ABSTRACT

FLOWERS, HENRY JARED. Methods for Monitoring and Assessing Sturgeon Populations Using Technology. (Under the direction of Joseph E. Hightower.)

Sturgeons (Acipenseridae) are one of the most threatened taxa worldwide, including populations of Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*. This subspecies is found in rivers and marine areas of the Atlantic Coast of the United States. The National Oceanic and Atmospheric Administration listed Atlantic Sturgeon under the Endangered Species Act in 2012. The listing delineated five Distinct Population Segments (DPS), one classified as threatened (Gulf of Maine) and five as endangered (New York Bight, Chesapeake Bay, Carolina, and South Atlantic). Populations are significantly reduced from historic levels by a combination of intense fishing and habitat loss. Successful restoration of Atlantic Sturgeon depends on a solid foundation of biological data.

Traditional fisheries sampling approaches are often limited for federally-listed species such as Atlantic Sturgeon. One alternative is to develop less-intrusive methods using new technologies. Side-scan sonar is an emerging fisheries technology with advantages over traditional sampling techniques, including the ability to efficiently sample large areas and survey fish without physically handling them – important for species of conservation concern. Acoustic telemetry is another area of rapid technological advances, including smaller, longer-lived tags and new designs for submersible receivers. Online databases facilitate data-sharing between researchers operating autonomous receiver arrays, enabling telemetry studies to incorporate expansive spatial areas.

The first objective for this study was to develop methodology using side-scan sonar to survey and assess Atlantic Sturgeon populations. This was accomplished by surveying six North and South Carolina rivers, using a combination of side-scan sonar, telemetry, and video cameras (to sample jumping sturgeon). We surveyed lower reaches of each river, near the saltwater/freshwater interface, on three occasions (generally successive days) and used occupancy modeling to analyze these data. We were able to detect sturgeon in five of six rivers, with estimated gear-specific detection probabilities ranging from 0.2-0.5 and river-specific occupancy estimates (per 2-km river segment) ranging from 0.0-0.8.

Next we used count data from the same side-scan sonar surveys to estimate abundances of sturgeon >1 m in length in conjunction with N-mixture and distance models. Estimated abundances in the Carolina DPS were 2,031 (95% confidence interval: 1,075-3,858) and 1,912 (1,016-3,616) using N-mixture and distance models, respectively. The Pee Dee River, South Carolina had the highest overall abundance of any river at 1,944 (1,036-3,646) and 1,823 (976-3,406) using count and distance models, respectively. These estimates do not account for sturgeon occurring in unsurveyed riverine reaches or marine waters. Comparing the two models, the N-mixture model produced similar estimates using less data than the distance model with only a slight reduction of estimated precision.

The third objective was to use telemetry to describe long-term movements of Atlantic Sturgeon from the Roanoke River, North Carolina. Six adult Atlantic Sturgeon (presumably males) were implanted with acoustic telemetry tags from 2010-2012. Sturgeon were monitored through a network of passive receivers in North Carolina and eight additional states. A multi-state model was used to estimate movement probabilities among riverine, estuarine, and marine areas. From September 2010 to June 2014, five of six Atlantic Sturgeon were detected in marine portions of three different DPSs. Seasonally, sturgeon were observed to either spend the entire year in marine waters or winter-spring in marine waters, summer in Albemarle Sound and fall in the Roanoke River for spawning. The multi-state model suggests seasonally variable movement probabilities. Estimated annual mortality was relatively low (0.03) and detection probability high (>0.50) in most study regions. Sturgeon were observed to spawn in consecutive years or with a year in between spawning events. The complexity of Atlantic Sturgeon movements and the mixing of populations in marine waters add to the potential difficulty in managing the recovery of this species.

Methods for Monitoring and Assessing Sturgeon Populations Using Technology

by
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A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements of the Degree of
Doctor of Philosophy

Fisheries, Wildlife, and Conservation Biology

Raleigh, North Carolina

2015

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BIOGRAPHY

I was born in Augusta, GA, to Hank and Debra Flowers. I was raised and schooled in the Augusta, GA area, graduating from Greenbrier High School in 1998. I also spent a significant amount of time in southwest Georgia, fishing, hunting, and exploring the outdoors with my grandparents, Opa and Oma; and uncle, Mick. These experiences, along with fishing trips with my dad, exploring the backyard with my sister, Ami, and high school FFA program with teacher Larry Moore, spurred my interest in natural resources and fisheries. I started college at the Georgia Institute of Technology in 1998, and then transferred to Abraham Baldwin Agriculture College in 2001, where I received my A.S. degree in Forest Resources. I then enrolled at the University of Georgia where I completed my B.S.F.R. in both Fisheries Management and Forest Environmental Resources. After graduation I worked as a field technician with the University of Georgia in Michigan with Lake Sturgeon on the Muskegon River and then worked as a field technician with the University of Arkansas, Fayetteville USGS Coop Unit on trout species in the White River system. I then attended the University of Florida, receiving my M.S. in 2008, this time working on Gulf Sturgeon. Afterwards I embarked on my career at North Carolina State, seeking a Ph.D., this time working with Atlantic Sturgeon. After graduation I will continue at NCSU in a post-doctoral position with Tom Kwak.

ACKNOWLEDGEMENTS

I would first like to thank my family. They have been there my entire life and have largely made me who I am today. My parents, Hank and Debra, have always been caring, supportive, and encouraged me to think for myself. My dad, grandparents- Opa and Oma, and Uncle Mick introduced me to fishing and the outdoors. My sister Ami has always been a fellow outdoor explorer and followed me into natural resources.

I'd like to think my Master's advisor, Bill Pine, for taking a chance on my when I was wet-behind the ears technician. He encouraged me and really opened up the world of possibilities fisheries had to offer. Both he and Michael Allen were responsible for encouraging me to come to NCSU and start a Ph.D. Also at UF, Carl Walters was also an inspiration, exposing students to serious stock assessment science and a lifetime of fisheries experience and advice. I want to thank my Ph.D. advisor Joe Hightower all he's done. I've learned a great deal from him during my time at NCSU and have enjoyed sharing a common passion for sturgeon and Georgia football. I am most thankful that he has been willing to put up with me over these past years. I would like to thank Tom Kwak for his support and advice while at NCSU and making me feel like one of the group. I want to thank my committee members and all the other professors at NCSU that have taught me many things, sharing their unique view of the world, during my time here. I thank Stephania Bolden at NOAA Fisheries for funding support during both my M.S. and Ph.D. projects. Last, but certainly not least, Wendy Moore for always having the right answers and always being willing to deal with petty problems and lost receipts.

I'm thankful for the many people I've interacted with during my time at UF and NCSU. I've seen technicians and grad students become professors and scientists and have enjoyed knowing them all. Nick Cole, Aaron Prince, and Taylor Jackson were great technicians who were critical in my research. I thank all of my friends and colleagues who have helped me through the years, especially Dan Gwinn, Tamara Pandolfo, Jessica Stocking, and Gus Engman. You and everyone else have made this adventure an incredible journey.

Finally, I would like to thank my girlfriend Amy Comer. It’s only too fitting that we met at a fisheries meeting and were both working on sturgeon and side-scan sonar. Although she hasn’t been there the whole time, she has been there for me during the most important time and maybe longer.

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CHAPTER 1

INTRODUCTION

The Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* is a federally threatened and endangered fish species found in rivers and marine areas of the Atlantic Coast of the United States. In its listing decision, the National Oceanic and Atmospheric Administration (NOAA) divided individual populations into five Distinct Population Segments (DPS), from north to south: Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (ASSRT 2007). The Gulf of Maine population was listed as threatened, while all others were considered to be endangered (NOAA 2012). The major reason for the decline of Atlantic Sturgeon populations range-wide was overharvest, particularly during the early 1900s (Secor 2002). Commercial fisheries reduced populations to fractions of their original size within a matter of a few decades. Due to life history characteristics such as slow growth and late age-at-maturation, populations did not recover, even after harvest reductions or fishery closures. Concern about low population sizes led to the eventual closure of the United States Atlantic Sturgeon fishery in 1998 and the subsequent ESA listing in 2012 (NOAA 2012).

Atlantic Sturgeon is a large, long-lived fish species, attaining maximum sizes in excess of 3 m and ages to 60 years (Gross et al. 2002). They are anadromous, spending much of the year feeding and migrating in marine environments and using freshwater rivers for spawning and a summer dormant period (ASSRT 2007). During summer sturgeon may aggregate in lower portion of rivers, often in deep holes near the freshwater-saltwater interface, although the exact location can vary by individual river characteristics and flow conditions (Moser and Ross 1995; Collins et al. 2000). Sturgeon are known to move large distances in marine environments and individuals from different populations mix, although the extent to which this happens is not well known (ASSRT 2007).

As a result of low population sizes and fishery closures, there has not been a great deal of research on Atlantic Sturgeon when compared to other important fishery species

(Peterson et al. 2008). Notable exceptions in the Southeastern United States include studies by Armstrong and Hightower (2002), Collins et al. (1996, 2000a, 2000b), Collins and Smith (1997), Peterson et al. (2008), Moser and Ross (2005), and Laney et al. (2007). Most of these studies focused on individual river systems and many involved shorter term telemetry and tagging studies. Only one of these studies (Peterson et al. 2008) looked at population sizes and some individual river systems were overlooked. Major questions that were not addressed by these studies included estimates of population status and trends, identifying spawning sites and spawning habitat, and ocean movement patterns.

Listing of Atlantic Sturgeon created new interest in conducting research. The informational requirements of the ESA process, such as critical habitat designation, recovery plans, and status reviews, identified data needs to be addressed by future research (NOAA 2012). However, a consequence of endangered status is that researchers are more restricted in the methods that they can employ to sample sturgeons. The need for data coupled with concerns about causing harm to endangered populations is a catalyst for finding and developing new sampling techniques that can provide similar information about populations as traditional gears while reducing or eliminating the need to handle target species.

Technology in fisheries is continually advancing, presenting challenges to fisheries scientists to develop ways to both utilize techniques in the field and analyze acquired data. New technologies may include those that are entirely new or just new to the study of fishes. An example of an older technology that is being newly applied to fisheries is side-scan sonar, a hydroacoustic technology originally designed for oceanographical surveys of the seafloor (Johnson and Helferty 1990). Side-scan sonar uses sound waves to create static images of the underwater environment, including objects on and above the bottom. The large size and distinct body shape of sturgeon make them an ideal candidate species to be sampled with side-scan sonar, with the added advantage that individuals do not have to be handled. Because of limited past use in fisheries applications, methods must be developed to employ side-scan sonar, combined with appropriate statistical analyses, in order to use this tool in a meaningful way.

Acoustic telemetry is an older fisheries technology that has been improved in recent years. Improvements in battery technology have allowed tags to become smaller, but have longer lifespans. Affordable, simple automated telemetry receivers are available that can collect data around the clock. The result is more data, with better temporal and spatial coverage with less effort. Affordability has led to widespread usage of compatible receivers, leading to even wider coverage outside of research studies' focal areas. Tagged fish have the potential to be detected on multiple receiver arrays at locations from Florida to Maine. In the past it was rather difficult to track down the owner of an unknown tag or find out who may have detected your tags. A solution to this problem was another application of technology made possible by the internet. Telemetry networks have been established for sharing information coast-wide about tags and receivers. On the Atlantic Coast, notable networks include the Atlantic Cooperative Telemetry Network (ACT; www.theactnetwork.com), the Ocean Tracking Network (OTN; oceantrackingnetwork.org) and the Florida Acoustic Cooperative Telemetry.

The objective of this study is to develop methods to employ these technological tools in the study of an endangered species, Atlantic Sturgeon. Chapter 2 illustrates the use of side-scan sonar to rapidly survey large areas of river to establish the location and distribution of sturgeon. Observations of sturgeon presence and absence at discrete sites were used with occupancy modeling to describe the detection probability of side-scan gear and the occupancy of sturgeon in the surveyed rivers. Chapter 3 describes a method to produce abundance estimates from count data acquired through side-scan surveys. Two different estimation procedures, N-mixture and distance modeling, were used to estimate abundance of sturgeon in six major sturgeon rivers in North and South Carolina and the Carolina DPS. These estimates were scaled up to represent the entire area of the survey reach. Chapter 4 discusses a long-term study of Atlantic Sturgeon movement based on acoustic telemetry. Six adult Atlantic Sturgeon (presumably males) from the Roanoke River were implanted with acoustic telemetry tags from 2010-2012. These sturgeon were monitored through a network of passive receivers in North Carolina and eight additional states. We used a multi-state model to estimate movement probabilities among riverine, estuarine, and marine areas.

Planning Atlantic Sturgeon recovery and management will require a great deal of reliable and up-to-date information. This study will attempt to fill some of the knowledge gaps in several aspects of Atlantic Sturgeon life history that have management implications. Knowing where and when sturgeon are found will enable managers and researchers to create sampling and monitoring programs to answer other questions about sturgeon biology. Current abundance estimates allow for the establishment of recovery targets for different populations. Insight into sturgeon movements allows managers to evaluate fisheries regulations, schedule activities like dredging to be less impactful, and adjust riverine flow regimes to accommodate spawning. By providing this information, new techniques and technologies could satisfy data needs and serve as the foundation for future Atlantic Sturgeon conservation strategies.

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CHAPTER 2

A NOVEL APPROACH TO SURVEYING STURGEON USING SIDE-SCAN SONAR AND OCCUPANCY MODELING

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Published in Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science (2013) 5:211-223.

Abstract

Technological advances represent opportunities to enhance and supplement traditional fisheries sampling approaches. One example with growing importance for fisheries research is hydroacoustic technologies such as side-scan sonar. Advantages of side-scan sonar over traditional techniques include the ability to sample large areas efficiently and potential to survey fish without physical handling – important for species of conservation concern, such as endangered sturgeons. Our objectives were to design an efficient survey methodology for sampling Atlantic Sturgeon using side-scan sonar and to develop methods for analyzing these data. In North Carolina and South Carolina, we surveyed six rivers thought to contain varying abundances of sturgeon by using a combination of side-scan sonar, telemetry, and video cameras (i.e., to sample jumping sturgeon). Lower reaches of each river near the saltwater/freshwater interface were surveyed on three occasions (generally successive days), and we used occupancy modeling to analyze these data. We were able to detect sturgeon in five of six rivers using these methods. Side-scan sonar was effective in detecting sturgeon, with estimated gear-specific detection probabilities ranging from 0.2 to 0.5 and river-specific occupancy estimates (per 2-km river segment) ranging from 0.0 to 0.8. Future extensions of this occupancy modeling framework will involve use of side-scan sonar data to assess sturgeon habitat and abundance in different river systems.

Introduction

Sturgeon populations worldwide have declined from historic levels as a result of a combination of factors, including over-harvest and habitat alteration (Secor 2002; Pitkitch et al.2005). In the eastern United States, Shortnose Sturgeon *Acipenser brevirostrum* and Atlantic Sturgeon *A. oxyrinchus* have been listed as endangered under the Endangered Species Act (ESA) in 1967 and 2012, respectively. Endangered status restricts the methods that researchers can employ to sample sturgeons, and extra care must be taken when sampling and handling specimens (Damon-Randall et al. 2010; Kahn and Mohead 2010). Concerns about causing harm to endangered populations create a need to find and develop new sampling techniques that can provide similar types of information about populations as provided by traditional gears while reducing or eliminating the need to handle target species.

The most common technique for sampling Atlantic and Shortnose Sturgeon is netting, typically with set trammel and gill-nets (Collins et al. 1996; Moser et al. 2000; Peterson et al. 2008). Electrofishing and other methods are much less effective (Moser et al. 2000) and are prohibited as a capture method for Gulf *A. oxyrinchus desotoi*, Green *A. medirostris*, Atlantic and Shortnose Sturgeon (Kahn and Mohead 2010). Most of the netting in southeastern rivers occurs during summer months (Moser and Ross 1995; Collins and Smith 1997; Zehfuss et al. 1999), when water temperatures are approaching upper thermal tolerances for Atlantic Sturgeon and Shortnose Sturgeon (>30°C) (Ziegeweid et al. 2008), and handling individuals can induce stress and potential mortality (Moser and Ross 1995; Collins et al. 1996). Riverine netting is often performed in summer since both sturgeon species are commonly available and easily sampled (Moser and Ross 1995; Collins and Smith 1997).

Hydroacoustics may represent a non-intrusive alternative to sample endangered species. Sturgeon and related Paddlefish *Polyodon spathula* have been identified as potentially suitable targets for hydroacoustic studies (Hale et al. 2003; Nealson and Brundage 2007; Bergman 2011). Hydroacoustics includes sonar technologies that use sound waves to provide information about underwater environments and in various forms has been used in oceanographic studies to locate and map underwater features. With recent improvements in technology and decreases in cost, hydroacoustics has become more attractive for use in fisheries studies. Several different forms of hydroacoustics have been used in fisheries studies, including split-beam sonar, Dual-frequency IDentification SONar (DIDSON; Sound Metrics Corp.), and side-scan sonar, each with its own characteristics and applications. Targets that are imaged by hydroacoustics, including side-scan sonar, often produce silhouettes or acoustic shadows that yield shape information about the target and can be used to identify fish (Moursund et al. 2003; Langkau et al.2012).

Side-scan sonar is a relatively old hydroacoustic technology that has been used increasingly in fisheries studies in recent years (Kaeser and Litts 2008; Foote 2009). Side-scan sonar units can produce high-quality still images of the bottom, allowing detection of subsurface objects (e.g. sunken vessels) and geologic features (Johnson and Helferty 1990). These images can be geo-referenced and combined into a mosaic image of the bottom in a survey area. Historical fisheries applications of side-scan sonar have primarily focused on habitat (Oliver and Kvitek 1984; Kaiser and Spencer 1994; Kaeser and Litts 2008), but side-scan sonar can also detect fish, which appear as distinct targets in the image. The ability of side-scan sonar to detect fish depends on specifications of the individual unit, with higher-frequency units typically having greater image resolution. Software plays a part in imaging as well, and advances in this area have improved the processing and interpretation of side-scan sonar data (Johnson and Helferty 1990). Side-scan sonar has been used to count fish (Barton 1982; Barton 2000), but in those cases the identification of species was unnecessary.

Our study in the Carolinas encountered both Shortnose Sturgeon and Atlantic Sturgeon populations, but we chose to focus primarily on Atlantic Sturgeon, as they are more abundant than Shortnose Sturgeon in these systems, attain larger sizes, and are of heightened interest because of their recent listing status. Both species were found historically throughout the southeastern United States, but their numbers are greatly reduced in many systems (Secor 2002). Sturgeons have not been well studied in many Southeastern systems since the closure of commercial sturgeon fisheries in 1998 (ASSRT 2007; Peterson et al. 2008).

The large body size and distinctive shape of Atlantic Sturgeon make them ideal hydroacoustic target. Atlantic Sturgeon can attain maximum sizes in excess of 3 m and live for approximately 60 years (Gross et al. 2002). Atlantic Sturgeon are anadromous, spending large amounts of time feeding and migrating in marine environments and using freshwater rivers for spawning and a summer dormant period (ASSRT 2007). During summer both Shortnose Sturgeon and Atlantic Sturgeon may aggregate in lower portion of rivers, often in deep holes near the freshwater-saltwater interface, although the exact location can vary by individual river characteristics and flow conditions (Moser and Ross 1995; Collins et al. 2000).

The objective of our study was to develop a sampling protocol for rapidly surveying rivers by using side-scan sonar to detect the presence of sturgeon. Conservation concern and lack of status knowledge across the range of these sturgeons indicate a need for new methodologies and surveys, especially those involving non-invasive technologies like hydroacoustics. This method may allow for efficient, effective sampling to confirm the presence-absence of sturgeon in systems without the need for direct handling of the sturgeon. The use of side-scan sonar should be an improvement over current protocols that require a large amount of effort using traditional sampling gears, (e.g., gill nets) and handling of sturgeon. The survey protocol should be effective regardless of whether there is prior knowledge of sturgeon habits in a specific system. We utilized occupancy modeling to analyze data and to estimate (1) detection probability achieved by the side-scan sonar and (2) the probability of sturgeon presence in various rivers.

Methods

Study Sites

Field work took place in six river systems in North Carolina and South Carolina (Figure 1, Table 1). Systems were chosen based on available information about the status of sturgeon populations or the potential for sturgeon presence in that system. The goal was to sample rivers with sturgeon populations ranging from high to low abundance. Population status was approximate – based primarily on anecdotal observations or limited directed sampling. Mark-recapture studies and other types of population studies have not been performed in these systems.

Side-scan Sonar Unit

Our side-scan sonar unit was an Edgetech model 4125-P dual frequency unit, which is a high-end, towed, portable unit primarily for marine waters and large water bodies. The sonar unit operates at frequencies of 450 and 1,250 kHz, with a maximum side-to-side scan range of 300 m and 100 m, respectively. The side-scan sonar unit was towed behind a 5.5-m fiberglass work boat operating at optimal speeds between 6.4 and 9.6 km/h. We used Chesapeake Technology's SonarWiz.Map software to capture, process, and analyze the side-scan sonar data. This software creates a real-time, geo-referenced mosaic display of sonar imagery while the survey is performed, allows the marking and measuring of potential sonar targets, and can export data into a GIS program for further processing.

Side-scan Surveys

Side-scan sonar surveys were performed over 3 d on each of the six rivers. The three sampling days were selected to be as close as possible (often consecutive) in order to reduce the chance of fish movement between sites. Sturgeon have been previously found in lower portions of coastal rivers near the freshwater-saltwater interface (Moser and Ross 1995; Collins et al. 2000; Peterson et al. 2008), and we designed our surveys accordingly. Riverine survey reaches began downstream in tidal portions of elevated salinity (>15 mg/L) and ranging upstream a distance of at least 30 km inland on the main stem or to a point where river depths were too shallow to permit effective operation of the side-scan sonar. Several rivers had multiple braids, and surveys included the main-stem river channels and significant branches. As a result, the total distance surveyed in each river varied from 40 to 80 km.

The side-scan sonar unit was deployed at a depth of approximately 1 m below the water's surface. Depth remained constant for all systems and surveys except where occasional shallow depths required us to temporarily pull the tow-fish at a shallower depth. We used our side-scan sonar in high-frequency (1250-kHz) mode, with a total swath width of 60 m. In previous trials, these settings were found to be the best compromise in terms of area swept and target detail. In most cases, we could not scan the river bank to bank at the 60-m range; as a result, we followed the center of the river, usually the main channel, during surveys.

Side-scan sonar data were later analyzed in the laboratory by reviewing each side-scan sonar file and identifying potential sturgeon targets. When a potential sturgeon was observed, the target was marked, GPS coordinates were taken, and length was measured. Target body length was the standard measurement; however, in few cases where the body image was weak, distorted, or obscured, the length of the target's shadow was used. The target was described in terms of quality and shape and then classified as being either a sturgeon ("yes"), not a sturgeon ("no"), or possibly a sturgeon ("maybe"; see example images in Appendix B). Classification was a subjective judgment of the observer, made generally on the basis of target size and shape. Two independent observers processed the side-scan sonar files and classified targets; neither observer was explicitly aware of whether sturgeon were detected by one of the other gears at the individual sites. The observers had different levels of experience viewing side-scan sonar files; one observer had used and viewed side-scan sonar images for several years, whereas the other observer had done so for only a few months.

To assess the assumption of closure, we simultaneously attempted to detect telemetry tagged sturgeon during side-scan surveys. In four of the six study systems, Atlantic Sturgeon had been tagged with VEMCO telemetry transmitters within the past year as a part of a separate, ongoing research project. Although sturgeon were not tagged in the other two systems, it could have been possible for tagged sturgeon to migrate into those systems from other systems. A VEMCO VR-100 receiver with an omnidirectional hydrophone was submerged and attached to the side-scan sonar cable. Although we found we could detect tagged fish while collecting side-scan data, acoustic noise limited the speed at which we could travel. When a fish was detected, individual tag code, time, and GPS location were recorded. Locations were approximate since we could not stop the side-scan sonar run to determine the exact position of the fish; however, tag reception range was likely limited to less than 300 m.

Atlantic Sturgeon also have a habit of jumping entirely out of the water (ASSRT 2007), and this behavior could be used to assess presence. To detect jumping sturgeon in a standardized manner, two video cameras were mounted on the boat, one looking front and one looking rearward. We used simple webcams connected to two computers to constantly record video footage during surveys. Each camera had a fixed viewing angle, and video quality was optimized for detail and file size. We chose a smaller video size (640 x 480 pixels) and medium quality option, although exact settings may vary by camera and software set-up. Observations of jumping sturgeon were recorded, and positions were estimated by using video time stamps to coordinate with the side-scan sonar file times and locations.

Side-scan sonar, video camera, and telemetry detections all were plotted in ArcGIS and were recorded by site and day. It is important to note that failure to detect sturgeon using side-scan sonar in a site known to be occupied, (i.e., observations with the video camera, telemetry, or both) was not solely a function of an inability to identify a sturgeon with the side-scan sonar. Limited side-scan sonar swath size could result in sturgeon not being ensonified and therefore not observed.

The large amount of data collected during the surveys required extended time for analysis. Every survey day created approximately 16 h of video and over 30 km of side-scan files to be analyzed. Side-scan sonar file processing took 1-3 d per survey day, depending on how many targets had to be recorded. Maps generated by using detection data provided an excellent overview of sturgeon positions in each system (Appendix A). Mapping illustrated the spatial similarities between sturgeon located by side-scan sonar and sturgeon detected by other gear types.

Occupancy Modeling

Occupancy modeling has been suggested as a useful approach to sampling rare and elusive species for which the acquisition of sufficient data to estimate abundance is difficult (MacKenzie et al. 2004, MacKenzie et al. 2005). An occupancy modeling approach is based on repeated sampling of a given study area to estimate the proportion of the area in which the species of interest is present (Mackenzie et al. 2002; Mackenzie et al. 2006). A key aspect of occupancy models is that they can account for imperfect detection by sampling gear. Because the method only requires presence-absence data, an occupancy approach tends to require less effort than studies that are designed to estimate abundance (Mackenzie et al. 2002). Our occupancy model assumptions include (1) the occupancy state of sites is constant during all single-season surveys; (2) the probability of occupancy is equal across all sites within a river; (3) the gear-specific probability of detection given occupancy is equal across all sites and rivers; (4) detection of the target species during each survey of a site is independent of those on other surveys; and (5) detection histories at each location were independent (Mackenzie et al. 2006). These assumptions can be relaxed depending on model specification.

In our study repeated sampling occurred over three survey days. The study area is typical broken into sampling units, or sites, suitable for the species and study objective. Our objective was to determine (1) sturgeon presence in river systems and (2) the areas where they were present within individual river systems. For this purpose each river was an individual study area divided into 2-km sites; thus, there was a total of 179 sites. The 2-km size was selected based on telemetry data, since this distance was greater than the maximum distance traveled in 1 d by any telemetry-tagged sturgeon (~1 km) during the study. It was also the smallest size to contain movement while also providing some information about local habitat if desired. We compared the model based on 2-km sites with those based on study areas divided into 1-km sites (n=358) and 4-km sites (n=90) in order to evaluate site size and closure assumptions.

Occupancy modeling incorporated three sampling methods, but not the same three gears used in the survey. Telemetry-tagged Atlantic Sturgeon were not available throughout all systems, so we excluded those data from occupancy analysis. Instead, we used video cameras and two independent observers of side-scan sonar data. Side-scan sonar data for each observer were kept separate and treated as two independent observations (i.e., each observer represented a "gear"). Only targets identified as sturgeon ("yes") were used in the occupancy analysis. Side-scan observer and video camera data were compiled into a binary 9 x N detection history matrix, where a 1 was entered if at least one sturgeon was detected in a site by a given gear and a zero was entered if no sturgeon were detected. Individual rivers were used as site level covariates for model scenarios.

We used the free program PRESENCE (Hines 2006) to perform our occupancy modeling. PRESENCE is specifically designed to run a wide variety of different occupancy models that take into account different study designs. We chose the single-season, multiple-method model (Nichols et al. 2008), which is designed for studies using multiple gears on multiple occasions during a single sampling season. Model-estimated parameters included site occupancy (ψ), detection probability (p), and the probability that animals, if present, are available to be detected by a given gear (θ). For our model, ψ is the proportion of sites occupied within a given river and p is the probability of a gear detecting sturgeon at a site if sturgeon were present. The θ is used to model the case in which individuals may be present at the sampling site but are not necessarily available to the gear. For example, this could be used to account for the fact that the swath width of our sonar did not cover the entire site area. By fixing θ at a value of 1.0 we would assume that individuals were fully available for detection if a site was occupied.

We evaluated candidate occupancy models that were chosen based on biological factors; Akaike's Information Criterion (AIC) was used to evaluate the support for each model. Candidate models included those in which p was constant or varied by gear type but remained constant across rivers and survey days. It is possible that there could be differences in cameras and side-scan sonar and that experience levels differed between the observers, thereby influencing p. We evaluated models that allowed p to vary by river, but there was little reason to assume that p would vary by day or river. It was possible that characteristics of individual sites (turbidity, depth, etc.) varied, but this variation was similar across the different rivers based on their summer low-flow conditions and similarity in geographical setting. We evaluated models in which ψ varied across rivers or were constant for all rivers but did not vary by survey day. Differences among rivers would be expected given anecdotal reports and target counts among rivers systems.

We used Pearson's Chi-square test to assess independence in observations between gears; the null hypothesis was that observations made by video cameras and telemetry were independent of side-scan sonar observations. Fisher's exact test was used to test for independence in a similar manner, but we also examined the odds ratio provided by this test. The objective of these tests was to compare raw results among the different gears. Both of these tests utilized observation data for each individual site summarized by gear in a 2x2 contingency table. Sites were grouped in categories based on whether or not sturgeon had been detected at a given site by a given gear, and separate tables were used for each side-scan sonar observer.

Results

The strongest AIC supported occupancy model was ψ(r), p(g), θ(.) (this model and other models are defined in Table 2), where ψ varied across river, p varied with gear, and θ was constant across all gears and surveys. There was also weak support for the ψ(r), p(g), θ(g) model, which differed by estimating individual values of θ for each gear. Models with θ fixed to 1.0 were not supported as strongly as their counterparts (Table 2), suggesting that sturgeon may have been present at a site but were not available for detection by a gear during that survey. Despite the varying amount of AIC support, model parameter estimates were similar across different models. Estimates of ψ ranged from a minimum of zero to a maximum of approximately 0.88 across all rivers and models (Table 3). No sturgeon were observed in the Santee River. Estimates were generally similar to the anecdotal estimates of abundance proposed for each river (Table 1).

