

USING SIDE-SCAN SONAR TO QUANTIFY THE SPAWNING RUNS OF ATLANTIC
STURGEON IN THE ALTAMAHA RIVER, GEORGIA

by

CORTNEY JO BUNCH

(Under the Direction of Adam G. Fox and Cecil A. Jennings)

ABSTRACT

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is an endangered, anadromous fish that occurs off the east coast of North America. Many populations were nearly extirpated by commercial harvest and dam construction on spawning rivers. Cost-effective remote sensing technology offers a new method for estimating the abundance of adult spawners during their upstream migrations. I used side-scan sonar to investigate adult Atlantic Sturgeon in the Altamaha River from September-November of 2017-2018. Using N-mixture models, I found that there were 115 spawners in 2017 (95%CI: 104-129) and 82 in 2018 (95%CI: 70-95) spawning runs. Depth and bedrock were significant covariates that predicted putative spawning locations. This study provides important quantitative data about the Atlantic Sturgeon population and preferred habitat characteristics. Compared to previous mark-recapture estimates of spawning run size, side-scan sonar was less invasive and required less effort while indicating that the Altamaha River spawning population has remained relatively stable since 2007.

INDEX WORDS: Atlantic Sturgeon, Side-scan sonar, N-mixture model, Spawning, Abundance, Remote sensing, Altamaha River, Ocmulgee River, Oconee River, *Acipenser oxyrinchus oxyrinchus*

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DEDICATION

I would like to dedicate this work to my hyperactive but loving dog, Ruger, and my genuinely patient husband, Calvin. I would also like to dedicate this to my parents, who gave me so many opportunities to appreciate and explore the outdoors growing up and who have always been supportive of my goals and choices.

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	ix
CHAPTER 1	1
Introduction.....	1
Atlantic Sturgeon Biology and Status.....	2
Remote Sensing	6
References.....	15
Tables and Figures	25
CHAPTER 2	27
Abstract.....	28
Introduction.....	29
Methods.....	32
Results.....	39
Discussion.....	42
Acknowledgements.....	53
References.....	54
Tables and Figures	66
CHAPTER 3	79
References.....	84

LIST OF TABLES

	Page
Table 2.1: Field effort for side-scan sonar surveys in the Altamaha River system in October 13 th -14 th in both 2017 and 2018. Effort is given in hours and river kilometers surveyed. Oconee and Ocmulgee river sections were surveyed concurrently by one boat each, which met at the confluence of the two tributaries and surveyed concurrently in the mainstem Altamaha River.....	69
Table 2.2: Number of Atlantic Sturgeon targets identified in side-scan sonar imagery during peak 2017 and 2018 surveys, both occurring October 13 th -14 th of each year. Oconee and Ocmulgee river sections were surveyed concurrently by one boat each, which met at the confluence of the two tributaries and surveyed the mainstem Altamaha River together, hence two replicate counts are reported for the Altamaha River. Targets were removed from analysis if length was <1.1 m. Total ATS targets represent the total number of targets identified in all rivers and passes after removal of fish below the cutoff length. Mean total targets reflects the sum of Oconee and Ocmulgee River counts, plus the mean of the two Altamaha River replicate counts	70
Table 2.3: Parametric bootstrap goodness-of-fit (GoF) test results for the base Zero-Inflated Poisson models on side-scan sonar survey data collected in the Altamaha River in October 13 th -14 th in both 2017 and 2018. One-hundred bootstrap iterations were used. Three statistics were used for the GoF test: Error Sum of Squares (SSE), Chi-square, and Freeman-Tukey. Estimates of the t-statistic (t0) resulting in probability (p) near	

0.5 indicate good fit of Zero-Inflated Poisson probability distribution to the sample data distribution	71
Table 2.4: Model selection AIC table for N-mixture models estimating Atlantic Sturgeon abundance from a side-scan sonar survey in October 2017 in the Altamaha River, Georgia. Each model includes potential covariates affecting sturgeon abundance (λ) and detection probability (p). The number of parameters (K), Akaike's Information Criterion (AIC), and difference in model AIC from the top model's AIC (Δ AIC) were identified for each model. The dashed line represents the threshold of models with Δ AIC <2.00.....	72
Table 2.5: Estimates of detection probability (\pm standard error [SE]) and abundance (95% Confidence Interval [CI]) of Atlantic Sturgeon spawners in the Altamaha River system in Fall 2017 and 2018	73
Table 2.6: Model selection AIC table for N-mixture models estimating Atlantic Sturgeon abundance from a side-scan sonar survey in October 2018 in the Altamaha River, Georgia. Each model includes potential covariates affecting sturgeon abundance (λ) and detection probability (p). The number of parameters (K), Akaike's Information Criterion (AIC), and difference in model AIC from the top model's AIC (Δ AIC) were identified for each model. The dashed line represents the threshold of models with Δ AIC <2.00.....	74

LIST OF FIGURES

	Page
Figure 1.1: The Altamaha River System in central Georgia	24
Figure 1.2: The five distinct population segments (DPSs) of the North American Atlantic Sturgeon: Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (NOAA 2012a, 2012b).....	25
Figure 2.1: Map of the Altamaha River system in Georgia including the Ocmulgee and Oconee river tributaries and dam locations on the upper reaches of each tributary. The side- scan sonar study area in Fall 2017 is depicted in dark gray, and the study area in Fall 2018 is depicted by the dark gray plus additional blue reaches.....	75
Figure 2.2: Mean daily water temperatures during the putative Atlantic Sturgeon fall spawning season from September 15 th through November 15 th , 2017-2018 in the Altamaha River system, Georgia. Peak survey period from each year is highlighted in red. Data retrieved from USGS streamgage 0221500 at rkm 412 on the Ocmulgee River in Hawkinsville, GA, and streamgage 02225000 at rkm 180 on the Altamaha River in Baxley, GA	77
Figure 2.3: Kernel Density Estimation (KDE) of Atlantic Sturgeon targets in the upper Altamaha River System (in population per square kilometer) from data collected during side-scan sonar surveys in 2017 and 2018. Analysis was conducted using GIS- based KDE with targets in the Altamaha River assigned half the weight of those in the Oconee and Ocmulgee rivers	78

Figure 2.4: Percentage of hard substrates (bedrock, rocky boulder, rocky fine) in the Altamaha River System by river kilometer. Kernel Density Estimation (KDE) of ATS targets > 1.1 m in 2017 and 2018 is shown in shades of red above each river. Analysis was conducted using GIS-based KDE with targets in the Altamaha River assigned half the weight of those in the Oconee and Ocmulgee rivers. The ‘X’ and horizontal black line at y>80 marks the boundaries and extent of the side-scan sonar surveys in relation to the entire Altamaha River system. Modified from Ingram and Peterson (2016).

Substrate data from Litts and Kaeser (2016)80

Figure 2.5: Atlantic Sturgeon spawner abundance estimates for the Altamaha River, Georgia.

Includes POPAN estimates from Peterson et al. (2008), Schnabel estimates from Schueller (2010), extrapolations of both of those estimates by Kahn et al. (2019) and the authors of this study, and N-mixture estimates of Atlantic Sturgeon abundance from side-scan sonar surveys of the putative spawning areas of the Altamaha River, Georgia.....81

CHAPTER 1

ECOLOGY OF THE ATLANTIC STURGEON (*ACIPENSER OXYRINCHUS*)

Introduction

Sturgeon are long-lived cartilaginous fishes that are members of the Acipenseridae family, which comprises 27 species of extant sturgeons and paddlefishes worldwide. These ancient fishes were historically abundant throughout their ranges, but populations have declined due to many anthropogenic and environmental factors (Smith 1985). Worldwide, 63% of Acipenserids are currently listed as Critically Endangered on the International Union for the Conservation of Nature (IUCN) Red List for Threatened Species (IUCN 2019). Of the nine extant North American species, all have at least one population listed as threatened or endangered under the Endangered Species Act (ESA), Canada's Species at Risk Act, or the Committee on the Status of Endangered Wildlife in Canada status reports.

Much is still unknown about North American sturgeon populations. In particular, gaps in knowledge persist regarding adult spawning populations and their habitat requirements; quantitative data about spawners are especially lacking. This information gap is due in part to the dynamic and cryptic life histories of sturgeon and the status of protected populations, which requires a stringent permitting process to be able to investigate. Recent advances in technology, including remote sensing, have provided an opportunity to monitor sturgeon populations noninvasively and economically, and is allowing researchers to obtain quantified data on spawning population abundances, extent of annual spawning migrations, and distribution of spawning habitats.

Atlantic Sturgeon Biology and Status

Species Description

Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus* [ATS]) are an anadromous, iteroparous fish belonging to the Acipenseridae family. They are found on the east coast of North America from the St Johns River, Florida to the St. Lawrence River, New Brunswick, Canada (ASSRT 2007). This species once spawned in 35 major coastal rivers, but now spawns in only 20 of these rivers (ASSRT 2007). Atlantic Sturgeon are primarily cartilaginous and possess an elongated body lined with five rows of bony scutes positioned along the dorsal, lateral and ventral surfaces. The species is characterized by a large heterocercal tail. Atlantic Sturgeon are benthic and have a ventral protractile mouth for bottom feeding. Individuals live up to 60 years and can reach weights of 368 kg (Bain 1997; Gross et al. 2002) and total lengths of 549 cm (DeKay 1842, cited by Kahnle et al. 2007).

Status

Atlantic Sturgeon have experienced major population declines due mainly to overharvest and habitat degradation. Throughout the 19th and 20th centuries, ATS were fished heavily for caviar and meat, which resulted in the collapse of nearly all populations (Smith 1985). Continued population declines prompted the United States (U.S.) National Marine Fisheries Service to enact a federal fishing moratorium in 1998 (ASFMC 1998), although many state agencies had already closed state fisheries by that time. Georgia allowed commercial fishing for ATS, focused around a directed gillnet fishery for roe females, until a state moratorium was enacted in 1997 (Smith and Clugston 1997). Dams on many rivers block ATS from accessing historical spawning areas, which has prevented or slowed recovery in many systems (Smith and Clugston 1997; ASSRT 2007). The Altamaha River in Georgia is undammed below the fall line and retains much of its presumed historical ATS spawning habitat in its two main tributaries, the Oconee and Ocmulgee

rivers (Figure 1.1). Atlantic Sturgeon also remain vulnerable to urban, agricultural, and industrial development, which pose numerous indirect threats such as heated water and pollutant discharges (Sloan 1987; Rogers and Weber 1994; Smith and Clugston 1997; ASSRT 2007). Dredging operations directly affect sturgeon by potentially entraining individuals in the dredging gear and indirectly by altering critical habitat and natural channel morphology (ASSRT 2007; Smith and Clugston 1997). Additional major threats to ATS include ship strikes (Brown and Murphy 2010; Balazik et al. 2012b), incidental bycatch (Collins et al. 1996; Smith and Clugston 1997), and poaching (ASSRT 2007). Due to the major declines to ATS populations and continuing threats to the species, Atlantic Sturgeon were listed under the Endangered Species Act in 2012 (NOAA 2012a, 2012b). The ATS's entire range along the East Coast of the U.S. was divided into five distinct population segments [DPS]: Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (Figure 1.2). All DPSs were listed as endangered except for the Gulf of Maine DPS, which was listed as threatened (NOAA 2012a, 2012b). The interim recovery plan for ATS outlines major priorities for the species, including gaining a better understanding of population dynamics, distribution, and trends, and developing standardized methods for determining abundance (NOAA 2017).

Atlantic Sturgeon population assessment data generally are limited or lacking, especially for adults. The Altamaha River is the largest river system in Georgia and is thought to host a robust adult ATS population, though the current estimate may represent less than 2% of the historic population (ASSRT 2007). Capture-mark-recapture (CMR) surveys completed in the mid-2000s in the Altamaha River indicated consistent juvenile recruitment, which suggests that the population was relatively stable (Schueller and Peterson 2010). From 2004-2007, adult ATS abundance in the Altamaha River was estimated by using intensive mark-recapture surveys and

an open population model in the POPAN® software package; adult abundance was estimated at 89-213 ($\pm 76 - 258$) individuals annually from 2004-2007 (Peterson et al. 2008; Schueller 2008). Although that study attempted to estimate the number of migratory spawners, the estimates were confounded by the presence of non-spawning adults: most adults (>95%) examined in 2006 and 2007 were not running ripe (i.e., showing indications of being ready to spawn; Schueller 2008). Clearly, accurately quantifying adult population size requires further study. Although monitoring of the juvenile population has continued over the past decade (Sturgeon lab, University of Georgia, unpublished data), the adult ATS population has not been assessed since 2007.

Life Cycle

Atlantic Sturgeon have an anadromous life cycle that consists of several distinct life stages, each with unique habitat requirements. Eggs are spawned over hard substrates by adults in upriver spawning areas; a sticky coating allows the eggs to attach to substrate and prevents them from being swept downstream. Eggs hatch within 92 – 140 hours (Dean 1893, 1895; Vladykov and Greeley 1963; Smith et al. 1980, 1981), and the free embryos inhabit interstitial rocky substrate where they develop into larvae within two weeks (Smith et al. 1981). The larvae travel downstream nocturnally during the first week after yolk-sac absorption and then make diel drifts for the remainder of their larval lifespan, eventually reaching the estuaries where they remain as river-resident juveniles (RRJs) for up to 4 years (Bain et al. 2000, Kynard and Horgan 2002). At age-2, some RRJs begin to outmigrate to the ocean and become marine migratory juveniles (MMJs), which inhabit nearshore coastal waters and may occasionally return to their natal estuaries (Fox and Peterson 2019). The MMJ life stage lasts until the fish mature, which in southern rivers may take 5 – 13 years for males and 7 – 19 years for females (Smith et al. 1982).

Adult ATS disperse throughout the nearshore waters of the western North Atlantic, but return to their natal rivers to spawn (Smith 1985). Spawning reportedly occurs once every 1 – 5

years for males (Smith 1985) and 2 – 5 years for females (ASSRT 2007). More recently, Van Eenennaam et al. (1996) concluded that males spawn in consecutive years and females spawn less frequently, and average spawning periodicity in the York River System was 1.1 years for males and 2.2 years for females (Kahn 2019). Atlantic Sturgeon exhibit latitudinal variation in the timing of spawning. Historically, ATS were thought to spawn mainly in the spring, although fall spawning migrations had been documented as far back as the early 1900s (Worth 1904, cited in Smith et al. 2015). Recently, dual (spring and fall) spawning migrations have been suggested for several rivers, including the Pamunkey and James rivers in Virginia (Balazik et al. 2012a; Hager et al. 2014; Balazik and Musick 2015), the Roanoke River in North Carolina (Smith et al. 2015), the Edisto and Combahee rivers in South Carolina (Smith et al. 1984; Collins et al. 2000), and the Savannah River on the Georgia/South Carolina border (Vine et al. 2019a). In the York River and the Altamaha River, Georgia, there appears to be a single fall spawning run (Kahn et al. 2019; Ingram and Peterson 2016).

