

Deepwater Horizon Open Ocean Trustee  
Implementation Group

Informing Gulf Sturgeon Population Status and  
Trends as a Baseline to Evaluate Restoration

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Summary of Project Results

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The following report is as a final deliverable for the Deepwater Horizon Monitoring and Adaptive Management Activity, *Informing Gulf Sturgeon Population Status and Trends as a Baseline to Evaluate Restoration*. NOAA is leading implementation of this project in collaboration with the Department of the Interior (DOI) for the Open Ocean Trustee Implementation Group to restore resources injured in the Gulf of Mexico by the 2010 *Deepwater Horizon* oil spill.

The following report was prepared by the project's Principal Investigator, Dr. William Pine (previously with the University of Florida), and other collaborators identified in the Acknowledgements section. This report includes detailed information on the results from several population analyses used to assess adult survival, population trends, and population viability for all seven Gulf Sturgeon populations. An Executive Summary will be released separately to highlight the findings, provide additional synthesis, and identify how these population analyses can inform future restoration opportunities.

# **Informing Gulf Sturgeon Population Status and Trends as a Baseline to Measure PDARP Actions to Promote Species Recovery**

Project period of performance: July 1, 2019–December 31, 2023

Project principal investigator: Dr. William Pine

# Contents

Executive Summary.....	1
Acknowledgments.....	2
1. Project Introduction and Summary.....	3
Task 1 Summary.....	4
Task 1 Results.....	6
Task 2 Results.....	7
References .....	8
2. Survival Estimation Using Multistate Models .....	14
Completed as part of Task 1.1 .....	14
Introduction .....	14
Methods.....	15
<i>Acoustic telemetry tagging and monitoring</i> .....	15
<i>Survival and movement rate estimation</i> .....	15
<i>Data characteristics and capture history formatting</i> .....	16
<i>Multistate model structures</i> .....	17
Results.....	18
<i>Tagging summary</i> .....	18
<i>Survival and detection probability estimation</i> .....	18
<i>Fidelity and exchange among rivers and regions</i> .....	19
<i>AIC model comparison</i> .....	20
Discussion .....	20
<i>Comparison with previous studies</i> .....	21
<i>Informing future research: monitoring time</i> .....	22
<i>Informing future research: transmitter deployments and tagged-fish pool size</i> .....	22
<i>Future research implications: planning</i> .....	24
Conclusions .....	24
References .....	25
Tables and Figures .....	27
Appendix.....	37
3. Survival Estimation Using a Barker Model .....	47

Completed as part of Task 1.1 .....	47
Introduction .....	47
Methods.....	47
<i>Data overview</i> .....	47
<i>Capture history format</i> .....	47
<i>Barker model parameterization</i> .....	48
<i>Barker model descriptions</i> .....	48
Results.....	49
<i>Data summary</i> .....	49
<i>Range-wide capture probability</i> .....	49
<i>Range-wide survival</i> .....	49
<i>River-specific capture probability</i> .....	49
<i>River-specific survival</i> .....	50
Discussion .....	50
Management and restoration recommendations.....	51
References .....	53
Tables and Figures .....	55
Appendix: Estimating survival from life history invariants and a discussion of true survival .....	70
4. Lambda Pradel Estimation .....	72
Completed as part of Task 1.2 .....	72
Introduction .....	72
Methods.....	72
Results.....	74
Discussion .....	75
References .....	79
Tables and Figures .....	82
Appendix.....	100
5. Population Viability Analysis.....	105
Completed as Task 1.3 .....	105
Introduction .....	105
Materials and Methods .....	105
<i>Model description</i> .....	105

<i>Model scenarios</i> .....	106
Results.....	107
<i>Creeping chronic mortality rates</i> .....	107
<i>Increasing episodic mortality event frequency</i> .....	107
<i>Increasing recruitment failure frequency</i> .....	107
Discussion .....	107
References .....	109
Tables and Figures .....	112
Appendix.....	117

## Executive Summary

We compiled and standardized all available Gulf of Mexico Sturgeon tagging data into a common database and used these data to assess trends in adult ( $\geq 1,350$  mm total length) Gulf Sturgeon populations from seven rivers from 1990–2022. We used these data to estimate the survival of adult Gulf Sturgeon by river, and found lower survival in the western Gulf of Mexico compared to other areas. Reasons for lower survival are unknown, as data resolution does not allow mortality to be partitioned into different sources. Overall, adult survival was similar to biological reference points for the species. We found a positive intrinsic rate of population growth in all seven rivers in 1990–2009, but population change was negative in four of seven rivers in 2010–2022; this negative trend may be driven by lower recruitment to adult size.

We used a population viability model to assess the extinction risk for Gulf Sturgeon due to episodic mortality events similar to those observed in recent decades. Extinction risk for all seven Gulf Sturgeon populations was low, but it will increase if the frequency or severity of episodic mortality events increases.

We also developed the Gulf Sturgeon Database to enable better coordination of physical and telemetry tagging data, and modernized Gulf Sturgeon field data collection workflows to reduce data entry errors. This resource provides information to managers to inform decision-making for on-the-ground recovery actions.

## Acknowledgments

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## 1. Project Introduction and Summary

The Gulf of Mexico Sturgeon (*Acipenser oxyrinchus desotoi*), hereafter Gulf Sturgeon, was listed under the US Endangered Species Act (ESA) in 1991 (50 CFR 17). Current management units for this species include seven river systems (Pearl, Pascagoula, Escambia, Yellow, Choctawhatchee, Apalachicola, and Suwannee rivers) and adjacent marine habitats across the northern Gulf of Mexico. The current Gulf Sturgeon Recovery Plan (GSRP) outlines criteria to be met before delisting can be proposed. A short-term goal of the GSRP is to ensure that populations are not declining. Its primary long-term goal is to establish self-sustaining populations that could allow delisting of the species, with a secondary goal of population recovery to a point at which directed fishing could be sustained (U.S. Fish and Wildlife Service and Gulf States Marine Fisheries Commission [USFWS and GSMFC] 1995).

Factors contributing to declines in Gulf Sturgeon populations include overfishing and habitat modifications (Clugston et al. 1995; Ahrens and Pine 2014; Flowers et al. 2020). Other factors that may have impacted the Gulf Sturgeon population recovery trajectory since about 2003 include paper plant effluent spill, significant hurricanes, recurring red tide events, and the 2010 *Deepwater Horizon* oil spill.

Natural events such as hurricanes have caused a type of episodic mortality throughout the evolutionary history of the species. Anthropogenic disturbances may contribute additional mortality. Following the *Deepwater Horizon* oil spill, the Programmatic Damage Assessment and Restoration Plan and Programmatic Environmental Impact Statement identified that large numbers of Gulf Sturgeon were exposed to oil and were affected by that exposure (USFWS 2015; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). During this same period, Gulf Sturgeon experienced other extreme events, including drought in the eastern portion of the range (Leitman et al. 2016) and flooding in the west (Gledhill et al. 2020).

The GSRP recommends using population models to assess restoration and management options for Gulf Sturgeon, identify future research needs, and forecast time to population recovery (USFWS and GSMFC 1995). Capture-recapture models have been used to assess Gulf Sturgeon population status in several rivers (USFWS and National Marine Fisheries Service [NMFS] 2022), and age-structured models have been used to assess time to recovery (Flowers et al. 2020). In 2009, a stock assessment was completed for Gulf Sturgeon (Pine and Martell 2009). A key finding of this assessment was that long-term demographic data for completing assessment efforts were only available for the Apalachicola and Suwannee rivers. An analysis of these data revealed divergent trends in Gulf Sturgeon stock status depending on model structure because of confounding between low capture probability and survival parameters and changes in monitoring program design. This led to an effort led by NOAA (the National Oceanic and Atmospheric Administration) to estimate mortality range-wide using telemetry tags over five years (2010–2015).

This work was interrupted by the 2010 *Deepwater Horizon* oil spill, as some of the data from the NOAA effort were embargoed until after legal and regulatory processes related to the oil spill were completed. Using the data not embargoed from 2010 to 2012, Rudd et al. (2014) presented estimates of adult mortality for and transition probabilities between each of the Gulf Sturgeon rivers described in the critical habitat designation. The previously embargoed data are now available and have been integrated

into the Gulf Sturgeon Database (GSDB). Following the *Deepwater Horizon* spill, new sampling and research efforts began for Gulf Sturgeon (PDARP 2015). These efforts included transitioning from capture-recapture efforts for adult Gulf Sturgeon to a focus on juvenile Gulf Sturgeon ecology that expanded with NRDA (Natural Resource Damage Assessment) funding. This report represents efforts to synthesize information from these two distinct periods (1990–2010 and 2010 to 2022) to meet GSRP guidelines related to trends in Gulf Sturgeon populations to help inform future recovery actions.

Completing this goal required two tasks. Task 1 was to standardize and correct errors in all available historic Gulf Sturgeon capture-recapture data and integrate them into a common database (the GSDB) and to fit different models to these data to estimate trends in Gulf Sturgeon demographic parameters. Task 2 was to modernize Gulf Sturgeon data recording efforts, by updating and standardizing equipment used in the field to capture and record data in order to reduce errors, and then to integrate these data into the database created in Task 1.

### **Task 1 Summary**

As of December 2023, the GSDB contained over 500,000 contacts (capture, recapture, recovery, and acoustic telemetry detections) from over 21,500 individually marked Gulf Sturgeon from 1976 to the present. Records include about 65,000 marks of all types, including active and passive tags. The originally funded data compilation effort was designed to standardize information from passive tags—mostly PIT (passive integrated transponder) and Floy tags, which have been used for Gulf Sturgeon since the 1990s. At the request of NOAA, we expanded the database to include acoustic telemetry tags and integrated about 24 million such detections from hundreds of individual files created since about 2010. This was a significant work order change to the project. More than 70 database queries were custom-built to compile data as requested by cooperators. Multiple training sessions, in group and one-on-one format, were held with every Gulf Sturgeon research team to provide training on database use.

Pine and Martell (2009), Zehfuss et al. (1999), and Zehfuss (2000) highlight the importance of developing consistency in Gulf Sturgeon monitoring programs to improve the ability to detect changes in the species population size. For example, Zehfuss (2000) found that to detect a 5–10% decline in population size, standardized Gulf Sturgeon sampling using passive tags would need to be conducted for at least seven years. Rudd et al. (2014) assessed a portion of the 2010–2015 NOAA effort to estimate Gulf Sturgeon survival. They demonstrated empirically and through simulation that accurate and precise survival estimates could be obtained by marking relatively small numbers of Gulf Sturgeon in each river with telemetry tags. These telemetered Gulf Sturgeon could then be virtually recaptured by detecting their movement near a location monitored by an autonomous receiver.

Changes in Gulf Sturgeon field sampling procedures have occurred during the last three decades, including gillnet mesh size, how sampling sites are chosen, and when sampling occurs. This creates challenges to understanding underlying Gulf Sturgeon population dynamics, because changes in sampling could be misinterpreted as changes in the demographics of the population. As an example, plots of Gulf Sturgeon captures from the GSDB organized by total length (TL; y-axis) and year (x-axis) from the two rivers with the longest history of sampling, the Suwannee and Apalachicola, show different patterns in the number and size of fish captured (Figures 1.1 and 1.2).

In the Suwannee River, a wide size range of fish were collected in the late 1980s through 1990s, but since 2000 the number of fish captured each year has declined. For the Apalachicola River, the size frequency data demonstrate a higher catch of Gulf Sturgeon since about 2010 with increased frequency of younger, smaller fish (less than about 800 mm FL) since about 2014. Understanding whether these patterns over time reflect changes in Gulf Sturgeon populations (e.g., higher or lower trends in adult fish recruitment) within a river, or just changes in sampling programs, is essential to understanding trends in Gulf Sturgeon populations. Unfortunately, recovering information on monitoring program changes such as sampling efforts from GSDB data is not possible. This necessitated original approaches and assumptions in our analyses to understand long-term trends in Gulf Sturgeon populations from those data.

Two basic data types were available in the GSDB for assessing Gulf Sturgeon population dynamics range-wide: physical recapture of passively tagged fish (1990 to 2022), and virtual recapture using telemetry tags (2010 to 2022). The data in the first set were collected by physically capturing Gulf Sturgeon in nets and recording the tag information. Each Gulf Sturgeon is identified within the database with a unique fish ID, and every subsequent tag detection and recapture is linked back to that fish ID. This was necessary because some individual fish have carried multiple tags over their life, and the information captured from these tags had to be integrated. Failure to do this would lead to a strong negative bias in survival.

Because Gulf Sturgeon capture probabilities are low (about 5–15%; Zehfuss et al. 1999), and sampling programs have changed (recent efforts have primarily focused on capturing juveniles), recaptures in recent years of previously tagged adult Gulf Sturgeon can be limited. Recaptures of adult fish are very important for informing survival estimates. For every fish that is tagged and released, and for each sampling event, the goal is to determine one of three fates for previously tagged fish: alive and captured, alive and not captured, or dead. Our analytical efforts focused on assigning a probability to each of these three fates.

The data in the second set were gathered using telemetry tags. Detecting a fish passing near an acoustic receiver confirms that the fish is alive on a specific date and time. This is much simpler than capturing the fish in a net. This results in the virtual recaptures having a higher detection probability, often  $p = 60\text{--}80\%$  (Rudd et al. 2014), which is higher than passive captures or recaptures. Because of the higher capture probability, we consider the telemetry data a high-resolution dataset. Most field sampling efforts for Gulf Sturgeon since 2010 have focused on capturing and tagging a relatively small number of fish each year (10–50) with telemetry tags. These tagging efforts included NOAA-led efforts to estimate mortality patterns in adult Gulf Sturgeon (2010–2018), efforts led by the US Fish and Wildlife Service to mark juvenile Gulf Sturgeon, state and federal agency response to the *Deepwater Horizon*, including NRDA, and other efforts led by different state and academic cooperators. This objective—tagging a specific number of fish within a given size range each year with telemetry tags—is different from the objective of capturing and marking a representative population sample, which a population monitoring program might pursue. This is demonstrated in the size/frequency plots for the Suwannee River (Figure 1.1), where the decline in captures over time is most likely related to changes in sampling objectives.

## Task 1 Results

Because most of the available data in the GSDB reflect recaptures of previously marked fish, these data are most suitable for estimating trends in survival of adult Gulf Sturgeon, continuing the NOAA study objective defined after the 2009 Gulf Sturgeon stock assessment (Pine and Martell 2009). Using the high-resolution telemetry data from 2010–2022, including data previously embargoed, we updated the multistate analysis of Rudd et al. (2014) to estimate adult Gulf Sturgeon survival range-wide (Task 1.1). We assessed survival patterns over time, space (individual river), and genetic relatedness groupings while accounting for variation in detection probability within each river.

Overall, we found Gulf Sturgeon survival was lower in the western than the eastern Gulf of Mexico, with the Pearl River population generally having the lowest survival and the Choctawhatchee River population having the highest. We cannot partition data into different sources, so we do not know why survival rates may differ among river basins. We also found high fidelity to the river of tagging (>90%), suggesting that management actions within a river basin are most likely to benefit the Gulf Sturgeon population within that basin, not the range-wide population unit used by the GSRP.

We then used all GSDB data (from both passive and telemetry tags, collected from 1990–2022) in an original application of a Barker model (Williams et al. 2002) to estimate adult Gulf Sturgeon survival over three decades (Task 1.1). This model used unique capture probability terms to distinguish between field and virtual (telemetry) recaptures, in order to account for variation in capture probability by recapture type as well as by river system and time frame. We also calculated different biological reference points from life-history invariants to compare survival.

The key result from these analyses is that Gulf Sturgeon survival over space and time has remained relatively constant, with no clear trends, and values are similar to those expected based on life history. We consistently estimated survival in the western Gulf of Mexico to be lower than in the eastern Gulf of Mexico. This was demonstrated through our analyses of the full data set (passive and telemetry tags, 1990–2022) and our multistate analyses of the high-resolution data (telemetry tags only, 2010 to 2022). With the high-resolution data, we could detect occasional episodic mortality events, such as lower survival in the Apalachicola River in 2018, the same year as Hurricane Michael. If a pattern of increasing mortality over time was observed in the data, that could suggest a declining population (if rate of loss is greater than rate of replacement), which would not meet the GSRP's short-term goal of ensuring that populations are not declining.

Based on the relatively stable survival patterns predicted by the multistate and Barker modeling approaches, we derived the intrinsic rate of adult ( $\geq 1350$  mm total length [TL]) population growth (Task 1.2) and recruitment by estimating seniority probability from 1990–2022 using the Barker model survival estimates (which are from concurrent years). To account for changes in Gulf Sturgeon sampling programs after 2009, we organized the analyses in six epochs, 1990–1994, 1995–1999, 2000–2004, 2005–2009, 2010–2014, and 2015–2021. We found population growth was  $< 1$  for three rivers (Escambia, Apalachicola, and Suwannee rivers) in 2015–2021, but for Gulf Sturgeon across the entire Gulf of Mexico range, we found a positive population growth overall for the 2015–2021 time period. Estimated recruitment to the adult fish population in these three rivers with population declines has also declined since 2010–2014, but it is unclear whether this is because of changes in monitoring

program efforts or biological reasons. Thus, while the seniority probability and life-history theory indicated population growth was driven by adult survival, in this case, declining recruitment could be causing the change in population growth since 2010. Consistency in monitoring program design could reduce this uncertainty.

Finally, we used results from these analyses and the peer-reviewed literature to parameterize a population viability analysis model (Task 1.3) to forecast Gulf Sturgeon populations in the context of ongoing threats and assess fundamental concerns related to the risk of extinction for each population (see GSRP Section 1.3.2; USFWS and GSMFC 1995). Our population viability analysis results suggest the seven Gulf Sturgeon populations are robust to episodic mortality similar to the frequency and levels observed since 1990. However, if total mortality increases for Gulf Sturgeon, for example, due to episodic events or changing climate, then extinction probability increases.

These results suggest that efforts to promote adaptive capacity in Gulf Sturgeon populations by facilitating access to required habitat types and continuing efforts to minimize adult mortality from anthropogenic sources may be critical to the long-term persistence of Gulf Sturgeon populations.

## **Task 2 Results**

Our efforts to modernize Gulf Sturgeon data recording efforts (Tasks 2.1 and 2.2) were a success, as demonstrated by the widespread implementation of new PIT tag scanners and tagging equipment and field crews' use of data entry tablets. This is best shown by requests for custom database queries from cooperators to support ongoing research efforts (more than 70 developed, Task 2.3). Ongoing research efforts were improved by a reduction in data entry errors facilitated by the updated equipment and workflow designed and implemented as part of Task 2, which integrated data collected in the field with the GSDB created in Task 1.

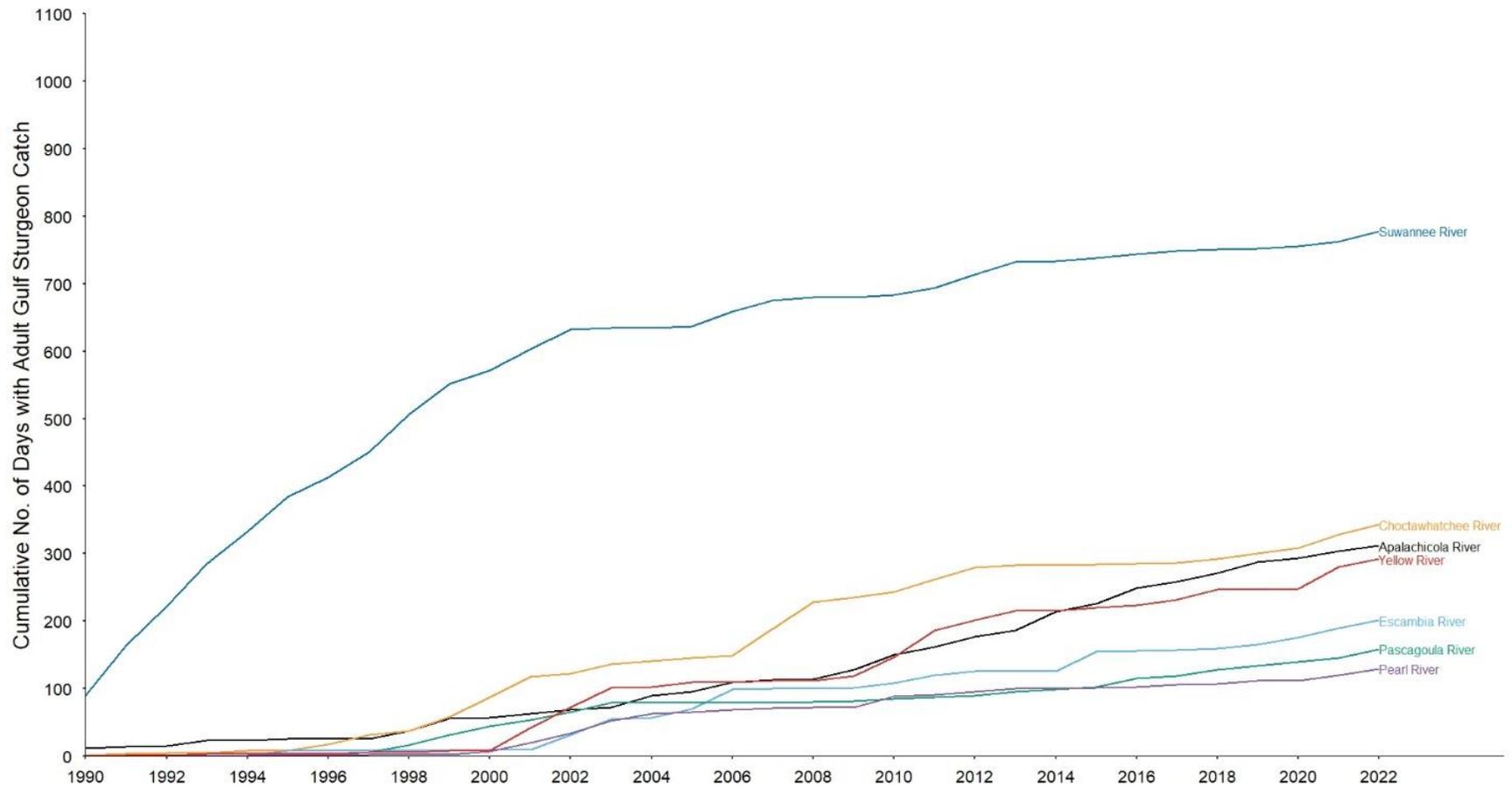
Data summaries and summary graphics requested by NOAA or USFWS in their review of the draft report are located after the references for this summary section.

## References

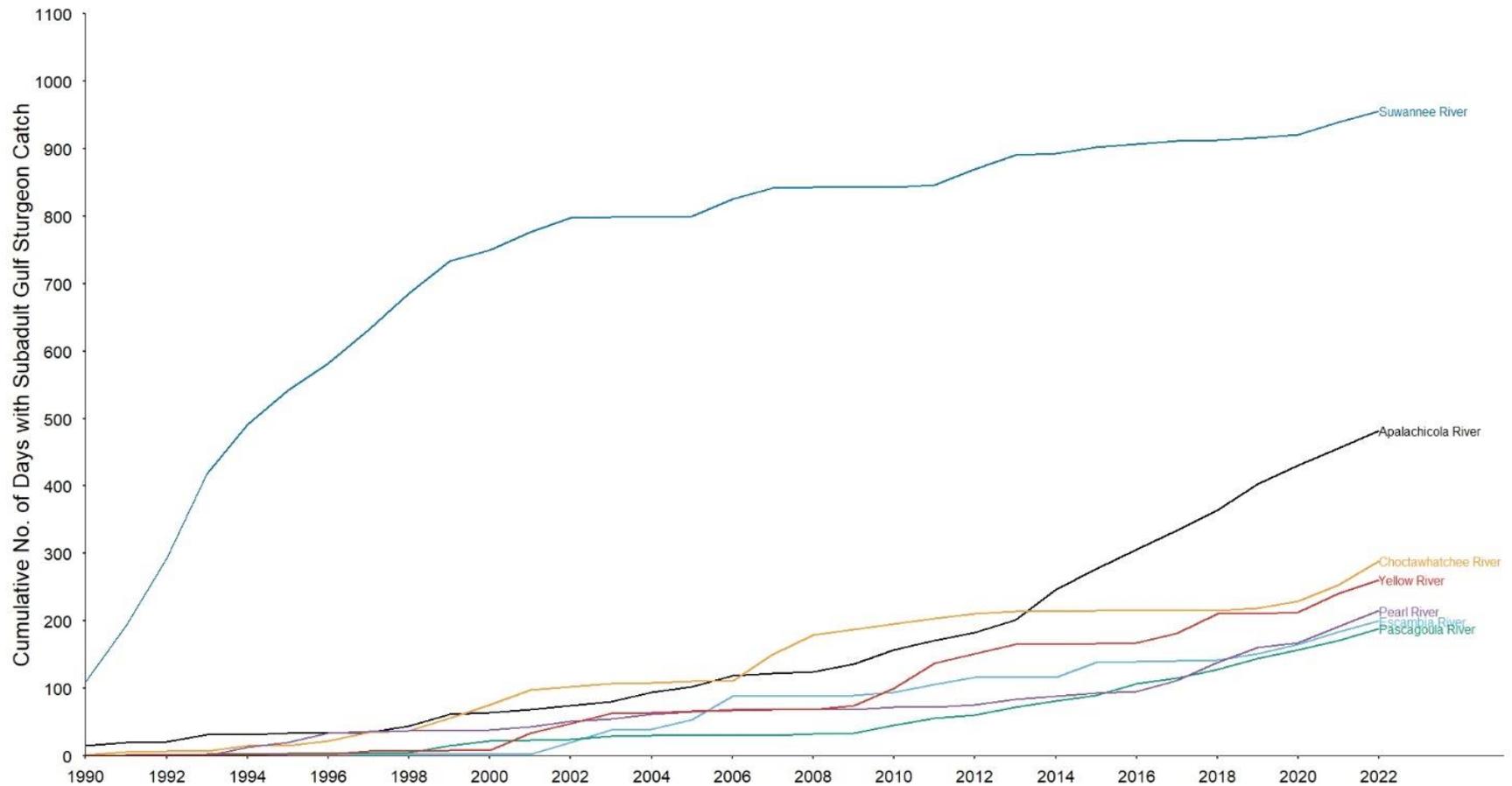
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**Table 1.1. Total number of receivers active in each river in each year and included in the Gulf Sturgeon Database.**

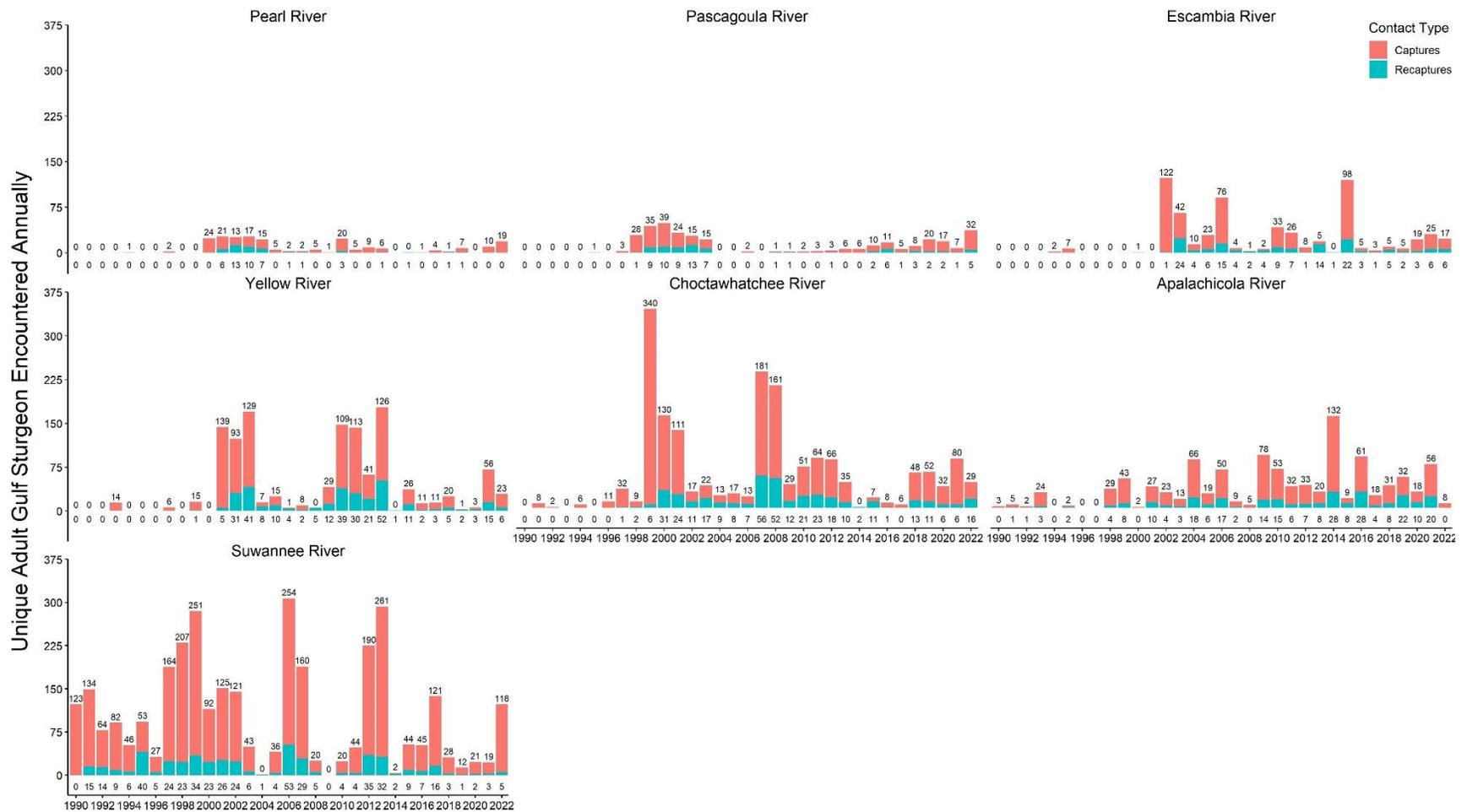
River	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Pearl River	0	0	0	0	0	5	5	5	5	5	5	5	6	3	3	45	70	21
Pascagoula River	0	0	0	0	0	3	3	5	5	5	5	4	4	4	8	31	57	29
Escambia River	11	14	12	0	0	0	2	2	10	11	19	17	2	2	12	36	34	34
Yellow River	0	1	1	0	0	0	3	2	4	2	5	8	19	20	18	18	21	21
Choctawhatchee River	12	6	1	0	0	1	8	10	5	3	6	2	4	6	21	38	44	32
Apalachicola River	0	0	0	0	0	0	13	10	30	30	26	24	26	24	24	34	31	36
Suwannee River	0	0	0	0	0	3	3	3	3	3	3	3	3	6	6	32	32	31

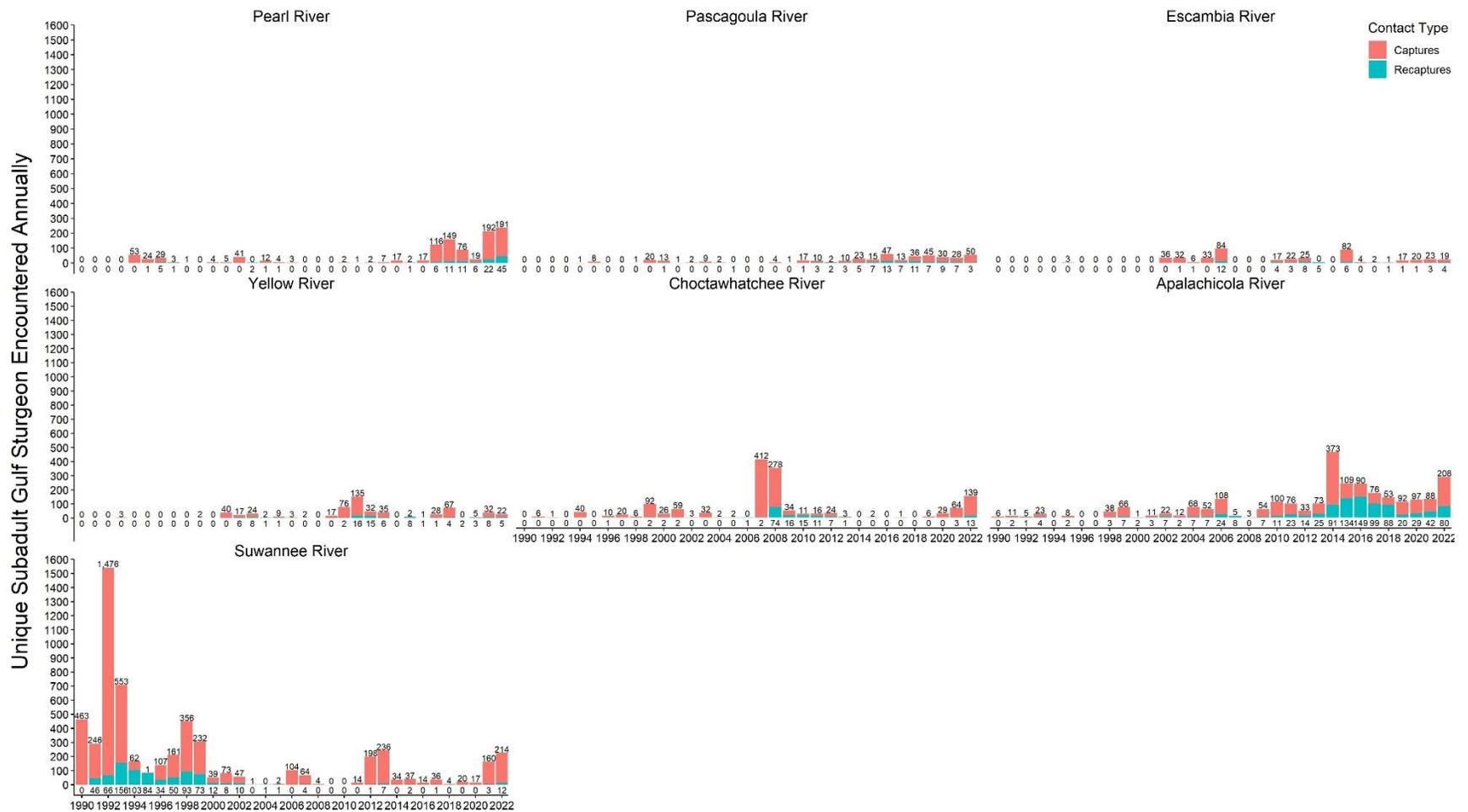


**Figure 1.1. Cumulative number of days (y-axis) adult ( $\geq 1350$ -mm TL) Gulf Sturgeon were captured from 1990-2022 (x-axis) for each river (colored lines). This plot describes the accumulation of days Gulf Sturgeon were caught, but does not include days when Gulf Sturgeon were not caught, because those data are not available.**



**Figure 1.2. Cumulative number of days (y-axis) subadult Gulf Sturgeon (< 1350-mm TL) were captured from 1990-2022 (x-axis) for each river (colored lines). This plot describes the accumulation of days Gulf Sturgeon were caught, but does not include days when Gulf Sturgeon were not caught, because those data are not available.**





## 2. Survival Estimation Using Multistate Models

### Completed as part of Task 1.1

#### Introduction

Gulf Sturgeon are anadromous. They require riverine spawning habitat, estuarine feeding areas, and movement corridors between these habitats to complete their life cycle (USFWS and NOAA 1991). Because Gulf Sturgeon need multiple habitat types to persist, and these habitats each have unique and shared threats, it is necessary to understand and characterize survival over time and space to inform conservation and recovery planning efforts.