Estimates of p varied by gear and were higher for side-scan sonar than for the video cameras (Table 3). There was stronger support for models with differences in p for each side-scan observer than for those with observer p-estimates pooled. Estimates of p were influenced by θ, with decreasing θ values producing an increasing in p-estimates. This implies that the availability of sturgeon to be observed by a given gear at a given site was variable. Models that allowed p to vary among rivers produced unrealistic parameter estimates and did not properly differentiate the effects of p and ψ.

We successfully detected sturgeon in five of the six surveyed rivers, and in most cases sturgeon were detected with multiple gears (Table 1) over 179 2-km sites. Telemetry tagged sturgeon were generally observed to move less than 1 km during the course of the surveys, supporting our occupancy modeling assumption of closed sites. We had some prior knowledge about sturgeon whereabouts in several systems, but in at least one system (Edisto River) we had no knowledge at all but were still able to detect sturgeon. Side-scan sonar targets that could potentially be sturgeon were detected in all rivers systems, ranging in number from 58 to 1,331 targets/river for both observers. A vast majority of potential sturgeon targets were classified as "maybe" and fewer were classified as "yes," but the proportion varied by river and between observers. Most targets classified as sturgeon were at least 1 m in length (Figure 2), and this appeared to be a minimum length required to provide sufficient information about body shape. The Santee River had a high number of side-scan targets, but all were classified as "maybe", with most being smaller and having indistinct shape.

Video cameras were effective in detecting jumping sturgeon (Figure 3), despite the apparent random and infrequent character of those events. In total, 39 jumping events were detected during all surveys in approximately 290 h of video footage. Cameras could detect sturgeon outside the swath covered by side-scan sonar, but most sturgeon present in an area would not jump at precisely the time to be recorded. In total, 40 individual telemetry-tagged sturgeon were detected during the side-scan sonar surveys in three systems: the Cape Fear, Pee Dee, and Edisto rivers.

Our study rivers were relatively shallow, with maximum depths in the range of 8-10 m (excluding the Cape Fear River shipping channel); these depths did not present an issue with our choice to use a fixed tow-fish depth. There were isolated areas in which the water was too shallow and side-scan sonar image quality was poor, although targets could still be seen. Where the water was too deep, side-scan sonar beams could not reach the bottom and only objects in the water column were detected. This was the case at two sites in the shipping channel of the lower Cape Fear River, where the bottom could not be consistently scanned; as a result, we excluded those two sites from our occupancy analysis.

In general side-scan sonar image quality was good across all rivers, and better image quality improved target detection. Only on a few occasions was image quality impaired, primarily by environmental conditions or boat traffic (Figure 4). Only a few of our side-scan sonar targets exhibited high-quality acoustic shadow shapes that made it easy to identify them as sturgeon. Most of the sturgeon targets with lower-quality silhouettes were classified based on a combination of size and shape information (Figure 5, Appendix B). In most systems sturgeon were expected to be the largest fish species commonly encountered, with a few exceptions. The fish most similar to sturgeon encountered during surveys, both by side-scan sonar and visually by jumping, were Tarpon *Megalops atlanticus*, but they were observed in areas with much higher salinity than sturgeon and their acoustic shadows differed from those of sturgeon (Figure 6). Longnose Gar *Lepisosteus osseus* were commonly seen in areas where sturgeon could be found, but the shape of this species was distinctive. Common bottlenose dolphins *Tursiops truncatus* were encountered, but these were usually observed visually before scanning and they had distinctive shapes.

Overall, the two side-scan sonar observers were able to detect sturgeon at approximately 70% of the sites where sturgeon were also detected by telemetry, video camera observations, or both. The null hypothesis was that side-scan sonar sturgeon detections were independent of sturgeon detections by other gears. Results of Pearson's chi-squared test suggested that side-scan sonar observations of sturgeon were dependent on sturgeon presence and were not random (side-scan observer 1: $X^2 = 53.92$, df=1,179, $p = 2.09 \times 10^{-13}$, side-scan observer 2: $X^2 = 46.54$, df=1,179, $p = 8.98 \times 10^{-12}$, for side-scan sonar observer 1 and 2, respectively). Additionally, odds ratio estimates from Fisher's exact test suggested that the odds of sturgeon being detected at a site by telemetry, video camera observations, or both was 16.54 times greater (95% confidence interval = 7.10-40.94) if sturgeon were detected by side-scan sonar observer 1 and 12.06 times greater (95% confidence interval = 5.35 - 28.58) if sturgeon were detected by side-scan sonar observer 2.

Discussion

Our results demonstrated that we could reliably detect sturgeon in multiple systems by using side-scan sonar. Sturgeon locations agreed with historic observations based on netting and telemetry. Within the Cape Fear River, we detected sturgeon in the same areas that Moser and Ross (1995) selected for gill-net sampling locations. Similarly, side-scan sonar results were similar to those reported by Collins and Smith (1997), who reported large numbers of sturgeon in the Pee Dee-Waccamaw and Edisto rivers during netting studies. They observed Atlantic Sturgeon ranging in size from 33 to 254 cm TL in these systems, representing both juvenile and mature individuals. Their upper bound for observed lengths is consistent with those of our side-scan sonar estimates (Figure 2). Collins and Smith (1997) observed Atlantic Sturgeon in the Santee River previously during summer months, but those fish were all subadults (< 105 cm TL) and the river discharge was much greater than during our surveys. Few sturgeon–mainly juveniles–have been observed in the Neuse River (Oakley 2003) or Roanoke River (Armstrong and Hightower 2002); however, adult Atlantic Sturgeon have recently been captured and observed in the Roanoke River (Smith et al. 2015; Chapter 4).

As our study and other studies have shown (Moser and Ross 1995; Collins and Smith 1997; Peterson et al. 2008), Atlantic Sturgeon use riverine habitat during summer. It is generally believed that juvenile Atlantic Sturgeon remain in riverine habitats over the summer (Moser and Ross 1995; Collins and Smith 1997; Peterson et al. 2008), but the considerable number of sturgeon larger than 1.5 m based on measurements using side-scan sonar seems to indicate that adult sturgeon are present as well (Figure 2). Riverine summer habitat use by at least some adults may be a characteristic shared by southern Atlantic Sturgeon and Gulf Sturgeon populations (Wooley and Crateau 1985; Zehfuss et al. 1999). Knowledge that sturgeon can be found reliably in riverine habitats during summer is useful for monitoring programs, as it establishes a potential time for locating sturgeon in rivers when they may be relatively stationary and accessible. At other times of the year, sturgeon are spawning and migrating, which can be problematic for sampling programs. This is exacerbated when spawning runs are small in size and their seasonality is unknown.

Even though we tried to monitor fish movement, closure was the assumption that was most likely to have been violated during our study. There probably were instances in which sturgeon moved from one site to another during our study, especially for individuals that were close to a site boundary. This occurrence may have been mitigated by high sturgeon abundance at some sites, such that even though a particular individual moved, the net site occupancy did not change because additional individuals where present. Larger sites could protect against some of this movement. Varying site size from 2 km to either 1 km or 4 km did not change the relative ranks of rivers or the relative performance of the gears, suggesting that closure was not violated (Figure 7). It makes sense that occupancy would increase as site size increased.

The AIC scores suggested that our survey data were better described by an occupancy model that decomposed the detection process into availability (i.e., θ) and detection given availability (i.e., p; Hines et al. 2010). Those models have proven useful for large-scale surveys where detection is a local process within a much larger site (Hines et al. 2010). In our case, there are several possibilities for why this decomposition might be useful. The most obvious is for a site that is occupied by sturgeon but in which the sturgeon are unavailable for detection by video camera because of the fish's low probability of jumping. Given that a sturgeon was available for detection by video (i.e., jumped), the probability of detection would depend on the fraction of the site within the field-of-view for the two cameras, at the instant when the fish jumped. Similarly, detection given availability could account for a sturgeon within the path of the sonar but produced an image with insufficient clarity to allow for confident classification of that individual as a sturgeon. Availability to the side-scan sonar would depend on the cross-channel distribution of sturgeon. Our field observations suggest that sturgeon tend to be concentrated in the deeper parts of a river channel and therefore are available for detection.

One approach for refining the estimate of θ would be to include, as separate gear types, side-scan sonar passes in different depth zones. If fish are mostly concentrated in the deeper parts of the channel, θ would be low for shallow sonar passes and higher for mid-channel passes. Another approach that might improve the decomposition of the detection process would be to include a separate side-scan pass at a swath width that encompassed the entire river cross-section. Availability could be fixed at 1.0 for that gear type, and then estimated for all other types.

Acoustic image quality was dependent on several factors, including target orientation, water turbidity and turbulence, vessel motion, and bottom features. These factors were site-specific and were randomly encountered within all rivers. Boat wakes and wind created surface motion, resulting in wavy distortion in side-scan sonar images. Wind, tidal motion, and other factors could increase the amount of reflective small particulates and air bubbles in the water column, producing "cloudy" images in which objects might be obscured. Other environmental factors, (e.g., bottom type or reflectivity) and the presence of schools of small fish could also affect image quality.

Prior to the study, informal field trials were conducted to evaluate the ability of side-scan sonar to identify fish, including sturgeon, but the trials produced mixed results. Our side-scan sonar unit was accurate for determining the lengths of fish and other targets but was not generally successful in determining species, although most target fish were less than 1 m in length. Tethered and netted Atlantic Sturgeon were presented to the side-scan sonar in the field, but these did not maintain natural swimming positions and did not represent good targets. At least one other study (Bergman 2011) involved attempts to ensonify and identify a 1-m frozen sturgeon with poor success; however, a lower resolution (800 kHz) side-scan sonar unit was used in that study. Side-scan sonar units are likely to be most effective when targeting larger species over 1 m in length (Bergman 2011; Gonzalez-Socoloske and Olivera-Gomez 2012).

The critical issue in our study was the certainty with which we could positively identify sturgeon. Since we could not fully validate our field observations, we relied on independent evidence to support our side-scan observations; such evidence included historical records of distribution patterns, our telemetry data, our observations of jumping sturgeon, and sturgeon size relative to other species. Unlike other hydroacoustic systems, with side-scan sonar it is difficult to create a fully objective method for identifying fish. With DIDSON, swimming motion as well as target shape can be evaluated to identify species; using split-beam sonar, it is possible to quantify target strength with prior calibration (Nealson and Brundage 2007; Mueller et al. 2008). While DIDSON may be more useful for identifying species, it is more limited in scanning range, more expensive than side-scan sonar units, is more cumbersome to deploy in the field, and lacks mapping capability.

Improving the quality of side-scan sonar images should increase detection ability. We could have improved our image quality by reducing the width of the side-scan sonar swath, but this would incur the tradeoff of reduced area swept by our surveys. Higher resolution side-scan sonar units used in combination with software that better processes and displays side-scan sonar data should also improve the ability to detect and identify fish. Software that can automatically process data is available for other hydroacoustic systems and can decrease analysis time, although there are identification errors associated with these analyses (Mueller et al. 2008). Increasing the number of surveys in a season could also improve occupancy estimates, but there would be a tradeoff in terms of field and processing time. In systems that are significantly deeper, it may be necessary to evaluate different towing arrangements, such as those that allow for variable depth, to achieve optimal side-scan sonar performance.

Human observers are an integral part of side-scan sonar usage, and the skill and experience of the observer will affect results of side-scan sonar analysis. Even though experience varied between the observers, the less experienced observer was estimated to detect sturgeon with a probability greater than 0.5, and detection results were similar when examined for individual sites (Table 4). Observer effects could be better quantified by additional means, such as laboratory trials evaluating the ability of observers to correctly classify example side-scan sonar images. Incorporating additional information sources, (e.g., video cameras and telemetry data as in the present study) can help to reduce observer uncertainty by confirming the presence of sturgeon at a site.

Side-scan sonar could be used independently or in conjunction with standard fisheries sampling approaches. Use of side-scan sonar could eliminate the need to handle sturgeon unless dictated by the study (e.g., mark-recapture or genetic studies). Stand-alone side-scan sonar surveys have the potential for time and monetary savings in comparison with traditional sampling. Although the initial cost of the side-scan sonar may be higher, use of a side-scan sonar unit instead of other gears could pay for itself in time. Sturgeon sampling using traditional gears such as nets require a large amount of effort. For example, a minimum of 288 net-hours over 8-10 weeks was suggested for determining Shortnose Sturgeon presence in a single river system (Moser et al. 2000). This might require a sizeable field crew and associated logistical supplies to support sampling efforts. The time required to review side-scan files would be less than that required to perform netting surveys over a similar area, although including video data would extend overall processing time.

Side-scan sonar data could be used with other occupancy and non-occupancy modeling approaches. We used a basic occupancy model, but more sophisticated occupancy models could be created, incorporating covariates into the model to assess different environmental, biological, and behavioral conditions that may affect occupancy and the ability to detect individuals (Mackenzie et al. 2006). Occupancy models can be modified to produce abundance estimates as well (Royle and Nichols 2003; Mackenzie et al. 2006). Non-occupancy approaches, like N-mixture abundance models (Royle 2004), could be used to incorporate counts of individuals at sites to generate abundance estimates from surveys. Estimates of density or abundance in specific areas could improve traditional surveys, such as gill-netting, by providing estimates of gear efficiency for capturing or detecting target species. Repeated standardized side-scan surveys over a series of years could also be used to monitor population changes in a CPUE framework by identifying changes in fish density in designated areas. A program like this could be performed relatively cheaply, requiring only a few days in the field each year.

An ideal combined side-scan sonar and netting sampling approach would incorporate (1) side-scan surveys to rapidly and efficiently identify areas where sturgeon are present and (2) subsequent netting to positively assess fish species and size and to allow for other measurements and tagging. Side-scan sonar could be used to identify areas where sturgeon are present, leading to a reduction in the amount of effort (including length of time for net sets) required to find sturgeon for a sampling program. Side-scan sonar images can also be used to identify bottom hazards that may interfere with sampling operations.

A common application of side-scan sonar is to map and characterize habitat in areas where fish are found. The relatively small sturgeon populations in many river basins have made habitat utilization patterns difficult to establish with certainty (Collins et al. 2000). Methods for using side-scan sonar to map habitat have previously been described, and doing so is a relatively simple process (Kaeser and Litts 2010). Summer habitat in multiple rivers can be surveyed in just a few weeks, although file processing takes considerable time if individual fish positions and sizes are determined. This information could be used to better inform monitoring programs and to identify areas that need protection under the auspices of Endangered Species Act requirements. Side-scan sonar surveys could provide data on habitat types and usage, which are valuable since little detailed information about specific sturgeon habitats is available in all river systems. Habitat data could also be used with occupancy models to describe factors that influence sturgeon habitat use.

Conclusions

Our results demonstrate that side-scan sonar can be used to survey sturgeons and potentially other large fishes. A primary advantage of using side-scan sonar to sample sturgeon was that physical handling of sturgeon was not required, thus eliminating the risk of mortality. We detected individual fish with a multitude of gears and even identified targets to species with some confidence. Video cameras were surprisingly effective for detecting jumping sturgeon, and the use of telemetry-tagged individuals helped inform our study. An occupancy modeling approach was well suited for analyzing side-scan sonar data, providing useful information about the status of sturgeon within our sampled rivers systems. We were able to confirm presence of sturgeon in river systems using a fraction of the effort associated with traditional netting programs and without having to handle the target species.

Side-scan sonar and other hydroacoustic methods should become a more attractive option for sampling as technology improves and as prices decrease. New ideas and uses should develop as more researchers and managers use hydroacoustic technologies. We plan to extend our side-scan sonar data analysis to an evaluation of sturgeon abundance and habitat use in the study systems. The greatest potential for side-scan sonar may lie in situations where it can be used in conjunction with traditional sampling methods and integrated into monitoring programs. Combined approaches to studying fish populations should always be considered when practical.

Acknowledgements

Funding for this project was provided by National Oceanographic and Atmospheric Administration. We thank T. Jackson for his work in the field and laboratory and in reviewing side-scan and video data. We appreciate C. Collier and M. Loeffler (North Carolina Division of Marine Fisheries) and W. Post (South Carolina Department of Natural Resources) for allowing us to use their telemetry-tagged sturgeon during the course of the study. We also thank N. Cole, J. Hughes, and A. Prince for assistance during preliminary phases of our side-scan sonar work. The Cooperative Fish and Wildlife Research Unit is jointly supported by North Carolina State University, North Carolina Wildlife Resources Commission, U.S. Geological Survey, U.S. Fish and Wildlife Service, and Wildlife Management Institute. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 1. Results of river surveys for each sampled system with prior anecdotal abundance. Sturgeon were detected in 5 of 6 rivers and by all 3 gears. The last column is the number of 2-km sample sites where sturgeon were detected over the total number of sites surveyed in each river.

River	Anecdotal Population Level	Side-scan Sturgeon Detection	Video Sturgeon Detection	Telemetry Sturgeon Detection	Sites with a detection/total sites
Roanoke, NC	Low	Yes	Yes	No	12/30
Neuse, NC	Low	Yes	No	No*	3/22
Cape Fear, NC	Medium	Yes	Yes	Yes	19/38
Pee Dee / Waccamaw, SC	High	Yes	Yes	Yes	24/37
Santee, SC	Low	No	No	No*	0/30
Edisto, SC	Medium / High	Yes	Yes	Yes	18/22

* No sturgeon were telemetry-tagged in the Neuse or Santee rivers, although it could be possible that tagged individuals immigrated from other systems.

Table 2. Candidate occupancy models denoted by parameterization: “r” for river, “g” for sampling gear, “ss” for side-scan”, and “v” for video.

Model	AIC	deltaAIC	AIC weight	Likelihood	# Par.	-2*LogLike
ψ(r), p(g), θ(.)	954.71	0.00	0.807	1	10	934.71
ψ(r), p(g), θ(g)	957.77	3.06	0.1747	0.2165	12	933.77
ψ(r), p(ss,v), θ(.)	962.68	7.97	0.015	0.0186	9	944.68
ψ(r), p(ss,v), θ(g)	965.73	11.02	0.0033	0.004	11	943.73
ψ(r), p(g), θ(fixed)	997.09	42.38	0	0	9	979.09
ψ(r), p(ss,v), θ(fixed)	1001.79	47.08	0	0	8	985.79
ψ(.), p(g), θ(.)	1008.27	53.56	0	0	5	998.27
ψ(r), p(.), θ(.)	1010.52	55.81	0	0	8	994.52
ψ(.), p(g), θ(g)	1011.33	56.62	0	0	7	997.33
ψ(r), p(.), θ(g)	1013.57	58.86	0	0	10	993.57
ψ(r), p(.), θ(fixed)	1040.05	85.34	0	0	7	1026.05
ψ(.), p(g), θ(fixed)	1050.65	95.94	0	0	4	1042.65
ψ(.), p(.), θ(.)	1064.08	109.37	0	0	3	1058.08
ψ(.), p(.), θ(g)	1067.13	112.42	0	0	5	1057.13
ψ(.), p(.), θ(fixed)	1093.61	138.90	0	0	4	1089.61

Table 3. Parameter estimates of the top five occupancy analysis scenarios with estimates of detection probability (p) for each gear, occupancy (ψ) for each river, and individual availability (θ). Side-scan Observer 1 was the more experienced observer of the two. Models denoted by parameterization: "r" for river, "g" for sampling gear, "ss" for side-scan", and "v" for video.

	Ψ(r), θ(.), p(g)		Ψ(r), θ(g), p(g)		Ψ(r), θ(.), p(ss,v)		Ψ(r), θ(g), p(ss,v)		Ψ(r), θ(fixed), p(g)	
Parameter	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
p[Side-scan Obs. 1]	0.701	0.045	0.701	0.045	0.607	0.036	0.607	0.036	0.484	0.035
p[Side-scan Obs. 2]	0.526	0.045	0.526	0.045	0.607	0.036	0.607	0.036	0.363	0.033
p[Video Camera]	0.266	0.037	0.266	0.037	0.263	0.037	0.263	0.037	0.184	0.026
θ[Side-scan Obs. 1]	0.653	0.046	0.611	0.069	0.660	0.047	0.618	0.069	1.000	-
θ[Side-scan Obs. 2]	0.653	0.046	0.654	0.069	0.660	0.047	0.661	0.070	1.000	-
θ[Video Camera]	0.653	0.046	0.696	0.069	0.660	0.047	0.704	0.070	1.000	-
ψ[Roanoke]	0.431	0.097	0.430	0.097	0.431	0.097	0.430	0.097	0.408	0.091
ψ[Neuse]	0.147	0.079	0.147	0.079	0.147	0.079	0.147	0.079	0.139	0.075
ψ[Cape Fear]	0.453	0.087	0.453	0.087	0.453	0.087	0.453	0.087	0.429	0.082
ψ[Pee Dee]	0.699	0.086	0.698	0.086	0.699	0.086	0.698	0.086	0.662	0.080
ψ[Santee]	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ψ[Edisto]	0.881	0.091	0.880	0.091	0.881	0.091	0.880	0.091	0.834	0.084

Table 4. Survey detection contingency tables for both observers. Note the similarity in detections across methods.

		Telemetry and Video Camera		
		Detections	Non-detections	Totals
Side-scan observer 1	Detections	36	17	53
	Non-detections	14	112	126
	Totals	50	129	179

		Telemetry and Video Camera		
		Detections	Non-detections	Totals
Side-scan observer 2	Detections	34	19	53
	Non-detections	16	110	126
	Totals	50	129	179

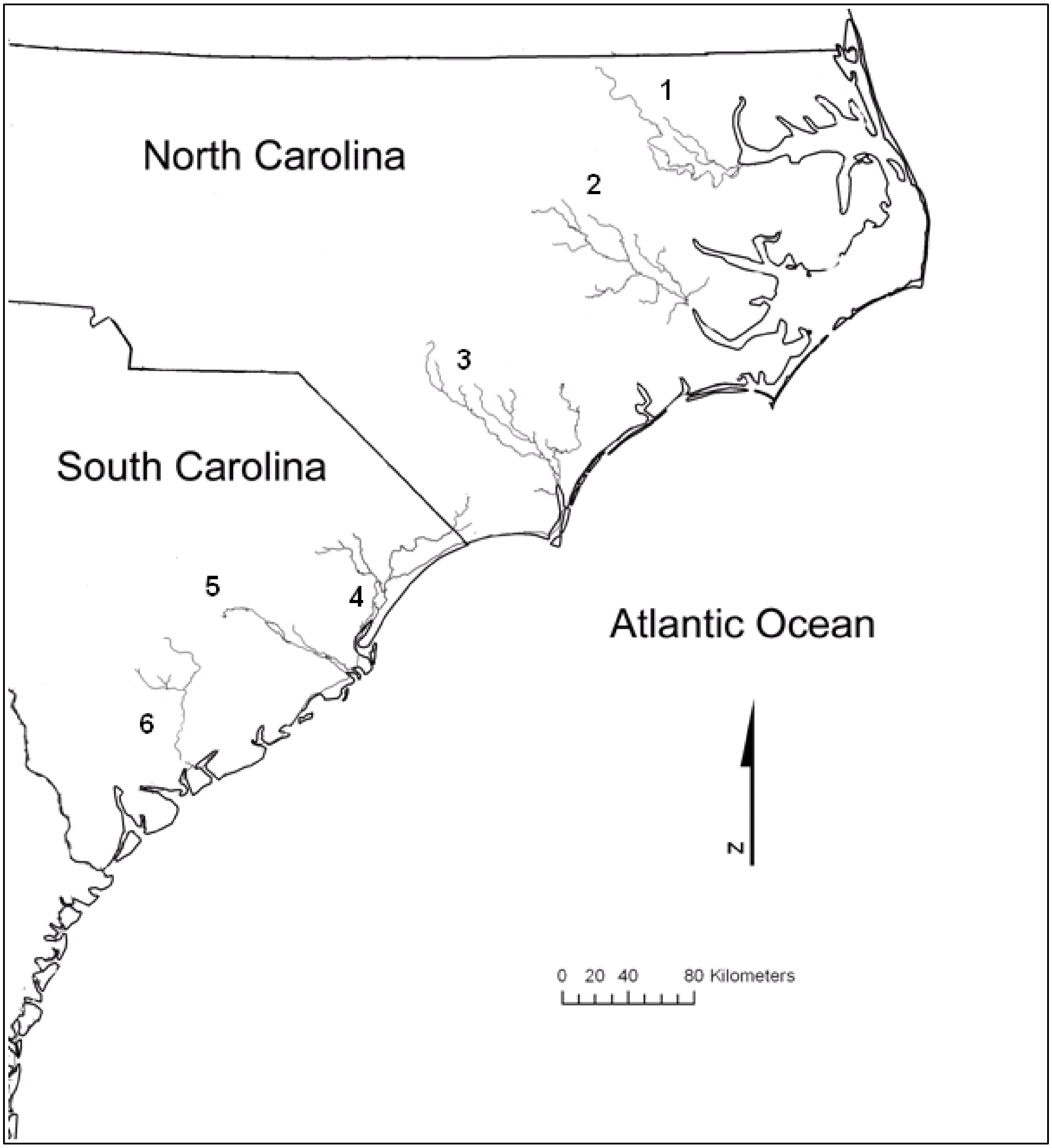

Figure 1. Lower portions of six river systems were sampled during our study. From north to south: (1) Roanoke, (2) Neuse, and (3) Cape Fear rivers in North Carolina and (4) Pee Dee/Waccamaw, (5) Santee, and (6) Edisto in South Carolina.

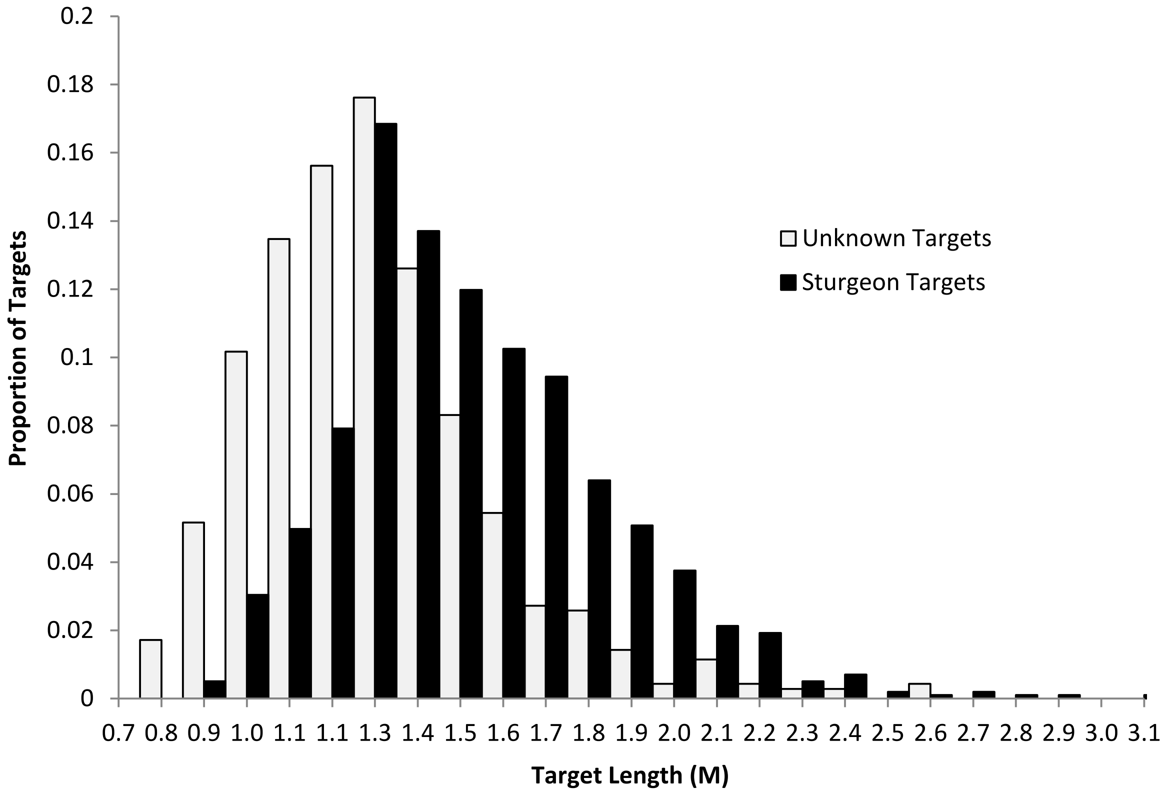

Figure 2. Proportional length-frequency histogram of detected side-scan targets for all rivers. Smaller targets (N=985) were more difficult to positively identify, while targets identified as sturgeon (N=698) were generally larger. Targets longer than 2.5 m were probably distorted.

Figure 3. Video frame capture of a jumping sturgeon, Edisto River, SC.

