EFFECTS OF HURRICANE MICHAEL ON ANNUAL RECRUITMENT, MORTALITY, AND MIGRATION OF GULF STURGEON IN THE APALACHICOLA RIVER, FLORIDA

by

BRENDAN THOMAS DULA

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

ABSTRACT

Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) populations have experienced significant declines because of human activity since the early 20th century, leading to their listing as threatened in 1991. Increased hurricane activity presents an additional threat to vulnerable Gulf Sturgeon populations. In 2018, Hurricane Michael struck the Apalachicola River and caused a hypoxic event, which triggered a fish kill that included adult sturgeon. We used a variety of data sources to estimate the effect of the hurricane on Gulf Sturgeon recruitment, mortality, and migration behavior. Juvenile recruitment remained stable following the hurricane; however, apparent annual adult mortality was 4 - 5 times greater than the preceding 2 years. There was also a rapid out-migration of the surviving adults after the storm, but subsequent migrations returned to normal. These findings suggest that hurricanes pose a major threat to Gulf Sturgeon, and that an increase in hurricane frequency may threaten species recovery and population stability.

INDEX WORDS: Hurricane effects, Apalachicola River, Mark-recapture, Population estimation, Hypoxia, *Acipenser oxyrinchus desotoi*

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DEDICATION

I would like to dedicate this work to my parents for everything they have done for me throughout my life to give me the opportunity to pursue a Master's degree. They have always provided support and love to me in every path I chose, and I can never thank them enough for all they have done. I would also like to dedicate this to my brothers, Will and Matt, for their support and for helping create my interest in nature and conservation from a young age. I would especially like to dedicate this to my girlfriend Julie for her constant support making my time in graduate school as enjoyable and stress-free as possible, and for making the past year of quarantine more fun and exciting than it had any right to be. Finally, I would like to dedicate this to my in-home writing partners who provided daily support and constantly supervised my work, Ginkgo and Buster.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Species Description

Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) is a subspecies of the Atlantic Sturgeon (*A. oxyrinchus oxyrinchus*) found in the northern Gulf of Mexico (GOM). Their range extends from the Pearl River on the Louisiana-Mississippi border to the Suwannee River in Florida. They are anadromous and spawn in upriver reaches of coastal rivers (Huff 1975). Gulf Sturgeon are characterized by their large size (>2 m), ventral mouth, five rows of bony scutes, and a heterocercal tail (Gilbert 1989). There are both genetic (Ong et al. 1996) and physical differences from the Atlantic Sturgeon, with a longer spleen as the most reliable difference (Vladykov 1955). Gulf Sturgeon live about 25 - 40 years (Huff 1975, Sulak and Clugston 1999).

Spawning Location and Timing

Gulf Sturgeon is a late-maturing species, not capable of spawning until reaching a fork length of 1.2 m; females typically require 8 - 12 years to develop active gonads while males require 7 - 10 years. In both cases, spawning does not seem to occur until a few years after maturity is reached (Huff 1975, Sulak et al. 2016). Ripe adult Gulf Sturgeon reach their spawning grounds in March and April (Wooley and Crateau 1985, Marchant and Shutters 1996, Sulak and Clugston 1998, Fox et al. 2000, Heise et al. 2004, Kreiser et al. 2008, Flowers et al. 2009). Males enter rivers earlier than females, and ripe adults of either sex enter before nonspawning individuals (Carr et al. 1996, Fox et al. 2000). Their spawning locations may be >200 km upriver (Marchant and Shutters 1996, Sulak and Clugston 1998). Spawning occurs about March to mid-May when water temperatures are 17 - 24 °C in sites with surface water velocities of 0.5 - 1.5 m/s (Marchant and Shutters 1996, Sulak and Clugston 1998, Fox et al. 2000, Heise et al. 2004, Kreiser et al. 2008, Flowers et al. 2009). Benthic substrates at confirmed spawning sites have been characterized as hard, rocky, limestone outcroppings with a gravel top layer where adhesive eggs can attach (Sulak and Clugston 1998, Fox et al. 2000, Heise et al. 2004, Flowers et al. 2009). Steep banks at these locations may help create the ideal flow and substrate conditions for spawning (Fox et al. 2000).

Adult Gulf Sturgeon typically return to their natal river every spring. They may travel to neighboring rivers to spend the summer; the frequency of this behavior appears to vary depending on the conditions in the natal river system (Wooley and Crateau 1985, Stabile et al. 1996, Sulak and Clugston 1999, Parauka et al. 2011, Rudd et al. 2014). This tendency to return to their natal river annually is reflected in the haplotype diversity. Mitochondrial DNA analysis has documented that four regionally distinct genetic populations are present for Gulf Sturgeon across the eight river systems in their range (Stabile et al. 1996, Waldman et al. 2002).

There is increasing evidence of a fall spawn in September to November by a subset of the population. In the Suwannee River during the fall, acoustically tagged adults were tracked moving up to spawning grounds, ripe sturgeon were captured, and courtship abrasions were observed (Randall and Sulak 2012). In both the Suwannee and Apalachicola rivers, some captured young-of-the-year juveniles appeared smaller than the expected size range for spring-spawned fish (Randall and Sulak 2012, Marbury 2016, UGA Sturgeon Lab unpublished data). The strongest support for fall spawning came with the collection of 35 eggs between October 11 and November 4 of 2019 in the Choctawhatchee River, Florida (Fox et al. 2020, Rider et al. 2020). Genetic analyses are still needed to determine if fall-spawning individuals are opportunistically spawning in the fall or represent a distinct subpopulation.

Early Life History

Much is known about Gulf Sturgeon development from egg to juvenile fish. Egg survival is highly dependent on water temperature: maximum survival rates occur when water temperature is between 15 - 20 °C; 25 °C is the upper limit for survivability (Chapman and Carr 1995). Low and variable flows could also decrease spawning habitat availability and egg survival (Flowers et al. 2009). Newly hatched Gulf Sturgeon seek cover within the substrate at the spawning site to begin their development as free embryos (Kynard and Horgan 2002, Kynard and Parker 2004). After they emerge from the substrate and begin exogenous feeding, larvae migrate downstream; little is known about their foraging behavior, but they most likely engage in drift-feeding (Kynard and Parker 2004). Post-larval Gulf Sturgeon develop into young-of-the-year (YOY) juveniles before moving downriver to overwinter in the estuary with the older juveniles in late January or early February. Over winter, they feed on aquatic insect larvae, amphipods, grass shrimp, isopods, polychaetes, and oligochaetes (Mason and Clugston 1993, Sulak and Clugston 1999, Kynard and Parker 2004). Exactly where juvenile sturgeon overwinter within the bays and estuaries is still unknown.

Juvenile and Adult Behavior

After overwintering in the estuary, all juvenile and adult sturgeon, including the YOY, return upriver from February to April. All fish remain upriver for the duration of the summer (Chapman and Carr 1995, Carr et al. 1996, Foster and Clugston 1997, Fox et al. 2000, Marbury

2016, Hancock 2019). All Gulf Sturgeon exit the rivers during September to November, after which they then spend the winter in nearshore marine habitats (Huff 1975). This movement pattern is consistent throughout the species' range and has been observed in the Suwannee (Foster and Clugston 1997, Edwards et al. 2003), Apalachicola (Wooley and Crateau 1985, Odenkirk 1991), Choctawhatchee (Fox et al. 2000), Pascagoula (Heise et al. 2004), and Pearl (Rogillio et al. 2007) river systems.

Gulf Sturgeon aggregate in specific staging and holding sites for most of their freshwater migration and residency. These holding sites tend to be relatively deep holes or channels (Wooley and Crateau 1985, Foster and Clugston 1997, Sulak and Clugston 1999, Sulak et al. 2007). Carr et al. (1996) suggested that deep holes could create thermal refugia where Gulf Sturgeon can avoid the warmer ambient river water; however, Gulf Sturgeon in the Suwannee River did not show a preference for cool water when selecting habitat (Foster and Clugston 1997, Sulak et al. 2007). Instead, deep pools may allow Gulf Sturgeon to conserve energy by avoiding the high flow areas of the river (Wooley and Crateau 1985, Sulak et al. 2007); these pools also serve as staging areas during spring and fall migrations (Wooley and Crateau 1985, Sulak and Clugston 1999). Gulf Sturgeon migrate from rivers to nearshore marine habitats when temperatures decrease to around 21°C in the fall (Carr et al. 1996, Foster and Clugston 1997).

Adult Gulf Sturgeon primarily overwinter in feeding grounds within shallow water (2 - 7 m) bays and nearshore (1.5 - 12 km) habitats, but occasionally travel farther into the GOM, (Fox et al. 2002, Harris et al. 2005, Ross et al. 2009, Parauka et al. 2011) with detections recorded >20 km offshore (G. Alvarez, University of Georgia, personal communication). They typically forage at one location (<1 km^2) for several weeks before rapidly traveling large distances to new foraging grounds (Fox et al. 2002, Edwards et al. 2003, Ross et al. 2009, Parauka et al. 2011).

Acoustically tagged adult Gulf Sturgeon were most often detected via telemetry in areas with sand or sand and shell substrate and high concentrations of their benthic prey, (Fox et al. 2002, Harris et al. 2005, Ross et al. 2009, Parauka et al. 2011). Their main prey are nearshore, benthic, marine macroinvertebrates such as branchiopods, amphipods, polychaetes, lancelets, small mollusks, and echinoderms (Mason and Clugston 1993, Harris et al. 2005, Ross et al. 2009). The relative proportions of the different prey species in their diet are dependent on location within the GOM. Marine invertebrates comprise most of what adult Gulf Sturgeon eat, which can only be obtained during their over-wintering period in the GOM (Gu et al. 2001, Sulak et al. 2012). During their summer river residency, Gulf Sturgeon do not actively forage because of the low abundance of prey and relatively high energetic costs to foraging, which causes them to lose 4 - 15 % of their total body weight throughout the summer (Wooley and Crateau 1985, Mason and Clugston 1993, Carr et al. 1996). To compensate for summer weight loss, they must consume large quantities of prey during their marine and estuarine residency, on average gaining 20% of their body weight from when they enter the estuary (Carr et al. 1996). Juvenile Gulf Sturgeon (age 2 - 6 years) are thought to overwinter closer to shore than the adults, remaining in the brackish waters of their natal estuary (Sulak and Clugston 1999, Peterson et al. 2016).

Status of Gulf Sturgeon

Historically, Gulf Sturgeon thrived in most large GOM river systems from the Mississippi River in Louisiana to the Hillsborough River in Tampa Bay, Florida (Wooley and Crateau 1985). At the end of the 19th century, large-scale commercial fisheries for Gulf Sturgeon meat and caviar began in Florida (U.S. Commission of Fish and Fisheries 1902, Huff 1975). Overharvest caused range-wide population declines, and Gulf Sturgeon populations were extirpated from some rivers. Dams and other impediments exacerbated the problem by blocking

Gulf Sturgeon from reaching their upstream spawning grounds in many rivers, thus reducing spawning success. In 1984, Florida passed a law prohibiting the harvest of Gulf Sturgeon, and the species was officially listed as threatened under the Endangered Species Act in 1991 (Huff 1975, Federal Register 1991, USFWS and GSMFC 1995).