Additive anthropogenic mortality (additional mortality to natural mortality processes) may have occurred for Gulf Sturgeon populations in recent decades at various spatial scales, from single rivers (e.g., Temple-Inland paper mill spill; Louisiana Department of Wildlife and Fisheries 2011) to potentially a large portion of Gulf Sturgeon range (*Deepwater Horizon* oil spill; USFWS 2015; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). These events are considered a threat to recovery within the Gulf Sturgeon species recovery plan (USFWS and NOAA 1995). While threats and events that may be associated with such mortality are identifiable at specific spatial scales (e.g., observed Gulf Sturgeon mortality in a single river during or after some event), information on how the spatial scale of such threats relates to the spatial scale of Gulf Sturgeon habitat use is lacking because of uncertainties in how Gulf Sturgeon use space. This knowledge gap makes it difficult to rank threats or prioritize Gulf Sturgeon conservation actions. For example, if Gulf Sturgeon space use is highly restricted to a river basin, then a conservation action directed at a population within an individual river will only benefit the population that uses that river. If space use is distributed across multiple river systems, then a conservation action in one watershed could benefit multiple riverine populations that use that watershed. Threats can be viewed similarly; some threats may only impact a single population, while others may impact multiple populations. Improving our understanding of how Gulf Sturgeon use space within the current critical habitat designation under the Endangered Species Act (ESA; USFWS and NOAA 2003) will help to inform conservation planning and threat assessment efforts as part of ongoing Gulf Sturgeon recovery work.

This task builds on previous studies that documented different Gulf Sturgeon survival or mortality rates among river populations (e.g., Morrow et al. 1998; Rudd et al. 2014) and how Gulf Sturgeon move between river systems. Previous efforts such as Rudd et al. (2014) represented relatively short-term studies, and our current effort takes advantage of a more complete and longer data record to (1) estimate survival rates of adult Gulf Sturgeon while accounting for incomplete detection; (2) estimate adult Gulf Sturgeon river fidelity and straying rates (i.e., movement into rivers not associated with the initial tagging event); and (3) provide initial insight to inform future conservation planning based on these results.

## Methods

### *Acoustic telemetry tagging and monitoring*

A standardized acoustic telemetry monitoring program for adult ( $\geq 1350$  mm TL) Gulf Sturgeon began in 2010 in the seven rivers designated as Gulf Sturgeon critical habitat (Figure 2.1). This program was designed to reduce uncertainty in estimates of survival and movement identified in a Gulf Sturgeon stock assessment (Pine and Martell 2009) to inform ongoing recovery efforts and inform range-wide estimates of adult mortality. Adult Gulf Sturgeon were captured using drifted or anchored gill nets, and telemetry tags were surgically implanted (Table 2.1) following standard methods developed for the congeneric Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* (Kahn and Mohead 2010). Tagged Gulf Sturgeon were virtually recaptured using a network of VEMCO VR2W (and other model) acoustic receivers (Vemco-Amirix Systems, Halifax, Nova Scotia), which were maintained by agency and academic partners as part of the Gulf Sturgeon Working Group. 2.

Gulf Sturgeon movements between the seven river systems included in the ESA critical habitat designation were extracted from the Gulf Sturgeon Database (GSDB; Task 1.1). The rivers of interest included the Pearl, Pascagoula, Escambia, Blackwater/Yellow, Choctawhatchee, Apalachicola, and Suwannee rivers (USFWS and NOAA 2003; Figure 2.1). Due to their proximity and shared estuary (Pensacola Bay), all Blackwater River sampling, including physical captures to initially tag fish and virtual recaptures, were included as part of the Yellow River. We used virtual recaptures of fish detected near the mouth of each river because these locations consistently had receivers deployed in these locations throughout the study. This receiver location protocol maximized the likelihood of Gulf Sturgeon detection during the in and out-migration periods by monitoring areas of the river that functioned as geographically restricted gates and within the detection range of redundant receivers deployed in the river mouths. Data quality assurance, including removal of false detections, was maintained as part of the GSDB. We assumed acoustic transmitter tag longevity based on manufacturer specifications, censoring telemetry tags from analysis after the assigned tag expiration date (Table 2.A1). When these expiration estimates were unavailable, we assumed that transmitter longevity was five years from the initial deployment.

### *Survival and movement rate estimation*

We used a maximum likelihood framework to estimate river- and region-specific survival and movement rates from virtual recaptures (Hightower et al. 2001). We converted virtual recaptures to standard capture history format for multistate capture-recapture models (Williams et al. 2002) in Program MARK (White and Burnham 1999) through RMark (Laake 2013) in Program R (R Core Team 2022). We developed *a priori* models as different hypotheses related to how Gulf Sturgeon survival and transition probabilities may be best represented (similar to Rudd et al. 2014). Models fit to these data assessed temporal and spatial trends in survival and transition probability. Each multistate model estimated the following three parameters:

1. true survival — the probability of surviving to the next time step
2. detection probability — the probability of virtual recapture during each time interval

3. transition rate — the probability that a Gulf Sturgeon moves between rivers or regional areas in a given model

As an extension of the Cormack–Jolly–Seber (CJS) model, the multistate model shares the same basic assumptions (Williams et al. 2002). The traditional CJS framework estimates apparent survival as the joint probability that the animal is alive (true survival) and remains in the study area (Lebreton et al. 1992). Because our receiver array network included all rivers classified as Gulf Sturgeon critical habitat, we assume all individuals stayed in the study area and the survival estimates in this framework represent true survival. Building models which allow the detection probability parameter to vary by river allows us to account for variations in the number of receivers in each river over time. An important aspect of this work is that river mouth receiver locations were maintained throughout the available data period. These receivers were placed to maximize detections of telemetered Gulf Sturgeon as the fish transitioned to or from the riverine environment.

#### *Data characteristics and capture history formatting*

Data on virtual recaptures were compiled, normalized (i.e., organized/reformatted for greater consistency and data integrity), and converted to capture-history format. We condensed virtual recaptures from the receiver array into daily contacts and removed observations that resembled false detections (i.e., daily contacts represented by a single acoustic detection). We then generated individual capture histories on annual time steps for Gulf Sturgeon encountered within the seven rivers of the critical habitat designation between 2010 and 2022. Some Gulf Sturgeon with telemetry tags were implanted prior to 2010 and their tags were viable entering our study period of 2010–2022. We included these 72 individuals tagged between 2005 and 2009 to inform capture histories within the 2010–2022 timeframe. In instances in which transmitter longevity may not have covered the complete period of the study, some Gulf Sturgeon received multiple telemetry tags, and the virtual recaptures of these multiple tags were collapsed into a single capture history (Table 2.1) using the unique fish identification number given to each individual Gulf Sturgeon within the GSDB. Previously embargoed data not available for use in Rudd et al. (2014) is now available, and these data were included in the GSDB for these analyses.

A total of 1,017 Gulf Sturgeon informed our analyses; 985 were tagged as adults (Table 2.1) and 32 were initially tagged as sub-adults (<1350-mm TL; Tables 2.A2–2.A3). Individuals initially telemetered as sub-adults did not contribute to capture histories informing these multistate models until they were physically recaptured, measured, and determined to satisfy the adult length threshold (Table 2.A4).

Other approaches to compiling data to create capture histories exist. For example, only Gulf Sturgeon that were adults at the initial capture size could be included in the analyses, and fish that were observed to grow into the adult size class could have been excluded. Incorporating data associated with fish observed as adults (instead of only those telemetered as adults) led to a larger pool of marked fish across the entire time period. Tables 2.A2–2.A4 summarize these sub-adult data in numbers of acoustic tags deployed in sub-adults, telemetered sub-adult totals as unique fish, and the timing of when these telemetered sub-adults recruited into the adult fish pool for contribution to these analyses.

For Gulf Sturgeon contacts with only FL measurements, we generated a linear model informed by over 42,500 Gulf Sturgeon contacts in the GSDB to predict TL measurements from FL measurements using the following equation:

$$(1) \quad TL = 1.098 * FL + 20.993$$

Capture histories for individual Gulf Sturgeon detected within a given year were denoted with a letter code to represent the state (i.e., river unit in the multistate model) where the detection occurred (Rudd et al. 2014). If we detected an individual Gulf Sturgeon in multiple states (rivers) within a given year, it received the state associated with the most detection days for that occasion (year). Because our capture histories represented annual time steps, we used insight from Gulf Sturgeon life history and assumed that the occupied state was the river a Gulf Sturgeon entered during the spring migration and over-summering period. We also assumed these adult fish left river habitats during fall or early winter (Wooley and Crateau 1985).

### *Multistate model structures*

We fit models estimating detection probability by river and transition probabilities among rivers. While all models shared a common parameterization for detection and transition rates, each model uniquely estimated survival over various spatial and temporal scales representing discrete hypotheses about how Gulf Sturgeon survival patterns may be best represented by these data. Spatial groupings for survival estimation included:

- a range-wide grouping that represented Gulf Sturgeon survival as a single constant rate
- a “region” grouping that collapsed the seven rivers in the critical habitat designation into four geographically separated regions. These regions also represent four genetically distinct units by allele frequency (Stabile et al. 1996): (1) the western Gulf: Pearl and Pascagoula rivers; (2) Pensacola Bay: Escambia and Yellow rivers; (3) Choctawhatchee River; and (4) the eastern Gulf: Apalachicola and Suwannee rivers (Stabile et al. 1996; Figure 2.1). Models with this spatial grouping estimate survival rates by regional group.
- a “river” grouping in which survival was estimated separately for each of the seven river populations.

To explore the potential effects of time on survival, we fit models estimating the additive and multiplicative effects of time on these spatial groupings. A comprehensive suite of models and their associated hypotheses are presented in Table 2.2. We used the delta method to calculate normal-approximated 95% confidence intervals (CI) for all region and river fidelity estimates. We compared models using Akaike Information Criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2004) and AIC weights to determine which spatiotemporal resolution best described the survival patterns in the data. Regional transition rates among genetically distinct units were estimated in a separate regional model as this change to the spatial scale of analysis and the associated likelihood prevented this model from inclusion in the AIC model selection process (which used rivers, not regions, as capture history states).

## Results

### *Tagging summary*

The number of acoustic transmitters annually deployed in adult Gulf Sturgeon ranged from 0 to 64 in each river for a total of 42–343 telemetered adults in each river between 2010 and 2022 (Table 2.1). The annual number of tagged Gulf Sturgeon was lower for rivers in the western Gulf of Mexico (Pearl and Pascagoula; Table 2.1). Because tag longevity was less than the study length for some tags (Table 2.A1), we calculated the annual number of active acoustic tags per river per year (i.e., deployed acoustic tags that were potentially available for virtual recapture based on longevity information). However, accounting for annual fish movement and possible fish death (as indicated by the year following the last known detection) changes the interpretation of number of active transmitters in each river (Tables 2.A5–2.A7). If we account for tag expiration and fish movement, the annual number of active acoustic tags in each river ranged from 2 to 179, with the mean number of active tags each year spanning 14.8–125.6 (Table 2.A6). A more conservative approach that accounts for fish movement and assumes fish died once they were no longer detected yields suggests the mean number of active tags each year spans 8.5–108.8 (Table 2.A7). The percentage of Gulf Sturgeon virtually recaptured in their river of initial tagging ranged between 65.1% (Pearl River) and 93.1% (Choctawhatchee River; Table 2.A8).

### *Survival and detection probability estimation*

Because Gulf Sturgeon research and management occur at multiple spatial scales, we present model results first and then evaluate statistical fit of models from an  $AIC_c$  framework. This ensures that model results of interest that may be used to inform management decisions are not excluded due to their relative performance compared to other models. Information theoretic approaches, such as  $AIC_c$ , can be informative when considering which model of a limited candidate suite best explains the variation observed in the data with relation to the other models evaluated. We use this tool to evaluate which of these models best describes the adult Gulf Sturgeon survival patterns in these data. However, model selection cannot define, and is not informed by, aspects of Gulf Sturgeon ecology or potential management interests such as preserving genetic diversity.

### Spatial estimates

Our null model (Model 1; fewest number of parameters) estimated a constant, range-wide survival rate of 0.89 with a 95% CI of 0.88–0.90 (Table 2.3). Constant regional survival rates (Model 3) were lowest for the western region (0.83) and highest for the Choctawhatchee River (0.93; the Choctawhatchee River population represents its own regional group; Table 2.3). Standard errors for all regional survival rate estimates were low (0.01–0.02; Table 2.3). The Choctawhatchee River survival rate 95% CI did not overlap with any of the other regional confidence intervals, suggesting that the Choctawhatchee River had the highest adult Gulf Sturgeon survival of any region (Table 2.3).

Constant riverine survival rates (Model 3) ranged from 0.85 to 0.92 for all rivers but the Pearl River, where survival was estimated to be 0.71, and the 95% confidence intervals for the Pearl River did not overlap with the other rivers (Table 2.2). Overall, constant river survival estimates were precise (SE smaller than estimate of survival), with relatively small 95% CI ranges (Table 2.3). River-specific

detection probability estimates, which account for variations in the number of receivers in each river, were  $\geq 0.90$  for all rivers except the Yellow River, and standard error estimates were low for all rivers (about 0.01) except the Pearl River (Table 2.3).

#### Time-varying estimates

Across time-varying models (Models 4–8), survival was generally high ( $\geq 0.85$ ). The time model (Model 4; Table 2.3), which considered Gulf Sturgeon as a single stock, suggested that 2013, 2015, and 2016 represented years of lower survival. Annual regional and river survival rates (Models 7–8) support this and suggest that 2015 and 2016 represent the most distinct and most ubiquitous years of lower survival. The 2013 period of low survival was most evident in the Pensacola Bay rivers and the Apalachicola River (Figures 2.2–2.3).

Annual survival rates ranged from 0.32 for the Pearl River in 2015 to 1.0 (Figure 2.3). Survival estimates of 1.0 can be an indicator of poor model parameter fit. We reviewed detection patterns of individual fish in each year and these detection patterns show year-over-year patterns of detecting the same group of marked animals. Therefore, these estimates represent periods of high survival. Precision around estimates of annual survival was more variable between rivers than within rivers across time (Figure 2.3), likely due to differences in sample sizes among rivers. Our results suggest it is more likely that an estimate of 1.0 would occur when the pool of tagged individuals in a river is  $< 50$  (Figure 2.3; Tables 2.A5–2.A7). Pearl River annual survival estimates were the lowest and the most uncertain, exceeding 0.73 only once between 2010 and 2016 (Figure 2.3). In contrast, Choctawhatchee River survival rates were below 0.79 once and remained consistently high (between 0.91 and 1.0) in most years (Figures 2.2–2.3).

#### *Fidelity and exchange among rivers and regions*

Fidelity to the river of tagging ranged from 63% (Escambia River) to 99% (Suwannee River; Table 2.5). Fidelity was  $\geq 80\%$  for all rivers except the Escambia River, and the precision around these estimates was relatively high (Table 2.5). Grouping the Escambia and Yellow rivers together estimated the regional fidelity of Pensacola Bay to be similarly high at 90% (Table 2.6). The exchange between rivers ranged from movement from the river of tagging to one other river (observed in the Pearl River) to movement to four other rivers (observed in the Pascagoula, Escambia, Yellow, Choctawhatchee, and Apalachicola rivers; Table 2.5). Overall, exchange rates were generally low (1–4%) for most rivers (Table 2.5). Riverine transition probabilities that were  $\geq 10\%$  annually included Pearl-to- Pascagoula (11%), Escambia-to- Yellow (24%), Escambia-to-Choctawhatchee (10%), and Yellow-to-Escambia (11%). The highest estimated exchange rate between regions was estimated as 9% for Gulf Sturgeon transitioning from the Pensacola Bay rivers to the Choctawhatchee River (Table 2.6). The only other regional transition probability estimate  $> 2\%$  was the reciprocal rate of Gulf Sturgeon moving from the Choctawhatchee River to the Pensacola Bay rivers (8%; Table 2.6). There was a  $\sim 2\%$  annual probability of Gulf Sturgeon leaving the eastern or western regions and being detected in another region (Table 2.6).

All observed transitions between rivers are summarized in Figure 2.A1. For example, we observed 961 instances of Choctawhatchee River-tagged fish being detected in the Choctawhatchee River in two consecutive years. If a particular fish was detected in four consecutive years in the Choctawhatchee

River, that would represent three observed transitions back to the Choctawhatchee River. In contrast, only one Choctawhatchee River-sourced fish was observed in the Choctawhatchee River one year and in the Pascagoula River the next year.

### *AIC model comparison*

Information-theoretic model selection suggests best statistical fit for Model 7 (lowest  $AIC_c$  value, highest AIC weights), a model with unique survival parameters for each region and year (Table 2.7). The river-specific model received an AIC weight of 1, and no other models had a  $\Delta AIC_c < 10$  (Table 2.7). The model with the most parameters (114 parameters; Model 8) received the second most support, and the model with the fewest parameters (31; Model 1) received the least support (Table 2.7). Models that estimated survival over time were ranked the higher than models that did not. Models that estimated shared trends in survival across the Gulf (additive models; Models 5–6) did not perform as well as models that generated independent estimates of survival over both space and time (interactive models; Models 5–6).

## **Discussion**

We address a key knowledge gap by estimating spatially explicit survival and transition rates for all Gulf Sturgeon river populations designated as critical habitat. Years of low survival were generally characterized by sudden declines beneath some baseline survival rate, followed by similarly sharp increases back towards this baseline. Such large, sudden departures from baseline survival may suggest these sources of mortality are episodic (i.e., event-based mortality that is separate and/or more intense than normal chronic mortality), which is consistent with threats associated with documented Gulf Sturgeon mortality events such as red tide, spills, and major hurricanes (USFWS and NMFS 2022). We found adult Gulf Sturgeon survival rates in the western U.S. Gulf of Mexico were lower and more uncertain than in the eastern Gulf. Additive models which estimated the same temporal trends for all populations had higher  $AIC_c$  values than models that estimated differing temporal survival trends for different regions and rivers. Model selection results suggest that Gulf Sturgeon survival is best represented by individual estimates for each region and year. Collectively, these results indicate that chronic and/or episodic mortality differs among these populations but is most similar within geographic regions.

Annual river-specific survival estimates (Figure 2.3) suggest lower survival rates in the Pearl River (a western Gulf of Mexico River) than in the other six rivers where survival was estimated. This suggests that the lower estimated survival in the Pearl River may be the driver for lower survival for the pooled western Gulf of Mexico estimate, but the Pascagoula River also had high uncertainty around annual survival estimates related to low sample sizes (Figures 2.2–2.3; Tables 2.A5–2.A7). These lower annual survival rates in the western Gulf of Mexico (first identified by Morrow et al. 1998) likely reflect higher annual adult mortality, from unknown sources, within the western portion of the Gulf Sturgeon range.

We observed low survival in the Apalachicola River in 2018 (0.69), the same year Hurricane Michael made landfall as a category 5 hurricane in this region. Our survival estimate for this year in the Apalachicola is concordant with the empirical mortality calculation of undetected fish by Dula et al.

(2022) in their evaluation of the effects of Hurricane Michael on Gulf Sturgeon in the Apalachicola River. Empirical estimates of episodic mortality intensity and frequency are of critical importance to future evaluations of the effects of possible mortality scenarios on individual population viability and species persistence as a whole.

We documented high adult Gulf Sturgeon fidelity rates (generally  $\geq 90\%$  to the river/region of detection), which supports the hypothesis that the differential survival we observed may be a result of different threats facing different river populations/regions. If fidelity was low and widespread exchange among populations was occurring, it would be harder to assess whether threats differ across space. If adult survival rates were the same across the Gulf, we would have reason to believe the threats facing these fish, or the resilience of these populations, were similar. Our estimates of differential survival highlight the importance of considering whether these differences are a function of different risks or reflect natural variation in the life history of Gulf Sturgeon across its range.

To assess the robustness of our conclusions about adult Gulf Sturgeon population dynamics to different ways the data could be organized, we performed the same analyses with a dataset that only included Gulf Sturgeon tagged as adults. This dataset did not include Gulf Sturgeon tagged as juvenile who were included in the analyses once they were known to reach adult size based on physical recapture. The results were nearly identical as the larger dataset which exhibited marginal increases in precision because of the inclusion of additional fish. This suggests that creating capture histories including fish tagged as sub-adults that grew into the adult size class to inform our analyses did not lead to substantial increases in precision or any other changes in our inferences from these analyses.

### *Comparison with previous studies*

The multistate model estimates in our study expand on earlier efforts (Rudd et al. 2014) to estimate these parameters before the *Deepwater Horizon* oil spill and subsequent data embargo related to the associated litigation. Making use of all available telemetry data via the GSDB to generate the most informed estimates of survival and transition probability were a major motivation for these analyses. The estimation methods, models, and assumptions in Rudd et al. (2014) and this chapter are the same, but this effort represents a much larger sample size than Rudd et al. (2014), both in the number of telemetered fish available for analyses in each year, relocation data available in each year, and the number of years of study. The Rudd et al. (2014) spatial patterns in river-specific survival estimates were generally the same as what was observed in this study. The Rudd et al. (2014) survival estimates, which were informed only by less than three years of data (June 2010 to June 2012) were higher than those in this study for all rivers except the Pascagoula River. Our survival estimates, informed by data from 2010 to 2022, were within the 95% CI's associated with the survival estimates in Rudd et al. (2014) for all rivers except the Pascagoula River. In the Pascagoula we estimated survival to be 0.87 and Rudd et al. (2014) estimated survival as 0.51. The annual survival estimates in Model 8 show that we also estimated survival to be low in 2010 (0.50) and 2011 (0.75), which are similar to the estimates for the same years included in Rudd et al. (2014). After 2011 (data not included in Rudd et al. (2014)), we saw survival increase and remain above 0.85 in most years which demonstrates an improving period of survival for Pascagoula River Gulf Sturgeon. Estimated capture probabilities from virtual recaptures were high in

both studies compared to traditional mark-recapture tagging estimates (not informed by virtual recaptures) for Gulf Sturgeon (generally  $\sim 0.10$ ; Zehfuss et al. 1999; Sulak et al. 2014).

#### *Informing future research: monitoring time*

We improved the precision of survival and transition probability estimates for adult Gulf Sturgeon from estimates in Rudd et al. (2014). There was significant uncertainty following the 2009 Gulf Sturgeon stock assessment as to whether survival could be estimated from a telemetry study over a three-year time period because it was possible that survival would be near 100% over the short time period of observation based on Gulf Sturgeon life history and previous survival estimates (Pine et al. 2001). Rudd et al. (2014) simulated the bias and precision of the same multistate capture-recapture model under a variety of scenarios involving different numbers of tags deployed each year and the number of years the tags were monitored. Their assessment of the tradeoffs between increased sample size or monitoring program length suggested that longer monitoring periods led to more precise parameter estimates (Rudd et al. 2014). An important outcome of this task is that our results empirically support the Rudd et al. (2014) simulations and demonstrate that extended monitoring time ( $>5$  years), represented by the total years of array deployment and the pool of active tags in each river, yielded more precise survival estimates than the shorter ( $<5$  year) study.

#### *Informing future research: transmitter deployments and tagged-fish pool size*

Variations in the capture rate and tagging effort in each river created patterns of how the pool of telemetered fish in each river was created and how additional sturgeon were added to the population of marked animals. These variations allow basic assessments of different strategies that can be used to inform the allocation of sampling resources (e.g., effort, telemetry tags) to estimate adult Gulf Sturgeon survival. For example, only 43 acoustic tags were implanted in the Yellow River in Gulf Sturgeon over the last 9 years of the study. But because most Gulf Sturgeon that were tagged in the Yellow River were marked with long-lived 5- to 10-year tags near the beginning of our study, these tagged fish were observed over a longer period of time (Table 2.A1). Since Gulf Sturgeon survival is high relative to shorter-lived species, the pool of marked Gulf Sturgeon in the Yellow River persisted throughout the study resulting in a precise river-specific survival estimate ( $SE=0.014$ ; Model 3). In contrast, annual acoustic transmitter deployments were consistent in the Pascagoula River where smaller numbers of shorter-lived tags were deployed each year. Despite the Pascagoula River representing the second lowest average number of active transmitters available for detection, the difference in standard errors for the Pascagoula River and Yellow River survival estimates was about 0.006 (Model 3; Table 2.3), and the survival estimates in both systems covered the same number of years, despite their differences in tag longevity (Table 2.A1). The tagging approach in the Pascagoula River is similar to the staggered-entry design described by (Pollock et al. 1989). Both this staggered-entry approach in the Pascagoula River and the alternate approach of deploying a larger number of long-lived tags early in the study period in the Yellow River resulted in adequate sample sizes for river-specific survival estimation with relatively high precision. In both of these cases the pool of marked fish was maintained or supplemented over a long period of time, an outcome that would not result from the deployment of a large number of short-lived tags over a short period of time.

Despite differences in the numbers of total tags deployed, tag longevity, and active transmitters available for detection each year in each river, we generated precise survival estimates (SE 0.01–0.02; Model 3; Table 2.3) for rivers that averaged at least five acoustic tag deployments per year (Table 2.1). Estimating river-specific survival rates was the motivating factor for range-wide telemetry tagging efforts following the 2009 Gulf Sturgeon stock assessment. An examination of the trends in both the number of transmitters and transmitter longevity showed that a variety of tag deployment strategies are likely viable within this extended monitoring time framework, where monitoring time appears to be the greatest limiting factor on precision for estimating river-specific survival.

Models that estimate annual survival rates for each river (as in Model 8) instead of single, constant rates (as described above in Model 3) have greater data requirements due to the greater number of survival parameters estimated. These data requirements can be thought of in terms of observations of telemetered fish each year in each river. From the available data for adult Gulf Sturgeon, we can use the Choctawhatchee River (which represents largest number of telemetered adult Gulf Sturgeon and largest pool of 10-year acoustic tags) to establish our expectations for attainable precision levels. For the Choctawhatchee River we estimated a constant river-specific survival rate with SE=0.008 (i.e., represented by a 95% CI  $\pm$  0.01–0.02 of the estimate; Model 3). Annual survival estimates for the Choctawhatchee River showed a decline in precision to about SE=0.029 (i.e., represented by 95% CIs generally  $\pm$  0.03–0.11 around the estimate). This precision range associated with annual survival estimation likely represents a best-case scenario approximating the upper limit of resource allocation and parameter precision than can be achieved.

To further inform future sampling efforts, we empirically evaluated the tradeoffs between parameter precision and the number of adult Gulf Sturgeon available for detection by plotting the number of active acoustic transmitters available for detection by river (as defined in Table 2.A7) vs. the precision of the annual survival estimate for the same river and year (Figure 2.A2). By using the definition of “active acoustic transmitters available for detection by river” from Table 2.A7, we explicitly accounted for annual fish movement between rivers (as opposed to only generating this number from annual tag deployments) and also generated a conservative estimate of tags available for detection that more closely resembles how the models interpret these data each year by assuming fish were no longer available for detection after the last year they were detected (instead of when the tag was assumed to expire). As expected, the annual survival estimates with the least precision were associated with the years with the fewest telemetered fish. As the tag pool size increased, there is an inflection point at between 30 and 50 telemetered fish where the precision does not improve at the same rate with greater numbers of tagged adult Gulf Sturgeon. However, there were increases in precision beyond this point as the most precise estimate was associated with a tagged-fish pool size of 111 individuals. Because this investigation into the relationship between tag pool size and annual survival rate precision uses real data, and these monitoring programs did not control for tag longevity or standardize deployment schedules, exploration into this relationship via simulation is needed to further quantify precision thresholds relevant to management decisions, and to better understand the influence of longer capture histories on precision. The continued evolution of tagging technology, which has improved tag reliability and battery life, coupled with long-term monitoring, may result in larger improvements in parameter estimates of survival than other actions (see below).

### *Future research implications: planning*

If survival or transition probabilities are the primary parameters of management interest, we recommend continued monitoring of previously tagged Gulf Sturgeon and the maintenance of a living data system (Yenni et al. 2019). To efficiently manage funding in the context of uncertain research budgets, future acoustic tag deployments in these rivers to increase or maintain tagged pools of telemetered Gulf Sturgeon must be informed by estimates of the current tagged-fish pool size and motivated by a quantifiable expectation of what these efforts will yield in parameter precision needed to inform decision-making. To increase efficiency, minimize cost, and maximize inference gained from a telemetry-based monitoring program we provide the following recommendations: (1) clearly define population parameters of interest and commit to monitor those parameters. Virtual recaptures using telemetry tags and autonomous receivers are a recaptures only data type (Williams et al. 2002), which is appropriate for estimating survival but not in estimating abundance (because there is no information on unmarked animals). As demonstrated in this project, the virtual recaptures from an autonomous telemetry array designed to capture animal movements into more restricted movement habitats (rivers) from open estuarine habitats provided higher capture probabilities than passive tagging studies, which resulted in lower uncertainty in estimates of survival. However, this improvement in survival estimates is only realized if survival is the parameter that informs management decisions; (2) determine acceptable levels of precision for parameter estimates. In a classic paper, Robson and Regier (1964) offer precision levels of 0.1 as the required minimum level for “careful research into population dynamics” for determining sample size in estimating abundance, and this level of precision likely applies to survival as well. Ultimately the level of precision required to inform decision making should be determined prior to beginning the tagging study and then informed through simulation or empirical assessments such as Rudd et al. (2014) and this effort.

### **Conclusions**

These analyses of Gulf Sturgeon survival and fidelity patterns across their range suggests spatially distinct mortality patterns, and thus realized threats, on these populations which may delay population recovery across the range of Gulf Sturgeon (Flowers et al. 2020). Future research assessing these potentially differing threats should focus on the sources of mortality and whether or not this can be influenced by management actions. For example, if the differences in mortality are related to large-scale environmental conditions such as red tide, then management actions to reduce red tide mortality risks are likely limited solely to benefit Gulf Sturgeon. Alternatively, if the mortality source is an in-river effect, then the high fidelity rate suggests a local management action to reduce this mortality would likely benefit that population. Restoration actions intended to facilitate Gulf Sturgeon population recovery overall should consider these differences in survival among river populations and not expect localized restoration actions to have benefits that extend beyond the populations within an individual population. Our results combined with age-structured modeling work in Flowers et al. (2020) suggest that management actions that increase adult survival in the western Gulf of Mexico may be beneficial to Gulf Sturgeon population recovery as a whole.