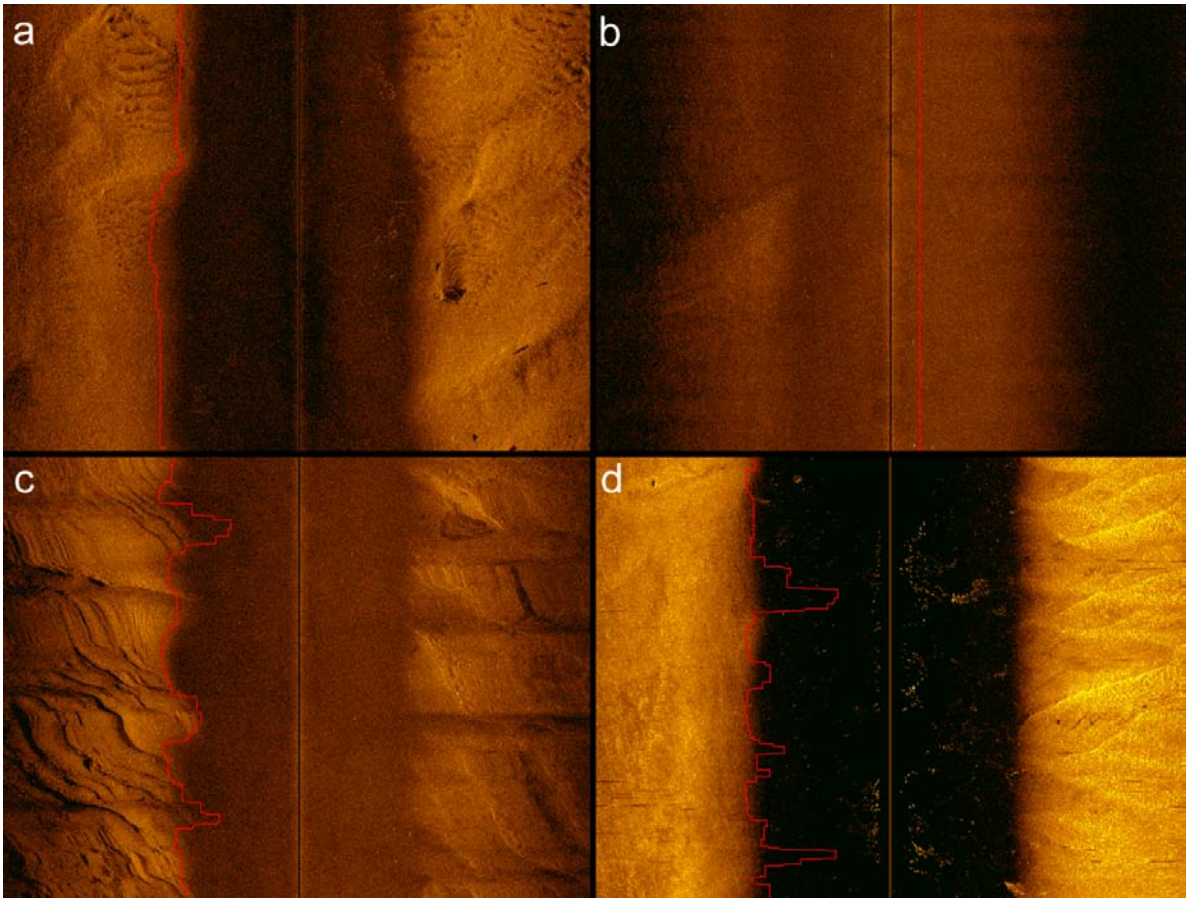

Figure 4. Example side-scan images showing variability in image quality. Width of each image is 60 m. Images: a) typical side-scan image; b) image from same location with high turbidity or turbulence; c) image showing distortion from surface waves (horizontal banding in image) and moderate turbidity or turbulence; d) image showing small fish and other objects in the water column. The red line in each image represents the river bottom as perceived by the side-scan sonar software (prior to any manual correction): a) typical image; b) excessive turbidity or turbulence obscures bottom from detection; c & d) interference prevents software from properly tracking bottom.

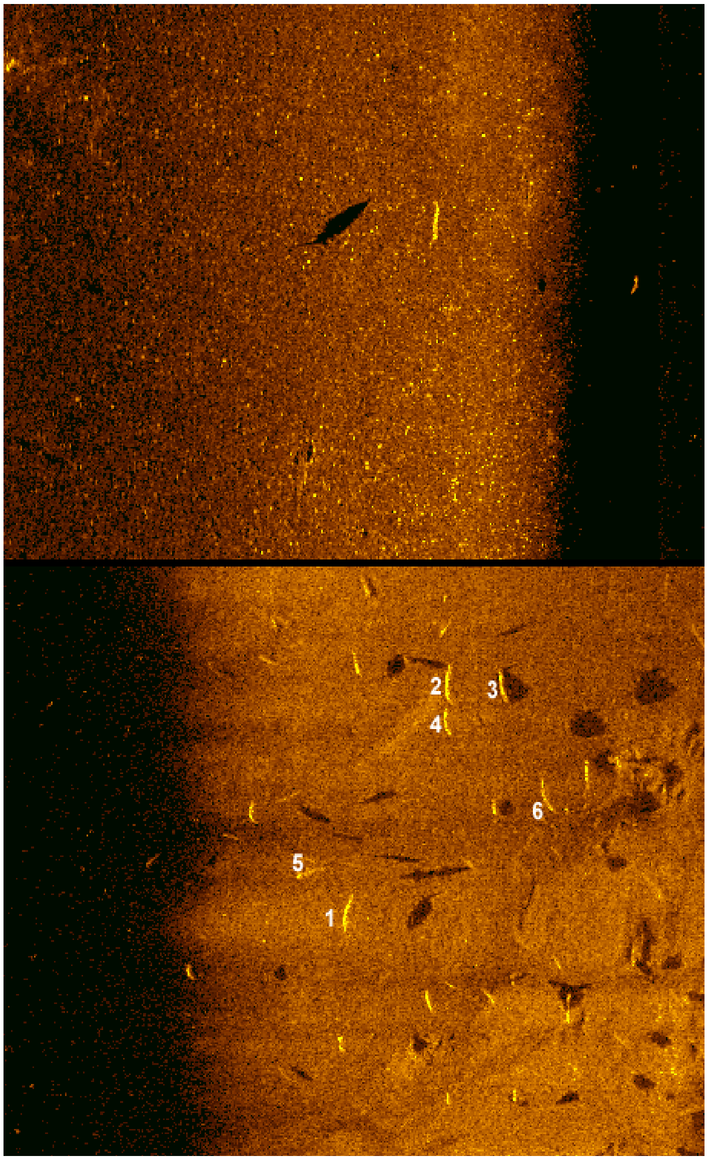

Figure 5. Composite image showing target identified as 1.9 m sturgeon (top) in the Roanoke River, and multiple targets in the Pee Dee River (bottom) identified as sturgeon and unknowns. Sturgeon in bottom image are numbered. Lengths are as follows: 1) 1.5 m, 2) 1.6 m, 3) 1.4 m, 4) 1.3 m, 5) 1.2 m, 6) 1.6 m. Other targets range in size from 0.4- 1.2 m.

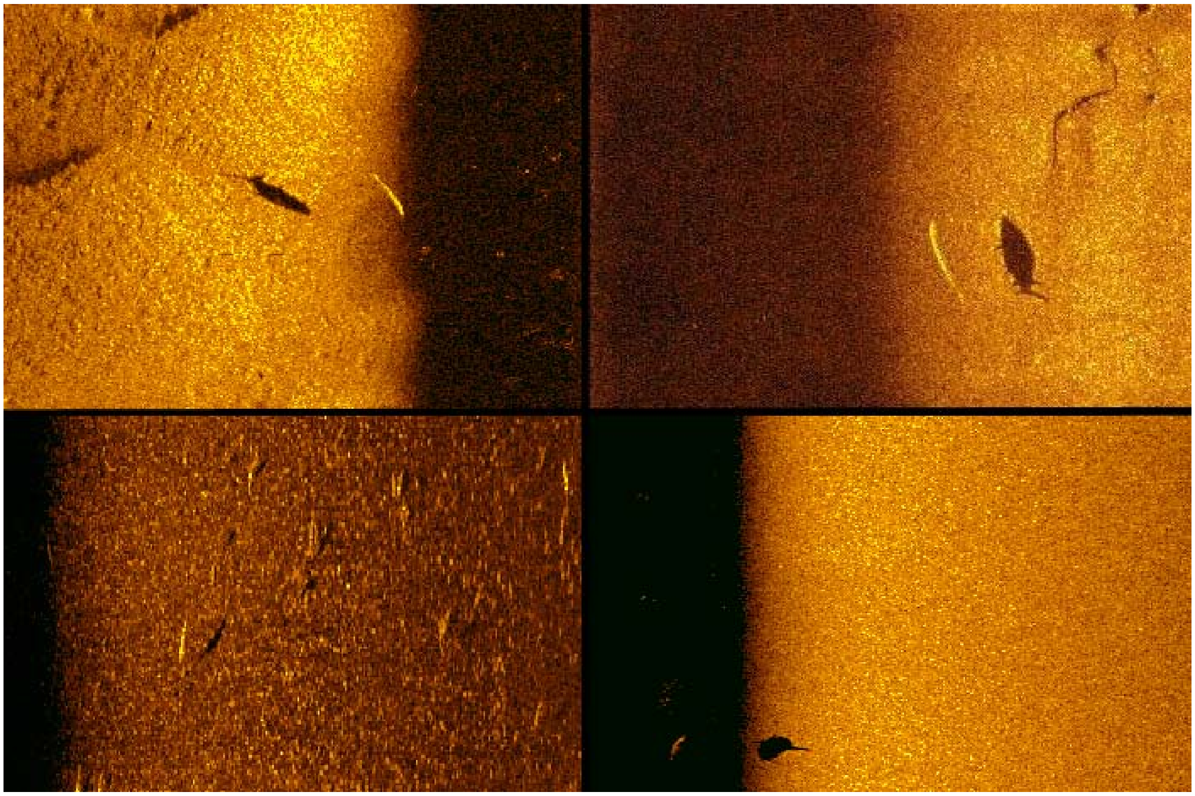

Figure 6. Examples of different large fish targets as seen on side-scan sonar. (Clockwise from top right): Atlantic Sturgeon (1.8 m length); bottlenose dolphin (1.2 m, confirmed visually), Longnose gar (0.9 m, confirmed by netting), Tarpon (1.6 m, confirmed visually). These images demonstrate the detail that can be seen in the acoustic shadows of each target. Notice body shape, proportion, and fin position for each.

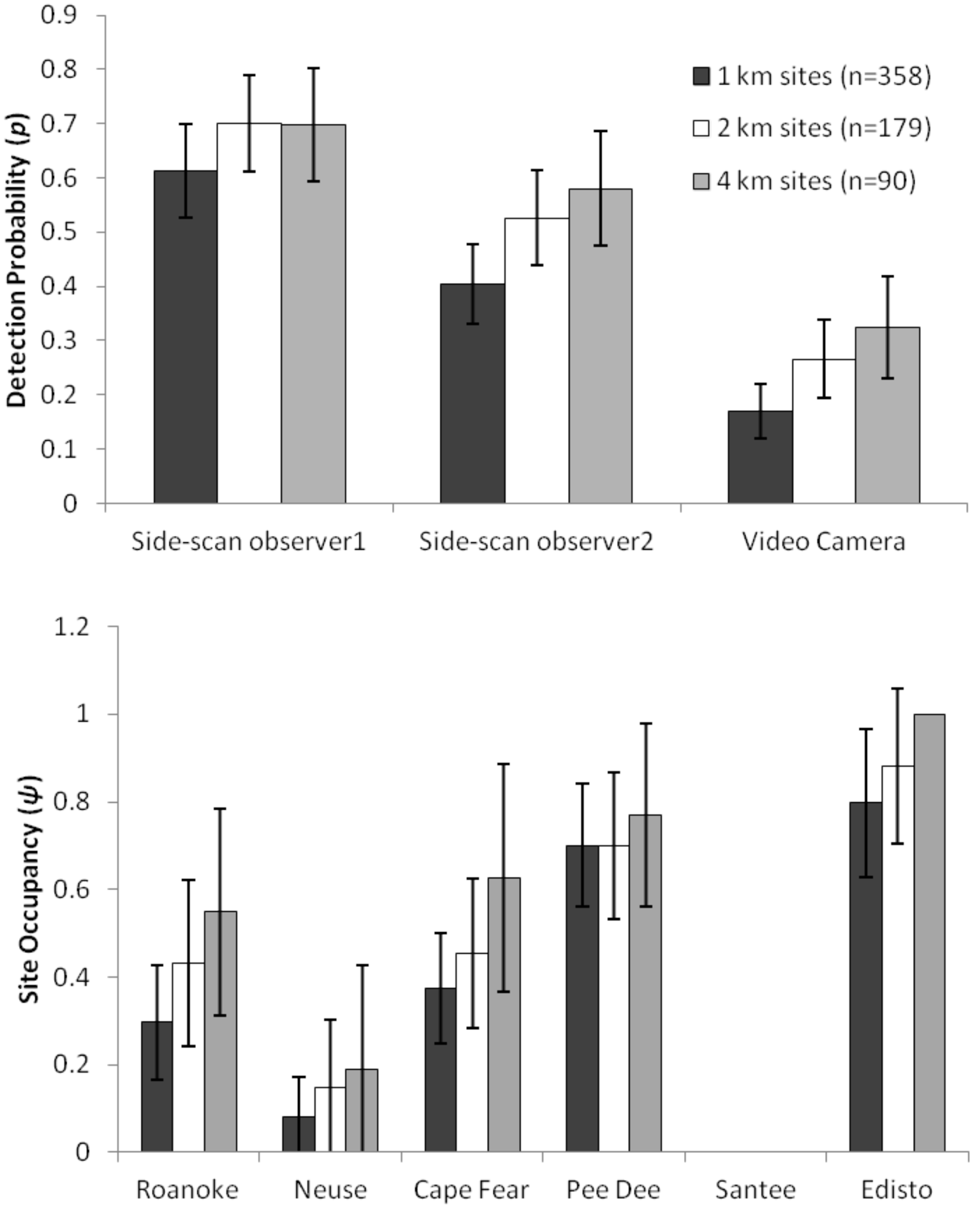

Figure 7. Parameter estimates of detection probability (*p*) for each gear (top), occupancy (ψ) for each river (bottom). Error bars denote 95 % confidence intervals of estimates. No sturgeon were detected in the Santee River.

CHAPTER 3

ESTIMATING STURGEON ABUNDANCE IN THE CAROLINAS USING SIDE-SCAN SONAR

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Chapter in press in Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science

Abstract

Sturgeons (Acipenseridae) are one of the most threatened taxa worldwide, including species in North Carolina and South Carolina. Populations of Atlantic Sturgeon *Acipenser oxyrinchus* in the Carolinas have been significantly reduced from historic levels by a combination of intense fishing and habitat loss. There is a need for estimates of current abundance, to describe status, as well as historic estimates of abundance in order to provide realistic recovery goals. In this study we used N-mixture and distance models with data acquired from side-scan sonar surveys to estimate abundance of sturgeon in six major sturgeon rivers in North Carolina and South Carolina. Estimated abundances of sturgeon greater than 1 m TL in the Carolina distinct population segment (DPS) were 2,031 using the count model and 1,912 using the distance model. The Pee Dee River had the highest overall abundance of any river at 1,944 (count model) and 1,823 (distance model). These estimates do not account for sturgeon less than 1 m TL or occurring in riverine reaches not surveyed or in marine waters. Comparing the two models, the N-mixture model produced similar estimates using less data than the distance model with only a slight reduction of estimated precision.

Introduction

Sturgeon (Acipenseridae) populations worldwide have declined from historic levels as a result of a combination of factors, including over-harvest and habitat alteration (Secor 2002; Pitkitch et al. 2005; Nelson et al. 2013). In the eastern USA, Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* was listed as "endangered" under the Endangered Species Act (ESA) in 2012. Under the listing, five separate Atlantic Sturgeon distinct population segments (DPS) were established. One DPS was categorized as threatened, but the other four were listed as endangered, including the Carolina and South Atlantic DPSs (Figure 1). The Carolina DPS includes riverine populations ranging from the Roanoke River in North Carolina to the Santee-Cooper system in South Carolina. The South Atlantic DPS includes rivers from the Ashepoo-Combahee-Edisto Basin in South Carolina to the St. Johns River, Florida. Given the status of sturgeons, it is important to assess and monitor the state of populations. Unfortunately, sturgeons have not been well studied in many Southeastern systems since the closure of commercial U.S. fisheries in 1998 (ASSRT 2007; Peterson et al. 2008). Reliable estimates of abundance are necessary for making management decisions and developing recovery strategies.

A common method for estimating absolute abundance of fish species is mark-recapture; however, there are drawbacks to these studies, including cost and potential harm to the study species. The endangered status of sturgeon limits the sampling methods researchers can employ because extra care must be taken when sampling and handling specimens (Damon-Randall et al. 2010; Kahn and Mohead 2010). Hydroacoustics provides a non-intrusive method for sampling endangered species. Sturgeon and related paddlefish *Polyodon spathula* have been identified as potentially suitable targets for hydroacoustic studies (Nealson and Brundage 2007; Bergman 2011; Nelson et al. 2013). Side-scan sonar is a relatively old hydroacoustic technology that has been used increasingly in fisheries studies in recent years (Kaeser and Litts 2008; Foote 2009). In a previous paper, we described a procedure to rapidly survey sturgeon populations using side-scan sonar and occupancy modeling approaches (Flowers and Hightower 2013). We reexamine those data here, with a goal of estimating Atlantic Sturgeon abundance in the Carolina DPS. Large body size, including a maximum length of over 3 m (Gross et al. 2002) and distinctive shape make this species an ideal hydroacoustic target. This anadromous species spends large amounts of time feeding and migrating in marine environments, using freshwater rivers for spawning and a summer dormant period (ASSRT 2007). During summer, Atlantic Sturgeon may aggregate in lower portions of rivers, often in deep holes near the freshwater-saltwater interface, although locations vary with river characteristics and flow conditions (Moser and Ross 1995; Collins et al. 2000).

Sturgeon density can be obtained from counts based on side-scan images and the length and width of the survey transect. These counts can be analyzed with an N-mixture model (Royle 2004) that uses a distribution, such as a Poisson, to simulate abundance and a binomial distribution to simulate detection. Count data can also be analyzed using distance sampling methods (Buckland et al. 2001; Royle et al. 2004) based on the distance on side-scan images from sturgeon to the survey transect. We compare results from the various data types and models and provide abundance estimates for Atlantic Sturgeon recovery planning.

Methods

Study sites

Field work took place in six river systems in North Carolina and South Carolina (Figure 1). Systems were chosen based on available information about the status of sturgeon populations or the potential for presence of sturgeon in that system. Five of the rivers were located in the Carolina DPS (Roanoke, Neuse, Cape Fear, Pee Dee, and Santee) while the sixth was located in the South Atlantic DPS (Edisto). The Tar River was the only Carolina DPS river excluded from the survey, based on smaller size (Oakley and Hightower 2007) and lack of recent anecdotal evidence of sturgeon. Mark-recapture studies or other types of sturgeon population studies have not been performed on these systems.

Side-scan surveys

Surveys were conducted in coastal rivers near the freshwater/saltwater interface where sturgeon have been observed (Moser and Ross 1995; Collins et al. 2000; Peterson et al. 2008). Repeated side-scan sonar surveys were performed over 3 d at each of the six rivers. The three sampling days were as close as possible, often consecutive, in order to reduce the chance of movement between sites, as needed to minimize violations of the population closure assumptions of these methods. Riverine survey reaches began downstream in tidal portions of elevated salinity (>15 mg/L) and ranging upstream a distance of at least 30 km inland on the main stem or to a point where river depths were too shallow to effectively operate the side-scan sonar. The total distance surveyed in each river varied, ranging from 40-80 km because of braids and side channels. Full details regarding survey methods were provided in Flowers and Hightower (2013).

We used an Edgetech 4125-P side-scan sonar unit operated in high-frequency (1,250 kHz) mode, with a total swath width of 50 m. The unit was deployed at a constant depth of approximately 1 m below the water's surface for all systems and surveys. Side-scan sonar data were collected and processed using Chesapeake Technology's SonarWiz.Map software. When a potential sturgeon was observed on side-scan images, the target was marked, its GPS coordinate was taken, and the target's body length and distance from transect measured.

Each river was an individual study area divided into 2-km sites, for a total of 179 sites. Sites of 1 km and 4 km size were previously evaluated for their effect on occupancy, with results bracketing the 2 km sites (Flowers and Hightower 2013). The large amount of data collected during the surveys required extended time for analysis. Side-scan sonar file processing took 1-3 d/survey day, depending on how many targets needed to be recorded.

Abundance estimation

Only targets clearly identified as sturgeon (Flowers and Hightower 2013) were used in our analyses. For the N-mixture model, side-scan observer data were compiled into a data matrix containing river, site, and the three daily counts of individual sturgeon. Sites were arranged in rows (N=179) while river index and daily counts were listed in columns (N=4). A separate matrix for distance sampling data incorporated corrected horizontal distance from a side-scan transect's centerline to each sturgeon identified in a given site for each survey day. The number of rows in this matrix was equal to the number of distance observations by site (N=1,436) and had columns representing river, site, sample day, and distance (N=4). A "slant range correction" was used to account for positioning errors because the cross-track coordinates of a side-scan image are a function of range to the sonar rather than horizontal distance on the bottom (Cobra et al. 1992). Although our side-scan swath was 25 m/side, based on slant-range, the maximum horizontal range was actually 24 m.

The counts and distance data sets were analyzed using procedures in package unmarked (Fiske and Chandler 2011) in program R (R Development Core Team 2014). For both analytical methods, we assumed that we correctly identified targets classified as sturgeon, although additional sturgeon were assumed to be present but not identifiable from a particular side-scan image. Count data were analyzed in unmarked using the pcount procedure, based on the N-mixture framework proposed by Royle (2004). The general form of the N-mixture model for site abundance is:

$$N_i \sim f(\lambda, \theta) \text{ for } i = 1, 2, \ldots, M \qquad (1)$$

and for the detection process is:

$$y_{ij} \mid N_i \sim \text{Binomial}(N_i, p) \text{ for } j = 1, 2, \ldots, J_i, \qquad (2)$$

where λ is the mean abundance per site and p is the detection probability. A discrete distribution such as the Poisson or negative-binomial, is used for f, with support restricted to $N_i \geq 0$ (Fiske and Chandler 2011). The θ are additional parameters of f other than the abundance rate for distributions such as the negative binomial (Fiske and Chandler 2011).

This method uses temporally repeated counts of individuals at a site to estimate the abundance of a closed population. The framework uses a combination of two different processes to model detection and abundance. Detection probability is modeled using a binomial distribution while abundance is modeled using a Poisson, negative binomial, or zero-inflated Poisson distribution. Sites were assumed to be closed for the duration of the experiment, and probability of detecting an individual animal was assumed to be constant (Royle 2004).

Distance sampling data were analyzed using the gdistsamp function based on the method proposed by Royle et al. (2004) and extended by Chandler et al. (2011). This model is similar to the N-mixture model, although it adds a component to the likelihood to address variability in detection probability as a function of range from the survey transect. Here transect-level abundance is modeled the same as the N-mixture model, but the detection process is modeled as:

$$y_{ij} \mid N_i \sim \text{Multinomial}\ (N_i, \pi_{ij}) \quad \text{for } i = 1,\ldots,M \ \ j=1,\ldots,J, \tag{3}$$

where N_i is the latent abundance at site i, as with the N-mixture model, and π_{ij} is the multinomial cell probability for transect i in distance class j, computed by integrating a detection function such as the half-normal (with scale parameter σ) over each distance interval (Fiske and Chandler 2011). Abundance is modeled using a Poisson or negative-binomial distribution. Four functions (uniform, half-normal, exponential, hazard), described in further depth by Buckland et al. (2001), were used to model detection, with distance data formatted in 4-m bins over the 24 m/side width of the side-scan swath. As above, sites were assumed to be closed over sampling occasions. Additional assumptions related to distance sampling were (1) sturgeon were distributed according to some stochastic process based on an underlying density, (2) sturgeon were detected at their initial locations, prior to any movement (to avoid double-counting), and (3) distances were correctly grouped by intervals (Buckland et al. 2001). It is generally assumed for distance surveys that survey lines are randomly placed but here a single mid-river survey line was used. Thus, we further assumed that sturgeon were randomly distributed so that our estimated abundances were representative of the entire surveyed sections of rivers.

For all models, scenarios were run using river as a site-level covariate to model the variability in abundance across rivers. For each method (count and distance), the most appropriate model was selected using Akaike's Information Criterion (AIC). We evaluated model selection using ΔAIC, i.e., the difference between the best model and each model, and AIC weight (AICwt), representing the relative likelihood of each model. Goodness-of-fit for the best models was evaluated using the parametric bootstrapping function in unmarked, parboot. One hundred bootstraps were run for each model and the Freeman-Tukey test was used to assess fit. Estimates of abundance and 95% confidence intervals were calculated for each of the best models using the predict function in unmarked.

We estimated the proportion of the river scanned based on the total surface area and the area surveyed by side-scan sonar (48 m x 179 2 km sites). River area measurements were performed in Google Earth Pro (Google Inc.). Our side-scan surveys only covered 17.2 sq km, which was 0.13 of the area of the survey reach for all rivers combined. Proportions for individual rivers were: 0.13 (Roanoke), 0.08 (Neuse), 0.26 (Cape Fear), 0.11 (Pee Dee), 0.29 (Santee), and 0.11 (Edisto).

Results

Counts of sturgeon during surveys ranged from 0 to 109 across sites (Figure 2). Of the 179 sites, 113 had no sturgeon detected, 55 had between 1 and 10 sturgeon, and only 11 had more than 10 sturgeon. Clearly, sturgeon were not uniformly distributed across sites or systems. When detected, they were predominantly alone or in small numbers and not in large aggregations, except in a few instances.

The best performing N-mixture model used a negative binomial distribution for abundance and included river as a covariate (Table 1). There was negligible support for a Poisson distribution for abundance (with or without zero inflation) or models without river-specific estimates. Estimated abundance varied substantially among sites and rivers, with highest observed and estimated counts for the Pee Dee and Edisto rivers (Table 2; Figure 3). The Pee Dee River had the highest estimated abundance for a single river (1,944), and comprised a large fraction of estimated total abundance for the Carolina DPS (Table 2). The selected model appeared to be adequate based on a goodness-of-fit test (Figure 4). The data do appear to be overdispersed, with estimated dispersion $\alpha>0$, at 0.13.

The best performing distance model also utilized a negative binomial distribution for abundance, with river as a covariate (Table 3). As in the N-mixture models, there was negligible support for a Poisson distribution for abundance. The preferred model used a half-normal distribution for describing detection probability. The pattern of detections by range bins (Figure 5) was not well described by the half-normal distribution (or any other alternative), but the half-normal did account for the low detections at ranges greater than 20 m. Detections probably decreased at the far edge of the swath because acoustic shadows would have been outside the sonar image field-of-view. Detections increased gradually at distances of 8-20 m off the transect, perhaps because the more gradual angle relative to the sonar provided a clearer acoustic shadow for identification. Abundance estimates from the distance model were quite similar to those of the N-mixture model, the Carolina DPS estimate being 1,823 (Table 2; Figure 3). The preferred distance model was supported by the goodness-of-fit test (Figure 4). The data do appear to be overdispersed, with estimated dispersion $\alpha>0$, at 0.27.

Discussion

Our abundance estimates are the first of any kind on these rivers and only the fifth estimate of Atlantic Sturgeon abundance rangewide (Kocik et al. 2013; Kahn et al. 2014).. Sturgeon have been observed in these rivers and sampled in various studies (Collins and Smith 1997; Collins et al. 2000; Moser and Ross 1995, Armstrong and Hightower 2002, Oakley and Hightower 2007, authors' unpublished data), but no assessments have been undertaken. A recent range-wide study estimates that there may be 6,615-29,784 ocean-going Atlantic Sturgeon in the Carolina DPS (Kocik et al. 2013).

Our Atlantic Sturgeon population estimates are not all-inclusive. Estimates are limited to sturgeon >1 m because smaller sturgeon are difficult to identify confidently using side-scan images. Thus, all identified sturgeon were likely Atlantic Sturgeon due to their greater abundance and larger overall size. Only the largest Shortnose Sturgeon *A. brevirostrum* would be close to the 1 m size threshold for identification. Estimates are also limited to the reaches of rivers surveyed. This zone, encompassing the freshwater/saltwater interface, likely contained most of a river's available Atlantic Sturgeon ≥1 m, although side-scan detections of sturgeon sometimes occurred to the upper extent of survey reaches (Flowers and Hightower 2013, Supplement A). We did not observe sturgeon in our surveyed portion of the Santee River, resulting in a 0 population estimate, but sturgeon have been observed there in the past (Collins et al. 2000). A different survey design would be required in order to produce estimates that would apply to each entire river.

Both models require that sites be closed with respect to mortality, recruitment, and movement. Our survey passes were typically done on successive days in order to minimize these events, and telemetry data showed limited movement between sampling occasions (Flowers and Hightower 2013). Prior studies have shown that Atlantic Sturgeon occupy deep areas and show little or no movement for extended periods during summer (Moser and Ross 1995). Distance sampling assumes that transects are located randomly and independent of animals' locations (Thomas et al. 2010). Our transects extended through the entire study reach so were therefore independent of sites containing sturgeon. However, we do recommend that future side-scan surveys of sturgeon be done with transects at varying locations cross-channel.

Based on telemetry studies (Erickson et al. 2011; Parauka et al. 2011; Oliver et al. 2013), sturgeon are known to move between river systems. Therefore a sturgeon detected in a given river system may not belong to that river's reproductive population. We also do not know what proportion of sturgeon remain in river systems during summer versus move to marine habitats. Generally it is thought that juvenile Atlantic Sturgeon stay in riverine areas year-round, while adults move into rivers during spring for spawning but move out into marine environments during other times (Smith 1985; Bain 1997). Our study and others (Moser and Ross 1995; Collins et al. 2000) have observed adult and subadult Atlantic Sturgeon in riverine areas during summer. In an ongoing study in the Roanoke River-Albemarle Sound system, most sonic-tagged adult Atlantic Sturgeon were present during the summer months (two of three in 2011, five of five in 2012, and three of six in 2013), not offshore in marine waters (Chapter 4). This summering behavior may be similar to observations for Gulf Sturgeon *A. o. desotoi* (Wooley and Crateau 1985; Clugston et al. 1995). Additionally, presence of adult sturgeon in rivers during summer may be related to fall spawning (Smith et al. 1984; Balazik et al. 2012; Smith et al. 2015).

The best individual model for each method used a negative binomial distribution because the data appeared to be overdispersed, based on estimated values of the overdispersion parameter α. Precision was similar for both models, although the distance model had slightly narrower confidence intervals. The distance model used replicate counts to provide information about the probability of being available for detection (Chandler et al. 2011). The replicate counts allow the model to relax the assumption that detection probability is 1 on the transect.

