Effects of Dams on Migratory Fishes in the Alabama River: Laying the Groundwork for Restoration

by

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Abstract

To understand the effects of dams on migratory fishes in the Alabama River Basin and support conservation of these species, I conducted studies on the past, present, and potential future of the system. The first study was to describe the ranges of migratory fish in the Mobile River Basin prior to the construction of dams (Pre-1890). Given the lack of scientific data from this period, I used archived newspapers and other historical sources to find occurrences of six imperiled migratory fish species and show how their ranges have declined over time. The second study was to track migrating Paddlefish after translocating them above a dam impeding their migration. I sought to know whether fish would be able to navigate the reservoir upstream and find potential spawning habitat if passage at the dam was improved. The majority of fish surviving translocation made upstream movements through the reservoir, but their survival during passage back downstream through the dam may have been limited. Finally, I conducted a simulation study to test how improving fish passage at dams on the Alabama River might affect a fragmented metapopulation of Paddlefish in the future. I programmed an agent-based model and explored the consequences of various parameterizations on the likelihood of population segment extirpation. At low levels of downstream entrainment, and levels of natural mortality slightly higher than estimated for the metapopulation, persistence of all segments was possible across diverse upstream passage scenarios. However, increasing passage led to more positive effects, which is promising for future mitigation efforts at the dams.

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Chapter 1: Introduction

Fish migration evolved as a strategy to maximize individual fitness in periodically changing environments (Lucas and Baras 2001). During certain periods, habitats may become suboptimal for survival, growth, spawning, etc., and the costs of residency may outweigh the costs of migrating to better habitat. Fishes have evolved diverse migration strategies to adapt to dynamic habitat conditions (Thurow 2016). The first of these strategies to be formally described was diadromy: migration between salt and freshwater. Diadromy was further classified into three syndromes: catadromy (adults live in freshwater and migrate to the ocean to spawn), anadromy (adults live in the ocean and migrate to freshwater to spawn) and amphidromy (adults spawn in tidal freshwater, juveniles migrate to sea for a brief period) (McDowall 2007). These broad definitions, while useful, do not account for wide diversity within syndromes, and particularly the variability in migration patterns of early life stages (e.g., larval residency, smoltification, etc.). Also, amphidromy is sometimes used as a catch-all for fishes that do not fit the conventional definitions of the other two syndromes but still make large scale movements for refuge, feeding, or spawning (Pauly 2004; Northcote and Hinch 2004). The term typically pertains to estuarine generalists, and amphidromous fishes may be experiencing selective forces, driven towards anadromy or catadromy (Gross 1987). The other strategy described was potamodromy: migration solely within freshwater (Myers 1949). Similar to diadromy, potamodromy has been broken down into syndromes based on the habitats involved: fluvial, adfluvial, lacustrine, and allacustrine (Varley and Gresswell 1988). Fishes may make any of these migrations for refuge, spawning, feeding and/or growth depending on the season and their life stage. They can make migrations passively (e.g., downstream larval drift) or actively (e.g., spawning runs upstream), and they may change their strategy over time in response to habitat alteration, sometimes even switching entire syndromes (Gross 1987; Bronmark et al. 2013). However, many species are unable to persist in altered habitat, which has led to large population declines (Limburg and Waldman 2009).

Overfishing, pollution, and habitat loss due to dam construction are the three most pervasive threats to migratory freshwater fishes worldwide (Waldman et al. 2016, Tamario et al. 2019). Migratory fish are particularly vulnerable to overfishing due to their predictable movements, and their tendency to aggregate during migration. Many overharvested fishes (e.g., salmonids, sturgeons, etc.) migrate up rivers *en masse* at the same time every year. As they swim up through natural bottlenecks like estuaries and narrow river channels, anglers can strategically focus their effort, and harvest substantial proportions of the population with relative ease. Over time, these devastating culls have decimated many spawning stocks, leading to their local and global extinction (e.g., Chinese Paddlefish *Psephurus gladius*, Zhang et al. 2019), and potential ecosystem collapse (Allan et al. 2005). Pollution has also contributed to the decline of migratory species (Brungs et al. 1977). While catastrophic events like oil spills can impact populations, steady increases in environmental contaminants such as heavy metals and PCBs have contributed to declines via bioaccumulation in many species groups, especially benthic species such as American eels *Anguilla rostrata* and predators such as salmonids (Belpaire et al. 2008; Ray 1978). Finally, the construction of dams has contributed to migratory fish declines via a suite of effects (Nilsson and Berggren 2000). The most obvious effect is the restriction of movement, particularly the obstruction of spawning migrations, although dams have also altered or destroyed essential habitat for migratory fishes. Altering or ceasing water flow in riverine ecosystems can decimate migratory fish populations, especially rheophilic ones that require flow for spawning and feeding (Birnie-Gauvin et al. 2017).

Migratory fishes have been in decline globally for centuries, and restoration efforts have been disproportionate among the different migration strategies (Limburg and Waldman 2009). Much more attention has been given to diadromous species because of their higher economic value, despite the fact that the majority of migratory freshwater fishes in the temperate and tropical zones are potamodromous, and can make up a substantial portion of the biomass in riverine ecosystems (Flecker et al. 2010). Basic understanding of the life histories of many potamodromous taxa is lacking, which has undoubtedly slowed potamodromous fish conservation and restoration (Northcote 1998; Lucas and Baras 2001). Potamodromous fish can be ecologically important due to the roles they play in ecosystem connectivity, providing seasonal subsidies of nutrients and energy (Flecker et al. 2010). Therefore, their extinction can represent the loss of essential components of ecosystem connectivity and function. Additionally, potamodromous fishes can have cultural and economic value, playing large roles in the mythology, folklore, and livelihoods of people globally (Lynch et al. 2016; O’Brien et al. 2019).

To protect and potentially restore these species, certain data are required. Current threats must be identified, species biology and life history described, and their population status assessed within a historical context. Some species lack historical data which has hindered efforts to protect them via legislation (Young et al, 2012). For my dissertation I studied the effects of one key threat (dams) on native potamodromous species holistically, incorporating a diverse set of approaches. In my first chapter, I researched the history of the most threatened and exploited migratory species of the Mobile Basin in Alabama (as defined by management and conservation experts), describing their historic distribution, and how those ranges may have declined over time since the mid 19th century. The second chapter is an experiment with a more applied focus. Although fish passage mitigation efforts have shown promise for restoration of migratory species, the ultimate outcomes of many passage solutions are not fully evaluated. To determine the potential of mitigation solutions to improve production of migratory fishes, fish that successfully pass the dam must proceed to their spawning grounds. In this experiment, I tracked the fates of fish translocated above an essentially impassable hydropower dam to assess the potential of restoring spawning runs of migratory fish along the Alabama River. In my final chapter, I used individual- (agent-) based simulation models to assess the potential impacts of improving passage rates at Alabama River dams on overall migratory fish population stability. The model I programmed has broad applicability to potamodromous fish populations in other fragmented systems around the world. Overall, my objective was to produce a holistic and interdisciplinary dissertation that would provide critical information and approaches to be used by multiple disciplines within ecology, biology, and fisheries management, toward the end of supporting appropriate conservation and management of fishes in human-altered systems.

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Chapter 2: **Pre-impoundment fish migrations in the Mobile Basin, Alabama**

Abstract:

Assessing the status of several migratory fishes in the Mobile River Basin, Alabama, has been complicated due to a general lack of historical data on their life history, habitat requirements, and distributions. Whether distributions were restricted by natural or human-made barriers to migration is difficult to assess because few scientific collections were made before dams were built (before 1890). Likewise, the earliest dams were built at the largest biogeographic barrier in the basin: the geological fall line. Therefore, we used anecdotal information, primarily records from archived newspapers and government reports published between 1850 and 1930, to describe the ranges of six migratory species prior to the construction of dams in the Mobile Basin. We describe the complicated history of Alabama Shad *Alosa alabamae* and show that range declines may have been masked by the stocking of American Shad *Alosa sapidissima* in the late 19th century. We document that Gulf Sturgeon *Acipenser oxyrinchus desotoi* probably migrated well above the fall line in the Coosa River, and may have been sympatric with Lake Sturgeon *Acipenser fulvescens*. We found no records of Alabama Sturgeon *Scaphirhynchus suttkusi* above the fall line. American Eel *Anguilla rostrata* migrated above the fall line in every Mobile Basin river before dams were built. Finally, Paddlefish *Polyodon spathula* may have once occurred above the fall line in at least two rivers, but they persist today in impounded reaches in the coastal plain, unlike some other species. These results demonstrate the utility and value of archival sources of information for re-tracing the histories of imperiled species.

Introduction:

The Southeastern region of the United States is the most biodiverse region for aquatic species in the country, but also ranks among those with the highest extinction rates. In 2000, an assessment of the conservation status of native freshwater fishes of the region reported a 125% increase in jeopardized fishes since 1980 (Warren et al. 2000). Within the region, the Mobile River Basin in Alabama has the second highest number of imperiled freshwater and diadromous fish species (n=57) of any ecoregion in North America (Jelks et al. 2008). Although some species have been Federally listed, others which are apparently imperiled have yet to be given the same protections due to data deficiencies and lack of historical understanding. The status of imperilment for several species have been shrouded due to insufficient collection records, lack of consensus on population structure, and lack of taxonomic status recognition (i.e. distinguishing between separate species vs. separate populations of the same species). As a result, the Federal listings of several taxa in Alabama have been delayed (e.g. Mayden and Kuhajda 1996; Smith and Clugston 1997), a need has developed to identify and fill data gaps where information is available.

Without historical records of abundance, low occurrence in current collections is not conclusive evidence of population decline or range reductions. Historical collections may not have captured the entire native range of species if they occurred after those ranges had already changed. Another issue is the historical records that do exist may predate the species description, so accurately attributing records to current taxa may be challenging (Burke and Ramsey 1995; Campton et al. 2000). Also, studying habitat preferences of rare species can be extremely difficult, due to the sampling effort required to obtain sufficient distribution and occupancy data.

One particular question that hinders our understanding of the distribution of imperiled migratory fishes in the Mobile Basin is whether the physiogeographic feature known as the fall line represents an historical migration barrier (Mudre et al. 1985; Mettee et al. 1996). Some of the first and largest dams in the basin were built at the fall line to use the hydraulic head generated by the sudden change in elevation for power generation and provide locks for navigation. These dams almost certainly halted fish migrations, but many of them pre-date the first collections of fishes in the state (e.g. Lay Dam, ca. 1913). Therefore, lack of species collections above the dams located on the fall line is not conclusive evidence that those dams affected species distributions, or if these species ever existed above the fall line prior to dam construction. These points combine to make for an extremely frustrating challenge for managers seeking to restore native migratory species in streams tributary to the Gulf of Mexico (i.e. which species are appropriate to restore upstream of the dams without well-documented distributions prior to dam construction ca. 1890).

Data that are typically used to inform extinction risk models for migratory fishes are a mix of quantitative and qualitative information that is evaluated based on “informed professional judgment” by panelists (Grogan and Boreman 1998). Several aspects of species’ biology are considered, but when even crude estimates of abundance are lacking, additional sources of information are required to inform both the current and historical status (Wainwright and Kope 1999). The two main sources of information typically used in status assessments are scientifically collected data (e.g. museum collections) and commercial information such as landings and trade records. However, when those records are lacking or insufficient, appropriate defensible evidence is difficult to find. Anecdotal evidence typically lacks the weight of scientific evidence in decision making and may be less precise and/or accurate, but increasing evidence has shown that incorporating local, particularly indigenous, knowledge systems into decision making can be a more effective strategy than relying solely on the scientific method (Gadgil et al. 1993; Reid et al. 2021). While verification of these sources is not always possible, the stakes of management decisions may be sufficiently high to warrant consideration of all information sources. Managers must leverage as many credible sources as are available to best assess a species status.

Several case studies have demonstrated the utility of anecdotal information in applied historical ecology. Applications have established historical baseline ranges and abundances for imperiled native species (Foster 2018), retraced the spread of biological invasions (Clavero and Villero 2014) and even quantified historic climate and habitat changes (Van Dyke and Wasson 2005). However, baselines can be difficult to establish when past conditions are confounded by human influence. It is difficult to determine whether any particular baseline was representative of pre-historical natural equilibrium conditions.

The purpose of this study is to combine scientific and anecdotal records to describe the historical ranges (and changes thereto) of six migratory species of varying conservation concern in the state: Gulf Sturgeon *Acipenser oxyrinchus desotoi*, Lake Sturgeon *Acipenser fulvescens,* Alabama Sturgeon *Scaphirhynchus suttkusi*, Alabama Shad *Alosa alabamae*, American Eel *Anguilla rostrata,* and Paddlefish *Polyodon spathula*. We selected these species because of their high conservation priority, but also because we expected that captures or sightings of these species would be more newsworthy than smaller and more common species, and more records would be available. Providing evidence of changes in species' distributions over time may provide insights for biogeography, conservation, and potential restoration strategies. For example, if Alabama Shad was never abundant in Alabama, then efforts to restore them may not be justified. Similarly, if sturgeon species were never found above the fall line, then providing fish passage at fall line dams for these species may not be necessary. In this study, we provide the results of a strategic and exhaustive search of available information sources, including local public libraries, historical archives, and collections databases for records of these species throughout the Mobile Basin. We hope that re-tracing historical fish migrations in the Mobile Basin will provide a useful baseline for future work, including the potential for restoration.

Methods:

We conducted two major search efforts: (1) to describe the history of dam construction in the Mobile Basin, and (2) to describe the ranges of a set of important migratory fish species as they changed concurrently.

We focused (but did not limit) the first search to the five largest Mobile Basin tributaries (Tombigbee, Alabama, Cahaba, Coosa, Tallapoosa), because the dams on these tributaries were built and owned by either governmental or publicly traded entities, while dams on smaller tributaries were typically privately owned and not documented as well in the public record. To find records of dam construction, we searched the JSTOR, the USACE Mobile District library catalog, and the Alabama Department of Archives and History using the terms "Alabama" AND “dam” and read materials with pertinent titles or abstracts. Records of structures like wing dams or bulwarks that did not span the river were screened. From records of dams, we collected the following data: the name of the dam and its owner, the start and completion dates of the project, and the location, size, type and purpose of the project. When applicable, we also recorded dates of important modifications to the dams, name changes, and the date of removal or destruction if relevant.

We also searched the W.S. Hoole Special Collection digital archives (University of Alabama Libraries), the Alabama Maps project website (Cartographic Research Laboratory, UA), and the Alabama Department of Archives and History Digital Collection (State of Alabama) for maps, photographs and aerial imagery to locate dams and describe potential barriers to migration before dams were built (University of Alabama). The aerial surveys were conducted beginning in 1939, which does not pre-date the earliest dams, but if they were conducted during periods of low water, human-made structures could be identified and noted.

The second search effort was to find records (both scientific and anecdotal) of the study species within the Mobile Basin. We first compiled collection records for each of the target species using the Global Biodiversity Information Facility (GBIF) database. We queried the database for the scientific name of each target species, but also included records of “Acipenser oxyrhinchus” for Gulf Sturgeon. In addition to GBIF records, we also requested data from the Alabama Department of Conservation and Natural Resources (ADCNR) database, and the Alabama Natural Heritage Program database. We only requested occurrences of the target species. We then screened the query results from each of the three databases. We excluded records without geographic coordinates and records occurring outside the Mobile River Basin.

Records that passed screening were then cross-referenced among the three databases and redundant records were removed. Details of the queries and screening can be found in Appendix A. We recorded the coordinates and date of each occurrence for mapping.

Finally, we performed a snowball search through primary sources for anecdotal records of captures, collections, landings, and sightings of the study species in the Mobile Basin. We began the search by querying Newspapers.com, a digital Newspaper archive, with a Boolean search for common names of the target species AND the word “caught”. We learned about additional names used for our target species as we searched, and broadened our search terms as new common names were discovered (Table 1.1). We first filtered the query results to exclude records from outside Alabama, but then performed additional Boolean searches for the most popular common names (e.g., spoonbill, sturgeon, shad) AND either “Tombigbee” OR “Etowah” OR “Coosa” to include occurrences that may have been published within the Mobile Basin, but outside the state. Further detail on the search for anecdotal records is available in Appendix B.

Each record matching our search terms was accessed and briefly reviewed for relevance. We filtered articles, only selecting ones that described the capture or sighting of a fish in the waters of the Mobile Basin (e.g. some articles were just vague fishing reports, only discussed the biology of the species, or discussed fisheries in other parts of the world). Then we gleaned all relevant information we could from the record, including the fish size, location, date of capture, and in some cases, abundance. If a photograph was included, we have reproduced it in Appendix C. If only the river name was provided, we assigned the record to the closest Cartesian coordinate on the river to the city the newspaper was published in. If no river name was given, we assumed the record came from the nearest river. If a specific location was named that could not be found on contemporary maps, we used the Historical Atlas of Alabama (Remington and Kallsen 1999) and the Historical Map Archive (UA Cartographic Research Laboratory) to try to determine the exact location. When the same record was published in numerous papers (i.e. copied verbatim from one newspaper to another, or referencing identical details about the occurrence) we only used the earliest published record.