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## Tables and Figures

**Table 2.1. The annual number of acoustic transmitters surgically implanted in adult ( $\geq 1350$ -mm TL) Gulf Sturgeon by river and year of deployment. Tag models and performance characteristics vary.**

River	Year													Total
	Before	2010	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	
Pearl	0	23	3	0	5	0	0	1	2	0	0	0	8	42
Pascagoula	0	2	3	3	5	5	8	9	3	7	13	8	5	71
Escambia	9	27	16	6	0	0	17	5	5	6	5	0	0	96
Yellow	27	64	41	21	0	0	17	10	9	6	1	0	0	196
Choctawhatchee	34	46	33	29	30	0	0	11	5	60	60	7	28	343
Apalachicola	1	21	15	18	0	0	8	13	13	16	4	9	0	118
Suwannee	2	20	31	24	0	0	0	16	13	15	5	23	0	149
	73	203	142	101	40	5	50	65	50	110	88	47	41	1,015

**Table 2.2. Model numbers, names, and associated hypotheses for eight multistate models estimating adult Gulf Sturgeon survival probability. All models shared the same parameterizations for detection probability and transition probability.**

<b>Model number</b>	<b>Model name</b>	<b>Model hypotheses</b>
1	Null	Adult survival is constant across space and time, and can be best represented by a single range-wide rate across time
2	Region	Adult survival rates differ among regional groups of river populations, but survival rates over time are constant within each regional group
3	River	Adult survival rates differ among river populations, but survival rates over time are constant within each river population
4	Time	Adult survival rates are the same for all river populations, but survival trends over time are variable
5	Region plus time	Adult survival rates differ among regional groups of river populations, but the survival trends over time are the same for all regional groups
6	River plus time	Adult survival rates differ among river populations, but the survival trends over time are the same for all river populations
7	Region over time	Adult survival rates differ among regional groups of river populations, and the survival trends over time also differ among these regional groups
8	River over time	Adult survival is so different across space and time that each river is best represented by its own survival estimate each year

**Table 2.3. Survival probabilities for adult Gulf Sturgeon ( $\geq 1350$ -mm TL) with upper (UCL) and lower (LCL) 95% confidence limits from Models 1–4. Each model provides spatial estimates that are constant over time or temporal estimates that are shared across space.**

Model number	Area or time	Estimate	LCL	UCL
<u>Range-wide</u>				
1	Constant	0.89	0.88	0.90
<u>Region</u>				
2	West	0.83	0.79	0.87
2	Pensacola Bay	0.87	0.84	0.89
2	Choctawhatchee	0.93	0.91	0.94
2	East	0.88	0.86	0.90
<u>River</u>				
3	Pearl	0.71	0.61	0.79
3	Pascagoula	0.87	0.83	0.90
3	Escambia	0.86	0.82	0.90
3	Yellow	0.87	0.84	0.90
3	Choctawhatchee	0.93	0.91	0.94
3	Apalachicola	0.86	0.82	0.89
3	Suwannee	0.89	0.87	0.92
<u>Year</u>				
4	2010	0.91	0.85	0.95
4	2011	0.92	0.88	0.95
4	2012	0.89	0.85	0.92
4	2013	0.76	0.71	0.80
4	2014	0.89	0.84	0.92
4	2015	0.72	0.66	0.78
4	2016	0.76	0.70	0.81
4	2017	0.95	0.91	0.98
4	2018	0.93	0.89	0.95
4	2019	0.97	0.94	0.98
4	2020	0.96	0.93	0.98
4	2021	0.97	0.93	0.98

**Table 2.4. River-specific detection probabilities for adult Gulf Sturgeon from Model 3 ( $\geq 1350$ -mm TL) with upper (UCL) and lower (LCL) 95% confidence limits.**

<b>River</b>	<b>Estimate</b>	<b>LCL</b>	<b>UCL</b>
Pearl	0.90	0.76	0.96
Pascagoula	0.98	0.95	0.99
Escambia	1.00	0.11	1.00
Yellow	0.72	0.68	0.77
Choctawhatchee	0.99	0.97	1.00
Apalachicola	0.94	0.90	0.96
Suwannee	0.99	0.98	1.00

**Table 2.5. Transition probabilities of adult Gulf Sturgeon ( $\geq 1350$ -mm TL) movement between rivers with 95% confidence intervals (CI) in parentheses. Columns indicate the river occupied in a given sampling occasion, and rows denote possible destinations in the following sampling occasion. Estimates along the diagonal represent river fidelity rates. An “x” represents an unobserved transition during the study.**

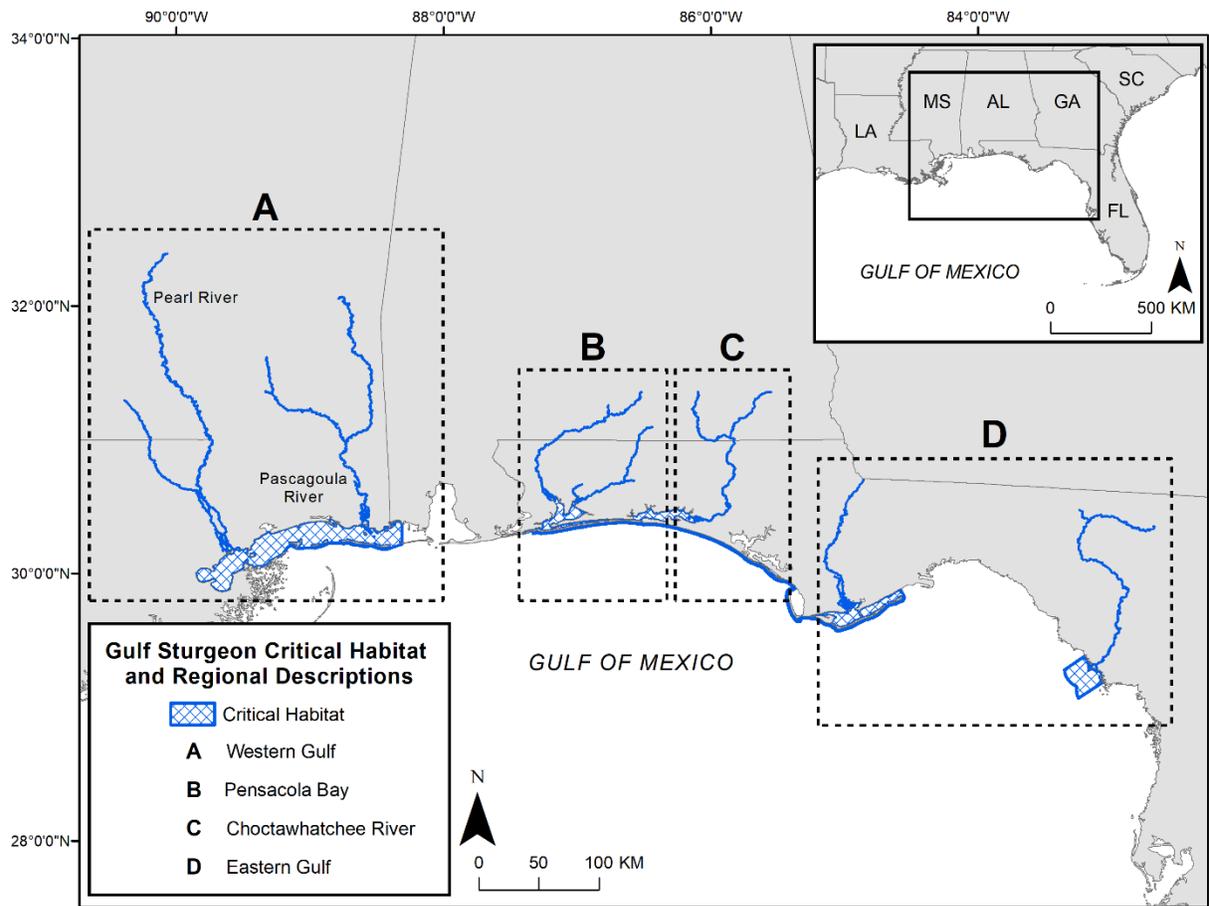
	Pearl	Pascagoula	Escambia	Yellow	Choctawhatchee	Apalachicola	Suwannee
Pearl	0.89 (0.81, 0.96)	0.02 (0.01, 0.05)	x	x	x	x	x
Pascagoula	0.11 (0.06, 0.21)	0.95 (0.93, 0.98)	0.01 (0.00, 0.03)	0.01 (0.00, 0.02)	0.00 (0.00, 0.01)	x	x
Escambia	x	0.02 (0.01, 0.04)	0.63 (0.57, 0.69)	0.11 (0.09, 0.13)	0.03 (0.02, 0.04)	0.01 (0.00, 0.02)	x
Yellow	x	0.00 (0.00, 0.03)	0.24 (0.19, 0.30)	0.80 (0.77, 0.83)	0.05 (0.03, 0.06)	0.01 (0.01, 0.04)	0.00 (0.00, 0.01)
Choctawhatchee	x	0.00 (0.00, 0.03)	0.10 (0.07, 0.14)	0.08 (0.06, 0.11)	0.91 (0.89, 0.93)	0.03 (0.02, 0.05)	x
Apalachicola	x	x	0.01 (0.00, 0.04)	0.00 (0.00, 0.01)	0.01 (0.01, 0.02)	0.93 (0.91, 0.96)	0.01 (0.00, 0.02)
Suwannee	x	x	x	x	x	0.02 (0.01, 0.04)	0.99 (0.98, 1.00)

**Table 2.6. Regional transition probabilities of adult Gulf Sturgeon ( $\geq 1350$ -mm TL) movement with 95% confidence intervals (CI) in parentheses. Columns indicate the region occupied in a given sampling occasion, and rows denote possible destinations in the following sampling occasion. Estimates along the diagonal represent fidelity estimates. An “x” represents an unobserved transition during the study.**

	<b>West</b>	<b>Pensacola Bay</b>	<b>Choctawhatchee</b>	<b>East</b>
West	0.98 (0.97, 1.00)	0.01 (0.00, 0.02)	0.00 (0.00, 0.01)	x
Pensacola Bay	0.02 (0.01, 0.04)	0.90 (0.88, 0.92)	0.08 (0.06, 0.10)	0.01 (0.01, 0.02)
Choctawhatchee	0.00 (0.00, 0.02)	0.09 (0.07, 0.11)	0.91 (0.89, 0.93)	0.01 (0.01, 0.02)
East	x	0.01 (0.00, 0.01)	0.01 (0.01, 0.02)	0.98 (0.97, 0.99)

**Table 2.7. Model selection table describing Akaike Information Criterion corrected for small sample size ( $AIC_c$ ), including the difference between each model's  $AIC_c$  score and the top model's  $AIC_c$  score ( $\Delta AIC_c$ ), the number of parameters (K), the negative log-likelihood (nll), and the weight of each model for three competing models characterizing adult Gulf Sturgeon survival (S), detection probability (p), and transition probability (Psi).**

Model number	Model name	Model parameterization	$\Delta AIC_c$	K	nll	AIC weight
7	Region over time	$S(\text{region}*\text{time}) p(\text{river}) Psi(\text{river to river})$	0.00	78	6001.14	1.00
8	River over time	$S(\text{river}*\text{time}) p(\text{river}) Psi(\text{river to river})$	12.91	114	5938.19	<0.01
6	River plus time	$S(\text{river}+\text{time}) p(\text{river}) Psi(\text{river to river})$	25.84	48	6089.07	<0.01
5	Region plus time	$S(\text{region}+\text{time}) p(\text{river}) Psi(\text{river to river})$	29.10	45	6098.48	<0.01
4	Time	$S(\text{time}) p(\text{river}) Psi(\text{river to river})$	49.99	42	6125.51	<0.01
3	River	$S(\text{river}) p(\text{river}) Psi(\text{river to river})$	207.36	37	6293.10	<0.01
2	Region	$S(\text{region}) p(\text{river}) Psi(\text{river to river})$	215.35	34	6307.21	<0.01
1	Null	$S(\text{constant}) p(\text{river}) Psi(\text{river to river})$	240.35	31	6338.32	<0.01



**Figure 2.1.** Map of Gulf Sturgeon critical habitat in the Gulf of Mexico. River populations included in this study from west to east are the Pearl, Pascagoula, Escambia, Yellow, Choctawhatchee, Apalachicola, and Suwannee rivers. Letters indicate genetically distinct regional units identified by Stabile et al. (1996) that represent regional groupings of river populations. Inset: map of the US Gulf coast. This map was produced using the WGS1984 projection and Gulf Sturgeon critical habitat GIS data sourced from NOAA (Available at <https://www.fisheries.noaa.gov/resource/map/gulf-sturgeon-critical-habitat-map-and-gis-data>).

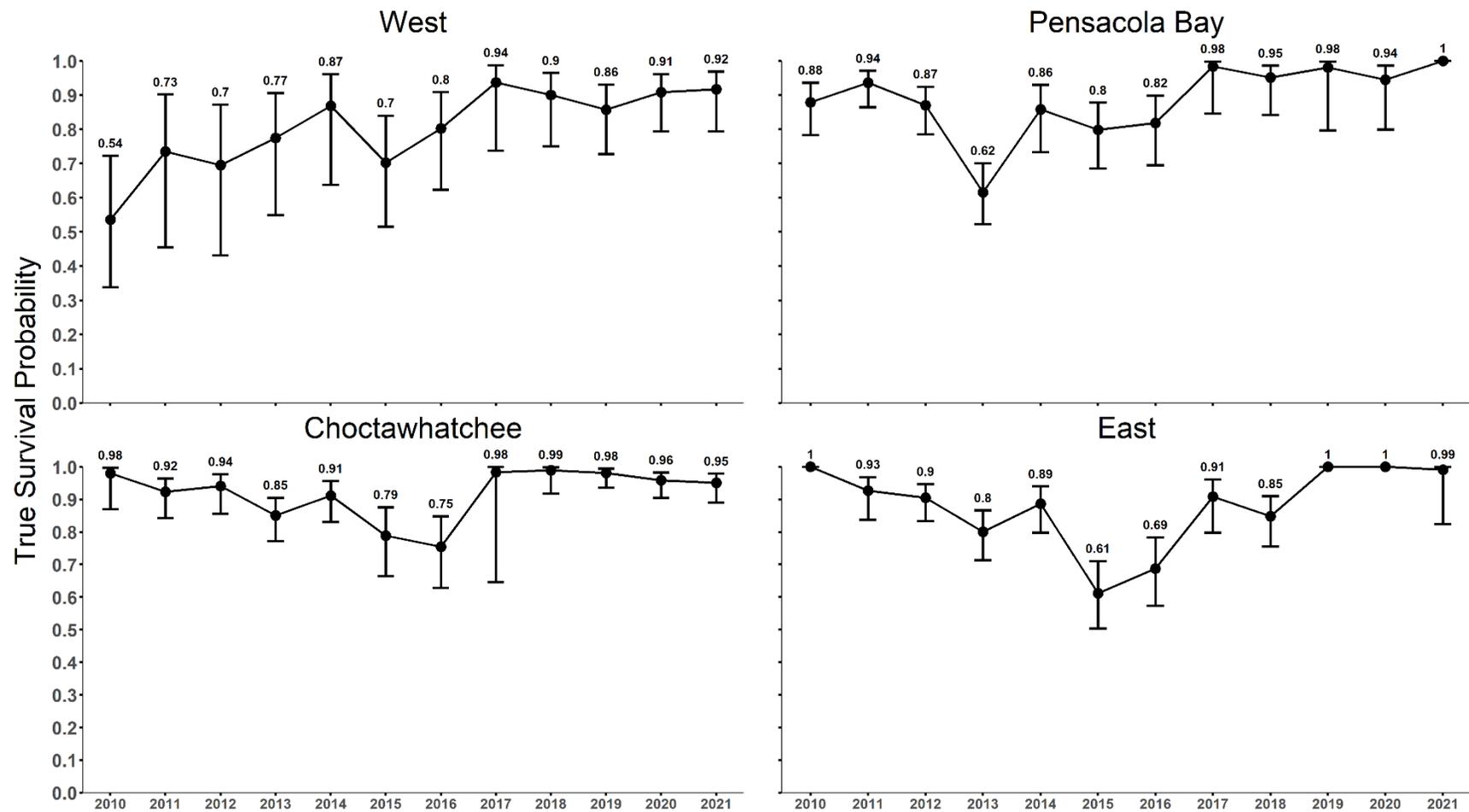


Figure 2.2. Annual regional survival probabilities for adult Gulf Sturgeon ( $\geq 1350$ -mm TL) from Model 7.

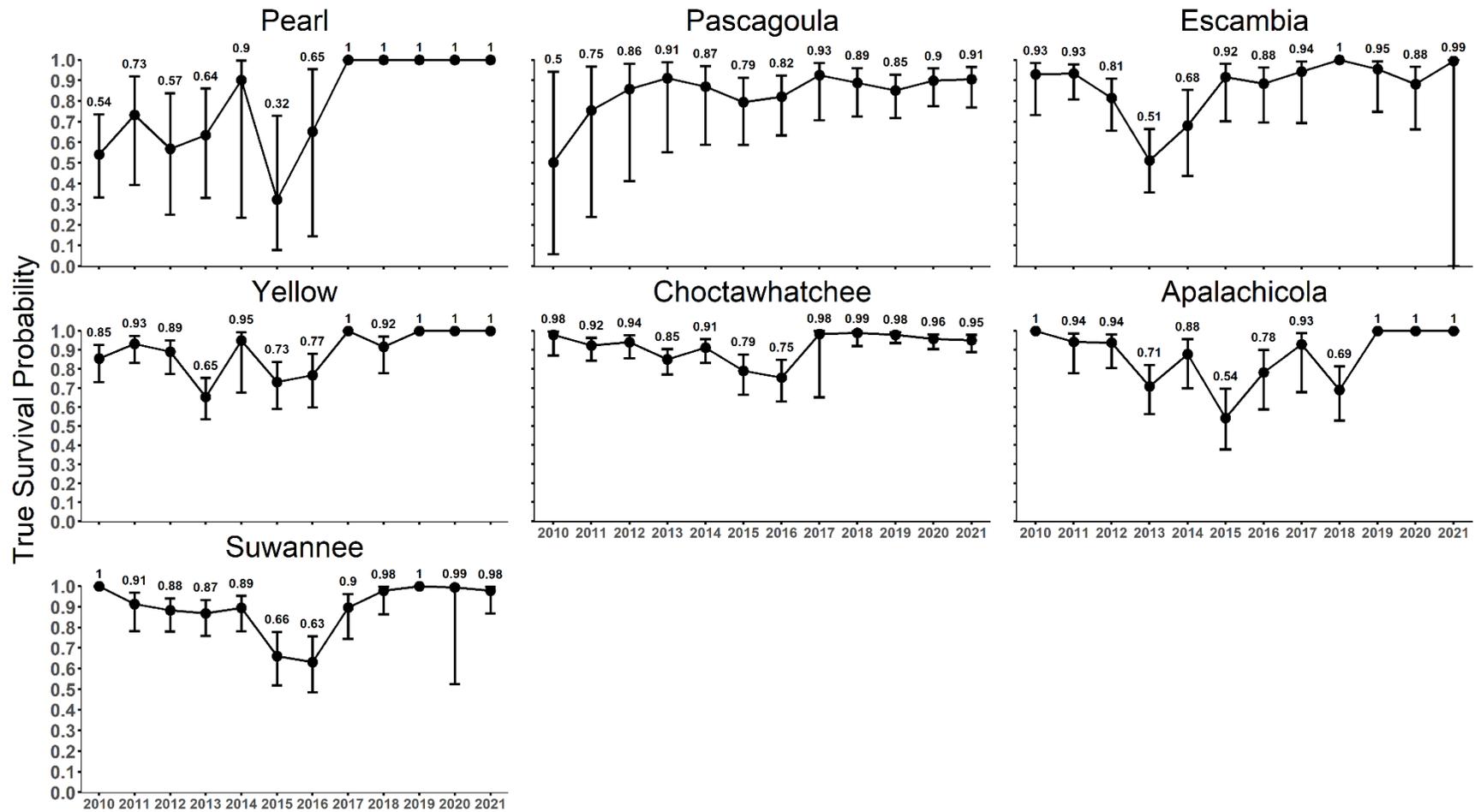


Figure 2.3. Annual river-specific survival probabilities for adult Gulf Sturgeon ( $\geq 1350$ -mm TL) from Model 8.

## Appendix

**Table 2.A1. Number of acoustic tags implanted in adult ( $\geq 1350$ -mm TL) Gulf Sturgeon summarized by battery life and river of deployment. Only tags that informed analyses (deployed before 2022) are summarized. Tags without longevity information were assumed to have a five-year longevity.**

River	Acoustic tag battery life										Total
	1-year	2-year	3-year	4-year	5-year	6-year	7-year	8-year	9-year	10-year	
Pearl	1	13	0	0	2	17	0	0	1	8	42
Pascagoula	0	1	0	0	12	14	0	0	17	27	71
Escambia	3	0	0	6	36	29	0	0	0	23	97
Yellow	4	0	1	22	46	97	0	0	0	26	196
Choctawhatchee	23	25	19	13	85	60	0	0	0	120	345
Apalachicola	8	0	1	0	0	52	0	0	9	48	118
Suwannee	1	10	0	0	0	60	0	0	0	78	149
	40	49	21	41	181	329	0	0	27	330	1018

**Table 2.A2. The annual number of acoustic transmitters surgically implanted in sub-adult Gulf Sturgeon (<1350-mm TL) by river and year of deployment. Individual fish that were implanted with an acoustic tag in multiple years contributed to more than one annual total. Each sub-adult Gulf Sturgeon later contributed to analyses (i.e., grew into inclusion) once it was recaptured and determined to be an adult (≥1350-mm TL).**

River	Year												Total
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	
Pearl	0	0	0	0	0	0	0	2	0	0	0	0	2
Pascagoula	6	3	1	1	4	1	6	3	5	1	0	0	31
Escambia	1	0	0	0	0	0	0	0	0	0	0	0	1
Yellow	1	0	0	0	0	0	0	0	0	0	0	0	1
Choctawhatchee	1	0	1	0	0	0	0	0	0	0	0	0	2
Apalachicola	0	1	2	0	0	0	0	0	0	0	0	0	3
Suwannee	0	0	0	0	0	0	0	0	0	0	0	0	0
	9	4	4	1	4	1	6	5	5	1	0	0	40

**Table 2.A3. Annual totals of telemetered sub-adult Gulf Sturgeon (<1350-mm TL) by river and initial year of tagging. Each sub-adult fish only contributed to the total associated with its initial capture. Each sub-adult Gulf Sturgeon contributed to analyses (i.e., grew into inclusion) once it was recaptured and determined to be an adult (≥1350-mm TL).**

River	Year												Total
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	
Pearl	0	0	0	0	0	0	0	2	0	0	0	0	2
Pascagoula	5	1	1	0	3	1	5	3	3	1	0	0	23
Escambia	1	0	0	0	0	0	0	0	0	0	0	0	1
Yellow	1	0	0	0	0	0	0	0	0	0	0	0	1
Choctawhatchee	1	0	1	0	0	0	0	0	0	0	0	0	2
Apalachicola	0	1	2	0	0	0	0	0	0	0	0	0	3
Suwannee	0	0	0	0	0	0	0	0	0	0	0	0	0
	8	2	4	0	3	1	5	5	3	1	0	0	32

**Table 2.A4. Annual totals representing the first year that Gulf Sturgeon tagged in these rivers as sub-adults (<1350-mm TL) grew into inclusion in our adult dataset (≥1350-mm TL). Each sub-adult was initially telemetered during a year prior to the totals summarized here. These totals do not reflect all years these fish contributed to analyses, but rather the first year they recruited into our adult dataset.**

River	Year												Total
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	
Pearl	0	0	0	0	0	0	0	0	1	0	0	1	2
Pascagoula	0	0	0	1	0	1	2	1	3	3	8	4	23
Escambia	0	1	0	0	0	0	0	0	0	0	0	0	1
Yellow	0	1	0	0	0	0	0	0	0	0	0	0	1
Choctawhatchee	0	0	0	0	0	0	0	0	2	0	0	0	2
Apalachicola	0	0	0	0	2	1	0	0	0	0	0	0	3
Suwannee	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	2	0	1	2	2	2	1	6	3	8	5	32

**Table 2.A5. Annual totals of Gulf Sturgeon with active acoustic transmitters available for detection by river. Gulf Sturgeon with viable transmitters (informed by longevity information) only contribute to annual active transmitter totals for the river associated with their initial tag deployment. This summary excludes 2022 tag deployments that didn't inform analyses.**

River	Year												
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Pearl	23	24	23	16	16	17	18	11	8	8	3	12	12
Pascagoula	2	5	8	14	19	28	37	37	45	60	70	71	71
Escambia	26	49	54	54	54	65	55	45	39	40	40	23	23
Yellow	62	123	146	148	147	143	127	95	62	43	43	26	26
Choctawhatchee	67	109	118	123	114	113	101	85	126	137	143	171	171
Apalachicola	20	34	52	52	54	62	75	59	61	47	57	57	55
Suwannee	22	45	73	74	69	66	82	73	69	54	78	78	72
	222	389	474	481	473	494	495	405	410	389	434	438	430

**Table 2.A6. Annual totals of Gulf Sturgeon with active acoustic transmitters available for detection by river. This summary accounts for movement between rivers. Gulf Sturgeon with viable transmitters (informed by longevity information) contribute to annual active transmitter totals for the river associated with their most recent detection.**

River	Year												
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Pearl	23	24	23	16	16	16	17	11	9	8	6	13	11
Pascagoula	2	5	9	14	19	30	39	38	45	60	67	70	72
Escambia	26	56	51	57	60	68	53	40	31	32	38	20	29
Yellow	62	119	138	132	131	138	121	94	66	42	42	25	27
Choctawhatchee	67	107	127	134	121	113	106	91	129	145	148	179	166
Apalachicola	20	33	54	55	56	62	76	56	60	47	53	53	53
Suwannee	22	45	72	73	70	67	83	75	70	55	80	78	72
	222	389	474	481	473	494	495	405	410	389	434	438	430

**Table 2.A7. Annual totals of Gulf Sturgeon with active acoustic transmitters available for detection by river. This summary accounts for movement between rivers, simulated tag death, and possible fish death. Gulf Sturgeon with viable transmitters (informed by longevity information) contribute to annual active transmitter totals for the river associated with their most recent detection. Individuals are considered to be dead, even if they have a viable transmitter, one year after the year in which they were last detected.**

River	Year												
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Pearl	23	13	9	11	7	6	3	5	4	3	5	12	9
Pascagoula	2	4	7	11	15	24	29	25	34	48	53	53	49
Escambia	26	54	45	42	26	34	30	24	24	30	34	14	22
Yellow	62	108	117	93	60	74	50	47	49	36	35	20	22
Choctawhatchee	67	105	119	119	96	81	64	54	111	143	143	169	144
Apalachicola	20	33	52	49	36	37	35	31	42	33	39	39	39
Suwannee	22	45	68	63	56	50	49	40	48	52	77	74	68
	222	362	417	388	296	306	260	226	312	345	386	381	353

**Table 2.A8. The percentage of acoustically tagged adult ( $\geq 1350$ -mm TL) Gulf Sturgeon virtually recaptured in each river. Columns indicate the river associated with the initial tagging event and rows indicate the river of detection. Each Gulf Sturgeon may contribute to percentages in multiple rivers of detection.**

River of detection	River of capture						
	Pearl	Pascagoula	Escambia	Yellow	Choctawhatchee	Apalachicola	Suwannee
Pearl	65.1%	5.4%	×	×	×	×	×
Pascagoula	7.0%	89.1%	2.2%	1.0%	0.3%	×	×
Escambia	×	2.2%	71.4%	26.6%	8.1%	0.8%	×
Yellow	×	1.1%	37.4%	69.8%	11.1%	0.8%	0.7%
Choctawhatchee	×	1.1%	22.0%	10.9%	93.1%	8.5%	×
Apalachicola	×	×	2.2%	1.6%	2.1%	83.9%	2.0%
Suwannee	×	×	×	×	×	3.4%	92.6%

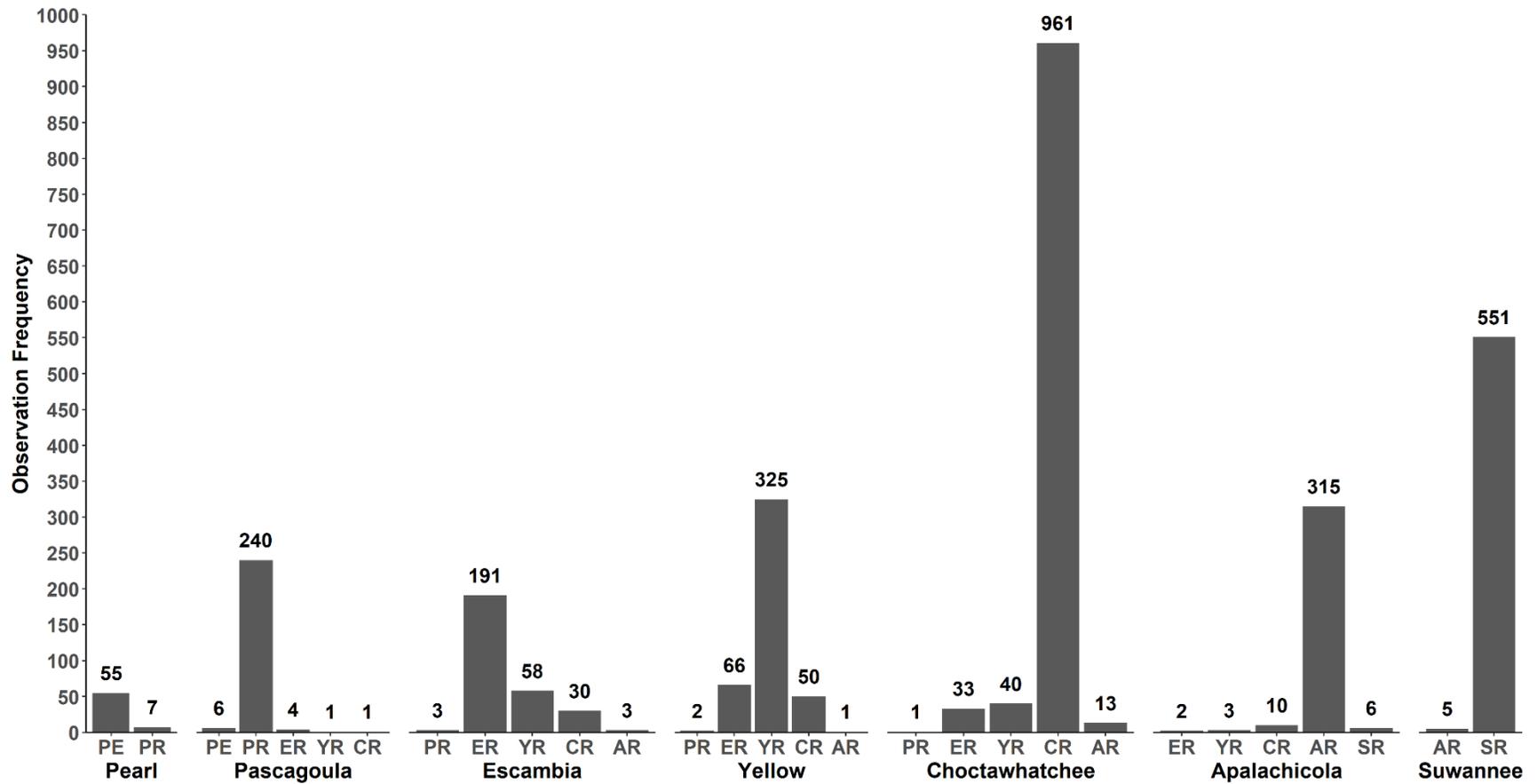


Figure 2.A1. Transition frequencies between observable states represented by rivers of detection. Totals summarize each observed transition between rivers and are grouped by the river occupied in the first year. Abbreviated rivers represent transition destinations: PE–Pearl, PR–Pascagoula, ER–Escambia, YR–Yellow, CR–Choctawhatchee, AR–Apalachicola, SR–Suwannee.