For both models, estimated detection probability was a product of true detection probability and availability of an animal within the site to be detected by the survey. These two components can sometimes be estimated separately, such as in occupancy modeling with multiple gears (Hines et al. 2010; Flowers and Hightower 2013). However, there is insufficient information available in this study to parse the effects of detection probability and availability using only one survey gear. While our assumption of site closure was probably not violated for the 2 km sites, it was likely that all sturgeon did not remain within our side-scan swaths during our surveys, based on the variability of sturgeon counted in individual sites over the course of our surveys. If sturgeon were moving randomly in and out of our survey swaths, our abundance estimates should reflect the numbers of sturgeon in our surveyed rivers. If sturgeon movement was more limited, abundance estimates may need to be scaled up to account for areas not surveyed by the sonar.

The distance model incorporates information about the spatial distribution of animals within the survey swath to make inference about changes in detection probability with distance, while the N-mixture model assumes an average detection probability throughout the swath. Even though the half-normal function was selected as the best to model detection across the sampling swath, it did not appear to fit the distance observations well (Figure 5). We evaluated the results of other poorer fitting distributions, but abundance estimates were comparable to the half-normal. Another option was to truncate our data observations to a maximum distance of 20 m. In this case the uniform distribution fit best and estimates were more similar to those of the N-mixture model. Distance-sampling methods may not be well suited for use with side-scan sonar since the survey width is arbitrarily truncated by the width of the sonar swath, which explains why estimates were so similar for each model. Apparent changes in detection probability across the swath may be more of an artifact of interpreting side-scan images, rather than of detection itself. Distance sampling may be more effective over wider swath widths, where there is greater contrast between image quality of near and far targets.

Conclusion

Side-scan sonar can be used to survey sturgeons and potentially other large fishes and various analytical approaches, such as N-mixture and distance models, are well suited for side-scan data. It is interesting that both abundance estimation models provided such similar estimates despite using different datasets and assumptions about detection. The N-mixture model requires less data (counts only, no distances off transect) than distance-sampling model, and only had slightly more uncertainty around abundance estimates. Further study is needed to determine whether the pattern in our distance data is a result of the distribution of sturgeon within our study, characteristics of side-scan data, or both. If patterns are related to side-scan characteristics, then new detection functions and analysis techniques may be needed to properly analyze data.

Our abundance modeling provided useful information about the status of sturgeon within our sampled rivers systems. We were able to produce estimates of sturgeon populations in river systems using a fraction of the effort of traditional netting programs and without having to handle our target species. Covariates that could influence abundance can also be incorporated into all models (Kéry and Schaub 2012). Abundance estimates from side-scan surveys can be used in conjunction with other data sources, such as genetic abundance estimates or traditional mark-recapture tagging studies to improve population abundance estimates. Side-scan sonar can provide absolute abundance estimates in discrete areas while tagging (especially with sonic tags) could provide the information needed for expanding to system-wide estimates. Netting would also allow for information to be collected on smaller-sized individuals and species composition. Side-scan sonar can also provide habitat information about sturgeon locations and identify potential areas where netting operations could be performed safely.

Acknowledgements

Funding for this project was provided by National Oceanographic and Atmospheric Administration. We thank T. Jackson for his work in the field and in the laboratory reviewing side-scan and video data. We appreciate C. Collier and M. Loeffler (North Carolina Division of Marine Fisheries), and W. Post (South Carolina Department of Natural Resources) allowing us the use of their sonic-tagged sturgeon during the course of the study. We also thank N. Cole, J. Hughes, and A. Prince for assistance during preliminary phases of our side-scan sonar work. B. Gardner and K. Pollock provided comments on an earlier version of the manuscript. The Cooperative Fish and Wildlife Research Unit is jointly supported by North Carolina State University, North Carolina Wildlife Resources Commission, U.S. Geological Survey, U.S. Fish and Wildlife Service, and Wildlife Management Institute. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 1. Comparison of N-mixture models as applied to Atlantic Sturgeon in the Carolina and South Atlantic distinct population segments with and without river as a covariate for abundance and using alternative distributions for abundance. Model fit is compared using Akaike's Information Criterion (AIC); a lower value indicates a better performing model. The number of parameters in each model is denoted by nPars, ΔAIC is the difference between AIC value and the best model, and AICwt represents the relative likelihood of each model.

Model	nPars	AIC	ΔAIC	AICwt
Negative binomial, with river	8	1208.48	0.00	1.00
Negative binomial	3	1292.65	84.17	<0.001
Zero-inflated Poisson, with river	8	2147.44	938.96	<0.001
Zero-inflated Poisson	3	2663.59	1455.11	<0.001
Poisson, with river	7	2735.87	1527.39	<0.001
Poisson	2	3909.23	2700.75	<0.001

Table 2. Abundance estimates and 95% confidence intervals for riverine Atlantic Sturgeon >1 m TL within six North Carolina and South Carolina rivers (see Figure 1). Results for each analytical approach are from the model with lowest Akaike Information Criterion. Maximum counts (per survey day) and number of survey sites for each river system are listed for comparison. The Carolina Distinct Population Segment (DPS) estimate is a total for all rivers except the Edisto.

River	N sites	Maximum Count	N-mixture Estimate	Distance Estimate
Roanoke	30	4	10.9 (3-36)	10.3 (3-34)
Neuse	22	1	2.7 (0-23)	2.7 (0-21)
Cape Fear	38	23	73.1 (35-152)	75.8 (37-156)
Pee Dee	37	419	1,943.8 (1,036-3,646)	1,823.3 (976-3,406)
Santee	30	0	0.0 (0-0)	0.0 (0-0)
Edisto	22	104	343.5 (150-788)	326.3 (143-744)
Carolina DPS	157	447	2,030.5 (1,075-3,858)	1,912.0 (1,016-3,616)

Table 3. Comparison of distance models as applied to Atlantic Sturgeon in the Carolina and South Atlantic distinct population segments with and without river as a covariate for abundance and using alternative distributions for abundance and detection. Model fit is compared using Akaike's Information Criterion (AIC); a lower value indicates a better performing model. For all but the top performing model, AIC weights were <0.001. The number of parameters in each model is denoted by nPars, ΔAIC is the difference in a model's AIC value and the best model, and AICwt represents the relative likelihood of each model.

Model	nPars	AIC	ΔAIC	AICwt
Negative binomial, half-normal, with river	9	443.54	0.00	1.00
Negative binomial, exponential, with river	9	462.09	18.55	<0.001
Negative binomial, uniform, with river	8	480.34	36.81	<0.001
Negative binomial, half-normal	4	528.58	85.04	<0.001
Negative binomial, exponential	4	547.13	103.59	<0.001
Negative binomial, uniform	3	565.38	121.84	<0.001
Negative binomial, hazard, with river	10	980.19	536.65	<0.001
Negative binomial, hazard	5	1061.96	618.43	<0.001
Poisson, hazard, with river	9	1864.23	1420.69	<0.001
Poisson, half-normal, with river	8	1980.57	1537.03	<0.001
Poisson, exponential, with river	8	1999.12	1555.58	<0.001
Poisson, uniform, with river	7	2017.37	1573.83	<0.001
Poisson, hazard	4	3031.24	2587.7	<0.001
Poisson, half-normal	3	3147.59	2704.05	<0.001
Poisson, exponential	3	3166.14	2722.6	<0.001
Poisson, uniform	2	3184.39	2740.85	<0.001

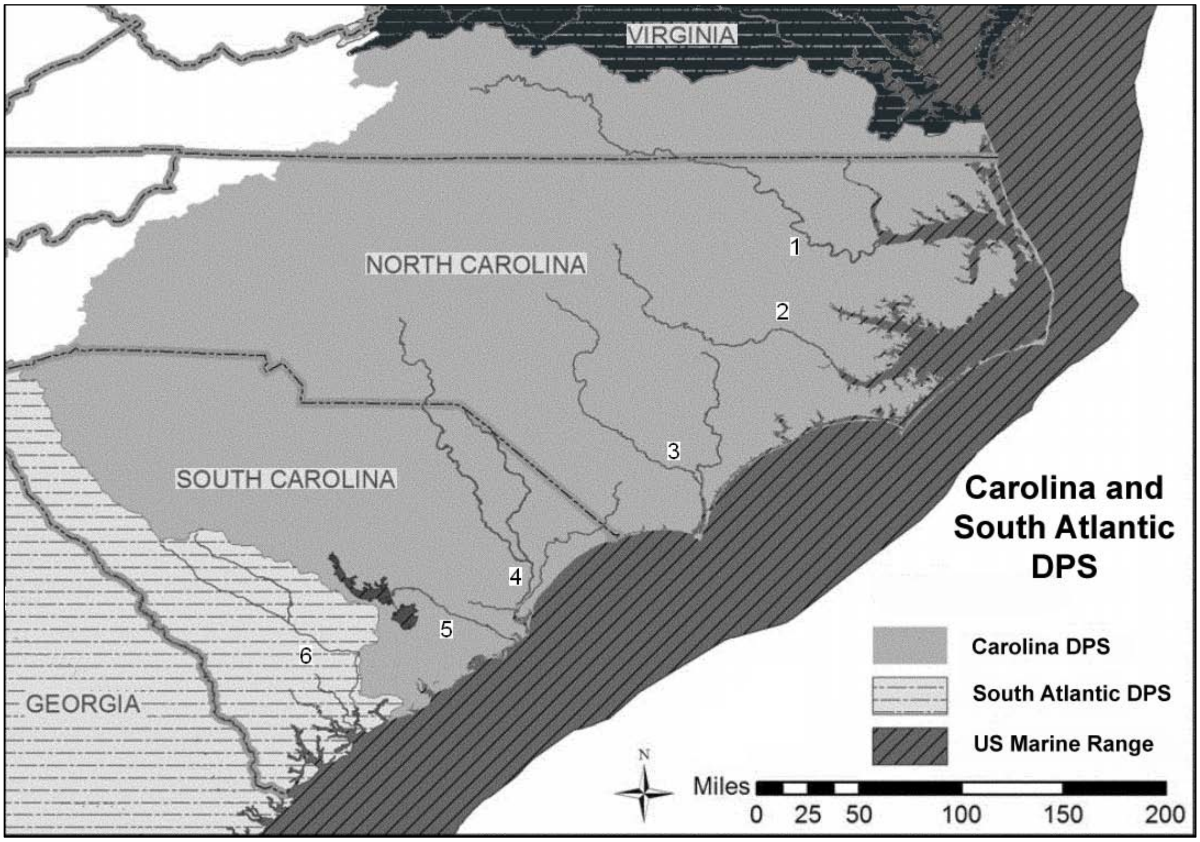

Figure 1. Lower portions of six river systems in the Carolina and South Atlantic distince population segments (DPS) surveyed using side-scan sonar; from north to south they are the Roanoke (1), Neuse (2), and Cape Fear (3) rivers in North Carolina and Pee Dee/Waccamaw (4), Santee (5), and Edisto (6) in South Carolina.

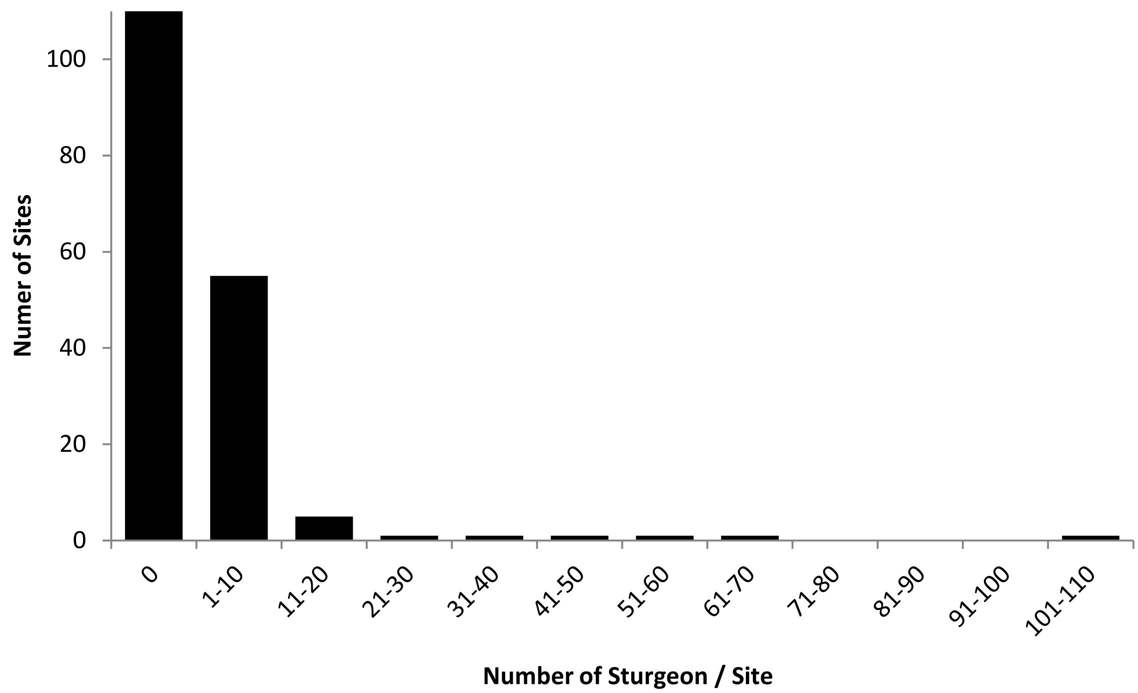

Figure 2. The distribution of Atlantic Sturgeon counts per site across all rivers (179 sites) sampled in the Carolina and South Atlantic distinct population segments. Most sites had dtections of either no sturgeon or 1-10. The maximum number of sturgeon counted at a single site was 109.

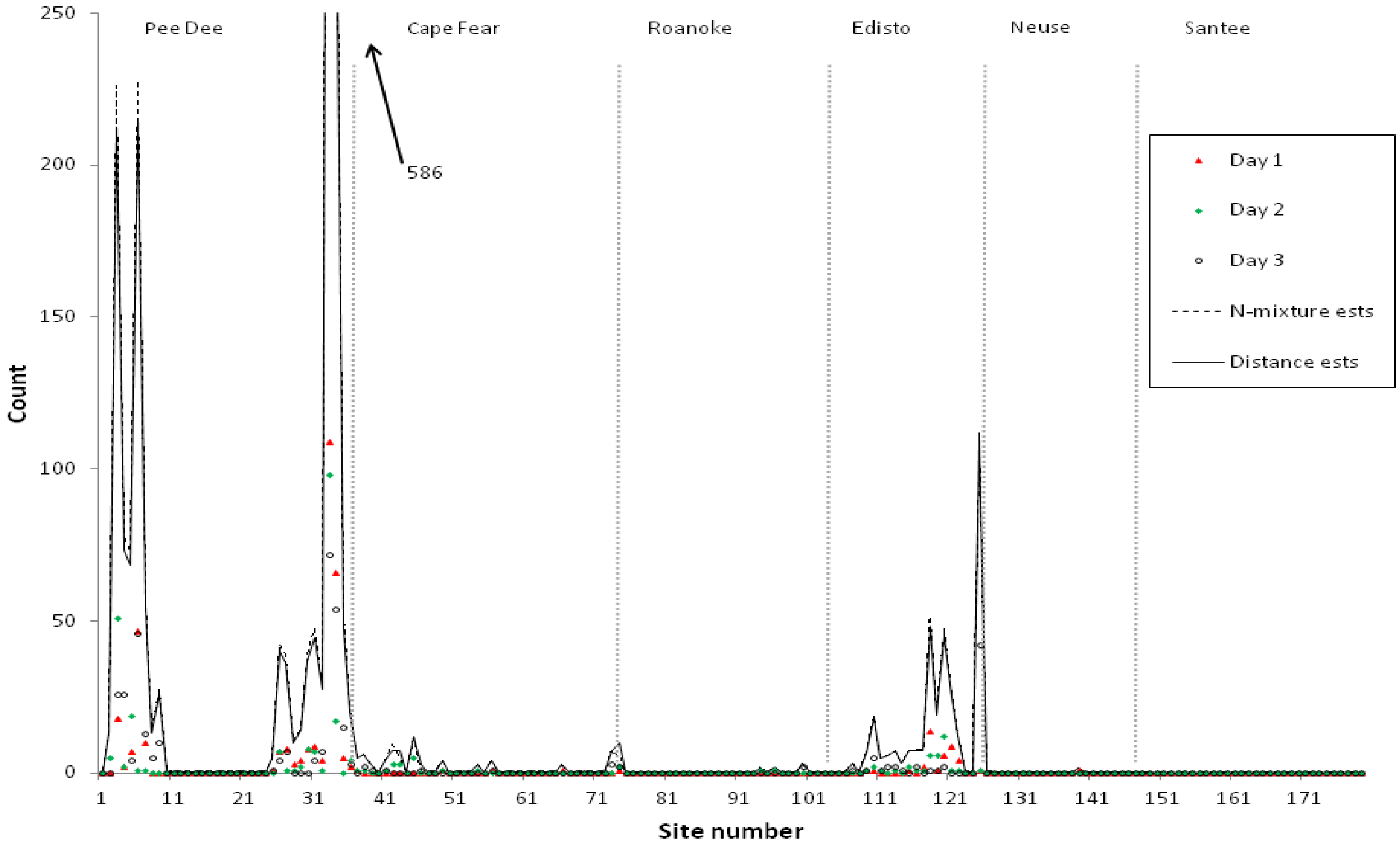

Figure 3. Site-specific estimates of Atlantic Sturgeon abundance in the Carolina and South Atlantic distinct population segments derived by the distance (solid) and N-mixture (dashed) models and overlaid onto counts of sturgeon per site for each survey day. Model estimates followed trends in site counts, and there was little difference in estimates between models.

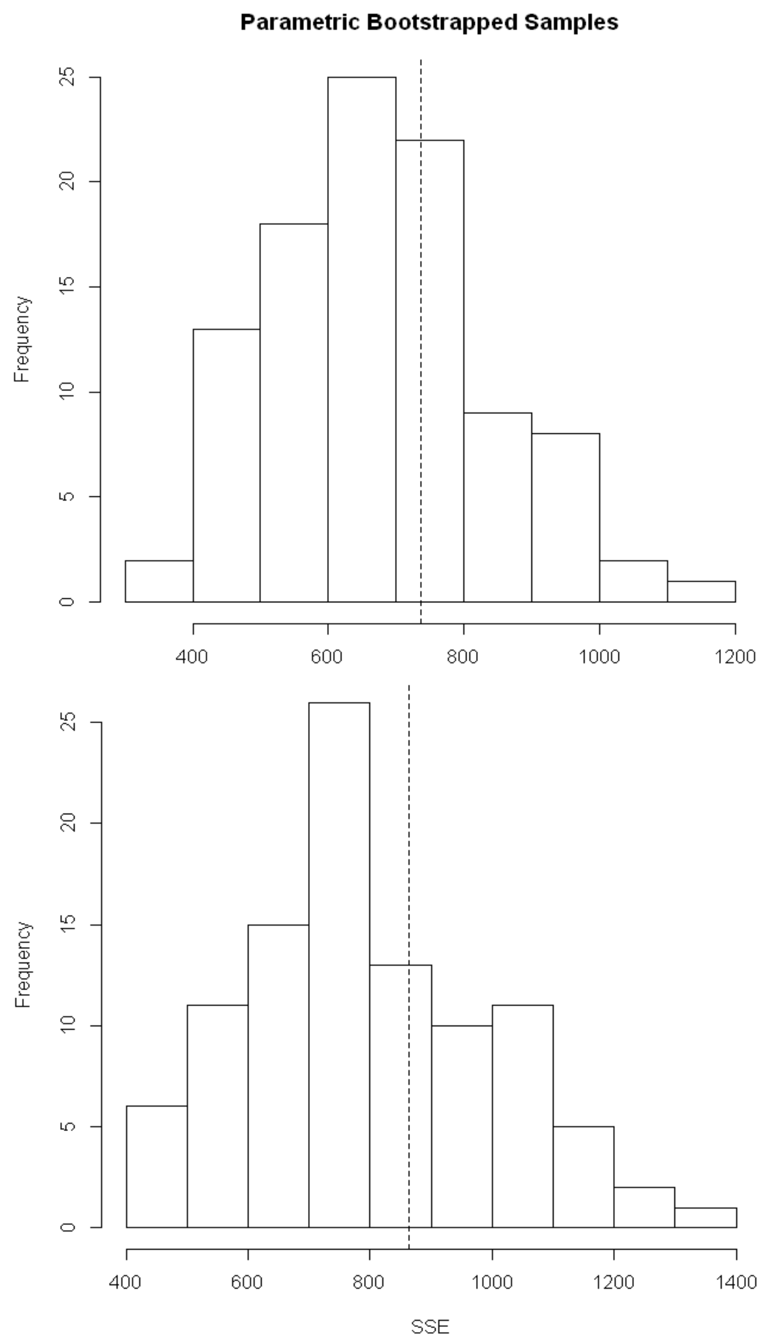

Figure 4. Results of parametric bootstrap goodness-of-fit testing as related to Atlantic Sturgeon in the Carolina and South Atlantic distinct population segments. The upper panel is for the N-mixture model; the lower panel is for the distance model. The dotted line is the Freeman-Tukey test statistic. Both models adequately explain the observed data.

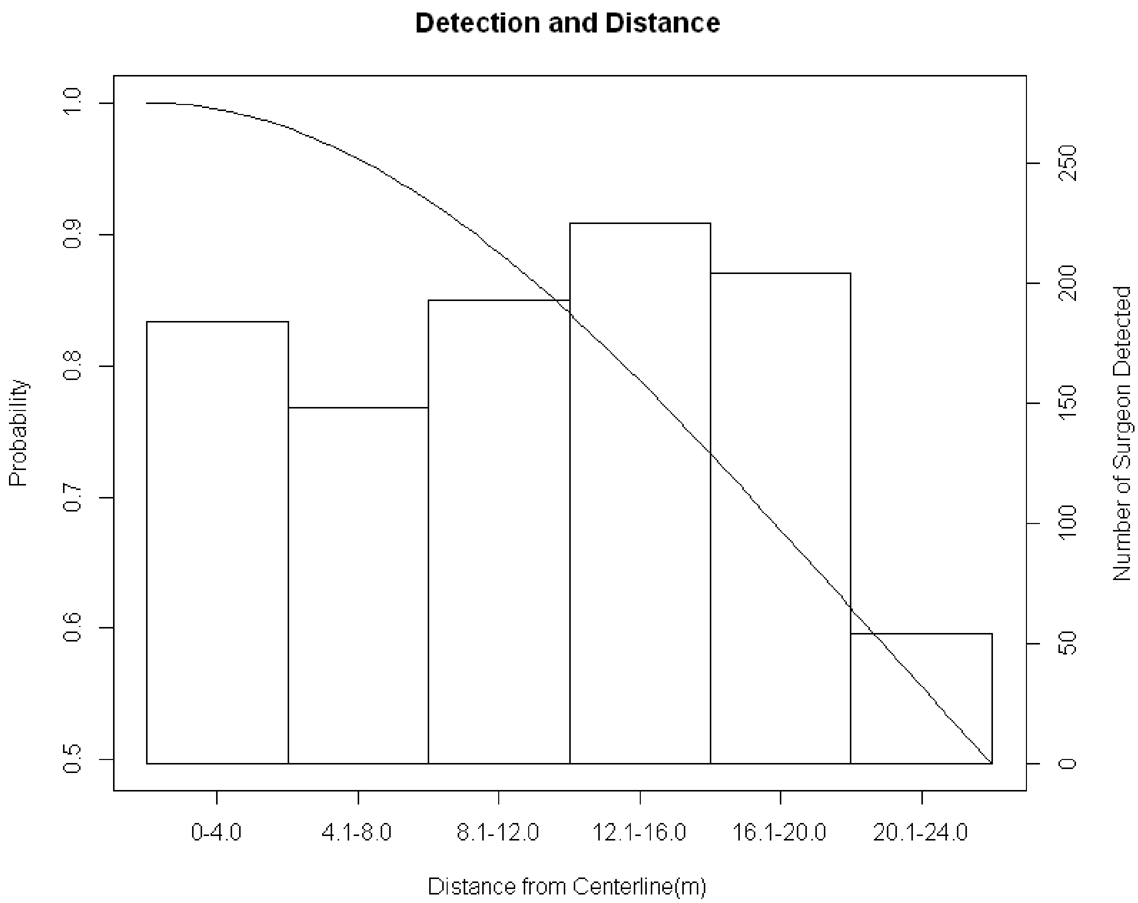

Figure 5. Detection probability for the distance model and distribution of side-scan sonar targets (i.e., Atlantic Sturgeon in the Carolina and South Atlantic distinct population segments) across the scan swath for all surveyed rivers (see Figure 1). Target distance is measured from centerline of side-scan image to body of sturgeon target. The detection probability function shown is the half-normal for the top AIC selected distance model, σ=20.3.

CHAPTER 4

ANNUAL MOVEMENT PATTERNS OF ROANOKE RIVER ATLANTIC STURGEON, INCLUDING INTER-DPS MARINE MOVEMENTS AND SPAWNING PERIODICITY

H. Jared Flowers and
Joseph E. Hightower

Abstract

Successful restoration of the endangered Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* depends on a solid foundation of biological data. For Roanoke River, North Carolina Atlantic Sturgeon, there are questions regarding annual migration patterns, including spawning timing and movements, and marine movements. Six adult Atlantic Sturgeon (presumably males) from the Roanoke River were implanted with acoustic telemetry tags from 2010-2012. These sturgeon were monitored through a network of passive receivers in North Carolina and eight additional states. We used a multi-state model to estimate movement probabilities among riverine, estuarine, and marine areas. From September 2010 to June 2014, five of six of our Atlantic Sturgeon were detected in three different marine areas defined by the National Oceanic and Atmospheric Administration as Distinct Population Segments. Seasonally, sturgeon were observed to either spend the entire year in marine waters or winter-spring in marine waters, summer in Albemarle Sound and fall in the Roanoke River spawning. The multi-state model suggests that movement probabilities were seasonably variable. Annual estimated Atlantic Sturgeon mortality during the study was low (0.03) and detection probability high (>0.50) in most study areas. Sturgeon were observed to spawn in consecutive years or with a year in between spawning events. The complexity of Atlantic Sturgeon movements and the mixing of populations in marine waters add to the potential difficulty in managing the recovery of this species.

Introduction

Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* are an anadromous fish species, meaning they use both marine and freshwater habitats throughout their life (Atlantic Sturgeon Status Review Team [ASSRT] 2007). Atlantic Sturgeon populations have been observed to mix in coastal marine waters (Waldman et al. 1996; Dunton et al. 2012), while returning to spawn in natal rivers (Wirgin et al. 2000; King et al. 2001; Grunwald et al. 2008). Throughout their historic range, populations have been reduced by the effects of overharvest and habitat destruction (Secor 2002; Pitkitch 2005). Atlantic Sturgeon are listed as endangered along most of the Atlantic Coast of the United States (NOAA 2012). As part of the listing, populations were broken up into five Distinct Population Segments (DPS): (from north to south) Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (ASSRT 2007). These distinctions were based on genetic and behavioral differences among populations.

The Roanoke River begins in southwestern Virginia and flows southeast into northeastern North Carolina, discharging into western Albemarle Sound. The river has a total length of approximately 568 km and the first impoundment is located at Roanoke Rapids, North Carolina, 221 river kilometers (rkm) upstream of the mouth near the Piedmont fall zone (Armstrong and Hightower 2002; Oakley and Hightower 2007). The river and sound are the most northerly in the Carolina DPS. A historic Atlantic Sturgeon fishery existed on the river around the turn of the 20th century, tapering off as sturgeon stocks declined (Worth 1904; Chestnut and Davis 1975). The Roanoke River was long believed and now confirmed to have a spawning population of Atlantic Sturgeon (Smith et al. 2015). Small population size and uncertainty about behavior have made it difficult to study adult Atlantic Sturgeon, especially members of the spawning population, in the Roanoke River and Albemarle Sound. This changed after 2009, when adult sturgeon were observed in the Roanoke River during summer and fall.

In this study, we used acoustic telemetry tags to characterize the movements of Roanoke River Atlantic Sturgeon. Telemetry has been used to evaluate spawning characteristics, riverine and marine movement patterns, and habitat use of Atlantic Sturgeon

(Kieffer and Kynard 1993; Collins et al. 2000a; Armstrong and Hightower 2002; Hatin et al. 2002) and the Gulf subspecies *A. o. desotoi* (Wooley and Crateau 1985; Fox et al. 2000; Rudd et al. 2014). Technological advances in telemetry equipment have resulted in smaller, longer-lived, more reliable tags and autonomous receivers that can continually detect tagged animals. In our study we used an array of VEMCO VR2W autonomous telemetry receivers distributed throughout the Roanoke River and Western Albemarle Sound, and acoustic tags with predicted battery life of up to 4 years. The receivers functioned as gates to track animal movements through distinct sections of river, continuously monitoring an approximately 300 m radius area surrounding the receiver for the presence of any sturgeon with a VEMCO tag. Sequential detections of a sturgeon through the receiver array indicated directional movement patterns.

In addition to our VR2 array, receivers deployed by other research groups along the Atlantic Coast could detect our tagged Atlantic Sturgeon. These included, but were not limited to those located in Albemarle Sound (North Carolina State University [NCSU]; North Carolina Division of Marine Fisheries [NCDMF]), the Cape Fear River (NCDMF), coastal North Carolina (East Carolina University [ECU]), South Carolina (South Carolina Department of Natural Resources [SCDNR]), Virginia and Chesapeake Bay (United States Navy [USN]; Virginia Commonwealth University [VCU]), coastal Delaware (Delaware State University [DESU]), the Hudson River (New York State Department of Environmental Conservation; DESU), coastal New Jersey and Long Island (Stony Brook University [SBU]) and Long Island Sound (Connecticut Department of Natural Resources [CT DNR]). Additionally, several autonomous gliders equipped with VR2 receivers were operating intermittently during the course of the study off the mid-Atlantic Coast. Communication between groups was facilitated by the Atlantic Coast Telemetry Network (ACT) based at DESU. The availability of this network allowed us to address questions about migration including inter-DPS movements on a coast-wide scale.