When newspaper articles mentioned stocking or introduction of the study species, we attempted to verify the events by searching Newspapers.com for other mentions of the names of the people or agencies responsible. We also accessed stocking reports by the U.S. Fish Commission (1871-1903) on the Penobscot Bay Watch organization website (penbay.org, 2023), and tabulated all stocking events listed in the reports. We treated these as scientific, rather than anecdotal records of the species.

Due to the uncommon practice of using scientific names in newspapers, and the scarcity of photographs, we were not able to identify all records of “sturgeon” to species. When photographs were provided, we sought expert opinion to confirm the species identification. Otherwise, we considered weight information when provided to infer identification. Given that Lake Sturgeon and Alabama Sturgeon have never been recorded at weights greater than 100 kg in Alabama, we assumed that any record of a “sturgeon” over that weight was a Gulf Sturgeon. Similarly, records of “shad” were rarely identified to species, making it nearly impossible to discern among congeners (e.g., American shad *Alosa sapidissima*, Hickory Shad *A. mediocris*, Skipjack Herring *A. chrysochloris, etc.)*. We provide our best guess at the identity of unknown sturgeons and shads on a case-by-case basis along with our rationale.

We also performed searches of the target species common and scientific names on the Alabama Department of Archives and History Digital Collections database, the Auburn University Library Archive Catalogue, and the University of Alabama Library's W.S. Hoole Special Collections Digital catalogue to find potential occurrences of the species. We briefly reviewed each query result for relevance, but found no pertinent records.

To present our findings, we begin with a history of dam construction in the Mobile Basin, with a focus on mainstem dams, but provide some historical context for general development of the basin's rivers. We present the results of our search for records of each species in the basin, and discuss how the records relate spatiotemporally to these potential migration barriers for each of the target species in the major Mobile Basin rivers. For broad overview mappings of our findings, scientific collection records (with sturgeon species distinct) and anecdotal records (with sturgeons grouped) were aggregated within HUC 8 sub-basins (National Hydrography Dataset; U.S. Geological Survey 2018). Due to indemnity agreements, we are not allowed to disclose the exact locations of the scientific collections and occurrences, but we do plot the estimated locations of the anecdotal ones. The complete dataset, including locality information for each anecdotal record is available upon request.

Results and Discussion:

Summary of Potential Fish Migration Barrier Construction in the Mobile Basin

The first survey to design "improvements" of the Alabama River was in 1814 (Tatum 1814). As the demand for commercial boat traffic increased throughout the 19th century, the U.S. Army Corps of Engineers began funding projects to remove natural obstacles, clear debris, and reinforce river banks. In the early 1870s, funds were appropriated to widen and deepen the shipping channels by dredging and excavating shoals in the Tombigbee, Black Warrior, and Alabama rivers, making them navigable year-round (USACE 1880). With the industrial revolution accelerating development, low-head dams were built on smaller tributaries to power mills and small factories that mainly processed agricultural products like cotton into textiles. The first mill dam built on a major river in the Mobile Basin was at Tallassee, AL, at the fall line on the Great Falls of the Tallapoosa River in 1844 (FERC 1994).

At first, commercial navigation in the Mobile Basin was largely restricted to the low-gradient reaches of Mobile Basin rivers below the fall line. Larger projects like the construction of wing-dams and jetties were underway in those reaches in the 1880s to improve navigation, but in the 1890s, work began on the Black Warrior River that would allow commercial traffic to navigate above the fall line (USACE 1895). Three lock-and-dam structures were begun on the Black Warrior River to overcome the fall line at Tuscaloosa in 1888 (USACE 1895). Later, the River and Harbor Acts of 1902 and 1907 approved funding for an additional 14 lock-and-dam structures that spanned the river from its mouth at Demopolis up to near Birmingham, AL (U.S. House of Representatives 1840).

The original surveys of the Coosa River by the USACE called for a system of 25 locks and dams between Wetumpka, AL, and Rome, GA, in the headwaters, and included plans for a canal that would connect the Upper Coosa to the Tennessee River (USACE 1872). This plan was later modified to include 31 locks and dams, but eliminated the canal (USACE 1883). By the late 1880s, the construction of six locks was underway: five between Riverside, AL, and Greensport, AL, and one in Wetumpka, AL. Another lock and dam was added at Mayo's Bar in Georgia in

1913. Lock 5 failed in 1915 and was never repaired (USACE 1916). Construction of Lock 31 in Wetumpka was halted in 1896 and never completed (USACE 1897). The rest of the locks and dams were never built. By the late 1920s, shipping traffic had all but ceased on the Coosa River, and in 1940, USACE abandoned all the existing locks and dams (USACE 1940).

Around the turn of the 20th century, the expansion of railways into Alabama combined with a boom in manufacturing simultaneously reduced the need for river navigation, and increased demands for electricity (Jackson 1995). The construction of the first hydropower dam in Alabama was on Big Wills Creek, a tributary of the Coosa River, in 1886, but impounding mainstem rivers for hydropower did not begin until the construction of Lay Dam on the Coosa River in Chilton County, AL, in 1913. Since then, a total of 16 hydropower projects have been constructed on the mainstems of the five major Mobile Basin rivers (Figure 1.1).

The original 17 locks and dams on the Black Warrior River and six on the Coosa River were replaced or flooded by 12 hydropower dams, (six on each river). The Tallapoosa River was never developed for commercial traffic, but three hydropower dams were built above the fall line in the 1920s, beginning at the former site of the Tallassee Mill Dam at the fall line. A small mill dam was built in the upper Tallapoosa River near Heflin, AL, in 1935 but removed in 2019. An additional hydropower dam above Lake Martin (R.L. Harris Dam) was completed in 1983 and remains the most recently completed hydropower dam in the Mobile Basin. The Cahaba River has remained free-flowing except for a few low-head dams and small impoundments near Birmingham, AL (Jefferson County).

In the 1970s, two major navigation projects were built with the anticipation of a revitalization of industry in the region. The Tenn-Tom Waterway, a system of locks and dams connecting the upper Tombigbee River and Tennessee River, was built starting in 1977 (completed 1985) to provide a direct navigation route from the Tennessee River to the Gulf of Mexico, bypassing the Ohio and Mississippi Rivers (USACE 2010). Around the same time, six low-head locks and dams were built in the lower Tombigbee and Alabama Rivers below the fall line. The two downstream-most dams (Coffeeville and Claiborne) are unique in that they were built with fixed crest spillways that inundate during high-water events. They are currently the first migration barriers encountered by fish moving upstream from the Gulf of Mexico, but fish passage has been documented at Claiborne (Simcox et al. 2015, Mettee et al. 2006, Hershey et al. 2022), and is likely also occurring at Coffeeville due to its similar characteristics.

The earliest dams in Alabama did not likely represent complete barriers to fish passage, given that they were generally low-head dams (<5 m) that inundated during high water or wing-dams that did not reach all the way across (USACE 1894). Interestingly, the original locks and dams on the Black Warrior River were equipped with wooden vertical-slot fishways (Mower 1915). We did not find any records of fish using these ladders, but we assume that their use by large-bodied fishes like sturgeon and Paddlefish was negligible due to poor passage efficiencies in similar modern designs (Hershey 2021). However, fish may have passed the dams incidentally via the locks with barge traffic (Mettee 2019).

Our search for other human-made barriers to fish migration resulted in the locations of several stone fish-weirs, which were distinguished from natural shoals by characteristic V- or W-shaped notches, designed to funnel fish towards the downstream entrance. Many of these rock weirs were built by Native Americans and were later used, and sometimes owned, by European settlers to capture migrating fish (Hubbert and Wright 1987). The age of some indigenous fish weirs of the same construction in the Eastern United States exceeds thousands of years. They were probably less obstructive to fish passage than low head locks and dams, but at low water they were highly effective at trapping fish, especially when settlers built on top of existing weirs, and attached wood and metal traps. Traps were common in reaches above the fall line due to the availability of boulders which were stacked in shallow bedrock shoals (Hubbert and Wright 1987). However, they were also built in coastal plain reaches of the Mobile Basin, including the Tombigbee River, and were supposed to have been designed to capture eels, shad, and sturgeon (Mistovich 1981; Connoway 1982; Figure 1.2).

The use of traps to capture fish was outlawed in the 1930s, and many weirs were flooded by the dams in the mid-20th century. We could not confirm whether every weir we found was used by European settlers, but some certainly obstructed fish migrations to some extent, and increased the efficiency with which fish could be captured. One example, Willingham's Trap, was located about 4k m upstream of where Logan Martin Dam currently impounds the Coosa River (Figure 1.3). We found multiple records of target species being captured there, including sturgeons and eels. In 1951, before Logan Martin Dam was built, Donald Scott (Department of Biology, University of Georgia) sampled the site and one further downstream near Childersburg, and caught a Lake Sturgeon at the downstream site in a hoop net. We were also able to estimate the location of another fish trap in the Black Warrior Basin called "Nichol's Trap", which was flooded by the construction of Lock 17 (later modified and called Bankhead Dam).

Summary of fish records:

Relative to the various sources we used, by far, the most valuable resource in this effort was Newspapers.com. Relative to taxa, search results varied among species, with the highest-yielding search being for the keywords “sturgeon” AND “caught” (2,725 hits). We found 129 newspaper reports of sturgeon caught in the Mobile Basin that had not previously been counted in the scientific literature (Figure 1.4). We did not find any records or photographs of Alabama Shad in the newspaper archive, but did find many potentially informative records and reports of “shad” in the basin (Figure 1.5). We found 67 anecdotal records of American Eel, spanning from 1880-1962 (Figure 1.6). They ranged in size from 30.5 to 274 cm in length, and up to 15 pounds. Finally, we found 51 anecdotal records of Paddlefish spanning 1875-1990 (Figure 1.7). Data from each record is available in the supplementary materials.

Sturgeon species

Very few scientific collections of Gulf Sturgeon have ever been made in the Mobile Basin, therefore we omitted a range map of scientific records for those species (Figure 1.4). Seven specimens were collected in 1970-71 and preserved in the Tulane University Ichthyological Collection, most from Mobile Bay and surrounding estuaries. In the first comprehensive review of historical records of Gulf Sturgeon (Sulak et al. 2016), the authors present findings that the Mobile Basin supported a commercial fishery in the late 19th century that harvested hundreds of thousands of pounds of sturgeon over the span of decades. After around 1920, records were limited to sightings of individuals mostly in Mobile Bay and the surrounding estuaries. Most recently, eDNA and telemetry detections have confirmed the species’ presence in the lower Tombigbee and Alabama Rivers, and Mobile Bay although their range once extended much farther upstream (Pfleger et al. 2016, Greenheck 2023).

Sulak et al. (2016) also used newspaper records to ascertain the historical range of Gulf Sturgeon, but we located 112 additional records that may expand the known range of the species prior to dam construction. Also, according to Sulak (2016), the largest Gulf Sturgeon ever recorded (417 lbs) was captured at Tallassee, AL, in 1930. We found a record of a sturgeon weighing 420 lbs captured near Fairhope, AL, in Mobile Bay, but without a photo to verify its size. The furthest upstream mention of any sturgeon we could find in the upper Tombigbee River was from the Clarion Ledger in 1929, which stated that “sturgeon weighing from 60 to 70 pounds have been brought here [Amory, MS] from the river once or twice in the past…” Additional records of sturgeon up to 300 lbs came from newspapers near Columbus, MS (see supplemental materials). Therefore, Gulf Sturgeon could have once migrated that far upstream, but such migrations could not occur after construction of the Tenn-Tom Waterway that now impounds the Tombigbee River from Pickensville, MS, up to the Tennessee border. The last record of sturgeon being captured prior to dam construction in the Tombigbee River was of a 2.5ft sturgeon captured four miles upstream of Columbus, MS, in May 1956. Based on its size, this could have been *Scapiyrhynchus suttkusi*, although the paper states the fish was “of the saltwater variety”, suggesting it was more likely an immature Gulf Sturgeon.

In the Black Warrior River, no records of “sturgeon” were found above the fall line. The earliest record of a sturgeon capture in this drainage was from the Tuscaloosa Times, published May 8th, 1872, before any dams had been built.

> "A sturgeon [sic. Gulf Sturgeon] was recently caught in the fish-traps, above our city wharf, measuring seven feet and three inches in length, more than one foot across the back, and weighing about two hundred pounds."

Incidentally, this is also one of the furthest upstream records for any sturgeon in the entire basin. The last record of a Gulf Sturgeon caught in the Black Warrior River after dam construction began was in 1898 near Eutaw, AL, more than 80 km upstream of the junction with the Tombigbee River. By 1902, the first three locks had been constructed downstream on the lower Tombigbee River.

In the Cahaba River, most of the anecdotal records we found state that sturgeon were caught in fish traps at the fall line near Centreville, AL. However, one record from 1952 states that a 244 pound sturgeon was caught snagging near Montevallo (Reynolds 1993). The nearest point on the Cahaba River to Montevallo is approximately 20km upstream of the fall line. However, this was the only such record we found, and since the exact location could not be confirmed, we caution that this may not be evidence that the range of any sturgeon extended beyond the fall line in this drainage. This is the most recent record of a potential Gulf Sturgeon we could find in the Cahaba River.

In the Tallapoosa River, records of sturgeon captures were limited to the downstream reaches below the fall line. We were only able to find two records in addition to the record-breaking one published in Sulak (2016). However, for the Coosa River, we found records of "sturgeon" from the mouth at Wetumpka up into the headwaters in North Georgia. Anecdotal records of sturgeon up to 247 lbs were found as far upstream as Riverside, AL, (ca. 1877; St. Clair County) well above the fall line. The specific identify of the fish in these records could not be confirmed, but their sizes suggest they were most likely Gulf Sturgeon, given that Lake

Sturgeon in the southern portion of their range were not likely to grow larger than 100 kg (Peterson et al. 2006). In addition to the records near Riverside that pre-dated dam construction, we found several records of sturgeon caught in the tailraces of Coosa River dams. We found three records of two large adult sturgeon captured in the tailrace of Mitchell Dam, which was the second hydropower dam to impound the mainstem Coosa River, built in 1923. The two sturgeon weighed 335 and 227 pounds, caught in 1924, and 1926, respectively. Interestingly, another sturgeon was caught in the area in 1891, weighing 300 pounds. Based on their sizes, these were undoubtedly Gulf Sturgeon that had migrated up from the Gulf of Mexico to spawn. Mitchell Dam was built at a shoal called Duncan Riffle, which may have been a spawning site for Gulf Sturgeon before downstream Jordan Dam was built in 1928 (Figure 1.2). We were unable to find any records of sturgeon greater than 200 lbs above Jordan Dam after its construction, although they were caught below it down to Wetumpka until around 1940. We found one record from the Wetumpka Herald from 1954 that stated a sturgeon weighing 85 pounds was caught “in the bend of the river”, but the location could not be verified, and the size does not exclude the possibility of its identity as a Lake Sturgeon. Therefore, it is possible that Jordan Dam (completed in 1928 and still operating today) was the final impoundment that fully sealed off the Coosa River from diadromous fish migration. Lake Sturgeon records from the Coosa persisted until 1963 when a large Lake Sturgeon was caught in the tailrace of Lock 4 near Riverside, AL, and photographed for the Talladega Daily Home newspaper (see Appendix). They were presumed extirpated by the 1970s, and were not seen again in the river until 2002 when Georgia Department of Natural Resources (GADNR) began to stock juveniles spawned in a hatchery from broodstock acquired from Wisconsin (Bezold 2007).

Their reintroduction program continues today, and Lake Sturgeon have since been captured as far downstream the Coosa River as the tailrace of Jordan Dam (Rider 2023, personal communication).

Since 1985, only 26 captures or credible sightings of Alabama Sturgeon have occurred, none of which came from the Tombigbee River (Kuhajda and Rider 2016). We were able to find four other records of Alabama Sturgeon that were verifiable by photographs. One record of an Alabama Sturgeon in the Cahaba River is from the Selma Times, published September 27, 1956: "Quite by accident, an eleven-year-old fisherman pulled a four-pound sturgeon out of the Cahaba while he and his father were fishing on the river Saturday." Thanks to the included photo by Gene Wood, we were able to verify its identity as an Alabama Sturgeon. Three other photographs of Alabama Sturgeon have been published in various newspapers located in the Alabama River Basin, so we assumed they were caught in the Alabama River, although their precise location could not be verified (see photos in Appendix).

Alabama Shad

The story of Alabama Shad *Alosa alabamae* in Alabama is complicated because American Shad *Alosa sapidissima* was introduced into the Mobile Basin in the 1850s before the native species had even been described. Very little information exists about the status of Alabama Shad in the Mobile Basin prior to American Shad introduction, and records after the introduction are confusing because the authors of the articles we found rarely distinguish between the species, generally referring only to "shad". Newspaper articles that reported the capture of "shad" in the late 19th century were common around the same time that the U.S.