Today, there are seven major river systems that support spawning Gulf Sturgeon populations, but Gulf Sturgeon abundances in these river systems are often far below historic levels (USFWS and NMFS 2009, Baremore and Rosati 2013). Currently, the Suwannee River population of Gulf Sturgeon, estimated at 10,000 (age-1+) individuals in 2004, is considered to be the largest (USFWS and NMFS 2009). In contrast, the Apalachicola River, which may have historically contained the largest population of Gulf Sturgeon, sustains a much smaller population of ≤2,000 (age-1+) individuals, as of a 2005 estimate (USFWS and NMFS 2009).

Challenges to Conservation

Habitat loss is one of the main barriers to Gulf Sturgeon recovery. Dams, in addition to blocking access to historic spawning grounds in many systems, can negatively affect downstream spawning habitat. Reduced and variable flows caused by dams can harm recruitment by reducing the available spawning habitat and lowering egg and larval survival through increased sedimentation and decreased dissolved oxygen (Fox et al. 2000, Flowers et al. 2009). Across the Gulf Sturgeon's range, accessible habitat has been reduced by more than 75% in many rivers. In the Apalachicola River, the Jim Woodruff Lock and Dam (JWLD), constructed in 1957, blocks 78% of the historic range of sturgeon within the Apalachicola-Chattahoochee-Flint (ACF) river system (USFWS and GSMFC 1995). Much of this is suitable spawning habitat (Kaeser et al. 2012) and was likely the historic spawning grounds within the system. Despite the ban on fishing for Gulf Sturgeon for over 30 years, many populations, including in the

Apalachicola River, have not rebounded; the reduction of available spawning grounds may be limiting recovery (Ahrens and Pine 2014). Full recovery may require the removal of dams or creation of passages (e.g., fish ladders) to allow sturgeon to migrate past the dams to reach historic spawning grounds. Trap and transfer of adult Gulf Sturgeon above dams to allow them to access their historic range has been tested within the ACF river system with limited success but could cause individuals to become trapped above the dams (Marbury et al. 2021). Artificial reefs that mimic the substrate necessary for spawning may mitigate some of the effects of dams by creating new spawning habitats downstream of the dams (Bouckaert et al. 2014). Changing flow regimes from dams to match run-of-the-river flows has restored downstream spawning grounds and increased recruitment in Lake Sturgeon (*Acipenser fulvescens*) (Auer 1996, Haxon et al. 2015) and may be a useful tool for Gulf Sturgeon recovery. Restoration of spawning grounds by creating access to historic upriver sites or improving the quality of currently available sites may be crucial to recovery of Gulf Sturgeon.

Habitat degradation and accidental mortalities from human activities also pose a threat to Gulf Sturgeon. Human development, water use, dredging, and agricultural activities can alter substrate composition, riverbed shape, and water quality within rivers and bays, potentially reducing the amount of suitable habitat for sturgeon spawning and foraging (USFWS and GSMFC 1995, USFWS and NMFS 2009). Increasing aquatic contaminants may be negatively affecting Gulf Sturgeon (Berg 2006). Boat strikes, dredging activities, and bycatch have all directly contributed to Gulf Sturgeon mortality, and mortalities have also been reported within the Gulf of Mexico following toxic algal bloom events caused by anthropogenic eutrophication (USFWS and NMFS 2009).

Threat from Hurricanes

Natural events such as hurricanes can affect fish assemblages directly and indirectly. Although the immediate effects of hurricanes (e.g., strong storm surges) on fish communities are not well understood, the effects of natural processes triggered by hurricanes are well-documented. Decreased dissolved oxygen (DO) caused by organic materials washed into a river by a hurricane can kill or displace fish (Mallin et al. 2002, Mallin and Corbett 2006, Stevens et al. 2006, van Vrancken and O'Connell 2010). The likelihood and intensity of hypoxic events depends on a variety of factors, including land use in the location of landfall, the storm's trajectory after landfall, damage to the power grid, and time of year (Mallin and Corbett 2006). The largest decreases in DO are caused by hurricanes that make landfall in areas with large amounts of potential human or animal waste contamination and follow a path through the upper watershed (Mallin et al. 1999, Mallin and Corbett 2006). Damage to infrastructure and power loss can increase the amount of organic waste that leaks into river and prolong the time required to make repairs to stop leakage (Mallin and Corbett 2006). The effects of low DO are most prominent within the lower freshwater reaches and river mouth because of the influx of organic debris collecting and decomposing. Gulf Sturgeon's reliance on Gulf Coast rivers during most of the hurricane season (June 1– November 30) puts them at potential risk from hurricanes (Mallin and Corbett 2006, Stevens et al. 2006, van Vrancken and O'Connell 2010, Lewis et al. 2011).

From 1995 to 2013, there was an increase in tropical storm activity in the southeast United States. This increased activity may be explained by natural variations with historic periods of high and low activity (Burn and Palmer 2015, Klotzbach et al. 2015); however, some weather models cannot explain the increased activity by natural variation alone (Smith et al. 2010). As global temperatures continue to rise, the possibility for hurricane activity increases, and current weather forecast models predict a possible decrease in overall tropical storm activity but a 2- to 7-fold increase in strong (category 3 or higher) hurricanes in the coming decades (Bender et al. 2010, Grinsted et al. 2013, Knutson et al. 2013). The area most affected by these stronger storms will be the western Atlantic Ocean above 20°N latitude, which includes the Gulf coast of the United States (Bender et al. 2010).

Population Estimation Techniques

Accurately estimating abundance of fish populations has long been a goal of fisheries managers. Many approaches, each with their own advantages and disadvantages, have been used to estimate population abundance. Some of the most common sampling techniques are depletion, genetic, point or transect counts, and capture-mark-recapture (CMR).

Removal or depletion sampling involves capturing fish and removing them from the population over multiple occasions and using the intercept of the depletion trend line to determine initial abundance. This technique has its origins in using fisheries harvest and catch-per-unit-effort data to calculate population size (DeLury 1947). The two mathematical approaches to obtaining an estimate from removal sampling data are linear regression analysis (Hayne 1949) and maximum likelihood estimation (Zippin 1956, Carle and Strub 1978). A large proportion of the population needs to be captured for either technique to give accurate estimates (Zippin 1956), and field comparison studies have found removal sampling to be more biased and inaccurate than CMR sampling (Peterson and Cederholm 1984, Rosenberger and Dunham 2005). In cases where time or resources are limited or removal was already occurring for other purposes, such as commercial harvest (Young et al. 2004), this technique can still be used to provide relatively accurate population estimates

Use of genetic analyses in population monitoring can provide information about population size that was previously difficult or impossible to attain (Schwartz et al. 2006). Much of the work on population abundance focuses on estimating the effective population size (N_e), which is the size of an ideal population that would undergo the same amount of genetic change as the real population. Although N_e can be orders of magnitude smaller than some marine population sizes, dramatic declines in populations can still be reflected in shrinking N_e (Hare et al. 2011, Ruggeri et al. 2016). Some populations' abundances may be more closely linked to N_e and annual changes in abundance will be reflected in the N_e (Ovenden et al. 2016). Genetics can also be used in mark-recapture type studies where juveniles can be assigned to previously captured parents as a recapture and produce accurate spawning abundance estimates (Rawding et al. 2014). Full population abundance estimates are more difficult using genetics alone.

Point and transect counts are becoming an increasingly viable means of estimating fish abundance with advancing technology. SCUBA divers and underwater cameras have been used in reef ecosystems for decades (Bohnsack and Bannerot 1986, Ellis and DeMartini 1995). Fish behavior plays a large role in determining the best technique to accurately estimate abundance (Samoilys and Carlos 2000, Colvocoresses and Acosta 2007). With high-definition video now widely available and affordable for underwater use, stationary cameras are being used increasingly because of their cost effectiveness and ability to be used in a wide range of conditions. Stationary cameras detect fewer species but comparable abundance and diversity compared to transect counts (Pelletier et al. 2011). Using variable abundance indices and detection probability, population size can be estimates from multiple repeated counts (Royle and Nichols 2003). A new type of transect count being used in riverine environments employs side-scan sonar to observe individual fish. N-mixture modeling of the detection data has been used to get adult abundance estimates of Atlantic Sturgeon (Flowers and Hightower 2015, Vine et al. 2019). This technique is limited to counting species and individuals that can be accurately distinguished from neighboring fishes.

The most common technique for estimating population size is CMR sampling. Peterson (1896) and Lincoln (1930) first introduced the premise of capturing individuals, marking them, and then using the recapture rate of marked individuals to estimate the size of the population. The formula used with such data is called the Lincoln – Peterson model. Schnabel (1938) modified the model to allow for multiple recapture events and Chapman (1951) further modified this model to reduce its bias when dealing with small populations. All these models share the assumptions that the populations are closed (no immigration, emigration, births, or deaths) during sampling, all individuals have the same probability of being captured, marks are maintained by the individual and not overlooked by the reader, and marked individuals mix randomly into the rest of the population. As natural populations do not follow these assumptions, especially for long sampling periods, new models have been introduced to help account for violation of these assumptions when estimating abundance. One example is the Huggins closed capture model, which allows for the capture probability to vary based on individual heterogeneity and previous capture history (Huggins 1989, Huggins 1991). These models can be very accurate when sampling closed populations but lose effectiveness when dealing with open populations and years of data.

Open population CMR models allow for abundance estimation of populations, but they don’t have assumptions about population closures; they also allow for the estimation other useful population parameters (e.g., recruitment). The Cormack-Jolly-Seber model can provide apparent annual survival and abundance estimates for a population sampled over multiple years (Cormack

1964, Jolly 1965, Seber 1965). Recruitment and growth rate can also be estimated from open population models through inverting capture probabilities to determine the probability that individuals were part of the population at previous capture events (Pradel 1996).

Robust models combine both closed and open capture-mark-recapture models to estimate population parameters. This approach uses closed population models to estimate within-year abundance estimates and open population models to estimate between-year population parameters (Pollock 1982). If the assumptions of closure are met during an annual sampling season, then robust models can provide more accurate annual population estimates from closed population models, while still using open population models to estimate inter-annual population parameters.

Research Needs

Understanding the dynamics and trajectories for all Gulf Sturgeon populations within the GOM will require monitoring, which is also legally required under the Endangered Species Act to determine the effectiveness of conservation efforts. One of the recovery goals identified for Gulf Sturgeon is achieving populations that are self-sustaining over a 12-year period (USFWS and GSMFC 1995). Annual abundance estimates for each river will be critical when assessing population trends throughout their range and will allow for assessments following mass mortality events. Continued monitoring following any mortality event will help determine the annual maximum growth rate for Gulf Sturgeon populations and estimate how long recovery may take.