In the Altamaha River, ATS adults exhibited either a two-step or one-step migration pattern. Fish began the two-step migration in April – May and moved to summer holding areas partway up the river, followed by a fall migration the remainder of the way to spawning sites. Fish began the one-step migration in August – September and moved from the ocean directly to spawning grounds (Ingram and Peterson 2016). Spawning habitat occurs in river reaches near where the coastal plains transition to the upland region (i.e., below the fall line). Such areas are characterized by rocky shoals and coarse substrates. Altamaha ATS have been documented near hard substrate upriver when water temperatures at the nearest temperature gauge at Darien, GA declined below 20 °C in the fall (Ingram 2014). After spawning, the adults migrated downriver and exit Altamaha Sound between late November and the first week of January (Ingram 2014;

Ingram and Peterson 2016). This outmigration generally took a few weeks, with the shortest documented outmigration lasting only 8 days (Ingram 2014; Ingram and Peterson 2016).

Although the general timing of spawning migrations in this population has been documented, much remains unknown about the specific spawning sites, exact timing of spawning, and abundance of adult spawners in the Altamaha River and other southern rivers.

Remote Sensing

Remote sensing is the process of using non-invasive technology to obtain information and measurements about physical characteristics of objects from a distance. For instance, satellites and aircraft are able to use a variety of active and passive remote sensing techniques to collect topographic or bathymetric data. Passive data collection uses instruments that are only capable of receiving a one-way signal containing information from an object. For example, satellites that contain radiometers are able to passively measure electromagnetic radiation on Earth. Active data collection uses instruments that transmit a signal and detect the echoes of that signal after it reflects off an object (Fish and Carr 1990). Examples of active remote sensing include radio detection and ranging (radar), light detection and ranging (lidar), and sound navigation and ranging (sonar).

Sonar is unique in that it uses sound to acquire information about distant objects. A sonar unit transmits an acoustic signal, and a hydrophone on the unit detects the echoes of that sound; distance to an object is calculated as a function of the time the echo takes to return to hydrophone. It is useful for remote sensing in aquatic environments where light and radio waves cannot penetrate. In the early 20th century, sonar use became more prevalent because of an increasing need to detect submarines during naval conflicts. Subsequently, hydroacoustic sonar

surveys have been used for mapping bathymetry and substrate of large bodies of water. Types of sonar include single-beam and multibeam echo sounders. Single-beam echo sounders use a single acoustic beam to obtain information, traditionally depth data, from directly below the transducer. Multibeam echo sounders use a fan-shaped array to obtain data from a wider swath of the waterscape. Hydroacoustic mapping studies typically use multibeam sonar to collect bathymetry data.

Side-Scan Sonar

Side-scan sonar (SSS) was an innovation developed in the 1950s to produce high resolution images of the benthic substrate (Bjørnø 2017). It differs from other sonars in that it typically uses dual sonar beams angled to the left and right side of the transducer. The fan-shaped beams collect almost-continuous data based on the frequency of pings per second and the speed of the vessel. As the transducer moves through the water, the SSS produces a sonogram whose image resemble the substrate condition. Variation in tone in the image depends on many factors of the object being insonified, including the distance to, material makeup, density of the object, and the angle of incidence of the sound wave reflecting back to the hydrophone (Fish and Carr 1990).

Historically, side-scan sonar required the use of a transducer mounted to a “towfish” that is attached to a cable and suspended below the vessel; towfish can generally only be operated in deep-water systems – typically offshore marine habitats or large inshore rivers. Traditional applications for SSS throughout the 20th century include target location, substrate mapping, petroleum pipeline operations, dredging, naval mine hunting, environmental effluent monitoring, and pinpointing power cable breakages (Fish and Carr 1990, Carr and Fish 1992). Early fisheries applications included surveying fish schools, reefs, and shellfish beds (Fish and Carr 1990). In

the past two decades, SSS technology has improved dramatically in quality, while becoming much smaller, cheaper, and easier to operate. Consumer-grade sonar units can be used easily in shallow-water aquatic environments including rivers for smaller-scale applications including recreational fishing and fisheries science.

Improvements in SSS equipment and technology have provided fisheries scientists with a new tool for remotely sensing fish populations and their habitat, while eliminating the negative effects of traditional sampling methods. Recently, consumer-grade SSS equipment has been used to create detailed maps of benthic riverine and estuarine habitats (Edsall. et al. 1989; McHugh et al. 2004; Kaeser and Litts 2008, 2010; Hook 2011; Kaeser et al. 2012; Litts 2013; Gruber 2015; Litts and Kaeser 2016; Schooley and Neeley 2017). Side-scan sonar also has been used to detect several large fish species such as Alligator Gar (*Atractosteus spatula*; Fleming et al. 2018), American Paddlefish (*Polydon spatula*; Hale et al. 2003), and several sturgeon species including White Sturgeon (*Acipenser transmontanus*; Hughes et al. 2018), Atlantic Sturgeon (Flowers and Hightower 2013, 2015; Flowers 2015; Vine et al. 2019b), and Gulf Sturgeon (*Acipenser oxyrinchus desotoi*; Adam Kaeser, USFWS personal communication). All of these species are large (>1 m long) with distinctive shapes and hard body characteristics that reflect sound waves relatively well, which can help distinguish the fish in SSS imagery. Traditional survey methods for large adult Acipenserids involved the use of gillnets and trammel nets to capture and tag individuals for mark-recapture studies; those procedures are stressful, invasive, and disruptive for the fish. Netting is also a time-intensive activity for researchers, and it reveals little about the habitat occupied by the fish. Using SSS, fishery researchers have been able to identify sturgeon aggregation locations, count individuals, develop indices of abundance, and estimate actual

abundance. Because it is non-invasive, SSS may be a more cost-effective and efficient method for monitoring and quantifying sturgeon populations than traditional methods such as netting.

Sturgeon Detection

For many reasons, sturgeon are relatively ideal candidates for SSS detection. They tend to be benthic and orient into the current when occupying riverine habitat (Flowers and Hightower 2013), which distinguishes them from other taxa. Their bony scutes help reflect sound waves and their distinctive heterocercal tails can sometimes be identified in sonar images (Flowers and Hightower 2013; A. Kaeser, USFWS, personal communication). The large size of adult sturgeon also sets them apart from other riverine species; across the U.S Atlantic coast, mature ATS vary from 117 – 549 cm TL (DeKay 1842, as reported in Kahnle et al. 2007; Smith et al. 1984; Van Eenennaam and Doroshov 1998; Kahnle et al. 2007; Schueller 2008; Hagar et al. 2014; Smith et al. 2015; Taylor and Litvak 2017; Ingram and Peterson 2016; Pendleton et al. 2019). Although Shortnose Sturgeon (*Acipenser brevirostrum*; SNS) may co-occur with ATS in some systems (Rogers et al. 1994; Rogers and Weber 1994; Fernandes et al. 2010), SNS tend to be substantially smaller than ATS. In the Altamaha River, the mean FL for adult ATS collected between 2010 and 2013 was 161.8 cm (range: 125.5 – 203.0 cm); the mean FL for adult SNS collected during that same time period was 70.1 cm (range: 57.4 – 83.0 cm) (Ingram 2014; Ingram and Peterson 2018). In the Altamaha River, SNS and ATS appear to use the same spawning habitat, but their use is temporally segregated: ATS spawn in the fall and leave the system by early January, and SNS begin to migrate upstream in January to spawn in the spring. However, because SNS have occasionally been observed upriver in the fall, timing alone cannot reliably distinguish between species (Ingram 2014; Ingram and Peterson 2018; UGA Sturgeon Lab unpublished data). Because target length can be measured in sonar imagery, a sturgeon

target larger than a known SNS can logically be classified as an ATS if exhibiting characteristics of sturgeon.

Accuracy of SSS Detection

Although SSS has been used increasingly to detect large fishes, its reliability as a tool for quantitative fisheries research is still being assessed. Issues related to the effects of environmental conditions as well as user proficiency all can affect the accuracy and precision of the information generated with this technology. Environmental and operational variables can affect a sonar beam's ability to insonify (hit and reflect off of) a fish, and the SSS's ability to produce clear, high-quality, interpretable imagery (Fish and Carr 1990). Wind, waves, and currents may affect the trajectory path and stability of the transducer. Water temperature and salinity density gradients change the attenuation of the acoustic signal. The material makeup of the substrate or targets being imaged all can affect the angle and strength of the return signal. Although environmental variables cannot be manipulated, survey periods can be selected for optimal conditions. There are several operational factors that must be considered as well. Survey speed and sonar ping rate are extremely important because they determine how much information is collected per unit of time in a survey. The ratio of water depth to beam range, known as depth:range ratio, must be appropriate to collect high quality data; depth should be 10-20% of the range (Fish and Carr 1990). To maintain optimal depth:range ratio, surveys can be conducted during flow events that create appropriate depth. Sonar frequency, gain settings, slant range correction, and beam range per side all affect the resolution, sensitivity, and final representation of SSS imagery. The amount of river channel covered by the sonar beams (swath) affects whether a fish can be detected at all. All of these factors contribute to the probability of insonification of a fish.

Side-scan sonar data quality is also affected by reader recognition - the ability of the operator to recognize a sturgeon target in the SSS imagery after it has been insonified. Correct identification of targets is important, as miscounts will affect the estimate of the population size, any inferences and conclusions of a study as well as any management decisions based on the data. A fish's depth, proximity to the transducer, movement during insonification, orientation (aspect angle in relation to sonar beam), and distance from transducer may affect its sonar image representation. Background substrate and sunken debris can affect a reader's ability to differentiate a sturgeon target from a background of boulders or large woody debris. Although habitat factors cannot be manipulated, reader experience and training are positively correlated with accurate target identification (Fleming et al. 2018; A. Kaeser, USFWS, personal communication). In a controlled experiment, Fleming et al. (2018) reported that reader false detection (7%) and misidentification (4%) of Alligator Gar in stocked ponds were relatively low. However, in natural systems, the accuracy of reader target identification cannot be easily verified; therefore, training the reader(s) to identify sturgeon is very important and cannot be overemphasized. Using multiple independent readers can reduce potential reader bias, and the percent of agreement between readers can serve as a measure of likelihood of the object being correctly identified as a sturgeon and provide data on the precision of the estimate. Side-scan sonar can be a powerful tool for fisheries scientists, but recognizing and accounting for the factors that affect insonification and target recognition are necessary for accurate enumeration of targets.

Population Estimation Techniques

There are several methods for estimating fish population size depending on factors including water body characteristics, species life history, and available capture methods. The

most traditional methods for estimating animal abundances involve subsampling the target population and then using CMR or depletion analysis. More recently, genetic analyses and point count methods have been developed to estimate abundance. Each design method lends itself to several abundance estimator options.

In its simplest form, CMR involves capturing fish, giving each individual a retainable mark or tag, releasing them, and subsequently recapturing them. Subsequent recaptures allow scientists to calculate abundance based on the proportion of previously-marked fish that were recaptured. Estimation methods for this type of sampling include Schnabel, Huggins, spatial capture, Pradel, Cormack-Jolly-Seber, Lincoln-Peterson, and Chapman Peterson methods (Ricker 1975), among others. For example, DeVries (2006) used robust Jolly-Seber models within program MARK (White and Burnham, Colorado State University) to estimate SNS abundance in the Altamaha River, Schueller and Peterson (2010) used Pradel models to estimate Altamaha River ATS juvenile recruitment, and unpublished analyses by the University of Georgia sturgeon lab used Huggins closed capture and spatial CMR models to estimate ATS recruitment in the Altamaha River. Each of these models is based on a set of assumptions – for example, some models work only for populations that are closed during sampling, but others can account for immigration and emigration. Care must be taken to select an appropriate model or results may be inaccurate. Additionally, all of these models make assumptions about mark retention and identification, distribution of the marked fish, and about the capture and recapture probability of unmarked and marked fish.

Depletion or removal sampling is often conducted in streams. A sampling method (e.g., electrofishing or seining) is used to capture target species in repeated passes at the same site where the specimens are temporarily removed without replacement until sampling has ended.

Study designs include single-pass, two-pass, and multiple-pass surveys (Lockwood and Schneider 2000). Abundance is then estimated using the Leslie method, DeLury method (Walter III et al. 2007), K-Pass Removal, multinomial-Poisson mixture modeling (Dorazio et al. 2005), among many other variations. Generally, depletion sampling requires the assumptions of population closure, constant catchability, and gear-species vulnerability; violations of those assumptions can lead to biased catchability coefficients and incorrect estimates of abundance (Ogle 2013).

Genetic analysis tools can be used to gain information about abundance by examination of microsatellites and single nucleotide polymorphisms (SNPs), for example. Generally, effective population size (N_e) is the size of a population experiencing random genetic change at the same rate as the actual population, and N_e can be estimated using genetic information. It does not always represent direct abundance due to sampling biases, but retains a relationship to abundance (Waldman et al. 2018). By examining microsatellite markers in the DNA of juvenile ATS from several rivers, Waldman et al. (2018) were able to estimate contemporary N_e for those populations. Additionally, Rawding et al. (2014) used juvenile genetic samples from Chinook Salmon to obtain an estimate of successful spawners; their results were statistically similar to independently estimated abundances based on redd counts, carcass tagging, and area-under-the-curve methods.

Modeling abundance based on point counts is an approach that was developed for terrestrial species, but has recently been adopted among some fisheries researchers. Repeated surveys based remotely sensed data allow researchers to count individuals of some fish species within a site. Using input from repeated count surveys, a hierarchical model (i.e., a multinomial mixture [N-mixture] model) can be used to estimate detection probability and abundance (Royle

2004; Kéry and Royle 2016). Detection of individuals is expected to be imperfect - by comparing observations from repeated counts within a site, it is possible to model the probability of detecting a target individual. Using that detection probability information, imperfect raw counts are adjusted to reflect an estimate of true abundance.