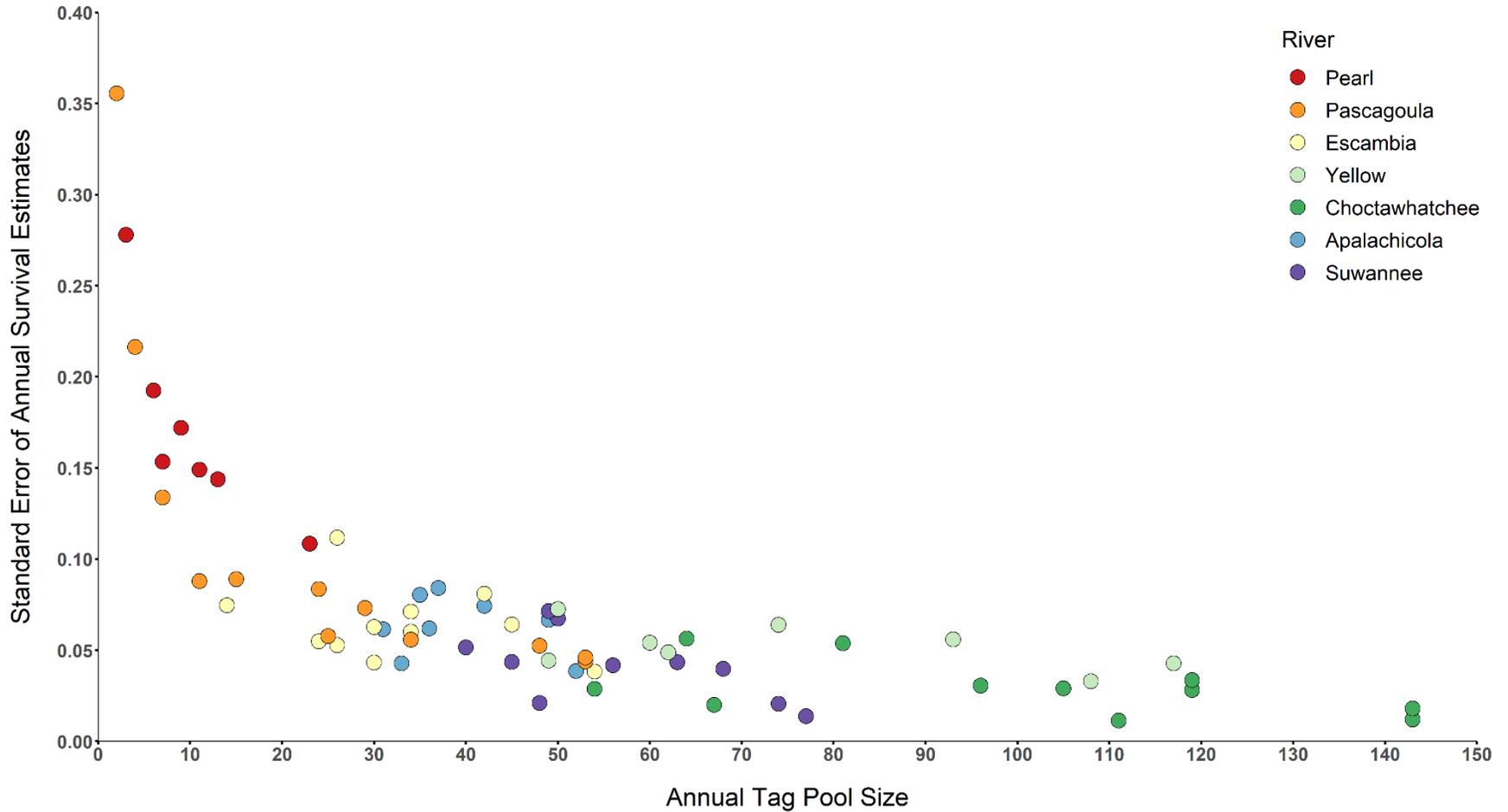


Figure 2.A2. Annual river-specific totals of telemetered fish available for detection (Table 2.A7) plotted against the corresponding standard error of the annual river-specific survival estimates for the same year (Figure 2.2) representing the relationship between the tag pool size and the precision of these survival rates for a given river and year. Estimates of 1.0 that had do not have confidence intervals (standard errors of zero) were excluded from this figure.

### 3. Survival Estimation Using a Barker Model

#### Completed as part of Task 1.1

#### Introduction

We use all active and passive tagging data from 1990–2022 provided to the Gulf Sturgeon Database (Task 1) to estimate long-term trends in survival for adult ( $\geq 1350$ -mm TL) Gulf Sturgeon at a Gulf of Mexico and individual river system levels. We also compare these survival estimates from capture-recapture models to life-history-based survival estimates commonly used in data-limited stock assessments as a reference point. Understanding trends in adult Gulf Sturgeon survival over time and space is important for multiple reasons, such as assessing the likelihood of Gulf Sturgeon populations declining due to the loss rate exceeding the replacement rate. Previous Gulf Sturgeon research has identified that the rate of species recovery is influenced by adult mortality (Flowers et al. 2020), and examining trends in mortality over time can provide insight into how Gulf Sturgeon populations respond to management actions or events of conservation concern described in the five-year status review such as recurring red tide (USFWS and NMFS 2022) or long-term effects of the *Deepwater Horizon* oil spill. Reducing uncertainty in mortality estimates can also lead to improved estimates of time-to-recovery and prioritize spatial locations for management actions that may influence adult mortality rates.

#### Methods

##### *Data overview*

Within the Gulf Sturgeon Database every marked fish collected is assigned a unique fish identification number, and all subsequent encounters (real or virtual) are recorded and linked to this fish identification number. Other information collected each time a Gulf Sturgeon is physically handled, including biological information such as size, is also linked to this fish identification number, which allows a reconstruction of the capture history of an animal and changes in physical characteristics. Using the capture information from each unique fish identification number, we generated two sets of annual capture histories for this analysis: one informed exclusively by PIT tag capture and recaptures and one informed exclusively by acoustic telemetry virtual recaptures. Capture histories summarized PIT tag data from 1990–2022 and telemetry data from 2010–2022. Leading zeroes were included with the telemetry capture histories to ensure the two types had the same number of annual occasions. Our data included adult Gulf Sturgeon (i.e., contacts associated with a minimum recorded TL of at least 1350-mm) implanted with PIT tags or acoustic telemetry tags at some point (i.e., not necessarily during the same occasion; Table 3.1).

##### *Capture history format*

Our application of a Barker model (Barker 1997; Williams et al. 2002) to these data types is original and requires some modification of the data structure from the traditional format. The standard Barker model follows an “LDLDD” capture history where a “1” in the “L” portion signifies a live capture, a “1”

in the “D” portion represents a recovery (i.e., dead individual), and a “2” in the “D” portion represents a resight event (i.e., the individual was reported alive during the interval; Barker 1997). To use the “D” portion for telemetry contacts and thereby convert a traditional Barker model into a joint live-recapture/live resight/tag-recovery parameterization of this model (Barker 1997), we represented all telemetry contacts with a “2” and combined the PIT tag and telemetry capture histories such that subsequent “L” and “D” occasions corresponded to PIT tag and telemetry contacts for the same sampling interval. Treating acoustic telemetry virtual recaptures as resight events allowed us to estimate the probabilities of detection associated with each tag type.

### *Barker model parameterization*

Field sampling efforts could not be summarized from the data provided and available in the Gulf Sturgeon Database. We inferred years without sampling for each river from the total number of annual contacts for each tag type (i.e., PIT tags and acoustic transmitters). If there were no contacts for a specific river and tag type in a given year, we informed the models that there were no data to inform parameter estimates for that year. Using the Barker model parameterization summarized in Table 3.2, we estimated parameters of interest (using the Barker notation): survival probability ( $S$ ); capture probability (i.e., PIT tag detection probability –  $p$ ); and the probability that an individual survived and was resighted alive between sampling occasions (i.e., acoustic telemetry detection probability –  $R$ ). We also estimated the probability of dead recovery ( $r$ ), but this parameter was generally uninformative as our data only included 16 dead recovered individuals (from GSDB). We also estimated the probability that a fish died but was resighted alive between capture events before dying ( $R'$ ) to facilitate model performance (R. J. Barker, University of Otago, personal communication). The probability of temporary site fidelity ( $F$ ) was fixed to 1, and the probability of temporary emigration ( $F'$ ) was fixed to 0 to represent our comprehensive sampling area coverage of all documented spawning populations designated as critical habitat (USFWS and NOAA 2003). A conceptual diagram representing the differences in these data streams and how they informed the estimation of specific Barker model parameters is in Figure 3.1.

### *Barker model descriptions*

We fit various models to comprehensively characterize spatiotemporal  $S$  dynamics for adult Gulf Sturgeon over the last three decades. We accommodated changes in sampling programs design by allowing  $p$  to vary over space and time with corresponding  $S$  estimates. Because of complicated changes in sampling programs over time,  $S$  was estimated over blocks of years where sampling efforts were similar. For example, a five-year  $S$  group could include sampling from years 2000–2004, but only a single  $S$  parameter estimate for that grouping of years would be estimated, and this  $S$  estimate would represent the average  $S$  for 2000–2004, and the SE for  $S$  would capture the variability in  $S$  within the block. Model parameterizations are summarized in Table 3.3. Models 1 and 2 were range-wide parameter estimates of  $S$ ,  $p$ , and  $R$ , with Model 1 estimating a single value of  $S$  and  $p$  over time and Model 2 estimating these parameters in five-year blocks of time. Models 3 and 4 included river-specific estimates of  $S$ ,  $p$ , and  $R$ , with Model 3 estimating a single value of  $S$  and  $p$  over time for each river and Model 4 estimating these parameters in five-year blocks for each river. We were interested in how

survival varied over time, as an indication of Gulf Sturgeon population status, and how survival varied over space because of different threats to specific river populations. We did not have reason to believe there were meaningful changes in  $R$  (acoustic tag detection probability) over time because a core group of autonomous receivers was consistently maintained, and we examined river and annual variability in  $R$  through our work with the telemetry-only data in the multistate model (Task 1.1). Therefore, we estimated each model's constant rate of  $R$  (Table 3.3). We estimated  $r$  and  $R'$  to be constant rates over time for similar reasons.

## Results

### *Data summary*

The Gulf Sturgeon Database contained data for 7,191 Gulf Sturgeon tagged between 1990 and 2021 that were available for recapture between 1991 and 2022 (Table 3.1; Figure 3.1). The total number of Gulf Sturgeon that only received PIT tags (6,221) was higher than the number of Gulf Sturgeon that received both PIT and acoustic telemetry tags (970). River-specific totals of Gulf Sturgeon that exclusively received PIT tags ranged between 141 and 2,681 (Table 3.1). Between 30 and 351 Gulf Sturgeon were implanted with both PIT and acoustic tags in each river (Table 3.1). The number of tagged Gulf Sturgeon was lower for rivers in the western Gulf of Mexico (Pearl and Pascagoula), likely because of lower Gulf Sturgeon catch rates.

### *Range-wide capture probability*

Model 1 estimated a constant, range-wide  $p$  of 0.04 and  $R$  of 0.80 (Table 3.4). Time-varying (Model 2) range-wide  $p$  estimates ranged from 0.02 to 0.07 and generally decreased over time, with the lowest PIT tag capture probability estimates representing more recent sampling years (Model 2; Table 3.5). All range-wide estimates of  $p$  had high precision (SE approximately 0.01; Tables 3.4–3.5).

### *Range-wide survival*

We estimated  $S$  for five-year groupings between 1995 and 2009 with relatively high precision (SE range of 0.01–0.02; Models 1 and 2; Tables 3.4 and 3.5). For range-wide models, Gulf Sturgeon  $S$  was consistent over time, with estimates mostly ranging between 0.90 and 0.93 (Figure 3.2; Tables 3.4–3.5). Model 1 estimated a constant survival rate across all years and rivers of 0.90 and a 95% CI of 0.89–0.91 (Table 3.4). The 95% CI of  $S$  overlapped with annual estimates of  $S$  from Model 2 (time-dependent) for all years except for a lower estimate representing 1995–1999 and a higher estimate representing 2015–2021 (Figure 3.2; Tables 3.4–3.5).

### *River-specific capture probability*

Estimates of  $p$  from Models 3 and 4 were low across individual rivers (generally 0.02–0.07; Tables 3.6–3.7; Figures 3.3–3.4). There was also a trend of increasing precision in estimated  $p$  over time (Table 3.7; Figure 3.4). Precision for most  $p$  estimates was high (SE 0.01). Most river-specific time-varying  $p$  estimates  $\geq 0.12$  had higher uncertainty with SE  $\geq 0.02$  (Table 3.7; Figure 3.4), and values of  $p < 0.12$  were more precise (generally SE  $\leq 0.01$ ; Table 3.7; Figure 3.4).

### *River-specific survival*

For Model 3, we observed lower  $S$  in the western Gulf of Mexico Rivers than eastern. Lowest  $S$  was in the Pearl River  $S = 0.76$ , which was lower than all other rivers (0.87–0.89; Table 3.6; Figure 3.3). Lower survival was also estimated for the Pascagoula River in the western Gulf of Mexico in 2000–2009 (Model 4; Table 3.7, Figure 3.5). Uncertainty around estimates of  $S$  was also higher for rivers in the western Gulf of Mexico (Tables 3.6–3.7; Figures 3.3 and 3.5).

Precision in estimates of  $S$  generally increased over time (Table 3.7; Figure 3.5) as the tagged fish pool increased (up to the point of diminishing returns; see Figure 2.A2, Task 1.1), and most Gulf Sturgeon populations exhibited relatively constant survival rates (Table 3.7; Figure 3.5). Only three time-varying  $S$  estimates from Model 4 were lower than 0.81, and there was uncertainty around each of these low  $S$  estimates (SE 0.08–0.19; Table 3.7; Figure 3.5).

### **Discussion**

We used all available tagging data (active and passive) in an original application of a Barker capture-recapture model to estimate Gulf Sturgeon survival over more than three decades across the entire range of the species. Assessing survival over decadal time scales allows us to assess survival patterns both as chronic mortality (i.e., mortality from natural processes) and episodic mortality from specific events of management concern, which may or may not be anthropogenically influenced (e.g., hurricanes, red tide events).

Do our capture-recapture survival estimates represent actual Gulf Sturgeon population survival? To answer this, we compared the estimates of survival from Model 2 (Gulf-wide, time-dependent model with 5-year time steps) where  $S \geq 0.90$  across most periods (Figure 3.2) to multiple life-history-based invariants of survival similar to those widely used for data-limited stock assessments (see the Appendix). The capture-recapture-based Model 2 estimates and life-history based estimates of  $S$  are similar, which suggests the capture-recapture-based estimates are reasonable, and it is unlikely a significant component of mortality is unaccounted for in our models or that our models are estimating unrealistic values for  $S$  for the data provided in the GSDB.

We also observed stable, generally high survival over time within most river populations, and these estimates were similar to our more straightforward (fewer model parameters) range-wide estimates (Models 1–2). The Pascagoula and Pearl rivers represented exceptions to this pattern. We estimated lower survival for the Pascagoula River than for other systems for periods between 2000 and 2009, but more recently, the Pascagoula survival estimates are similar to other rivers. This suggests that survival in the Pascagoula River may have increased since 2000–2009 or that threats facing this population were isolated to this period. Survival in the Pearl River was also generally lower than other river systems in the eastern Gulf of Mexico, and these results of lower survival in the Pearl River have been previously noted (Morrow et al. 1998; Rudd et al. 2014; Task 1 multistate analyses). The lower baseline survival observed for the Pearl River across different datasets and multiple model parameterizations over more than twenty years of assessments suggests that the Pearl River Gulf Sturgeon population is exhibiting lower survival than other Gulf Sturgeon populations and may, therefore, be experiencing different threats than other populations. This is an important result that suggests some Gulf Sturgeon populations

may be realizing various threats to survival than others, as expressed through lower fluctuating survival rates around some baseline over time.

Most episodic mortality events for Gulf Sturgeon need to be better documented because the mortalities are observed after the event, and baseline survival rates from before the event may not be available. For example, following the Temple-Inland paper mill spill on the Pearl River in 2011 (Louisiana Department of Wildlife and Fisheries 2011), dead Gulf Sturgeon were recovered. Let's examine survival estimates for the 2010-2014 time period in the Pearl River. These estimates are similar to other periods (Figure 3.5), but the high uncertainty around the survival estimates that predate this event obscure our ability to further assess this event.

The *Deepwater Horizon* oil spill impacted a large area of the Gulf of Mexico, and USFWS (2015) estimated that between 1,100 and 3,600 Gulf Sturgeon were potentially exposed during the *Deepwater Horizon* oil spill, including sturgeon populations in the Pearl, Pascagoula, Yellow, Escambia, Yellow/Blackwater, and Choctawhatchee rivers (USFWS 2015; PDARP 4-416; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). This exposure also potentially caused injury to Gulf Sturgeon (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). We assessed the available Gulf Sturgeon data to assess whether there was evidence of an episodic mortality signal in 2010 that could be related to the injury related to the *Deepwater Horizon* oil spill. For other marine species, including Bottlenose Dolphins (*Tursiops truncatus*), post-*Deepwater Horizon* injury has been documented, including reduced birth rate due to reproductive failure (Lane et al. 2015; Kellar et al. 2017) and mortality (Litz et al. 2014; Schwacke et al. 2017).

Our range-wide  $S$  estimates for the periods before and after the oil spill are similar (Table 3.5; Figure 3.2). If we examine patterns in individual rivers, we estimated decreases in survival between the periods of 2005–2009 and 2010–2014 for the Escambia, Yellow, and Choctawhatchee rivers (rivers which may have been impacted by oil from the *Deepwater Horizon*; USFWS 2015; PDARP 4-416; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016), but we generally did not observe lower survival rates for the 2010–2021 period. This result does not necessarily mean that the *Deepwater Horizon* oil spill did not have other unknown effects on Gulf Sturgeon populations.

Assessments of individual events on individual river systems are likely best made using high-resolution data, such as the telemetry-only analyses used in the multistate analyses (Task 1.1). However, the 2015-2021 period for the Apalachicola River, including Hurricane Michael, saw lower survival. Therefore, an event like Hurricane Michael may produce a signal that may be discernable in analyses where time-varying estimates represent sequential groupings of years.

## **Management and restoration recommendations**

These models of Gulf Sturgeon survival over three decades provide a new perspective on a key demographic parameter for understanding the resilience and persistence of this species across a landscape where threats to species recovery are changing. The most important result unique to this analysis is the stability in adult mortality during the last three decades, with a slight increasing trend over the past two decades. Flowers et al. (2020) identified the closure of the commercial Gulf sturgeon fishery as likely being the species' single most effective recovery action. This result and the stability in

mortality over the last three decades we document in this analysis should promote age-structure recovery facilitating Gulf Sturgeon population resilience to current and future threats to long-term viability and recovery.

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## Tables and Figures

**Table 3.1. Summary of the number of Gulf Sturgeon in each river marked with PIT tags or both PIT and acoustic telemetry tags between 1990 and 2022.**

<b>River</b>	<b>PIT tags</b>	<b>PIT and telemetry tags</b>
Pearl	141	30
Pascagoula	178	83
Escambia	417	102
Yellow/Blackwater	804	169
Choctawhatchee	1,201	351
Apalachicola	799	97
Suwannee	2,681	138

**Table 3.2. Barker model parameter definitions within the context of this study.**

<b>Parameter</b>	<b>Study definition</b>
$S_i$	the probability that a fish alive at $i$ is alive at $i + 1$
$p_i$	the probability that a fish at risk of capture at $i$ is captured at $i$
$R_i$	the probability that a fish that survives from $i$ to $i + 1$ is resighted (virtually detected via acoustic telemetry) between $i$ and $i + 1$
$R'_i$	the probability that a fish that died in $i$ was first resighted alive in $i$ before it died
$r_i$	the probability a that fish that dies in $i$ , is reported dead in $i + 1$
$F_i$	the probability that a fish at risk of capture at $i$ is at risk of capture at $i + 1$
$F'_i$	the probability that a fish not at risk of capture at $i$ is at risk of capture at $i + 1$

**Table 3.3. Barker model summaries including model-specific hypotheses and spatiotemporal parameterization of survival (S), PIT tag capture probability (p), and rate of acoustic tag detection (R).**

Model no.	<i>S</i> and <i>p</i>		<i>R</i>	
	Spatial groups	Temporal groups	Spatial groups	Temporal groups
1	Range-wide	Constant	Range-wide	Constant
2	Range-wide	1990–1994, 1995–1999, 2000–2004, 2005–2009, 2010–2014, 2015–2021	Range-wide	Constant
3	Rivers	Constant	Rivers	Constant
4	Rivers	1990–1994, 1995–1999, 2000–2004, 2005–2009, 2010–2014, 2015–2021	Rivers	Constant

**Table 3.4. Range-wide Gulf Sturgeon survival estimates, standard errors (SE), and associated 95% confidence intervals (lower confidence limits [LCL] and upper confidence limits [UCL]) from a Barker model (Model 1) estimating constant survival (S), constant PIT tag capture probability (p), and a constant rate of acoustic tag detection (R). Other parameters are defined in Table 3.2.**

Parameter	Years	Estimate	SE	LCL	UCL
<i>S</i>	Constant	0.90	<0.01	0.89	0.91
<i>p</i>	Constant	0.04	<0.01	0.04	0.04
<i>R</i>	Constant	0.80	0.01	0.79	0.81
<i>R'</i>	Constant	0.00	<0.01	0.00	0.00
<i>r</i>	Constant	0.00	<0.01	0.00	0.00
<i>F</i>	Fixed	1.00	–	–	–
<i>F'</i>	Fixed	0.00	–	–	–

**Table 3.5. Five-year survival estimates, standard errors (SE), and associated 95% confidence intervals (lower confidence limits [LCL] and upper confidence limits [UCL]) for Gulf Sturgeon 1990–2014 and a single seven-year survival estimate representing 2015–2021 from a Barker model (Model 2) estimating river-specific survival (S), river-specific PIT tag detection probability (p), and a constant rate of acoustic tag detection (R). Other parameters are defined in Table 3.2.**

Parameter	Years	Estimate	SE	LCL	UCL
<i>S</i>	1990–1994	0.97	0.03	0.86	0.99
<i>S</i>	1995–1999	0.80	0.02	0.76	0.84
<i>S</i>	2000–2004	0.90	0.01	0.86	0.92
<i>S</i>	2005–2009	0.91	0.02	0.87	0.93
<i>S</i>	2010–2014	0.93	0.01	0.91	0.94
<i>S</i>	2015–2021	0.95	0.01	0.93	0.96
<i>p</i>	1990–1994	0.05	0.01	0.04	0.07
<i>p</i>	1995–1999	0.07	0.01	0.06	0.09
<i>p</i>	2000–2004	0.06	<0.01	0.06	0.07
<i>p</i>	2005–2009	0.04	<0.01	0.04	0.05
<i>p</i>	2010–2014	0.04	<0.01	0.03	0.04
<i>p</i>	2015–2021	0.02	<0.01	0.01	0.02
<i>R</i>	Constant	0.79	0.01	0.77	0.80
<i>R'</i>	Constant	0.00	<0.01	0.00	0.00
<i>r</i>	Constant	0.00	<0.01	0.00	0.00
<i>F</i>	Fixed	1.00	–	–	–
<i>F'</i>	Fixed	0.00	–	–	–

**Table 3.6. Gulf Sturgeon survival estimates, standard errors (SE) and associated 95% confidence intervals (lower confidence limits [LCL] and upper confidence limits [UCL] from a Barker model (Model 3) estimating river-specific survival (*S*), river-specific PIT tag capture probability (*p*), and a constant rate of acoustic tag detection (*R*). Other parameters are defined in Table 3.2.**

Parameter	River	Estimate	SE	LCL	UCL
<i>S</i>	Pearl	0.77	0.03	0.71	0.82
<i>S</i>	Pascagoula	0.87	0.01	0.84	0.89
<i>S</i>	Escambia	0.90	0.01	0.87	0.92
<i>S</i>	Yellow	0.91	0.01	0.90	0.93
<i>S</i>	Choctawhatchee	0.93	0.01	0.92	0.94
<i>S</i>	Apalachicola	0.90	0.01	0.88	0.92
<i>S</i>	Suwannee	0.90	0.01	0.89	0.91
<i>p</i>	Pearl	0.09	0.02	0.06	0.13
<i>p</i>	Pascagoula	0.07	0.01	0.05	0.09
<i>p</i>	Escambia	0.05	0.01	0.04	0.06
<i>p</i>	Yellow	0.05	<0.01	0.05	0.06
<i>p</i>	Choctawhatchee	0.03	<0.01	0.03	0.04
<i>p</i>	Apalachicola	0.05	<0.01	0.04	0.06
<i>p</i>	Suwannee	0.03	<0.01	0.02	0.03
<i>R</i>	Pearl	0.86	0.04	0.78	0.92
<i>R</i>	Pascagoula	0.97	0.01	0.94	0.98
<i>R</i>	Escambia	0.81	0.02	0.77	0.85
<i>R</i>	Yellow	0.65	0.02	0.62	0.68
<i>R</i>	Choctawhatchee	0.79	0.01	0.77	0.81
<i>R</i>	Apalachicola	0.82	0.02	0.78	0.86
<i>R</i>	Suwannee	0.89	0.01	0.86	0.91
<i>R'</i>	Constant	0.00	<0.01	0.00	0.00
<i>r</i>	Constant	0.00	<0.01	0.00	0.00
<i>F</i>	Fixed	1.00	–	–	–
<i>F'</i>	Fixed	0.00	–	–	–

**Table 3.7. Five-year survival estimates, standard errors (SE) and associated 95% confidence intervals (lower confidence limits [LCL] and upper confidence limits [UCL]) for Gulf Sturgeon 1990–2014 and a single seven-year survival period representing 2015–2021 from a Barker model (Model 4) estimating river-specific survival (S), river-specific PIT tag capture probability (p), and a constant rate of acoustic tag detection (R). Other parameters are defined in Table 3.2. Data-deficient estimates, as identified by years without river-specific sampling or data that did not result in model convergence, were removed. Estimates of 1 or 0 do not have 95% confidence intervals.**

Parameter	River	Years	Estimate	SE	LCL	UCL
S	Pearl	1990–1994	–	–	–	–
S	Pearl	1995–1999	–	–	–	–
S	Pearl	2000–2004	0.83	0.09	0.59	0.94
S	Pearl	2005–2009	0.81	0.13	0.44	0.96
S	Pearl	2010–2014	0.82	0.06	0.69	0.90
S	Pearl	2015–2021	0.87	0.05	0.76	0.94
S	Pascagoula	1990–1994	–	–	–	–
S	Pascagoula	1995–1999	1.00	<0.01	1.00	1.00
S	Pascagoula	2000–2004	0.71	0.08	0.52	0.84
S	Pascagoula	2005–2009	0.51	0.16	0.23	0.78
S	Pascagoula	2010–2014	0.93	0.04	0.79	0.98
S	Pascagoula	2015–2021	0.94	0.01	0.90	0.96
S	Escambia	1990–1994	–	–	–	–
S	Escambia	1995–1999	0.84	0.16	0.35	0.98
S	Escambia	2000–2004	0.78	0.06	0.64	0.88
S	Escambia	2005–2009	0.99	0.05	0.07	1.00
S	Escambia	2010–2014	0.92	0.02	0.87	0.95
S	Escambia	2015–2021	0.90	0.02	0.85	0.94
S	Yellow	1990–1994	0.69	0.19	0.29	0.93
S	Yellow	1995–1999	1.00	<0.01	1.00	1.00
S	Yellow	2000–2004	0.83	0.03	0.76	0.88
S	Yellow	2005–2009	1.00	<0.01	1.00	1.00
S	Yellow	2010–2014	0.93	0.01	0.90	0.96
S	Yellow	2015–2021	0.99	0.01	0.76	1.00
S	Choctawhatchee	1990–1994	–	–	–	–

**Table 3.7. Continued.**

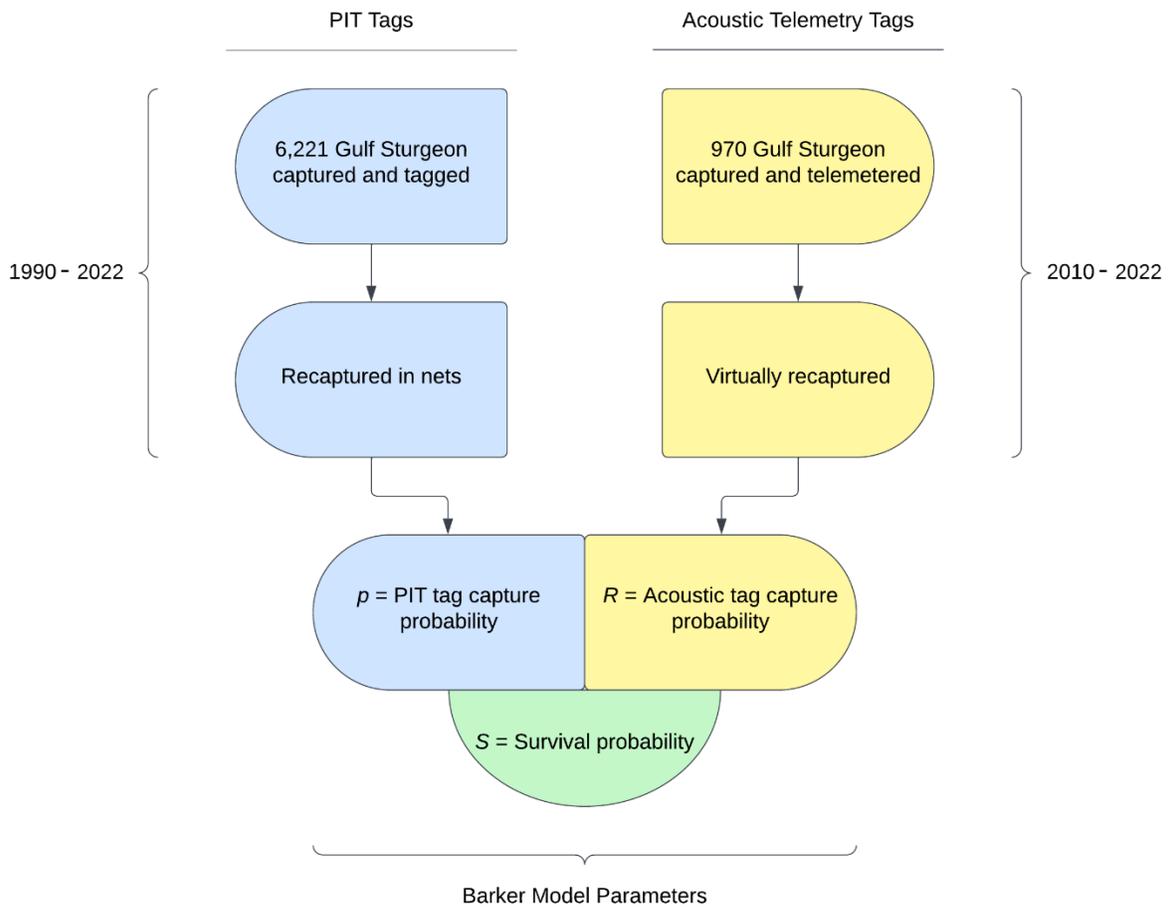
Parameter	River	Years	Estimate	SE	LCL	UCL
<i>S</i>	Choctawhatchee	1995–1999	0.84	0.06	0.69	0.92
<i>S</i>	Choctawhatchee	2000–2004	0.86	0.02	0.81	0.90
<i>S</i>	Choctawhatchee	2005–2009	0.97	0.03	0.81	1.00
<i>S</i>	Choctawhatchee	2010–2014	0.95	0.01	0.92	0.96
<i>S</i>	Choctawhatchee	2015–2021	0.98	0.01	0.96	0.99
<i>S</i>	Apalachicola	1990–1994	0.82	0.09	0.57	0.94
<i>S</i>	Apalachicola	1995–1999	0.94	0.07	0.57	0.99
<i>S</i>	Apalachicola	2000–2004	0.97	0.05	0.60	1.00
<i>S</i>	Apalachicola	2005–2009	0.82	0.03	0.75	0.88
<i>S</i>	Apalachicola	2010–2014	0.94	0.02	0.90	0.97
<i>S</i>	Apalachicola	2015–2021	0.90	0.02	0.86	0.93
<i>S</i>	Suwannee	1990–1994	0.99	0.03	0.46	1.00
<i>S</i>	Suwannee	1995–1999	0.86	0.03	0.80	0.91
<i>S</i>	Suwannee	2000–2004	0.94	0.03	0.85	0.98
<i>S</i>	Suwannee	2005–2009	0.97	0.03	0.85	0.99
<i>S</i>	Suwannee	2010–2014	0.96	0.01	0.92	0.97
<i>S</i>	Suwannee	2015–2021	0.93	0.01	0.89	0.95
<i>p</i>	Pearl	1990–1994	–	–	–	–
<i>p</i>	Pearl	1995–1999	–	–	–	–
<i>p</i>	Pearl	2000–2004	0.26	0.06	0.16	0.39
<i>p</i>	Pearl	2005–2009	0.01	0.01	0.00	0.04
<i>p</i>	Pearl	2010–2014	0.02	0.01	0.01	0.07
<i>p</i>	Pearl	2015–2021	0.02	0.01	0.00	0.06
<i>p</i>	Pascagoula	1990–1994	–	–	–	–
<i>p</i>	Pascagoula	1995–1999	0.27	0.07	0.15	0.43
<i>p</i>	Pascagoula	2000–2004	0.12	0.03	0.07	0.18
<i>p</i>	Pascagoula	2005–2009	0.25	0.25	0.02	0.83
<i>p</i>	Pascagoula	2010–2014	0.00	<0.01	0.00	0.00
<i>p</i>	Pascagoula	2015–2021	0.06	0.01	0.04	0.09
<i>p</i>	Escambia	1990–1994	–	–	–	–

**Table 3.7. Continued.**

Parameter	River	Years	Estimate	SE	LCL	UCL
<i>p</i>	Escambia	1995–1999	0.00	<0.01	0.00	0.00
<i>p</i>	Escambia	2000–2004	0.13	0.03	0.09	0.20
<i>p</i>	Escambia	2005–2009	0.05	0.01	0.03	0.08
<i>p</i>	Escambia	2010–2014	0.03	0.01	0.02	0.05
<i>p</i>	Escambia	2015–2021	0.03	0.01	0.02	0.05
<i>p</i>	Yellow	1990–1994	–	–	–	–
<i>p</i>	Yellow	1995–1999	0.05	0.05	0.01	0.31
<i>p</i>	Yellow	2000–2004	0.14	0.02	0.11	0.17
<i>p</i>	Yellow	2005–2009	0.03	0.01	0.02	0.04
<i>p</i>	Yellow	2010–2014	0.09	0.01	0.08	0.11
<i>p</i>	Yellow	2015–2021	0.01	<0.01	0.01	0.02
<i>p</i>	Choctawhatchee	1990–1994	–	–	–	–
<i>p</i>	Choctawhatchee	1995–1999	0.07	0.03	0.04	0.14
<i>p</i>	Choctawhatchee	2000–2004	0.05	0.01	0.04	0.06
<i>p</i>	Choctawhatchee	2005–2009	0.06	0.01	0.05	0.08
<i>p</i>	Choctawhatchee	2010–2014	0.03	<0.01	0.02	0.04
<i>p</i>	Choctawhatchee	2015–2021	0.01	<0.01	0.01	0.02
<i>p</i>	Apalachicola	1990–1994	0.37	0.16	0.13	0.70
<i>p</i>	Apalachicola	1995–1999	0.13	0.04	0.07	0.22
<i>p</i>	Apalachicola	2000–2004	0.07	0.01	0.05	0.10
<i>p</i>	Apalachicola	2005–2009	0.05	0.01	0.04	0.07
<i>p</i>	Apalachicola	2010–2014	0.06	0.01	0.04	0.07
<i>p</i>	Apalachicola	2015–2021	0.04	<0.01	0.03	0.05
<i>p</i>	Suwannee	1990–1994	0.05	0.01	0.03	0.06
<i>p</i>	Suwannee	1995–1999	0.06	0.01	0.05	0.07
<i>p</i>	Suwannee	2000–2004	0.02	<0.01	0.02	0.03
<i>p</i>	Suwannee	2005–2009	0.02	<0.01	0.02	0.03
<i>p</i>	Suwannee	2010–2014	0.01	<0.01	0.01	0.02
<i>p</i>	Suwannee	2015–2021	0.005	<0.01	0.00	0.01
<i>R</i>	Pearl	Constant	0.86	0.04	0.77	0.91