Historically, most population assessments included only adults (USFWS and NMFS 2009), and there is sparse information on juvenile populations because recruitment has only been estimated from open-population models on the adult populations (Pine and Martell 2009). Gulf

Sturgeon population growth is highly vulnerable to increased mortality during early egg to age-1 life stages (Pine et al. 2001, Tate and Allen 2002) and even small increases in mortality rate can cause decreased population growth and eventual population declines (Pine et al. 2001, Gross et al. 2002, Tate and Allen 2002). By estimating the age-1 population (i.e., recruitment), researchers and managers can quickly detect changes to the juvenile population as they occur, instead of waiting 8 - 12 years for those changes to be reflected in the adult population (Peterson et al. 2000, Schueller and Peterson 2010). This technique has been used to successfully quantify annual recruitment in the Apalachicola River by Marbury (2016) and Hancock (2019); those authors found annual recruitment of 22 - 210 age-1 individuals per year over a 6-year period. Continued long-term monitoring of this population will allow for analysis of the effects of environmental factors (e.g., temperature, flow duration and variability) on changes in recruitment. Monitoring annual recruitment could serve as a useful tool for comparing population health among rivers. Because of the seasonal migratory behavior of Gulf Sturgeon, all juveniles return to their natal river every summer. Therefore, juvenile survival can be calculated based on repeated abundance estimates of the same cohort (i.e., cohort size at age 1 and then at age 2); the 2009 Gulf Sturgeon Recovery Plan Update identified investigations of recruitment and juvenile mortality as critical areas of research (USFWS and NMFS 2009).

There is increasing interest in the role hurricane activity may play in shaping Gulf Sturgeon recovery. Hurricanes were not mentioned in the Gulf Sturgeon Recovery/Management Plan laid out in 1995 (USFWS and GSMFC 1995), but recent studies have noted the potential for hurricanes to cause large-scale Gulf Sturgeon mortality (Havrylkoff 2010, Rudd et al. 2014, Ahrens and Pine 2014, Sulak et al. 2016). Following Hurricane Ivan in 2004 and Hurricane Katrina in 2005, dead Gulf Sturgeon were reported among the fish kills (Havrylkoff 2010).

Although many sturgeon are believed to have died as a result of the storms, little quantitative or demographic data were available for those populations before or after the storms (USFWS and NFMS 2009). A detailed assessment of a Gulf Sturgeon population's response to a hurricane still does not exist.

In October 2018, Hurricane Michael, made landfall as a category 5 hurricane just west of the Apalachicola River. The storm traveled upriver along the ACF system and north into Georgia. Immediately following the storm, the Apalachicola River experienced a hypoxic event and a fish kill in which dead adult sturgeon were observed (A. Strickland, FWC, personal communication); the full effects of the storm on the Apalachicola Gulf Sturgeon population are not yet known. Prior to the hurricane, the University of Georgia and United States Fish and Wildlife Service were conducting a long-term Gulf Sturgeon population monitoring study, which allowed us to compare hurricane effects to recent baseline data. Using a combination of mark-recapture, side-scan sonar, and acoustic telemetry data, we estimated annual Gulf Sturgeon recruitment, adult mortality, and examined adult migration behavior in the Apalachicola and Brothers rivers before and after the hurricane. This provided a unique opportunity to study how a hurricane may affect Gulf Sturgeon populations, which will help determine their vulnerability to predicted future increased hurricane activity.

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CHAPTER 2

EFFECTS OF HURRICANE MICHAEL ON ANNUAL RECRUITMENT, MORTALITY, AND MIGRATION OF GULF STURGEON IN THE APALACHICOLA RIVER, FLORIDA[1]

[1]B.D. Dula, A.J. Kaeser, C.A. Jennings, and A.G. Fox. To be submitted to *Transactions of the American Fisheries Society*.

Abstract

Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) populations have undergone significant declines since the start of the 20th century because of overfishing and habitat loss. A predicted increase in frequency and severity of hurricanes, driven by climate change, presents an additional but poorly-understood threat to vulnerable Gulf Sturgeon populations. In October 2018, Hurricane Michael made landfall 50 km west of the Apalachicola River in the Florida Panhandle, causing a hypoxic event and an ensuing fish kill that included adult sturgeon. Because the storm occurred in the middle of a long-term study of the Apalachicola River Gulf Sturgeon population, we were able to assess the effects of Hurricane Michael by comparing population metrics in 2018 to non-hurricane years. Using mark-recapture, side-scan sonar, and acoustic telemetry data we estimated Gulf Sturgeon annual recruitment and apparent adult mortality and examined adult migration behavior in the Apalachicola River system following the hurricane. Juvenile recruitment for the 2018 cohort was greater than five of the previous six years, indicating the hurricane did not cause a year class failure. However, apparent annual mortality for adult Gulf Sturgeon in 2018 (0.44) was 4 - 5 times greater than the preceding 2 years. Within days of Hurricane Michaels' landfall, there was an early and rapid out-migration of the surviving tagged adults, which coincided with a major hypoxic event. One year after Hurricane Michael, estimated recruitment was still high compared to previous years, and apparent adult mortality and migration behavior returned to normal. These findings suggest that hurricanes pose a major threat to adult Gulf Sturgeon, and that an increase in hurricane frequency may threaten species recovery and population stability. However, strong recruitment following the hurricane might provide the potential for recovery from these adult mass-mortality events.

Introduction

Gulf Sturgeon (*Acipenser oxyrinchus desotoi*, Vladykov 1955) is a subspecies of the Atlantic Sturgeon (*A. oxyrinchus oxyrinchus*) that is found only in the northern Gulf of Mexico (GOM) from the Pearl River on the Louisiana-Mississippi border to the Suwannee River in Florida. They are an anadromous species that does not spawn every year; however, an entire population enters its natal river in the spring regardless of spawning condition (Huff 1975). Historically, Gulf Sturgeon thrived in most GOM river systems (Huff 1975, Wooley and Crateau 1985), but at the end of the 19th century, large-scale commercial fisheries for Gulf Sturgeon meat and caviar began in Florida (U.S. Commission of Fish and Fisheries 1902, Huff 1975). Overharvest caused range-wide population declines, and Gulf Sturgeon populations were extirpated from some rivers. Dams and other impediments further contributed to the decline by preventing Gulf Sturgeon from reaching their upstream spawning grounds, thus reducing spawning success. These factors eventually led to a 1984 harvest moratorium in Florida and a threatened listing under the Endangered Species Act in 1991 (Huff 1975, Federal Register 1991, USFWS and GSMFC 1995).

Natural events like hurricanes can affect fish assemblages directly and indirectly. Although the immediate effects of hurricanes (e.g., strong storm surges) on fish communities are not well understood, the effects of other natural processes triggered by hurricanes are well-documented. Decreased dissolved oxygen (DO) events following a hurricane are the largest threat to fish populations as they can kill or displace fish (Mallin et al. 2002, Mallin and Corbett 2006, Stevens et al. 2006, van Vrancken and O’Connell 2010). The likelihood and intensity of these hypoxic events depends on the increase in biological oxygen demand caused by the influx of organic materials washed into the river. This is affected by a variety of factors including strength of the storm, land use at the location of landfall, the storm's trajectory after landfall, damage to the power grid, and time of year (Mallin and Corbett 2006). Densely populated areas, farmland, and blackwater swamps have the potential for releasing large amounts of organic debris; thus, a hurricane making landfall in those areas is likely to cause hypoxic events in the surrounding rivers (Mallin et al. 1999, Mallin and Corbett 2006). Damage to infrastructure and power outages can also increase the amount of organic waste that leaks into a river and prolong the time required to make repairs and prevent further leakage (Mallin and Corbett 2006). The effects of low DO are most prominent within the lower freshwater reaches and river mouth because of the influx of organic debris that collects and decomposes there. Gulf Sturgeons' reliance on Gulf coast rivers and estuaries puts them at potential risk from hurricanes (Mallin and Corbett 2006, Stevens et al. 2006, van Vrancken and O'Connell 2010, Lewis et al. 2011).

Because of the predicted rise in hurricane activity and storm strength over the coming century (Bender et al. 2010, Grinsted et al. 2013, Knutson et al. 2013), determining the vulnerability of Gulf Sturgeon populations to the negative effects of hurricanes has become increasingly important. In October 2018, Hurricane Michael made landfall as a category 5 hurricane in the Florida Panhandle, just west of the Apalachicola River (Figure 2.1). The storm's track carried it north into Georgia, moving upriver along the Apalachicola-Chattahoochee-Flint (ACF) river system. Immediately following the storm, the Apalachicola River experienced a hypoxic event and a fish kill in which dead adult sturgeon were observed (A. Strickland, FWC, personal communication). Because Hurricane Michael occurred during the 7th year of a long-term recruitment and telemetry study, there was a unique opportunity to study how a hurricane may affect annual recruitment, mortality, and migration behavior. Therefore, the objectives of this study were to determine the effects of Hurricane Michael on recruitment, mortality, and behavior of Gulf Sturgeon within the Apalachicola River.

Methods

Study System

The Apalachicola River is the largest river in Florida by discharge, with a mean daily discharge of 555 m^3/s (Couch et al. 1996). It flows 171 km from the Jim Woodruff Lock and Dam to Apalachicola Bay and the Gulf of Mexico. The dam was constructed at the confluence of the Chattahoochee and Flint rivers in 1957 and formed Lake Seminole. The three rivers and their watersheds together comprise the ACF River Basin, which encompasses over 4.85 million hectares of land (Ruhl 2005). The dam blocks Gulf sturgeon from accessing 78% of their historic range in the ACF system (USFWS and GSMFC 1995). The Brothers River is a coastal plain tributary of the Apalachicola River that flows into the Apalachicola River at river kilometer (rkm; as measured from the mouth) 19 and is a known site in which juvenile and adult Gulf Sturgeon congregate during their freshwater residency (Wooley and Crateau 1985, Marbury 2016, Hancock 2019).

Environmental Data

The United States Geological Survey (USGS) streamgage stations on the Apalachicola River in Sumatra, Florida (USGS 02359170, rkm 33) and Chattahoochee, Florida (USGS 02358000, rkm 170) were used to obtain river discharge, water temperature, and dissolved oxygen data. These are the two stream gages within the Apalachicola river, and the gage at rkm 33 is just north of our netting locations. The Apalachicola National Estuarine Research Reserve has five water quality stations throughout the Apalachicola River estuary and Apalachicola Bay.

Only two of the stations remained operational through Hurricane Michael, and of those the station in the Little St. Marks River (APALMWQ, LSM rkm 4), a distributary of the Apalachicola River, was also used to obtain dissolved oxygen data.

Recruitment Estimation

From 2013-2018, the University of Georgia and U.S. Fish and Wildlife Service monitored annual recruitment of Gulf Sturgeon in the Apalachicola River (Marbury 2016, Hancock 2019); we continued to collect recruitment data in 2019-2020. We sampled for sturgeon 3 to 5 days per week from May through August with occasional sampling events in September and October of each year. The sites we fished were within the Brothers River (Figure 2.1), as well as just downstream of Jim Woodruff Lock and Dam, which is another known juvenile holding site. Our study design also included intermittent sampling in the mainstem of the Apalachicola River to ensure we did not miss any juvenile sturgeon congregations. We used bottom-anchored gill nets (45.7 x 3.0 m) consisting of three randomly-ordered 15.2 m panels of 7.6, 8.9, and 10.2 cm stretch monofilament mesh to capture juvenile sturgeon. We used a YSI® Pro 2030 (Yellow Springs Instruments, Yellow Springs, OH, USA) to ensure water temperature and dissolved oxygen were within allowable range for netting at each site. The nets soaked for up to 2 hours in deep channels within the river before retrieval.