The issues researchers face by attempting to estimate endangered species like the Atlantic Sturgeon may be countered by using remoting sensing techniques like side-scan sonar. Combining count data from sonar imagery with population estimation models, such as N-mixture models, may allow for efficient abundance estimation of adult Atlantic Sturgeon in the Altamaha River, Georgia.

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Tables and Figures

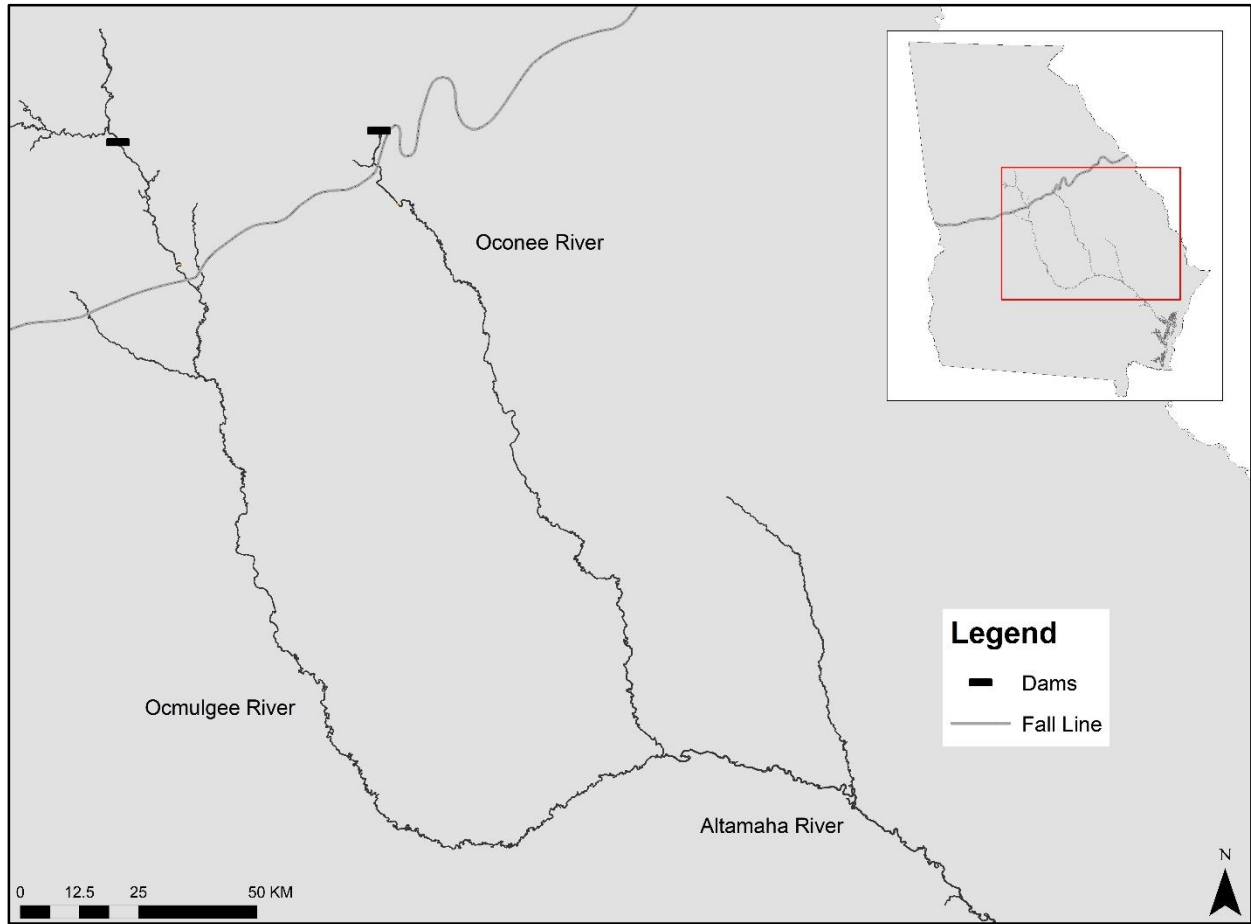


Figure 1.1. The Altamaha River System in central Georgia.

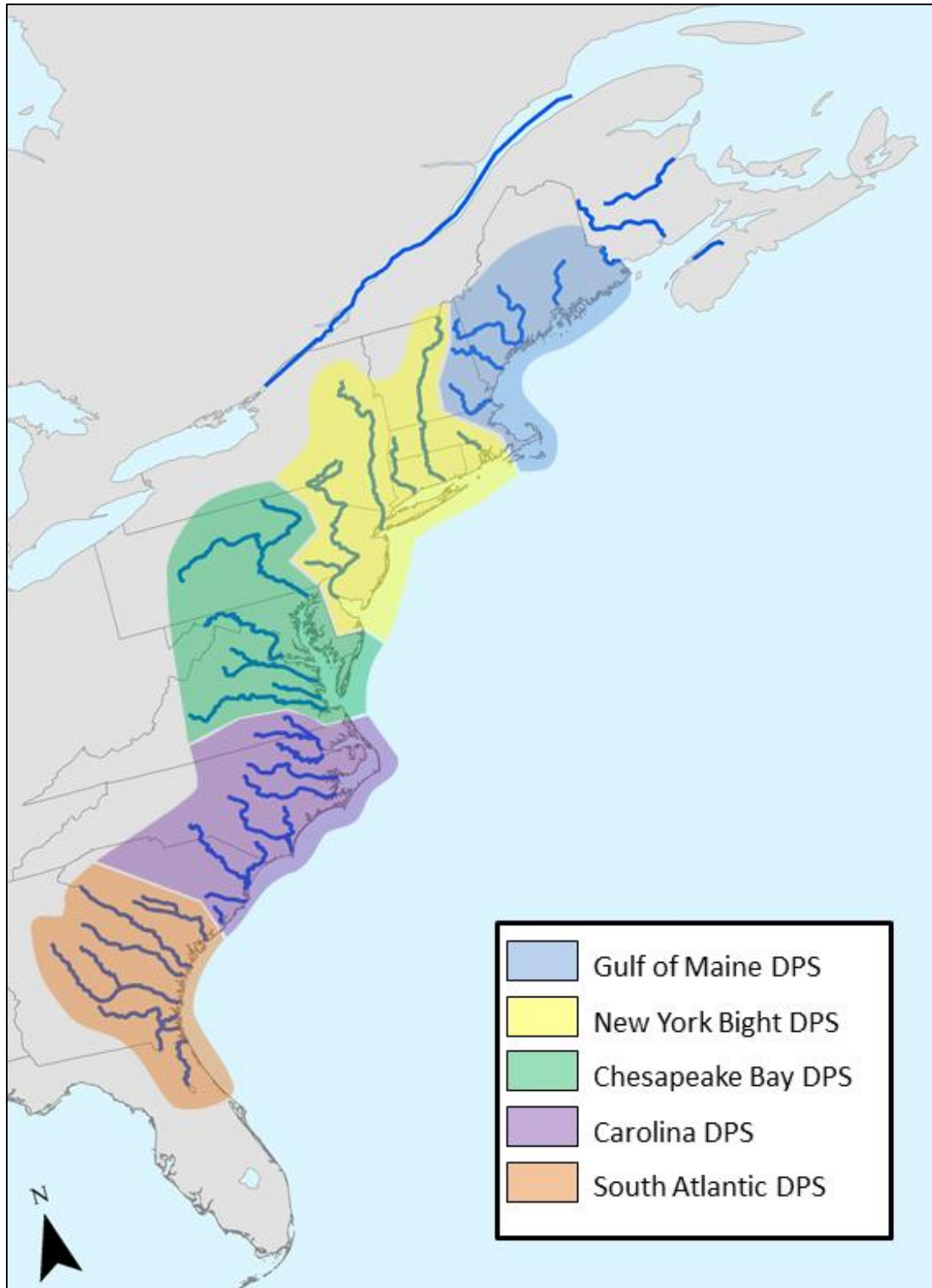


Figure 1.2. The five distinct population segments (DPSs) of the North American Atlantic Sturgeon: Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic.

CHAPTER 2

USING SIDE-SCAN SONAR TO QUANTIFY THE SPAWNING RUNS OF ATLANTIC
STURGEON IN THE ALTAMAHA RIVER, GEORGIA¹

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Abstract

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is a large, benthic, anadromous fish that occurs off the east coast of North America. Many populations were nearly extirpated by commercial harvest and the construction of dams on spawning rivers, which resulted in the species being listed as federally endangered in 2012. Recruitment studies indicate that the Atlantic Sturgeon population in the Altamaha River, Georgia is among the most robust within the South Atlantic Distinct Population Segment (DPS). Unfortunately, population estimates for the large, migratory adults are lacking because quantifying them is logistically challenging. The recent availability of cost-effective remote sensing technology offers a new method for estimating the abundance of adult spawners during their upstream migrations. In this study, I used side-scan sonar surveys to assess the run size of Atlantic Sturgeon throughout the entire navigable reach of potential spawning habitat (~550 river km) in the Altamaha River system, from September-November of 2017 and 2018. I used N-mixture models to estimate that there were 115 (95% CI: 104-129) and 82 (95% CI: 70-95) adult Atlantic Sturgeon in the 2017 and 2018 spawning runs. Abundance was positively associated with river depth in both years and availability of bedrock in 2018. Detection probabilities were 0.42 (SE = 0.13) and 0.14 (SE = 0.13), respectively. This study provides the first estimate of ATS spawner abundance in the Altamaha River since 2007 and the first since the species was listed as threatened, and my results suggest that the population has remained stable over the last decade. My results also provide managers with important quantitative data about the spawning habitat locations and characteristics. Compared to previous mark-recapture estimates of spawning run size, side-scan sonar was less invasive and required substantially less sampling effort.

Introduction

Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus* [ATS]) are anadromous, iteroparous fish belonging to the Acipenseridae family. They are found on the east coast of North America from the St Johns River, Florida to the St. Lawrence River, New Brunswick, Canada (ASSRT 2007). This species once spawned in 35 major coastal rivers, but currently spawns in only 20 (ASSRT 2007). Atlantic Sturgeon have experienced major population declines due mainly to overharvest and habitat degradation throughout the 19th and 20th centuries (Smith 1985), prompting the United States (U.S.) National Marine Fisheries Service to enact a federal fishing moratorium in 1998 (ASFMC 1998). Due to the major declines to populations and continuing threats, ATS were listed as Endangered under the Endangered Species Act in 2012 in four of five distinct population segments (DPS) and threatened in the remaining DPS (Figure 1.2; NOAA 2012a, 2012b).

Dams on many rivers block ATS from accessing historical spawning areas, which has prevented or slowed recovery in many systems (Smith and Clugston 1997; ASSRT 2007). Atlantic Sturgeon also remain vulnerable to numerous threats posed by urban, agricultural, and industrial development (Sloan 1987; Rogers and Weber 1994; Smith and Clugston 1997; ASSRT 2007) in addition to ship strikes (Brown and Murphy 2010; Balazik et al. 2012b), incidental bycatch (Collins et al. 1996; Smith and Clugston 1997), and poaching (ASSRT 2007).

The life cycle of Atlantic Sturgeon consists of both residential and migratory periods. Eggs are spawned over hard substrates by adults in upriver spawning areas. Larvae travel downstream, eventually reaching the estuaries where they remain as juveniles for up to 4 years (Bain et al. 2000, Kynard and Horgan 2002). Juveniles eventually outmigrate to the ocean and inhabit nearshore coastal waters and may occasionally return to their natal estuaries (Altenritter

et al. 2017; Wippelhauser et al. 2017; Fox and Peterson 2019). In southern rivers, males mature at 5 - 13 years and females at 7 - 19 years (Smith et al. 1982). Adult ATS disperse throughout nearshore waters of the western North Atlantic, but return to their natal rivers to spawn (Smith 1985). This generally occurs once every 1 - 5 years for males (Smith 1985) and 2 - 5 years for females. Recent evidence indicates that males spawn in consecutive years and females spawn less frequently (Van Eenennaam et al. 1996) and average spawning periodicity in the York River system, Virginia is 1.13 years for males and 2.19 years for females (Kahn 2019; Hager et al. 2020). Atlantic Sturgeon display sex-specific migratory behavior as well, where males generally enter spawning grounds earlier and stay longer, whereas females make directed runs to spawning grounds and leave soon after spawning (Van Eenennaam et al. 1996; Bain 1997; Kahn 2019). In Georgia, telemetered ATS of unknown sex make both types of migrations as they ascend the Altamaha River to spawn (Ingram and Peterson 2016). Adult ATS exhibit latitudinal variation in the timing of spawning; although the species is typically thought to spawn mainly in the spring, fall spawning migrations have been documented in some systems as far back as the early 1900s (Worth 1904, cited in Smith et al. 2015). In the York River and the Altamaha River, Georgia, there appears to be a single fall spawning run (Kahn et al. 2019; Ingram and Peterson 2016). Recently, dual (spring and fall) spawning migrations have been suggested for several rivers, including the Pamunkey and James rivers in Virginia (Balazik et al. 2012a; Hager et al. 2014; Balazik and Musick 2015), the Roanoke River in North Carolina (Smith et al. 2015), the Edisto and Combahee rivers in South Carolina (Smith et al. 1984; Collins et al. 2000), and the Savannah River on the Georgia/South Carolina border (Vine et al. 2019a). Despite the documentation of these apparent spawning runs, spawning (spring or fall) has not been directly observed in most

systems. Much remains unknown about the specific spawning sites, exact timing of spawning, and current abundance of adult spawners.

Although Atlantic Sturgeon are endangered, population assessment data generally are limited or lacking, especially for adults. The Altamaha River, located in the South Atlantic DPS, is the largest river system in Georgia and is thought to host a robust adult ATS population (ASSRT 2007). Mark-recapture surveys completed in the mid-2000s through present indicate consistent juvenile recruitment, suggesting that the population was relatively healthy (Schueller and Peterson 2010; Sturgeon lab, University of Georgia, unpublished data). Juvenile recruitment estimates are key to monitoring populations because they can provide timely information on current recruitment failures and successes (Peterson et al. 2000) and may provide insights on the number of successful spawners (Waldman et al. 2019). Regulation restrictions (Kazyak et al. 2020), migratory behavior, and varying spawning timing make quantifying adult sturgeon populations difficult. Peterson et al. 2008 and Schueller (2008) used a variety of population models and estimated the adult ATS population in the Altamaha River in 2004-2007 to be 89-385 adults. However, the abundance of adults in the Altamaha River in the period after the species was listed has not been estimated.