Fish Commission began to stock millions of American Shad in the Mobile Basin (USFC 1883). In a molecular phylogenetic analysis, the two species were found to be sister taxa (Bowen et al. 2008). The two species are morphologically distinct and there is no evidence of hybridization. We have mapped all anecdotal records of "shad" captures prior to 1930 in Figure 1.5.

We found two records of "shad" captures published before stocking began. The earliest record we found was from a newspaper article published in the Jacksonville Republican in 1844:

> "SHAD—We were, a few evenings since, invited to partake of a shad supper, and, as will be expected, we did not refuse. These fish, the greatest delicacy of the fish order– (in our humble estimation) are now being caught in the Cahawba [sic] river, a thing unheard of before. Those of which we partook were exceeding fine, and were the first fresh shad that we had eaten in eight years".

Given the absence of reports of "shad" in the Mobile Basin prior to this record, we believe the author had probably eaten the native species, Alabama Shad. However, the origin of the shad he ate eight years prior was not stated, so it could potentially have been shipped from the U.S. East Coast where commercial fisheries for American Shad were already well established, or he could have been at the East Coast himself. However, Alabama Shad may not have been vulnerable to the fisheries at the time, since they do not strike at lures or take bait during their upstream migration in freshwater, and large-scale commercial fishing in general was not common in Mobile Basin streams until later in the 1800s (Sulak et al. 2016).

By the following decade (1850s), the origins of shad caught in rivers had become a subject of debate because in 1848, the USFC started experimenting with stocking American Shad in the Mobile Basin. A letter from W.C. Daniel to the U.S. Fish Commissioner published in an 1873 report said that an experimental stocking of "white shad" [sic. *Alosa sapidissima*] in the

Etowah River was conducted by a “Major Mark A. Cooper” in 1848. The author stated that he presumed that shad captured in subsequent years originated from this stocking experiment.

> “The first white shad known to have been taken was in 1851 or 1852 in traps placed at the foot of the Black Warrior, near Tuscaloosa, Ala…About the same time the white shad was taken in traps at the foot of the falls of the Alabama River, near Wetumpka. In 1858 (or ten years, as I suppose, after the deposit of the eggs by Major Cooper) they were taken in abundance in the traps near Tuscaloosa”. (USFC 1874)

In a letter penned by Cooper himself, he describes the receipt of “a great number” of fertilized eggs in a package from the Savannah River. He then placed them in a small tributary of the Etowah River. He did not say whether he observed successful hatching, but noted that the eggs gradually disappeared over some time (USFC 1874). It is highly unlikely that these eggs survived, therefore we posit that this 1848 stocking experiment by Cooper was probably unsuccessful, despite the fact that reports of “genuine white shad” were reported at the time. Instead, the shad caught in the fall line cities (i.e. Wetumpka, Tuscaloosa) in the early 1850s were probably the native Alabama Shad. The people there were apparently aware that there was a native species but insisted that the American Shad stocking was successful. In 1849, an article in the Daily State Guard (Wetumpka) stated that:

> “The real genuine White shad are caught frequently [in Wetumpka]. We have doubted their being the white shad, until the other day, an old friend who had been ‘raised on shad’ in Georgia, give [sic] us his opinion that there was nothing more genuine than those caught in the Coosa. We know that a fish resembling the white shad very much, has been caught in the waters of Alabama, for several years, but, from the fact of them being very ‘bony’ we are confident they could not be of the ‘old sort,’ those the fishermen catch here are different–being clear of the little thousands of fibre bones, and perhaps are just about as delicious as the imagination would require.”

This article is the earliest we could find that makes a distinction between “white shad” and a native shad species. It seems impossible that American Shad were being caught frequently in Wetumpka only a year after the first stocking experiment, while native shad were already there. Later articles also express confusion about the origins of shad in the Coosa River. In 1857, the author of an article in the Wetumpka Spectator tried to explain recent captures of “genuine white shad” in the nearby traps.

> “If these fish ran up the river (as it is supposed all shad do,) how does it happen that none have been caught in the Alabama River or the Coosa below Wetumpka, or indeed in any other river of the Gulf west of Florida? This singularity, as well as the fact that they were caught on traps (indicating that they were passing down stream) would seem to argue that the shad are permanent residents of the upper Coosa river. The only reason we can give… for shad not being caught at other places on the river, is that there are no traps in, and if there were, they would have to be made to catch as the fish run up stream. Owing to the fact of their being considerable fall above our city, the shad as they run up, get into the strong current running on the traps and are washed in. No doubt, if we could catch them as they come up, we should catch larger ones than we do, as it is now, the larger and stronger ones go up without being forced on the traps.”

In 1858, four shad weighing 7 pounds each were caught in Mobile Bay and were pronounced “genuine white shad”. Remarkably, the author of the report in The Weekly Advertiser (Montgomery) drew the conclusion that American Shad were native to the Mobile Basin.

> “This of course puts at rest the long mooted question of Coosa river shad; for we have proof positive that this delicious fish is becoming somewhat plenty in our waters, and without having been introduced by spawn or young fish from the Savannah river.”

The author could have been unaware of the stocking attempts, but claimed that they were not the origin of the shad caught in Mobile Bay. Regardless, 7 pounds is much more than the maximum recorded weight of an Alabama Shad (3lbs, Kentucky River, Smithsonian National Museum of Natural History; Catalog Number 21345, GBIF 2023) so the identity as well as the origin of the fish remains impossible to tell.

The confusion about the origin of Coosa River shad could be due to the fact that the native species was already rare by the time people started writing about it. One article from 1860 in the Independent American (Troy, AL) suggests that the native species was once abundant, but had declined to the point that conservation was required.

> "The shad [sic. *Alosa alabamae*] formerly caught in large numbers in the Chattahoochee river, were smaller than those of the Atlantic streams, but they were nevertheless pronounced to be of the same genus. It may be, and we incline to the opinion, that the shad of the Alabama and its tributary are identical in variety with those of the Chattahoochee, all possessing the flavor of the Atlantic shad, and only differing in size. We suggest to fishermen, that no more shad be taken from our waters, until they become more plentiful. When caught they should be returned alive to the water."

The same 1860 article mentions two other early attempts to stock American Shad in the Mobile Basin. The first was by a man named Albert J. Pickett, who "caused a number of live shad to be brought from the Savannah river and deposited in the Tallapoosa." The other attempt was by a "pair of agents" in Montgomery who "brought a large lot of young shad from the Oconee river in Georgia, and deposited them in the Alabama river." This other attempt was also recorded in an 1871 article from the Selma Morning Times which stated that

> "A genuine white shad was caught in a net this morning, from the Alabama river, near the railroad bridge, about six miles above Selma. Prior to 1858 no genuine

> shad had been seen in any river emptying into the Gulf of Mexico. In May of that year 1,300 young shad were delivered into the artificial pond at Montgomery, prepared for their reception by Mr. S. Hooker, and from thence turned into the Alabama River."

We suspect that some of the fish stocked in these efforts could have been captured shortly after, such as the one near the railroad bridge in Selma, but we believe that it is unlikely that stocking a few thousand shad led to the capture of hundreds in subsequent years given the time it would take for reproduction, growth, and harvest. In 1873, an article in the Tuscaloosa Gazette reported that "shad proper" were being caught daily (presumably in the Black Warrior River) which we do not think could have been American Shad if so few had been stocked up to that point, and in rivers hundreds of miles away.

Reports of "shad" catches began to increase in 1876, following the first substantial stocking of American Shad. The first report of a U.S. official stocking American Shad in the Mobile Basin comes from an 1883 report by USFC, which stated that 90,000 shad were stocked in the Alabama River at Montgomery in July 1876. In 1878, T.S. Doron, from Montgomery, sent a shad caught from the Coosa to Washington, D.C. where it was identified as an American Shad "although not quite so large as it is found in Northern waters…" by the U.S. Fish Commissioner S.F. Baird. (Birmingham Iron Age 1878). The author of the article which enclosed the letter from Baird remarked

> "This settles the question as to the kind of shad now being caught in the Alabama and Coosa rivers, and will be gratifying news to those who are fond of that delightful fish. It will be interesting, however, to consider whether these shad are the product of the spawn placed in the river many years ago by Dr. Gesner and Mr. Hooker, or those placed in the river here a year or two ago by U.S. Fish

> Commission. Our opinion inclines toward Dr. Gesner and Mr. Hooker, but in a year or more the latter additions will cause a heavy increase in the shad product."

The author ignored the possibility that the fish caught in the Coosa River prior to the Federal stocking of American Shad could have been native. In fact, later study of that same specimen showed that it had been misidentified by the commissioner, as it was later vouchered as an Alabama Shad in the collections at the Field Museum of Natural History (Catalog No. 74569). With evidence that American Shad stocking was successful, USFC continued stocking throughout the Mobile Basin until 1892 (Table 1.2).

Landings of "white shad" in Wetumpka started out large after the 1876 Federal stocking. An 1878 article in the Livingston Journal reported that over a thousand pounds were caught in the Coosa in one week, and that "our market is so glutted with these delicious fish that they are selling for only 5 to 7 cents a pound." Catches of "white shad" were also being reported in the Black Warrior River at Tuscaloosa, and in the Alabama River at both Selma, and Montgomery. However, catches declined quickly. By 1883, only 23 shad were caught in the traps at Wetumpka, versus 1,000 in 1879. An 1883 article in the Montgomery Advertiser said, "Today there are still shad in the Alabama River, but the building of dams and locks restricts their running" (Napier 1983). Construction of several locks and dams began in the Black Warrior and Coosa Rivers in the mid-1880s (as described earlier), which could have prevented either shad species from migrating upstream to spawn. However, declines were also likely due to poor survival of stocked juveniles, and ultimately, whether surviving fish historically had returned from the Gulf of Mexico and migrated past the fall line to spawn remains unclear. Several catches of "shad" occurred sporadically throughout the coastal plain rivers of the Mobile Basin until around 1892, but we only found one record ever of shad caught above the fall line, despite having been stocked in the upper Coosa and Tallapoosa Rivers (Figure 1.5). An article in the Florence Gazette from May 1878 stated that "great quantities of young shad have been caught this spring in the Coosa, Etowah, and Oostanaula rivers, in traps and nets". It seems unlikely that these fish were hatched in the river if they were American Shad, but given that the Etowah River was not stocked until June 1878, it is possible that these were the progeny of either American Shad stocked in the Alabama River in 1876, or native shad that were already there. If these were native Alabama Shad, then it would be the only known occurrences of the species above the fall line in any Mobile Basin tributary from that time. Much later, between 1950 and 1964, Royal Suttkus collected hundreds of adult and juvenile Alabama Shad above and below the fall line in the Cahaba River (Rider et al. 2021). Interestingly, the Cahaba River was the only tributary without a dam.

In 1896, four shad were collected from the Black Warrior River, at Tuscaloosa, AL, and finally described by Jordan and Evermann as a newly recognized species of *Alosa*, the Alabama Shad (Evermann 1896). In his 1896 report to USFC, Evermann described a specimen he collected from the Black Warrior River:

> "This is undoubtedly the native shad of the Gulf of Mexico and tributary streams, though it is probably less abundant in those waters than *Alosa sapidissima*, which has extensively been introduced there by the United States Fish Commission."

After the description of Alabama Shad, it took a while for the name to catch on. Most articles still only referenced "shad", but records of "white shad" stopped after 1892. One from the Montgomery Advertiser in 1897 stated that

> "about two years ago there was a remarkable catch of shad at Tuscaloosa. At the foot of the lock works going on in the Warrior River it was no trouble to catch large quantities of them and they were as fine as those caught in any of the Eastern streams. Is it not possible that these shad have been going up the river for years without notice and that the obstructions caused them to be caught."

The rhetorical question posed by the author is a fascinating remark, and implies that the Alabama Shad were not vulnerable to fisheries and that their apparent abundance was unknown because they were rarely caught. The dams may not only have blocked their spawning migration, but concentrated them making them more vulnerable to fishing than they had ever been before. An article from the Daily Mountain Eagle in 1925 provides strong evidence for this hypothesis:

> "SHAD IN THE WARRIOR – The River shad are swimming up stream to spawn. The Warrior River at Lock Ten is alive with them. There are thousands of them. As a proof of this, all one has to do to catch a mess is to rig a heavy fishing line with snag hooks, put a weight on the end, tie to a pole and jerk through the water. One man caught 32 in this manner Saturday afternoon. He did not fish over an hour. They were about a half pound each.
>
> The shad in this part of the country are not extensively eatn [sic]. They taste all right, but contain so many bones that they are too tedious to fool with. The shad caught up around the mounth [sic] of the Delaware river weigh several pounds. They are heavy and fat. They are on the northern market at certain seasons of the year ad [sic] are considered a great delicacy when planked.
>
> The shad in the Warrior River are thin, small and bony. They do not possess much food value. Not many people attempt to eat them. They will not take a bait, either alive or artificial. They must confine their diet to soup or serials– Tuscaloosa News."

We believe that the scarcity of anecdotal records of Alabama Shad (*c.f.* "white shad") could be due in large part to their behavior, and early remarks about their scarcity may not be accurate given that they were probably not vulnerable to the same fisheries as American Shad. Alabama Shad do not feed or strike at lures when migrating upriver, so it would have been uncommon to capture one using a hook and line as are used to catch American Shad. Alabama Shad would have to be snagged or trapped to be captured, which was very rarely reported, especially in the coastal plain where traps were less common. Furthermore, it has been found that Alabama Shad prefer sand-bottom rivers with limestone outcrops for spawning, which are much more common below the fall line (Rider et al. 2021).

Whether the Alabama Shad was ever abundant remains an unanswered question, but it is definitely rare now. It has been listed as a Priority 2 species (High Conservation Concern) by the State of Alabama (Mirarchi et al. 2004), and has been petitioned for Federal listing under the Endangered Species Act. Only five individuals have been collected from the Mobile Basin since 1994 (Rider et al. 2021). Prior to 1994, scientific collections confirmed their presence in every major tributary except the Tallapoosa River (Table 1.3). Recent collection efforts in the Mobile Basin have been fruitless, and the species' decline has been attributed to the construction of dams and possible overfishing (Rider et al. 2021). Unfortunately, without more accurate historical records, the actual causes of its decline, and the full extent of its former range remains a mystery.

American Eel

Based on anecdotal and museum collection records, American eels (hereafter: "eels") were distributed throughout the Mobile Basin, and well into the headwaters of all major tributary basins except the Tallapoosa River (Figure 1.6). Eels likely migrated far up into the Tombigbee River headwaters. In addition to the anecdotal evidence, scientific collections of eels ranged upstream as far as Aberdeen, MS, as recently as 1979 indicating their migration probably extended into the tributaries of the upper Tombigbee River, and some individuals may have persisted there for some time after dam construction. However, more recent records do not exist, so the current status of American eel in the drainage is unknown.

Records of eels, both anecdotal and scientific, extended far upstream into the Black Warrior headwaters. One notable mention was from 1899 in the Gadsden Times which stated that “while the Warrior River near here [Walnut Grove] was muddy the boys had a good deal of fun catching eels and catfish and some very large eels were caught”. Anecdotal and scientific records of eel captures persisted well into the 20th century, despite the fact that dam construction had begun in the 1880s. The latest collection of an eel in the Black Warrior drainage was from 2007 in Lost Creek near Jasper, AL (Auburn Museum, Catalog No. 48844). Its origin is unknown, but barring the possibility of human transport, it could have migrated past the six dams between Lost Creek and the Gulf of Mexico.

In the Cahaba River, records of eels ranged as far up as Birmingham, AL, where several have been captured in the spillway of Lake Purdy, an impoundment of the Little Cahaba River built in 1923. The last record of an eel in the Cahaba River was a specimen collected in 1984 four miles upstream of the mouth (Auburn Museum, catalog No. 24760).

Anecdotal records of American eel in the Coosa River were scattered throughout the basin, but a few interesting records tell a story of decline. In 1913, around the completion of Lay Dam (known for the first few years as Lock 12) a commercial fisherman captured between 6,000 and 8,000 pounds of eels in Willingham’s Fish Trap upstream of the dam site (Figure 1.3) and took them to Gadsden, AL, for sale. The article states that the fisherman claimed that “the eel industry down his way [Talladega] is booming” (The Guntersville Democrat 1913).