**Table 3.7. Continued.**

<b>Parameter</b>	<b>River</b>	<b>Years</b>	<b>Estimate</b>	<b>SE</b>	<b>LCL</b>	<b>UCL</b>
<i>R</i>	Pascagoula	Constant	0.96	0.01	0.93	0.98
<i>R</i>	Escambia	Constant	0.81	0.02	0.77	0.84
<i>R</i>	Yellow	Constant	0.62	0.02	0.59	0.66
<i>R</i>	Choctawhatchee	Constant	0.77	0.01	0.75	0.79
<i>R</i>	Apalachicola	Constant	0.82	0.02	0.78	0.86
<i>R</i>	Suwannee	Constant	0.88	0.01	0.85	0.90
<i>R'</i>	Constant	Constant	0.00	<0.01	0.00	0.00
<i>r</i>	Constant	Constant	0.00	<0.01	0.00	0.00
<i>F</i>	Fixed	Fixed	1.00	–	–	–
<i>F'</i>	Fixed	Fixed	0.00	–	–	–



**Figure 3.1. Conceptual diagram outlining the differences in Gulf Sturgeon monitoring data between 1990 and 2022 used to inform Barker model survival estimates. These totals reflect the number of tags deployed through 2021 and available for detection through 2022.**

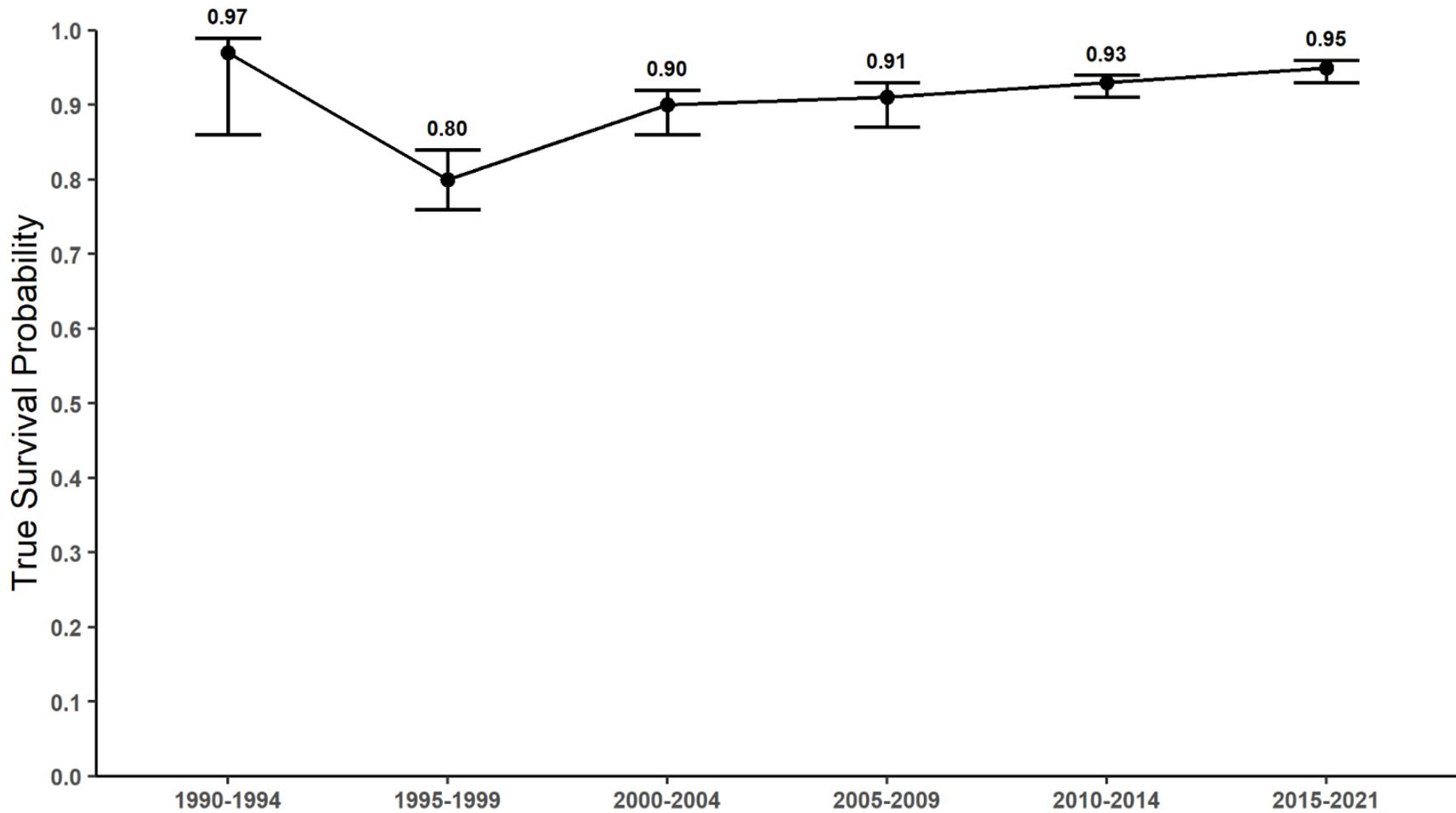


Figure 3.2. Five-year survival (S) estimates for Gulf Sturgeon 1990–2014 and a single seven-year survival estimate representing 2015–2021 from a Barker model (Model 2) estimating river-specific survival, river-specific PIT tag capture probability (p), and a constant rate of acoustic tag detection (R). The errors bars provided represent 95% confidence intervals.

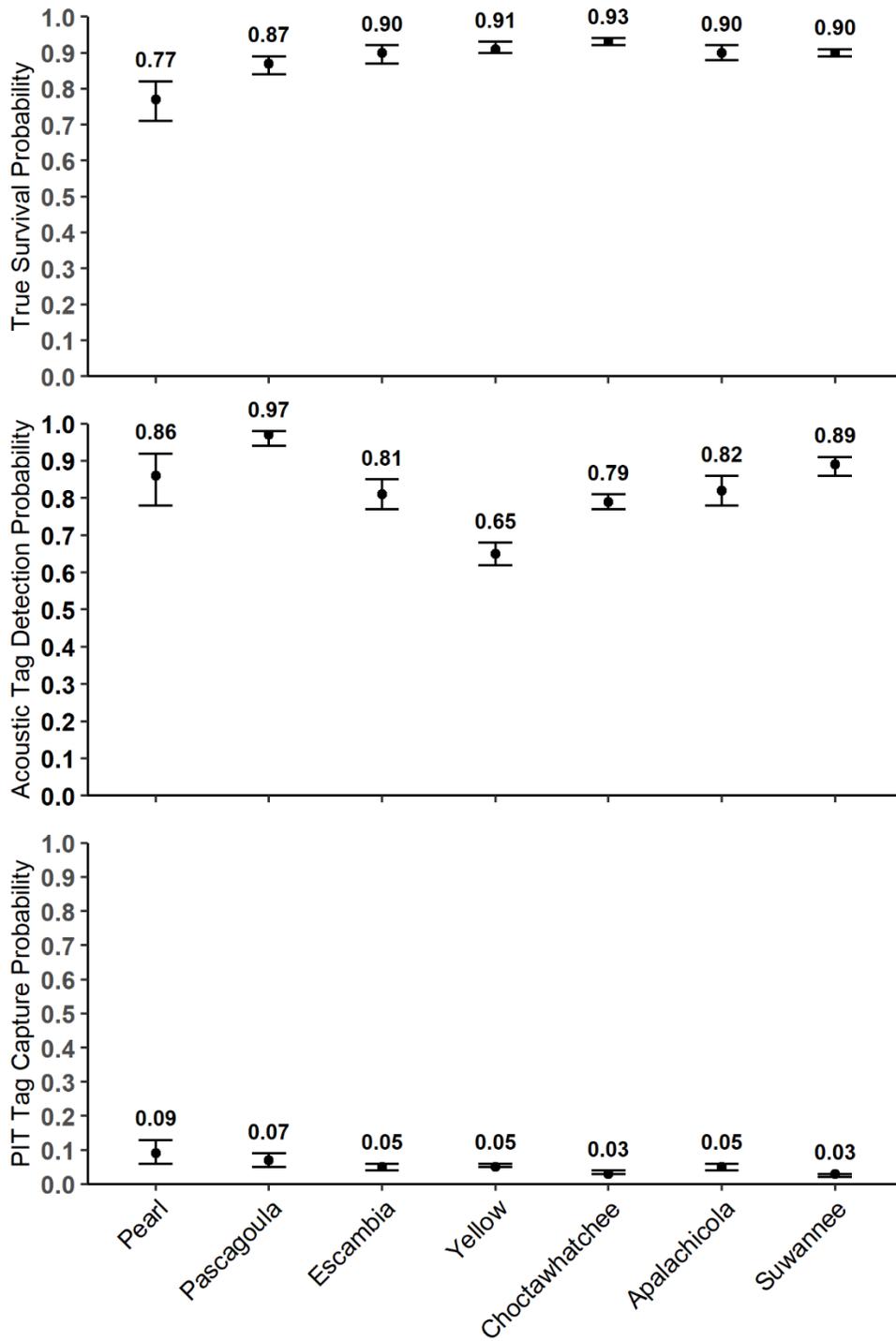


Figure 3.3. Gulf Sturgeon survival ( $S$ ) estimates and associated 95% confidence intervals from a Barker model (Model 3) estimating river-specific survival, river-specific PIT tag capture probability ( $p$ ), and a constant rate of acoustic tag detection ( $R$ ). Estimates of  $S$  are plotted on the top and  $p$  estimates are plotted on the bottom. Rivers plotted on the x-axis are arranged from west to east based on their location in the Gulf of Mexico.

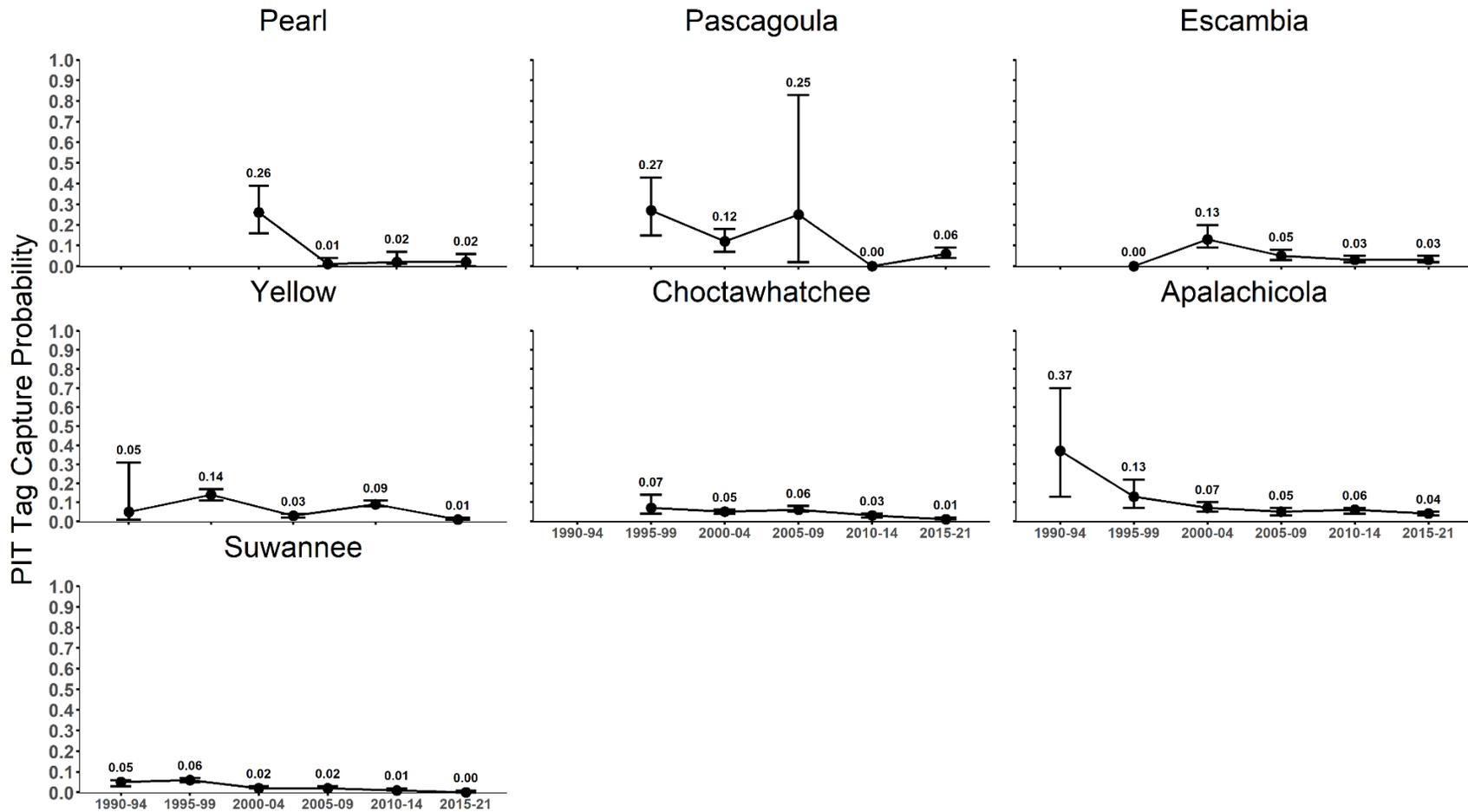


Figure 3.4. Passive Integrated Transponder (PIT) tag capture probability ( $p$ ) estimates and associated 95% confidence intervals estimated in five-year intervals for 1990–2014 tagging data and a single seven-year time period associated with 2015–2021 tagging from a Barker model (Model 4) estimating river-specific survival ( $S$ ), river-specific  $p$ , and a constant rate of acoustic tag detection ( $R$ ). The recapture process occurred in 1991–2022 and recaptured Gulf Sturgeon were initially tagged between 1990 and 2021, the range of years associated with survival estimates. Data-deficient estimates were removed. Estimates of 1.0 do not have 95% confidence intervals

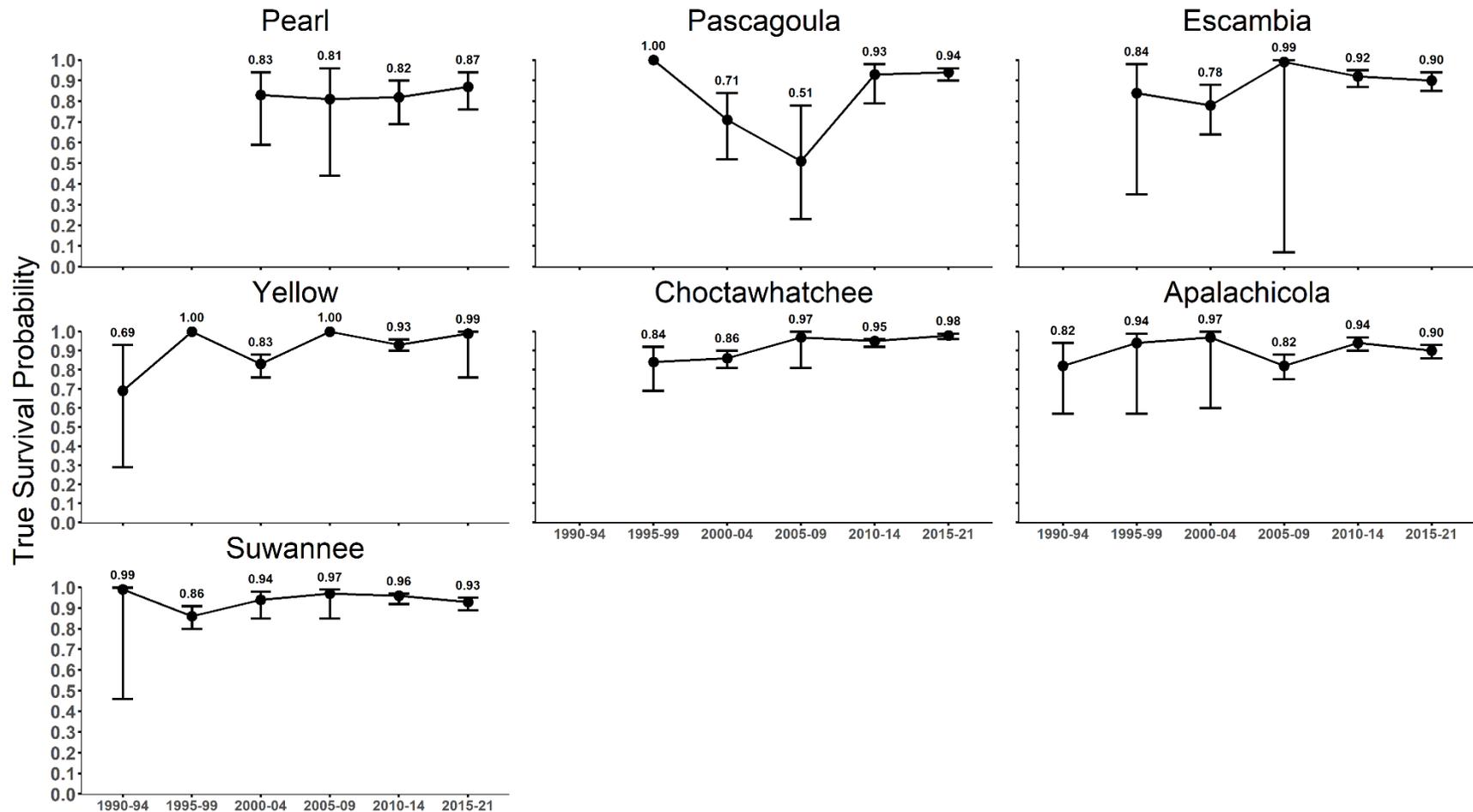


Figure 3.5. Five-year survival ( $S$ ) estimates and associated 95% confidence intervals for Gulf Sturgeon 1990–2014 and a single seven-year  $S$  period representing 2015–2021 from a Barker model (Model 4) estimating river-specific  $S$ , river-specific PIT tag capture probability ( $p$ ), and a constant rate of acoustic tag detection ( $R$ ). Data-deficient estimates, as identified by years without river-specific sampling or data that did not result in model convergence, were removed. Estimates of 1.0 do not have 95% confidence intervals.

## Appendix: Estimating survival from life history invariants and a discussion of true survival

Estimates of mortality are often difficult to measure directly in fish populations, so information-limited fisheries often assume constant values or use estimators informed by life history parameter estimates such as the Brody growth coefficient ( $K$ ) and maximum age ( $t_{max}$ ). We used the available tagging data and information on the time at liberty to calculate  $t_{max}$  for use in estimating  $M$  to compare to estimates derived from capture-recapture models. Alternative estimates of  $t_{max}$  from aging hard parts are unavailable for adult Gulf Sturgeon.

Two fish in the GSDB were at liberty for 26 years, one year greater than the maximum theoretical Gulf Sturgeon age reported in Sulak and Clugston (1999). The first (Fish 1) was captured in 1992, measuring 1403 FL/1600 TL in the Suwannee River, and was recaptured in the Suwannee River in 2018. The second (Fish 2) was captured in 1993, measuring 1765 TL (1586 FL from standard conversion in Task 1) in the Apalachicola River and was recaptured in the Apalachicola River in 2019. Using the river-specific direct aging von Bertalanffy parameter estimates in Flowers et al. (2010) for asymptotic length ( $L_{\infty}$ : Suwannee = 1697 mm; Apalachicola = 2168 mm),  $K$  (Suwannee = 0.21; Apalachicola = 0.13), and the theoretical age at zero-length ( $t_0$ : Suwannee = -0.63; Apalachicola = -0.83), we determined the ages of Fish 1 as 33.7 years old in 2018 and Fish 2 as 35.3 in 2019. Only Fish 2 was released alive. These empirical observations of fish at liberty for 26 years appear limited by the total number of years these data represent (32 years, 1990–2022). In their critique of empirical length-at-age curves for Gulf Sturgeon older than age 8–10, Sulak et al. (2016) suggest mature males tend to slow down in increasing in length such that a 1500–1600 mm TL male could be 10, 15, 20, or 30 years old. If this is true and Fishes 1 or 2 were males, the range of possible ages would be 36–56. Therefore, a maximum age for Gulf Sturgeon of 50 years, as estimated from life history characteristics by Ahrens and Pine (2014), is supported by these data and Atlantic Sturgeon *A. o. oxyrinchus* studies (Smith 1985).

With this empirical range of  $t_{max}$  values (35–50 years) and two possible  $K$  values (0.13 and 0.21; Flowers et al. 2010), we can now use these values to evaluate different mortality estimators given this study's direct vital rate estimates. The widely used Jensen (1996) estimator of  $M = 1.5K$  provides a range of  $M$  estimates for Gulf Sturgeon between 0.2 and 0.35. As Kenchington (2014) pointed out in a review of natural mortality estimators for information-limited fisheries, this estimator performs best when applied to archetypal exploited teleosts and therefore, would perform poorly in our application to Gulf Sturgeon. Then et al. (2015) evaluated the predictive performance of empirical estimators of  $M$  on over 200 fish species determined that *tmax-based* estimators performed better than methods that used  $t_{max}$  and  $K$  (e.g., Alverson-Carney method; Alverson and Carney 1975) or just  $K$  (e.g., Beverton-Holt method; Beverton and Holt 1959). They recommend using the updated Hoenig<sub>nls</sub> estimator of  $4.899t_{max}^{-0.916}$  when a  $t_{max}$  estimate is available (Then et al. 2015). Using the Hoenig<sub>nls</sub> estimator, a  $t_{max}$  of 50 provides a  $Z$  of 0.14, which is close to the Model 1 constant  $M$  estimate of 0.12 and is well within the range of time-varying, Gulf-wide direct estimates of  $M$  in this study ranging from 0.03 to 0.28. A  $t_{max}$  of 35 provides an  $M$  of 0.19, which is higher than most of the tagging-based estimates made for this study but within the range of estimates. If a pre-exploitation  $t_{max}$  can be observed, Kenchington (2014) recommends the estimator  $4.3/t_{max}$ , which estimates  $Z = 0.09$  for a  $t_{max}$  of 50 and  $Z = 0.12$  for a  $t_{max}$  of 35 for Gulf Sturgeon. These estimates are similar to the estimates generated from the capture-recapture data.

For a fish population recovering from fishery removals and age-structure erosion, life history-based mortality estimates, such as those from longevity or catch-curve type methods, would likely be positively biased due to the absence of older age classes. But as a reference point to compare tagging-based mortality estimates, these  $t_{max}$ -based estimators are a suitable starting point for comparison and planning. These life history-based estimators also provide additional lines of inference to give us greater confidence that our direct estimates of Gulf Sturgeon survival from available capture-recapture data sufficiently represent the true population survival. Further work is needed to determine how the direct and indirect mortality estimates presented here influence Gulf Sturgeon population viability.

In this study, we estimated actual survival,  $S$ , an analog of total mortality ( $Z$ ), from thirty years of tagging data. While these tagging data provide information on  $S$  from the last thirty years, to place the estimates in a greater biological context, we used standard fisheries approaches to estimate total mortality ( $Z$ ) as an analog for natural mortality ( $M = 1 - S$ ). Since much of the fisheries literature is reported regarding mortality, a key element in most population models used to assess stock status (Walters and Martell 2004; Flowers et al. 2020), we will shift to interpreting these results as mortality estimates. Total mortality is commonly calculated as the sum of  $M$  and fishing mortality ( $F$ ). Because  $M$  is almost always unobserved and fisheries management actions are most directed at  $F$ , quantifying population losses through  $M$  estimation is a necessary first step to understanding better sources of mortality that can be managed (e.g., bycatch, ship strikes). Therefore, an accurate estimate of  $M$  becomes a cornerstone of nearly all population models and in the planning and interpreting of the subsequent management actions that the population models were designed to inform. For Gulf Sturgeon, directed fishing has been closed for over two decades. Therefore,  $F = 0$  and  $Z \approx M$  vs will allow us to use  $1-S$  to evaluate mortality estimators for  $Z$  or  $M$  interchangeably.

## 4. Lambda Pradel Estimation

### Completed as part of Task 1.2

#### Introduction

We estimate seniority probability ( $\gamma_{i+1}$ ), which represents the relative contributions of adult survival ( $\phi$ ) and recruitment ( $f$ ) on the rate of population change  $\lambda$  for adult Gulf Sturgeon ( $\geq 1350$ -mm FL) over three decades. This information can be used to inform decisions related to “on the ground” restoration efforts by providing spatially explicit (by river basin) information on  $\lambda$  and  $\gamma_{i+1}$  as guides to target specific size classes (life stages), which use different habitat types. These decisions are informed by the relationships among  $\lambda$ ,  $\gamma_{i+1}$ , and  $\phi$  (Table 4.1). For example, the seniority rate is defined by  $\gamma_{i+1} = \phi_i / \lambda_i$ , and for values  $> 0.5$ , this shows how survival contributes proportionally more to  $\lambda$  than recruitment. In our case, if  $\lambda < 1$  and  $\gamma_{i+1} < 0.5$  in a specific river, it would suggest that the adult fish population is declining, and recruitment rates to adult size classes ( $\geq 1350$ -mm total length [TL]) are driving this decline (the recruitment rate is below replacement). Alternatively, a  $\lambda < 1$  and  $\gamma_{i+1} > 0.5$  would suggest an adult fish population in decline and that this decline is driven by the survival rate of adults (a rate of death higher than the rate of recruitment). Such estimates of  $\lambda$  and  $\gamma_{i+1}$  could be included in a decision analysis to prioritize conservation actions (Runge 2011; Gregory et al. 2012) that may improve the recruitment rate of pre-adult life stages (which primarily use riverine and estuarine habitats) or the survival of adult life stages (which use riverine, estuarine, and marine habitats).

#### Methods

Adult Gulf Sturgeon ( $\geq 1350$ -mm TL) capture-recapture data were compiled from a standardized database as capture histories with annual time steps (Gulf Sturgeon Database, GSDB; Insight Database Design, Tasks 1, 1.1, and 2.1). These data are a compilation of multiple short- and long-term studies between 1990 and 2022 led by governmental agencies and academic cooperators in seven river systems considered as part of designated Gulf Sturgeon critical habitat (Pearl, Pascagoula, Escambia, Yellow, Choctawhatchee, Apalachicola, and Suwannee rivers). Over the three decades of sampling, adult Gulf Sturgeon have been captured in riverine habitats primarily using gill nets (Chapman and Carr 1995; Carr et al. 1996; Fox et al. 2000) within freshwater habitats during spring before the spawning migration, in summer holding areas, or during the fall outmigration to estuarine environments. Captured fish are weighed and measured (all measurements standardized within the database environment) and tagged with a Passive Integrated Transponder (PIT) tag. Within the database, tagged fish are assigned a unique ID to track their respective initial and subsequent captures. This capture-recapture information was used to create capture histories on an annual time step for each

unique fish in each river. Summary information on the number of uniquely marked fish by river, and the number of adult fish PIT tagged each year by river is available in Appendix A.

We estimated  $\gamma_{i+1}$  using temporal symmetry models (TSM; Pradel 1996), a type of open-population capture-recapture model in Program MARK (White and Burnham 1999) through the RMark interface (Laake 2013; R Core Team 2023). We simplified the number of parameters in our model by fixing  $\phi$  and  $p$  to estimates from a detailed mortality study that used both PIT and telemetry tag information (Parker 2023, Task 1.1). We used river- and time-specific Barker model estimates of  $\phi$  and  $p$  (Task 1.1) to estimate  $\gamma_{i+1}$  for the same time steps of interest (5-year blocks of time, described below) for each river or range-wide. By using this information within the TSM framework, we can assess  $\gamma$  and the relationships among adult  $\phi$  and  $f$  to the adult size class. We then derived  $\lambda$  and  $f$  using the relationships described in Table 4.1. We estimated standard errors using the delta method and approximated the 95% confidence limits (Seber 1982). Because we restricted our analyses to adult Gulf Sturgeon, our estimates of  $\lambda$  represent the rate of change of the adult fish population, and  $f$  is the recruitment rate to the adult life stage.

The TSM approach has similar assumptions as the traditional Jolly-Seber model (Williams et al. 2002) and estimates  $\gamma_{i+1}$  using individual capture histories. An additional and essential assumption for TSM is that the study area and effort remain relatively constant through time (Hines and Nichols 2002; Franklin et al. 2004; Budy et al. 2017). We built four models (described in Table 4.2) to estimate  $\gamma$  and then derive  $\lambda$ . These models represent different hypotheses related to adult Gulf Sturgeon population demographics at different spatiotemporal scales, such as whether the data are best explained by a model where  $\gamma$  is relatively constant across rivers and variable over time (Model 2) or whether  $\gamma_{i+1}$  is unique to each of the seven rivers of management interest and generally constant across time (Model 3). Relative model fit to the data was evaluated by comparing Akaike's Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>; Williams et al. 2002).

None of the seven rivers in the Gulf Sturgeon recovery documents have had a consistent long-term monitoring program for 30 years. The data compilation used in this analysis is from a series of studies that all used PIT tags to mark animals (see Appendices for summaries of PIT tagging efforts). These studies represent different objectives, resulting in changes in sampling locations within each river, sampling timing, and the types of gillnets used for fish capture. We designed all models with the intent of avoiding fitting overly complex models whose assumptions we could not meet. For example, a model that estimated a range-wide  $\gamma$  for each year and then derived  $\lambda$  and  $f$  from fixed  $\phi$  and  $p$  values would be biased (and likely nonsensical) because of the non-constant sampling effort which would appear in model results as pulses of natural recruitment. To account for changes in sampling effort over time, which can bias estimates of  $\lambda$  and result in nonsensical estimates of  $f$  due to the "pulses" of sampling (which could incorrectly be interpreted as fish population recruitment pulses), we estimated  $f$

at either a range-wide level or for each river as a constant value over time periods of five years (1990-1993, 1995-1999, 2000-2004, 2005-2009, 2010-2014) or six years (2015-2021). Our time-varying models estimated  $\gamma_{i+1}$  for each time block to assess whether there were any discernable temporal trends in these data including the 2010 *Deepwater Horizon* oil spill, an event that exposed Gulf Sturgeon to oil and may have impacted populations (USFWS 2015; PDARP 4-416; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016).

## Results

The highest-ranked model using  $AIC_c$  (Model 4; Table 4.3) estimated  $\gamma_{i+1}$  and derived  $\lambda$  for five-year time periods 1990–2014 and a single seven-year time period 2015–2021 (Table 4.2; Figures 4.1–4.10). Figures 1–3 present parameter estimates for all rivers on a single plot (one plot for each parameter) to provide a range-wide snapshot of results. Figures 4.4–4.10 provide the same results, but are arranged to present trends in individual rivers over time (each plot displays parameter trends for a single river).

Range-wide  $\gamma_{i+1}$  was estimated as 0.86 (Model 1) and all values of  $\gamma_{i+1}$  by time period or river were  $\geq 0.64$  (Models 2–3; Table 4.4). Estimated 95% confidence intervals (CI) of  $\gamma_{i+1}$  by river exceeded 0.5 in all time periods except 2010–2014 in the Pascagoula River (Model 4; Table 4.5; Figures 4.1 and 4.5). These results collectively suggest that survival is the primary driver of population growth for Gulf Sturgeon across their range. Our derived estimates of  $\lambda$  suggest positive population growth in Gulf Sturgeon populations (lower 95% CI of  $\lambda > 1$ ) in most rivers and time periods (Table 4.5, Figure 4.2). Some  $\lambda$  estimates lack confidence intervals because their associated  $\gamma_{i+1}$  values were estimated to be 1.0 and, therefore, were represented by a single value. Three river systems (Escambia, Apalachicola, and Suwannee) had  $\lambda$  values  $< 1$  for the most recent time period 2015–2021 (Table 4.5, Figures 4.2, 4.6, 4.9, and 4.10). Among all river population trends in  $\lambda$  over time (Figures 4.4–4.10), the Pascagoula River is the only population that seems to exhibit an increasing trend as the 95% CI's associated with the first two  $\lambda$  estimates were  $< 1$  (2000–2009) whereas the two more recent estimates (2010–2021) had lower 95% CIs  $> 1$ . Most other rivers had  $\lambda$  estimates near 1 for each time block or an alternating pattern of  $\lambda$  above and below 1 over time (e.g., Choctawhatchee River, Figure 4.8). The Apalachicola and Suwannee rivers have the longest sampling history (estimates available 1990–2021). Over these three decades, the Suwannee River  $\lambda$  has generally been near or slightly above 1 whereas the  $\lambda$  estimates for the Apalachicola River have trended downward (but have overlapped) across time blocks, resulting in a most recent upper 95% CI of 0.97 (Table 4.5). Recruitment estimates are more difficult to interpret as this parameter represents recruitment to the adult fish population, and no clear recruitment patterns are apparent. Recruitment trends could be masked by changes in sampling effort (see Tables 4.A1–4.A4 and Figure 4.A1) or area over time, including changes that occurred in more recent time periods with a shift in sampling effort focused on juvenile Gulf Sturgeon.