Methods

Six adult Atlantic Sturgeon captured in the Roanoke River, North Carolina were surgically implanted with acoustic telemetry tags (Table 1). Three were tagged in September 2010, two in September 2011 and one in October 2012. Presence of Atlantic Sturgeon in the upper Roanoke River was related to Fall-spawning observed near Weldon,(Smith et al. 2015). Of the tagged sturgeon, 4 were identified as males whereas 2 were of unknown sex, but believed also to be males based on size and behavior during spawning season. Males tend to enter spawning areas earlier and linger longer, while females tend to make shorter, more directed spawning runs (Van Eenennaam et al. 1996; Bain 1997; Sulak and Clugston 1998). Based on their presence in upper portions of the Roanoke River, near spawning areas, during the observed spawning season, all tagged sturgeon were considered to be a part of the Roanoke River spawning population. Each tagged sturgeon received an acoustic telemetry tag, pit tag, and t-bar tag for individual identification.

Sturgeon tagged in 2010 were implanted with VEMCO V16-4H acoustic tags with a nominal lifespan of 1157 days, while sturgeon tagged in 2011 and 2012 were implanted with larger V16-6H tags with a nominal lifespan of 1633 days. Telemetry tags were surgically implanted using methods similar to those in Fox et al. (2000). In addition to our sturgeon, a number of Atlantic Sturgeon with compatible VEMCO tags were tagged in other areas throughout the Atlantic Coast. If these sturgeon moved into the range of our receivers, they would be detected.

Construction of the original Roanoke River VR2 array began during October 2010 and receivers were continually deployed until summer 2014. There was a minimum of 11 and a maximum of 28 receivers present during this period (Figure 1). The number and placement of deployed receivers varied slightly throughout the study due to equipment failures, loss/theft, variable river conditions, and varying study requirements. Nine receivers were temporarily placed in different parts of Western Albemarle Sound during summer 2012 to evaluate movements during this period (Figure 1). We used a unique receiver deployment system optimized for riverine environments (Appendix C).

Despite the extensive network of receiver arrays, there were temporal holes in coverage. Some arrays were not in place during the entire study period, especially during early 2011 (M. Loeffler, NCDMF personal communication; Keith Dunton, Stony Brook University, personal communication), while others were not in place seasonally, such as the DESU array which was removed each winter (Lori Brown, DESU, personal communication).

In order to quantitatively describe Atlantic Sturgeon movement patterns, we chose to use a multi-state modeling approach using Program R and WinBUGS. The model is based on those described by Kéry and Schaub (2012). It consisted of six different “states”, referring to the Roanoke River, Albemarle Sound, and marine waters of the three DPSs in which our sturgeon were observed, and a “death” state for apparent mortality (Figure 2). The model provided estimates of transition probabilities between these different states, as well as state specific detection probabilities and the probability of apparent mortality. A transition probability is the probability that animals move between given model states during a given time (Williams et al. 2002). Apparent mortality is the probability that an animal is not available to any state during subsequent time steps, but in our case apparent mortality would only differ from actual if a sturgeon permanently moved to an area where it could not be observed. An assumption is that the future state of the animal is dependent on the current state (Jackson 2011).

The basic form of state transition and observation matrices are provided in Table 2. We used a seasonal timeframe for movement probabilities, based on three month periods for winter (December-February), spring (March-May), summer (June-August), and fall (September-November). This structure was thought to reflect annual patterns in sturgeon movement. Because of limited data and the lack of evidence for time variation, we estimated a mean mortality probability over all states and detection probabilities for each individual spatial state. The model runs consisted of 50,000 iterations with 5,000 burn-in iterations. Model convergence was monitored using the R-hat statistic. R code for the model is provided in Appendix D.

Results

Our study covers telemetry tag observations from the first tag deployments in September 2010 until June 2014, at which point three tags were still active. The transmitters of two of three sturgeon tagged in 2010 were detected through the tag expiration date of November 2013. The third sturgeon tagged in 2010 (64090) was last detected six months before the tag was scheduled to expire.

Our telemetry tagged sturgeon were detected a total of 102,332 times by either our receiver array or those of 9 other researchers (Table 3). Approximately 30% of total detections of our sturgeon were made by others. The farthest south our sturgeon were detected was southwest of Cape Hatteras, North Carolina, while the farthest north was Long Island Sound off the coast of Connecticut (Figure 3). Sturgeon from our study were detected in both the Chesapeake and New York Bight DPSs to the north, but not in the South Atlantic DPS in the south. This was a relatively common occurrence, taking place in all of the three study years and including five of our six individual sturgeon. All detections were coastal or estuarine and our sturgeon were not observed to travel upstream in other rivers, including the Cape Fear River further south in North Carolina which contained an extensive array of receivers.

Both our observations and multi-state modeling supported a general Atlantic Sturgeon movement pattern (Figure 4; Table 4). We lacked data for some states (e.g. winter Roanoke River), resulting in movement probabilities that were equivalent to the prior distributions. In winter, spawned-out sturgeon moved from Albemarle Sound to marine waters. During spring, sturgeon returned to Albemarle Sound or dispersed out to the ocean DPSs. In summer sturgeon tended to stay in their previous location, moving little. The exception were spawning sturgeon, which began to return to Albemarle Sound and started to enter the Roanoke River. During fall, spawning sturgeon ran up the Roanoke River to spawn, then began to return Albemarle Sound and the marine waters.

Annual timing of events was relatively consistent (Figures 4-5), with first movements in and last movements out of riverine areas being within approximately two weeks of each other in consecutive years. The exception was date of spring entry into Albemarle Sound, which varied considerably by year. The timing of these movements may have been related to water temperatures in the Roanoke River, especially entry into the Roanoke River at the beginning of the spawning run. Across all years and sturgeon the mean temperature at fall river entry was 27.8 (27.3-28.3) ºC (Figure 6).

Annual Atlantic Sturgeon mortality was low over the course of the study, estimated to be 0.03 (0.00-0.09). Detection probability varied spatially throughout the study. Detection probability was highest in the Roanoke River and New York Bight while the lowest detection probabilities were estimated for the Chesapeake DPS and marine portions of the Carolina DPS (Table 5).

Over the four spawning seasons of our study there was not a clear pattern of spawning periodicity. We observed both consecutive year spawning and periodic spawning (interval of at least one year) by individuals. Four of six sturgeon were observed to spawn in consecutive years. All sturgeon, when in the Roanoke during spawning season, remained in the upper river area for an extended period of time, cruising adjacent to spawning areas.

In addition to our six sturgeon, we detected thirteen additional sturgeon tagged by other researchers. Ten were tagged by NCDMF researchers in Albemarle Sound. On average these sturgeon were smaller than ours and were likely juveniles or sub-adults. All of these sturgeon were observed in Albemarle Sound, but only one larger individual, 1499 mm TL, made what appeared to be a possible spawning run in 2012 and 2013. Three sturgeon tagged off the coast of Delaware by DESU researchers were detected in Albemarle Sound in 2011, 2012 and one again in 2014. Two of these sturgeon were assigned to the Savannah River, SC/GA population based on genetics (Lori Brown, DESU, *personal communication*). None of these DESU-tagged sturgeon were observed to move up the Roanoke River.

Discussion

Atlantic Sturgeon tagged in the Roanoke River did not remain within the Carolina DPS but regularly migrated northward to the Chesapeake and New York Bight DPSs. This suggests that recovery plans for Atlantic Sturgeon based on individual DPSs may not be the most effective option. Mixing of populations has also been observed in genetic studies of

Atlantic Sturgeon sampled in marine habitats (Waldman et al. 1996; Dunton et al. 2012). Only one of our tagged Atlantic Sturgeon was detected south of Albemarle Sound, just south of Cape Lookout, North Carolina, and none were detected in the South Atlantic DPS. At the same time no sturgeon from the Cape Fear River, the next river to the south with tagged sturgeon, were detected by our receivers in Western Albemarle Sound, even though these populations were estimated to be genetically similar (Wirgin et al. 2007).

Despite our observation of regular inter-DPS movement, there was no observed spawning activity associated with these movements. Our tagged sturgeon were only observed in coastal areas, and not upstream in freshwater areas more suited for spawning. Similarly, no sturgeon tagged in other systems were observed to make spawning runs in the Roanoke River, supporting observations of genetic differentiation among riverine populations (Wirgin et al. 2007; Grunwald et al. 2008). Marine movements of sturgeon were largely concentrated in areas close to shore; the furthest offshore a sturgeon was detected was 16 km. Several deployments consisted of receivers in a line perpendicular to shore and in most cases sturgeon were detected on inner receivers of the array. This observation was consistent with other studies on Atlantic Sturgeon (Stein et al. 2004; Laney et al. 2007; Dunton et al. 2010) and related Gulf sturgeon (Edwards et al. 2007) showing sturgeon tend to move through near-shore marine habitats.

It appeared that our Atlantic Sturgeon spent the largest amount of time throughout the study in Albemarle Sound, the Roanoke River, and the New York Bight DPS. These areas seem to be more permanent destinations, while sturgeon may be more transient through the Carolina DPS marine waters and the Chesapeake DPS. This observation may be confounded by the more limited receiver coverage in these two areas (Figure 3), highlighted by the low estimates of detection probability in these areas (Table 5).

The multi-state model generally performed well and provided seasonally-appropriate probabilities for remaining within an area versus moving among riverine, estuarine and marine areas. However some credible intervals ranged from 0.00-1.00 (Table 4), indicating insufficient data for that model state. A combination of low sample size and low detection probability in some areas may have led to empty observations, as no sturgeon were present to inform the model. Model estimates could be improved with greater number of telemetry-tagged individuals, a longer study period, and increased receiver coverage (especially within marine waters of the Carolina DPS).

Estimated mortality of tagged sturgeon was low during the study. We evaluated models using individual mortality estimates for each area, but these were essentially the same (with strongly overlapped credible intervals) as the single estimate. Because of this and the small sample size, we believed a single estimate of mortality made the most modeling sense. Only one sturgeon, 64090, was observed to disappear before the expiration date of its tag. The fate of sturgeon 64090 is unknown, but possible explanations include: the tag expired prematurely, the fish moved to an area without receivers and the tag expired as scheduled, the tag was detected on another array but the data have not been delivered, or the sturgeon died. It is worth noting that, in 2011, fish 64090 also had only few detections, again from within the New York Bight DPS.

The primary threats to survival facing Roanoke River sturgeon in their natal river and Albemarle Sound are similar to those threats found across the species' range, including habitat degradation, dams, and commercial fishing bycatch. A major threat outside of their natal system, especially in areas featuring shipping traffic, are vessel strikes, where individual Atlantic Sturgeons are entrained through the propellers of vessels or collide with vessel hulls (ASSRT 2007; Brown and Murphy 2010). Numerous vessel strikes have been observed in Chesapeake Bay (Balazik et al. 2012), Delaware River (Brown and Murphy 2010) and Cape Fear River (W. Laney, USFWS, personal communication). In these areas vessel strikes are a significant source of mortality, with the added impact that most sturgeon killed are of adult, spawning size (Brown and Murphy 2010; Balazik et al. 2012). Associated with shipping, dredging is also a threat to sturgeon survival in these areas (ASSRT 2007; Brown and Murphy 2010).

Migration of Atlantic Sturgeon across regions complicates management strategies. Fishing mortality is a concern throughout their range, but types of fishing and regulations vary based on location. Complicating this is the listing of the Gulf of Maine DPS as threatened while all others are endangered; meaning the level of protection varies across the range (NOAA 2012). Directed harvest of sturgeon ended in 1995; however poaching is still an issue and has been observed in several states (ASSRT 2007). A greater concern is sturgeon bycatch associated with other fisheries, primarily gill nets and trawling (ASSRT 2007). In Albemarle Sound and neighboring Pamlico Sound, gill net fisheries for Southern Flounder *Paralichthys lethostigma* and Striped Bass *Morone saxitilis* pose the greatest threat to Atlantic Sturgeon populations (ASSRT 2007; Armstrong and Hightower 2002). For U.S. Atlantic Sturgeon populations coast-wide, two distinct fisheries regions are present, based on threats, approximately split north and south by Cape Hatteras.

In the southern part of their range, anchored gill net fisheries for American Shad *Alosa sapidissima* may represent the greatest threat to sturgeon populations (Collins et al. 1996; ASSRT 2007; Bahn et al. 2012). Mortality in these fisheries has been reported to range from very low to almost 50% (Moser and Ross 1995; Collins et al. 1996; ASSRT 2007; Bahn et al. 2012). Trawls, often targeting Penaeid shrimp, are also a significant source of bycatch in these areas (Collins et al. 1996). Trawls in the southern part of their range may cause more mortality than those in the north as they tend to be longer in duration and water temperature greater (ASSRT 2007).

Anchored and drift gill net fisheries are the greatest threat to sturgeon populations in northern marine waters (Stein et al 2004; ASSRT 2007). Fisheries targeting species such as Monkfish *Lophius americanus*, Dogfish *Squalus* spp., Striped Bass and Atlantic Cod *Gadus morhua* have the greatest potential for mortality (ASSRT 2007). In the late 1990s, the Monkfish fishery had sturgeon bycatch mortality rates of up to 70%, although since 2000, regulations have changed to reduce this mortality rate. Mortality rates still ranged from between approximately 20-30% for other gill net fisheries in this region (Stein et al. 2004). Trawl fisheries had very little mortality, approach 0%, due to shorter durations and colder water temperatures in this region.

Albemarle Sound appears to be an important area for Atlantic Sturgeon. During late-spring and summer months, sturgeon were regularly found in western portions of the sound and in the extreme lower portions of the Roanoke River. Until initiating a spawning migration, sturgeon tended to circulate throughout the western part of Albemarle Sound, in the area roughly bounded by the NC Hwy 32 bridge across the middle of the sound, the US Hwy 17 bridge across the mouth of the Chowan River and the lower Roanoke River. This likely serves as a staging area for spawning runs and possibly a feeding area. Sturgeon were not dormant and concentrating in discrete areas as observed with other southern Atlantic Sturgeon populations (Moser and Ross 1995; Collins et al. 2000b; Flowers et al. 2013), but were constantly moving throughout the area. This movement could be a result of physical characteristics of the sound being large, relatively shallow, with little current, allowing sturgeon to move around more freely with less energy costs. During the summer salinity tends to rise in this part of the sound, suggesting the presence of the freshwater-saltwater interface where sturgeon are often found (Kieffer and Kynard 1993; Moser and Ross 1995).

Atlantic Sturgeon spawning runs may be negatively impacted by stochastic environmental events and therefore have adapted to these through behaviors like periodic spawning (Secor 1999; Peterson et al. 2007). During August 2011, Hurricane Irene passed through the eastern portion of Albemarle Sound. The resulting seiche and rainfall flooded the lower portion of the Roanoke and other rivers in the western part of Albemarle Sound. The result was a large, month-long anoxic zone at the mouth of the Roanoke River, causing a fish kill and effectively separating Albemarle Sound from the upper Roanoke River. While no sturgeon mortalities were observed, this event may have had the effect of halting or seriously impeding the spawning run that year. Several tagged sturgeon were observed to be upstream of the anoxic portion of the river while others, including one fish in the lower part of the river as Irene passed, remained in Albemarle Sound. While the storm may have interrupted one year’s spawning effort, since the whole spawning population was not involved the long-term survival of the population was not adversely affected.

Fall spawning activities have been confirmed in the Roanoke River (Smith et al. 2015) and suspected in other rivers (Collins et al. 2000a; Balazik et al. 2012). None of our tagged sturgeon exhibited any spawning behavior or even entered the Roanoke River during the spring. The earliest a sturgeon was observed in Albemarle Sound after exiting in the prior December was March 12. The traditional annual movement pattern of Atlantic Sturgeon following a spring-spawning strategy is thought to include spawning in late-spring or early summer followed by a return to marine waters to feed (Smith 1985; Bain et al. 1996; Caron et al. 2002). Sturgeon making fall spawning runs were present in Albemarle Sound by May or June prior to the run, after spring spawning might occur. Our study may be biased towards fall spawning since we collected our sturgeon during fall spawning migrations; however, there has been no recent evidence of a spring spawning run in the Roanoke River.

Timing of runs seems to be predominantly dependent on temperature cues in the Roanoke River. River temperature upon entering the river was highly consistent across all years and individuals (95% confidence interval 27.3-28.3 ºC) (Figure 6). These temperatures were much warmer than those seen in spring Atlantic Sturgeon and Gulf Sturgeon spawning populations (Bain 1997; Sulak and Clugston 1998; Flowers et al. 2006). Date of river entry was much more variable than temperature across years (Figure 5). Other theorized spawning cues such as moon phase (Sulak and Clugston 1998) were not likely based on high variability of dates and corresponding phase during runs. River discharge (Auer 1996) was less likely a factor since the Roanoke River is highly regulated during this time of year with daily peaking and few, if any, large pulses.

Individual Roanoke River Atlantic Sturgeon may follow two different annual movement patterns, with some individuals spending summers in marine waters and some spending summer in Albemarle Sound (Figure 4). Non-spawning sturgeon remained in marine waters and did not return to Albemarle Sound until their next spawning year. Sturgeon spawning in consecutive years returned to Albemarle Sound in summer. While it is generally stated that male sturgeon have an interval of 1-5 years between spawning (Smith 1985), based on our results and at least one other observation (Collins et al. 2000a), Atlantic Sturgeon are capable of spawning in consecutive years. This may be characteristic of populations in the warmer, southern part of the Atlantic Sturgeon range. The timeframe of our study was too short to sufficiently observe possible maximum intervals between spawning events.

Conclusions

While genetic studies for Atlantic Sturgeon have typically shown rivers to be genetically distinct, there is mixing of populations in marine and estuarine environments. Restoration and management actions in marine waters will need to consider the effects on all populations that include ocean-going sturgeon. Also important to management is the timing of sturgeon movements. Knowing when sturgeon are likely to be in an area is useful when considering fisheries regulations, hydrologic regimes, dredging, and other human activities. Based on our results, some proportion of adults may be present in both freshwater and marine environments at different times within the year. Behavior related to fall spawning also requires a shift in spring-spawning oriented management strategies. Although there is no clear pattern in the period between individual spawning years, some Atlantic Sturgeon were observed to spawn in every year of the study. Long-term, multi-DPS studies of Atlantic Sturgeon movements will be crucial to further improve our understanding of sturgeon behaviors and movement throughout their range.

Acknowledgements

We thank the many researchers who provided us data regarding our fish during the course of our study. These include: Mike Loeffler (NC DMF); Dewayne Fox, Lori Brown, and Matthew Breece (DESU); Dan Brown, Julie Harris, Sean Buczek, and Jody Callihan (NCSU); J. Carter Watterson (USN); Tom Savoy (CT DNR); Matt Balazik (VCU); and Jennifer Cudney-Burch (ECU). This project was funded using NOAA Section 6 funds. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of IACUC permit 13-037-O and federal scientific research permit (NOAA Fisheries) 16375-01.

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Table 1. Biological data for Roanoke River telemetry tagged Atlantic Sturgeon. All were tagged in proximity to the spawning grounds except 45491, which was tagged downstream, post-spawn. Four sturgeon were positively identified as males, while the other two were likely males based on size and movement patterns. For Sex, "M" is male while "ND" is not determined.

Date	Capture Latitude	Capture Longitude	Rkm	FL (cm)	TL (cm)	Wt (kg)	Sex	Pit Tag	Expiration Date	Tag Code
9/28/2010	36.42486	-77.58974	204	157.5	177.8	29.0	M	41632E1749	11/28/2013	64090
9/28/2010	36.42486	-77.58974	204	132.0	146.0	20.5	ND	4163334826	11/28/2013	64089
9/28/2010	36.42486	-77.58974	204	141.0	164.0	23.5	M	41633B4A45	11/28/2013	64088
9/29/2011	36.42402	-77.58249	202	167.6	193.0	37.0	M	470B40483D	3/19/2016	45476
9/29/2011	36.42402	-77.58249	202	134.6	150.5	27.2	M	985121014361269	3/19/2016	45492
10/19/2012	35.93587	-77.07731	78	152.4	170.2	33.0	ND	41632D4030	4/9/2017	45491

Table 2. Structure of the multi-state model. State transition matrix (top) represents the transition probabilities between different model states. Survival is represented by Φ while Ψ is the movement probability between states. The observation matrix (bottom) simulates the detection probability at each state, represented by p.

State transition matrix		Observed State					
		Roanoke River	Albemarle Sound	Carolina DPS (marine)	Chesapeake DPS	New York Bight DPS	Mortality
True State	Roanoke River	$\Phi(1\text{-}\Psi_{AB})$	$\Phi\Psi_{AB}$	0	0	0	$1\text{-}\Phi$
	Albemarle Sound	$\Phi\Psi_{BA}$	$\Phi(1\text{-}\Psi_{BA}\text{-}\Psi_{BC})$	$\Phi\Psi_{BC}$	0	0	$1\text{-}\Phi$
	Carolina DPS (marine)	0	$\Phi\Psi_{CB}$	$\Phi(1\text{-}\Psi_{CB}\text{-}\Psi_{CD})$	$\Phi\Psi_{CD}$	0	$1\text{-}\Phi$
	Chesapeake DPS	0	0	$\Phi\Psi_{DC}$	$\Phi(1\text{-}\Psi_{DC}\text{-}\Psi_{DE})$	$\Phi\Psi_{DE}$	$1\text{-}\Phi$
	New York Bight DPS	0	0	0	$\Phi\Psi_{ED}$	$\Phi(1\text{-}\Psi_{ED})$	$1\text{-}\Phi$
	Mortality	0	0	0	0	0	1

Observation matrix		Observed State					
		Roanoke River	Albemarle Sound	Carolina DPS (marine)	Chesapeake DPS	New York Bight DPS	Not detected
True State	Roanoke River	p_A	0	0	0	0	$1\text{-}p_A$
	Albemarle Sound	0	p_B	0	0	0	$1\text{-}p_B$
	Carolina DPS (marine)	0		p_C	0	0	$1\text{-}p_C$
	Chesapeake DPS	0	0	0	p_D	0	$1\text{-}p_D$
	New York Bight DPS	0	0	0		p_E	$1\text{-}p_E$
	Mortality	0	0	0	0	0	1

Table 3. Counts of sturgeon telemetry tag detections (receiver owner/transmitter owner) from September 2010 through June 2014 based on NCSU and other arrays.

Detections Year	Rec/Tran NCSU/All	NCSU/NCSU	NCSU/Others	All/NCSU	Others/NCSU
2010	1276	1276	0	1295	19
2011	6522	2743	3779	4778	2035
2012	59395	41943	17452	57949	16006
2013	42635	15274	27361	26736	11462
2014	9362	8773	589	11574	674
Totals	119190	70009	49181	102332	30196

Table 4. Transition probability results of the multi-state model. Each table contains movement probabilities and 95% credible intervals for each season, with the month ranges listed. Labels are Roanoke River (RR), Albemarle Sound (AS), Carolina DPS marine (CAR), Chesapeake DPS (CHE), New York Bight DPS (NYB). Diagonal elements are highlighted for clarity.

Fall September-November

	RR	AS	CAR	CHE	NYB
RR	0.301	0.699	-	-	-
	(0.13-0.51)	(0.49-0.87)	-	-	-
AS	0.001	0.428	0.571	-	-
	(0.00-0.01)	(0.21-0.67)	(0.33-0.78)	-	-
CAR	-	0.002	0.989	0.009	-
	-	(0.00-0.02)	(0.89-1.00)	(0.00-0.07)	-
CHE	-	-	0.991	0.004	0.005
	-	-	(0.89-1.00)	(0.00-0.03)	(0.00-0.05)
NYB	-	-	-	0.587	0.413
				(0.16-0.93)	(0.07-0.84)

Winter December-February

	RR	AS	CAR	CHE	NYB
RR	0.495	0.505	-	-	-
	(0.00-1.00)	(0.00-1.00)	-	-	-
AS	0.010	0.012	0.979	-	-
	(0.00-0.11)	(0.00-0.15)	(0.74-1.00)	-	-
CAR	-	0.05	0.827	0.122	-
	-	(0.01-0.14)	(0.41-0.97)	(0.01-0.52)	-
CHE	-	-	0.076	0.068	0.856
	-	-	(0.01-0.92)	(0.00-0.87)	(0.04-1.00)
NYB	-	-	-	0.533	0.467
	-	-	-	(0.00-1.00)	(0.00-1.00)

Table 4. (cont.)

Spring	March-May				
	RR	AS	CAR	CHE	NYB
RR	0.499	0.502	-	-	-
	(0.00-1.00)	(0.00-1.00)	-	-	-
AS	0.001	0.998	0.002	-	-
	(0.00-0.01)	(0.97-1.00)	(0.00-0.02)	-	
CAR	-	0.525	0.282	0.193	-
	-	(0.24-1.00)	(0.01-0.64)	(0.00-0.51)	-
CHE	-	-	0.620	0.393	0.000
	-	-	(0.00-1.00)	(0.00-1.00)	(0.00-0.00)
NYB	-	-	-	0.083	0.917
	-	-	-	(0.00-0.62)	(0.38-1.00)

Summer	June-August				
	RR	AS	CAR	CHE	NYB
RR	0.997	0.003	-	-	-
	(0.96-1.00)	(0.00-0.04)	-	-	-
AS	0.420	0.578	0.002	-	-
	(0.22-0.64)	(0.36-0.78)	(0.00-0.03)	-	-
CAR	-	0.161	0.186	0.652	-
	-	(0.01-1.00)	(0.01-1.00)	(0.01-1.00)	-
CHE	-	-	0.393	0.576	0.031
	-	-	(0.00-1.00)	(0.00-1.00)	(0.00-0.50)
NYB	-	-	-	0.007	0.993
	-	-	-	(0.00-0.08)	(0.92-1.00)

Table 5. Quarterly detection probability (*p*) for each of the study areas.

	mean	95% credible interval
Roanoke River	0.96	(0.85-1.00)
Albemarle Sound	0.89	(0.77-0.97)
Carolina DPS (marine)	0.04	(0.01-0.10)
Chesapeake DPS	0.50	(0.21-0.79)
New York Bight DPS	0.52	(0.29-0.75)

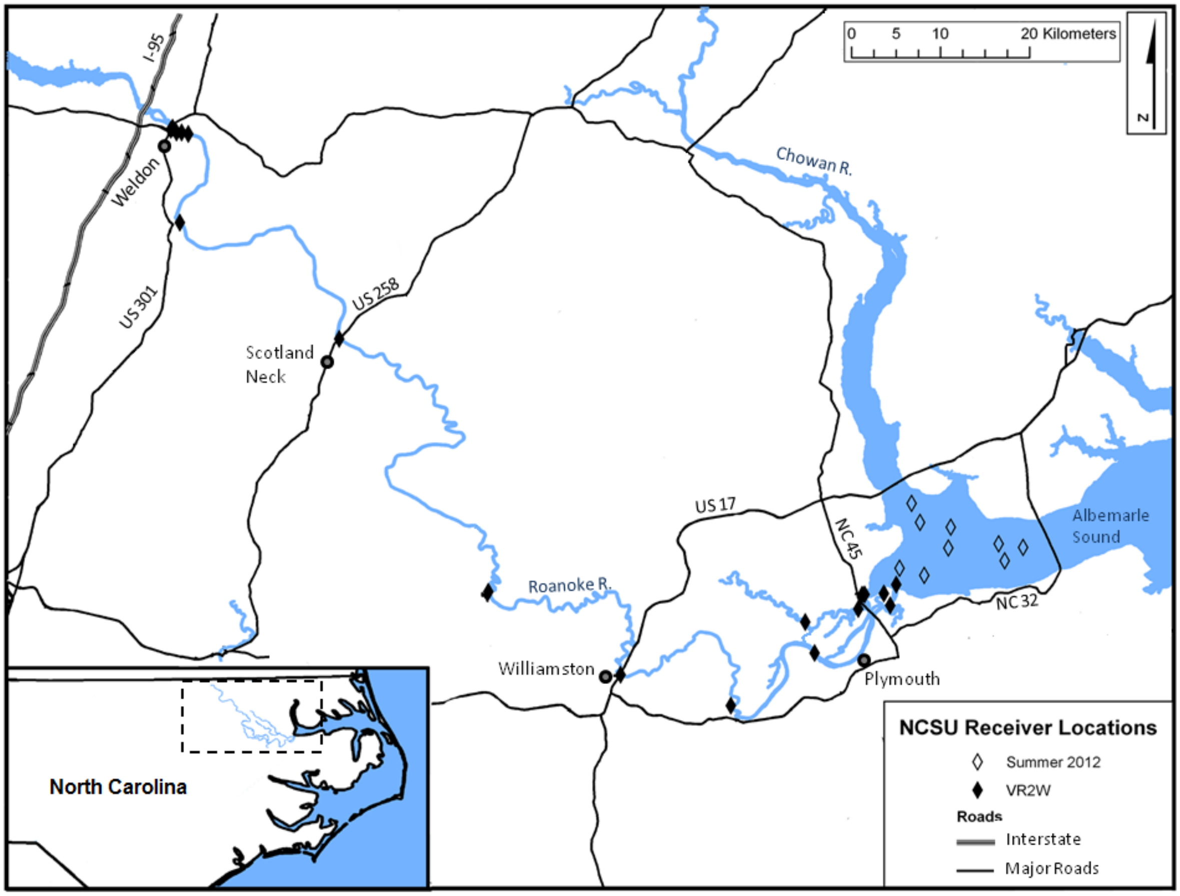

Figure 1. NCSU receiver locations in the Roanoke River and Western Albemarle Sound. The concentration of receivers near Weldon, NC, was intended to provide detailed movement data on that confirmed spawning site. Receiver locations and availability varied slightly over time due to occasion maintenance and deployment issues.

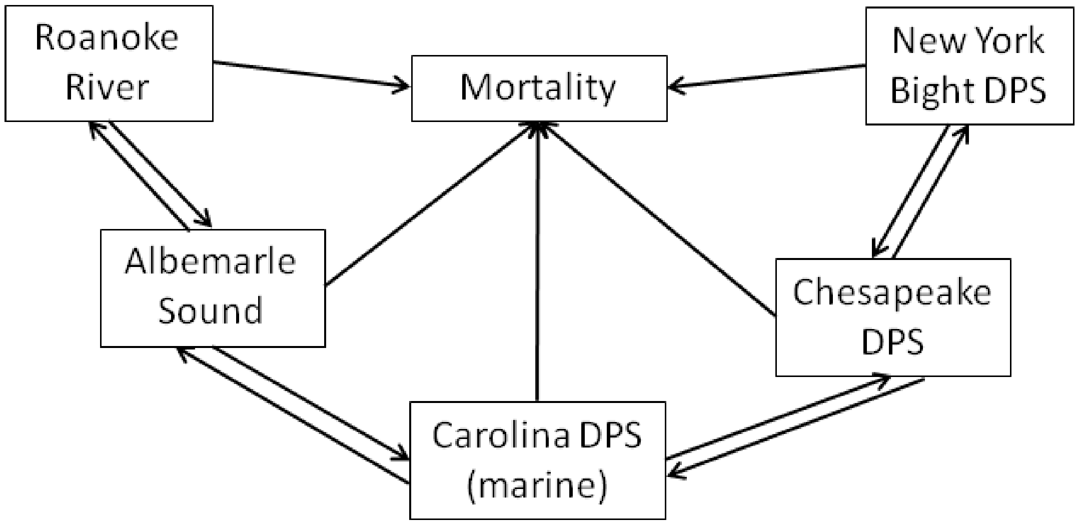

Figure 2. Multi-state model structure. Each box represents a model state and arrows are transition routes between states.