Interestingly, MacGregor et al. (2017) claimed that a commercial fishery for eels never existed in Alabama. This may be the only record of such an industry in the state, and it may not have been common. On August 15, 1926, an article was published in the Birmingham News in which the author wrote

> "Those who claim to know say the eel goes back to salt water to spawn, often going long distances over land, but if this is true I want to know where the young eels that are swarming in and around the powerhouse at Lock Twelve came from and how did they get there? These eels are no longer than a lead pencil, and about as large, and it doesn't seem reasonable that they could have come the thousands of miles from the salt water to this place. Many can remember the wagon loads of big eels that were brought into Birmingham and sold on the streets a few years ago. They were caught in traps in the Coosa River. When a rise would come in the river they would run on the traps by the thousands, much faster than they could be taken off. No doubt they are still plentiful in the Coosa but as the traps are all under water few are taken."

By 1926, Mitchell Dam (the next downstream structure from Lay Dam) had been operating for three years, but according to this article, juvenile eels were apparently still migrating up to the face of Lock 12. It seems unlikely that they could have passed these dams, but it is possible.

In 1952, an article published in the Anniston Star stated that a man brought to the office "a rarity in this part of the state– an eel caught in the Coosa River below Riverside. Eels seldom work their way up the river this far, a local fisherman explained, because of the locks… The eel was about two and one-half feet long and weighed about two and one-half pounds". Another was caught and photographed just upstream at Lock 4 in 1962 (see photo in Appendix). We did not find any records of juvenile eels in the Coosa River after the 1926 article, and collections of adults were mostly limited to below Jordan Dam by the 1980s. Occurrence records of eels in the Alabama River persist to the present day.

Only 14 collections of eels have ever occurred in the Tallapoosa Basin, seven in coastal plain tributaries, and seven in the mainstem below the fall line, the most recent of which took place in 1990 one mile below Thurlow Dam (ADCNR). Several other eel specimens were collected from research ponds at Auburn University, but did not likely migrate into the ponds on their own. Their exact origins are unknown. The only record of eels (anecdotal or scientific) above the fall line in the Tallapoosa River was from the Covington Crescent in 1891, which stated that a mill in Sandy Creek, a tributary now inundated by Lake Martin, was "so choked with eels that it would not revolve" and "on the same stream, two miles lower, Mr. Bell Brown caught 175 eels, weighing two to four pounds each, in a trap." The only evidence we have to judge whether eels were able to pass the falls prior to dam construction is the aforementioned record from Sandy Creek in 1891.

Paddlefish

Collection records of Paddlefish were dispersed throughout the Mobile Basin, including the Mobile-Tensaw Delta and Mobile Bay. Although studies have shown that populations in the Alabama River are now fragmented by dams, their range may not have declined as a result of dams (Kratina et al. in press). They ranged up the Tombigbee River into the Noxubee River, and although not found in collection records, are known to occur in the Hamilton Noxubee National Wildlife Refuge (Gilliland 2019). No occurrences of Paddlefish were found in the Tombigbee River above the confluence with the Noxubee River. Collections in the Black Warrior drainage spanned from the mouth in Demopolis upstream into the Mulberry Fork above the fall line, where larvae were collected at a powerhouse intake in 1975 and 1979, well after dams had been constructed downstream (Auburn University Museum of Natural History, Catalog No. 21738, 18636, and Alabama Natural Heritage Program EOID 2859). These records are perplexing, given that adults have never been documented in that area. We found no other anecdotal records of Paddlefish above the fall line, but it is possible that a small population of Paddlefish once existed above the fall line in the Black Warrior River if enough individuals were present above Bankhead Lock and Dam before it was built.

Collection records from the Alabama River range from the mouth up to the origin at the confluence of the Tallapoosa and Coosa Rivers. Occurrences in these collections were most dense in the lower Alabama River between Claiborne Lock and Dam and the mouth near historic Fort Mims. Although absent from official collection records, Paddlefish have been collected in the Coosa River, below Wetumpka in the Walter Bouldin Dam Tailrace (Personal observation, unpublished data, 2018). They have also been collected in the Tallapoosa between Thurlow Dam and the mouth near Wetumpka (Lein and DeVries 1998).

We found two anecdotal records from above the fall line in the Tallapoosa and Coosa rivers. We do not believe that these substantiate an expansion of the known range of the species in the Mobile Basin, but they are interesting nonetheless. One is from an article from 1912 when a Paddlefish was allegedly caught near Lock 3 in the Coosa River, well above the fall line near Ohatchee, AL. It weighed 25 lbs and measured 4 ft 5 in (Birmingham Post-Herald 1912). The record from the Tallapoosa River is from an article in the Montgomery Advertiser (1931) which provides some conflicting information. It quotes A.J. Lilley of Tallassee who said

> “I am 78 years old. I was born at Tallassee. I have been fishing in the Tallapoosa River ever since I was large enough to go fishing. I have fished with nets of

> different kinds, trot lines, hooks and in other ways and have never seen a gar, a blue cat, a drum, a buffalo or a spoonbill cat caught above the Tallassee Falls."

Later in the same article, a Mr. Frank Clements "of the Advertiser" was quoted saying that a "Mr. Peeples of near Cherokee Bluff caught a large spoonbill cat out of Martin Lake sometime ago" (Montgomery Advertiser 1931). This is the only record of Paddlefish above the fall line in the Tallapoosa River that we could find, and its validity is questionable at best.

Conclusions:

When combined with scientific records, the anecdotal records we found provide a much more detailed understanding of pre-dam fish migration in the Mobile Basin. We found important evidence that Gulf Sturgeon migrations once extended farther upstream in the Mobile Basin than previously thought, and that fish may have reached sizes larger than previously reported. Although not confirmed, it cannot be ruled out that Alabama Sturgeon may have ranged above the fall line. Little is known about Alabama Sturgeon habitat requirements, although the species is supposed to prefer large sand bottom rivers like its congener, the Shovelnose Sturgeon *Scaphirhynchus platorynchus* (Kuhajda and Rider 2016). Nevertheless, the records we found represent a substantial contribution to the scant existing database for this species.

Lake Sturgeon may have ranged below the fall line in the Coosa River, but based on their requirements for rocky substrate, and the dearth of records (scientific or otherwise) in the coastal plain, we conclude that this was unlikely (Peterson et al. 2007). Importantly, we have presented the first evidence that Lake Sturgeon and Gulf Sturgeon ranges once overlapped in the Coosa River. We are unaware of any record that these species were sympatric in any other part of their native range. As for the impacts of dams on Lake Sturgeon distribution, it is likely that the earliest dams (Locks 1-5 on the Coosa River) presented seasonally passable barriers to migration. However, after the construction of Weiss Dam in 1958, fish that persisted in the middle Coosa River (between Greensport and Wetumpka) were completely blocked from moving upstream to the Oostanaula and Etowah Rivers. Lake Sturgeon stocked by GADNR in the upper Coosa River occasionally migrate downstream through these hydropower dams, but spawning has only been confirmed in the upper reaches, and upstream passage has never been documented (Personal communication, Martin Hamel, 2023).

As for American eel, based on the anecdotal records we found, we conclude that the fall line did not represent a complete barrier to their migration in the Mobile Basin before dam construction. Furthermore, the first dams were also not likely a complete barrier, given that individuals were apparently observed swimming through turbines in Coosa River dams. In contrast to Gulf Sturgeon, eel records persisted after dam construction. We attribute this to life history differences between the species. Whereas anadromous sturgeon migrate upstream annually to spawn, eels may spend up to 50 years in freshwater habitats before returning to the ocean to spawn. Therefore, it is more likely that the individuals captured upstream of the locks and dams were there before the locks and dams were built.

Given that no “shad” was ever caught above the fall line even after American Shad were stocked there, this is indicative that neither species ever migrated upstream beyond the coastal plain. Little is known about the swimming performance of Alabama Shad, and translocation of individuals across dams has been used in other parts of their range to evaluate the potential for fish passage mitigation. Attempts to pass the species via lock operations have only been successful at Jim Woodruff Lock and Dam on the Apalachicola River, FL. Burkhead et al. (1997) hypothesized that Alabama Shad once migrated to the upper Coosa River and its tributaries, but this was based on the assumed swimming performance of American Shad in the high gradient Atlantic Slope rivers. Given that Alabama Shad are smaller, it is likely that their swimming abilities would be considerably lower than that of American Shad. Therefore, they were probably only native above the fall line in the Cahaba River, where the gradient is much less than the other tributaries.

We attribute the differences in the extent of migrations among sub-basins prior to dam construction to two main causes: differences in the gradients, and the habitat available upstream of the fall line. Most notably, prior to dam construction, elevation changes in the Coosa River were much less severe than in the Black Warrior, Cahaba, or Tallapoosa Rivers, although the average gradient of the river is relatively steep (Figure 1.8). The Coosa River's original course intersected the fall line a few miles downstream of where Mitchell Dam stands today, but followed the edge of the fall line for miles, falling over a series of smaller drops before crossing the fall line at the Jordan Dam site. In the other rivers, the fall line lies perpendicular to the course of the river, resulting in large waterfalls that were probably impassable to many species. The tributary with the largest drop in elevation at the fall line is the Tallapoosa River (see photos of falls in Appendix), which would explain the lack of sturgeon and Paddlefish found above it in that system. Another unique attribute of this tributary that probably impacted species distributions is its location in the Piedmont Ecoregion, which is characterized by granite, gneiss, and schist lithology, and high-gradient, spring-fed streams. This contrasts with tributaries in the neighboring Coosa Basin which are generally lower gradient, nutrient-rich streams in the Ridge and Valley Ecoregion.

These differences probably also account for some of the perplexing distributions of other fishes in the Mobile Basin. There are several species whose distributions are currently limited to the coastal plain sections of the Tallapoosa River, but found above the fall line in other Mobile Basin rivers, including Smallmouth Buffalo *Ictiobus bubalus*, Longnose Gar *Lepisosteus osseus*, and Freshwater Drum *Aplodinotus grunniens* (Boschung and Mayden 2004). Interestingly, in Homer Swingle's 1954 survey of the Tallapoosa River above the fall line, Blue Catfish, and Gizzard shad were also absent (Swingle 1954), although they are common now, potentially due to translocation by humans. As we have shown for Gulf Sturgeon, just because collection records do not indicate the presence of a species above the fall line, does not mean that they never inhabited those reaches. We emphatically warn that assuming the fall line as a biogeographic barrier for species distributions without pre-impoundment collections records could lead to erroneous conclusions about many species, including non-migratory ones with even less historical data.

Status assessments of these species have shown range-wide declines, but many are not Federally listed, for a variety of reasons. Rarity of most of the target species in the wild makes them difficult to study, and lack of data is currently a major roadblock to their protection. We have shown that much can be learned from leveraging information from sources other than purely scientific ones. Exploring archival sources allows us to re-learn forgotten information and elucidate the factors that led to the unfortunate status quo for these species. We believe this case study in historical ecology represents a significant contribution to the literature on imperiled riverine fishes of the Southeastern United States, and we hope that future research will continue to build on this ever-growing foundation of re-discovered archival information.

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Table 1.1 Scientific and common names used in popular articles for our target species.

Scientific Name	**Common Names**
Acipenser oxyrinchus desotoi	“Gulf sturgeon”, “sturgeon”, “Atlantic sturgeon”
Acipenser fulvescens	“Lake sturgeon”, “sturgeon”
Scaphirhynchus sutkussi	“Alabama Sturgeon”, “sturgeon”, “hackleback”, “shovelnose sturgeon”
Alosa alabamae	“Alabama shad”, “shad”, “skipjack”, “white shad”
Anguilla rostrata	“American eel”, “eel”
Polyodon spathula	“Paddlefish”, “spoonbill cat(fish)”, “shovelnose cat(fish)”, “shovelhead cat(fish)”

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Table 1.2. Dates, locations, numbers stocked and origins of American Shad stocked in the Mobile Basin between 1876 and 1892.

Date	River	Locale	Number stocked	Origin
July 11, 1876	Alabama	Montgomery	90,000	Holyoke, MA
May 29, 1877	Tallapoosa	Montgomery	75,000	Havre de Grace, MD
April 13, 1878	Tombigbee	Demopolis	116,000	Albermarle Sound, NC
May 15, 1878	Tombigbee	Fulton, MS	90,000	Havre de Grace, MD
May 15, 1878	Tombigbee	Aberdeen, MS	60,000	Havre de Grace, MD
June 9, 1878	Etowah	Cartersville, GA	50,000	Havre de Grace, MD
June 9, 1878	Tallapoosa	Salisbury, AL (Historic, Alexander City)	50,000	Havre de Grace, MD
June 13, 1879	Coosa	Lebanon, AL	45,000	Unknown

May 21, 1882	Coosa	Rome, GA	1,000,000	Central Station, Washington D.C.
May 27, 1882	Alabama	Selma	250,000	Central Station, Washington D.C.
1889	Alabama	Montgomery	500,000	unknown
1889-1890	Alabama	Montgomery	1,290,000	unknown
1889-1890	Tombigbee	Demopolis	490000	unknown
1891-1892	Alabama	Montgomery	2,499,000	unknown
1891-1892	Dog River	Mobile	1,400,000	unknown

Table 1.3. Scientific Collections of Alabama Shad in the Mobile Basin

Drainage	Collected	Source
Tombigbee River	Last observed in the 1950s	Mettee et al. 1987
Black Warrior River	Observed once in 1998, the only time since it was first collected in 1896.	Mettee and O'Neil 2003
Cahaba River	800 adult and juvenile specimens collected between 1954-1968	Pierson et al. 1989
Coosa River	Collected once in 1878	T.S. Doron (FMNH 1878)
Alabama River	Collected below dams between 1994 and 2001	O'Neil et al. 2000

Figure 1.1 Map of historic and current dams in the Mobile Basin, with a timeline of dam construction for each of the five impounded tributaries. The orange line marks the fall line.

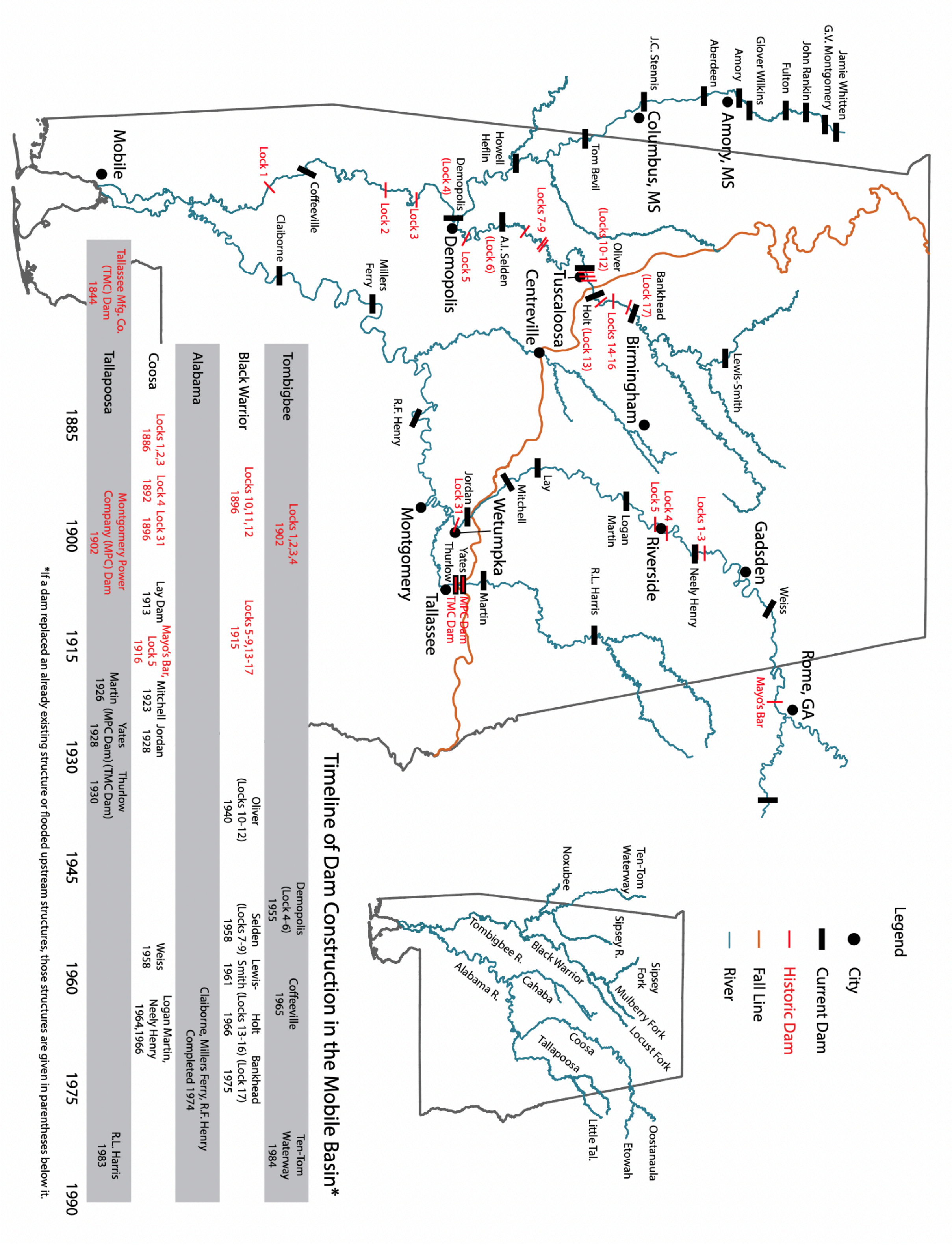


Figure 1.2 Painting of a wooden slat fall trap on the Tombigbee River (Unknown Artist, ca. 1885-1910, reproduced from article by Rufus Ward) courtesy of The Dispatch, Columbus, MS.