Side-scan sonar (SSS) is an emerging remote sensing technology that provides a new, efficient method for assessing ATS populations. This technology uses acoustic waves to produce images of sub-surface substrates and objects in water bodies and has been used effectively to map benthic habitats in riverine and estuarine areas (Kaeser and Litts 2008, 2010; Kaeser et al. 2012; Litts and Kaeser 2016; Richter et al. 2016; Walker and Alford 2016; Graham et al. 2017; Schooley and Neely 2017). Recently, SSS has been used to detect and count several large fish species such as Alligator Gar (*Atractosteus spatula*; Fleming et al. 2018), Paddlefish (*Polydon*

spatula; Hale et al. 2003), and several sturgeon species (Nealson and Brundage 2007; Flowers and Hightower 2013, 2015; Flowers 2015; Hughes et al. 2018; Vine et al. 2019b; Andrews et al. 2020; Kazyak et al. 2020). Adult ATS are suitable for SSS detection because their large size, air bladder, and bony scutes reflect sonar well. Their benthic, upstream orientation in rivers presents a relatively distinct target that can be identified in sonar images (Flowers and Hightower 2013).

Quantified population estimates are vital and legally required for assessing the recovery of endangered species like the Atlantic Sturgeon. The interim recovery plan for ATS outlines major priorities for the species, including gaining a better understanding of population dynamics, distribution, and trends, and developing standardized methods for determining abundance (NOAA 2017). Estimates of the number of adult spawners can provide important information about population trends within a river and allow for comparisons among populations in different rivers. With a better understanding of abundance and population dynamics, managers can take specific actions to increase recruitment and survival and to help meet recovery goals and ensure sustainable populations. The primary objective of this study was to estimate the abundance of the adult ATS spawning run within the Altamaha River system and its tributaries during the putative fall spawning period.

Methods

Study Area

This study occurred in the upper Altamaha River system in central-northern Georgia (Figure 2.1). It is longest free-flowing river system occupied by ATS in the South Atlantic DPS of the species' range and the largest drainage area east of the Mississippi River (Rogers et al. 1994). In this system, the Ocmulgee and Oconee rivers flow together to form the mainstem Altamaha River; from this confluence, the Altamaha River then flows uninterrupted to its mouth

at the Atlantic Ocean for 207 river kilometers (rkm). Above the confluence, the Ocmulgee River is impounded by Juliette Dam at rkm 368. The Oconee River is impounded by Sinclair Dam 231 rkm above the confluence. Both tributaries originate in the Piedmont ecoregion, and the fall line (which marks the boundary between the Piedmont and the coastal plain) begins in the Ocmulgee River at rkm 329 and the Oconee River at rkm 224.

Above the fall line, the rivers' natural substrates feature rocky shoals interspersed with sand and loam substrates. Below the fall line, substrates are mostly sand with occasional shoal habitat sparsely distributed in the Altamaha River and more abundantly in the Ocmulgee and Oconee rivers (EPD 1998, 2003; Litts and Kaeser 2016). Gradients of each river range from 0.17-0.26 inclusively (Litts 2013). The depths of the rivers during the fall months range from < 1 m to 10 m. The average wetted widths of the rivers vary among the Oconee (89 m), Ocmulgee (77 m) and Altamaha mainstem (110 m: Rogers et al. 1994; 160 m: Litts 2013); river width and depth are greatly influenced by drought and short-term rain events. The Ocmulgee and Oconee rivers contribute about the same discharge and are generally in phase during cool, wet periods and generally out of phase during warmer, tropical storm periods (Rogers et al. 1994). The entirety of the Altamaha River system below Juliette and Sinclair dams is designated as Atlantic Sturgeon critical habitat (NMFS et al. 2017).

The study area encompassed 432.7 contiguous rkm (Figure 2.1), including 227.0 rkm of the Ocmulgee River, 156.2 rkm of the Oconee River, and 49.4 rkm of the Altamaha River below the confluence. Preliminary SSS survey work was conducted in 2015 to test the equipment and technology, and to ensure that the study area was navigable. These river reaches were selected based on Ingram and Peterson's (2016) telemetry study of putative spawning ATS from 2011 to 2014. Although potential suitable spawning habitat (i.e., rocky shoals) has been identified

throughout the Altamaha River system (Litts and Kaeser 2016), specific ATS spawning locations have not yet been confirmed (Rogers and Weber 1994; DeVries 2006; Ingram and Peterson 2016). In 2018, the study area was expanded to include additional reaches on the upper ends of the Oconee and Ocmulgee rivers, encompassing a total of 550.3 contiguous rkm, including 276.3 rkm of the Ocmulgee River, 224.6 rkm of the Oconee River, and 49.4 rkm of the Altamaha River below the confluence.

Data Collection

Side-scan sonar surveys were conducted during September-November in 2017-2019. Surveys were accomplished using two identically-equipped 4.3-m motorized boats outfitted with consumer-grade Humminbird 1199ci HD SI combo sonar units with bow-mounted sonar transducers (Humminbird, Johnson Outdoors, Racine, Wisconsin). Range was set to 30 m per side, frequency was set to 455 kHz, and ping per second rate was set to 'auto' for the duration of all surveys. Each boat was equipped with flood lights to allow for nighttime operation. During surveys, the boats traveled downriver at ~6-10 kph to maximize sonar image quality (Flowers and Hightower 2013; Litts 2013). Full river system surveys consisted of continuously recording sonar data while traveling the entire study area. Beginning at the upper ends of the study area, two crews - one in each of the Oconee and Ocmulgee rivers - traveled continuously downstream. Both crews met at the confluence of the Ocmulgee and Oconee rivers and traveled the mainstem Altamaha River reach together. The boats followed the same path, with the second boat trailing 200 m behind the lead boat, except when shallow sandbars or immovable objects required an alternative path - because both boats surveyed the same area, I considered these to be "replicate passes" of sites. Each full survey took approximately 40-50 hrs, with crews working in 6-9 hr shifts. The continuous nature of these surveys allowed us to assume population closure (i.e.,

abundance did not change between replicate passes), as the survey did not contain pauses during which sturgeon could migrate up- or downriver to be double-counted.

During each survey, SSS data - including imagery, depth, latitude, longitude, date, and time - were logged using the Humminbird unit for later processing. Sonar imagery was recorded in one-hour segments to minimize computer memory issues during data processing. Survey crews also documented location information data for visual observations of ATS and other large aquatic species like longnose gar (*Lepisosteus osseus*), blue catfish (*Ictalurus furcatus*), channel catfish (*Ictalurus punctatus*), flathead catfish (*Pylodictis olivaris*), alligators (*Alligator mississippiensis*), and turtles (Families *Chelydridae*, *Emydidae*, *Kinosternidae*, *Trionychidae*).

Data Processing

I used SonarTRX SI with PlusPack (Leraand Engineering, Honolulu, Hawaii) to convert raw data into georeferenced image tiles, which were uploaded into ArcGIS suite (v 10.7, Environmental Systems Research Institute [ESRI], Redlands, California). ArcCatalog was used to mosaic tiles into a rectified sonar image mosaic, or “sonar image map,” with the water column intact by following steps outlined by A. Kaeser (personal communication). Images were then imported into ArcGIS by creating empty mosaic datasets, adding rasters, building footprints, generating seamlines, and building overviews. Finished mosaic images for each survey were visually examined in ArcMap.

In ArcMap, river channel polygons obtained from Litts and Kaeser (2016) were manually rectified to match 2017 satellite imagery (United States Department of Agriculture-Farm Service Agency Aerial Photography Field Office [USDA-FSA APFO]). Because the study rivers are dynamic, reported rkms for various features, including the confluence, varied by literature source (i.e., Rogers and Weber 1994; Litts and Kaeser 2016). I standardized rkms by placing the confluence at rkm 207, the same location reported by Litts and Kaeser (2016), and delineating

up- and down-river rkms accordingly. Substrate data were obtained from Litts and Kaeser (2016). The entire study area (concurrent with 2018 surveys) was divided into 0.1 km sections to create a total of 5503 sites (2763 in the Ocmulgee, 2246 in the Oconee, and 494 in the mainstem Altamaha). For each site, I calculated the area of each specific hard substrate type defined by Litts and Kaeser (2016; rocky fine, rocky boulder, bedrock) as well as total area of combined hard substrate types. Depth for each site varied for each survey and was calculated from recorded sonar data, averaged over each site.

Ensonified targets that appeared to be adult sturgeon (“potential sturgeon targets”) were marked in ArcMap by visually examining SSS imagery. The primary sonar imagery reader used a training module developed to identify sturgeon targets in side-scan sonar imagery (A. Kaeser, personal communication) and had ~3 years of experience analyzing SSS imagery. Potential sturgeon targets were identified based on shape, benthic orientation, and “sonar shadow” characteristics. Although there are few other fish that grow to the size of adult ATS in the Altamaha River, Shortnose Sturgeon (*Acipenser brevirostrum*; SNS) do occur in the system. I established a minimum size cutoff of 1.1 m to distinguish between SNS and ATS. This was based on the fork lengths (FL) of the smallest adult ATS (1079 cm) and the largest adult SNS (1330 cm) observed during gill net surveys in the Altamaha River by Schueller and Peterson (2010) and Peterson and Bednarski (2013). The length of each potential sturgeon target was measured using tools within ArcMap. The difficulty of low-frequency ensonification of the long dorsal lobe of a sturgeon’s heterocercal tail has been documented (Kaeser et al. 2016); to be conservative, I assumed that GIS measurements of ensonified sturgeon represented FL of each fish. If the target itself did not provide clear enough contrast to the surrounding substrate to allow measurement, its shadow was measured instead, similar to Flowers and Hightower (2013). If a

sturgeon moved while being ensounded, length measurements could have been biased depending on the movement direction and orientation relative to the survey boat. I did observe some obviously distorted targets/shadows, but noted that these target lengths were unlikely to be accurate. I corroborated the GPS coordinates of visual sightings of ATS (jumping or surfacing) with some SSS detections of sturgeon targets to confirm presence and identification.

The survey with the greatest total number of ATS targets each year was chosen to represent peak abundance for that year. For the peak survey, I also calculated the “mean total targets” - the sum of all Ocmulgee and Oconee river targets, plus the mean of the replicate counts from the mainstem Altamaha River below the confluence (rounded up to the nearest whole fish). This indicated an exploratory analysis of the average number of targets that were observed via SSS that accounted for individuals that were potentially double-counted between replicate passes. Total ATS targets indicated the number representing all targets among all passes.

Abundance Estimation

I used a binomial N-mixture model (Royle 2004) to estimate the abundance of sturgeon. This model describes two processes: spatial variation in abundance and spatio-temporal variation in detection probability. Site-specific abundance is treated as a latent variable that must be estimated using repeated count data (Kéry and Royle 2016). The simplest formula for the N-mixture model is:

1. State process: $N_i \sim \text{Poisson}(\lambda)$
2. Observation process: $C_{ij}|N_i \sim \text{Binomial}(N_i, p)$

where N_i is the latent abundance state at site i ($i = 1, \dots, M$) within the study area; λ is the expected value of abundance at each site; C_{ij} is the count at site i on sampling occasion j ; and p is the probability of detecting an individual during a single occasion (Kéry and Royle 2016). The state process can be modeled using a count distribution such as the Poisson (P), Zero-Inflated

Poisson (ZIP), or Negative Binomial (NB) distribution. The latter two distributions both account for overdispersion of data (i.e., zero-inflated data), but because the NB distribution is known to result in unrealistic parameter estimates despite a seemingly better fit, the ZIP distribution is the preferred choice for overdispersed data (Joseph et al. 2009; Kéry and Royle 2016; Hughes et al. 2018).

The model requires replication in both space and time, with a recommendation of a minimum of 20 sites sampled and replication of some percentage of sites, with the most replication possible being preferable (Kéry and Royle 2016).

Key assumptions of the N-mixture model are:

1. Closure: within each site i , variation between counts from each repeat sampling is due to detection probability and not emigration or immigration of targets.
2. Zero false-positive errors: individual targets are not counted twice, and non-target species are not counted as targets.
3. Independence of detection probabilities: individuals are detected independently from each other.
4. Homogeneity of detection among N_i individuals: individuals at each site i on sampling occasion j have the same detection probability.
5. Parametric modeling assumption: an accurate distribution is chosen for the supplied data and distribution assumptions are checked using a goodness-of-fit (GoF) test.

Models were fit using the ZIP distribution for the state process. I performed Freeman-Tukey GoF tests on the base models by using the parametric bootstrap method with 1000 iterations to determine that the distribution fit my data.

My models included covariates based on the physical characteristics of the river. Because sturgeon spawn over hard substrates and are reported to occupy deep water (>11 m; ASSRT 2007), I included both as site covariates. I created a candidate set of 22 models for each year and

used Akaike's Information Criterion (AIC) to calculate AIC weights (ΔAIC) for each to determine which model best fit the data.

Site-specific abundance and total abundance were computed using the Empirical Bayes methods and 1000 iterations (Carlin and Louis 2000; Kéry and Royle 2016). These methods do not allow for the calculation of model-averaged estimates; therefore, my results represent the estimates from the single top model for each year. Data were analyzed using the R package 'unmarked' (Fiske and Chandler 2011). I conducted an exploratory data analysis to locate areas with a high concentration of sturgeon targets by estimating kernel density (sturgeon per km²) using ArcGISI (methods by Silverman 1986) for combined 2017-2018 ATS targets. Sturgeon were sometimes observed in groups, and a one-way analysis of variance (ANOVA) and post-hoc Tukey's Test was performed on sturgeon target group sizes to determine if they differed between rivers.

Results

In 2017 I completed three full river system surveys, each covering 432.7 rkm. In 2018 I completed two full surveys (550.3 rkm each) plus two tributary surveys (325.7 and 274.0 rkm). Unfortunately, in 2019 I was unable to conduct any full surveys due to low water levels. Completing each survey required 41 - 48 hours of continuous data collection (Table 2.1). In 2017, the greatest number of ATS targets occurred during the October 13th -14th survey; therefore, I used that survey in my analyses. Combined mean daily river temperatures from USGS streamgage stations 0221500 [Hawkinsville, GA; rkm 412] and 02225000 [Baxley, GA; rkm 180]) during the peak 2017 survey fluctuated from 25.2 - 27.3 °C (Figure 2.2). In 2018, the greatest total ATS targets of any full survey occurred during the October 13th -14th survey.

Combined mean daily river temperatures for the duration of the peak 2018 survey were 21.9-25.2 °C (Figure 2.2).