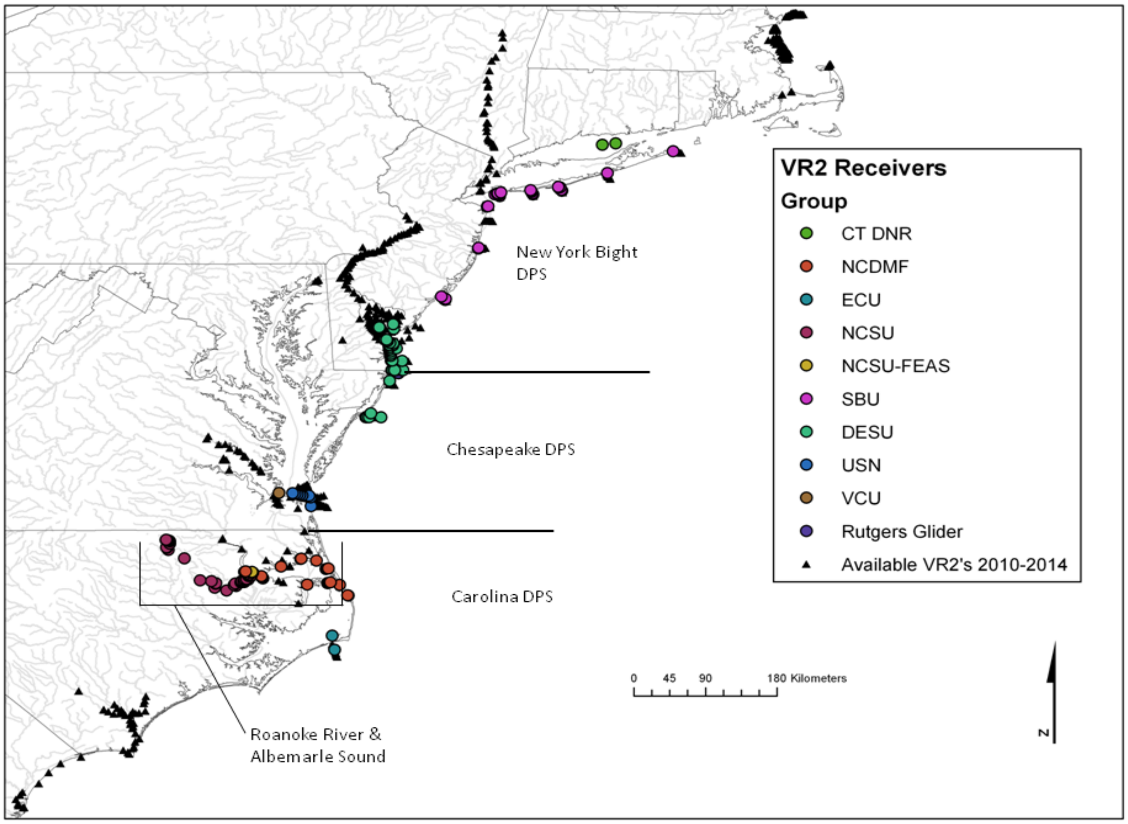

Figure 3. The range of detections of six adult Atlantic Sturgeon tagged in Roanoke River, North Carolina, 2010-2014. Circles are actual detections of our sturgeon and are color coded to receiver array owner. Triangles represent a partial list of receivers that were available during the study but where sturgeon were not detected. Major arrays with longer durations of deployment and/or large numbers of receivers are shown, although their temporal availability varied throughout the length of the study. Atlantic Sturgeon were detected in three Distinct Population Segments (labeled) in the coastal waters of seven states. The general trend was for Roanoke River sturgeon to travel north, but not south, from Albemarle Sound. The "Rutgers Glider" label refers to detections acquired by an autonomous glider from Rutgers University, while NCSU-FEAS refer to a separate group at NCSU that had receivers in Albemarle Sound.

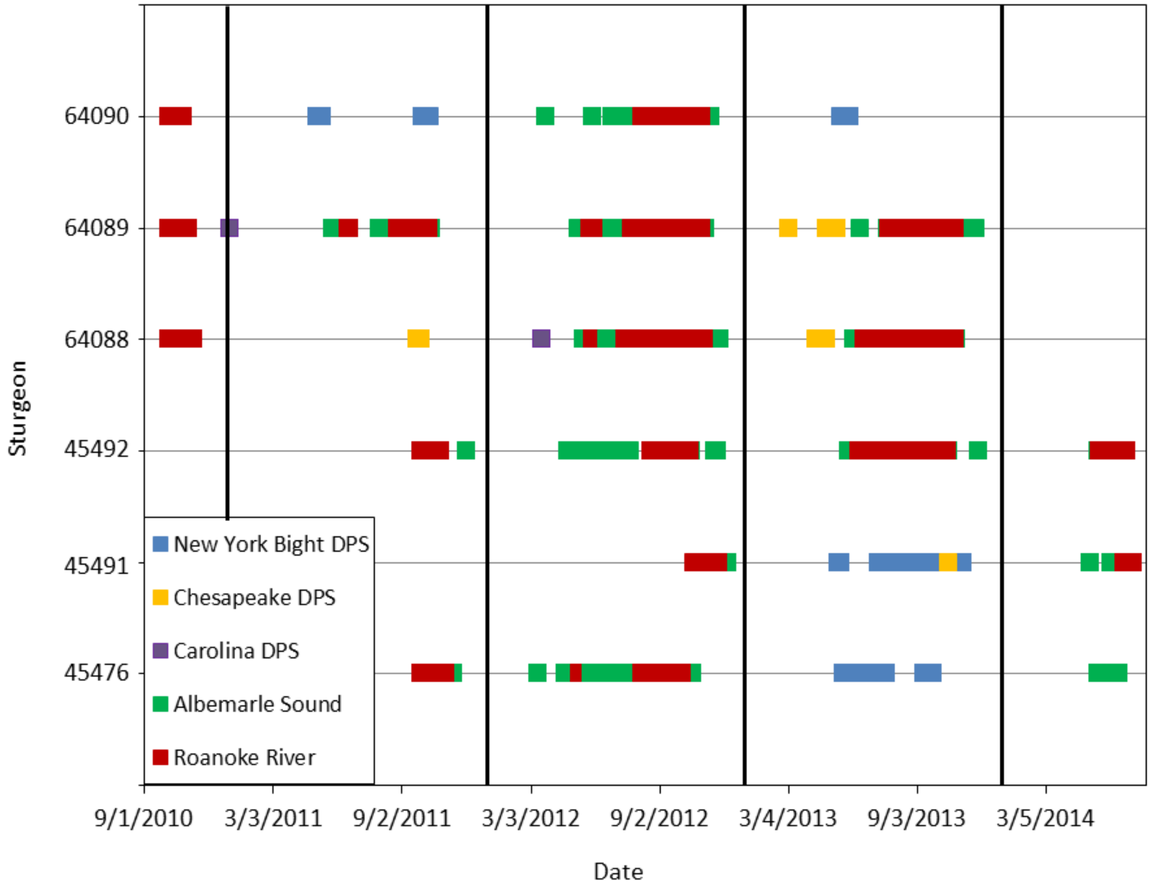

Figure 4. Annual movement patterns of tagged Atlantic Sturgeon. Colors represent different areas and vertical lines January 1. Batteries for tags 64088, 64089, and 64090 expired at the end of 2013.

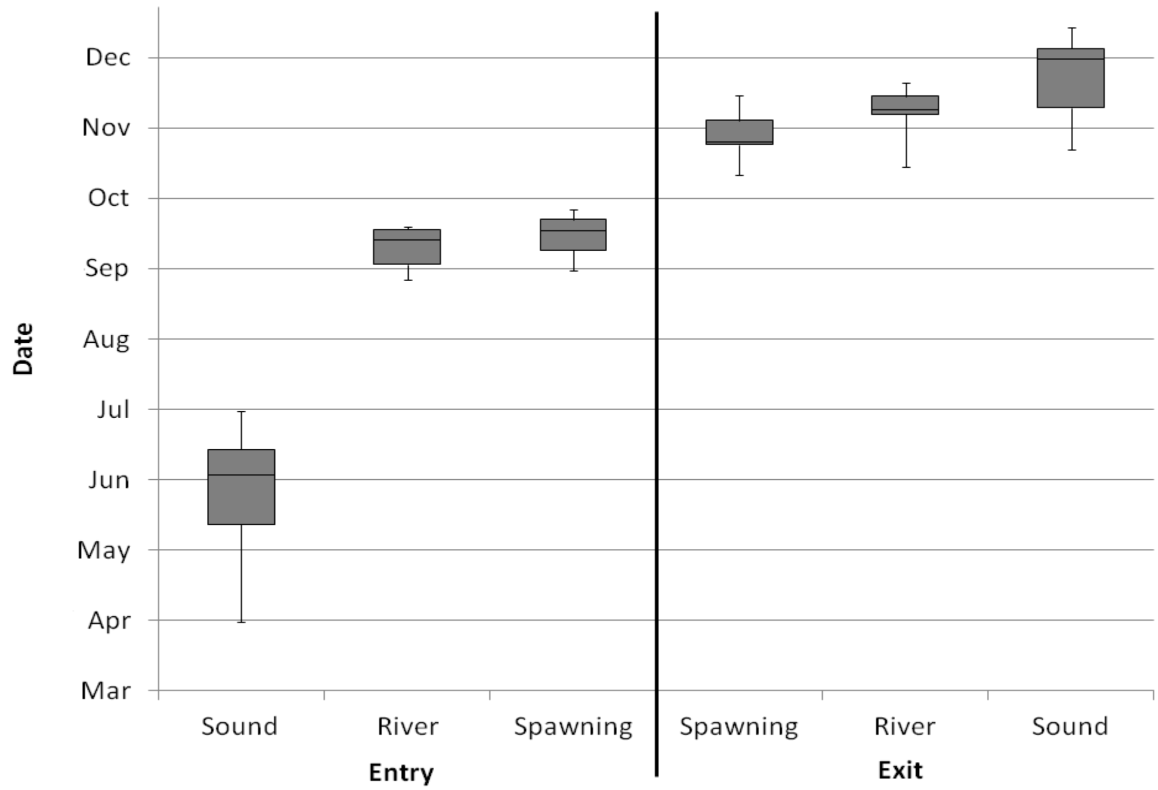

Figure 5. Tagged Atlantic Sturgeon mean date of entry and exit of Albemarle Sound and Roanoke River. Data are included for all individuals from 2010-2014. Sturgeon were considered to have entered or exited Albemarle Sound at Oregon Inlet, the Roanoke River at the mouth, and the spawning area at the Hwy 258 bridge near Scotland Neck, NC.

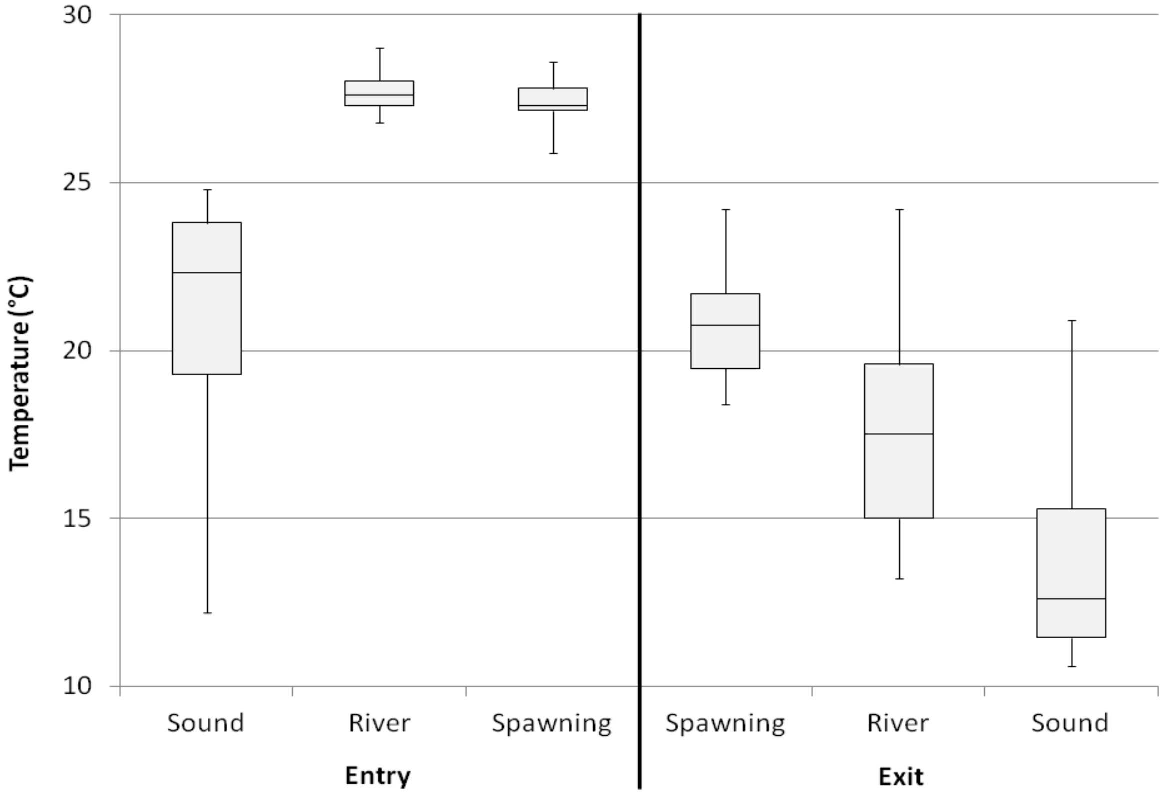

Figure 6. Tagged Atlantic Sturgeon mean temperature at entry and exit of Albemarle Sound and Roanoke River. Data are included for all individuals from 2010-2014. Sturgeon were considered to have entered or exited Albemarle Sound at Oregon Inlet, the Roanoke River at the mouth, and the spawning area at the Hwy 258 bridge near Scotland Neck, NC.

CHAPTER 5

Conclusion

New technologies can substantially advance fisheries science, once suitable field and analytical methods have been developed. We used side-scan sonar to identify and count an endangered species without the risks associated with capture and handling. This was done over a few weeks' time at a regional scale, with little prior knowledge of sturgeon abundance or distribution. Information from these same surveys made it possible to estimate abundance within multiple rivers and at the scale of a DPS. Long-life tags and a coast-wide network of receivers allowed us to follow fish across hundreds of kilometers of ocean. These new technologies often offer greater efficiencies in time and cost when compared to older techniques. For example, manual tracking of telemetered fish cannot be done at a coast-wide scale and even within a single river is quite labor-intensive. In comparison, automated telemetry receivers provide many thousands of detections year-round while only requiring a limited number of field days for tagging and receiver maintenance and downloading.

Since endangered species by definition are rare and not easy to find, information about seasonal locations of sturgeon will increase the efficiency of future studies. Side-scan sonar proved to be a useful tool to find Atlantic Sturgeon relatively efficiently in riverine environments. Knowing where sturgeon can be reliably found is a huge benefit for planning management activities and sampling regimes. Abundance estimates can be used to prioritize recovery efforts and as a baseline for future studies, including more intrusive methods such as capture-recapture through netting and tagging. Side-scan based abundance estimates could be used with capture-recapture methods to create more accurate and precise estimates of sturgeon abundance. A combined study would be able to address some of the weaknesses of side-scan, such as only being able to identify individuals > 1 m. Side-scan sonar could be used in a robust-design framework (Pollock et al. 1990), using side-scan survey for short-term abundance and a mark-recapture component for long-term survival.

The migration study in Chapter 4 would have been severely limited without the data sharing through telemetry networks. The most significant issue moving forward will be to maintain the participation and cooperation of individual researchers. Concerns over data rights have caused researchers to be hesitant about sharing data. These concerns must be resolved in order for studies of this type to continue.

In the preceding chapters, we used statistical methods (occupancy, N-mixture modeling, and distance sampling) that are rather common for terrestrial animal studies but less prevalent in fisheries research and monitoring. These methods may be less popular in fisheries because of differences in the estimated values they produce. Fisheries studies tend to focus on exploited species and demographic parameters such as individual and population growth, mortality, and exploitation rates, as well as abundance (Walters and Martell 2004). Mark-recapture studies are often used to estimate these parameters, despite being more expensive in terms of cost and effort (MacKenzie et al. 2004). Even when only relative abundance trends are needed, the historical convention for many fisheries programs is to use potentially flawed catch-per-unit-effort indices (Hilborn and Walters 1992). Occupancy and N-mixture models have more rigorous sampling requirements compared to catch-per-unit-effort (e.g. replicated sampling of sites) but may provide comparable or better information for management. For example, replicated sampling in occupancy studies can allow for site habitat characteristics to be related to detection and occupancy probabilities. This could be a substantial improvement over traditional (unreplicated) fisheries monitoring.

Occupancy modeling is a useful approach for studying rare and endangered species where encounter rates and population numbers are low since inference about population size can be made when individuals are too difficult or sparse to count or detection probabilities are low (MacKenzie et al. 2004; MacKenzie et al. 2005). Occupancy has been used in a few fisheries studies (Wenger and Freeman 2008; Falke et al. 2010), mainly involving rare species. N-mixture models have very rarely been used (Wenger and Freeman 2008). Distance sampling methods have been used primarily in visual surveys (Thresher and Gunn 1986; Kulbicki and Sarramégna 1999; McIntyre et al. 2013). Characteristics of side-scan sonar, such as the ability to rapidly survey areas (allowing for repeated surveys in a short time-span) and having a known swath width (enabling distance measurements from the transect centerline and providing area for density estimates) make it well suited for these analytical approaches.

The ultimate goal of any recovery plan is restoring populations to historic abundance levels. For Atlantic Sturgeon this could eventually mean reopening of fisheries. While Atlantic Sturgeon could not be harvested at the same rates as previous fisheries, sturgeon can be harvested sustainably at a reasonable level, like the Wisconsin Lake Sturgeon *Acipenser fulvescens* fishery (Bruch 1999). Recovered Atlantic Sturgeon populations could provide socioeconomic benefits to coastal and riverine communities both through the economic value of sturgeon products, such as caviar, and the sense of pride and accomplishment resulting from return of an iconic, yet somewhat forgotten species, to the waters.

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APPENDICES

Appendix A. Survey Target Detection Maps

Targets detected in sonar surveys were plotted on maps of each river. Rivers were broken up into 2 km sites and detections were recorded for each site.

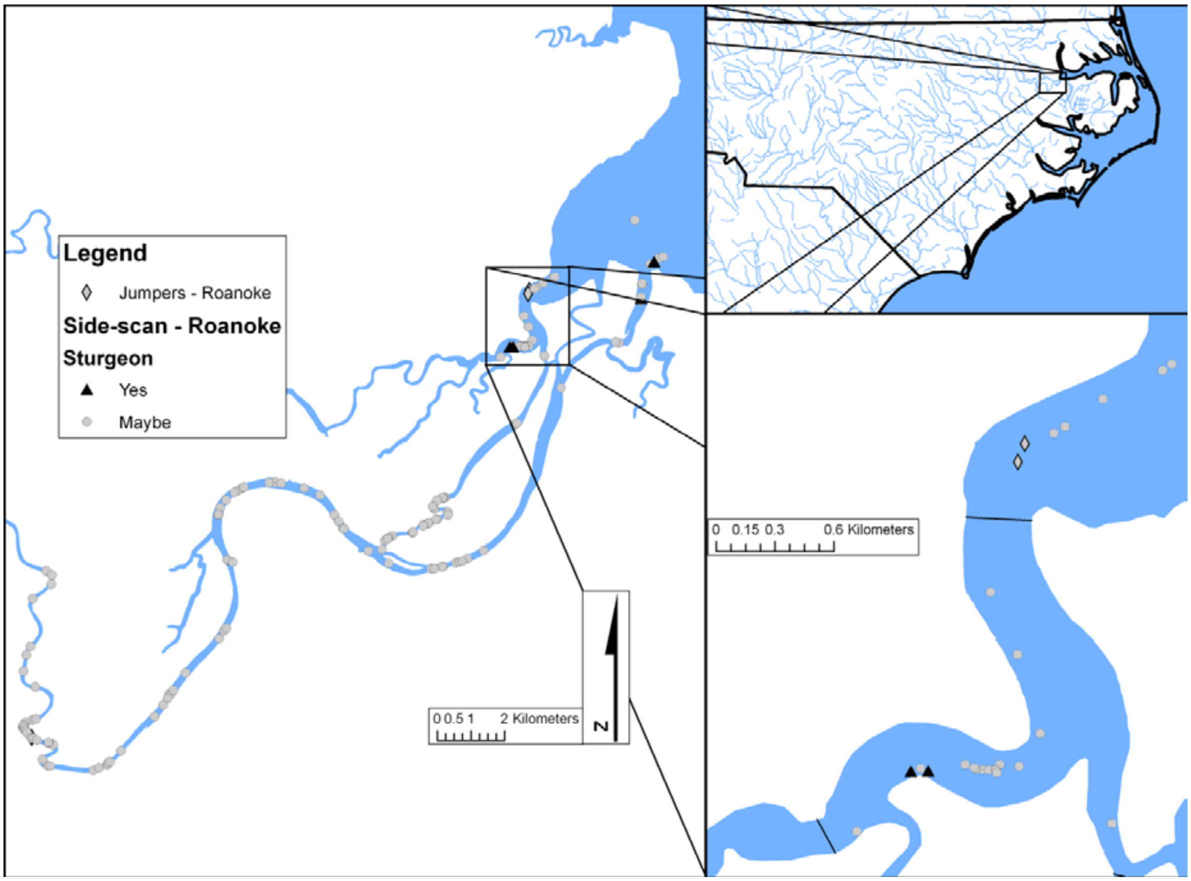

Figure A.1. Map of the Roanoke River, NC showing survey detections. Left pane shows extent of survey area while lower inset shows zoomed survey area with 2 km segments denoted by black lines. No telemetry detections were made. Only one side-scan observer's detections are plotted, for clarity.

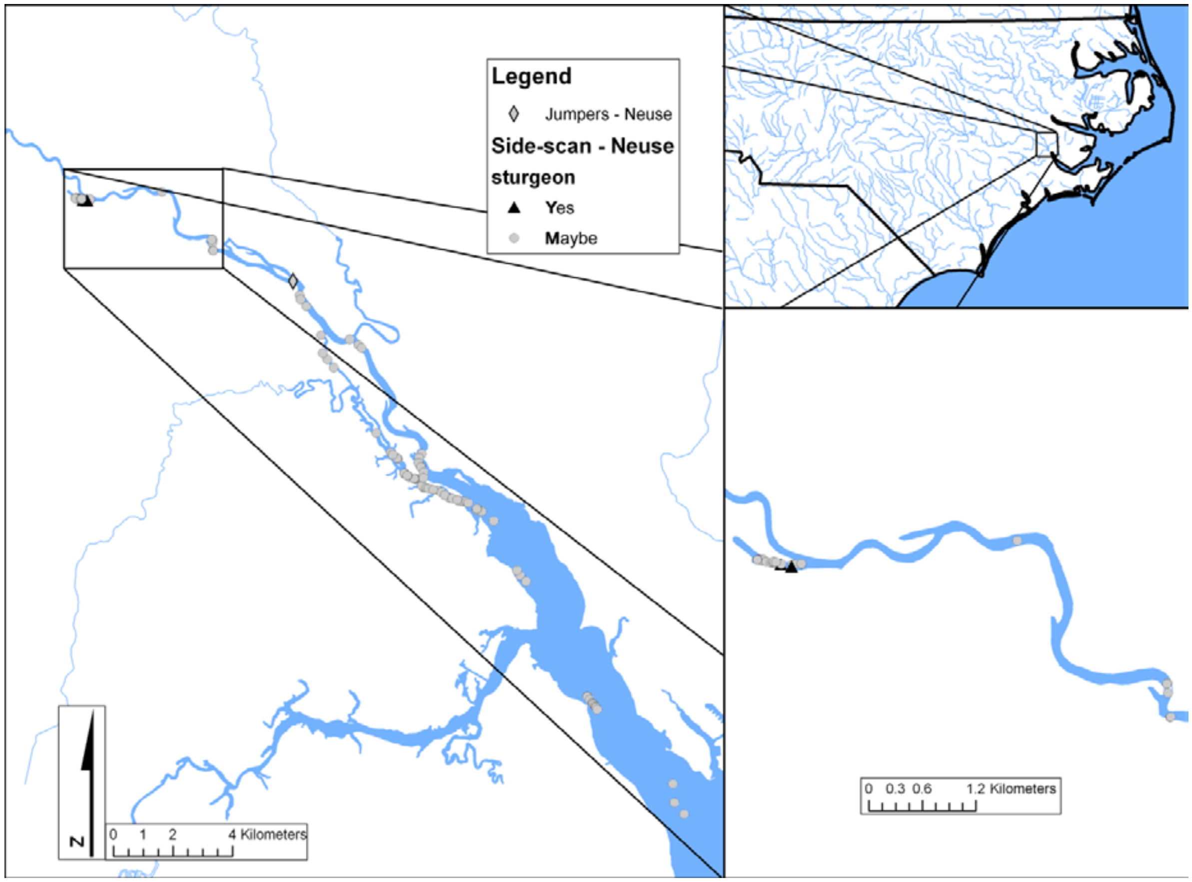

Figure A.2. Map of the Neuse River, NC showing survey detections. Left pane shows extent of survey area while lower inset shows zoomed survey area with 2 km segments denoted by black lines. No telemetry observations of sturgeon were made. Only one side-scan observer's detections are plotted, for clarity.

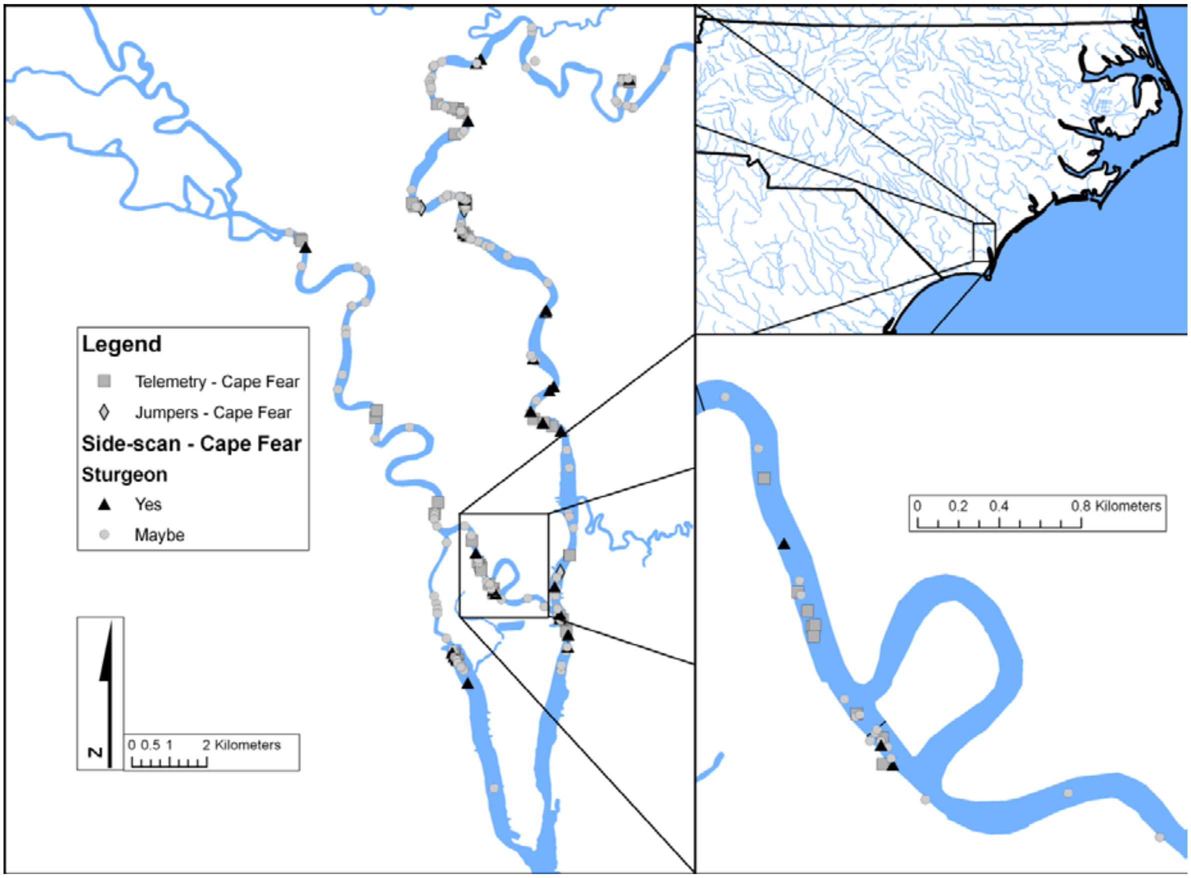

Figure A.3. Map of the lower Cape Fear River, NC area showing survey detections. Left pane shows extent of survey area while lower inset shows zoomed survey area with 2 km segments denoted by black lines. The Cape Fear River survey area also included portions of the Northeast Cape Fear River and the Brunswick River. Only one side-scan observer's detections are plotted, for clarity.