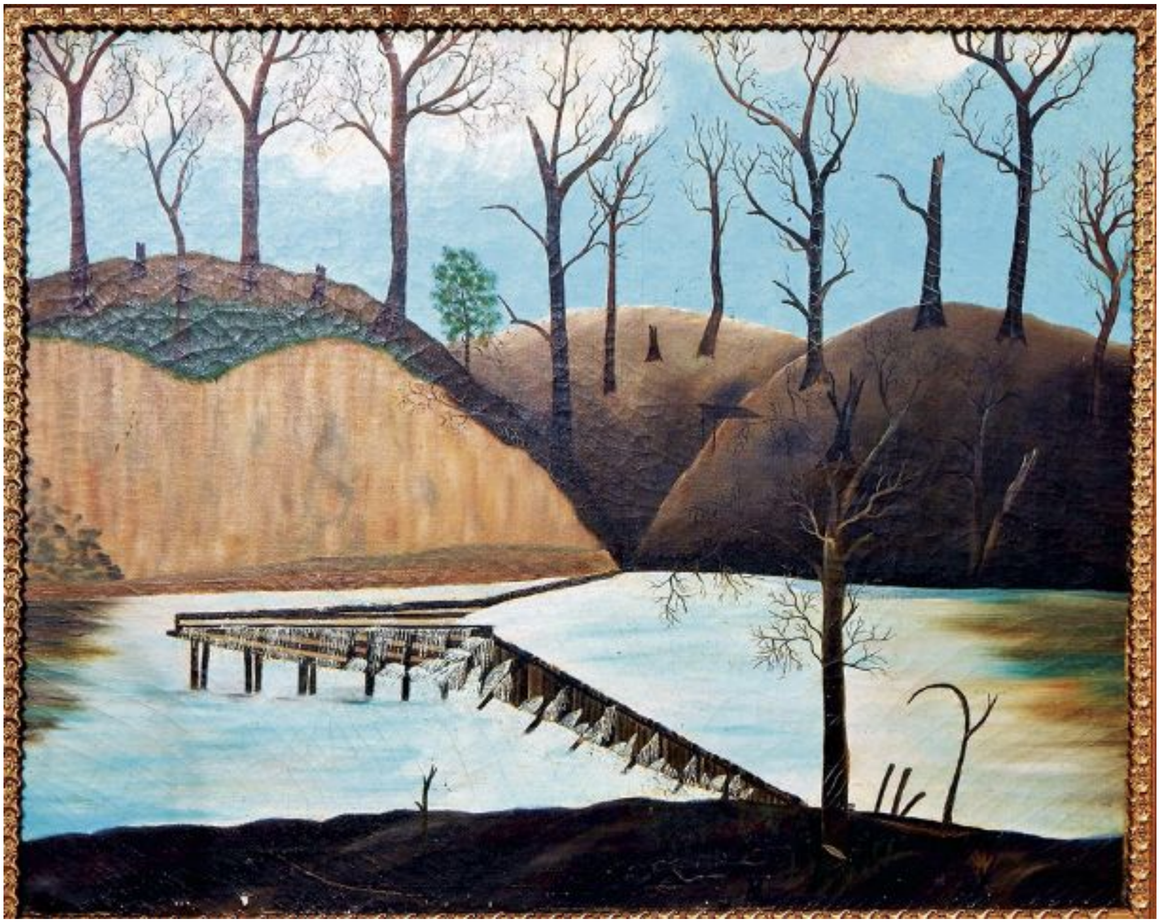


Figure 1.3 Map of the current area around Logan Martin Dam on the Coosa River, including inset aerial photographs of three possible sites of Willingham's Fish Trap taken before the dam's construction by the U.S. Department of Agriculture. Potential stone weirs in the top two photographs are circled. The bottom weir is still visible today at low water.

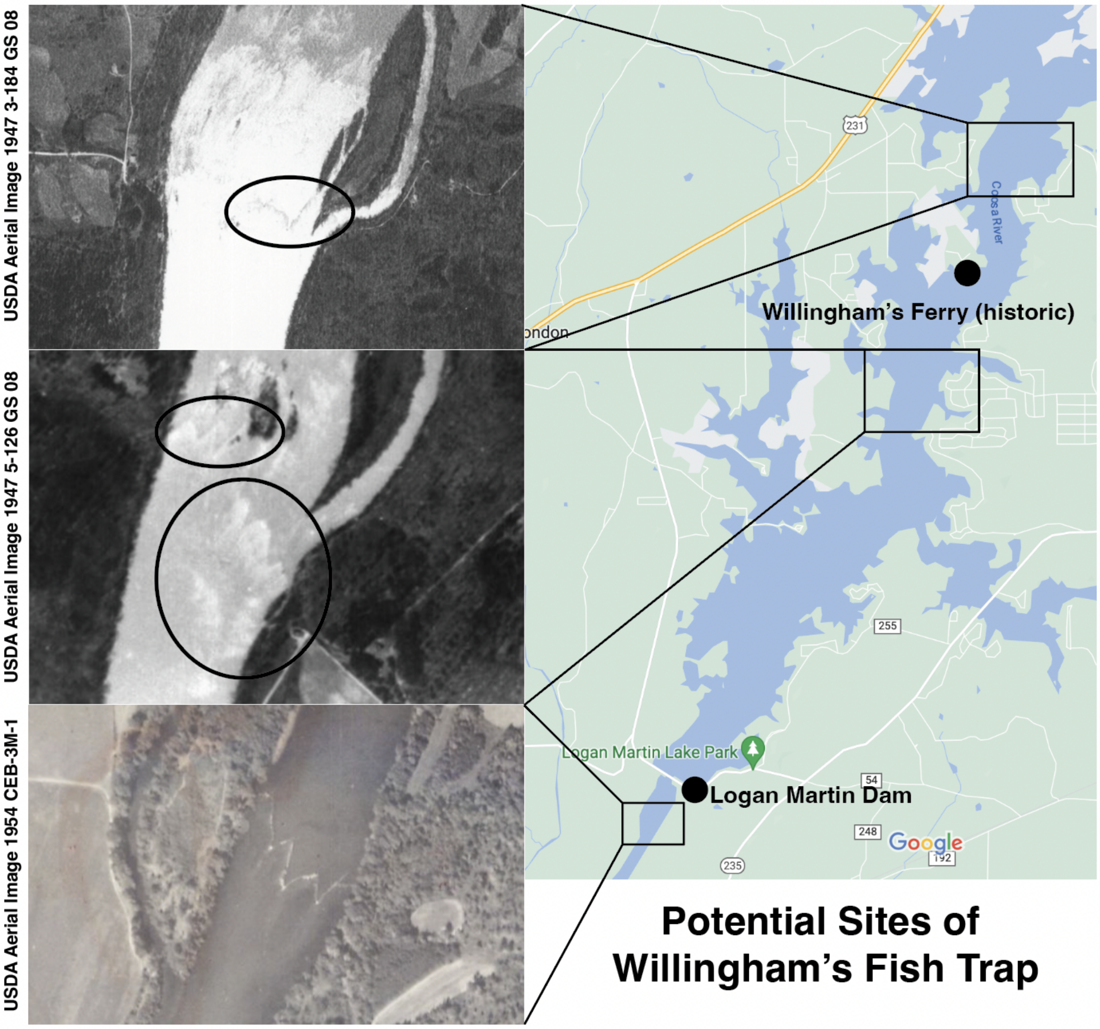


Figure 1.4 Scientific and anecdotal records of Sturgeon species in the Mobile Basin with HUC8 sub-basins colored by the number of records within them. The thick black line marks the fall line.

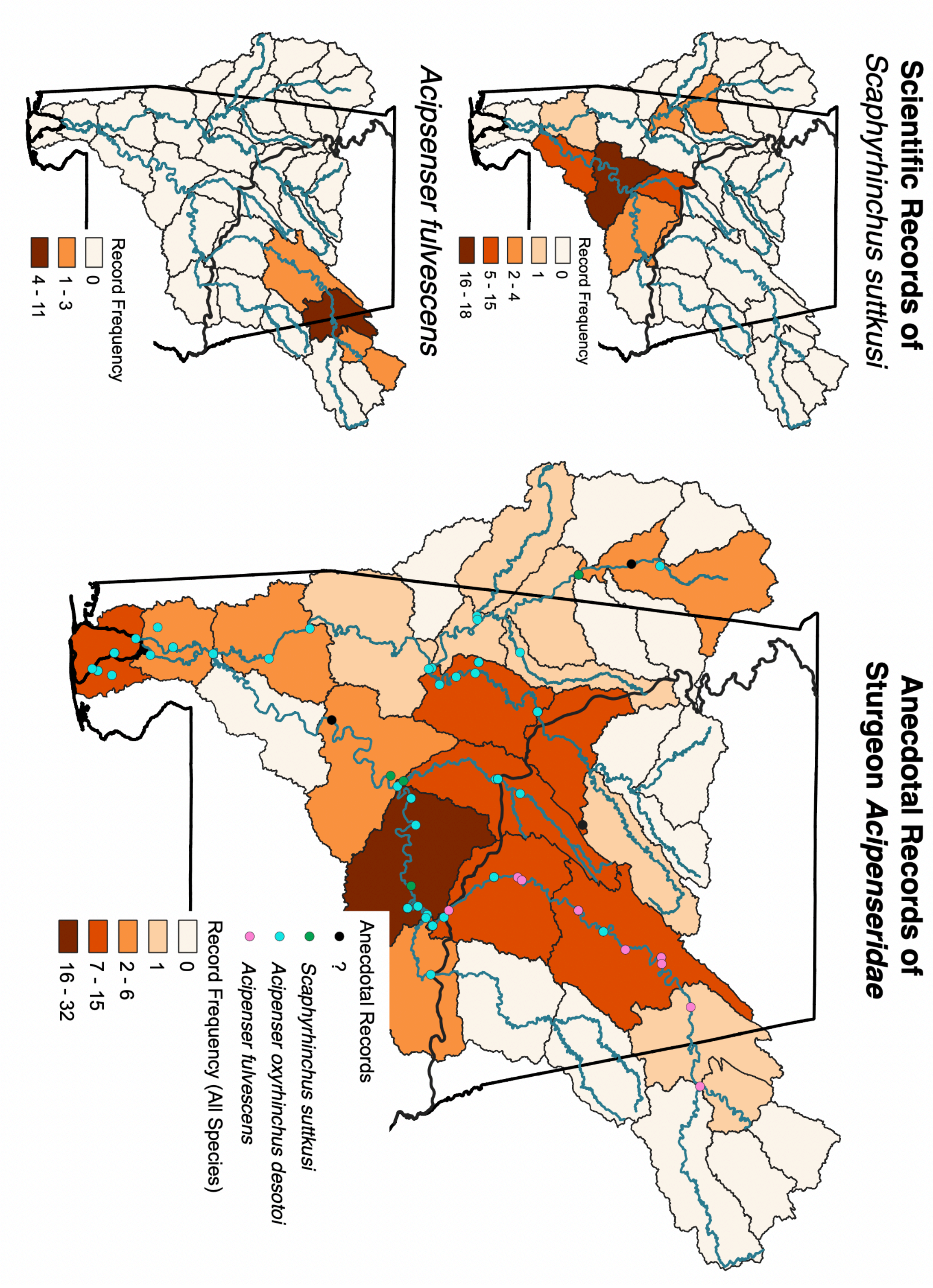


Figure 1.5 Scientific and anecdotal records of Alabama Shad in the Mobile Basin with HUC8 sub-basins colored by the number of records within them. Approximate locations of USFC stocking events given in green in the left panel. The thick black line marks the fall line.

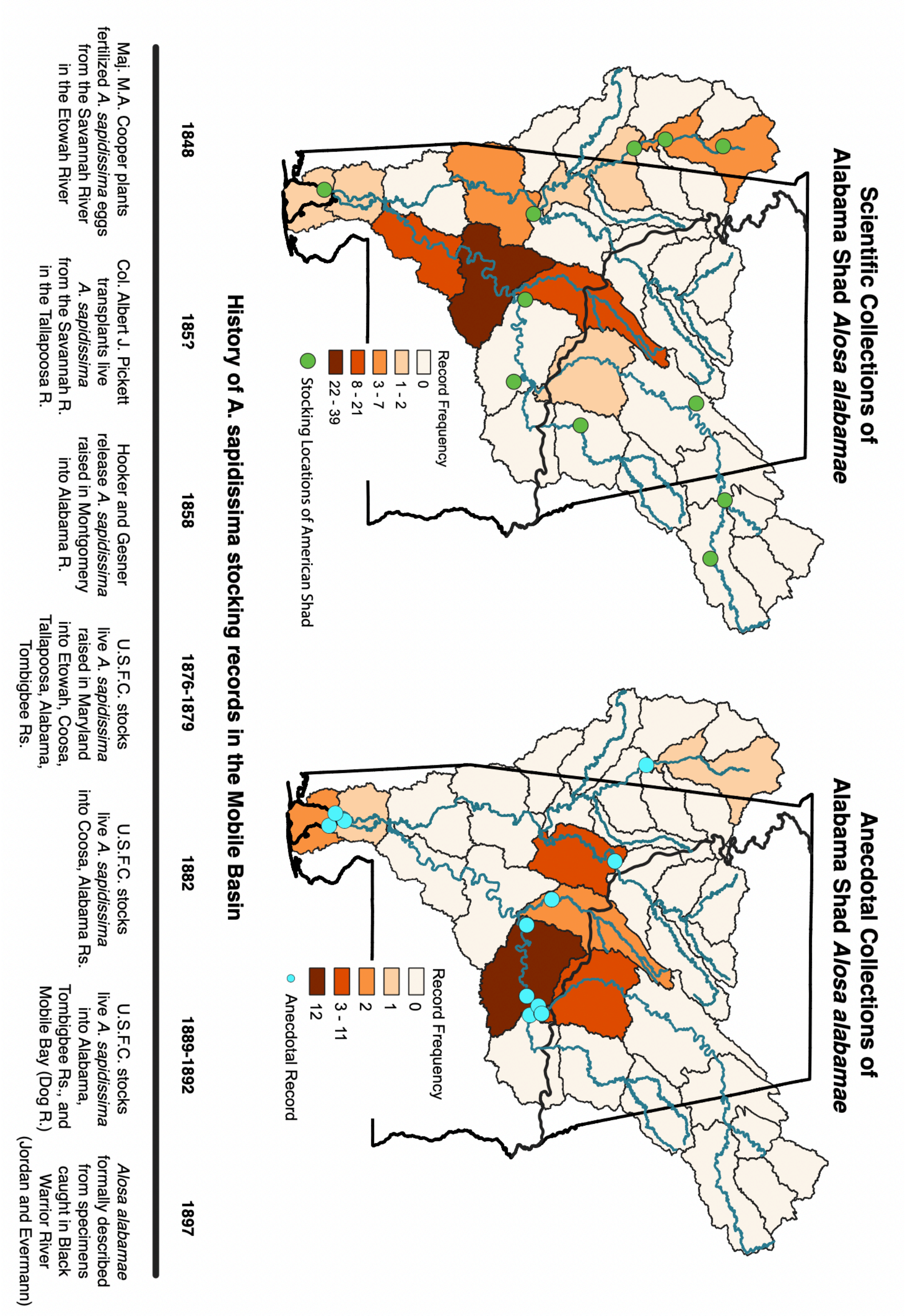


Figure 1.6 Scientific and anecdotal records of American Eel in the Mobile Basin with HUC8 sub-basins colored by the number of records within them. The thick black line marks the fall line.