## Discussion

Assessments of population growth over time are critical to informing recovery actions for listed species. For long-lived species such as Gulf Sturgeon, mismatches between periods for individual research efforts (e.g., 2–4 years of sampling) compared to the species' lifespan (likely 50 years or more) necessitate creativity in synthesizing data to assess the status of Gulf Sturgeon over time and space to inform management decisions related to species recovery. We quantified the rate of population change over three decades for Gulf Sturgeon using a TSM models fit to capture-recapture data building upon earlier applications of this modeling framework for this species from a single river system (Pine et al. 2001). Because the data used in this effort are from many studies collected in seven different river systems over three decades, we were concerned that changes in sampling effort, gillnetting locations, or gillnet mesh size could bias estimates of population growth rate by introducing different forms of heterogeneity (Pradel 1996; Hines and Nichols 2002; Budy et al. 2017). Including a detection probability function partially accounts for changes in sampling effort (Budy et al. 2017) in this modeling framework. Because information on sampling effort is not recoverable from field data, we could not use effort as a covariate. Marescot et al. (2011) found  $\lambda$  estimation approaches robust to heterogeneity in detection probability. We made use of the best available spatially-explicit rates of survival and capture probability (which are relatively constant over time, Task 1.2) estimated from a related Barker model fit to capture-recapture data from passive and active tags over the same period to estimate  $\phi$  (Parker 2023, Task 1.2), which informed our TSM model parameter estimates. We recognize that fixing survival and capture probability parameter estimates for inclusion in our TSM models may result in underestimating standard error and other parameter biases if the values we used are inaccurate. However, because of our detailed efforts to estimate survival and capture probability in Task 1.2, we feel these assumptions are reasonable, and may be our only option, to allow us to develop insight from these TSM models into the intrinsic rate of population growth.

Nonetheless, combining information from multiple approaches and simplifying models fit to data in a biologically reasonable framework, the TSM model results of  $\lambda$ ,  $f$ , and  $\gamma_{i+1}$  may provide an essential element within a decision framework to prioritize conservation actions for Gulf Sturgeon. Uncertainty in these results, and other Gulf Sturgeon demographic assessments, would be reduced if standardized sampling of adult Gulf Sturgeon with consistent effort and area sampled was completed on regular time intervals in each river of management interest.

To assess range-wide trends in  $\lambda$  and  $f$ , we fit a separate parameterization of Model 2 informed by a Barker model which estimated  $\phi$  and  $p$  by time-period (instead of by river and time period). Therefore, we were able to derive range-wide estimates of  $\lambda$  and  $f$  for all time-periods from these range-wide, time-specific  $\phi$  estimates. This model suggests that range-wide population growth has been relatively stable ( $\lambda \sim 1$ ) or increasing ( $\lambda > 1$ ) since the 2005–2009 time block. Estimates of  $\gamma_{i+1}$  remained high at  $\geq 0.83$  since the 2000–2004 time period,

suggesting adult survival is more important to these trends in  $\lambda$  over the past few decades than  $f$ . Range-wide  $f$  trends are variable, but there was a decrease in range-wide  $f$  in the 2010–2014 time period. A key point is from a range-wide, Gulf of Mexico scale (the spatial scale used in management) the most recent estimates of  $\lambda$  suggest an overall positive trend in Gulf Sturgeon populations even if the river-specific analyses (the spatial scale research efforts are conducted) suggest three rivers have a  $\lambda < 1$  in 2015–2021.

An assumption of TSM models (and many types of capture-recapture models) is that effort and sampling area remain constant over time. We examined the actual and cumulative number of new fish tagged each year by river (Figure 4.A1) which demonstrates variable numbers of fish tagged each year visually inferred from the stairstep pattern in the plot of the cumulative number of tags. Marking information (Tables 4.A1–4.A4) and summary statistics of the mean number of fish tagged in each time block show on average a decline in the number of adult fish PIT tagged in the Choctawhatchee and Suwannee Rivers after 2010 with increases in the number of adults tagged in the other five rivers. The cumulative tagging effort of new PIT-tagged fish demonstrates a pattern with different inflection points over time suggesting changes in the number of fish marked in different years. However, these changes in the numbers of tagged fish each year are not consistent with derived estimates of  $f$ , which estimate recruitment declines. We are unable to relate changes in the number of fish caught to sampling effort, or include an effort covariate, because of the lack of information on effort related to data provided to the GSDB. Additionally, we are unsure how robust derived estimates of recruitment are to heterogeneity in capture probability or changes in sampling effort and location, whereas estimates of  $\lambda$  are known to be robust to heterogeneity in capture probability (Marescot et al. 2011). Because we estimated  $f$  from a derived  $\lambda$  and a fixed  $\phi$ , the estimates of recruitment are likely robust to heterogeneity in capture probability, but how variation in effort and sampling location may or may not bias these estimates is unknown. As in Pine et al. (2001), it is important to recognize that these changes in the population, both the rate of  $f$  or  $\lambda$ , are for the adult portion of these Gulf Sturgeon populations, and thus changes in recruitment to the adult size class is of concern from a population recovery perspective.

The 2016 *Deepwater Horizon* Oil Spill Final Programmatic Damage Assessment and Restoration Plan and Final Programmatic Environmental Impact Statement (PDARP) presented a detailed framework explaining the injury determination and effects of oil exposure on Gulf Sturgeon (Chapter 4, <https://tinyurl.com/3wc2mv4w>). This determination, using multiple lines of inference (USFWS 2015), including observed movement patterns of telemetered Gulf Sturgeon compared to the surface oil footprint, concluded that a substantial portion of the telemetered Gulf Sturgeon from the Pearl, Pascagoula, Escambia, Blackwater, Yellow, and Choctawhatchee rivers were potentially exposed to *Deepwater Horizon* oil (USFWS 2015; PDARP 4-416; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016) and when extrapolated to the Gulf Sturgeon populations in these rivers, this represents about 63%

of the Gulf Sturgeon in these populations (USFWS 2015; PDARP 4-418; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). The PDARP report further states that Gulf Sturgeon exposure to oil likely resulted in genotoxicity and immunosuppression of Gulf Sturgeon, which “...can lead to malignancies, cell death, susceptibility to disease, infections, and a decreased ability to heal (USFWS 2015).”

We estimated general trend of  $\lambda \geq 1$  range-wide from 1990–2021 for Gulf Sturgeon, and no river had a  $\lambda$  estimate  $< 1$  for consecutive blocks of time. Recruitment patterns are more variable, and the declines in recruitment in the Escambia, Apalachicola, and Suwannee rivers in the most recent time block is likely driving the derived  $\lambda < 1$  in these same rivers for the same 2015–2021 time period. Of these rivers, only the Escambia River is included in the list of Gulf Sturgeon populations impacted by *Deepwater Horizon* oil exposure (impacted rivers are the Pearl, Pascagoula, Escambia, Yellow, and Choctawhatchee). The Apalachicola Gulf Sturgeon population has experienced other episodic mortality events since 2010, including recurring red tide (USFWS and NMFS [National Marine Fisheries Service] 2022) and one of the most powerful US landfalling hurricanes in recorded history (Hurricane Michael; Dula et al. 2022), which may or may not be anthropogenically influenced. Apalachicola River and Apalachicola Bay have also experienced extreme drought and other significant estuarine ecosystem changes since 2010 (Pine et al. 2015; Leitman et al. 2016), which could impact Gulf Sturgeon at different life stages in ways that are not clear. Flowers et al. (2020), using a detailed age-structured population model for Gulf Sturgeon, highlighted the importance of minimizing additive anthropogenic mortality on recovery trajectories and timelines for this species given the large erosion in the population age-structure following decades of commercial exploitation. These authors further suggested that additional mortality beyond the baseline used in their simulation ( $M=0.095$ ) would likely delay Gulf Sturgeon population recovery. A similar result, showing that additional levels of mortality as small as 10% could lead to delayed recovery, was found for Green Sturgeon (*Acipenser medirostris*; Beamesderfer et al. 2007).

Gulf Sturgeon research efforts in the last three decades have evolved from life history and basic demographic assessments of adult life stages to more recent efforts to address knowledge gaps on subadult and juvenile life stages. Our analyses of the best available information on trends in adult populations, combined with the general life history theory of long-lived species (Crouse et al. 1987; Winemiller and Rose 1992) and other Gulf Sturgeon population modeling work (Pine et al. 2001; Flowers et al. 2020), suggests species recovery may be more sensitive to adult demography than earlier life stages. This basic idea that restoration and management actions must be linked to influencing a life stage and associated demographic rate that makes meaningful contributions to population declines, or growth, is critical (Davis et al. 2023). Further research to identify sources of adult mortality, prioritizing efforts in rivers with upper 95% CI  $\lambda < 1$ , and implementing associated mitigation, if possible, may assist with recovery. If efforts to reduce adult mortality are not possible, then increasing recruitment may

benefit population recovery, but likely not as much as reducing adult mortality (Ahrens and Pine 2014; Flowers et al. 2020). If increasing mortality risks are from sources that are not easily managed (i.e., hurricanes and red tide) then mortality from these sources may need to be mitigated if these risks cannot be reduced. We suggest that these additional mortality sources be considered part of the species' baseline mortality rate in future recovery planning efforts. Doing so may help to streamline recovery targets and promote resilience to known and emerging threats, and enhance the viability of a stock with a higher baseline natural mortality rate than has been previously assumed thus far, given the assumed life history of the species (Pine and Martell 2009; Flowers et al. 2020). This shifting baseline as a function of increasing anthropogenic threats, which cannot be managed, is similar to changes in baseline  $M$  related to changing climate, which may be considered for many fish stock assessments (Thompson et al. 2021).

There is a chance that the diverse life history of Gulf Sturgeon, utilizing riverine, estuarine, and marine habitats, may, at first, appear to expose the species to a wider range of threats. Given the observed persistence of Gulf Sturgeon over the past ~200 million years, perhaps this actually represents the species' capacity for resilience and adaptation. We encourage consideration of a framework to assess management and recovery actions that promotes the resilience of this species to current and future threats. This approach could provide hope for future adaptation if the opportunity is provided to Gulf Sturgeon.

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## Tables and Figures

**Table 4.1. Relationships among seniority probability ( $\gamma$ ), lambda ( $\lambda$ ), and recruitment ( $f$ ), a description of the parameter, and a description of which parameters were fixed to allow estimation of derived parameters in analyzing adult Gulf Sturgeon capture-recapture data from 1990–2022.**

Parameter estimated and derivation	Description	Fixed Parameters
$\lambda$ $\lambda_i = \frac{\varphi_i}{\gamma_{i+1}}$	<p>The rate of population change of adult Gulf Sturgeon <math>\geq 1350</math>-mm TL between times steps <math>t_x \rightarrow t_y</math> where <math>t_x</math> is the first year of interest to estimate lambda between <math>x</math> and <math>y</math>. If <math>t_x</math> is the first year of sampling, then <math>t_{x+1}</math> is not estimable.</p>	<p><math>\phi</math> values by river from joint PIT and telemetry information in a Barker model.</p> <p>Capture probability (<math>p</math>) by river from PIT tag recaptures in the Barker model</p>
$\gamma$ $\gamma_{i+1} = \frac{\varphi_i}{\lambda_i}$	<p>Seniority probability. The probability that an adult Gulf Sturgeon in the population at time <math>t</math>, was alive and in the population at time <math>t-1</math>.</p>	<p><math>p</math> by river from PIT tag recaptures in the Barker model</p>
$f$ $f_i = \varphi_i \left( \frac{1 - \gamma_{i+1}}{\gamma_{i+1}} \right)$	<p>Rate of recruitment (new individuals in <math>i+1</math> per individual in <math>i</math>) to the tagged adult fish population <math>\geq 1350</math>-mm TL</p>	<p><math>\phi</math> values by river from joint PIT and telemetry information in a Barker model.</p> <p><math>p</math> by river from PIT tag recaptures in the Barker model</p>

**Table 4.2. Description of models considered for Gulf Sturgeon seniority ( $\gamma$ ), population growth ( $\lambda$ ) and recruitment rates ( $f$ ) estimated or derived from temporal symmetry models, using fixed apparent survival ( $\phi$ ) and capture ( $p$ ) probabilities for seven river systems from a Baker model described in Task 1.1. Derived parameters are calculated from estimated (“real parameters”) and fixed values.**

Model number	Real parameters	Fixed parameters	Derived parameters	Description
1	$\gamma(\text{constant})$	$\phi(\text{river and time period} = \text{fixed})$ $p(\text{river and time period} = \text{fixed})$	$\lambda, f$	An estimate of average range-wide seniority across all years, represented as a single value. Apparent survival and capture probability are fixed by river and time period.
2	$\gamma(\text{time periods})$	$\phi(\text{river and time period} = \text{fixed})$ $p(\text{river and time period} = \text{fixed})$	$\lambda, f$	Seniority estimates for five-year time periods 1990–2014 and a single seven-year time period 2015–2021.
3	$\gamma(\text{river})$	$\phi(\text{river and time period} = \text{fixed})$ $p(\text{river and time period} = \text{fixed})$	$\lambda, f$	River-specific estimates of seniority averaged over time.
4	$\gamma(\text{river and time period})$	$\phi(\text{river and time period} = \text{fixed})$ $p(\text{river and time period} = \text{fixed})$	$\lambda, f$	River-specific estimates of seniority averaged for five-year time periods 1990–2014 and a single seven-year time period 2015–2021.

**Table 4.3. Ranking of temporal symmetry models for Gulf Sturgeon seniority ( $\gamma$ ), survival ( $\phi$ ), and capture probability ( $p$ ) used to derive recruitment ( $f$ ) and population growth rates ( $\lambda$ ). Models include fixed parameters generated using a Barker mark-recapture model that estimated survival and capture probabilities for five-year time periods 1990–2014 and a single seven-year time period 2015–2021 (Task 1.1). Other abbreviations are defined as:  $K$  = number of model parameters,  $AIC_c$  = Akaike's Information Criterion adjusted for small sample sizes, and  $\Delta AIC_c$  = difference in  $AIC_c$  score between the given model and the top-ranked model.**

<b>Model number</b>	<b>Model parameters</b>	<b><math>K</math></b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>	<b>Model Weight</b>
4	$\gamma(\text{river}*\text{time period}) \phi(\text{fixed} = \text{Barker}) p(\text{fixed} = \text{Barker})$	35	152,214.70	0.00	1.00
2	$\gamma(\text{time period}) \phi(\text{fixed} = \text{Barker}) p(\text{fixed} = \text{Barker})$	6	154,240.10	2025.40	<0.01
3	$\gamma(\text{river}) \phi(\text{fixed} = \text{Barker}) p(\text{fixed} = \text{Barker})$	7	154,274.30	2059.62	<0.01
1	$\gamma(.) \phi(\text{fixed} = \text{Barker}) p(\text{fixed} = \text{Barker})$	1	155,223.90	3009.26	<0.01

**Table 4.4. Seniority probability ( $\psi$ ) estimates for adult Gulf Sturgeon ( $\geq 1350$ -mm TL) with upper (UCL) and lower (LCL) 95% confidence limits from Models 1–3. Each model provides spatial estimates that are constant over time or temporal estimates that are shared across space. Fixed estimates of survival and capture probability were consistent across each of these models and are presented in Table 5 with the results of Model 4.**

Model Number	Area or Time	Seniority probability			
		Estimate	SE	LCL	UCL
	<u>Range-wide</u>				
1	Constant	0.86	<0.01	0.86	0.86
	<u>Time Period</u>				
2	1990–1994	1.00	<0.01	1.00	1.00
2	1995–1999	0.64	0.01	0.62	0.65
2	2000–2004	0.95	0.01	0.93	0.96
2	2005–2009	0.83	0.01	0.82	0.85
2	2010–2014	0.90	0.01	0.88	0.92
2	2015–2021	0.89	0.01	0.87	0.90
	<u>River</u>				
3	Pearl	0.77	0.01	0.76	0.78
3	Pascagoula	0.73	<0.01	0.72	0.74
3	Escambia	0.87	<0.01	0.86	0.87
3	Yellow	0.86	<0.01	0.86	0.87
3	Choctawhatchee	0.87	<0.01	0.87	0.88
3	Apalachicola	0.82	<0.01	0.81	0.82
3	Suwannee	0.87	<0.01	0.87	0.88

**Table 4.5. Parameter estimates from the top ranked temporal symmetry model by river system and time period. Confidence intervals (95% CI) are provided in parentheses next to each estimate. Fixed survival and capture probabilities were estimated in Task 1.1 using Barker mark-recapture models. Assumed survival and capture probabilities were not estimated in Task 1.1 and were therefore fixed to the nearest estimated value for survival and fixed to zero for capture probabilities.**

River	Parameter	Time Periods					
		1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2021
Pearl	Seniority ( $\gamma$ )	–	–	0.76 (0.67–0.83)	0.63 (0.57–0.68)	1.00 (1.00–1.00)	0.73 (0.67–0.78)
	Survival ( $\phi$ )	0.83 (assumed)	0.83 (assumed)	0.83 (fixed)	0.81 (fixed)	0.82 (fixed)	0.87 (fixed)
	Capture ( $p$ )	0.00 (assumed)	0.00 (assumed)	0.26 (fixed)	0.01 (fixed)	0.02 (fixed)	0.02 (fixed)
	Population growth ( $\lambda$ )	–	–	1.10 (0.99–1.21)	1.30 (1.19–1.41)	0.82 (0.82–0.82)	1.19 (1.11–1.28)
	Recruitment ( $f$ )	–	–	0.48 (0.40–0.57)	0.63 (0.56–0.70)	0.17 (0.11–0.23)	0.54 (0.47–0.60)
Pascagoula	Seniority ( $\gamma$ )	–	0.43 (0.37–0.49)	1.00 (1.00–1.00)	0.97 (0.37–1.00)	0.43 (0.37–0.49)	0.78 (0.72–0.84)
	Survival ( $\phi$ )	1.00 (assumed)	1.00 (fixed)	0.71 (fixed)	0.51 (fixed)	0.93 (fixed)	0.94 (fixed)
	Capture ( $p$ )	0.00 (assumed)	0.27 (fixed)	0.12 (fixed)	0.25 (fixed)	0.00 (fixed)	0.06 (fixed)
	Population growth ( $\lambda$ )	–	2.34 (2.02–2.71)	0.71 (0.71–0.71)	0.53 (0.46–0.60)	2.16 (1.87–2.51)	1.20 (1.11–1.30)
	Recruitment ( $f$ )	–	1.16 (1.01–1.30)	0.15 (0.10–0.19)	0.15 (0.05–0.26)	1.07 (0.93–1.21)	0.52 (0.44–0.59)

**Table 4.5. Continued.**

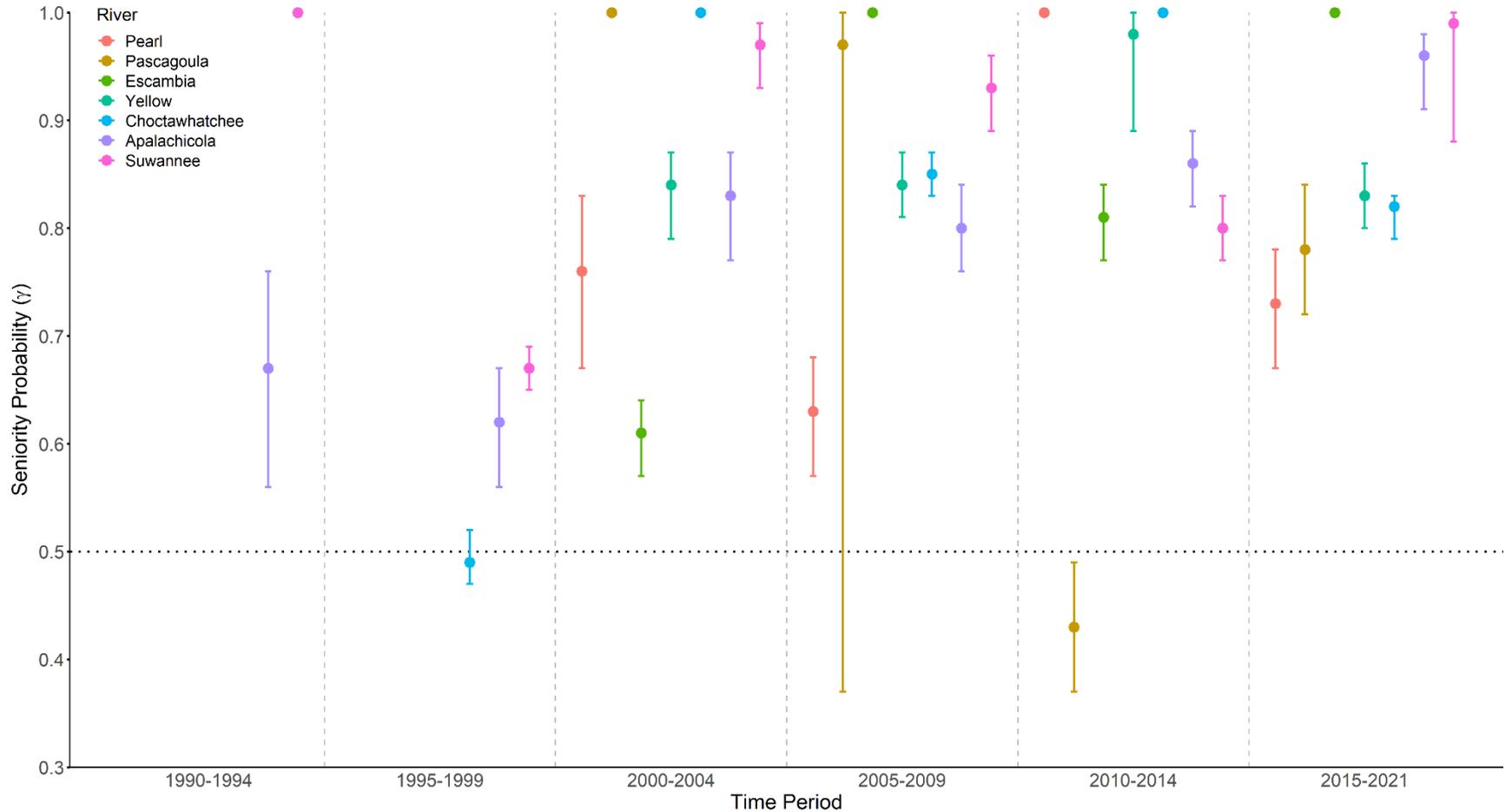
River	Parameter	Time Periods					
		1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2021
Escambia	Seniority ( $\gamma$ )	–	–	0.61 (0.57–0.64)	1.00 (1.00–1.00)	0.81 (0.77–0.84)	–
	Survival ( $\phi$ )	0.84 (assumed)	0.84 (fixed)	0.78 (fixed)	0.99 (fixed)	0.92 (fixed)	0.90 (fixed)
	Capture ( $p$ )	0.00 (assumed)	0.00 (fixed)	0.13 (fixed)	0.05 (fixed)	0.03 (fixed)	0.03 (fixed)
	Population growth ( $\lambda$ )	–	–	1.29 (1.21–1.37)	0.99 (0.99–0.99)	1.14 (1.09–1.19)	0.90 (0.86–0.94)
	Recruitment ( $f$ )	–	–	0.63 (0.58–0.68)	0.21 (0.13–0.28)	0.47 (0.43–0.52)	–
Yellow	Seniority ( $\gamma$ )	–	0.41 (0.31–0.51)	0.84 (0.79–0.87)	0.84 (0.81–0.87)	0.98 (0.89–1.00)	0.83 (0.80–0.86)
	Survival ( $\phi$ )	0.69 (fixed)	1.00 (fixed)	0.83 (fixed)	1.00 (fixed)	0.93 (fixed)	0.99 (fixed)
	Capture ( $p$ )	0.00 (assumed)	0.05 (fixed)	0.14 (fixed)	0.03 (fixed)	0.09 (fixed)	0.01 (fixed)
	Population growth ( $\lambda$ )	–	2.47 (1.94–3.14)	0.99 (0.94–1.04)	1.18 (1.14–1.23)	0.95 (0.92–0.99)	1.19 (1.15–1.23)
	Recruitment ( $f$ )	–	0.00 (0.00–0.00)	0.40 (0.35–0.44)	0.47 (0.43–0.51)	0.26 (0.19–0.33)	0.48 (0.44–0.52)
Choctawhatchee	Seniority ( $\gamma$ )	–	0.49 (0.47–0.52)	1.00 (1.00–1.00)	0.85 (0.83–0.87)	1.00 (1.00–1.00)	0.82 (0.79–0.83)
	Survival ( $\phi$ )	0.84 (assumed)	0.84 (fixed)	0.86 (fixed)	0.97 (fixed)	0.95 (fixed)	0.98 (fixed)
	Capture ( $p$ )	0.00 (assumed)	0.07 (fixed)	0.05 (fixed)	0.06 (fixed)	0.03 (fixed)	0.01 (fixed)
	Population growth ( $\lambda$ )	–	1.70 (1.60–1.80)	0.86 (0.86–0.86)	1.14 (1.12–1.17)	0.95 (0.95–0.95)	1.20 (1.17–1.23)
	Recruitment ( $f$ )	–	0.85 (0.80–0.90)	0.18 (0.16–0.20)	0.45 (0.43–0.47)	0.20 (0.16–0.23)	0.50 (0.47–0.52)

**Table 4.5. Continued.**

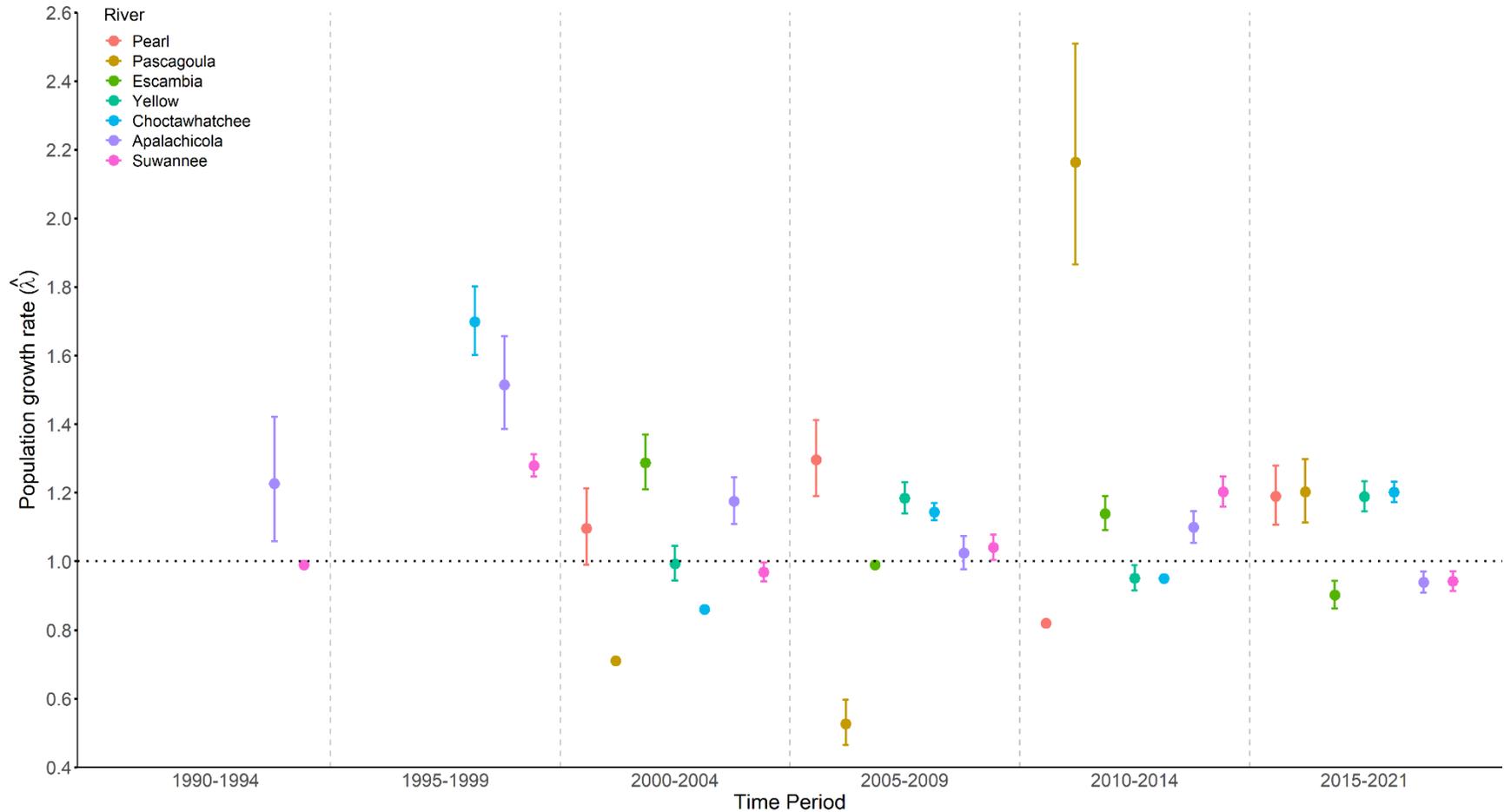
River	Parameter	Time Periods					
		1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2021
Apalachicola	Seniority ( $\gamma$ )	0.67 (0.56–0.76)	0.62 (0.56–0.67)	0.83 (0.77–0.87)	0.80 (0.76–0.84)	0.86 (0.82–0.89)	0.96 (0.91–0.98)
	Survival ( $\phi$ )	0.82 (fixed)	0.94 (fixed)	0.97 (fixed)	0.82 (fixed)	0.94 (fixed)	0.90 (fixed)
	Capture ( $p$ )	0.37 (fixed)	0.13 (fixed)	0.07 (fixed)	0.05 (fixed)	0.06 (fixed)	0.04 (fixed)
	Population growth ( $\lambda$ )	1.23 (1.06–1.42)	1.51 (1.39–1.66)	1.17 (1.11–1.24)	1.02 (0.98–1.07)	1.10 (1.05–1.15)	0.94 (0.91–0.97)
	Recruitment ( $f$ )	0.05 (0.04–0.06)	0.74 (0.65–0.82)	0.48 (0.42–0.54)	0.43 (0.39–0.47)	0.43 (0.38–0.47)	0.28 (0.24–0.33)
Suwannee	Seniority ( $\gamma$ )	1.00 (1.00–1.00)	0.67 (0.65–0.69)	0.97 (0.93–0.99)	0.93 (0.89–0.96)	0.80 (0.77–0.83)	0.99 (0.88–1.00)
	Survival ( $\phi$ )	0.99 (fixed)	0.86 (fixed)	0.94 (fixed)	0.97 (fixed)	0.96 (fixed)	0.93 (fixed)
	Capture ( $p$ )	0.05 (fixed)	0.06 (fixed)	0.02 (fixed)	0.02 (fixed)	0.01 (fixed)	0.005 (fixed)
	Population growth ( $\lambda$ )	0.99 (0.99–0.99)	1.28 (1.25–1.31)	0.97 (0.94–1.00)	1.04 (1.00–1.08)	1.20 (1.16–1.25)	0.94 (0.91–0.97)
	Recruitment ( $f$ )	0.21 (0.18–0.23)	0.60 (0.58–0.63)	0.28 (0.23–0.32)	0.34 (0.30–0.39)	0.51 (0.47–0.54)	0.24 (0.18–0.31)

**Table 4.6. Range-wide estimates from a temporal symmetry model by time period. Confidence intervals (95% CI) are provided in parentheses next to each estimate. Fixed survival and capture probabilities were estimated in Task 1.1 using Barker mark-recapture models.**