Captured sturgeon were placed into a floating net pen (approximately 1.2 x 0.8-meter) attached to the boat. Each fish was weighed, measured for total length (TL) and fork length (FL), and inspected for external tags and passive integrated transponder (PIT) tags. If a PIT tag was not present, one was injected into the muscle tissue beneath the dorsal fin. All fish were released back into the river at the site of their capture. We used length frequency analysis (based on Schuller and Peterson 2010) to estimate fish age based on length, and fin ray aging data from

2013 to 2018 (Marbury 2016, Moran 2018, Hancock 2019); Apalachicola River sturgeon with fork lengths of 370 – 530 mm were considered to be age 1.

We used R-software (R Core Team 2020) to create daily capture histories of PIT tagged individuals and used the Huggins closed capture model (Huggins 1989, Huggins 1991) within the RMark package (Laake 2013) to estimate the annual abundance of each age-1 juvenile cohort. This method has been used as a measure of annual recruitment for several sturgeon species (Bahr and Peterson 2016, Bahr and Peterson 2017, Hancock 2019). Using individual age (M_a) and capture occasion (M_t) as covariates, we created a candidate series of individual covariate and covariate-interaction models. We then used Akaike Information Criterion (AIC) (Akaike 1973) to determine our confidence models and weight for averaging.

Adult Mortality Estimation

We used side-scan sonar techniques described in Kaeser and Litts (2010) to estimate annual adult abundance sturgeon within index reaches in the Apalachicola and Brothers rivers. Humminbird® 900 and 1100 Series Side Imaging units with frequency set to 455 kHz and a range of 25.6 to 29.0 m to each side were used to scan known holding areas as part of an annual index count that began in 2012. There were 10 index reaches scanned within the river system that summed to a total of 44 rkm scanned. The data were processed in SonarTRX software (Leraand Engineering, Honolulu, Hawaii) into rectified images that were compiled in ArcGIS (v 10.7, Environmental Systems Research Institute [ESRI], Redlands, CA, USA) to display as a seamless mosaic. These mosaics were then visually inspected by a single counter at close range (1:200 scale) to identify targets as adult Gulf Sturgeon based on size, shape, position in the water column, and relationship to surroundings. Single-pass surveys with a single boat were conducted in 2012 and 2014-2016 to generate index counts, and triple-pass surveys were conducted in 2018 (prior to Hurricane Michael) and 2019. For the triple-pass surveys, three boats – following each other 0.5km apart – scanned the same index reaches and the three counts were averaged to calculate the number of adult sturgeon within all of the index reaches of the rivers. The surveys were conducted in the early fall (August or September, with the 2014 scan occurring in late July) of each year and in the same index reaches. Hurricane Sally prevented a triple-pass survey in the fall of 2020 because it caused an early outmigration of adult sturgeon before the scan was conducted.

Since 2011, U.S. Fish and Wildlife Service (USFWS) monitoring projects have tagged adult Gulf Sturgeon in the Apalachicola River with acoustic transmitters. These fish were captured with 45.7 x 3.0 m nets with 25.4 cm stretch monofilament mesh using the same technique outlined for juvenile sampling, although much of the sampling occurred during September and October. To implant the acoustic tag (Vemco® V-16, Vemco, Bedford, NS, Canada; lifespan ~10 years, 69 kHz, 16 x 68 mm, 24 g in air), each captured adult sturgeon was placed into a continuously irrigated live-well, an approximately 2-cm incision was made just beside the ventral line, and the tag was then inserted. The incision was closed with 2/0 absorbable monocryl suture (Monoswift™ L943) in a single interrupted pattern (Boone et al. 2013). At the time of Hurricane Michael’s landfall, more than 50 sturgeon with active transmitters were present in the Apalachicola River system.

To monitor post-release movements of tagged fish, an array of 24-27 stationary acoustic receivers (Vemco® VR2W) was deployed during 2016 within the Brothers River, throughout the lower reaches of the Apalachicola River, and into Apalachicola Bay (Figure 2.1). The receivers were attached with 0.32 cm stainless steel cable to trees and other stationary structures in the river and bay. The array was serviced and data were downloaded every 3 months throughout its deployment within the river. Acoustic detection data for Apalachicola River sturgeon also were obtained from receiver arrays in neighboring rivers via the iTAG Network and the Gulf Sturgeon Database.

These telemetry data provided an additional way to investigate adult mortality. The acoustic data were processed using Vemco VUE software and analyzed in R-software. An individual was considered an apparent mortality under two circumstances: 1) the individual was detected entering the river in the spring but not detected leaving in the fall; 2) the individual was detected leaving in the fall but not detected entering any array in the spring.

Fish Behavior

We used the array of acoustic receivers at the mouth of the Apalachicola River and the other distributaries that drain into Apalachicola Bay to monitor the timing of migrations and the rate of return for tagged adult fish (Figure 2.1). For each acoustically tagged individual, we recorded the day of first detection on the array in the spring (during in-migration) and fall (during out-migration). We compared the day of spring arrival and fall departure in three treatment groups: before the hurricane (fall 2016 – spring 2018), first migration after the hurricane (fall 2018 and spring 2019), and one year after the hurricane (fall 2019 and spring 2020). To test for normality, we used a Shapiro-Wilk W test (Shapiro and Wilk 1968). Day of departure was not normally distributed ($W = 0.925$, $p = <0.001$), so we used a Kruskal-Wallis test to compare day of arrival and departure (Kruskal and Wallis 1952). We used Dunn's test with Bonferroni adjustments (Dunn 1964) for post hoc comparisons across the three groups. To determine the annual return rate, we calculated the percentage of acoustically tagged adult sturgeon that spent the summer within the Apalachicola River between subsequent years. Apparent mortalities were removed before calculating return rate.

Results

During 2019 and 2020, we set 1082 gill nets for a total of 1004.9 net hours. We captured a total of 508 Gulf Sturgeon, including 125 recaptures, with sizes ranging from 264 to 2105 mm FL. Of the captured sturgeon, 126 were age-1 and 58 were age-2 juveniles (Table 2.1) as determined by their FL. In 2019, we observed 17 fish that were below the minimum expected summer size for an age-1 fish.

Environmental Data

The dissolved oxygen in the lower Apalachicola River (rkm 33) and estuary (LSM rkm 4) dropped to hypoxic conditions (< 2 mg/l) within 52 hours of Hurricane Michael's landfall. Conditions became anoxic (< 0.5 mg/l) within four days and remained that way for 21 days (Figure 2.3). The river reach immediately below JWLD (rkm 170) did not experience hypoxic conditions during or after the storm.

Recruitment Estimation

During the two years we sampled, estimated abundance of age-1 recruits ranged from 103 (95% CI: 87 – 132) in 2019 to 122 (95% CI: 88 – 189) in 2020 (Figure 2.2). The top model was the additive model of time and age (M_{t+a}) in 2019 and the interactive model of time and age (M_{t*a}) in 2020. Both models held >95% of the weight in each year and were the only models used to estimate recruitment. In addition to age-1 cohort size, our models also reported the abundance of other cohorts. The age-2 population for 2019 could not be estimated because only 5 individuals were caught during the sampling season. In 2020, we estimated 124 (95% CI: 90 – 193) age-2 individuals (531 – 709 mm FL). In 2019, the estimated abundance of sturgeon <370 mm FL was 39 (95% CI: 24 – 89).

Adult Mortality Estimation

There were many reports of dead adult sturgeon within the Apalachicola River following Hurricane Michael. Florida Fish and Wildlife Conservation Commission (FWC) officers and biologists surveyed the Apalachicola by boat and observed 50 to 100 dead Gulf Sturgeon among the fish kills (Lt. S. Cook, FWC, personal communication) and positively confirmed at least 10 dead adult sturgeon during their biological investigation 10 days post-storm (A. Strickland, FWC, personal communication). Unfortunately, FWC personnel were unable to collect any physical or tag data on these mortalities because of the advanced stage of decomposition.

Both side-scan sonar index counts and telemetry data indicate an increase in adult sturgeon mortality in 2018 compared to other study years. Prior to the storm, side-scan-sonar index counts were between 523 and 762 adult (>90-cm FL) sturgeon. In 2019, after Hurricane Michael, we observed only 241 (SD ± 12) sturgeon (Figure 2.4). In non-storm years, the mean (± SD) annual rate of change to the index count between two sequential years was -0.020 ± 0.205. Between the pre-storm 2018 count and the post-storm 2019 count, we saw a 0.607 reduction in sturgeon abundance. Based on acoustic telemetry, the mean apparent annual adult mortality for non-hurricane years was 0.07 ± 0.04 (range: 0.03 – 0.11; Table 2.1). In 2018, the year of Hurricane Michael, we observed an apparent annual mortality of 0.44. There was never a case of a detection on an array or recapture in a net by an individual that we had previously classified as apparent mortality.

Monitoring Behavior

From 2016 to 2020, adult Gulf Sturgeon entered the river in the spring between February 12 - May 12 and exited in the fall between August 15 - December 25. Fish that were classified as apparent mortalities had a mean of 252 detections per year (± 361, SD), whereas fish that were confirmed survivors had 8,642 ± SD 7,853 per year (Table 2.2). All tagged sturgeon that survived the hurricane were detected exiting the river between 32 - 55 hours after the storm made landfall. Median day of spring arrival occurred between March 26 – April 1 and median day of departure between occurred between October 12 – October 28 (Figure 2.5). Across all groups, differences in annual day of arrival to the river was not significantly different (H = 0.289, df = 2, $p = 0.865$). There was a significant difference among day of departure (H = 28.899, df = 2, $p < 0.001$), with the year of Hurricane Michael differing from both the years prior ($p < 0.001$) and the year after (p < 0.001). No difference was seen between the years 2016-2017 and 2019 ($p = 0.488$). The rate adult sturgeon returned to the river between subsequent years from 2016-2020 was 0.80 to 0.94 (Table 2.3).

Discussion

This study was able to successfully quantify some negative and apparent positive effects of a major hurricane on a Gulf Sturgeon population thanks to ongoing long-term monitoring in the Apalachicola River. The record of recruitment and other data prior to Hurricane Michael provided a baseline to which the effects of the storm could be compared. To our knowledge, this was the first study to quantitatively measure the effects of a hurricane on a sturgeon population.