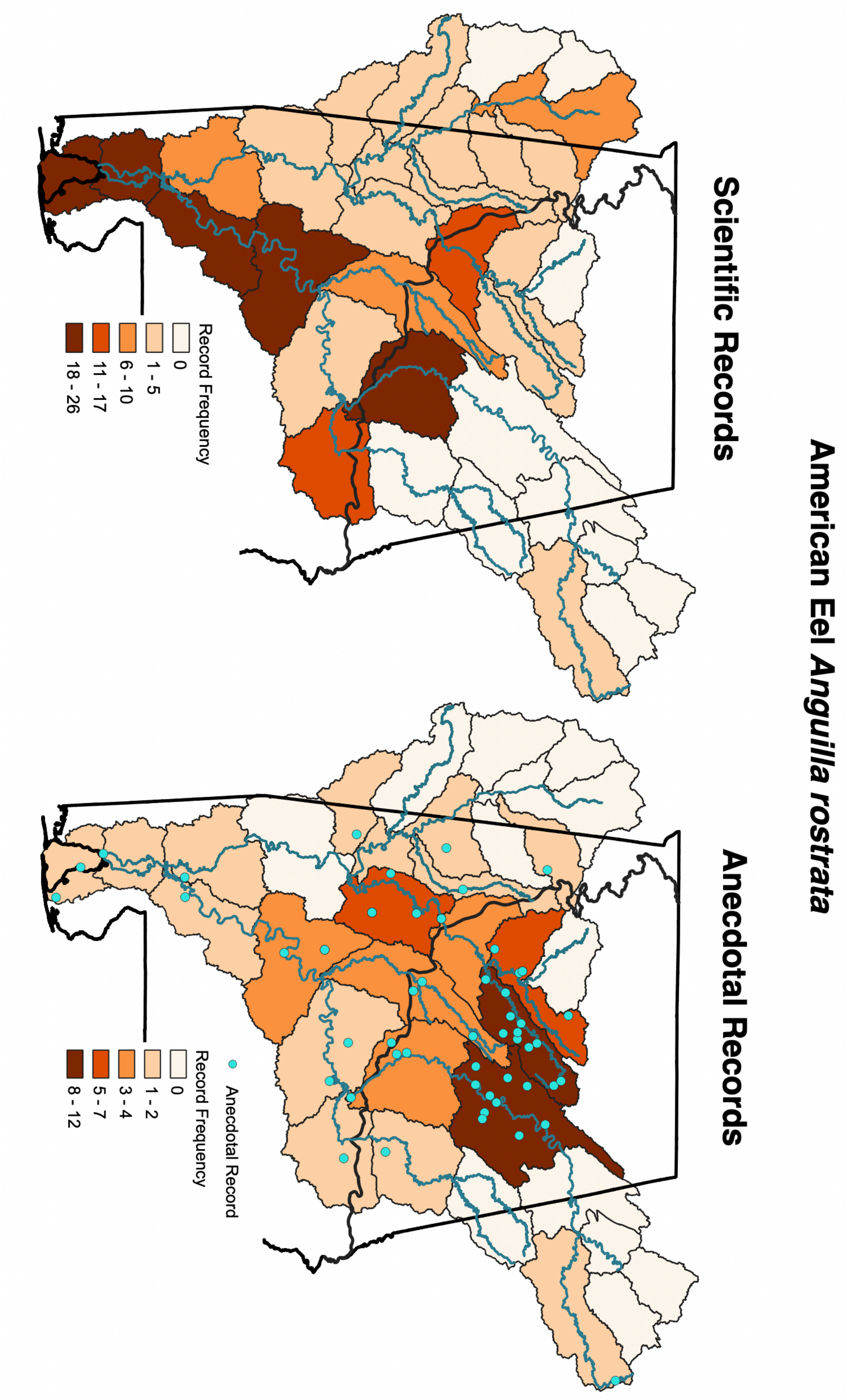


Figure 1.7 Anecdotal records of Paddlefish in the Mobile Basin with HUC8 sub-basins colored by the number of records within them. The thick black line marks the fall line.

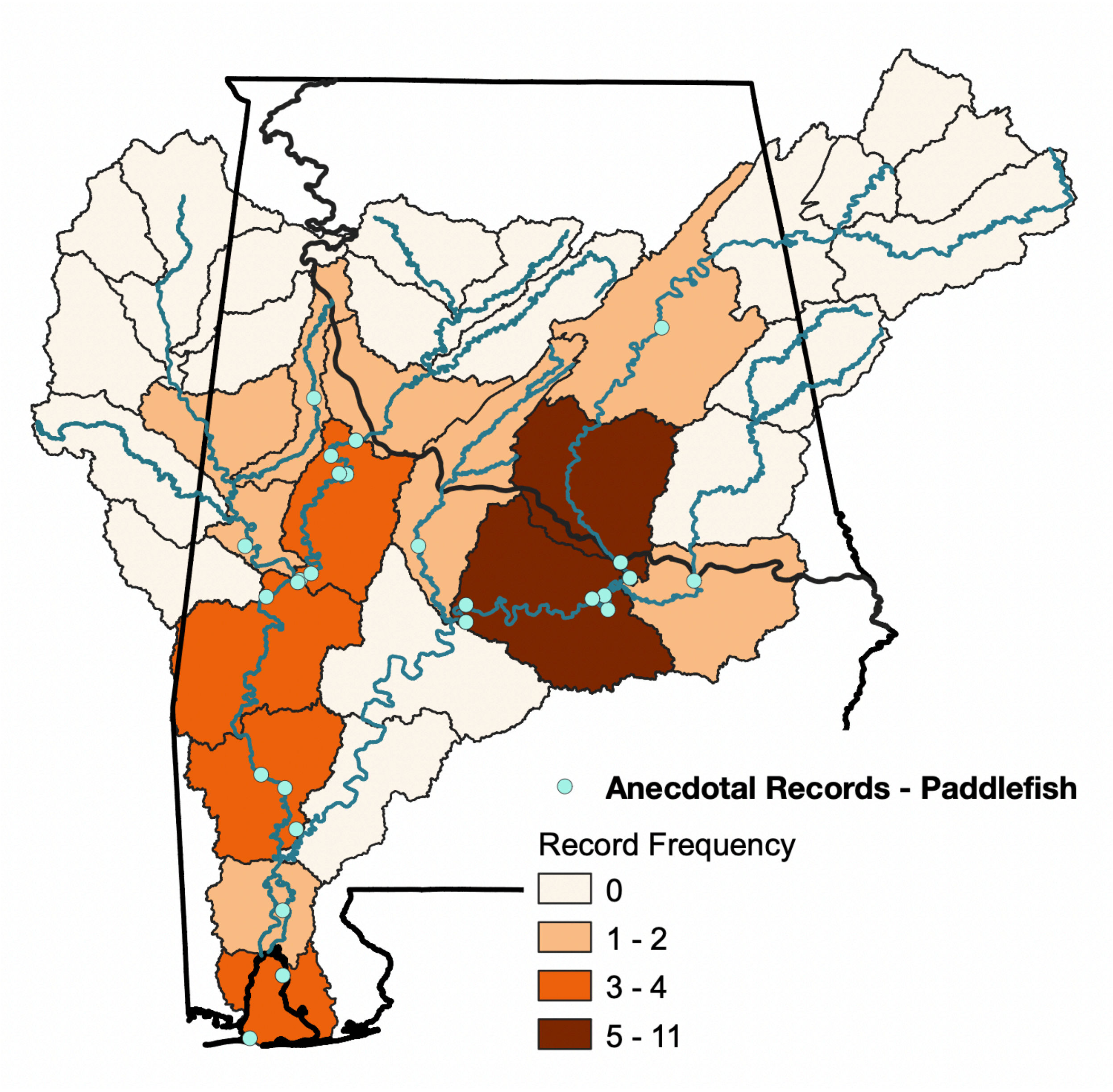
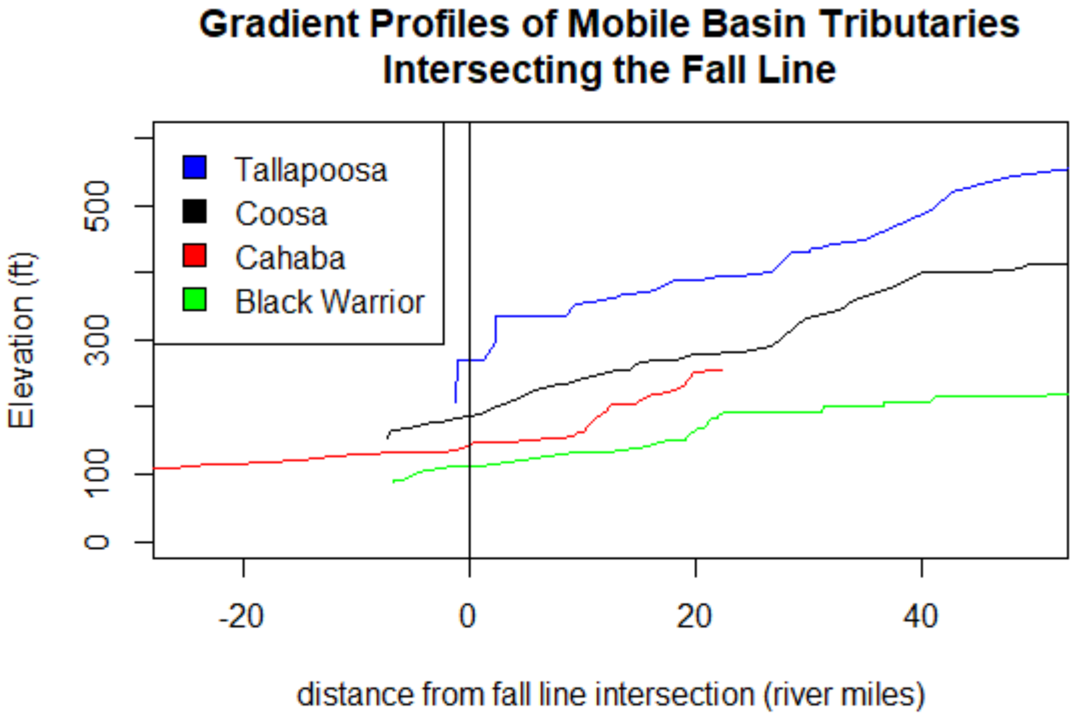


Figure 1.8. Elevation profiles of the four Mobile Basin tributaries that intersect the geological fall line, which is drawn at X=0. drawn from data produced by the Geological Survey of Alabama (1914) and U.S. Geological Survey (1904). By 1914, there were already two dams straddling the fall line on the Tallapoosa River, and elevation measures were taken at the crest of the dams, which confounds the river bottom elevation in that reach slightly, but the elevation change is still obviously more severe than on any of the other Mobile Basin tributaries.



Chapter 3: Movements and fate of migratory fish translocated above a hydropower dam

Abstract:

Increasing connectivity across barriers to fish migration may improve population stability in regulated rivers, but understanding how fish behave in novel environments before connectivity is restored is critical to ensuring the success of fish passage solutions. Therefore, in anticipation of a feasibility study for a bypass channel, we translocated 44 Paddlefish upstream of Millers Ferry Lock and Dam (MFLD) on the Alabama River to determine whether fish could navigate the upstream reservoir and continue their migration. In total, 23 of the translocated fish made a conspicuous upstream migration after release. The extent of the migration varied, but 12 of the migrants were detected 160 river kilometers (RKM) upstream at the next dam. Non-migrants tended to use the lower half of the reservoir, but were also detected around the mouth of a large tributary in the middle of the reservoir. At least 13 of the translocated fish moved back downstream below MFLD. Although the exact passage routes (via the lock chamber, the spillway gates or the powerhouse turbines) were undetermined, the timing of these downstream passage events closely aligned with periods of high flow when spillway gates would have been open. Survival (confirmed with detections) through the dam was limited, so it may be prudent to also include guidance for fish passing downstream of the dam in any fish passage efforts. These results can inform design of fishways in this system and others, and management of potamodromous species globally.

Introduction:

Fish passage restoration has been used to mitigate the effects of migration barriers on fishes globally (Bunt et al. 2012, Noonan et al. 2012). Restoration takes many forms depending on the species affected and the structure of the barrier, and those forms have led to variable success depending on their engineering, as well as on how success is defined (Kemp 2016). While the proximate goal of most fish passage solutions is to allow fish to migrate past barriers, the ultimate goal is to ensure the spawning success and long-term sustainability of the affected population (Castro-Santos et al. 2009). Many fishway evaluation studies sufficiently address the proximate goal, but fewer studies address the ultimate goal due to the difficulty of tracking test fish to their spawning habitat, combined with eventually quantifying spawning success (Bunt et al. 2012). The reason such evaluations of ultimate success are important is because even if fish passage is restored at a barrier, the ultimate goal may not be met and fish populations may not improve because the spawning success of passed individuals may be limited by other factors. This could be a particular problem for long-lived fish, where a lack of improved spawning success might not be apparent or manifested for many years.

Hydropower dams are well-known obstructions to fish spawning migrations. Technical fishways, bypass channels, locks, lifts, ladders and translocation have all been used to promote fish movement upstream, but their success ranges from 0% to 100% efficiency, and efforts to determine the exact causes of passage failure using meta-analysis have not been successful (Bunt et al. 2012; Noonan et al. 2012; Hershey 2021). Given the diversity of species, structures, and systems, there is no one size fits all solution to fish passage at hydropower dams, and the prohibitive costs of various approaches can make the task of implementing a solution difficult or sometimes even not possible. Therefore, it is imperative that researchers be able to accurately predict the expected outcomes of fish passage solutions based on the exact specifications of each dam, combined with the biological limitations of the species targeted for passage. Typically, this is done through experimentation and simulation. Behavioral models can be used to predict how many fish might be expected to use a passage solution under a range of flow conditions (Lindberg et al. 2013; Chen et al. 2019). But it is clearly much more difficult to predict eventual expected spawning success of those individuals given successful passage.

One way to predict the ultimate efficacy of a fish passage solution prior to its construction is by capturing fish downstream of the dam, transporting and releasing them upstream, and tracking their movements post-translocation (Irving and Modde 2000; Thomas in review; Marbury et al. 2021). The fate of these individuals would provide insight into the potential fates one could expect for fish that successfully passed a hypothetical mitigation structure, assuming that the stress impacts of translocation are similar to those due to passage via the structure (Jager et al. 2016). The fate of fish translocated into a reservoir above a dam depends on their condition post-translocation, on the availability of spawning habitat upstream, and on the ability of those fish to navigate upstream lentic waters and eventually locate suitable spawning habitat in more lotic conditions (Jager 2006, Marbury et al. 2021). If fish are too stressed by capture, translocation, or transmitter implantation surgery, they may exhibit fallback or delayed mortality (Frank et al. 2009). Furthermore, semelparous species that return downstream after spawning may attempt downstream passage through the dam and could require guidance if safe passageways are not available (Tripp et al. 2019). Also, spawning habitat must be confirmed to exist above the dam, given that reservoirs can inundate coarse spawning substrates with sediment, and some species require flowing water for egg survival (Zhong and Power 1996). Finally, many migratory fish are rheotactic and require flow cues for navigation (Montgomery et al.1997). These cues may be reduced or absent in the reservoir upstream, making it difficult for translocated fish to reach spawning habitat if it still exists (Xu et al. 2020; Silva et al. 2018).

One migratory freshwater species that may benefit from restored fish passage is the Paddlefish *Polyodon spathula.* The Paddlefish is a large, long-lived migratory species native to several large river basins tributary to the Gulf of Mexico. Paddlefish in the Mobile River Basin are genetically distinct from those in other tributaries (Epifanio et al. 1996), but similar in their life history. Individuals reach a maximum size of about 25kg and are capable of swimming hundreds of kilometers in a span of days (Mettee et al. 2006). Temperature and flow cues trigger the onset of their spawning migration in late winter, and they spawn at water temperatures between 12 and 17 C (Lein and DeVries 1998). In the Alabama River, a metapopulation of Paddlefish is fragmented by three dams, but may still spawn successfully in tributaries and tailraces (Mettee et al. 2009). Each of the fragmented subpopulations may be self-sustaining, and connectivity slightly varies across each dam, but increasing connectivity is expected to improve stability of the overall metapopulation (Pracheil et al. 2015).

The impetus for our translocation experiment was in anticipation of proposed mitigation efforts at a low-head low-use lock-and-dam structure that currently limits fish migration in the Alabama River (US Army Corps of Engineers 2023). Although the recommended alternative (a natural bypass channel) has not yet been designed, we set out to answer the question: Would fish resume their migration once allowed to pass upstream? The goal of the proposed passage project is to increase connectivity across the dam for a diverse array of taxa, but given the sensitivity of a few taxa and the difficulties of capturing and tracking them, we elected to use Paddlefish as our model species with the expectation that our findings will provide insight into both the behavior of other migratory species in this system and the behavior of Paddlefish in similar systems throughout their range.

Study Site:

The Alabama River is a large tributary of the Mobile River Basin that begins at the confluence of the Tallapoosa and Coosa rivers near Montgomery, AL, and continues downstream for over 450 km to its confluence with the Tombigbee River near Mobile, AL. Historically, migratory fish moved freely between the Gulf of Mexico and the headwaters of Mobile River tributaries in upland regions of the Alabama, Mississippi, and Georgia. However, dam construction began in the late 19th century and limited access to presumed ancestral spawning habitats. Overfishing, pollution, and channelization continued for more than a hundred years, contributing to the extirpation of several migratory taxa, including Gulf Sturgeon *Acipenser oxyrhinchus desotoi* (Sulak et al. 2016). In the early 1970s three low-head lock-and-dams were built on the previously unimpounded Alabama River between Montgomery and Monroe County for flood control, hydropower, navigation, and recreation. The lower-most dam, Claiborne Lock & Dam (CLD; RKM 116; measured going upstream from the river's mouth) included a fixed-crest spillway which has allowed migrating fish to pass during periods of high flow when it completely inundates. As many as 30% of fish tagged in the CLD tailrace have been observed migrating over the fixed-crest spillway (Simcox et al. 2015), and most of those fish continue their migration up to Millers Ferry Lock and Dam (MFLD; RKM 215 Hershey et al. 2022). However, passage rates at MFLD are negligible (Mettee et al.2009; Simcox et al. 2015; Hershey et al. 2022).