Target Detections

I detected 104 targets during the peak survey of 2017 (Table 2.2). Lengths of sturgeon targets varied from 0.83 to 2.26 m (presumed FL). Six targets <1.1 m were removed from further analysis, leaving a total of 98 ATS targets observed by both boats combined. Atlantic Sturgeon targets were located throughout the river system - 39% of the mean total targets observed in this survey were in the Ocmulgee River, 24% were in the Oconee River, and 37% were in the Altamaha River. The ratio of Oconee River to Ocmulgee River targets during this peak survey was 0.607. Sturgeon targets were found in sites with mean depths of 1.6-3.9 m, and at a maximum depth of 7.9 m. Thirty-four percent of total targets were observed alone, but most were observed in groups. In the Ocmulgee River, targets were observed alone and in groups of up to five fish; most sturgeon (71% of Ocmulgee River targets) were located between rkms 340 and 415. Oconee River targets were scattered throughout the range individually and in groups of up to 6 individuals, the latter of which were observed at rkms 249, 284, and 314. In the Altamaha River, targets were observed singly and in groups of up to 9 individuals. The 28 rkm below the confluence (rkms 179-207) contained most of mean total targets (92%). Fifteen total targets were detected (among both replicate surveys) in the 3-rkm stretch immediately below the confluence. A one-way ANOVA revealed that mean group size did not differ among the rivers ($F = 0.247$; $p = 0.863$).

I detected 54 targets during the 2018 peak survey (Table 2.2). Lengths of sturgeon targets varied from 0.80 to 2.41 m. Nine targets <1.1 m were removed from further analysis, leaving a total of 45 ATS targets observed by both boats. Atlantic Sturgeon targets were located throughout the river system. Of the mean total targets observed in this survey, 49% were

observed in the Ocmulgee River, 30% were in the Oconee River, and 22% were in the Altamaha River. The ratio of Oconee River to Ocmulgee River targets during this peak survey was 0.612. Sturgeon targets were found in sites with mean depths of 1.6-8.5 m and at a maximum depth of 9.7 m. Most targets were alone during the 2018 full survey (91%), with only two groups detected: one pair was observed at rkm 273 in the Ocmulgee River and another pair was observed at rkm 168 in the Altamaha River. In the Ocmulgee River, most sturgeon (67% of Ocmulgee River targets) were located between rkms 250 and 388. Four targets (22%) were also located within 7 rkm of the confluence. Oconee River targets were scattered throughout the range: 45% were located between rkms 269 and 286, two dispersed individuals (18%) were located at rkms 238 and 318, and four targets (36%) were located within 11 rkm of the confluence. In the Altamaha River, targets were scattered throughout the reach. Fifty-six percent of mean total targets were found in rkms 179 - 207, and the other 44% of targets were located further downstream in rkms 158-174. A one-way ANOVA revealed that mean group size did not differ among rivers ($F = 0.492$; $p = 0.69$).

Across both years, some river reaches appeared to be more heavily used by sturgeon than other reaches. More sturgeon targets were observed in the lower portion of the Oconee River than the upper portion. Specifically, 69% and 91% of targets were focused at rkm 280 and south, with kernel densities estimated to be greater between rkms 262-280, compared to the remainder of the Oconee where targets were more scattered (Figure 2.3). In the Ocmulgee River, targets occurred more frequently in the middle and lower reaches than in the upper portion of the river. Kernel densities were estimated to be slightly greater near the confluence and in several distinct river reaches (rkms 250-255, 369-392, and 405-418), compared to other river reaches (Figure 2.3). In the Altamaha River, many targets were located in sites at the confluence and in the 28

rkms immediately downstream. Specific locations of greatest sturgeon occurrence appeared to shift between study years.

Abundance and Detection Probability

A GoF Freeman-Tukey test performed on 2017 peak survey data revealed that the fit statistic indicated the data were a moderately good fit for the ZIP distribution (Freeman-Tukey = 159, $p=0.21$; Table 2.3; Kéry and Royle 2016). My top model in 2017 indicated that detection probability varied randomly among sites, and mean depth was a significant covariate in explaining the variation in abundance (Table 2.4). The model estimated that latent total abundance was 115 (95 % CI: 104 - 129) adult Atlantic Sturgeon and detection probability was 0.43 (SE=0.13; Table 2.5).

For the 2018 peak survey, a GoF Freeman-Tukey test showed that the observed data distribution was similar to the ZIP distribution (Freeman-Tukey = 81.1, $p=0.515$; Table 2.3). My top model indicated that none of the covariates explained the variation in my detection probability, but mean depth and area of bedrock explained the variation in abundance (Table 2.6). My top model estimated abundance and detection probability to be 82 (95 % CI: 72 - 95) adult Atlantic Sturgeon and 0.137 (SE=0.132; Table 2.5).

Discussion

This study provides the first estimate of ATS spawner abundance in the Altamaha River since 2007 and the first since the species was listed as threatened. In two of my three study years, I was able to scan nearly the entire potential spawning area, with the exception of some non-navigable river reaches above the study area. This is the most comprehensive SSS survey of spawning ATS in any southeastern river to date and one of the first to quantitatively link spawner

abundance to substrate type. The spatio-temporal nature of the hydroacoustic data I collected also provided insights into the specific timing of spawning and indicated potential spawning locations.

I estimated adult ATS spawner abundance in the upper Altamaha River system to be 115 (95 % CI: 104 - 129) during 2017 and 82 (95 % CI: 70 - 95) during 2018. These estimates are likely conservative counts of spawning ATS, in part because my estimates were based on the survey with peak sturgeon abundance, omitting any individuals that spawned before or after that peak survey. Also, because female ATS are present in spawning for a much shorter period than males (Van Eenennaam et al. 1996), I may have missed counting them during my surveys. However, based on the prior telemetry work by Ingram and Peterson (2016), my surveys occurred during the time period when most sturgeon were present on the spawning grounds. Although my study area was expanded in the second year of my surveys (2018), I believe these two estimates are comparable in number because only two targets (4% of all targets in the peak survey) were identified in the expanded reaches in 2018, both in the upper Ocmulgee River. I did observe some differences in the apparent orientation of ATS targets between the two years that may have contributed to the smaller spawning run size estimate for 2018.

In other rivers (e.g., the Hudson River), Atlantic Sturgeon congregate in groups as large as 100 fish in spawning and holding areas (Kazyak et al. 2020), but this does not seem to be the case in the Altamaha River. In 2017, 66% of all sturgeon targets were observed in groups of two - nine fish; in 2018, 90% of fish were detected alone.

Interestingly, Hurricane/Tropical Storm Michael passed through the study area just before the 2018 survey. Gulf Sturgeon (*Acipenser ocyrinchus desotoi*), subspecies of Atlantic Sturgeon in the Gulf of Mexico, outmigrated early following a hurricane event, potentially due to

increased river flows that may have triggered migratory behavior (Parauka et al. 2001; Heise et al. 2005). Recently, Hager et al. (2020) identified temperature, photoperiod, and a drop in barometric pressure (coinciding with onset of fall storms) as key characteristics instigating female ATS spawning.

Additionally, the 2017 peak survey occurred when water temperatures were 25.2-27.3 °C, above the upper limits of egg survival (Chapman and Carr 1995) and just before a drop in temperatures (Figure 2.2). In 2018, the peak survey occurred when water temperatures were 21.9-25.2 °C (Figure 2.2), within the limits of egg survival (ASFMC 2012). Because the 2018 survey occurred at lower water temperatures, peak spawning may have already passed and fish may have begun to outmigrate. Indeed, during the 2017 survey, most targets were in benthic positions facing upstream, as would be expected as if they were station-holding or staging to move upriver for a spawn. In contrast, many targets in the 2018 survey appeared to be suspended off the bottom of the river oriented in directions other than upstream.

Sturgeon distribution through the study area varied between study years, but distribution in the two major tributaries was similar in both years. In 2017, most ATS targets were observed either in the Altamaha (37% of all targets) or the Ocmulgee (39%) rivers; whereas, 49% of all targets were observed in just the Ocmulgee River in 2018. ATS staged in the upper Altamaha River before traveling up into the tributaries to spawn (Ingram and Peterson 2016). Because my surveys each represent only a ~45hr snapshot in time, I cannot conclude whether differences in target distribution actually correspond to a preference of one tributary over another during the entire spawning season. However, the ratio of targets in the Oconee River to targets in the Ocmulgee River was similar in both 2017 (0.607) and 2018 (0.611). Over a 3-year telemetry study, the ratio of Oconee:Ocmulgee spawning migrations was 0.689 (Ingram and Peterson

2016); this suggests that ATS in the system may demonstrate a consistent preference for spawning in the Ocmulgee over the Oconee River.

My sonar covered a swath of river 60 m wide, which was often less than the documented average wetted width of the Oconee (89 m), Ocmulgee (77 m), or Altamaha mainstem rivers (160 m), but there are several reasons why I believe my scans were sufficient to detect and count sturgeon. First, the wetted width data were collected during high spring flows for habitat mapping purposes (Litts and Kaeser 2016). The average depths of the Oconee, Ocmulgee, and Altamaha rivers during the spring habitat surveys (4.3 m, 3.7 m, and 2.7 m, respectively) were greater than mean depths during surveys in both October 2017 (2.0 m, 2.0 m, and 2.1 m) and October 2018 (2.2 m, 2.8 m, and 2.6 m). This difference indicates that the rivers were not at full wetted width during the SSS survey. Additionally, each boat attempted to remain in the thalweg, and sturgeon seemed unlikely to use the shallow edges of the river channels outside the reaches of my sonar swath.

Although bedrock appeared to be a factor affecting abundance in only the top model of 2018, many of the top models with $\Delta AIC < 2$ incorporated some form of hard substrate affecting abundance in both years of surveys. For both study years, bedrock consistently appeared to be the hard substrate that best explained variation in abundance. This finding suggests that during the spawning season, ATS are more likely to associate with bedrock than with other hard substrates classes (defined by Litts and Kaeser 2016), including rocky boulder, rocky fine, or combinations of hardbottom. Bedrock may be the preferred spawning substrate for ATS - in the Roanoke River, VA. Smith et al. (2015) captured fall-spawned Atlantic Sturgeon eggs in a shoal area near eddies created by bedrock outcroppings. Similarly, Gulf Sturgeon eggs have been collected at sites dominated by limestone bedrock and lesser amounts of fine gravel substrates in

the Suwanee, Choctawhatchee, Pea, and Apalachicola rivers (Sulak and Clugston 1998; Fox et al. 2000; Flowers et al. 2009).

The mainstem Altamaha River contained less availability of hard substrate than the two major tributaries, but hard substrate is prevalent in rkms 179-207 below the confluence, where 92% of mean total targets were located in 2017 (Figure 2.4). During 2018, sturgeon were dispersed through a wider area. Telemetered ATS were observed previously using this same reach below the confluence, particularly rkms 205-207 (Ingram 2014). This area is also a confirmed spawning ground for SNS (Devries 2006). Within this heavily used reach of the mainstem Altamaha River lies the Edwin Hatch Nuclear Plant, located at rkm 180. Across both study years, eight ATS targets were observed within 3 km near the plant in sites containing hard substrates - characteristics of potential spawning habitat. The plant conducts annual dredging activities between August and November and features river water intakes and hot water discharge pipes (Southern Nuclear Operating Company 2004), which may pose a hazard to ATS using adjacent potential spawning sites.

Generally, ATS target locations were widely dispersed throughout the Oconee River across both years, although they were frequently detected in between rkms 273-287 (Figure 2.3). Interestingly, sites in this reach featured a maximum of 0.37% hard substrate, though sites just above and below these contained up to 13.4% hard substrates. Litts and Kaeser (2016) identified rkms 320-366 as having higher portions of hard substrate relative to other substrates, but I only detected a total of three ATS targets in that reach, all in 2017 (Figure 2.3). Low flow may have been a barrier in the Oconee River for migrating sturgeon (Ingram and Peterson 2016). The Oconee River featured some of the shallowest depths I observed in the entire system in both 2017 and 2018. The difference in sturgeon target distribution between study years may indicate

that they use different spawning sites in different years, possibly when low flows impede access to some areas. Consequently, shallow depths may have limited detection of sturgeon in this river as well.

In the Ocmulgee River, targets appeared to occur more frequently in areas with greater availability of hard substrates (Figure 2.4), and Ingram (2014) also detected ATS in many of the areas where I detected them. Bedrock was less common in the Ocmulgee River than the Oconee River, with a maximum site availability of 10.6%. However, sites with the greatest concentration of targets featured total hard substrate availabilities of up to 82.7% (Figures 2.3, 2.4). Although bedrock is important for ATS spawning, other hard substrates are also used (Flowers et al. 2009).

Depth was an important covariate for predicting sturgeon abundance in my top models for both 2017 and 2018. This was expected because depth is known to be an important factor for Atlantic Sturgeon spawning (ASSRT 2007) and it was a significant site covariate for predicting abundance in the Savannah River (Vine et al. 2019b). However, depth, like flow, can change dramatically based on rain events or dam discharges, and the temporal variation in river depth may change the behavior (i.e., location) of ATS spawners. This weather-related change in behavior is the reason for my use of observed survey depths in my models. Targets were observed in sites with mean depths of 1.6-3.9 m (2017) and 1.6-8.5 m (2018), with maximum depths each year of 7.9 m (2017) and 9.7 m (2018). Potential spawning has been recorded at depths of 11-27 m (Borodin 1925, Leland 1968, Scott and Crossman 1973, Crance 1987, Bain et al. 2000), much deeper than my river system during my fall surveys (the deepest hole I observed was ~10 m). However, spawning Atlantic Sturgeon in the Saint John River, New Brunswick occupied mean depths of 3.85 m despite availability of depths up to 9 m (Taylor and Litvak 2017). Additionally, Smith et al. (2015) collected ATS eggs at depths of <5 m in the Roanoke

River, and Fox et al. (2000) collected Gulf Sturgeon eggs at 1.4-7.9 m in the Choctawhatchee and Pea rivers. Given the variations in reported spawning depths, the presence of ideal spawning substrate may be more important than depth in determining where ATS spawn.