Recruitment

In the summer following Hurricane Michael, we observed and estimated a strong age-1 year class, which indicates those young-of- year (YOY) fish were able to survive the storm and the resulting hypoxic event. Although the hurricane did not cause a year class failure, we cannot be sure that recruitment was unaffected by the storm. Sturgeon populations are highly vulnerable to increased mortality in egg to age-1 life stages (Gross et al. 2002, Tate and Allen 2002), and exposure over 10 days to high water temperature (26 °C) and low dissolved oxygen (3 mg/L) in a lab setting is lethal (0% to 50% survival) to YOY Atlantic Sturgeon (Secor and Gunderson 1998). The hypoxia and anoxia caused by Hurricane Michael may have increased juvenile mortality within a juvenile cohort that was initially substantially larger. Although we have no information about the behavior of the juvenile sturgeon in the river when the hurricane made landfall, they may have been widely distributed throughout the river (Kynard and Parker 2004), including reaches where hypoxia did not occur. Juvenile sturgeon in another river, without that oxygenated refuge, may not have fared as well.

The effects of a hurricane on recruitment have been documented in several species. We observed that Gulf Sturgeon recruitment in 2019 was within the range of previous estimates but was greater than five of the previous six years (Marbury 2016, Hancock 2019) (Figure 2.2). Hurricanes have increased young-of-year (YOY) abundance in the estuarine, fall-spawning Atlantic Croaker (*Micropogonias undulatus*), but this increase did not translate to increased age-1 recruitment the following year (Knott and Martore 1991, Houde et al. 2005, Montane and Austin 2005). Abundance of YOY also increased post-hurricane in anadromous species such as the Striped Bass (*Morone saxatilis*) and White Perch (*M. americana*), but because those species spawn in the spring, spawning did not coincide with when the hurricane struck. Increased spring river discharge – not caused by the hurricane – was the probable cause for this increase (Houde et al. 2005). Increased spring flows may also benefit spring-spawned juvenile Gulf Sturgeon by increasing available spawning habitat (Flowers et al. 2009). Increased fall flows resulting from Hurricane Michael may have potentially allowed juveniles to access additional foraging habitats by expanding the low salinity areas present in the estuary (Randall and Sulak 2007), but the storm-associated hypoxia would likely have prevented any YOY in the river from reaching the estuary. However, there is evidence of fall-spawning Gulf Sturgeon in the nearby Choctawhatchee River in Florida (Fox et al. 2020, Rider et al. 2020), and the conditions created following the storm in mid-October may have supported a fall spawn or facilitated survival of fall-spawned eggs and larval fish. Our capture of 17 fish in 2019 that were between 264 – 344 mm FL, smaller than the typical age-1 size, suggests that a fall spawn may have occurred in 2018 – these fish may have been 6 months younger than the "normal," spring-spawned age-1 juveniles. Only 9 juveniles less than 370 mm FL had ever previously been reported in the Apalachicola River system (Kirk et al. 2010, Marbury 2016). Three of these were <120 mm FL, which suggests they were recent spring-spawned fish (Kirk et al. 2010). If these fish do represent fall-spawned YOY, this suggests that fall spawning does not occur regularly. Although none of our acoustically tagged adult fish remained in the river after the storm, this should not be seen as evidence against a fall spawn. Spawning could have occurred in September (prior to Hurricane Michael) – as has been observed in some Atlantic Sturgeon (Smith et al. 2015) – however, water temperatures were above the upper limit of egg and larval survivability (25 °C) (Chapman and Carr 1995) until after the hurricane. Also, only non-tagged fish that were missed in our current sampling design may have engaged in fall spawning. If a fall spawn did occur in 2018, the estimated 39 (95% CI: 24 – 88) YOY individuals captured in 2019 would account for about one-third of Apalachicola River recruitment in 2020.

Adult Mortality

Adult Gulf Sturgeon mass mortality events have been documented in the wake of both Hurricane Ivan (F. Paruaka, USFWS, personal communication) and Hurricane Katrina (Peterson et al. 2008) that made landfall along the Gulf coast. The most likely cause for the increased mortality is the hypoxic events that follow major hurricanes, as sturgeon seem to be highly vulnerable to low DO (Secor and Niklitschek 2001). In the Pascagoula River, annual catch of adult sturgeon dropped from 42 fish from 1998-2003 to only 4 fish in the 2 years following hurricanes Rita and Katrina in 2005 (Havrylkoff 2010). However, intensive monitoring efforts necessary to assess the full effects of these hurricanes were not in place prior to any of those storms. In the Apalachicola River, we know that Hurricane Michael caused a major kill of adult sturgeon, and we were able to quantify the resulting mortality via the SSS index surveys and acoustic telemetry data.

Prior to Hurricane Michael, our index counts of adult sturgeon remained relatively stable between annual counts, supporting the hypothesis that the Apalachicola River population is stable or slightly increasing (Wooley and Crateau 1985, Zehfuss et al. 1999, Pine and Martell 2009). The dramatic decline (-0.607) of sturgeon in the index reaches the year after Hurricane Michael was almost double the previous greatest change between two subsequent years (Figure 2.4). After the storm, adult sturgeon that left the Apalachicola River may have moved to neighboring rivers rather than returning to the Apalachicola River, and such “relocations” could be one potential explanation for the post-hurricane reduction of sturgeon abundance in our index counts. However, this seems unlikely, as 92% of adults confirmed to have survived the storm returned to the Apalachicola in 2019 (Table 2.3). There were only 2 fish that did not return following the storm; in 2019, one was detected in the Choctawhatchee River and the other was detected in the Suwannee River. Another possible explanation for the reduction of fish in the index count is that the hurricane physically altered the river and caused a shift in holding areas within the Apalachicola and Brothers rivers; in this scenario, our regular sampling might have missed fish. However, we did not see evidence for this. We were able to capture juveniles and some adults in the usual holding areas in the summer of 2020, and our sampling and telemetry in other river reaches did not suggest heavy use of any new areas. Therefore, the dramatic drop in observed adult sturgeon abundance following Hurricane Michael can be reasonably attributed to increased mortality.

Our acoustic receiver array proved very effective at detecting individuals at least once per year, which is needed to determine if a fish is alive. The array was positioned to detect adult sturgeon throughout their freshwater residency; therefore, the likelihood of detecting each fish at least once during a year was high – in fact, most individuals were detected at least several hundred times (Table 2.3). The fish with the lower number of annual detections were tagged upriver during the fall and were only detected as they exited the river that year. Over the 4 years of telemetry data collection, sturgeon that did not meet our criteria for an apparent mortality were ever detected afterwards on our array (or in a neighboring river) or recaptured later in a net.

Our telemetry-based rates of adult annual mortality in non-hurricane years (0.03 to 0.11) fall within the range of previous annual mortality estimates for adult Gulf Sturgeon in the Apalachicola River (0.11, Rudd et al. 2014) and Suwannee River (0.16, Sulak and Clugston 1999; 0.17, Pine et al. 2001; 0.11, Randall and Sulak 2008 as cited in Sulak et al. 2016). Zehfuss et al. (1999) did report annual adult mortality rate of 0.33 for the Apalachicola River for 1982-1991; however, because of tag loss and limited netting locations, theirs is probably an overestimate. From 2018-2019, following Hurricane Michael, we estimated annual mortality of 0.44 – a 4-fold increase from any previous non-hurricane year. This telemetry-based mortality estimate is lower than our estimate based on side-scan sonar observations (0.607), which represents an uncalibrated index count and as such may be less accurate or precise. However, both methods indicate a mass mortality event in which a large proportion of the adult population was lost between fall 2018 and fall 2019.

Current Gulf Sturgeon populations appear to be recovering slowly (USFWS and NMFS 2009), but small increases to current annual adult mortality (e.g., from 0.16 current annual mortality to 0.20 in the Suwannee River) could cause populations to begin to decline (Pine et al. 2001) or drastically slow population recovery within the river (Flowers et al. 2020). The large increase in adult mortality in the Apalachicola River following Hurricane Michael is concerning for the already imperiled population. Despite this fact, relatively high recruitment following the hurricane is promising for future population recovery. The 2020 age-1 cohort was spawned in spring 2019, after Hurricane Michael and the associated adult mortality, yet it was one of the largest observed since monitoring began in 2013. Surprisingly, the apparent loss of >40% of the adult population did not appear to affect recruitment, possibly because of high fecundity – one adult female Gulf Sturgeon can produce 300,000-600,000 eggs (Parauka et al. 1991, Sulak et al. 2016). This suggests that recruitment within the Apalachicola River is limited by other factors beyond spawning population size, such as available spawning habitat (Flowers et al. 2009). Additionally, Gulf Sturgeon do not spawn every year, and if the adults that spawned in 2018 experienced higher mortality than the rest of the population because of their possibly weakened condition, recruitment may not be affected until 2-3 years after the hurricane, when those fish would have been due to spawn again.

Fish Behavior

The primary driver for Gulf Sturgeon out-migration in the fall is declining water temperatures reaching an average of 21 °C (Carr et al. 1996, Foster and Clugston 1997); however, in 2018, out-migration occurred when water temperature was about 5°C higher. Early fall out-migrations of adult Gulf Sturgeon have been documented following the Category 2 Hurricane Georges in both the Choctawhatchee (Parauka et al. 2001) and Pascagoula (Heise et al. 2005) rivers. These aberrant early migrations were believed to have been triggered by increased river discharge following the storm. Hurricane Michael also triggered an early and rapid departure from the river by surviving adult sturgeon (Figure 2.5). Although flow did increase following Hurricane Michael, the departure of adult sturgeon in the Apalachicola River was much more rapid and complete than reported in the studies in the aftermath of Hurricane Georges. We believe the primary driver of the early, rapid out-migration we observed was the precipitous decline in dissolved oxygen in the days following the storm – hypoxia avoidance is known in a variety of southeastern estuarine fishes (Wannamaker and Rice 2000). The timing of the spring 2019 in-migration and subsequent migrations returned to normal (Figure 2.5), so the hurricane did not appear to create any lasting effects on fish movements. In 2020, the Category 2 Hurricane Sally caused increased discharge in the Apalachicola River and apparently triggered another early out-migration similar to those reported following Hurricane Georges (A. Kaeser, USFWS, personal communication); however, because Sally was weaker and more distant, there was no hypoxic event associated with that storm. These early outmigration events following increased flows from hurricanes may be an adaptive behavior of Gulf Sturgeon to avoid potential hypoxic conditions that occur after hurricanes.

Conclusions

As global temperatures continue to rise, hurricane activity and the associated threat to imperiled fish populations will likely increase. Current climate forecast models predict a possible decrease in overall tropical storm activity but a 2- to 7-fold increase in strong (category 3 or higher) hurricanes in the coming decades (Bender et al. 2010, Grinsted et al. 2013, Knutson et al.

2013). The area most affected by these stronger storms may be the western Atlantic Ocean above 20°N latitude (Bender et al. 2010), which includes the entire range of Gulf Sturgeon. However, shifting hurricane trajectory patterns may spare part of the Gulf coast from some of these storms (Colbert et al. 2013). Given the small sizes of many Gulf Sturgeon populations (USFWS and NMFS 2009), hurricane-driven increases to adult mortality are of particular concern. Looking to the results from this study, Hurricane Michael increased the normal apparent annual mortality of adults at least 4-fold, and because of the long lifespan, late age of mortality, and intermittent spawning intervals, multiple hurricanes hitting the same population over just a few years could cause a complete population crash or genetic bottleneck.