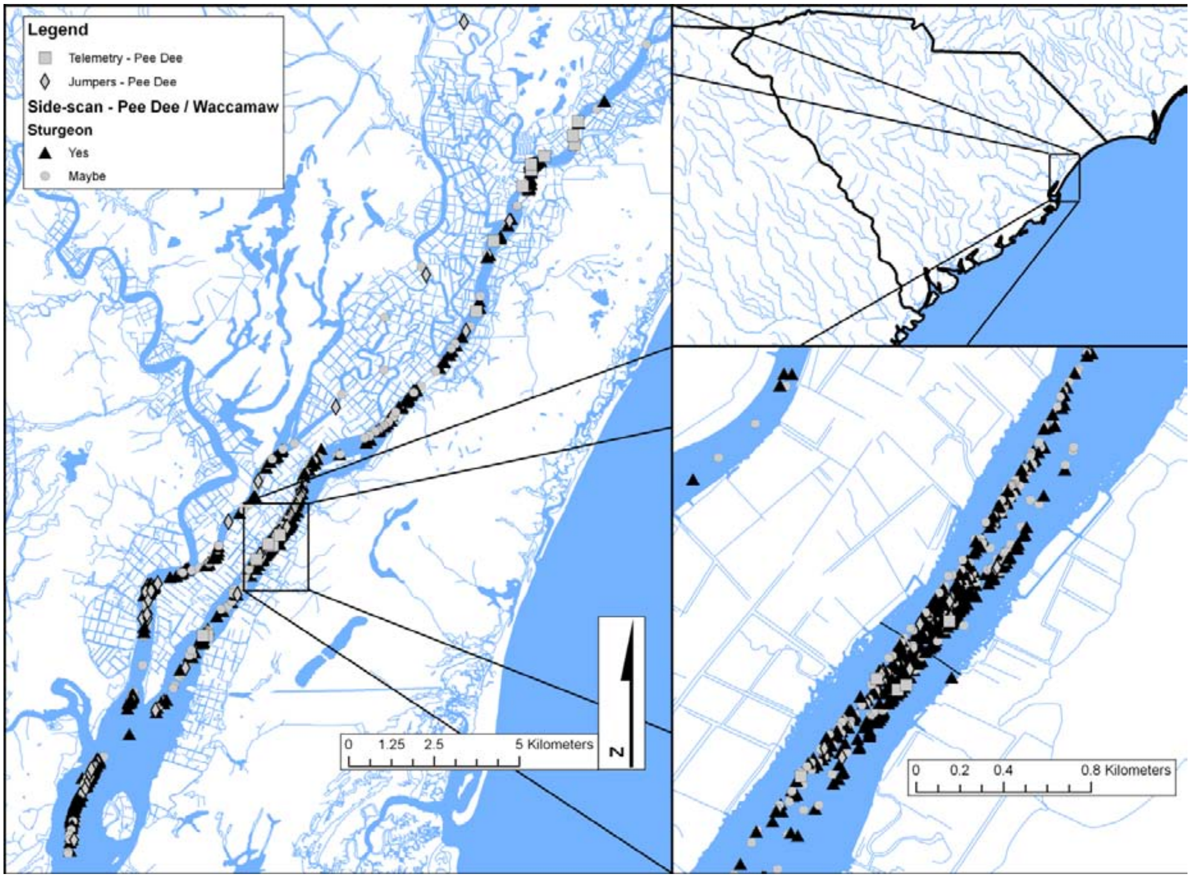

Figure A.4. Map of the lower Pee Dee / Waccamaw River area showing survey detections. Left pane shows extent of survey area while lower inset shows zoomed survey area with 2 km segments denoted by black lines. Portions of Winyah Bay, the Pee Dee River, and the Waccamaw River (including the intracoastal waterway) were included in the survey. Only one side-scan observer's detections are plotted, for clarity.

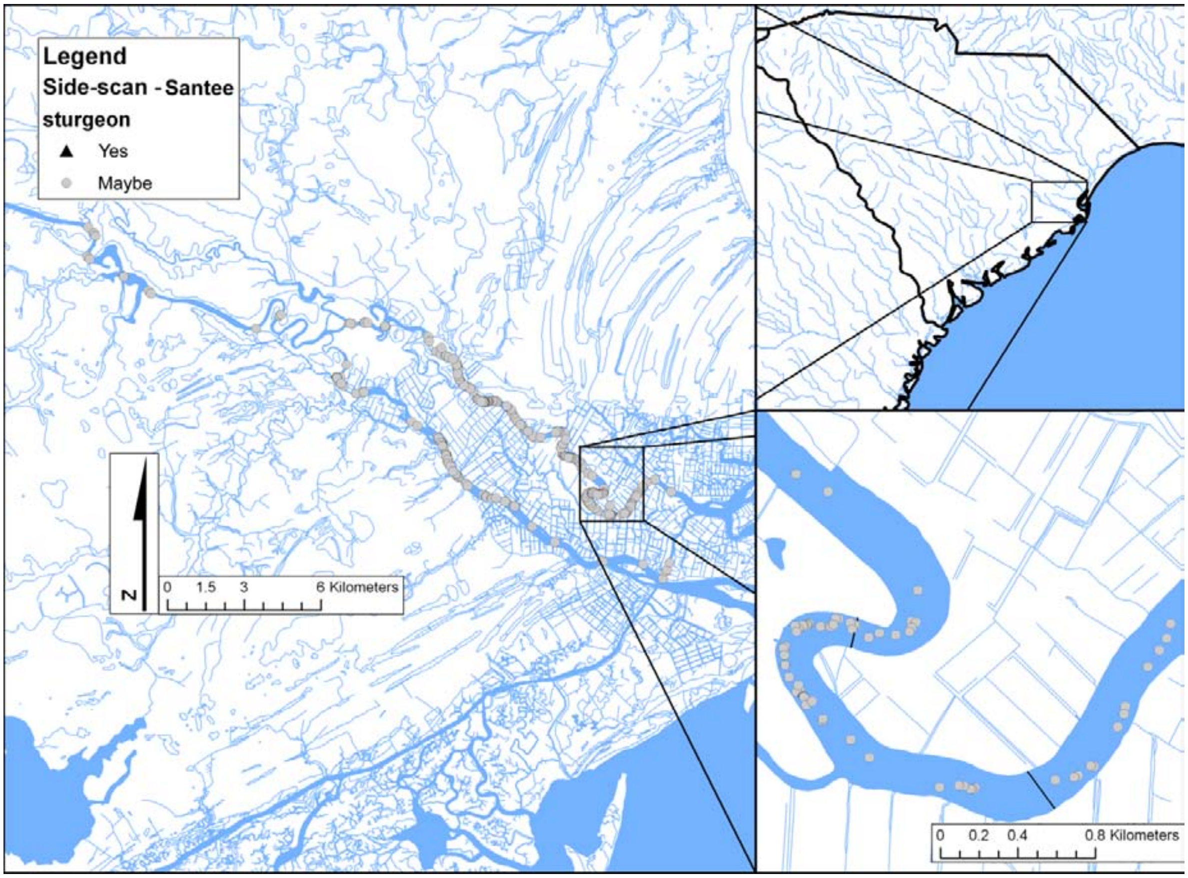

Figure A.5. Map of the Santee River showing survey detections. Left pane shows extent of survey area while lower inset shows zoomed survey area with 2 km segments denoted by black lines. No jumping or telemetry observations were made. The surveyed area included portions of both the North Santee and South Santee rivers. Only one side-scan observer's detections are plotted, for clarity.

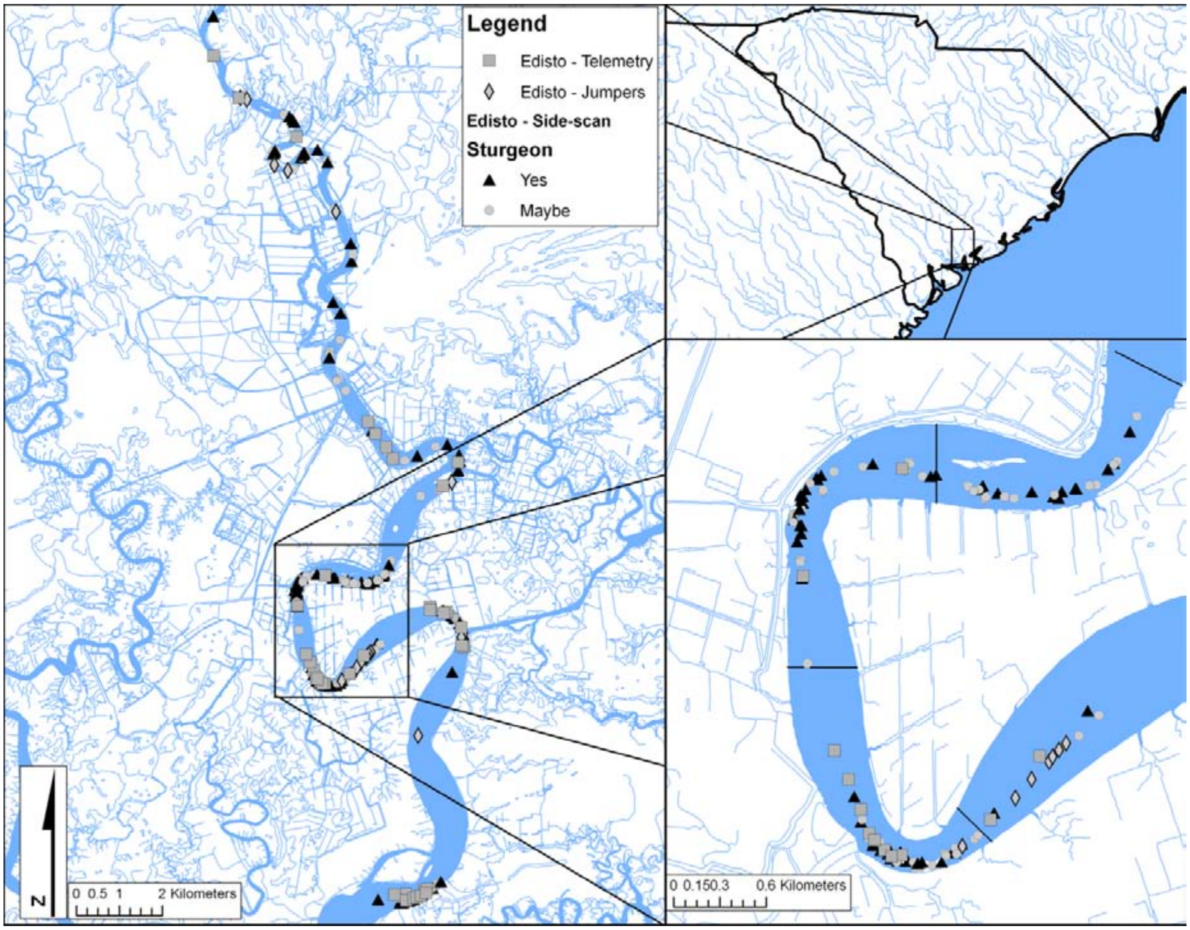

Figure A.6. Map of the Edisto River showing survey detections. Left pane shows extent of survey area while lower inset shows zoomed survey area with 2 km segments denoted by black lines. The lower portion of the river also contained the intracoastal waterway. Only one side-scan observer's detections are plotted, for clarity.

Appendix B. Example Side-scan images

Fish targets were identified and classified as sturgeon or not based on subjective factors decided on by the individual observer. These factors were usually body length, acoustic shadow shape, and possibly body shape. Following are images with different targets types to illustrate decisions made by the observers. Each selected target was classified the same by each observer.

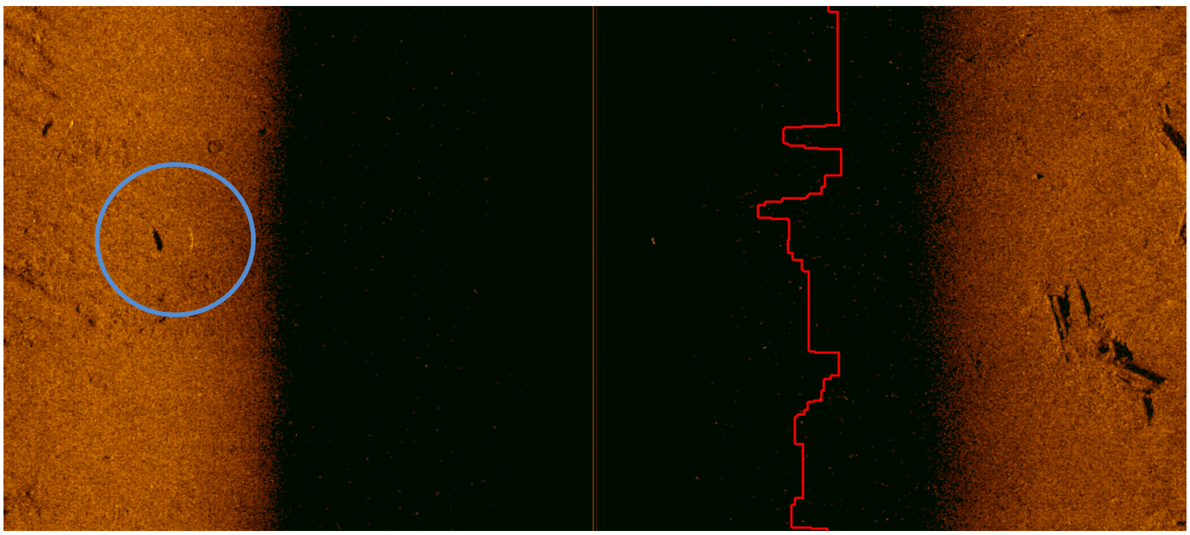

Figure B.1. A 1.7 m target identified as a sturgeon by both observers (circled) in the Cape Fear River. Classification was made based on length, and silhouette shape, showing some evidence of pectoral and anal fins, although caudal fin is somewhat obscured. Smaller target to upper left was classified as a sturgeon by observer 1 and a “maybe” by observer 2. Image width is 60 m.

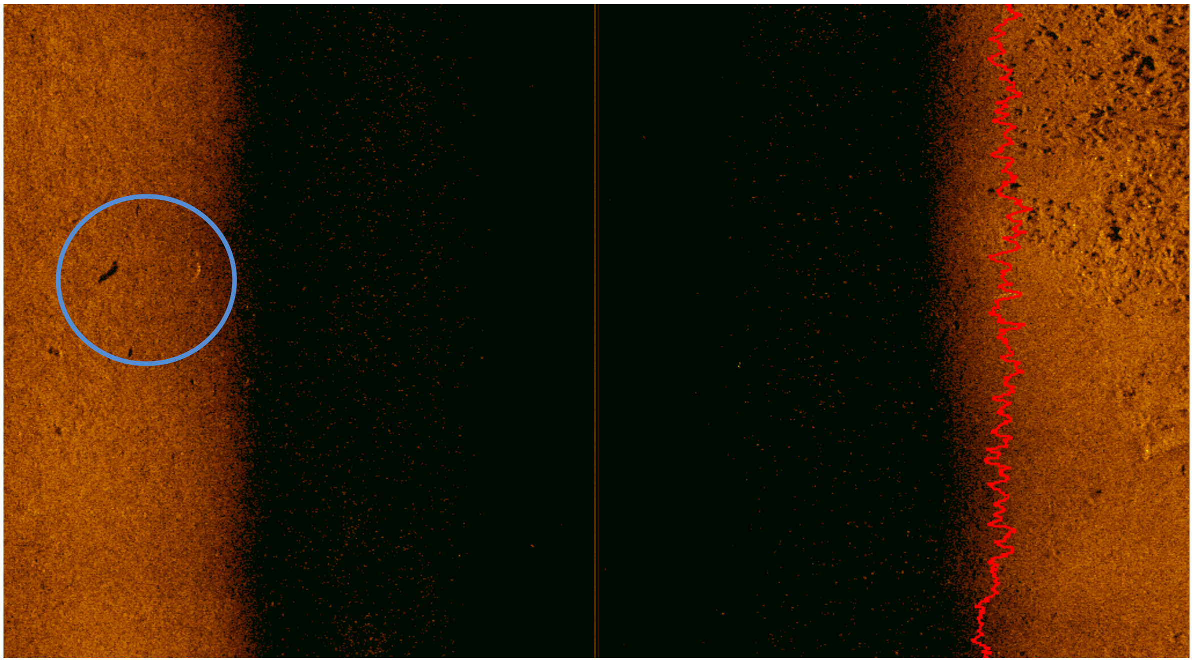

Figure B.2. A 1.6 m target identified as a sturgeon by both observers (circled) in the Cape Fear River. Classification was made based on length and silhouette shape. Image width is 60 m.

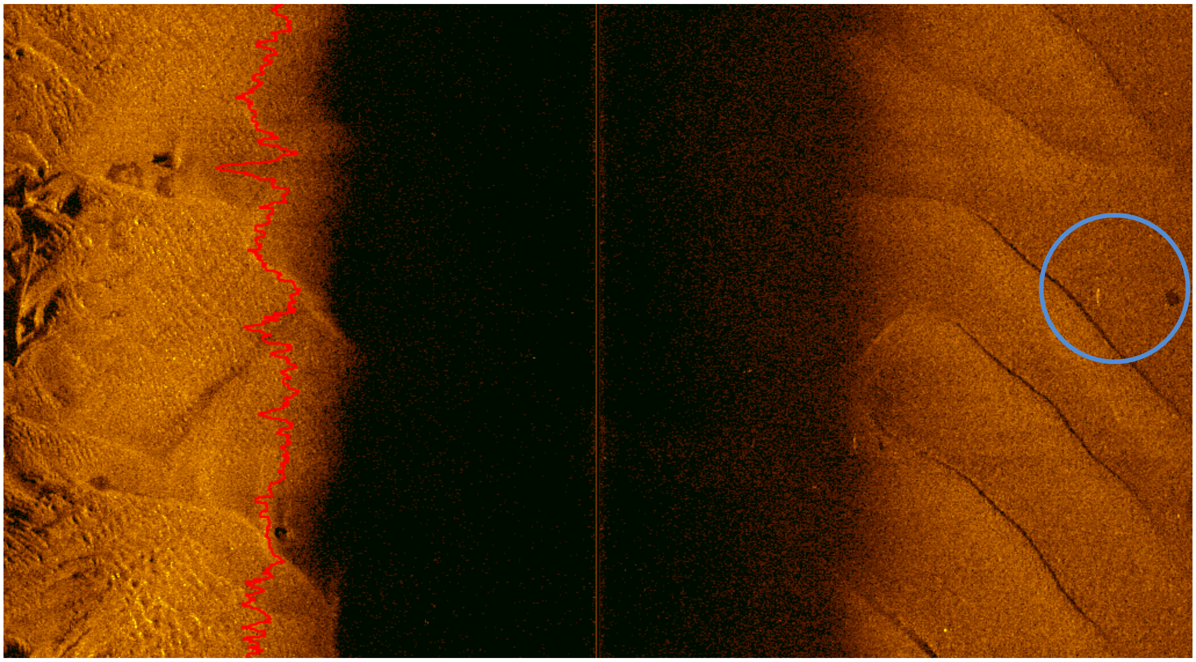

Figure B.3. A 1.1 m target identified as a sturgeon by both observers (circled) in the Cape Fear River. Classification was made based on length and silhouette shape, specifically the prominent upper caudal fin in shadow. Image width is 60 m.

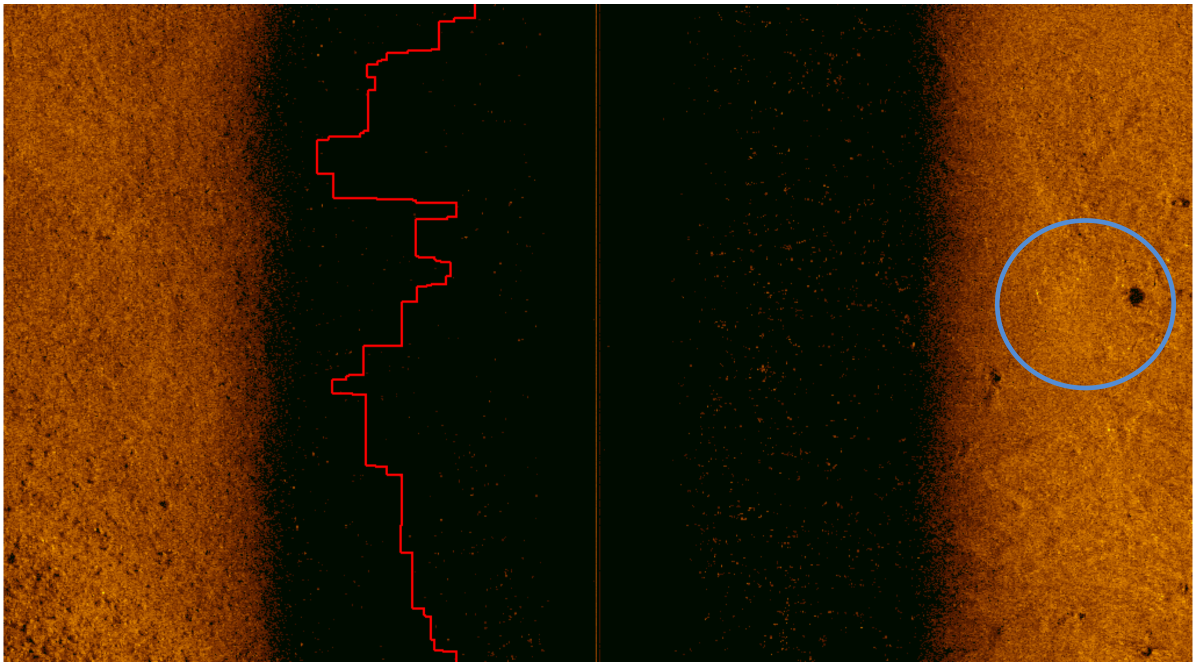

Figure B.4. A 1.6 m target identified as a sturgeon by both observers (circled) in the Cape Fear River. Classification was made based on length and silhouette shape, including caudal fin in shadow. Image width is 60 m.

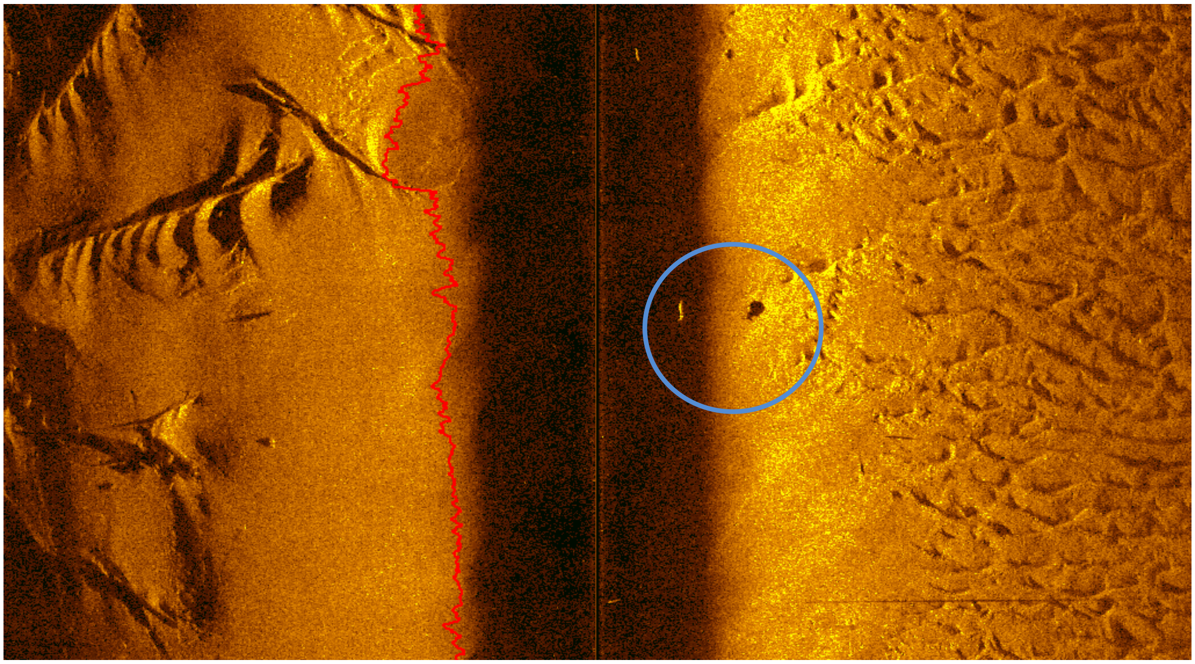

Figure B.5. A 1.6 m target identified as a sturgeon by both observers (circled) in the Edisto River. Classification was made based on length, body and silhouette shape, including caudal fin in shadow and evidence of caudal fin on body itself. Image width is 60 m.

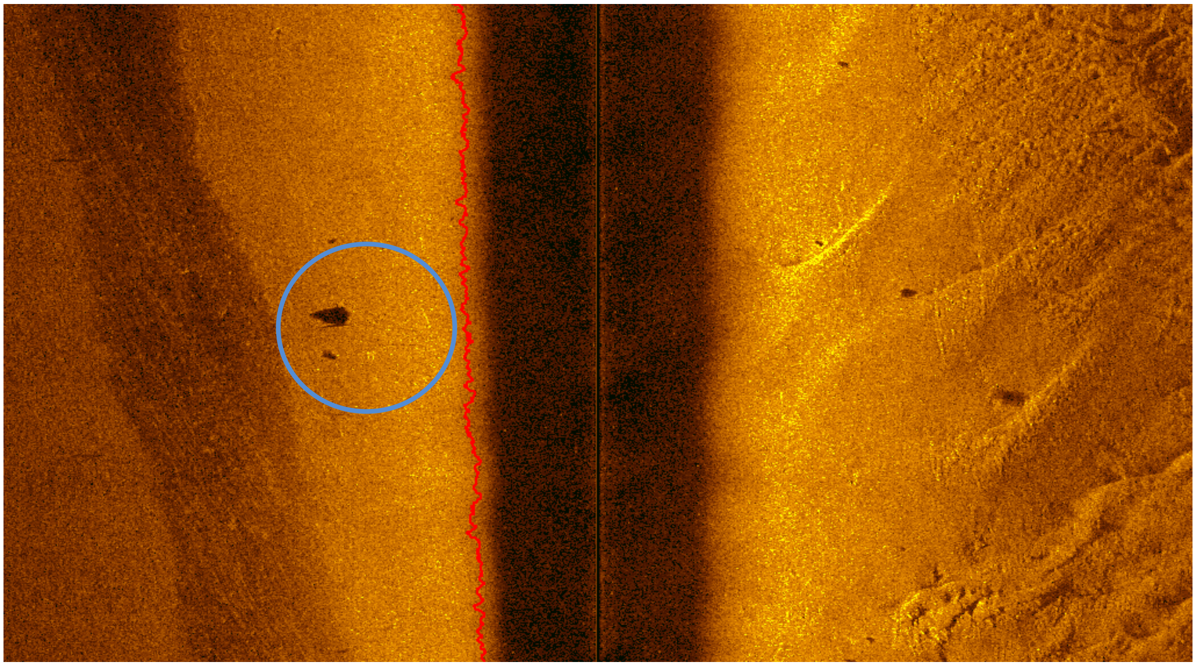

Figure B.6. A 1.5 m target identified as a sturgeon by both observers (circled) in the Edisto River. Classification was made based on length, silhouette shape, including caudal fin in shadow. Image width is 60 m.

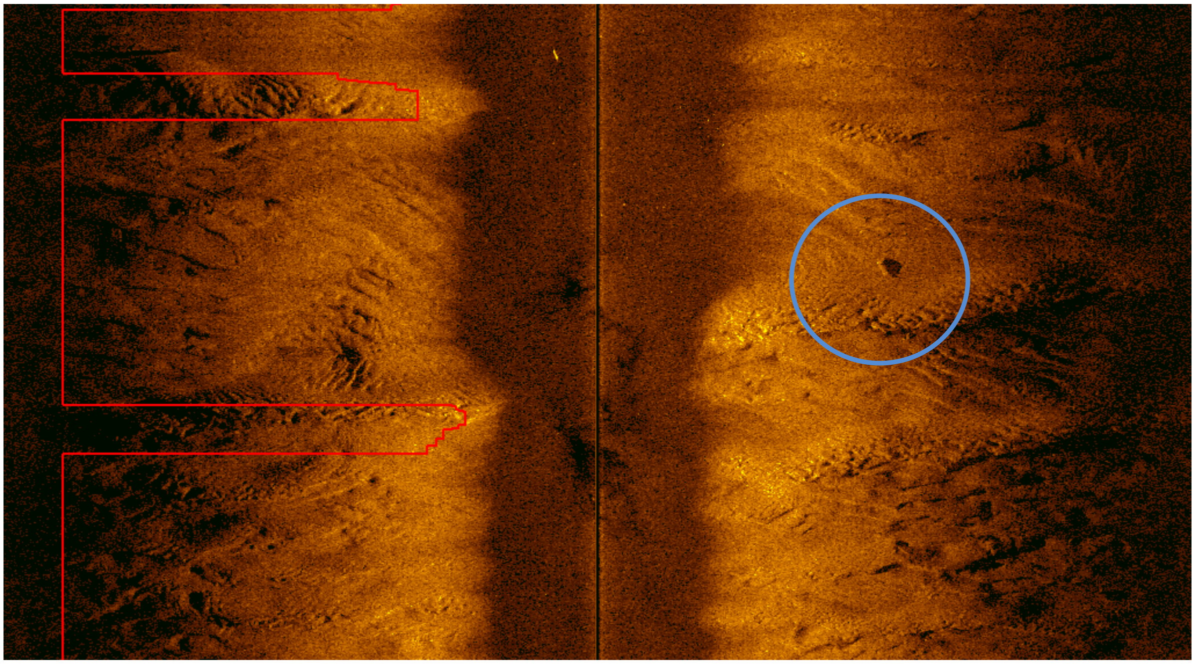

Figure B.7. A 1.7 m target identified as a sturgeon by both observers (circled) in the Edisto River. Classification was made based on length, silhouette shape, including caudal fin in shadow. Image width is 60 m.