Comparison to Previous Altamaha Spawning Run Estimates

My estimates of spawning run size (82 and 115 fish) were lower or equal to those previously produced by traditional mark-recapture studies in the Altamaha River estuary, depending on the estimation method (Figure 2.5). Peterson et al. (2008) used the Schnabel method to estimate a population of 324 adult ATS (95% CI: 143 - 667) in 2004 and 386 adults in 2005 (95% CI: 216 - 787). Schueller (2010) used open population POPAN models to estimate that there were 89 - 213 adults each year from 2004 - 2007. However, because those estimates were based on sturgeon tagged in the estuary, they may have overestimated the adult ATS population. Atlantic Sturgeon are periodic spawners and do not spawn every year (Smith 1985, ASSRT 2007, Kahn 2019). Non-natal fish may be utilizing the estuary (Fox et al. 2018a, 2018b), as well as non-migrating natal fish: telemetry data from Ingram and Peterson (2016) indicated 33-64% of adult ATS did not make a spawning run in the year they were tagged in the Altamaha River estuary. In fact, most of the adults (>95%) tagged in the Altamaha River estuary in 2006 and 2007 were not running ripe (i.e., not being ready to spawn; Schueller 2008). Similarly, historical commercial fisheries in South Carolina found that 39-61% of females were not ripe when captured in the estuary (Rogers et al. 1994). The documented presence of non-spawning and non-natal ATS in Georgia estuaries suggests that previous estimates of the estuarine population of adult ATS are not representative of the annual spawning run size located in the putative spawning area (where my estimates are based). Additionally, my estimates were most likely conservative compared to true spawning run abundance due to the nature of the targets I

decided to mark – targets were marked if all characteristics were met, but I excluded some targets with less reliable characteristics that may have been sturgeon.

Because this study occurred exclusively on the putative spawning grounds in the upper Altamaha River system, I should not have detected any non-natal or non-spawning fish; therefore, I expected that my 2017-2018 estimates of spawner abundance would be smaller than the previously reported adult abundances in the system. Kahn et al. (2019) suggested that an estimate of fall spawning run size could be derived from Peterson et al.'s (2008) estimate of estuarine adult abundance by modifying that estimate to account for the estimated proportion of adults in the estuary in the spring that were putative fall spawners. Ingram and Peterson (2016) estimated this number to be about 37 %. This modification resulted in adjusted estimates of 876-1043 spawning adult ATS per year in 2004-2005 (Figure 2.5) - still substantially more annual spawners than I observed in my study.

I propose a different approach to rectifying previous estimates, under the assumption that both two-step and one-step spawners mix in the estuary. By simply multiplying Schueller's (2008) estimate by the average proportion of Altamaha River fish that made spawning runs each year (71%; from Ingram and Peterson 2016), I derived an estimate of 64-153 adult ATS spawners annually in 2004-2007 - this is comparable to my SSS-based estimates and suggests that the population has remained relatively stable over the past decade.

The effort required to obtain data for my SSS-based spawner abundance estimates was considerably lower than what was required for Peterson et al.'s (2008) and Schueller's (2008) estimates. Obtaining viable population estimates via mark-recapture required 2-4 people to conduct 40-62 days of gill netting. I conducted 3-4 SSS surveys per season, with each survey requiring 4-6 people and taking ~45 hours of field effort; this resulted in considerable savings of

time, fuel, and fieldwork expenses. At present, the time required to process SSS data and manually count sturgeon was considerable (as also noted by Kazyak et al. 2020) and required specific software and familiarity with ArcGIS. For this study, a trained reader required ~3 days to review one complete (550 rkm) survey of the upper Altamaha River system, and surveys were examined multiple times for consistency. Model development and processing time were substantial but, once completed, my N-mixture models required only ~1 hr to return results. Some recent studies have successfully automated the counting of individual fish in SSS imagery (Lawson et al. 2019, Andrews et al. 2020); by incorporating automation of post-processing and counting, a SSS-based population study may eventually be streamlined to require far fewer resources than a traditional mark-recapture-based study. In addition to reducing fieldwork labor and costs, using SSS was non-invasive and did not require interaction with fish, essentially eliminating stress and the chance of injuring endangered ATS.

Comparison to Other ATS Populations

Although other researchers have used SSS to study ATS, dissimilar objectives and methodologies make direct comparisons of the results difficult. Flowers and Hightower (2013; 2015) reported abundances of 0 - 1944 ATS >1 m from SSS work in the coastal portions of six rivers in the Carolinas (North and South). However, the objective of that study was to estimate estuarine ATS, and those estimates almost certainly include non-natal and non-spawning ATS, as well potentially large adult SNS - a byproduct of a 1-m length cutoff.

Kazyak et al. (2020) estimated daily and cumulative seasonal spawner abundances in the Hudson River, likely the largest population of ATS in the U.S., by incorporating SSS with acoustic telemetry detection data. The cumulative seasonal spawner abundance in the Hudson River was estimated to be 466 (95% Credible Interval: 310-745), ~4-6 times larger than my estimates for the Altamaha River. However, because my estimates were calculated from a single,

peak SSS survey, they may be more directly comparable to Kazyak et al.'s daily spawning abundances, which varied from 93 (95% CrI: 61-149) to 118 (83-179) individuals. This credible interval overlaps with the 95% CI of my survey estimates. However, I surveyed almost the entire putative spawning area in the Altamaha River system, and Kazyak et al. only surveyed one large spawning reach. Therefore, the true number of daily spawners, and thus cumulative spawners, in the Hudson River is certainly larger than that in the Altamaha River.

Using SSS and an N-mixture model (with a different probability distribution and prediction method from what I used), Vine et al. (2019b) estimated 35-55 mean daily ATS spawners during the 2017 fall spawning period in the Savannah River, Georgia/South Carolina. Because the surveys did not cover the entire putative spawning area, this is likely an underestimate of the cumulative number of spawners in that system. Regardless, I would expect fewer spawners in the Savannah River, considering that the Altamaha River system is much larger, unimpounded, and is thought to have the largest ATS population in the southeastern U.S. (ASSRT 2007).

Kahn et al. (2014, 2019) used mark-recapture data and a Jackknife model in program CAPTURE to estimate spawning run abundances of 52-219 adults (lowest to highest 95% CI: 35 - 298) in the York River system, Virginia from 2013 - 2018. Although the 95% confidence intervals for my Altamaha River estimates overlap with Kahn et al.'s results, differences in study objectives, methods, and modeling preclude direct comparison of results. Kahn et al.'s (2019) spawning run abundances may represent total cumulative abundances; whereas, mine more closely represent daily abundance.

Clearly, there is not a "one-size-fits-all" method for using SSS to enumerate sturgeon, and that different objectives and study sites require different methods. The use of SSS in the Altamaha River system was quite challenging, compared to some other systems. The commercial

SSS systems used by many other fisheries studies (e.g., Flowers and Hightower 2015, Hughes et al. 2018, Kazyak et al. 2020) employ a towfish-mounted sonar transducer that would not be feasible in the shallow, rocky waters of the upper Altamaha River system. Subtle differences in research question (e.g., “daily spawner abundance” vs. “cumulative spawning run size”), or in survey extent (some or all of the putative spawning area), make comparing spawning run sizes between existing studies difficult. In addition, there are processes inherent in using remote sensing technology such as how environmental variables affect the ensonification and detection of (and ability to count) an individual sturgeon that have not yet been explored.

Management Applications

In addition to providing much needed updates to the decade-old estimates of adult ATS in the Altamaha River, my data can help inform the management and conservation of ATS in system in other ways. I observed Atlantic Sturgeon targets in likely spawning and holding habitats throughout the upper Altamaha, Oconee, and Ocmulgee rivers, including immediately upriver of the Edwin Hatch Nuclear Plant. The presence of potential spawning sites in such close proximity to this facility raises the question of whether plant operation and maintenance activities (e.g., dredging) may pose a potential hazard to spawning ATS (Reine et al. 2014); the hot water discharged by the facility may negatively affect all life stages. Bridge construction and maintenance projects were underway in the Altamaha River system during all years of my surveys, and these activities may have altered habitat and negatively affected sturgeon behavior. Future studies can refine detection of spawning sites by coupling fine-scale telemetry and egg/larval surveys in sites where SSS documented the occurrence of ATS targets in conjunction with hardbottom habitat; once identified, these spawning sites can be protected through targeted regulations by management agencies.

Using SSS to estimate spawning run size in the Altamaha River was much less invasive than

previous studies that relied on mark-recapture methods. My results suggest that the Altamaha River Atlantic Sturgeon population has remained relatively stable since the early 2000s, which implies that the current management practices are minimally sufficient for maintaining the current number of spawners. Assuming there is carrying capacity in the river, tweaking management strategies to enhance the number of spawning individuals may be desirable. Results from continued monitoring efforts would allow for refinement of management approaches as necessary. My estimates of the number of spawners are comparable to estimates derived from traditional mark-recapture methods and suggest that SSS coupled with N-mixture models may be a viable alternative for monitoring endangered Atlantic Sturgeon populations. My sonar surveys identified specific sites where ATS targets were found and which may be potential spawning sites. The N-mixture models I used allowed for the estimation of detection probability and abundance, as well as the identification of key covariates that may affect each parameter - a topic for future study. The methods used in this study can easily be adapted for use in other river systems to provide directly comparable information on spawner abundance and locations.

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Tables and Figures

Table 2.1. Field effort for side-scan sonar surveys in the Altamaha River system in October 13th-14th of 2017 and 2018. Effort is given in hours and river kilometers surveyed. Oconee and Ocmulgee river sections were surveyed concurrently by one boat each, which met at the confluence of the two tributaries and surveyed concurrently in the mainstem Altamaha River.

Survey Year	River	Survey Duration (hrs)	Km Surveyed
2017	Oconee	22	156.2
	Ocmulgee	34	227.1
	Altamaha	7	49.4
	<i>All</i>	<i>41</i>	<i>432.7</i>
2018	Oconee	28	224.6
	Ocmulgee	41	276.3
	Altamaha	7	49.4
	<i>All</i>	<i>48</i>	<i>550.3</i>

Table 2.2. Number of Atlantic Sturgeon targets identified in side-scan sonar imagery during peak 2017 and 2018 surveys, both occurring October 13th-14th of each year. Oconee and Ocmulgee river sections were surveyed concurrently by one boat each, which met at the confluence of the two tributaries and surveyed the mainstem Altamaha River together, hence two replicate counts are reported for the Altamaha River. Targets were removed from analysis if length was <1.1 m. Total ATS targets represent the total number of targets identified in all rivers and passes after removal of fish below the cutoff length. Mean total targets reflects the sum of Oconee and Ocmulgee River counts, plus the mean of the two Altamaha River replicate counts.

Survey Year	Oconee River	Ocmulgee River	Altamaha River		Overall Total Targets	n Targets Removed (<1.1 m)	Total ATS Targets	Mean Total Targets
			Replicate 1	Replicate 2				
2017	17	28	29	24	104	6	98	72
2018	11	18	6	10	54	9	45	37

Table 2.3. Parametric bootstrap goodness-of-fit (GoF) test results for the base Zero-Inflated Poisson models on side-scan sonar survey data collected in the Altamaha River in October 13th-14th in both 2017 and 2018. One-hundred bootstrap iterations were used to estimate Freeman-Tukey statistics. Estimates of the t-statistic (t_0) resulting in probability (p) near 0.5 indicate good fit of Zero-Inflated Poisson probability distribution to the sample data distribution.

Survey Year	Freeman-Tukey	
	t_0	p
2017	159.0	0.208
2018	81.1	0.515

Table 2.4. Model selection AIC table for N-mixture models estimating Atlantic Sturgeon abundance from a side-scan sonar survey in October 2017 in the Altamaha River, Georgia. Each model includes potential covariates affecting sturgeon abundance (λ) and detection probability (p). The number of parameters (K), Akaike's Information Criterion (AIC), and difference in model AIC from the top model's AIC (Δ AIC) were identified for each model. The dashed line represents the threshold of the Model Confidence Set with Δ AIC <2.00.

Model	K	AIC	Δ AIC
p(~1), λ (~depth)	4	724.13	0.000
p(~depth), λ (~1)	4	724.21	0.079
p(~depth), λ (~bedrock)	5	725.01	0.879
p(~1), λ (~depth + bedrock)	5	725.17	1.040
p(~1), λ (~depth + hard substrate)	5	725.34	1.212
p(~depth), λ (~depth)	5	725.37	1.239
p(~depth), λ (~hard substrate)	5	725.44	1.318
p(~depth), λ (~rocky fine)	5	725.63	1.502
p(~1), λ (~depth + rocky fine)	5	725.75	1.624
p(~depth), λ (~rocky boulder)	5	725.92	1.796
p(~1), λ (~depth + rocky boulder)	5	726.03	1.902
p(~depth), λ (~depth + bedrock)	6	726.22	2.094
p(~depth), λ (~depth + hard substrate)	6	726.56	2.432
p(~depth), λ (~bedrock + rocky boulder)	6	726.91	2.782
p(~depth), λ (~depth + rocky fine)	6	726.97	2.841
p(~1), λ (~depth + bedrock + rocky boulder)	6	727.15	3.024
p(~depth), λ (~depth + rocky boulder)	6	727.21	3.085
p(~depth), λ (~bedrock + rocky boulder + rocky fine)	7	728.09	3.966
p(~depth), λ (~depth + bedrock + rocky boulder)	7	728.18	4.057
p(~1), λ (~depth + bedrock + rocky boulder + rocky fine)	7	728.55	4.427
p(~depth), λ (~depth + bedrock + rocky boulder + rocky fine)	8	729.55	5.425
p(~1), λ (~hard substrate)	4	738.59	14.453

Table 2.5. Estimates of detection probability (\pm standard error [SE]) and abundance (95% Confidence Interval [CI]) of Atlantic Sturgeon spawners in the Altamaha River system in Fall 2017 and 2018.

Survey Year	Top Model	Overall Detection Probability (\pm SE)	Abundance (95% CI)
2017	$p(\sim 1), \lambda(\sim \text{depth})$	0.430 (0.130)	115 (104 - 129)
2018	$p(\sim 1), \lambda(\sim \text{depth} + \text{bedrock})$	0.137 (0.132)	82 (70 - 95)

Table 2.6. Model selection AIC table for N-mixture models estimating Atlantic Sturgeon abundance from a side-scan sonar survey in October 2018 in the Altamaha River, Georgia. Each model includes potential covariates affecting sturgeon abundance (λ) and detection probability (p). The number of parameters (K), Akaike's Information Criterion (AIC), and difference in model AIC from the top model's AIC (Δ AIC) were identified for each model. The dashed line represents the threshold of the Model Confidence Set with Δ AIC <2.00.