Going forward, continued adult population monitoring will be important to understand the full and continuing effects of Hurricane Michael on Apalachicola River Gulf Sturgeon. Adult population monitoring will also play an important role throughout their range to assess recovery of the species, as well as provide data for any future post-hurricane assessments. Triple-pass side-scan sonar counts over holding sites in conjunction with N-mixture models is a potential low-labor technique that could provide range-wide annual adult population estimates. Increased mark-recapture sampling of adults can also provide reliable annual population estimates to monitor trends. Continued recruitment assessments will reveal whether the 2018 loss of mature adults will affect juvenile production in the Apalachicola River. Additionally, if recruitment does remain stable for the next few years, other factors – beyond adult spawner abundance (e.g., juvenile mortality, habitat constraints) should be investigated to determine bottlenecks to population growth. Through continued monitoring of the Apalachicola River Gulf Sturgeon adult population, we can assess how long recovery to pre-hurricane levels will take.

Our mortality and recruitment estimates after Hurricane Michael made landfall in the Apalachicola River provide important new information that will need to be included in future models that assess the viability and recovery times of Gulf Sturgeon populations. Many Gulf Sturgeon populations appear to be vulnerable and small (USFWS and NMFS 2009), and the possibility of a large hurricane causing major adult mortality might result in local extirpation of the species from the affected rivers. Spawning Gulf Sturgeon populations have already likely disappeared from several rivers in their historic range (Sulak et al. 2016), and the loss of additional populations may necessitate a change in their status from threatened to endangered. In addition to the possibility of increased mortality due to hurricane activity, Gulf Sturgeon continue to face anthropogenic threats including loss of spawning habitat, habitat degradation, bycatch, the likely threat from climate change leading to increased water temperatures and habitat changes (USFWS and NMFS 2009). To mitigate or buffer these threats, species managers may need to consider taking actions to increase annual recruitment and survival to adulthood. Creating fish passage around dams (Ahrens and Pine 2014, Flowers et al. 2020), artificial spawning habitats (Bouckaert et al. 2014), supplemental stocking of YOY sturgeon (Bezold and Peterson 2008, Flowers et al. 2020), and releasing water from dams to more closely match run-of-the-river flows (Auer 1996, Haxton et al. 2015) may all help bolster Gulf Sturgeon populations and contribute to species recovery. Further, if successful in the Apalachicola River, these conservation measures may prove beneficial for recovering and maintaining Gulf Sturgeon populations range-wide.

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Tables and Figures

Table 2.1: Annual mortality rates for adult Gulf Sturgeon within the Apalachicola River from 2016 to 2019. Mortality rates were estimated from data on adult sturgeon that were surgically implanted with acoustic transmitters (Vemco® V-16, Vemco, Bedford, NS, Canada) dating back to 2011. An array of acoustic receivers (Vemco® VR2W) was in place throughout the study and was used to determine mortality rates. An individual was considered an apparent mortality under two circumstances: 1) the individual was detected entering the river in the spring but not detected leaving in the fall; 2) the individual was detected leaving in the fall but not detected entering any array in the spring.

Year	Tagged adults	Apparent mortalities	Mortality rate
2016	18	2	0.11
2017	26	2	0.08
2018	43	19	0.44
2019	31	1	0.03

Table 2.2: Mean number of detections for acoustically tagged adult Gulf Sturgeon within the Apalachicola River, FL for 2016 to 2020. An array of 24 - 27 stationary acoustic receivers (Vemco® VR2W) was deployed and maintained throughout the Apalachicola River, Brothers River, and Apalachicola Bay from 2016 to 2020.

Year	Mortality				Surviving			
	Mean	SD	Range	N	Mean	SD	Range	N
2016*	0	0	0 – 0	2	1773	5245	6 – 20328	16
2017	814	185	683 – 945	2	3548	2952	133 – 9152	24
2018*	216	417	0 – 1577	19	1313	2441	19 – 10829	24
2019	304	NA	304 – 3004	1	24867	21728	594 – 74133	30
2020ǂ	NA	NA	NA	NA	5616	2969	317 – 10742	26

* The fish with zero detections were tagged within the Brothers River the same year they are apparent mortalities. Tags were in working order when released and fish are presumed to have died before passing an acoustic receiver.

ǂ Data for year are only for January through July.

Table 2.3: Annual return rates for adult Gulf Sturgeon within the Apalachicola River from 2016 to 2020. Return rates were calculated with data from adult sturgeon that were surgically implanted with acoustic transmitters (Vemco® V-16, Vemco, Bedford, NS, Canada) dating back to 2011. An array of acoustic receivers (Vemco® VR2W) was in place throughout the study and was used to determine mortality rates. Annual return rate was the percentage of acoustically tagged adult sturgeon that spent the summer within the Apalachicola River between subsequent years.

Year	Surviving adults	Returned adults	Return rate
2016 – 2017	16	15	0.94
2017 – 2018	24	22	0.92
2018 – 2019	24	22	0.92
2019 – 2020	30	24	0.80

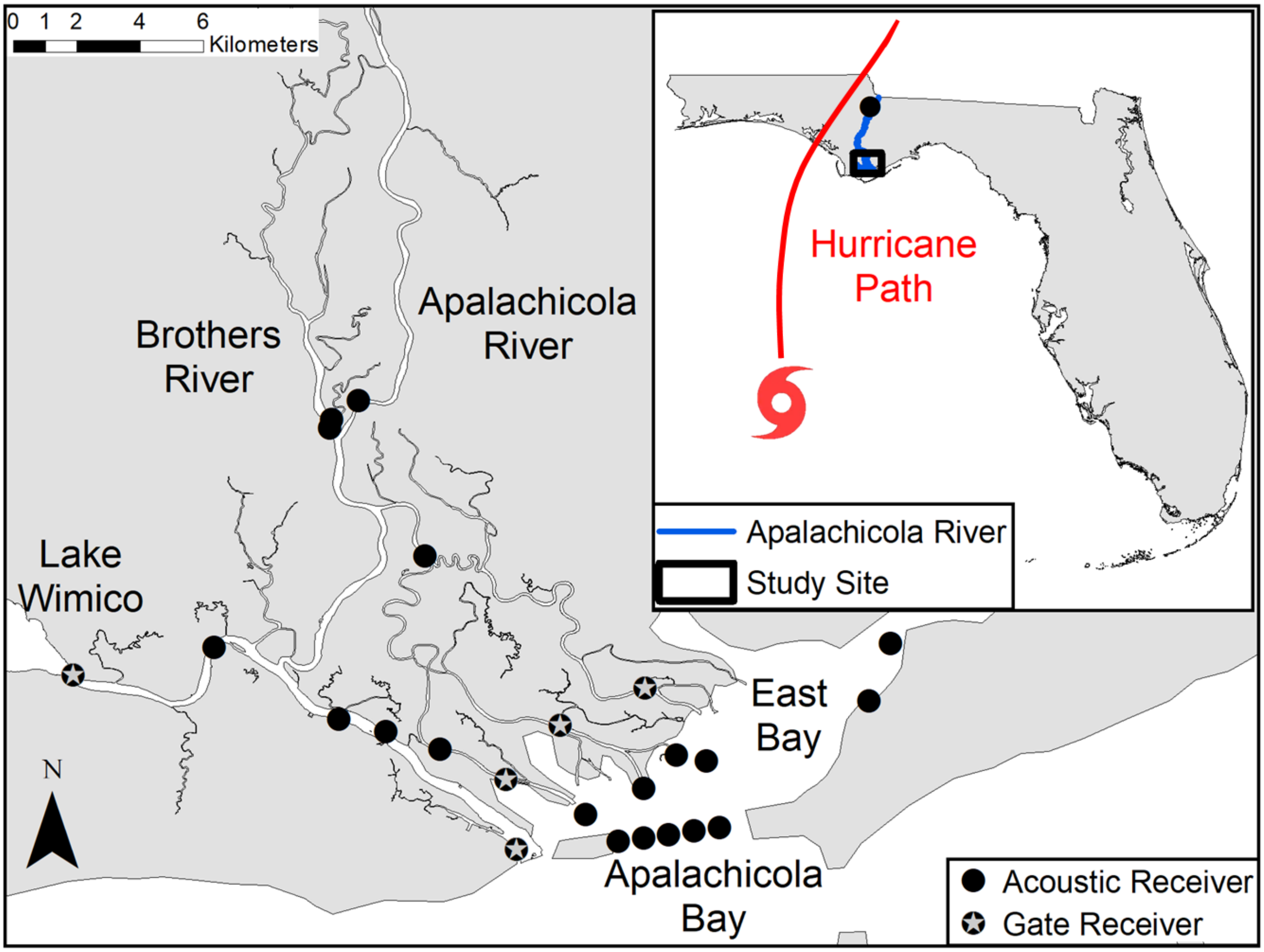

Figure 2.1: Map of the acoustic receiver (Vemco® VR2W) array within the Apalachicola and Brothers rivers during the study period (2016 to 2020). The gate receivers (indicated with a star) were used to determine arrival to and departure from the river. The inset shows the approximate path Hurricane Michael took during October of 2018.