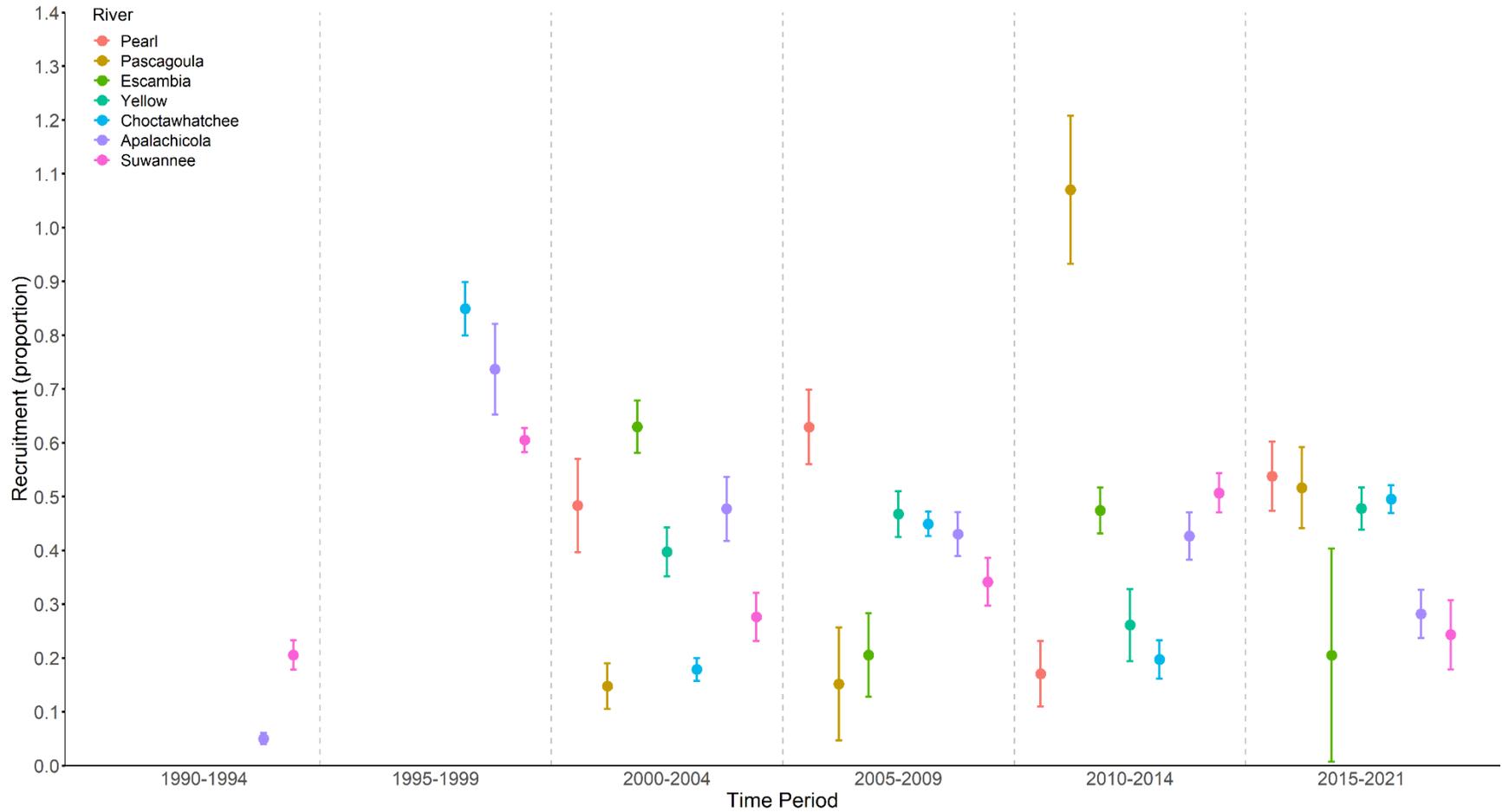
Parameter	Time Periods					
	1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2021
Seniority ( $\gamma$ )	1.00 (1.00–1.00)	0.59 (0.58–0.60)	0.97 (0.95–0.98)	0.83 (0.81–0.84)	0.93 (0.91–0.94)	0.91 (0.90–0.93)
Range-wide Survival ( $\phi$ )	0.97 (fixed)	0.80 (fixed)	0.90 (fixed)	0.91 (fixed)	0.93 (fixed)	0.95 (fixed)
Range-wide Capture ( $p$ )	0.05 (fixed)	0.07 (fixed)	0.06 (fixed)	0.04 (fixed)	0.04 (fixed)	0.02 (fixed)
Range-wide Population growth ( $\lambda$ )	0.97 (0.97–0.97)	1.36 (1.34–1.39)	0.93 (0.91–0.94)	1.10 (1.08–1.12)	1.00 (0.99–1.02)	1.04 (1.03–1.06)
Range-wide Recruitment ( $f$ )	0.20 (0.17–0.23)	0.67 (0.66–0.69)	0.27 (0.24–0.29)	0.45 (0.43–0.46)	0.33 (0.31–0.35)	0.36 (0.34–0.38)



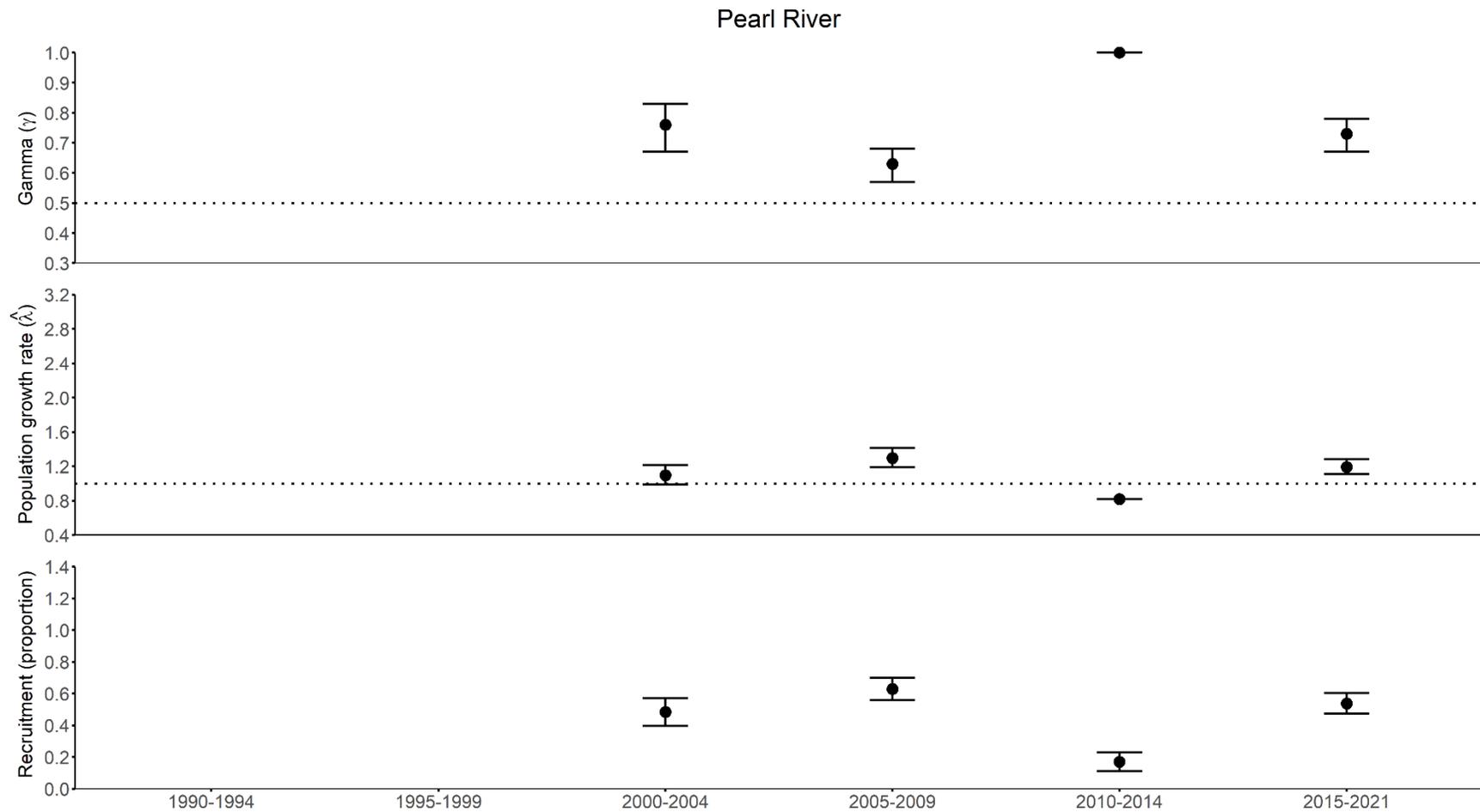
**Figure 4.1. River-specific estimates of seniority ( $\gamma$ ) for five-year time periods 1990–2014 and a single seven-year time period 2015–2021 from our top-ranked temporal symmetry model by  $AIC_c$  (Model 4; described in Table 2). The horizontal dotted reference line indicates the point at which adult survival is proportionally more important than recruitment ( $f$ ) to population growth rate ( $\lambda$ ) (i.e.,  $\gamma > 0.50$ ). Error bars indicate 95% confidence intervals for all estimates. Vertical dashed lines are visual aids separating time periods.**



**Figure 4.2. Derived river-specific estimates of population growth rate ( $\lambda$ ) for five-year time periods 1990–2014 and a single seven-year time period 2015–2021 from our top-ranked temporal symmetry model by  $AIC_c$  (Model 4; described in Table 2). The horizontal dotted reference line indicates a stable population ( $\lambda=1$ ). Error bars indicate 95% confidence intervals for all estimates. Vertical dashed lines are visual aids separating time periods.**



**Figure 4.3. Derived river-specific estimates of recruitment ( $f$ ) for five-year time periods 1990–2014 and a single seven-year time period 2015–2021 from our top-ranked temporal symmetry model by  $AIC_c$  (Model 4; described in Table 2). Error bars indicate 95% confidence intervals for all estimates. Vertical dashed lines are visual aids separating time periods.**



**Figure 4.4.** Pearl River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.

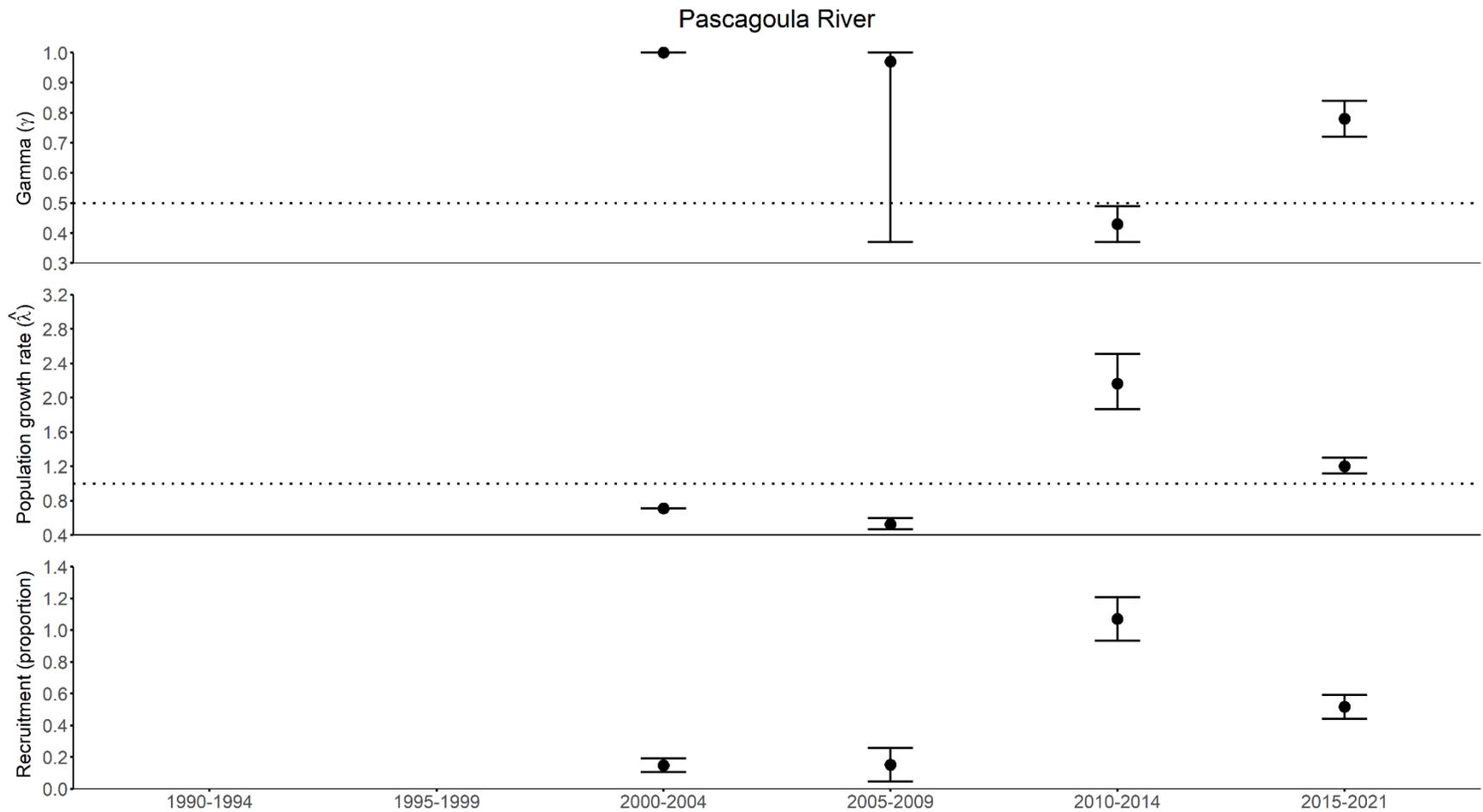


Figure 4.5. Pascagoula River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 4.2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.

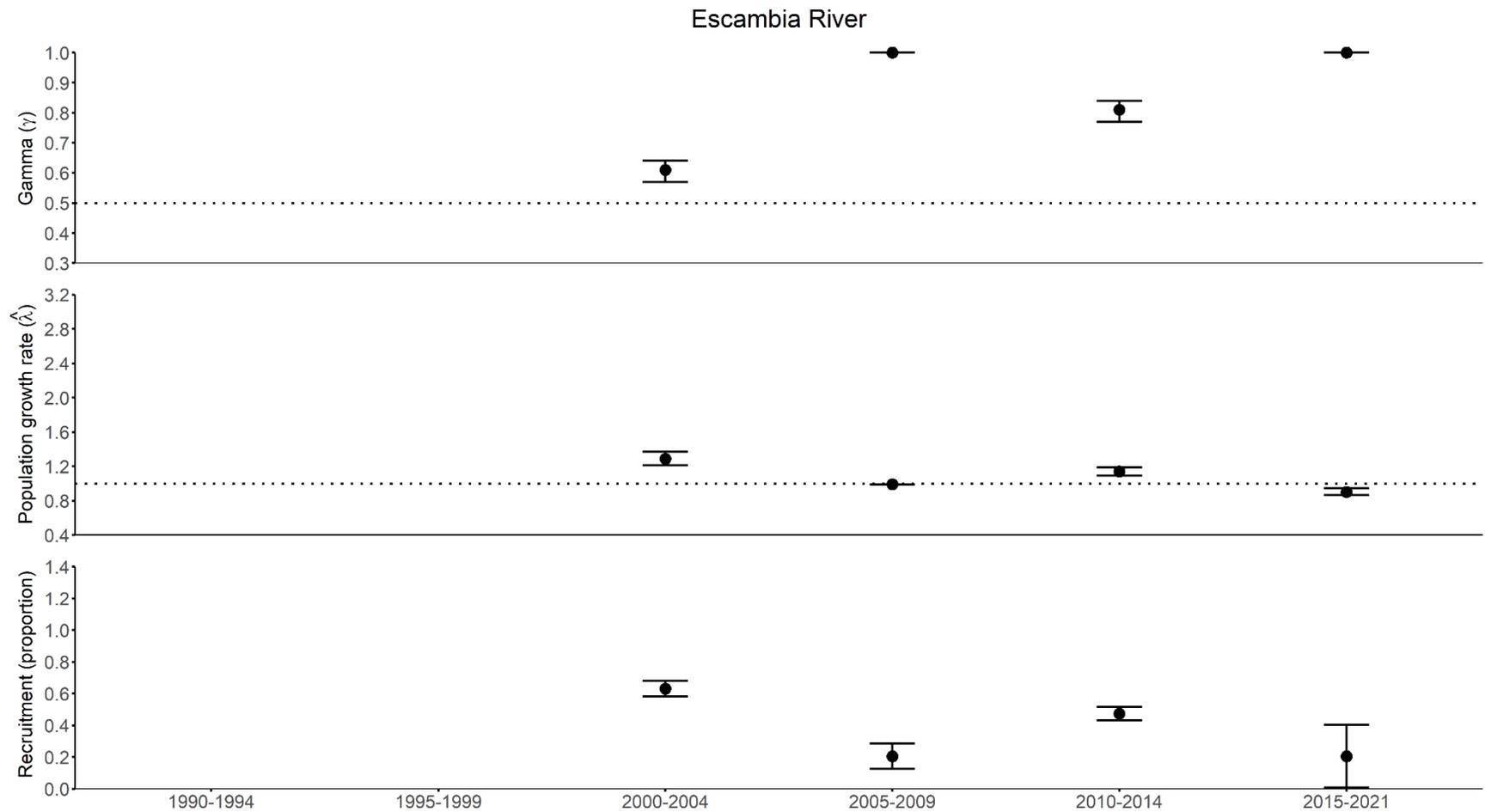
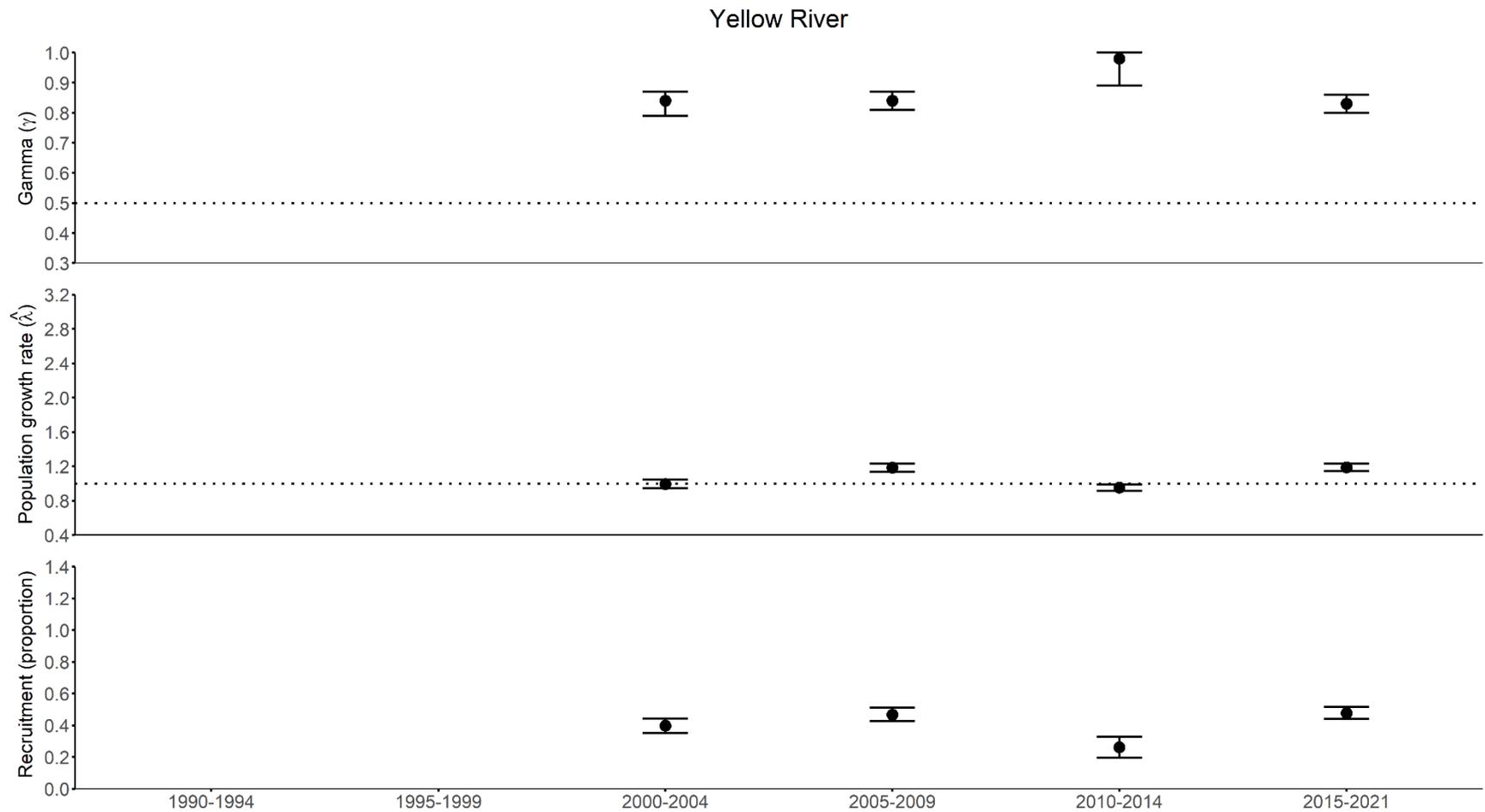


Figure 4.6. Escambia River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 4.2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.



**Figure 4.7. Yellow River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 4.2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.**

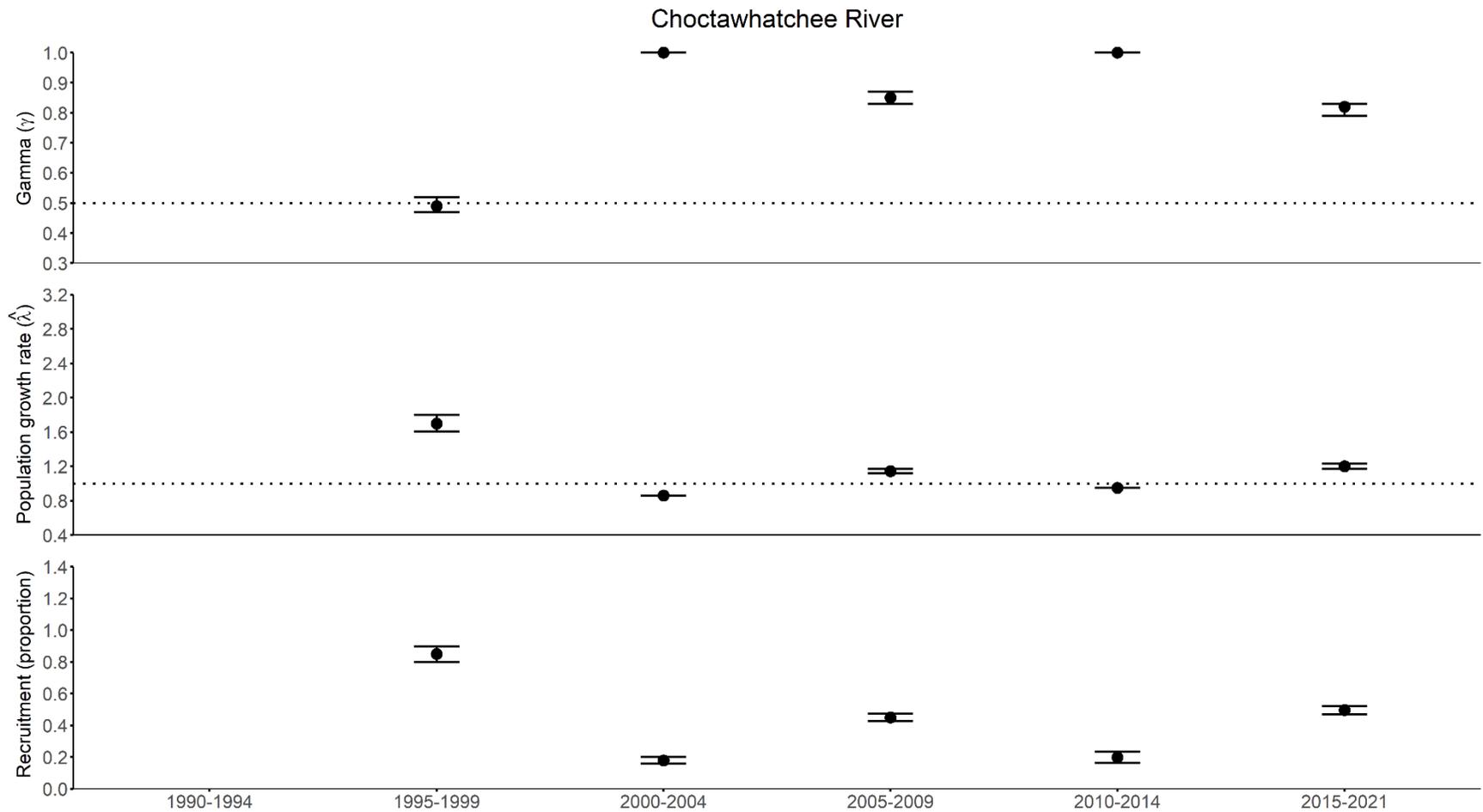
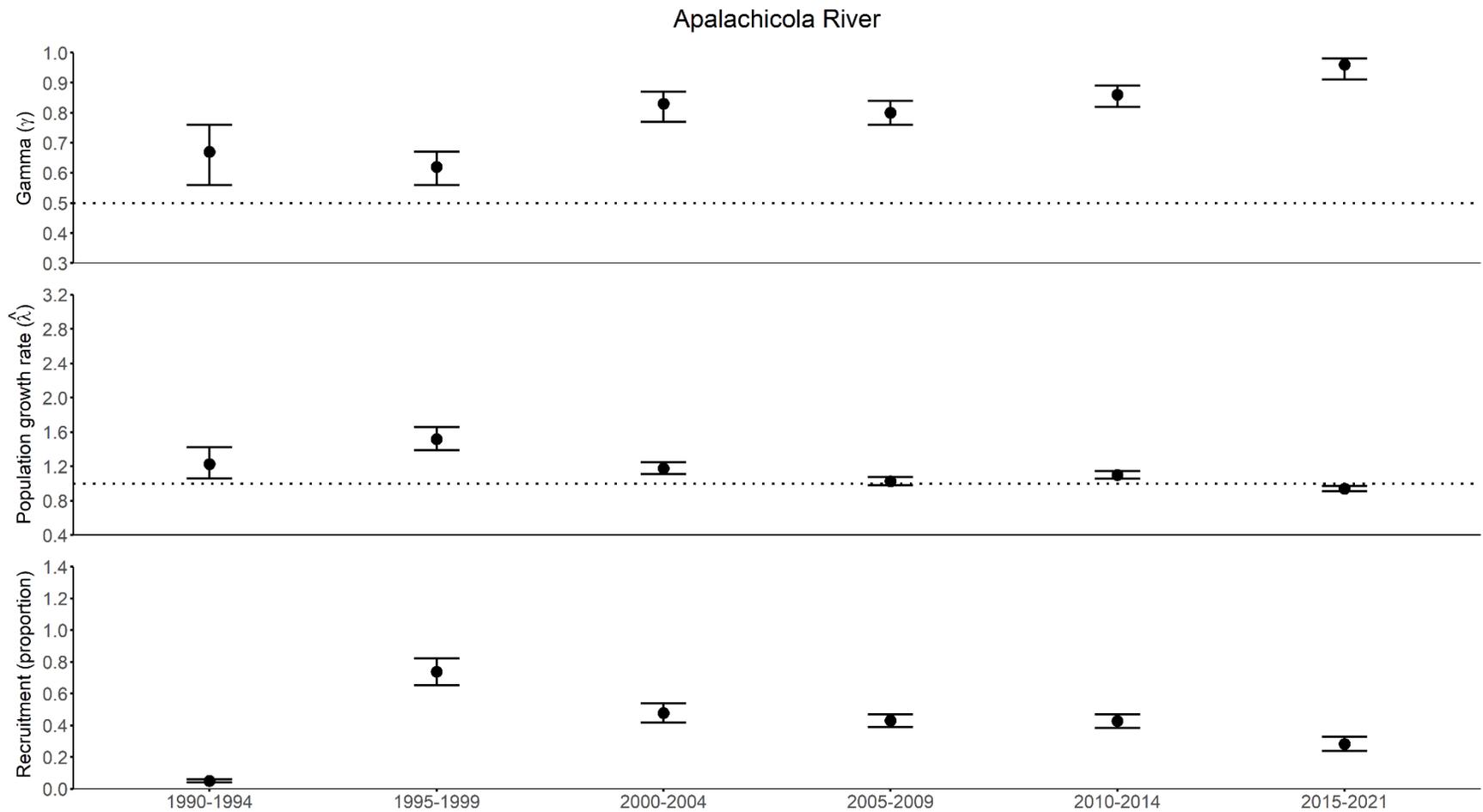


Figure 4.8. Choctawhatchee River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 4.2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.



**Figure 4.9.** Apalachicola River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 4.2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.

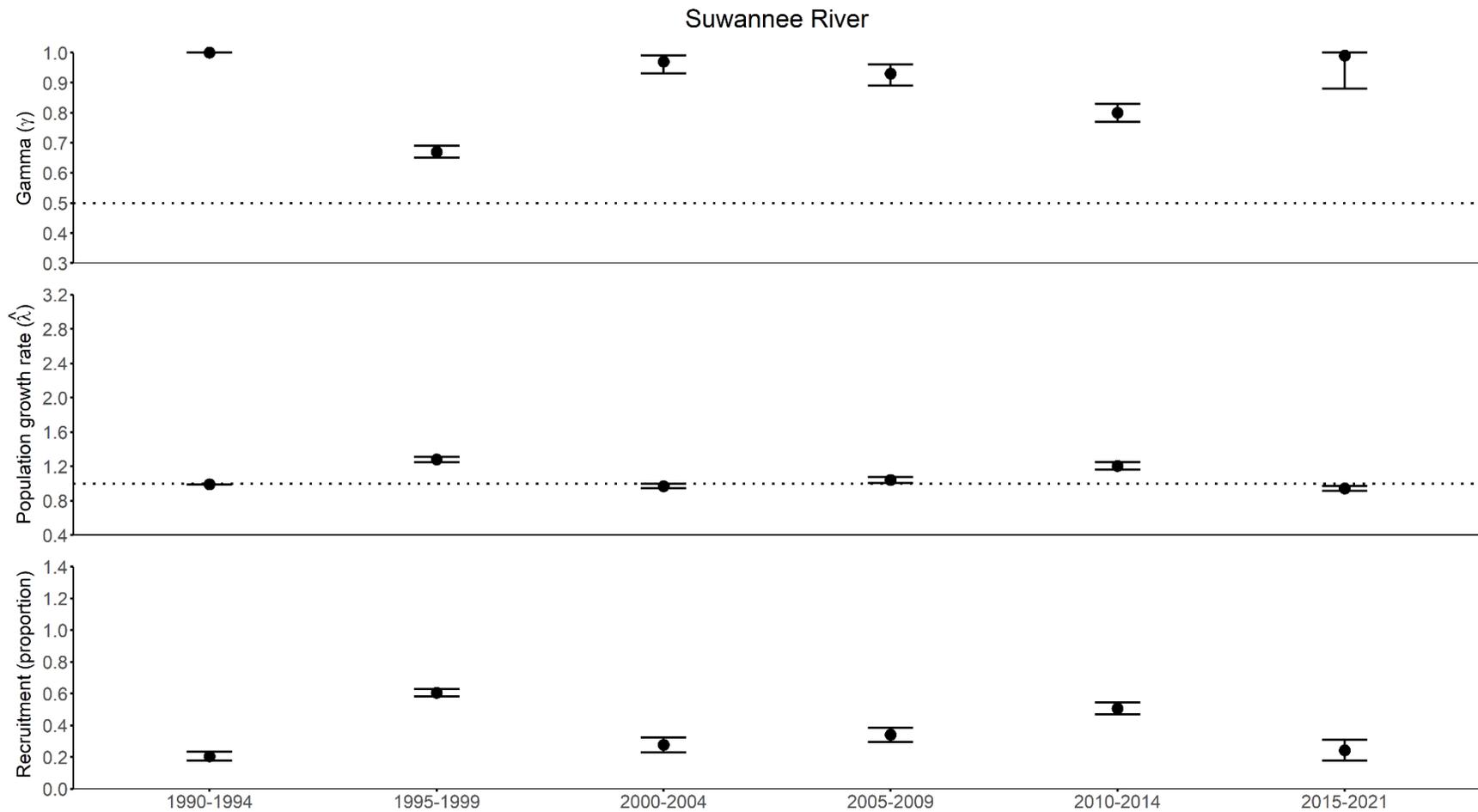


Figure 4.10. Suwannee River time period-specific estimates of seniority ( $\gamma$ ), and derived estimates of recruitment ( $f$ ; represented as a proportion) and population growth rate ( $\lambda$ ) from the top-ranked temporal symmetry model (Model 4; described in Table 4.2). Dashed reference lines indicate the point at which adult survival is proportionally more important than  $f$  to  $\lambda$  (i.e.,  $\gamma > 0.50$ ) and population stability ( $\lambda = 1$ ). Error bars indicate 95% confidence intervals.

