat use and run-size in the Hudson River Hyde Park reach. Delaware State University, Dover.
- Crossman, J. A., G. Martel, P. N. Johnson, and K. Bray. 2011. The use of dual-frequency identification sonar (DIDSON) to document White Sturgeon activity in the Columbia River, Canada. *Journal of Applied Ichthyology* 27(S2):53–57.
- 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* 31:218–229.
- Farrae, D. J., W. C. Post, and T. L. Darden. 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.
- Flowers, H. J., and J. E. Hightower. 2013. A novel approach to surveying sturgeon using side-scan sonar and occupancy modeling. *Marine*

- and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 5:211–223.
- Flowers, H. J., and J. E. Hightower. 2015. Estimating sturgeon abundance in the Carolinas using side-scan sonar. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 7:1–9.
- Gelman, A., and J. Hill. 2006. *Data analysis using regression and multi-level/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Hall, J. W., T. I. J. Smith, and S. D. Lamprecht. 1991. Movements and habitats of Shortnose Sturgeon, *Acipenser brevirostrum* in the Savannah River. *Copeia* 1991:695–702.
- Hightower, J. E., K. J. Magowan, L. M. Brown, and D. A. Fox. 2013. Reliability of fish size estimates obtained from multibeam imaging sonar. *Journal of Fish and Wildlife Management* 4:86–96.
- Hilton, E. J., B. Kynard, M. T. Balazik, A. Z. Horodysky, and C. B. Dillman. 2016. Review of the biology, fisheries, and conservation status of the Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus* Mitchell, 1815). *Journal of Applied Ichthyology* 32:30–66.
- Hughes, J. B., B. Bentz, and J. E. Hightower. 2018. A non-invasive approach to enumerating White Sturgeon (*Acipenser transmontanus* Richardson, 1863) using side-scan sonar. *Journal of Applied Ichthyology* 34:398–404.
- Ingram, E. C., and D. L. Peterson. 2016. Annual spawning migrations of adult Atlantic Sturgeon in the Altamaha River, Georgia. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 8:595–606.
- Kahn, J. E., C. Hager, J. C. Watterson, J. Russo, K. Moore, and K. Hartman. 2014. Atlantic Sturgeon annual spawning run estimate in the Pamunkey River, Virginia. *Transactions of the American Fisheries Society* 143:1508–1514.
- Kahn, J. E., C. Hager, J. C. Watterson, N. Mathies, and K. J. Hartman. 2019. Comparing abundance estimates from closed population mark-recapture models of endangered adult Atlantic Sturgeon. *Endangered Species Research* 39:63–76.
- Kellner, K. 2019. jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses, version 1.4.9. Available: <https://cran.r-project.org/package=jagsUI>. (July 2019).
- Kéry, M. 2018. Identifiability in *N*-mixture models: a large-scale screening test with bird data. *Ecology* 99:281–288.
- Kéry, M., and M. Schaub. 2011. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press, Cambridge, Massachusetts.
- Kéry, M., and B. R. Schmidt. 2008. Imperfect detection and its consequences for monitoring for conservation. *Community Ecology* 9:207–216.
- Lenhardt, M., I. Jaric, A. Kalauzi, and G. Cvijanovic. 2006. Assessment of extinction risk and reasons for decline in sturgeon. *Biodiversity and Conservation* 15:1967–1976.
- Limburg, K. E., and J. R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. *BioScience* 59:955–965.
- Mora, E. A., R. D. Battleson, S. T. Lindley, M. J. Thomas, R. Bellmer, L. J. Zarri, and A. P. Klimley. 2018. Estimating the annual spawning run size and population size of the southern distinct population segment of Green Sturgeon. *Transactions of the American Fisheries Society* 147:195–203.
- Musick, J. A. 1999. Ecology and conservation of long-lived marine animals. Pages 1–10 in J. A. Musick, editor. *Life in the slow lane: ecology and conservation of long-lived marine animals*. American Fisheries Society, Symposium 23, Bethesda, Maryland.
- Peterson, D. L., P. Schueller, R. DeVries, J. Fleming, C. Grunwald, and I. Wirgin. 2008. Annual run size and genetic characteristics of Atlantic Sturgeon in the Altamaha River, Georgia. *Transactions of the American Fisheries Society* 137:393–401.
- Royle, J. A. 2004. *N*-mixture models for estimating population size from spatially replicated counts. *International Biometrics Society* 60:108–115.
- Schueller, P., and D. L. Peterson. 2010. Abundance and recruitment of juvenile Atlantic Sturgeon in the Altamaha River, Georgia. *Transactions of the American Fisheries Society* 139:1526–1535.
- Seesholtz, A. M., M. J. Manuel, and J. P. Van Eenennaam. 2014. First documented spawning and associated habitat conditions for Green Sturgeon in the Feather River, California. *Environmental Biology of Fishes* 98:905–912.
- 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.
- Smith, T. I. J., and J. P. Clugston. 1997. Status and management of Atlantic Sturgeon, *Acipenser oxyrinchus*. North America. *Environmental Biology of Fishes* 48:335–346.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van Der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 64:583–639.
- Thomas, M. V., and R. C. Haas. 2002. Abundance, age structure, and spatial distribution of Lake Sturgeon, *Acipenser fulvescens*, in the St. Clair system. *Journal of Applied Ichthyology* 18:495–501.
- Vine, J. R., S. C. Holbrook, W. C. Post, and B. K. Peoples. 2019. Identifying environmental cues for Atlantic Sturgeon and Shortnose Sturgeon spawning migrations in the Savannah River. *Transactions of the American Fisheries Society* 148:671–681.
- Watanabe, S. 2013. WAIC and WBIC are information criteria for singular statistical model evaluation. *Proceedings of the Sixth Workshop on Information Theoretic Methods in Science and Engineering (WITMSE)* 2013:90–94.
- Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 62:872–885.