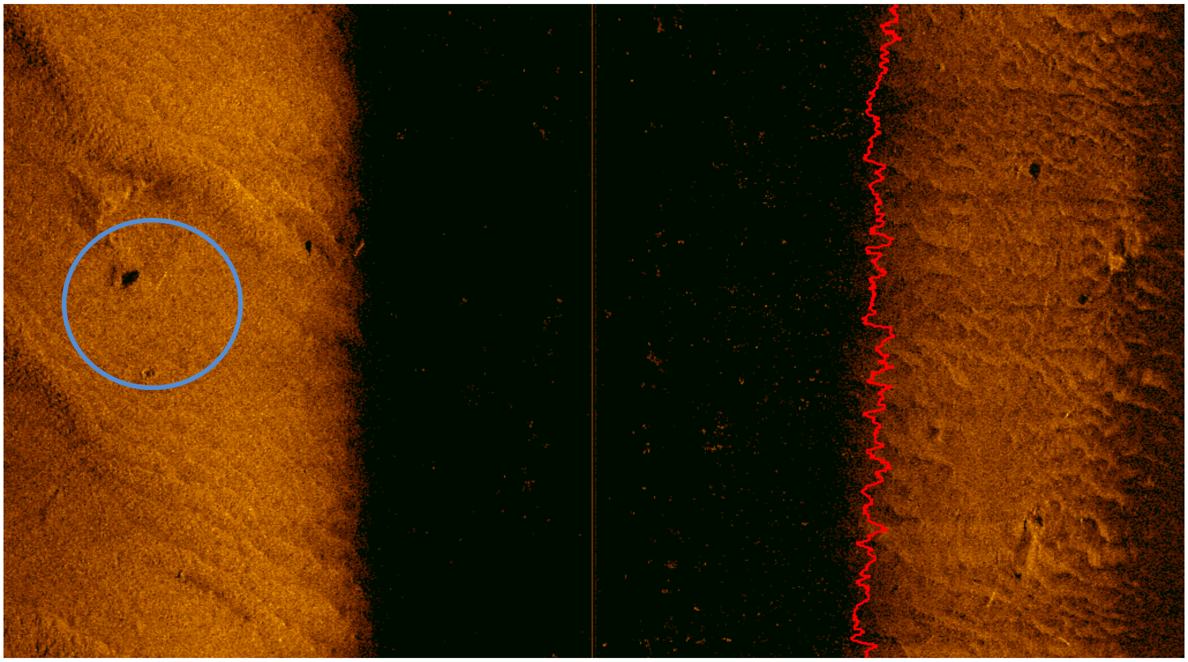

Figure B.8. A 1.3 m target identified as a sturgeon by both observers (circled) in the Edisto River. Classification was made based on length, silhouette shape, noting general evidence of fin position. Smaller target to right was classified as a sturgeon by observer 1 and a “maybe” by observer 2. Image width is 60 m.

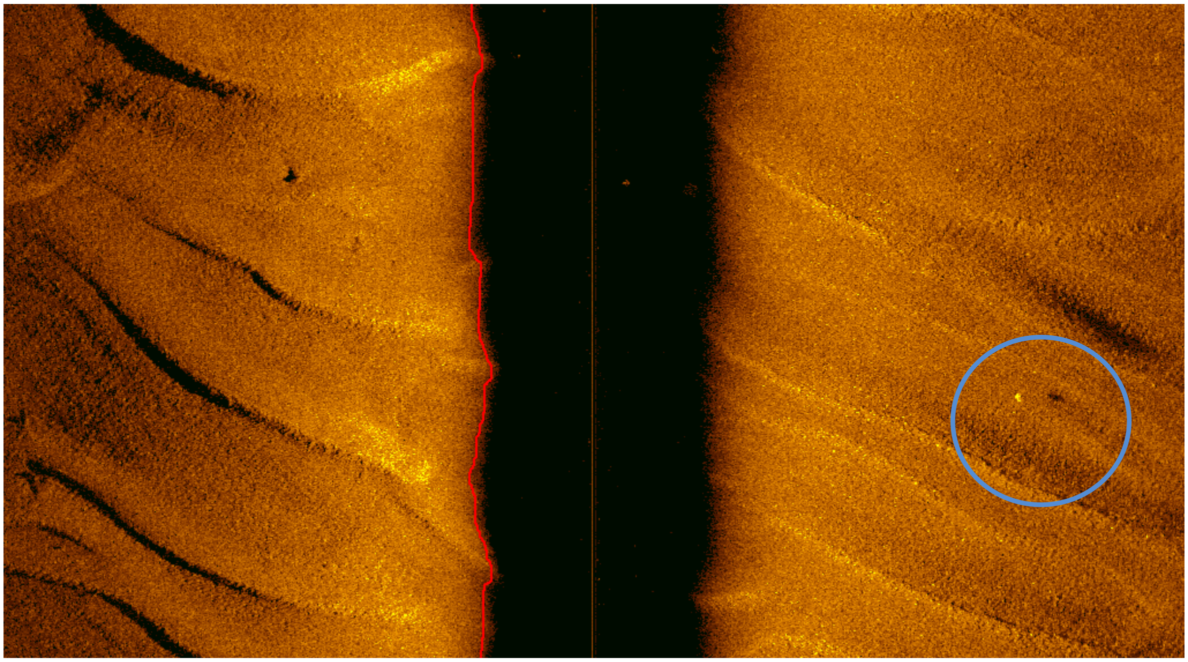

Figure B.9. A 0.9 m target identified as a “maybe” by both observers (circled) in the Cape Fear River. Classification was made based on length, but lack of any general shape information. Image width is 60 m.

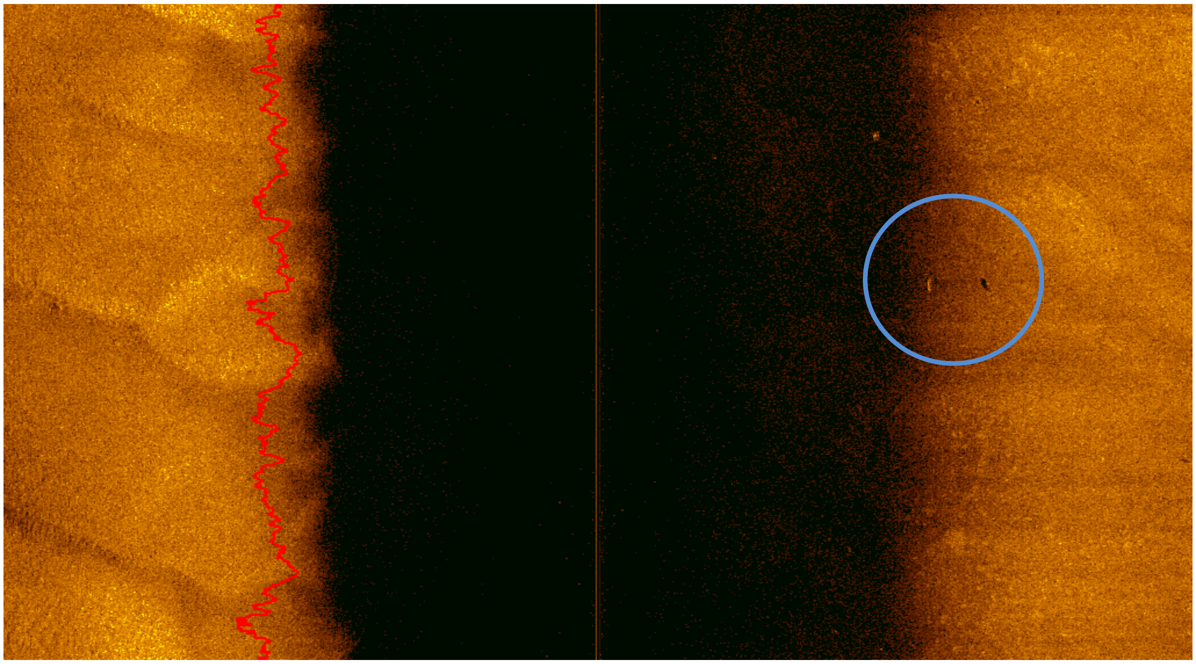

Figure B.10. A 1.0 m target identified as a “maybe” by both observers (circled) in the Cape Fear River. Classification was made based on length, but lack of any general shape information. Image width is 60 m.

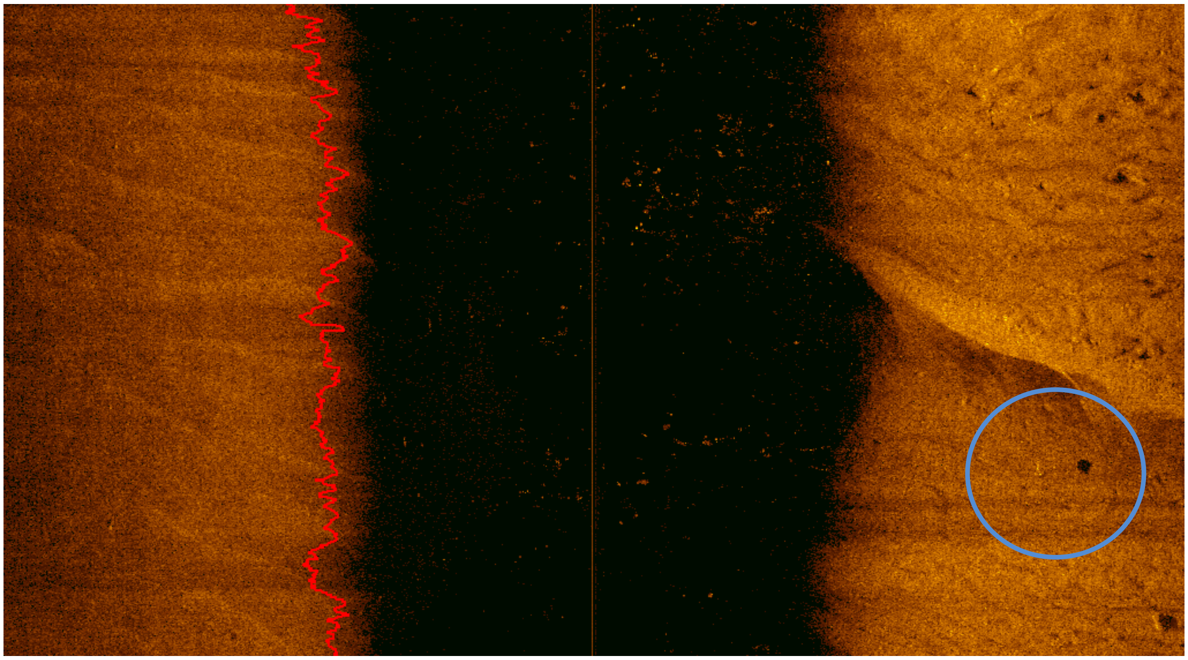

Figure B.11. A 1.0 m target identified as a “maybe” by both observers (circled) in the Cape Fear River. Classification was made based on length, but lack of any general shape information. Image width is 60 m.

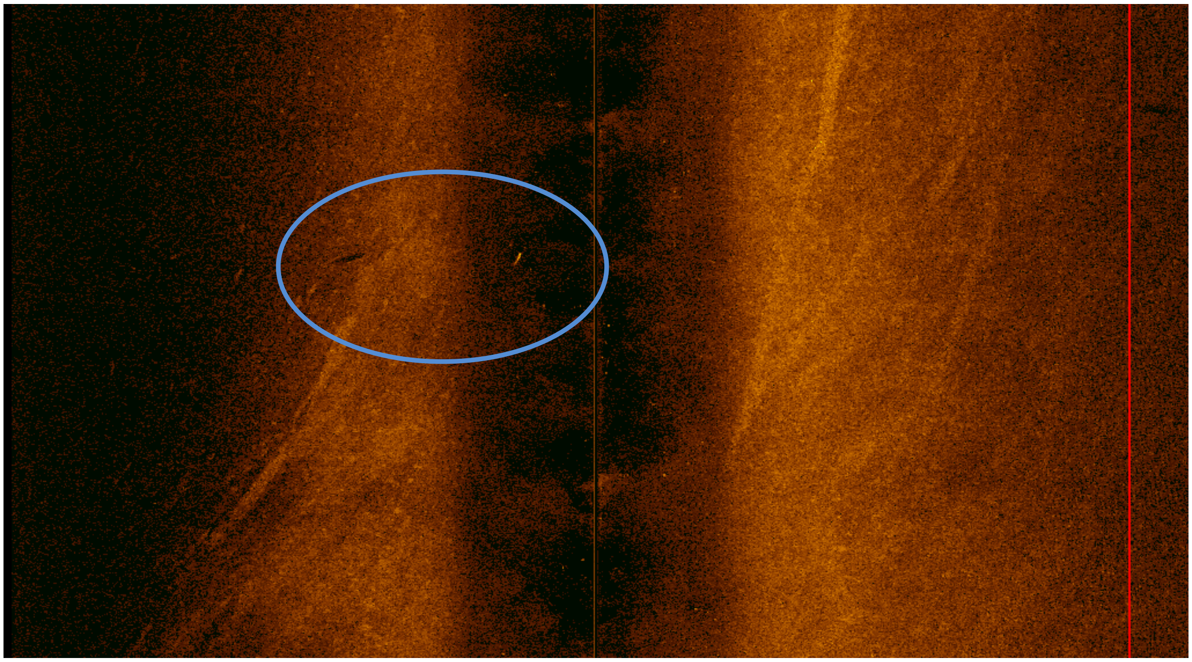

Figure B.12. A 1.0 m target identified as a “maybe” by both observers (circled) in the Edisto River. Classification was made based on length, but lack of any general shape information. Image width is 60 m.

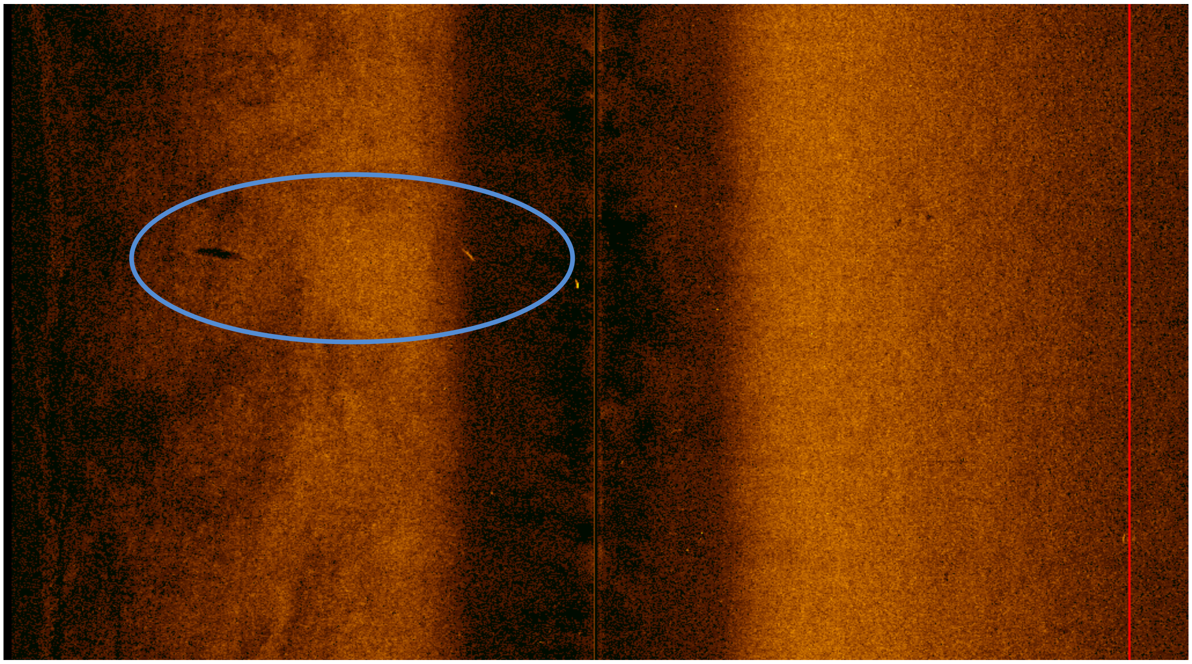

Figure B.13. A 1.2 m target identified as a “maybe” by both observers (circled) in the Edisto River. Classification was made based on length, but lack of any general shape information. Small target to right was not classified. Image width is 60 m.

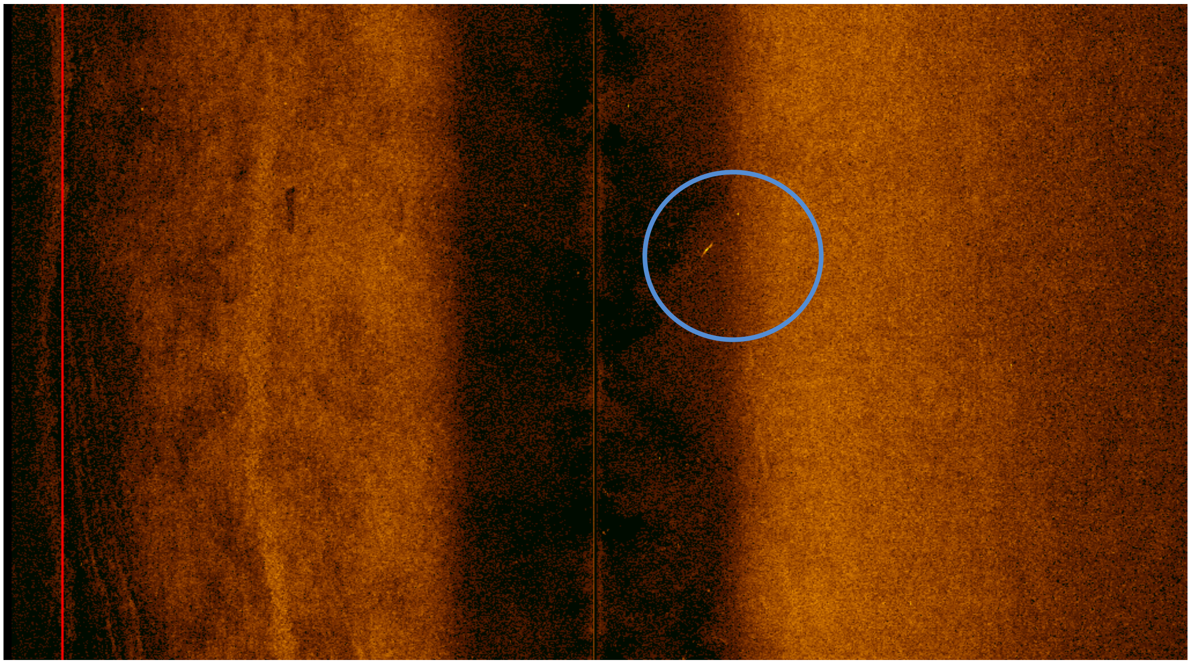

Figure B.14. A 1.2 m target identified as a “maybe” by both observers (circled) in the Edisto River. Classification was made based on length, but lack of any general shape information. Image width is 60 m.

Appendix C. Riverine Receiver Design

We used a specialized riverine deployment method where each VR2 was mounted on an anchor consisting of an L-shaped galvanized pipe structure set into a base of concrete formed by a 5-gallon bucket (Picture as supplement or Figure C.1). The VR2 was attached to the horizontal bar of the anchor using zip-ties and duct tape for reinforcement. A short length of chain was imbedded into the concrete base and served as the attachment point for the steel cable or rope, as well as protecting it from rubbing against the rough surface of the concrete. Anchors were attached to shoreline trees, docks, pilings, or other solid structures. This design has proved to be stable and robust, surviving flood events and a direct hit from a hurricane. Without having a float attached, they are also less prominent than other deployment methods and may be less susceptible to vandalism. Horizontally mounting the receiver also provides more room for shallow water deployments without a discernible change in detection performance. It was important to consider variation in water level when choosing deployment and tie-off locations as it is important that the receiver remains submerged at all times, but accessible when water levels rise. There was concern about receivers potentially becoming buried in sediment, but this was not an issue.

Figure C.1. VR2 receiver mounts. A round concrete anchor serves as a base with an upright pipe supporting a horizontal pipe arm used for VR2 attachment with zip-ties and duct tape. Note the chain embedded in the base for secure attachment.

Appendix D. Multi-state Model R Code

```
###R to WinBUGS code for multi-state sturgeon telemetry
###Model adapted from Kéry and Schaub 2012. by H. Jared Flowers

library(R2WinBUGS)      # Load package to run bugs from R

#read and format data
rC<-read.csv("MSMbugsriv3.csv",header=T)
rC<-as.matrix(rC)
rCH<-rC[1:6,]
seas<-as.vector(rC[7,])       #vector of numbers representing seasons

# Specify model in BUGS language
sink("msm2.txt")
cat("
model{

# -------------------------------------------------
# Parameters:
# phi: survival probability
# psiAB: movement probability from site A to site B
# psiBA: movement probability from site B to site A
# psiBC: movement probability from site B to site C
# psiCB: movement probability from site C to site B
# psiCD: movement probability from site C to site D
# psiDC: movement probability from site D to site C
# psiDE: movement probability from site D to site E
# psiED: movement probability from site E to site D
# pA: recapture probability at site A
# pB: recapture probability at site B
# pC: recapture probability at site C
# pD: recapture probability at site D
# pE: recapture probability at site E
# -------------------------------------------------
```

```
# States (S):
# 1 alive at A
# 2 alive at B
# 3 alive at C
# 4 alive at D
# 5 alive at E
# 6 dead
# Observations (O):
# 1 seen at A
# 2 seen at B
# 3 seen at C
# 4 seen at D
# 5 seen at E
# 6 not seen
# -------------------------------------------------

# Priors and constraints
  # Survival and recapture: uniform
pA ~dunif(0,1)
pB ~dunif(0,1)
pC ~dunif(0,1)
pD ~dunif(0,1)
pE ~dunif(0,1)
phi~dunif(0,1)

AnnS<-pow(phi,4)    #Calculates annual survival

# Transitions: multinomial logit
    # Normal priors on logit of all but one transition probs

for (t in 1:n.occasions){
for(i in 1:1){
 lpsiA[i,t] ~dnorm(0,0.001)
 lpsiE[i+3,t] ~dnorm(0,0.001)
 }
```

```
for(i in 1:3){
  lpsiB[i,t] ~dnorm(0,0.001)
  lpsiD[i+1,t] ~dnorm(0,0.001)
   }
for(i in 1:4){
  lpsiC[i,t] ~dnorm(0,0.001)
  }
  }

# Constrain the transitions such that their sum is < 1
for (t in 1:n.occasions){
 for (i in 1:1){
 psiA[i,t]<-exp(lpsiA[i,seas[t]])/(1+exp(lpsiA[1,seas[t]]))
 psiE[i+3,t]<-exp(lpsiE[i+3,seas[t]])/(1+exp(lpsiE[4,seas[t]]))
  }

 for (i in 1:2){
 psiB[i,t]<-exp(lpsiB[i,seas[t]])/(1+exp(lpsiB[1,seas[t]])+exp(lpsiB[2,seas[t]]))
  psiC[i+1,t]<-exp(lpsiC[i+1,seas[t]])/(1+exp(lpsiC[2,seas[t]])+exp(lpsiC[3,seas[t]]))
  psiD[i+2,t]<-exp(lpsiD[i+2,seas[t]])/(1+exp(lpsiD[3,seas[t]])+exp(lpsiD[4,seas[t]]))
      }

# Calculate the last transition probability
psiA[2,t]<- 1-psiA[1,t]
psiB[3,t]<- 1-psiB[1,t]-psiB[2,t]
psiC[4,t]<- 1-psiC[2,t]-psiC[3,t]
psiD[5,t]<- 1-psiD[3,t]-psiD[4,t]
psiE[5,t]<- 1-psiE[4,t]
}

# Define state-transition and observation matrices
for (i in 1:nind){
# Define probabilities of state S(t+1) given S(t)
  for(t in f[i]:(n.occasions-1)){
    ps[1,i,t,1]<- phi*psiA[1,t]
```

```
ps[1,i,t,2]<- phi*psiA[2,t]
ps[1,i,t,3]<- 0
ps[1,i,t,4]<- 0
ps[1,i,t,5]<- 0
ps[1,i,t,6]<- 1-phi
ps[2,i,t,1]<- phi*psiB[1,t]
ps[2,i,t,2]<- phi*psiB[2,t]
ps[2,i,t,3]<- phi*psiB[3,t]
ps[2,i,t,4]<- 0
ps[2,i,t,5]<- 0
ps[2,i,t,6]<- 1-phi
ps[3,i,t,1]<- 0
ps[3,i,t,2]<- phi*psiC[2,t]
ps[3,i,t,3]<- phi*psiC[3,t]
ps[3,i,t,4]<- phi*psiC[4,t]
ps[3,i,t,5]<- 0
ps[3,i,t,6]<- 1-phi
ps[4,i,t,1]<- 0
ps[4,i,t,2]<- 0
ps[4,i,t,3]<- phi*psiD[3,t]
ps[4,i,t,4]<- phi*psiD[4,t]
ps[4,i,t,5]<- phi*psiD[5,t]
ps[4,i,t,6]<- 1-phi
ps[5,i,t,1]<- 0
ps[5,i,t,2]<- 0
ps[5,i,t,3]<- 0
ps[5,i,t,4]<- phi*psiE[4,t]
ps[5,i,t,5]<- phi*psiE[5,t]
ps[5,i,t,6]<- 1-phi
ps[6,i,t,1]<- 0
ps[6,i,t,2]<- 0
ps[6,i,t,3]<- 0
ps[6,i,t,4]<- 0
ps[6,i,t,5]<- 0
ps[6,i,t,6]<- 1
```

```
# Define probabilities of O(t) given S(t)
  po[1,i,t,1]<- pA
  po[1,i,t,2]<- 0
  po[1,i,t,3]<- 0
  po[1,i,t,4]<- 0
  po[1,i,t,5]<- 0
  po[1,i,t,6]<- 1-pA
  po[2,i,t,1]<- 0
  po[2,i,t,2]<- pB
  po[2,i,t,3]<- 0
  po[2,i,t,4]<- 0
  po[2,i,t,5]<- 0
  po[2,i,t,6]<- 1-pB
  po[3,i,t,1]<- 0
  po[3,i,t,2]<- 0
  po[3,i,t,3]<- pC
  po[3,i,t,4]<- 0
  po[3,i,t,5]<- 0
  po[3,i,t,6]<- 1-pC
  po[4,i,t,1]<- 0
  po[4,i,t,2]<- 0
  po[4,i,t,3]<- 0
  po[4,i,t,4]<- pD
  po[4,i,t,5]<- 0
  po[4,i,t,6]<- 1-pD
  po[5,i,t,1]<- 0
  po[5,i,t,2]<- 0
  po[5,i,t,3]<- 0
  po[5,i,t,4]<- 0
  po[5,i,t,5]<- pE
  po[5,i,t,6]<- 1-pE
  po[6,i,t,1]<- 0
  po[6,i,t,2]<- 0
  po[6,i,t,3]<- 0
  po[6,i,t,4]<- 0
```

```
    po[6,i,t,5]<- 0
    po[6,i,t,6]<- 1
    }
   }

# Likelihood
   for(i in 1:nind){
  # Define latent state at first capture
    z[i,f[i]]<-y[i,f[i]]
    for (t in (f[i]+1):g[i]){
    # State process: draw S(t) given S(t-1)
     z[i,t]~dcat(ps[z[i,t-1],i,t-1,])
    # Observation process: draw O(t) given S(t)
     y[i,t]~dcat(po[z[i,t],i,t-1,])
     }
    }
    }
    ",fill=TRUE)
    sink()



# Compute vector with occasion of first capture
    get.first<-function(x)min(which(x!=6))
    f<-apply(rCH,1,get.first)

# Function to create known latent states z
    known.state.ms<-function(ms,notseen){
      state<-ms
      state[state==notseen]<-NA
      for (i in 1:dim(ms)[1]){
       m<-min(which(!is.na(state[i,])))
       state[i,m]<-NA
       }
       return(state)
       }
```

```
# Function to create initial values for unknown z
    ms.init.z<-function(ch,f){
      for(i in 1:dim(ch)[1]) {ch[i,1:f[i]]<-NA}
      states<-max(ch,na.rm=TRUE)
      known.states<-1:(states-2)
      v<-which(ch==states)
      ch[-v]<-NA
      ch[v]<-sample(known.states,length(v),replace=TRUE)
      return(ch)
      }

    g<-as.vector(c(40,40,40,46,46,46))

# Bundle data
   bugs.data<-list(y=rCH, f=f, g=g, seas=seas, n.occasions=dim(rCH)[2], nind=dim(rCH)[1],
      z=known.state.ms(rCH,6))

 # Initial values
   inits<-function(){list(pA=runif(1,0,1), pB=runif(1,0,1),
      pC=runif(1,0,1),pD=runif(1,0,1),pE=runif(1,0,1),z=ms.init.z(rCH,f))}

# Parameters monitored
   parameters<-c("AnnS","pA","pB","pC","pD","pE","psiA[1,1]","psiA[1,4]",
   "psiA[1,7]","psiA[1,10]","psiA[2,1]","psiA[2,4]","psiA[2,7]","psiA[2,10]",
   "psiB[1,1]","psiB[1,4]","psiB[1,7]","psiB[1,10]","psiB[2,1]","psiB[2,4]",
   "psiB[2,7]","psiB[2,10]", "psiB[3,1]","psiB[3,4]","psiB[3,7]","psiB[3,10]",
   "psiC[2,1]","psiC[2,4]","psiC[2,7]","psiC[2,10]","psiC[3,1]","psiC[3,4]",
    "psiC[3,7]","psiC[3,10]","psiC[4,1]","psiC[4,4]","psiC[4,7]","psiC[4,10]",
    "psiD[3,1]", "psiD[3,4]","psiD[3,7]","psiD[3,10]","psiD[4,1]","psiD[4,4]",
    "psiD[4,7]","psiD[4,10]","psiD[5,1]","psiD[5,4]","psiD[5,7]","psiD[5,10]",
    "psiE[4,1]","psiE[4,4]","psiE[4,7]","psiE[4,10]", "psiE[5,1]","psiE[5,4]",
    "psiE[5,7]","psiE[5,10]")
```

```
# MCMC settings
  ni<-50000
  nt<-2
  nb<-5000
  nc<-3

# Call WinBUGS from R
  ms4<-bugs(bugs.data,inits,parameters,"msm2.txt",n.chains=nc,n.thin=nt,
      n.iter=ni,n.burnin=nb,DIC=TRUE, digits=5, debug = TRUE)
```