## Appendix

**Table 4.A1. Summary of the number of Gulf Sturgeon in each river marked with PIT tags between 1990 and 2022.**

<b>River</b>	<b>No. Gulf Sturgeon</b>
Pearl	172
Pascagoula	263
Escambia	526
Yellow	974
Choctawhatchee	1,552
Apalachicola	897
Suwannee	2,837

**Table 4.A2. Summary of the number of adult Gulf Sturgeon in each river marked with PIT tags between 1990 and 2004.**

<b>River</b>	<b>1990</b>	<b>1991</b>	<b>1992</b>	<b>1993</b>	<b>1994</b>	<b>1995</b>	<b>1996</b>	<b>1997</b>	<b>1998</b>	<b>1999</b>	<b>2000</b>	<b>2001</b>	<b>2002</b>	<b>2003</b>	<b>2004</b>
Apalachicola	3	5	2	24	0	2	0	0	29	43	2	27	23	13	66
Choctawhatchee	0	8	2	0	6	0	11	32	9	340	130	111	17	22	13
Escambia	0	0	0	0	2	7	0	0	0	0	1	0	122	42	10
Pascagoula	0	0	0	0	0	1	0	3	28	35	39	24	15	15	0
Pearl	0	0	0	0	1	0	0	2	0	0	24	21	13	17	15
Suwannee	123	134	64	82	46	53	27	164	207	251	92	125	121	43	0
Yellow	0	0	0	14	0	0	0	6	0	15	0	139	93	129	7

**Table 4.A3. Summary of the number of adult Gulf Sturgeon in each river marked with PIT tags between 2005 and 2022.**

<b>River</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>2009</b>	<b>2010</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>2014</b>	<b>2015</b>	<b>2016</b>	<b>2017</b>	<b>2018</b>	<b>2019</b>	<b>2020</b>	<b>2021</b>	<b>2022</b>
Apalachicola	19	50	9	5	78	53	32	33	20	132	9	61	18	31	32	18	56	8
Choctawhatchee	17	13	181	161	29	51	64	66	35	0	7	8	6	48	52	32	80	29
Escambia	23	76	4	1	2	33	26	8	5	0	98	5	3	5	5	19	25	17
Pascagoula	0	2	0	1	1	2	3	3	6	6	10	11	5	8	20	17	7	33
Pearl	5	2	2	5	1	20	5	9	6	0	0	1	4	1	7	0	10	19
Suwannee	36	254	160	20	0	20	44	190	261	2	44	45	121	28	12	21	19	118
Yellow	15	1	8	0	29	109	113	41	126	0	26	11	11	20	1	3	56	23

**Table 4.A4. Summary statistics for the number of adult Gulf Sturgeon that were newly PIT-tagged in each river during each time period. The mean and coefficient of variation (CV) are provided for each river and time period.**

River	Time Period											
	1990–1994		1995–1999		2000–2004		2005–2009		2010–2014		2015–2021	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Pearl	0.20	223.61	0.40	223.61	18.00	24.85	3.00	62.36	8.20	90.19	3.29	118.81
Pascagoula	0.00	–	13.40	124.94	18.60	76.85	0.80	104.58	4.00	46.77	11.29	47.64
Escambia	0.40	223.61	1.40	223.61	35.20	147.61	21.20	150.63	14.60	97.18	23.14	150.93
Yellow	2.80	223.61	4.20	156.49	73.80	90.10	10.60	112.54	77.80	70.23	18.29	102.88
Choctawhatchee	3.20	113.54	78.40	187.13	58.60	97.26	80.40	104.11	43.20	62.83	33.29	85.20
Apalachicola	6.80	143.86	14.80	135.08	26.20	92.61	32.20	96.56	54.40	84.64	32.14	61.42
Suwannee	93.60	43.49	142.20	67.89	76.20	70.51	94.00	116.09	103.40	111.43	41.43	89.87

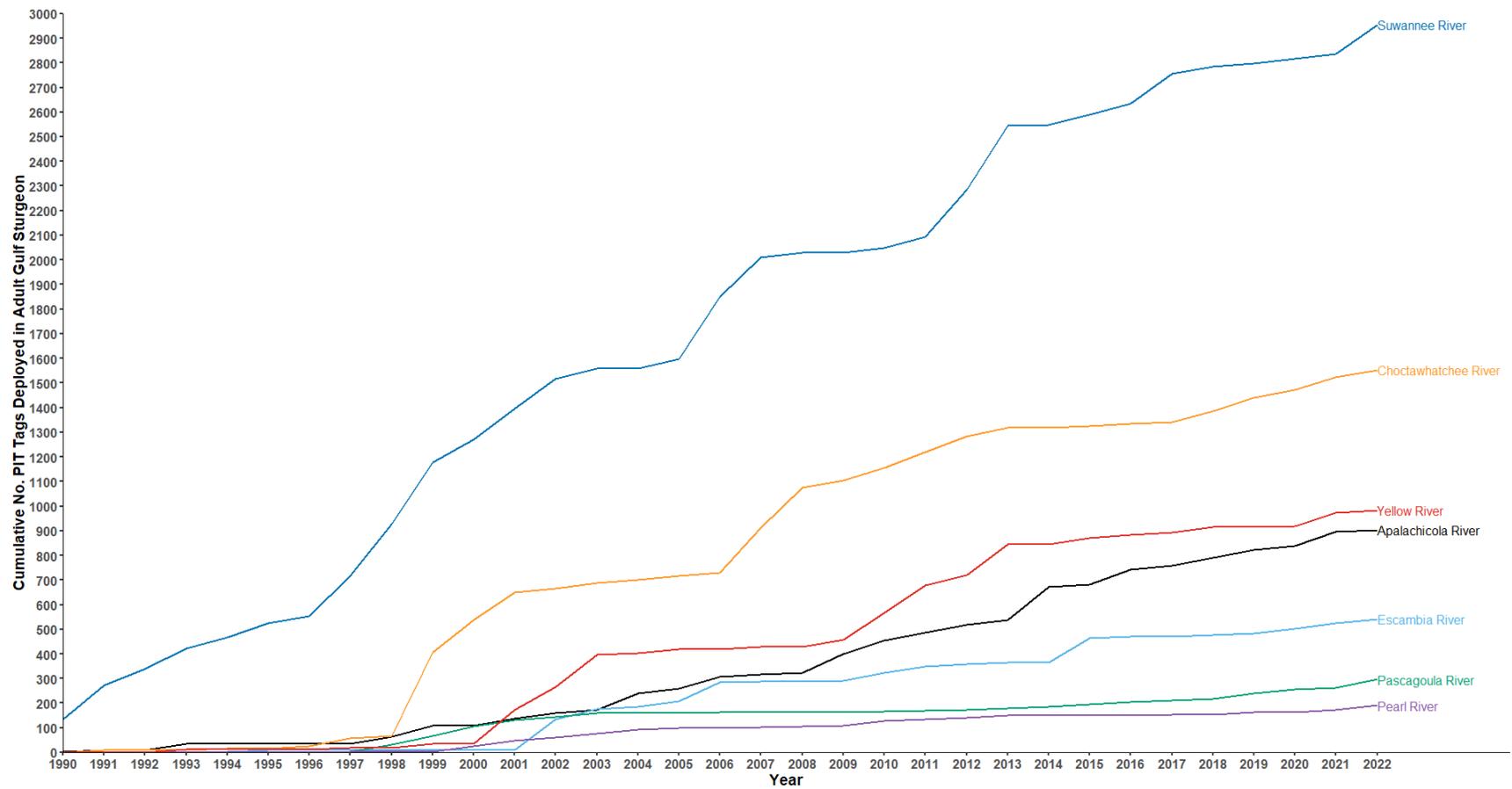


Figure 4.A1. Cumulative number of newly PIT tagged adult ( $\geq 1350$ -mm TL) Gulf Sturgeon (y-axis) in each River (colored lines) from 1990-2022 (x-axis).

## 5. Population Viability Analysis

### Completed as Task 1.3

#### Introduction<sup>1</sup>

We assess the extirpation risks for Gulf Sturgeon populations with a range of starting sizes and mortality rates estimated in Task 1.1. To evaluate the effects of various possible mortality sources on these populations, we simulated the following threats in the context of a range of population sizes. We estimated the probability of extirpation along various time horizons: (1) chronic increases in baseline mortality, (2) varying episodic mortality event frequency, and (3) varying recruitment failure frequency. A key finding was that Gulf Sturgeon population viability may be limited by creeping chronic rates of adult mortality.

#### Materials and Methods

##### *Model description*

We modified a PVA model described initially by Pine et al. (2013) for Humpback Chub *Gila cypha*. The original model was coded in Microsoft Visual Basic for Applications (VBA) by Carl Walters (University of British Columbia) and was migrated to program R (R Core Team 2022) and updated to its current form by Brett van Poorten (Simon Fraser University) and Lew Coggins (NOAA-Fisheries). Results from Task 1.1 inform input parameters for this model.

A summary of the equations used to inform the PVA model is included in Table 5.1. This model is an individual-based PVA model that simulates the dynamics of female fish only. Each PVA simulation was initialized by creating a list of  $N_0$  ( $i=1, 2, \dots, N_0$ ) individual female fish, which represents the number of female fish that were informed by a range of recent Gulf Sturgeon population estimates in rivers identified as critical habitat (NOAA and USFWS 2003; USFWS and NMFS 2022). Each fish was assigned an age based on an assumed initial stable age distribution based on age-specific survival rates  $S_a$ . For each subsequent simulation year,  $t = 1, 2, 3, \dots, T$ , the age of each fish increases by 1. Fish die and are removed from the population (list of individual female fish) with the probability of  $1-S(a_i)$ . The total count of surviving fish is the total surviving population at time  $N_t$ . Random stochasticity is introduced into each simulation based on the distribution of the initial age structure and survival and the  $N_0$  for each simulation. For age 1+ age classes, relative survival rates are used based on a Lorenzen function (Lorenzen 2000). We also assumed that older fish had a lower variance in survival than young fish. Random effects on survival were included to mimic environmental effects (Pine et al. 2013) by varying the maximum survival  $A_s$  (in the Beverton-Holt stock recruitment formulation, Walters and Martell 2004)

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<sup>1</sup> We received feedback from NOAA and USFWS in fall 2023 on a draft of the Task 1.3 report. Addressing the questions provided by NOAA and USFWS necessitated updating the PVA code to better assess how uncertainties in  $recK$  and  $M$  may influence estimates of population viability. These updated PVA simulations have required several weeks of high-performance computer time to complete and the final results from this updated PVA will be included in the submitted manuscript. We have provided a summary of the results from the updated reported in the Appendix to this chapter.

for each life history stanza included in the model (pre-recruit, juvenile/sub-adult, and adult). Life stanzas were used to screen specific scenarios of interest, such as recruitment failure (juvenile stanza) or changes to adult mortality (adult stanza). Each stanza and year were independent and assumed that maximum survival followed a normal distribution with a specified mean and standard deviation. Estimates from Task 1.1 informed this survival rate. Recruitment for each year was a function of the number of individual fry ( $E_i$ ) computed for that year (from the list of all female fish) and the survival of these fry through each of the life stanzas (stanza-specific survival rate). The number of recruits was added to the number of live fish at age 1.

Where possible, model inputs were informed by results from Task 1.1. Fish were recruited to the vulnerable population at age 4, and published estimates of Gulf Sturgeon recruitment compensation ratio (*reck*), the improvement in juvenile survival at low population levels relative to carrying capacity (Goodyear 1977, 1980), range from 3.9 to 5 (Flowers 2008; Flowers et al. 2009, 2020; Ahrens and Pine 2014). The sensitivity of model results to different values of *reck* is explored in the Appendix and will be further evaluated in a manuscript to be submitted for peer review in 2024.

### *Model scenarios*

We compared extirpation risk among the following three threats to understand better how risk may change if threats were realized. Threat 1 simulations represented increases in chronic mortality rates (“chronic creep”). Threat 2 simulations represented increases in episodic mortality frequency. Threat 3 simulations represented increases in recruitment failure frequency. These threats were informed by the Gulf Sturgeon Working Group discussions and reports over the last twenty years (USFWS and NMFS 2022; Dula et al. 2022). Evaluating these threats provides insight into the relative importance of juvenile mortality (recruitment failure) and adult mortality (chronic and episodic mortality) to population viability. The simulated scenarios are summarized in Table 5.3.

We varied PVA model input parameters, such as  $N_0$  and adult mortality, along a range of values to represent our best understanding of the present and possible future conditions within Gulf Sturgeon river populations. Initial vulnerable abundance (i.e., number of adult females;  $N_0$ ) in these simulations ranged between 100 and 10,000 individuals to represent the range of Gulf Sturgeon population sizes across the Gulf of Mexico; adult chronic mortality ranged between 0.11 and 0.15 (see summary in USFWS and NMFS 2022). These parameters informed various other equations related to survival at age, which then informed fecundity equations to determine recruitment. This recurring annual update of population size from these starting values occurred for 200 years. Future versions of this PVA will build upon this species-level analytical framework to include river-specific simulations.

The frequency of events (recruitment failure or episodic mortality) represents mean frequencies of occurrence over the maximum 200-year time horizons. Extirpation probabilities represent the percentage of the 1,000 trials of each scenario that resulted in population collapse over 50-year, 100-year, and 200-year time horizons. A simulation trial that resulted in extirpation in 50 years was also considered a population that went extinct over the 100-year and 200-year time horizons.

## Results

### *Creeping chronic mortality rates*

Baseline mortality rates of 0.11, informed by results from Task 1.1, resulted in no extirpation risk across all population sizes and time horizons (Scenarios 1–4; Tables 5.3–5.4; Figure 5.1). However, when adult mortality rates increased to 0.13, 200-year extinction probabilities ranged between 27.4% and 90.5% (Scenarios 5–8; Tables 5.3–5.4). A further increase in chronic mortality to 0.15 resulted in an 11.3% 50-year extirpation probability for populations starting with 100 fish. Additionally, 100-year time horizon extirpation probabilities were >26% for all populations starting with  $\leq 1000$  individuals, and all fish were extirpated at this mortality rate after 200 years (Scenarios 9–12; Tables 5.3–5.4).

### *Increasing episodic mortality event frequency*

When the average occurrence of episodic mortality events was 1/50 years, we observed a 15.9% 200-year extirpation probability for populations starting with 100 individuals (Scenario 13; Tables 5.3–5.4) and effectively no extirpation risk for populations starting with  $\geq 500$  fish (Scenarios 14–16; Tables 5.3–5.4). If mean event frequency increased to 1/25 years, 200-year extirpation probabilities ranged from 6.4–64.1% across all simulated populations (Scenarios 17–20; Tables 5.3–5.4). The maximum simulated mean episodic event frequency of 1/10 years resulted in an 11.8% 50-year extirpation probability for populations starting with 100 fish, 100-year extirpation probabilities >25% for all populations starting with  $\leq 1000$  individuals, and full extirpation of all populations after 200 years (Scenarios 21–24; Tables 5.3–5.4).

### *Increasing recruitment failure frequency*

Beginning with an adult mortality rate of 0.11, recruitment failure 1/10 years effectively reduced extirpation risk for populations with  $\geq 500$  initial individuals (Scenarios 30–32; Tables 5.3–5.4). When the mean frequency of recruitment failure increased to 1/5 years, extirpation probabilities ranged between 5.3% and 21.2% for these same  $\geq 500$  initial fish populations (Scenarios 30–32; Tables 5.3–5.4). Across both the five- and ten-year mean frequencies, there was a small probability (<5%) of extirpation for the smallest initial population size (Scenarios 25 and 29; Tables 5.3–5.4). Across a 200-year time horizon, these small populations also had the greatest extirpation probabilities (10.2% and 64.6%; Scenarios 25 and 29; Tables 5.3–5.4).

## Discussion

Overall, this work suggests that increases in adult Gulf Sturgeon mortality are a greater risk to viability than recruitment failure. Flowers et al. (2020) developed an age-structured population model for Gulf Sturgeon and found that higher annual mortality rates led to increased time to recovery. We observed that mortality frequency increases led to rapid extinction risk increases across all time horizons (50, 100, 200 years). Because the Gulf Sturgeon maximum age is likely more than 50 years (Tasks 1.1), these time horizons represent relatively few life spans of Gulf Sturgeon within a population recovery context.

Our PVA results suggest extinction risk is likely higher under certain population conditions, including (1) populations of 100 or fewer female adult fish with annual adult mortality rate  $\geq 0.13$ ; (2) populations of

≤1,000 adult females experiencing a ≥0.15 chronic adult mortality rate; (3) populations of 100 initial individuals facing a significant (~35%) episodic mortality event every 25 years on average; and (4) populations of ≤10,000 initial individuals facing a significant (~35%) episodic mortality event every ten years on average. These results were robust to various *reck* values (see the Appendix).

The mortality rates used in the different PVA simulations are informed by recent empirical evidence. For example, a chronic mortality rate of 0.15 is similar to a population experiencing a Hurricane Michael-level episodic event (Dula et al. 2022) about once every ten years. The consequence of such episodic mortality on population extirpation risk depends on the baseline mortality for the population. For the Pearl River, the mortality rate associated with the upper 95% confidence limit in Task 1.1 was about 0.21, 9% greater than the highest simulated adult mortality rate in this study. No other river had an estimated baseline mortality rate exceeding 0.15 (Task 1.1). With this chronic adult mortality rate and an assumed starting population size of 500 females, our PVA model estimates the 50-year extirpation probability to be >80%.

Our use of the upper 95% CI on survival for the Pearl River in the PVA is conservative because the chance of survival being lower is 95%. Using the upper 95% confidence interval in this way presents a cautionary example of how increases in mortality could increase the risk of localized extinction among these river populations. This is one reason why the population in the Pearl River has not gone extinct – survival rates in 500 years would only be expected to be 0.21 in 25 of the 500 years, which would not result in extinction.

This type of simulation is useful to assess risk to individual populations and inform allocation decisions for resources to support restoration and monitoring efforts. Our model is based on data from Task 1.1 and a recent estimate of episodic mortality (Dula et al., 2022). These empirical mortality values add realism to the PVA simulations. This iterative process of building models, testing, and collecting data to confront the models' predictions is often where significant learning and decision-making improvement occurs (Walters 1986).

## References

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## Tables and Figures

Table 5.1. A summary of the equations used to inform the population viability analysis simulations.

Equation no.	Study definition	Equation
1	Length-at-age	$l_a = 1 - e^{-Ka}$
2	Weight-at-age	$w_a = l_a^3$
3	Fecundity-at-age	$f_a = f(w_a - w_m)$
4	Size-based survival for recruited age-classes	$S_a = \exp\left(-\frac{M_\infty}{l_a}\right)$
5	Equilibrium egg density per recruit	$\varphi_0 = \sum_{a=1}^A l x_a f_a$
6	Maximum survival of Beverton-Holt recruitment function	$\alpha = \frac{\kappa}{\varphi_0}$
7	Carrying capacity parameter of Beverton-Holt recruitment function	$\beta = \frac{\kappa - 1}{R_0 \varphi_0}$
8	Maximum survival of Beverton-Holt recruitment function	$\alpha_s = \alpha e^{\left(\frac{M_s}{\sum M_s}\right)}$
9	Carrying capacity parameter of Beverton-Holt recruitment function	$\beta_s = B_s^* \frac{\beta}{\sum_{s'} (\beta_{s'}^* \prod_{s''=0}^{s'-1} \alpha_{s''})}$
10	The number of recruits in the first simulated year	$R_{t=1} = \frac{V_1}{\sum (l x_a v_a)}$
11	Gulf Sturgeon abundance in the first year	$N_{t=1} = R_{t=1} \sum l x_a$

**Table 5.2. Parameter estimates and sources.**

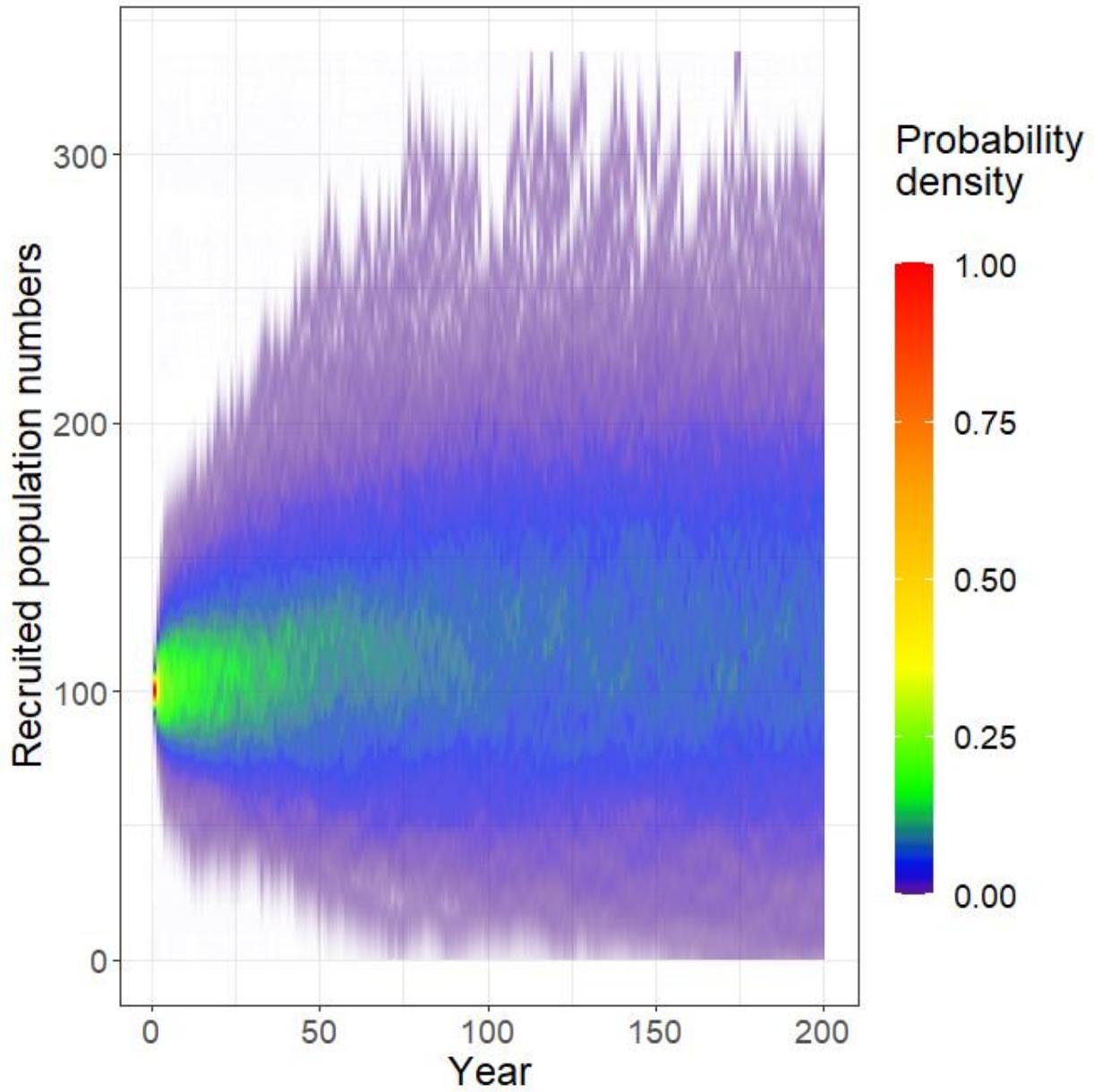
<b>Model parameter</b>	<b>Estimate</b>	<b>Comment and source</b>
Initial number of vulnerable fish ( $N_0$ )	100–10,000	Current population sizes are unknown. See USFWS and NMFS (2022) for a summary of river population abundance estimates.
Average long-term age 1 recruitment ( $R_0$ )	67	
Compensation ratio in recruitment ( $recK$ )	2.8	Assumed value. More conservative compensation than estimates from Flowers (2008) or Ahrens and Pine (2014)
Metabolic rate parameter of von Bertalanffy function ( $K$ )	0.13	Estimated from direct length-at-age and tagging data from 1978-2007 for the Apalachicola River by Flowers et al. (2010).
Minimum adult natural mortality rate ( $M_\infty$ )	0.0627	
Length at 50% selectivity ( $l_{50}$ )	0.27	
Selectivity shape parameter ( $l_{sl}$ )	0.045	
Weight at maturity relative to asymptotic weight ( $w_m$ )	0.15	Proportion of body weight lost to spawning estimated in Flowers et al. (2010).
Standard deviation of environmental effect on age 0 survival ( $\sigma_R$ )	0.6	Assumed to be high to reflect highly variable natural environment.

**Table 5.3. A summary of the various mortality scenarios we evaluated using population viability analysis simulations including the average frequency of occurrence for episodic events. The mortality rate is applied with this frequency on average.**

Scenario No.	Threat Definition	Adult Mortality	Vulnerable Abundance	Mean Freq.
1	Chronic mortality – baseline conditions	0.11	100	–
2	Chronic mortality – baseline conditions	0.11	500	–
3	Chronic mortality – baseline conditions	0.11	1,000	–
4	Chronic mortality – baseline conditions	0.11	10,000	–
5	Chronic mortality – creeping baseline	0.13	100	–
6	Chronic mortality – creeping baseline	0.13	500	–
7	Chronic mortality – creeping baseline	0.13	1,000	–
8	Chronic mortality – creeping baseline	0.13	10,000	–
9	Chronic mortality – creeping baseline	0.15	100	–
10	Chronic mortality – creeping baseline	0.15	500	–
11	Chronic mortality – creeping baseline	0.15	1,000	–
12	Chronic mortality – creeping baseline	0.15	10,000	–
13	Additional 35% episodic mortality	0.11	100	1/50 years
14	Additional 35% episodic mortality	0.11	500	1/50 years
15	Additional 35% episodic mortality	0.11	1,000	1/50 years
16	Additional 35% episodic mortality	0.11	10,000	1/50 years
17	Additional 35% episodic mortality	0.11	100	1/25 years
18	Additional 35% episodic mortality	0.11	500	1/25 years
19	Additional 35% episodic mortality	0.11	1,000	1/25 years
20	Additional 35% episodic mortality	0.11	10,000	1/25 years
21	Additional 35% episodic mortality	0.11	100	1/10 years
22	Additional 35% episodic mortality	0.11	500	1/10 years
23	Additional 35% episodic mortality	0.11	1,000	1/10 years
24	Additional 35% episodic mortality	0.11	10,000	1/10 years
25	Recruitment failure	0.11	100	1/10 years
26	Recruitment failure	0.11	500	1/10 years
27	Recruitment failure	0.11	1,000	1/10 years
28	Recruitment failure	0.11	10,000	1/10 years
29	Recruitment failure	0.11	100	1/5 years
30	Recruitment failure	0.11	500	1/5 years
31	Recruitment failure	0.11	1,000	1/5 years
32	Recruitment failure	0.11	10,000	1/5 years

**Table 5.4. Extirpation probabilities associated with 50-year, 100-year, and 200-year time horizons for all 32 simulated population viability scenarios.**

<b>Scenario No.</b>	<b>50-year Probability</b>	<b>100-year Probability</b>	<b>200-year Probability</b>
1	0%	0%	0.5%
2	0%	0%	0%
3	0%	0%	0%
4	0%	0%	0%
5	0.1%	18.5%	90.5%
6	0%	0%	58.2%
7	0%	0%	46.2%
8	0%	0%	27.4%
9	11.3%	90.8%	100%
10	0%	47.2%	100%
11	0%	26.2%	100%
12	0%	3.8%	99.6%
13	0.1%	1.3%	15.9%
14	0%	0%	0.6%
15	0%	0%	0.3%
16	0%	0%	0%
17	0%	9%	64.1%
18	0%	0.1%	20.4%
19	0%	0%	14.1%
20	0%	0%	6.4%
21	11.8%	78.9%	100%
22	0.5%	38.5%	99.9%
23	0%	25.7%	99.7%
24	0%	5.3%	99.1%
25	0%	0.3%	10.2%
26	0%	0%	0.1%
27	0%	0%	0.1%
28	0%	0%	0%
29	0%	4.4%	64.6%
30	0%	0%	21.2%
31	0%	0%	13.9%
32	0%	0%	5.3%



**Figure 5.1. Population projections from 1,000 simulations of Scenario 1, in which a chronic mortality rate of 0.11 was applied to an initial population of 100 adult female Gulf Sturgeon.**

## Appendix

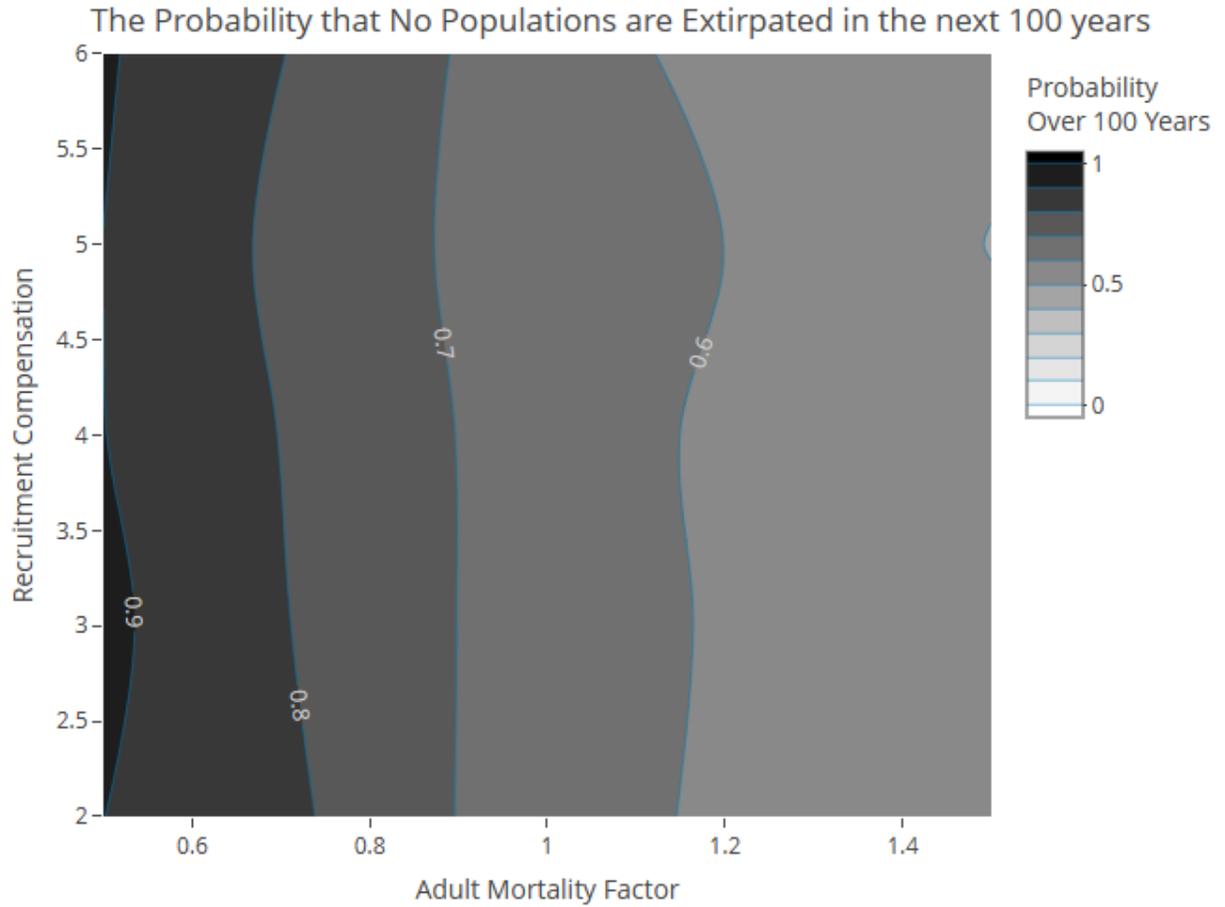
To evaluate the robustness of our population viability analysis (PVA) results to a range of recruitment compensation (reck) values, we conducted an ad-hoc sensitivity analysis to expand the included values of reck beyond a conservative assumed value of 2.8 to a range of values that included 2, 3, 4, 5, and 6. In addition, we wanted to investigate the relative importance of reck, a parameter with an assumed value, to adult mortality (Madult), a parameter we estimated. To explore the influence of varying values of Madult on extirpation risk, we multiplied the river-specific instantaneous Madult estimates by 0.5, 0.75, 1, 1.25, and 1.5. We then performed 1,000 simulations of each of these 25 pairwise combinations of varying reck and M values to assess their relative importance to population viability (25,000 total simulations). PVA parameters for this analysis are summarized in Table 5A.1. If the population size of any of these river populations dipped beneath 50 individuals during any of the 100 years of any single simulation, the population was deemed extirpated (Bowen and Avise 1990). We observed that reck had little effect on Gulf Sturgeon population viability as our estimates of extirpation risk were effectively the same when we only varied reck and held Madult constant. When Madult was held constant and reck changed from 2 to 6, the probability that no populations were extirpated didn't change by more than 0.02. In comparison, these probabilities changed up to 0.40 when Madult was varied and reck was constant. This suggests that our estimates of extirpation risk are much more sensitive to changes in Madult, the parameter that Gulf Sturgeon monitoring programs have shifted to measuring since 2010 (Pine and Martell 2009; Rudd et al. 2014).

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**Table 5.A1. Results of PVA sensitivity analysis.**

<b>RecK</b>	<b>Adult mortality factor</b>	<b>Probability no populations are extirpated within the next 100 years</b>
2	0.50	0.90
2	0.75	0.80
2	1.00	0.63
2	1.25	0.58
2	1.50	0.53
3	0.50	0.92
3	0.75	0.78
3	1.00	0.65
3	1.25	0.58
3	1.50	0.53
4	0.50	0.90
4	0.75	0.77
4	1.00	0.65
4	1.25	0.57
4	1.50	0.53
5	0.50	0.90
5	0.75	0.75
5	1.00	0.65
5	1.25	0.59
5	1.50	0.50
6	0.50	0.91
6	0.75	0.78
6	1.00	0.64
6	1.25	0.56
6	1.50	0.52



**Figure 5.A1. A plot of the probability that no river populations of Gulf Sturgeon are extirpated over the next 100 years is given a range of pairwise values of recruitment compensation and adult mortality.**