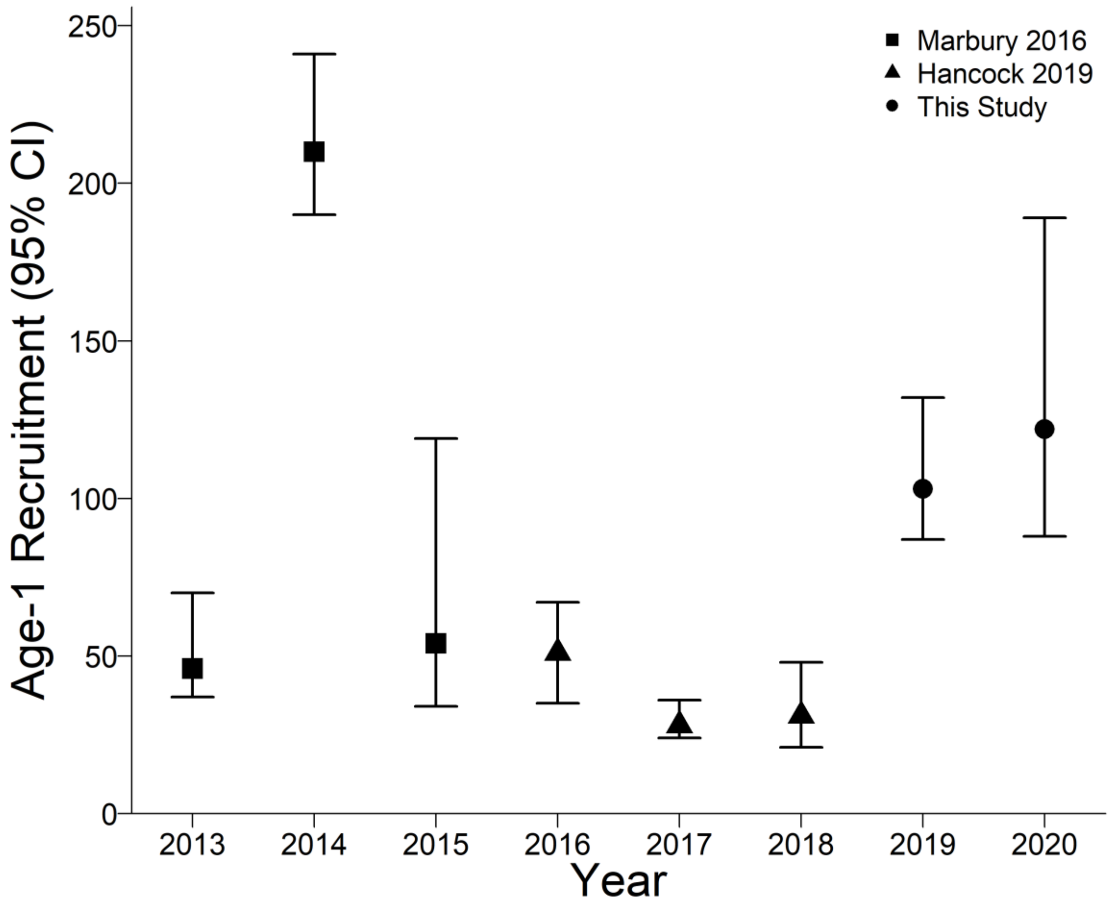

Figure 2.2: Age-1 recruitment estimates for Gulf Sturgeon within the Apalachicola River system from 2013 to 2020. Estimates were obtained from gill netting (45.7 x 3.0 m) data collected 3 - 5 days per week from May through August with occasional sampling events in September and October of each year. The sites fished were within the Brothers River, as well as just downstream of Jim Woodruff Lock and Dam. Unique capture histories for each individual sturgeon were analyzed using Huggins closed capture models in RMark to estimate recruitment cohort sizes. 2013 – 2018 data were collected and analyzed by Marbury (2016) and Hancock (2019).

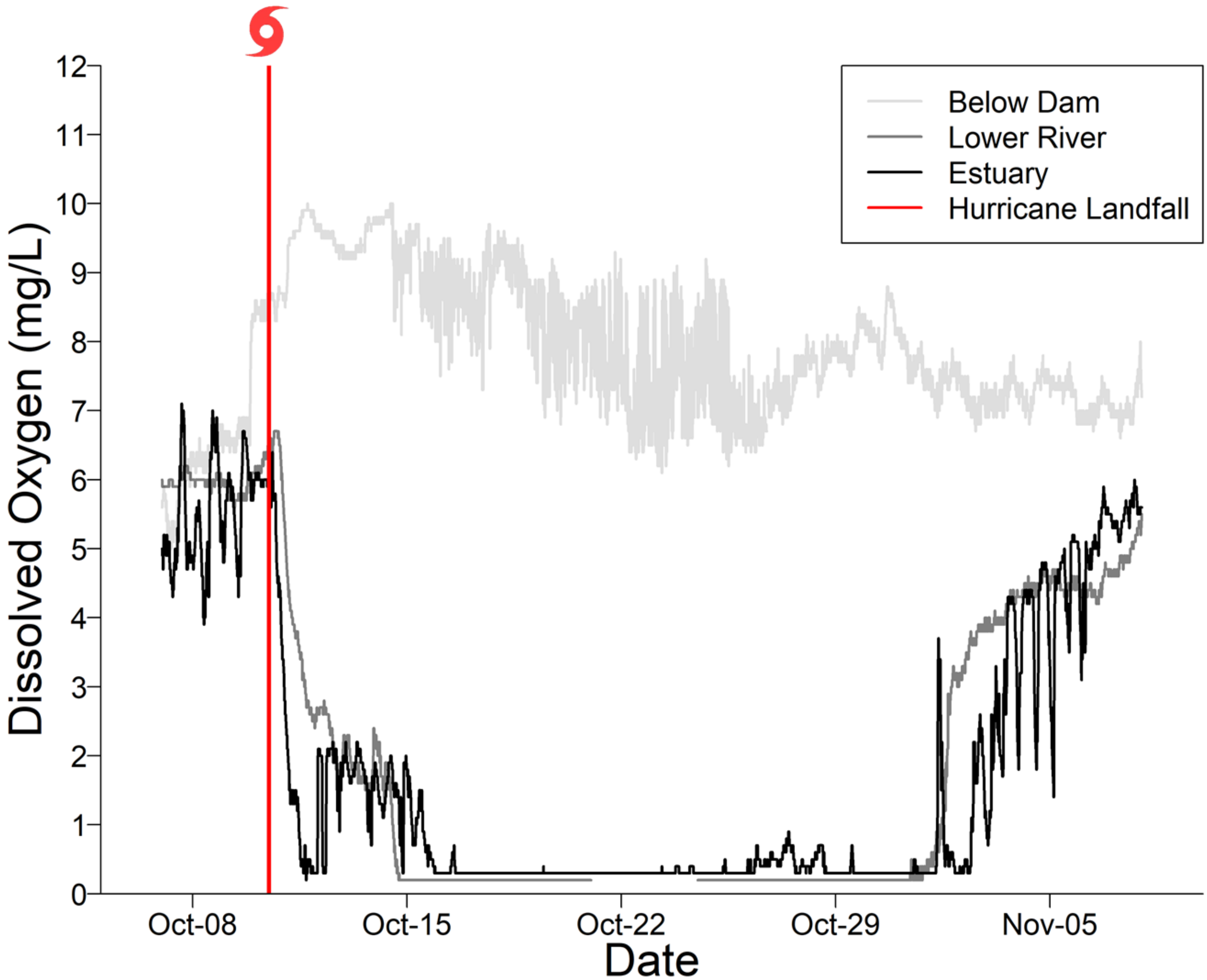

Figure 2.3: Dissolved oxygen within the Apalachicola River at three sampling sites from October 6 – November 8, 2018. Below Dam = USGS water station in Chattahoochee, Florida (rkm = 170, USGS 02358000), Lower River = USGS Water Station in Sumatra, Florida (rkm = 33, USGS 02359170), and Estuary = Apalachicola National Estuarine Research Reserve System water quality station in the Little St. Marks River (LSM rkm = 4, APALMWQ). The vertical red line indicates when Hurricane Michael made landfall.

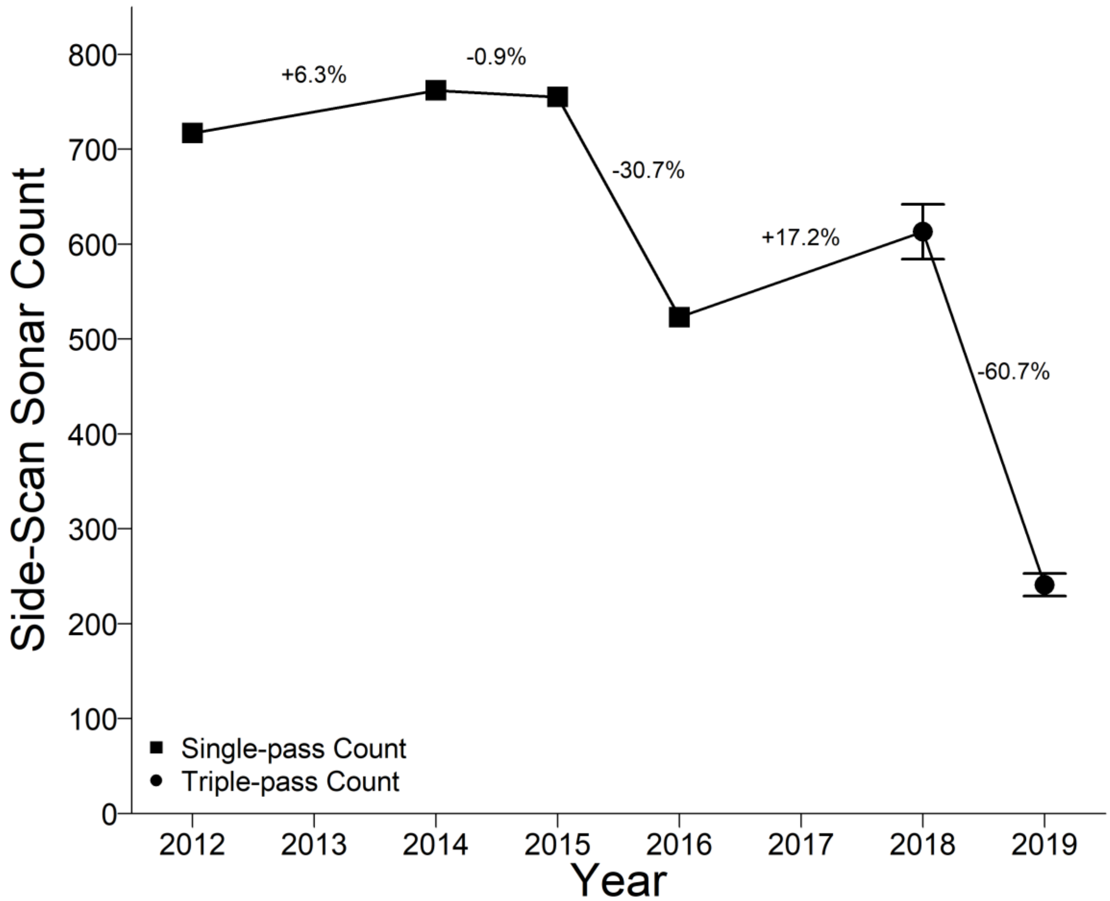

Figure 2.4: Side-scan sonar index counts and percent change between counts of adult (>90 cm FL) Gulf Sturgeon within the Apalachicola River system from 2012 to 2019. Annual index counts were done using Humminbird® 900 and 1100 Series Side Imaging units with frequency set to 455 kHz and a range of 25.6 to 29.0 m to each side to scan known holding areas. The data were processed in SonarTRX software and ArcGIS to create images of the scanned reaches to identify adult Gulf Sturgeon targets based on size, shape, position in the water column, and relationship to surroundings. Single-pass surveys with a single boat were conducted in 2012 and 2014-2016 to generate index counts, and triple-pass surveys were conducted in 2018 (prior to Hurricane Michael) and 2019 with the average and standard deviation of the 3 counts represented here.