Millers Ferry Lock and Dam was built with a fully gated spillway, a lock, and a separate hydropower dam that impounds a channel on the descending river left bank. The two structures are divided by a narrow island. Although a few fish passages have been observed via the lock chamber, this is an extremely rare occurrence compared to passage over the spillway at CLD (Mettee et al. 2006, Simcox et al. 2011, Hershey et al. 2022). MFLD impounds the Alabama River to form Bill Dannelly Reservoir, a complex shallow lake with a shipping channel that is maintained at a depth of approximately 8m. Although much of the lower half of the reservoir is flooded backwater habitat, lotic habitats are still common throughout, especially in the more channelized upstream reaches. The Cahaba River, Alabama River's largest free-flowing tributary, enters the reservoir at RKM 304, offering over 225 km of unimpeded lotic habitat with an average discharge of 85 m^3s^{-1}. The Alabama River continues another 80 km upstream past the mouth of the Cahaba River to R.F. Henry Lock and Dam (RFHLD), another fully gated structure with an attached powerhouse, past which no fish have ever been observed to migrate.

A similar study was performed at Claiborne Lock and Dam in 2018 and 2019 (Thomas, 2022) which found that translocated fish were able to navigate the reservoir upstream of the dam, and migrated upstream to Millers Ferry Lock and Dam. Our study may be considered an extension of this work, but with important differences: Dannelly Reservoir is a much larger and less channelized reservoir, with thousands of hectares of shallow backwater habitat, and several large tributaries. Based on the previous study, we expected that migrating individuals would be concentrated below the Millers Ferry Lock and Dam during their spawning season, and would continue their upstream migration when translocated above, but in lower proportions than at Claiborne Lock and Dam due to the possible lack of flow cues in Dannelly Reservoir.

Methods:

We translocated 20 and 24 Paddlefish over Millers Ferry Lock and Dam during March 2022 and 2023, respectively (Table 2.1). Water temperatures on translocation days ranged between 14 and 15 C. We captured fish with large-mesh gillnets in slack water eddies within 1km of the dam face with soak times not exceeding 1 hour. Paddlefish were assessed for injury upon capture, and freshly wounded individuals were immediately released. Paddlefish without injuries or with healed old wounds were held in an aerated live-well on the boat. Paddlefish were not held in the live-well longer than 4 hours. We transferred captured fish to a truck-mounted live-hauler (2 x 1.25 x 1 m) for translocation above the dam. We drove them approximately 16 km (road distance) to the release site at Shell Creek Park, which took about 15 minutes (N 32.114280382118025, W 87.40559078124909). The park is located in a backwater cove adjacent to the shipping channel, but approximately 2km upstream of the dam to protect fish from being swept downstream (Thomas 2022).

Before releasing the hauled fish, we treated the live hauler with buffered MS-222 and surgically implanted each individual with a Combined Acoustic and Radio Transmitter (CART; LOTEK Wireless model MM-MC-11-45 M; 536 day battery life). In 2022, each fish was removed from the live-well and weighed, then transferred to a surgery cradle where water was pumped over the gills with a small hose while the fish was measured. In 2023, we did not weigh the fish in an effort to further reduce any additional handling stress. Once a fish was measured, a small incision was made anterior to the left pelvic fin through which the tag was inserted, and the radio antenna was threaded through a 17 ga needle puncture in the skin posterior to the incision site. Sex was identified by examination of gonadal tissue inside the incision. If no eggs or testes were seen, we listed the sex as “unidentified”. The incision was closed with two interrupted sutures and sealed with veterinary grade surgical glue. Surgery took approximately three minutes per fish. Fish were revived by hand in the reservoir and only allowed to swim away once equilibrium and motor function were regained.

Post-release movements and fates of fish in Bill Dannelly Reservoir were monitored passively with 15 bank-tethered acoustic receivers (LOTEK Wireless model WHS 4350) spaced approximately 10km apart along the shipping channel up to RFHLD, as well as 10 receivers stationed in backwater side channels (Figure 2.1). An additional 17 receivers were maintained downstream of MFLD, and CLD to monitor fallback or downstream passage over the dams. Receivers were downloaded and batteries changed every three to four months, however, some receivers were inactive during April 2022 due to unsafe conditions for battery changes.

To describe the behavior of translocated fish we classified individuals into two groups: migrants, and non-migrants. Individuals were classified as migrants if they made a conspicuous upstream movement greater than 80 river kilometers within one month of release, or during the subsequent spawning season (February to May). Fish that exhibited any other behavior were classified as non-migrants. Upstream movements greater than 80 river kilometers outside of the spawning season in either year could be defined as migrations, but we were specifically focused on movements that could have been

Results:

In 2022, mean length of the 20 tagged fish was 866.6 ± 193.8 mm (µ ± SE). Putative fates of each translocated fish are given in Table 2.2. All but three were identified as male, with two females, and one unidentified. Apparent survival to one month after translocation was observed in all but two fish. One of the surviving fish never moved upstream, and was last detected in the MFLD forebay before being detected again in June 2022 in the CLD tailrace and, later, in the Lower Alabama River. Given the receiver outage in Claiborne Lake in April 2022, we assume that individual fell back downstream over MFLD shortly after its last detection in the forebay. Of the 17 other survivors, five did not migrate upstream, but 12 made conspicuous upstream migrations, seven of which reached RFHLD as early as March 15. The five non-migrants were detected consistently throughout the downstream half of the reservoir and spent long periods in the MFLD forebay. One of the 2022 non-migrants made a conspicuous upstream migration to RFHLD in late winter 2023, after which it returned to the MFLD forebay where it remained for the rest of the study period.

Of the 12 conspicuous migrants, all but two returned downstream to the translocation site within two months of their release. One remained in the RFHLD tailrace until June 11, 2022, before returning within 5km of MFLD on June 20, 2022, and the other moved down to RKM 236 before meandering throughout the reservoir for the remainder of the year. Of the 10 migrants that returned to the translocation site, three were last detected in the MFLD forebay, and five in the tailrace of MFLD. We suspect all eight of these made a downstream passage, and may have died due to the extreme hydraulic conditions in the spillway gates or powerhouse turbines. The remaining two of the ten conspicuous upstream migrants may have survived downstream passage at both MFLD and CLD, given that they were later detected in the Lower Alabama River after passage in summer 2022. However, only one of them made subsequent upstream movements after their downstream passage, which is the only way we could confirm their survival (see example in Figure 2.2A).

In 2023, mean-length of the 24 tagged fish was 911.3 ± 186.0 mm (μ ± SE). All but five were identified as male, and the remaining five were female. Weight was not measured. After their release, 9 fish were never detected, and one either died or shed its transmitter in the MFLD forebay within one week (it was detected constantly at one receiver for two weeks before the signal was lost). Of the 14 survivors, 10 made conspicuous upstream migrations, and 4 made smaller upstream movements.

Among the 10 conspicuous migrants, the extent of upstream migration varied. Four were detected in the RFHLD tailrace between March 18 and May 14, 2023. The upstream limit of the other six migrants was between RKM 296-325, (King’s Landing - Selma, AL). Following these upstream movements, five of the ten conspicuous migrants were either last detected downstream in the Lower Alabama River or Claiborne Lake after making a directed movement downstream. Although we know these fish moved downstream, we could not confirm their post-passage survival because downstream movements were not discernible from passive drifting by a dead fish. The remaining five conspicuous migrants stayed in Dannelly Reservoir for the remainder of the study period.

The four non-migrant fish all made smaller upstream movements during the study, but exhibited more meandering behavior, moving both up and downstream. One was last detected near the Cahaba River confluence, while the others spent more time near the MFLD forebay and were not detected farther upstream than RKM 264.

Five of the twenty fish released in 2022 were detected during 2023, all of which were within Dannelly Reservoir. One that made a conspicuous upstream migration in 2022 was detected sporadically in the upper half of the reservoir until it was last detected in early May 2023 near the Cahaba River. The other four did not migrate in spring 2022, but all exhibited another behavior, spending the spring and summer throughout the lower half of the reservoir until the fall when they moved upstream towards the Cahaba River (Figure 2.2B). Of these four, one was never detected again, and three returned downstream in the spring. In total, only one fish released in 2022 made a putative spawning migration up to R.F. Henry Lock and Dam in 2023 (Figure 2.2C). That fish returned to the MFLD forebay in March 2023.

We documented 19 downstream passages made by 13 fish. Seven fish passed both dams, while 6 only passed MFLD. The exact time of each passage event was not always possible to deduce, but the time between the last detection of a fish upstream of a dam and their first detection below it ranged from less than two hours up to 230 hours (Table 2.3). We overlaid these windows for each passage event over the gage height in the tailrace of the respective dams separated by year. Downstream passages at MFLD occurred as late as July 7 in 2022, and May 23 2023 (Figure 2.3). At CLD, downstream passages were limited to June in 2022, and occurred between April and May in 2023 (Figure 2.4). Almost all windows occurred during periods of increased tailrace gage height, which was most likely due to opened spillway gates. However, the maximum height during the windows ranged from 42 to 68 ft at MFLD, and from

13 to 35 ft at CLD, indicating that although passages tended to occur during flow pulses, they may not have been associated with pulse magnitude. At MFLD, during most of the downstream passage windows for each fish (12 out of 13 windows), other fish were detected in the MFLD forebay that did not pass during the window, indicating that passage is more likely due to individual behavior, than a specific flow condition that would force all fish present in the forebay to move downstream. For example, Tag ID 143 (the only fish in the study that exhibited fallback behavior) was detected below the dam within a few days of its release, but 11 other fish were detected in the forebay at the same time and did not move downstream during that window (Table 2.3).

Discussion:

Our primary goal was to determine whether Paddlefish would be able to navigate a novel lentic environment given the opportunity to pass upstream of a migration barrier. The goals of translocation above barriers to migration may vary depending on where suitable spawning habitat exists. Spawning sites of Paddlefish in Dannelly Reservoir have not been identified, but it is possible that fish spawn in the Cahaba River or other tributaries, as well as the tailrace of RFHLD, or other sections of the upper reservoir. Therefore, the proportion of translocated fish detected at the next-most upstream barrier may not be the most informative measure of success. However, 23 out of 44 (52.7%) translocated fish in this study did make a conspicuous upstream migration, which is the most conservative estimate of success for this study.

In 2019, 57 Paddlefish were translocated upstream of CLD (100 RKM downstream of MFLD) with the same goals as this study. Of those fish, 34 (59.6%) continued their migration up to MFLD, and none fell back downstream (Thomas 2020). Twelve of the fish in this study did not likely survive translocation, but 68.75% of surviving fish made conspicuous upstream migrations, and 34% reached the next barrier, suggesting that Paddlefish are able to navigate the reservoir habitat above the dam and potentially find spawning habitat upstream. However, fish that pass the proposed bypass structures may experience different stressors than our translocated fish, which could change their behavior, especially if they pass upstream of both structures in a single migration, which could be energetically taxing and stressful (Cooke et al. 2008).

The rate of conspicuous migration we observed is congruent with past work in this system, but higher than estimates reported on Acipenserids in other systems. Only two out of 10 (20%) Gulf Sturgeon translocated over Jim Woodruff Lock and Dam on the Apalachicola River were able to navigate Lake Seminole to find suitable spawning habitat. Six fish fell back over the dam, and four remained in the reservoir throughout the study period (Marbury et al. 2021). In the Mattagami River, Ontario, CN, 21 Lake Sturgeon *Acipenser fulvescens* were translocated over three hydropower dams to an isolated 34km river section from which the species had been extirpated. Six of the first 13 fish (46%) fell back over the downstream dam, and the remainder stayed in the lower portion of the segment. However, 10 years later, another eight fish were translocated and all but one (87.5%) were detected in the spawning area below the upstream dam (Boothroyd et al. 2019).

The goal of many translocations is to re-introduce a species to its former range, or improve genetic diversity within a small population (Boothroyd et al. 2018, Rust 2011). Therefore, downstream dispersal by translocated individuals before they become acclimated and reproduce is an undesirable outcome. We observed downstream dispersal by at least 12 fish (potentially up to 14; 22-32% of translocated fish) in this study, which was not unexpected (given previous observations at CLD; Thomas 2020) and not necessarily counter to our goal. Given that reintroduction was not the goal, whether fish emigrated from Dannelly Reservoir after potentially spawning should not have any bearing on the success of the project, and in fact, if a more natural migratory behavior is the goal, may be a desired long-term outcome. One fish exhibited fallback behavior (downstream movement immediately following release), but nine others were detected below MFLD after making a putative spawning migration. Seven that were detected downstream of MFLD only moved in a downstream direction. They may have survived but also could have died and been detected as they drifted downstream. The survival of the other two fish was confirmed based on having been detected making short movements upstream in Claiborne Lake after moving downstream past MFLD. Additionally, four fish were last detected in the MFLD forebay before the end of the study period, and were never detected again after that. We could not confirm whether these fish passed downstream, or the route that the confirmed passers took, although none were detected inside the MFLD lock chamber.

There are three ways for fish to pass downstream of MFLD: via the roller gates, the lock chamber, or the powerhouse turbines. Each passage route may have different mortality risks, and those risks may vary by species and by individual size within species. Surviving entrainment through hydropower turbines, in particular, may have significant impacts on population stability

(Harrison et al. 2019). Few studies have documented the passage routes and survival rates of potamodromous fishes, let alone Acipenseriform fishes, moving downstream of dams in other systems (Harrison et al. 2019; Jager et al. 2016). Our estimate of downstream passage through MFLD (22-32%) is comparable to other studies on Paddlefish in reservoirs, but downstream passage survival data for Paddlefish is still lacking in the literature. Pitman and Parks (1994) observed six out of 19 (31%) translocated juvenile Paddlefish emigrating from the B.A. Steinhagen Reservoir either through flood gates or over the spillway. Survival was not confirmed. Moen et al. (1992) tracked six out of 32 (19%) large adult Paddlefish moving downstream out of Pool 13 into Pool 14 on the Mississippi River through flood gates, but survival was not confirmed. Southall and Hubert (1984) found five out of eight (62.5%) Paddlefish that had first passed upstream of Lock and Dam 12 returned back downstream through the partially opened gates. This proportion may be higher than others because fish had already passed through the gates of their own volition and may have learned the route. Therefore, if a bypass channel is built at MFLD, a higher proportion of fish moving upstream over MFLD could potentially return downstream than our observations for translocated fish. However, whether they will pass back through the bypass channel or via previously existing routes could impact their survival.

Other studies on sturgeon species have been able to quantify survival in addition to downstream passage rates, which were similar to those found in this study. Out of 34 sub-adult Lake Sturgeon *Acipenser fulvescens* tagged above Slave Falls Generating Station in Manitoba, Canada, 11 (32%) moved downstream through the dam, with 10 surviving passage. Six were confirmed to have passed via the bottom-draw sluice gates in the powerhouse. (McDougall et al. 2014). At Kleber Reservoir, Michigan, a much smaller system than Slave Falls, about 55% of age-1 and age-2 Lake Sturgeon stocked in the reservoir were entrained through Kleber Dam, a hydropower facility. Most of the entrainment events occurred within 60 days of stocking (Hegna et al. 2020). In 2007, 18 out of 58 (31%) tagged White Sturgeon *Acipenser transmontanus* were documented moving downstream via open spill gates at the Dalles Dam on the Columbia River (Parsley et al. 2007). A bypass canal at Holyoke Dam on the Connecticut River was successful at passing Shortnose Sturgeon *Acipenser brevirostrum* downstream after it was modified to block sturgeon from the space between the bottom of the canal and a louver array that was an impingement risk (Ducheney et al. 2006). More work is needed to describe the routes and quantify the associated risks of downstream passage by Paddlefish in reservoir systems.

It is impossible to know the natal origins of the fish captured for this experiment (i.e., Claiborne Lake, or the Lower Alabama River), because philopatry (natal homing) has not been documented in the system (although it has been suggested that some Paddlefish in the Alabama River exhibit spawning site fidelity; Mettee et al. 2009). Detection of seven individuals in the lower Alabama River after their translocation above MFLD does not mean they originated there, but allowing fish passage at MFLD may enable fish from anywhere in the Mobile Basin downstream of MFLD to ultimately access Dannelly Reservoir and the Cahaba River. Conversely, it may allow for fish hatched upstream of MFLD to move downstream past both MFLD and CLD if they choose to emigrate downstream from Dannelly Reservoir. This has extremely important implications for fishway design.