Model	K	AIC	ΔAIC
p(~1), λ (~depth + bedrock)	5	515.56	0.00
p(~1), λ (~depth)	4	515.95	0.39
p(~depth), λ (~bedrock)	5	515.95	0.39
p(~depth), λ (~1)	4	516.31	0.75
p(~1), λ (~depth + rocky fine)	5	516.65	1.09
p(~depth), λ (~rocky fine)	5	517.02	1.46
p(~1), λ (~depth + bedrock + rocky boulder)	6	517.17	1.61
p(~1), λ (~depth + hard substrate)	5	517.46	1.90
p(~depth), λ (~depth + bedrock)	6	517.56	2.00
p(~1), λ (~depth + rocky boulder)	5	517.58	2.02
p(~depth), λ (~bedrock + rocky boulder)	6	517.59	2.03
p(~depth), λ (~hard substrate)	5	517.83	2.27
p(~depth), λ (~rocky boulder)	5	517.92	2.36
p(~depth), λ (~depth)	5	517.95	2.39
p(~1), λ (~depth + bedrock + rocky boulder + rocky fine)	7	518.06	2.50
p(~depth), λ (~bedrock + rocky boulder + rocky fine)	7	518.49	2.93
p(~depth), λ (~depth + rocky fine)	6	518.65	3.09
p(~depth), λ (~depth + bedrock + rocky boulder)	7	519.17	3.61
p(~depth), λ (~depth + hard substrate)	6	519.46	3.90
p(~depth), λ (~depth + rocky boulder)	6	519.57	4.02
p(~depth), λ (~depth + bedrock + rocky boulder + rocky fine)	8	520.06	4.50
p(~1), λ (~hard substrate)	4	521.77	6.21

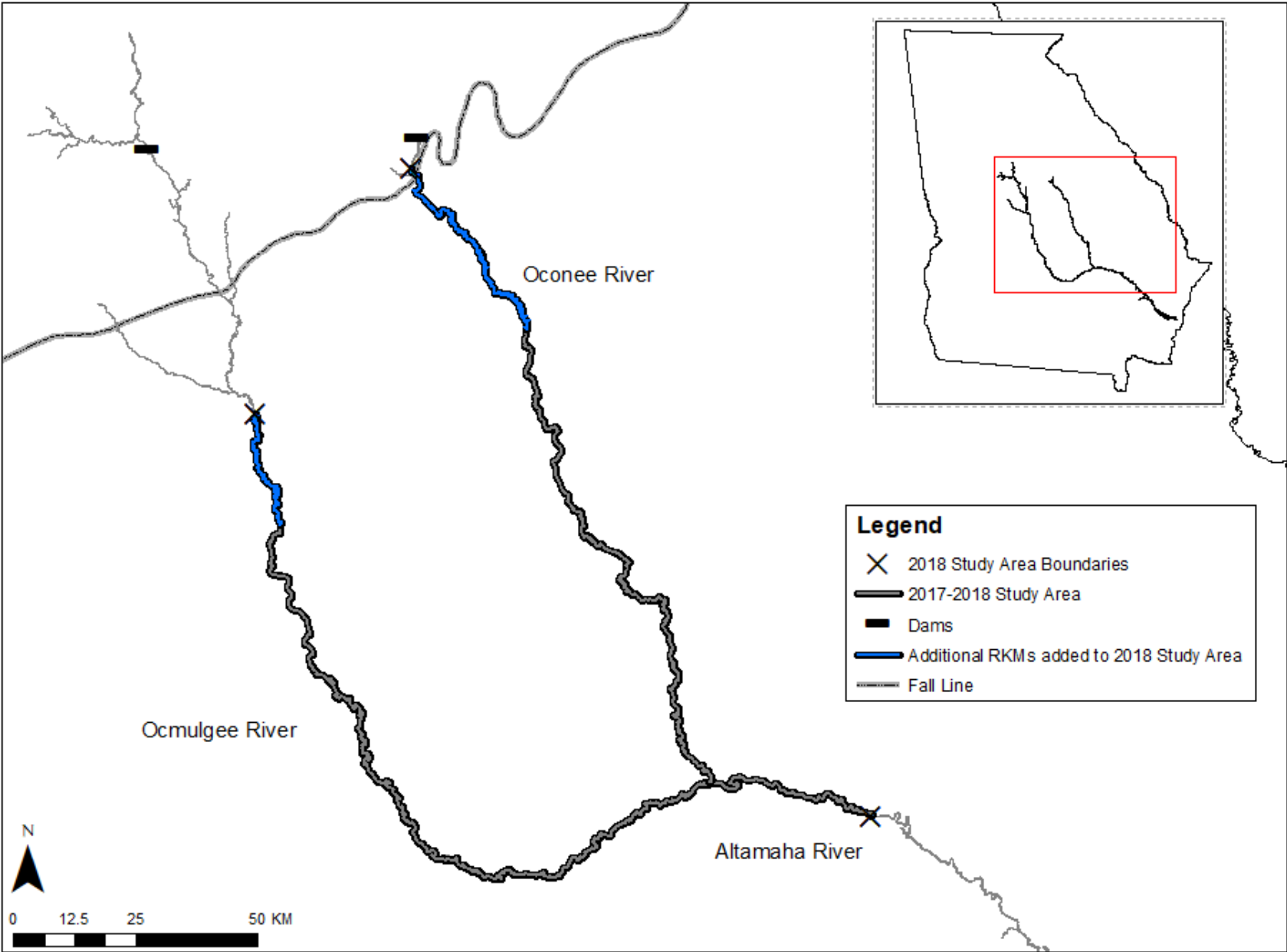


Figure 2.1. Map of the Altamaha River system in Georgia including the Ocmulgee and Oconee river tributaries and dam locations on the upper reaches of each tributary. The side-scan sonar study area in Fall 2017 is depicted in dark gray, and the study area in Fall 2018 is depicted by the dark gray plus additional blue reaches.

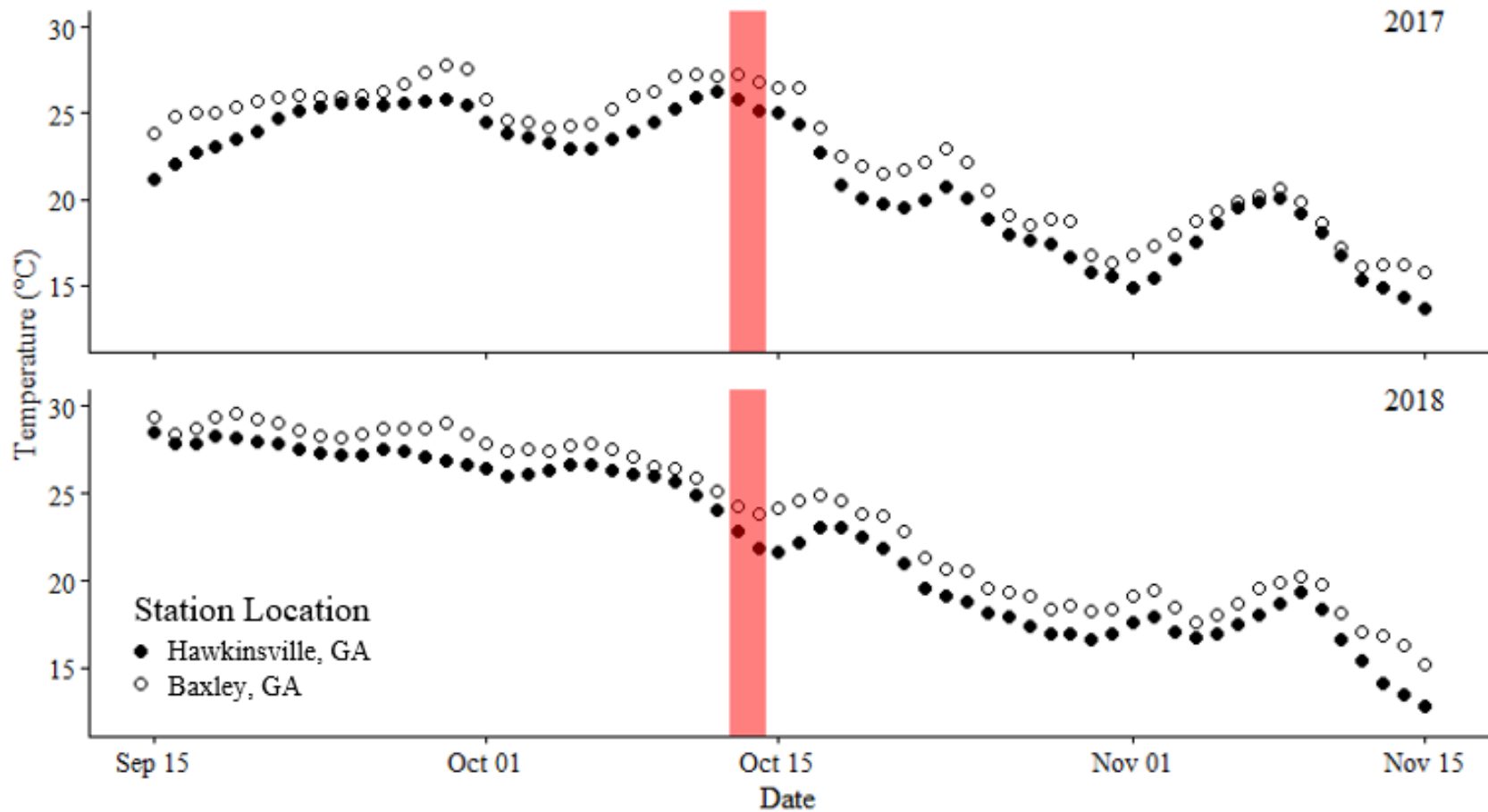


Figure 2.2. Mean daily water temperatures during the putative Atlantic Sturgeon fall spawning season from September 15th through November 15th, 2017-2018 in the Altamaha River system, Georgia. Peak survey period from each year is highlighted in red. Data retrieved from USGS streamgage 0221500 at river kilometer (rkm) 412 on the Ocmulgee River in Hawkinsville, GA, and streamgage 02225000 at rkm 180 on the Altamaha River in Baxley, GA.

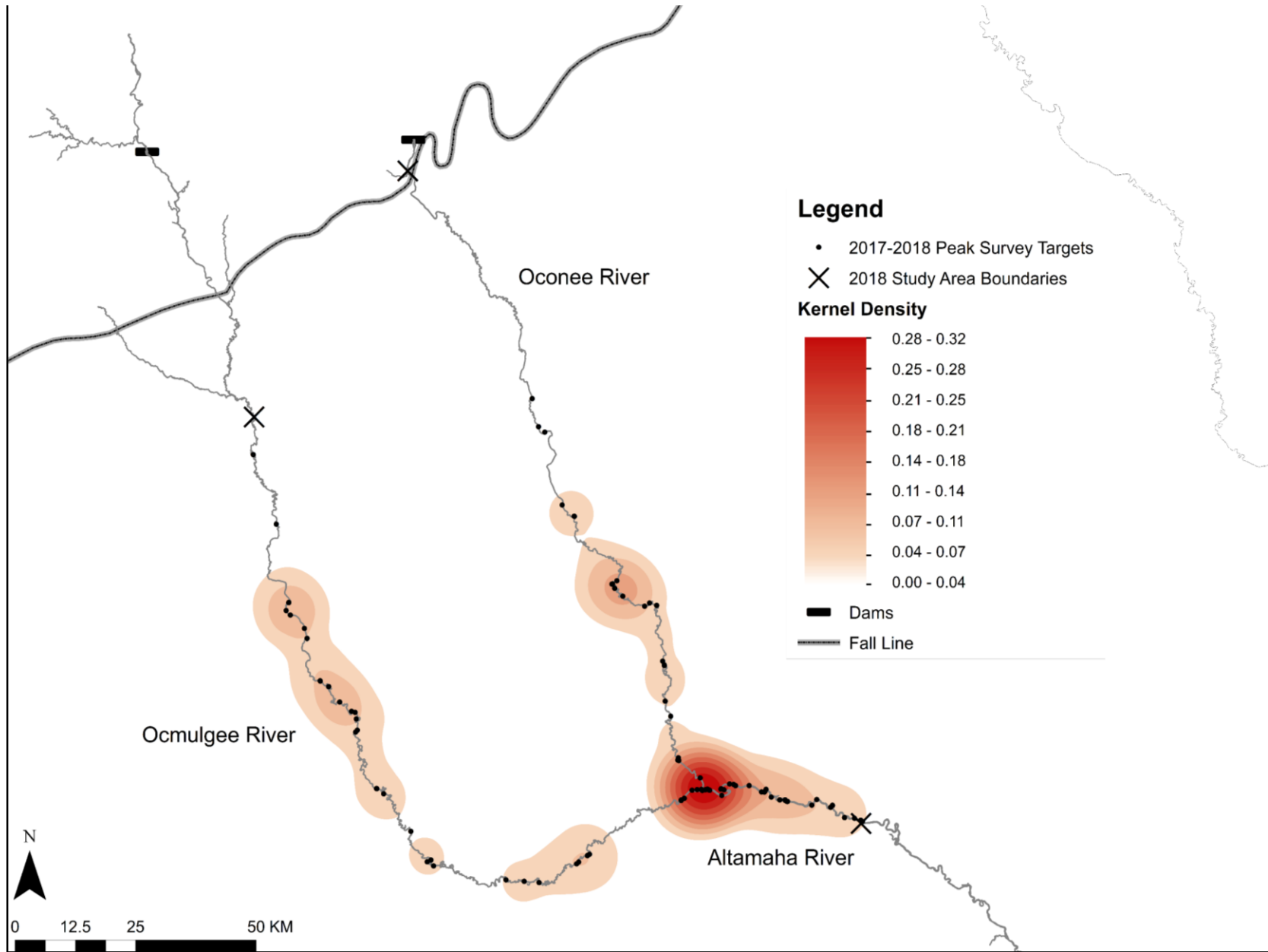


Figure 2.3. Kernel Density Estimation (KDE) of Atlantic Sturgeon targets in the upper Altamaha River System (in population per square kilometer) from data collected during side-scan sonar surveys in 2017 and 2018. Analysis was conducted using GIS-based KDE with targets in the Altamaha River assigned half the weight of those in the Oconee and Ocmulgee rivers.