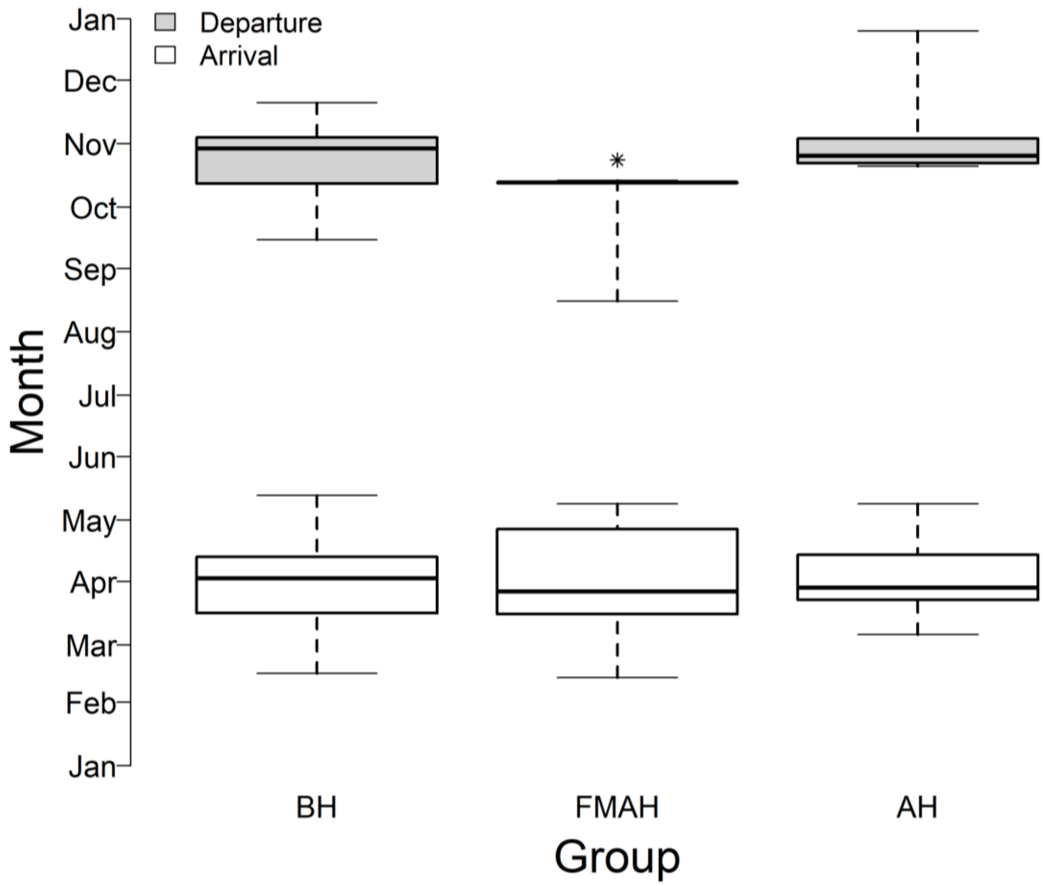

Figure 2.5: Boxplots representing the median, first quartile, third quartile, and range for day of arrival to and departure from the Apalachicola River of acoustically tagged adult Gulf Sturgeon. Adult Gulf Sturgeon were captured with gillnets and surgically implanted with acoustic transmitters (Vemco® V-16, Vemco, Bedford, NS, Canada) dating back to 2011. An array of acoustic receivers (Vemco® VR2W) was in place throughout the study and was used detect fish as they entered and exited the river each year. The arrival and departure days were broken into three groups: BH = before the hurricane (fall 2016 – spring 2018), FMAH = first departure and arrival after the hurricane (fall 2018 and spring 2019), and AH = first year after the hurricane (fall 2019 and spring 2020). For arrival groups (n = 40, 24, 27) and departure groups (n = 36, 24, 28).

* significant difference ($p < 0.001$)

CHAPTER 3

CONCLUSIONS

Long-term Gulf Sturgeon population monitoring is necessary to determine if recovery objectives outlined in the Gulf Sturgeon Recovery Plan are being met (USFWS and GSMFC 1995). Historically, population assessments were intermittent and included only adults (USFWS and NMFS 2009). Because of this, information on juvenile recruitment, habitat use, and mortality were identified as critical areas of research in the 2009 Gulf Sturgeon Recovery Plan 5-Year Review, as well as the need for standardized and regular census sampling (USFWS and NMFS 2009). Currently, many of the populations seem to be increasing slowly (USFWS and NMFS 2009); however, they are vulnerable to increases in mortality to adults and young-of-the-year (YOY) juveniles (Pine et al. 2001, Tate and Allen 2002). Further, a small increase in current mortality could cause populations to begin to decline (Pine et al. 2001, Gross et al. 2002, Tate and Allen 2002) or slow recovery substantially (Flowers et al. 2020).

There are many anthropogenic (e.g., fishery bycatch, mortalities from dredging operations, and pollution) and natural factors that may be causing additional mortality to Gulf Sturgeon populations. There is increasing interest in the role hurricane activity – as an additional source of mortality – will play in shaping Gulf Sturgeon recovery. Hurricanes were not mentioned at all in the Gulf Sturgeon Recovery/Management Plan laid out in 1995 (USFWS and GSMFC 1995), but recent studies have noted the potential for hurricanes to cause large-scale Gulf Sturgeon mortality (Havrylkoff 2010, Rudd et al. 2014, Ahrens and Pine 2014, Sulak et al.

2016). Adult Gulf Sturgeon mass mortality events have been documented in the wake of both Hurricane Ivan (F. Paruaka, USFWS, personal communication) and Hurricane Katrina (Peterson et al. 2008); however, long-term population monitoring programs necessary to determine the full effects of theses hurricanes were not in place prior to the storms' landfall.

In October 2018, Hurricane Michael, made landfall as a category 5 hurricane just west of the Apalachicola River. Immediately following the storm, the Apalachicola River experienced a hypoxic event and a fish kill in which dead adult sturgeon were observed (A. Strickland, FWC, personal communication). Our on-going long-term Gulf Sturgeon population monitoring study provided a unique opportunity to study how a hurricane may affect Gulf Sturgeon populations. Prior to this study, a detailed assessment of a Gulf Sturgeon population's response to a hurricane did not exist. We were able to estimate the effect Hurricane Michael had on annual recruitment, adult mortality, and migration behavior, which will help determine their vulnerability to predicted future increased hurricane activity.

From gill netting data collected during the two summers following Hurricane Michael, we were able to estimate age-1 recruitment within the Apalachicola River. Our results show that there was a strong age-1 year class in 2019, indicating that the YOY sturgeon were able to survive Hurricane Michael and the resulting drop in dissolved oxygen. We cannot be sure that recruitment was unaffected by the storm as methods to monitor juvenile mortality were not in place prior to the storm. In contrast, there is also the possibility that increased fall flows caused by the hurricane may have potentially allowed juveniles to access additional foraging habitats by expanding the low salinity areas present in the estuary, which could have led to increased recruitment (Randall and Sulak 2007). However, the storm-associated hypoxia would likely have prevented any YOY in the river from reaching the estuary and benefitting from the increase in foraging grounds. There is also evidence of fall-spawning Gulf Sturgeon in the nearby Choctawhatchee River in Florida (Fox et al. 2020, Rider et al. 2020), and the increased river discharge from the storm in mid-October may have created conditions that supported a fall spawn or facilitated survival of fall-spawned eggs and larval fish. Several juvenile sturgeon captured in 2019 were smaller than the typical age-1 size and suggests that a fall spawn may have occurred in 2018. There is little prior evidence of annual fall spawns within the Apalachicola River (Marbury 2016, Hancock 2019), so a successful spawn following Hurricane Michael would indicate a potential benefit to the recovery of the population following the mass mortality event. In fact, the estimated 39 (24 – 89) YOY individuals captured in 2019 would account for about one-third of Apalachicola River age-1 recruitment in 2020. Managers might be able to take advantage of fall spawns to aid in the recovery of the species by enacting a minimum river discharge during the fall that would allow for successful spawning and survival of eggs and larval fish (Flowers et al. 2009).

Adult Gulf Sturgeon mortality in the wake of a hurricane has been documented in several rivers prior to Hurricane Michael (Peterson et al. 2008, Havrylkoff 2010, F. Paruaka, USFWS, personal communication); however, we were the first to quantifying the resulting mortality via the SSS index surveys and acoustic telemetry data. A relatively greater frequency of strong hurricanes in the western side of Gulf Sturgeon’s range has been suggested as a possible explanation for the smaller western population sizes, but the amount that hurricanes have contributed to total mortality in these rivers is uncertain (Rudd et al. 2014). Prior to Hurricane Michael, our index counts of adult sturgeon remained relatively stable between annual counts, which supports the hypothesis that the Apalachicola River population is stable or slightly increasing (USFWS and NMFS 2009). We observed a dramatic decline (-0.607) of adult sturgeon in the index reaches the year after Hurricane Michael. This decline was most likely caused by a large increase in annual adult mortality, as 92% of adults confirmed to have survived the storm returned to the Apalachicola in 2019 and evidence of shifts in adult or juvenile holding sites was not seen in 2019 or 2020. We observed similar results in our acoustic telemetry data of adult sturgeon. Our telemetry-based rates of adult annual mortality in non-hurricane years (0.03 to 0.11) fall within the range of previous annual mortality estimates for adult Gulf Sturgeon (Sulak and Clugston 1999, Pine et al. 2001, Randall and Sulak 2008, Rudd et al. 2014). Following Hurricane Michael, we estimated annual mortality of 0.44 – a 4-fold increase from any previous non-hurricane year. These two methods for assessing adult mortality both indicate a mass mortality event in which nearly 50% of the adult population was lost between fall 2018 and fall 2019.

Hurricane Michael also triggered an early and rapid departure from the river by surviving adult sturgeon in 2018. We believe the primary driver of the early, rapid out-migration we observed was the precipitous decline in dissolved oxygen in that days following the storm – hypoxia avoidance is known in a variety of southeastern estuarine fishes (Wannamaker and Rice 2000). The timing of the spring 2019 in-migration and subsequent migrations returned to normal, so the hurricane did not appear to create any lasting effects on sturgeon migration behavior within the Apalachicola River.

As global temperatures continue to rise, hurricane activity and the associated threat to imperiled Gulf Sturgeon populations will likely increase. Current climate forecast models predict a 2- to 7-fold increase in strong (category 3 or higher) hurricanes in the coming decades (Bender et al. 2010, Grinsted et al. 2013, Knutson et al. 2013). The results from this study indicate that these storms can cause large-scale adult mortality events. Given the small sizes of many Gulf

Sturgeon populations, hurricane-driven increases to adult mortality are of particular concern. If hurricane activity does increase as predicted, we can expect an overall increase average annual mortality of adult Gulf Sturgeon within most to all of their natal rivers.

As we have seen with population recoveries since their listing as threatened in 1991, reduced adult populations can drastically slow the recovery speed of Gulf Sturgeon until they can rebuild a more balanced population age-structure (Flowers et al. 2020). The Suwannee River Gulf Sturgeon population underwent an estimated 5% annual growth rate during its recovery from 1986 to 1995 (Pine et al. 2001). If hurricanes can be expected to contribute an additional 40% to annual mortality, as seen in this study, then that population would require 10 years to recover to pre-storm levels. If intervals between strong hurricanes making landfall within a river system decreased to less than 1 per every 10 years, then that population would begin to decline unless population growth was increased above current rates. Future management may require techniques to increase annual recruitment (e.g., creation of artificial spawning habitat or stocking; Flowers et al. 2020), especially to those populations most affected by hurricanes. Continued monitoring of the Apalachicola River Gulf Sturgeon populations will determine if future recruitment is harmed by the loss to the adult population and the time required to recover to pre-hurricane levels. If major hurricanes become more frequent, Gulf Sturgeon populations may not have enough time to recover between storms and intervention may be necessary to protect the species. This study and future monitoring will provide important data to help determine the potential danger hurricanes pose to Gulf Sturgeon and if their populations can recover without intervention in the face of increased hurricane activity.

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