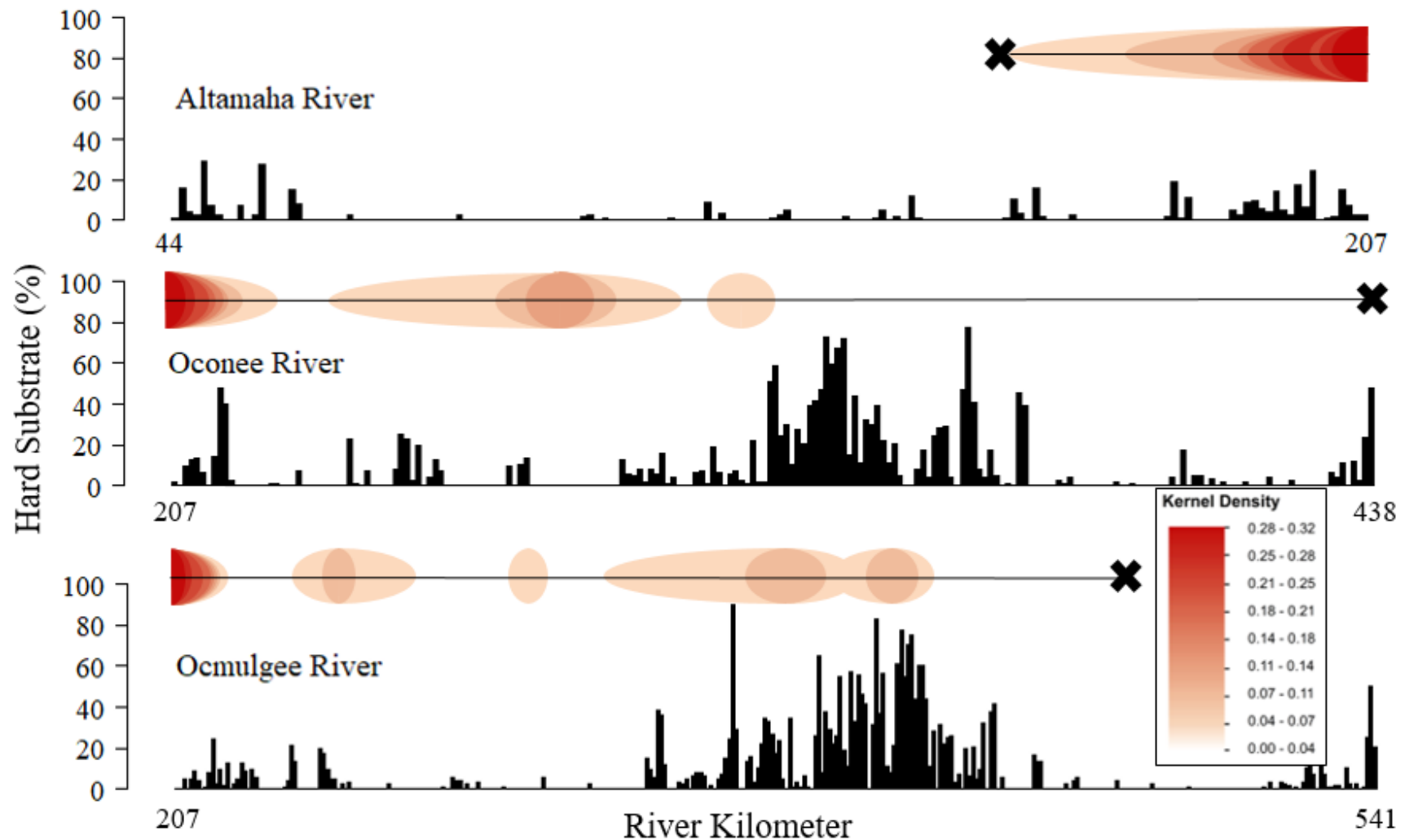


Figure 2.4. Percentage of hard substrates (bedrock, rocky boulder, rocky fine) in the Altamaha River System by river kilometer. Kernel Density Estimation (KDE) of ATS targets > 1.1 m in 2017 and 2018 is shown in shades of red above each river. Analysis was conducted using GIS-based KDE with targets in the Altamaha River assigned half the weight of those in the Oconee and Ocmulgee rivers. The 'X' and horizontal black line at $y > 80$ marks the boundaries and extent of the side-scan sonar surveys in relation to the entire Altamaha River system. Modified from Ingram and Peterson (2016). Substrate data from Litts and Kaeser (2016).

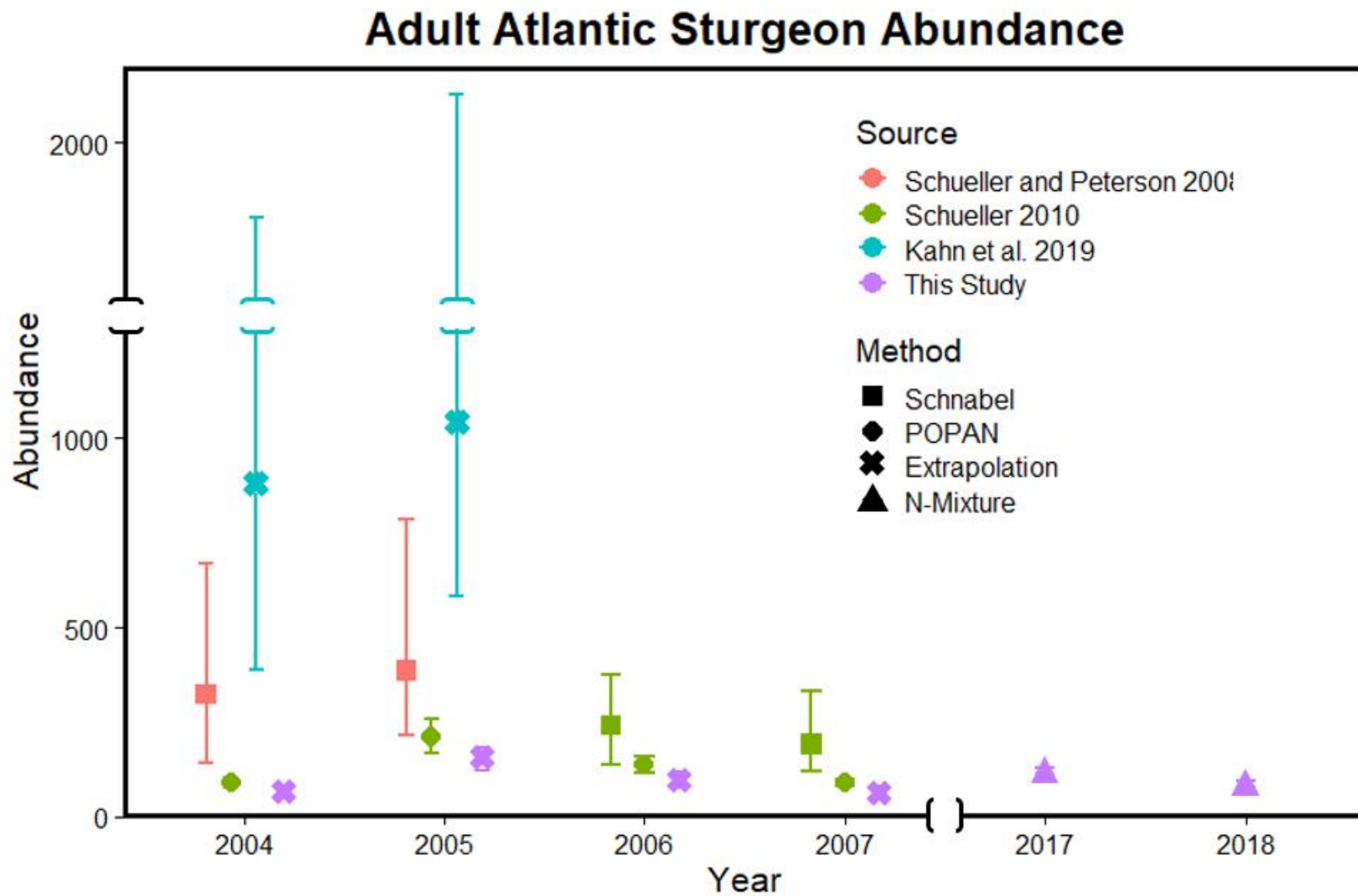


Figure 2.5. Atlantic Sturgeon spawner abundance estimates for the Altamaha River, Georgia. Includes POPAN estimates from Peterson et al. (2008), Schnabel estimates from Schueller (2010), extrapolations of both of those estimates by Kahn et al. (2019) and the authors of this study, and N-mixture estimates of Atlantic Sturgeon abundance from side-scan sonar surveys of the putative spawning areas of the Altamaha River, Georgia.

CHAPTER 3

CONCLUSIONS

Although scientists and managers agree that establishing a standardized, quantitative method for assessing ATS spawning runs is essential for evaluating species recovery, such a method currently exists but is not used consistently. The Atlantic Sturgeon Status Review Team (2007) identified three critical research needs that my study fulfills: spawning population abundance estimates, identification of spawning and nursery grounds and overwintering areas, and a long-term population monitoring program. Although a few researchers have successfully used mark-recapture sampling of river-resident juveniles to quantify annual ATS *recruitment*, this approach is typically not feasible for estimating adult populations because (1) the timing and locations of spawning runs is largely unknown and (2) obtaining a sufficient number of adult ATS captures/recaptures is logistically difficult (Schueller and Peterson 2010). Fortunately, recent advances in side-scan sonar technologies have been used successfully to identify adult sturgeon in many Atlantic and Gulf Coast river systems (Flowers et al. 2015, Kazyak et al. 2020). My multi-year study provides annual estimates of Altamaha River ATS spawning runs, pinpoints specific potential spawning sites, and the clear-cut methodology could easily be employed repeatedly over many years and in other river systems. These data fill the several critically important information gaps previously identified by state and federal management agencies (ASSRT 2007).

By using SSS and N-mixture models in a combined methodology, I was able to estimate annual ATS spawner abundances of 115 fish (95 % CI: 104 - 129) in 2017 and 82 fish (95 % CI: 70 - 95) in 2018, with detection probabilities of 0.43 (SE=0.13) and 0.14 (0.13), respectively. Although Peterson et al. (2008) and Schueller (2008) estimated “spring aggregations” of adult ATS, evidence indicates that these estimates likely inadvertently included non-spawning and non-natal individuals. However, the confidence intervals of my spawner abundance estimates overlap with those of the earlier studies, suggesting that the adult population has remained stable over the last decade.

Because my estimates are based on a single 48-hr survey during which the study site population was closed, they are most similar to the “daily spawner abundance” metric that some other studies have estimated. I saw approximately twice those that Vine et al. (2019) reported in the Savannah River, GA. The Altamaha River ATS population is thought to be the largest population in the Southeast (ASSRT 2007), likely due to the 800+ km of undammed river available as habitat for all life stages; even so, the Hudson River still likely has the largest population residing within the United States. Though my estimates were similar to the 93-118 (lowest to highest 95% Credible Interval: 61-179) daily spawners observed by Kazyak et al. (2020) in the Hudson River, my survey encompassed almost the entire available spawning area in the system, whereas that study investigated a single large aggregate spawning area. Therefore, total overall spawner abundance in the Altamaha River is undoubtedly smaller than the 466 (95% Credible Interval: 310-745) cumulative annual spawners estimated in the Hudson River (Kazyak et al. 2020). My estimates provide a critically important quantified reference point for the immediate status of the population, making possible future assessment of population trends. Thus, my data will be useful for current and future objective evaluation of species recovery range

wide. My estimates of spawning runs can be combined with existing methods for quantifying annual recruitment. This will allow us to examine stock-recruit dynamics in a quantified modeling framework that will lead to a new understanding of the biological and environmental interactions that directly affect spawning success of ATS. Inferences from such an analysis will greatly improve my understanding of how anthropogenic activities such as flow regulations, dredging, and incidental take, affect annual reproduction within specific populations.

The confluence of the Oconee and Ocmulgee rivers and the uppermost reaches of the mainstem Altamaha River consistently held the most ATS during my SSS surveys. More fish used the Ocmulgee than the Oconee River, and sturgeon in the Ocmulgee River were located in areas with higher percentages of hard substrate. In the Oconee River, sturgeon were dispersed throughout the lower portion of the river, and were not as closely associated with hard substrate. Ingram and Peterson (2016) determined the approximate locations (lower Oconee and Ocmulgee tributaries) of ATS spawning within the Altamaha system. During my surveys, I observed “hot spots” with higher densities of sturgeon in several locations in the mid-Ocmulgee, mid-Oconee, and upper Altamaha rivers; most of these sites were located near areas with hardbottom habitats that would potentially be suitable for spawning. Although these sites are within river reaches highly frequented by telemetered sturgeons (Ingram and Peterson 2016), this study was able to provide much more specific information about the exact positions of potential spawning sites.

To my knowledge, this study is one of the first to quantify how ATS presence, as observed using SSS, relates to hard substrate - specifically bedrock, a key component of spawning areas. Smith et al. (2015) suggest that hard bottom substrate including bedrock is important for ATS spawning and my results confirm this supposition. In my study, areas of high sturgeon use during the spawning period in the Altamaha River system coincided with or were

nearby to areas with hardbottom habitats. My findings confirm that hard substrate is important for ATS spawning and emphasize the need for protection of these areas during migration and the spawning season. My peak surveys, featuring the greatest numbers of observed sturgeon, occurred in mid-October; this falls within the October-December fall spawning period for ATS in the Altamaha River that had previously been reported based on telemetry (Ingram and Peterson 2016).

Currently, the entirety of the Altamaha River system is designated as Critical Habitat for Atlantic Sturgeon (NMFS et al. 2017), but bridge construction and dredging maintenance occurred at several locations throughout my study period. The data I collected on the areas most heavily used by sturgeon (including specific potential spawning sites) are vital for assessing how to proceed with future development projects within the watershed, including construction of roads, bridges, and water intake/discharge structures that could potentially affect the ATS population. Furthermore, by using nets and egg mats to sample for early life stages in the potential spawning locations I observed on SSS, future studies can confirm fall spawning and gain a better understanding of environmental variables associated with the activity.

My study established a relatively low-cost, quantitative methodology that can easily be used to conduct spawning run assessments on other river systems range-wide. By employing recreational-grade SSS technology and a study design that eliminated double-counts or missed sturgeon, I was able to produce peak daily spawning run and detection probability estimates without having to physically capture any fish. The creation of an established, affordable methodology using non-invasive, remote-sensing technology will assist management agencies in more easily identifying status of ATS spawner populations throughout the Eastern U.S. -

understanding the abundance and behavior of ATS spawners is critical for management agencies tasked with developing and implementing strategies to recover and maintain ATS populations.

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