Due to the survival of the fish translocated in this study, (73% initial survival, with possible additional downstream passage mortality) and the tendency of some fish to remain in Dannelly Reservoir after their translocation upstream (versus moving into the Cahaba River or upstream to RFHLD), we emphasize that designers of passage solutions must keep in mind the importance of safe downstream passage as well as successful upstream passage. A superior fish passage solution at any dam, let alone at MFLD, would provide balanced passage opportunities for both upstream and downstream migrants. Factors affecting downstream passage success in the system have not been studied, but our results suggest that at least half of the fish that move up through a mitigation structure would most likely subsequently return downstream, requiring avenues for safe passage and potential guidance to the mitigation structure entrance, given that the alternative pathways (through the spillway gates or powerhouse turbines) may be associated with increased mortality (Harrison et al. 2019).

Ultimately, improved connectivity for potamodromous fish in this system may hinge on a few key knowledge gaps. Priority should be placed on identifying spawning sites in the upstream reservoir, and its tributaries, as well as describing fine-scale movements of fish in the MFLD forebay and tailrace. Understanding how individuals approach and interact with this structure from both upstream and downstream will be crucial to ensuring success of any designed mitigation structure. Also, identifying the annual rate at which fish in Dannelly Reservoir pass downstream through the flood gates or powerhouse turbines will be highly valuable to managers of the species, particularly if injuries or mortality are more likely during passage. Our study provides insight into how Paddlefish and other potamodromous fish behave post-translocation, as well as how they might behave if they voluntarily passed upstream of any low-head lock and dam in a reservoir chain. Given the positive global trend in passage mitigation projects (, we hope this approach will continue to be used to characterize post-passage movements of other migratory species in these sorts of systems.

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Table 2.1 Dates on which Paddlefish were collected, tagged, and translocated, and the number of fish translocated on each date.

	# Paddlefish Translocated
March 7, 2022	10
March 8, 2022	6
March 9, 2022	4
March 6, 2023	9
March 7, 2023	15

Table 2.2 List of fish translocated in this study, their sex (M= Male, F= Female, U= Unidentified), whether they made a conspicuous upstream migration, where they were last detected, and their putative fate, inferred from telemetry data. The furthest upstream detection is given in parentheses for each upstream migrant.

Fish ID	Sex	Upstream Migrant	Last Detection	Putative Fate
146	M	No	Translocation Site	Died or shed transmitter within 1 week
147	M	No	NA	Never Detected
143	M	No	Lower Alabama River	Fell back over MFLD and CLD
140	M	Yes (376)	MFLD Tailrace	Emigrated downstream
141	M	Yes (325)	MFLD Tailrace	Emigrated downstream
142	M	Yes (376)	MFLD Tailrace	Emigrated downstream
145	M	Yes (376)	Lower Alabama River (Confluence)	Emigrated downstream
151	F	Yes (376)	MFLD Tailrace	Emigrated downstream
156	M	Yes (352)	Lower Alabama River	Emigrated downstream
160	M	Yes (376)	MFLD Tailrace	Emigrated downstream
144	M	Yes (325)	MFLD Forebay	Emigrated downstream
154	M	Yes (352)	MFLD Forebay	Emigrated downstream
155	M	Yes (352)	MFLD Forebay	Emigrated downstream
149	M	Yes (376)	Dannelly Reservoir	Remained in Dannelly Reservoir
152	M	Yes (376)	Dannelly Reservoir	Remained in Dannelly Reservoir
148	M	No	Dannelly Reservoir	Remained in Dannelly Reservoir
150	U	No	Dannelly Reservoir	Remained in Dannelly Reservoir
153	F	No	Dannelly Reservoir	Remained in Dannelly Reservoir
157	M	Yes (352)	Dannelly Reservoir	Remained in Dannelly Reservoir
158	M	No	Dannelly Reservoir	Remained in Dannelly Reservoir
29450	F	No	MFLD Forebay	Died or shed transmitter within 1 week
29482	M	No	NA	Never Detected
29484	M	No	NA	Never Detected
29470	F	No	NA	Never Detected
29452	M	No	NA	Never Detected
29468	M	No	NA	Never Detected
29418	M	No	NA	Never Detected
29422	M	No	NA	Never Detected
29426	M	No	NA	Never Detected
29438	M	No	NA	Never Detected
29446	F	Yes (325)	Lower Alabama River	Emigrated downstream
29434	M	Yes (310)	Lower Alabama River	Emigrated downstream
29436	M	Yes (325)	Lower Alabama River	Emigrated downstream
29428	M	Yes (376)	Lower Alabama River	Emigrated downstream

29444	F	Yes (376)	Claiborne Lake	Emigrated downstream
29458	M	No	MFLD Forebay	Emigrated Downstream
29480	M	Yes (325)	Dannelly Reservoir	Remained in Dannelly Reservoir
29474	M	Yes (376)	Dannelly Reservoir	Remained in Dannelly Reservoir
29420	F	Yes (310)	Dannelly Reservoir	Remained in Dannelly Reservoir
29488	M	Yes (376)	Dannelly Reservoir	Remained in Dannelly Reservoir
29430	M	Yes (296)	Dannelly Reservoir	Remained in Dannelly Reservoir
29486	M	No	Dannelly Reservoir	Remained in Dannelly Reservoir
29424	M	No	Dannelly Reservoir	Remained in Dannelly Reservoir
29432	M	No	Dannelly Reservoir	Remained in Dannelly Reservoir

Table 2.3 Downstream passage windows for each that moved downstream of MFLD in 2022 and 2023. Max Ht is the maximum tailrace gage height measured during the window, delimited by the last detection of the fish upstream of MFLD and its first detection downstream of MFLD. ΔT is the length of time of the window in hours. The last column lists the TagIDs of other individuals detected in the MFLD forebay during the window that did not pass during that window, but may have passed later. Fish that passed downstream in a later window are denoted with an asterisk.

TagID	Max Ht (ft)	Last Upstream Detection	First Downstream Detection	ΔT (hrs)	Other Tag IDs detected in MFLD Forebay During Window
143	32.35	2022-03-10 02:57:00	2022-03-13 05:58:49	74	160*, 146, 142*, 141*, 148, 157, 151*, 140*, 158, 150, 156*
151	38.54	2022-04-06 01:07:41	2022-04-07 01:08:37	24	150
140	44.5	2022-04-09 16:34:54	2022-04-09 20:22:34	3.8	NA
141	30.21	2022-04-15 22:37:18	2022-04-17 05:45:00	31	150, 142*
142	31.09	2022-04-17 05:44:33	2022-04-17 08:56:15	3.2	141*, 150
160	42.32	2022-04-18 18:15:00	2022-04-20 10:41:06	40	145*
156	30.91	2022-06-11 00:23:30	2022-06-11 04:18:27	3.9	157, 150, 145*
145	22.56	2022-07-11 02:18:28	2022-07-11 20:47:31	18	148, 150, 158
29434	45.98	2023-03-29 19:59:44	2023-04-08 10:43:44	230	29446*, 157, 29450, 29474
29446	45.98	2023-03-31 22:32:28	2023-04-05 01:16:58	98	157, 29450
29444	24.64	2023-05-02 22:25:20	2023-05-03 05:21:41	6.9	158, 29488, 29450
29428	23.03	2023-05-22 05:58:51	2023-05-25 20:26:11	86	29450, 157, 158, 29432

Figure 2.1. Map of the study area with acoustic receiver locations colored by reservoir or river section.

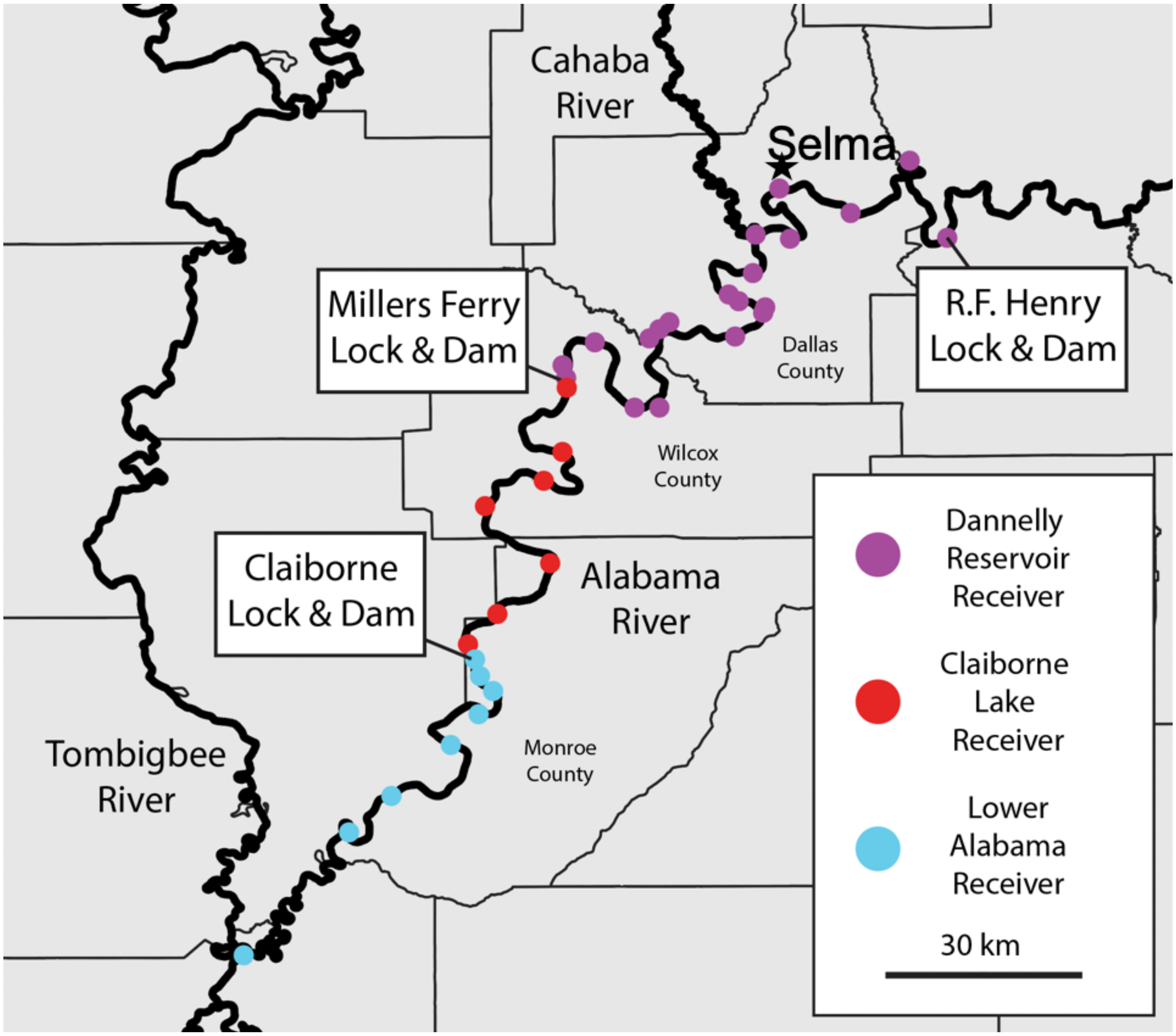


Figure 2.2 Examples of post-translocation movements above and below Millers Ferry Lock and Dam A) a conspicuous upstream migration to RFHLD in March, followed by a downstream migration in April, an extended period of residence in the MFLD forebay throughout May and June, downstream passage at both MFLD and CLD in July, and emigration from the Alabama River. B) no conspicuous migration in 2022, meandering behavior in the lower half of MFLD, a fall migration to the Cahaba River (RKM 305), and a return to MFLD forebay in April 2023. C) no conspicuous migration in 2022, a period of residence in the middle reservoir near the Cahaba River, and a conspicuous migration in February 2023 followed by a return to MFLD forebay in March.

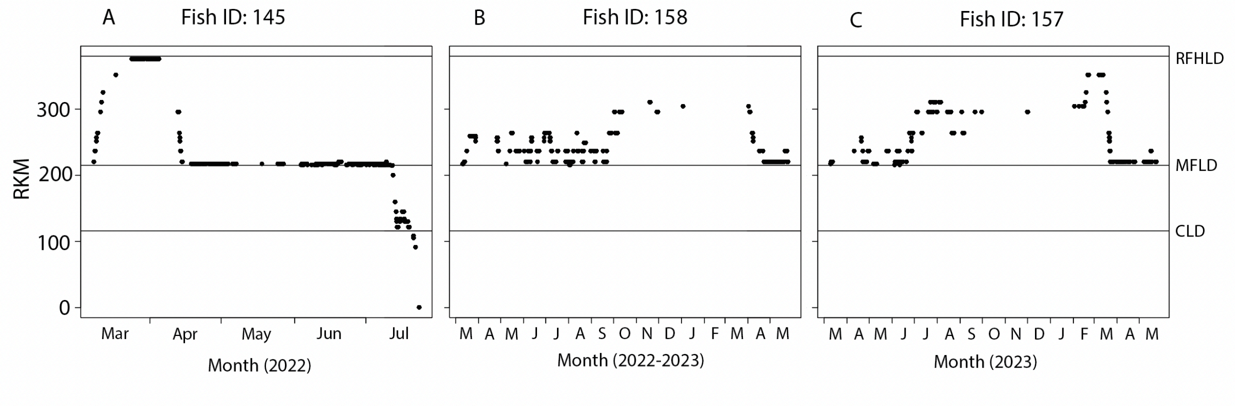


Figure 2.3 Gage height in the Millers Ferry Lock and Dam tailrace (black line) with downstream passage windows at MFLD overlaid in 2022 (top) and 2023 (bottom). Red lines indicate the last time a fish was detected above MFLD, and blue lines indicate the first time it was detected below MFLD. The level at which MFLD reaches flood stage (66 ft) is indicated by the horizontal black line.

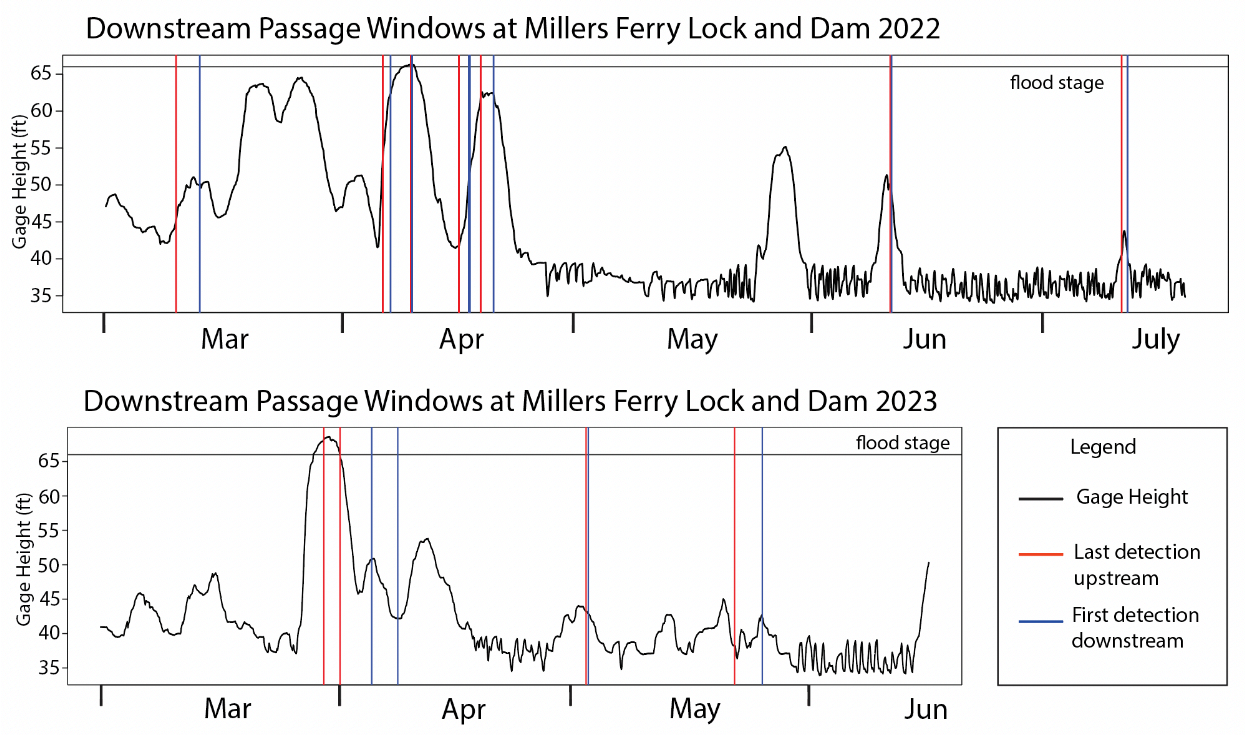
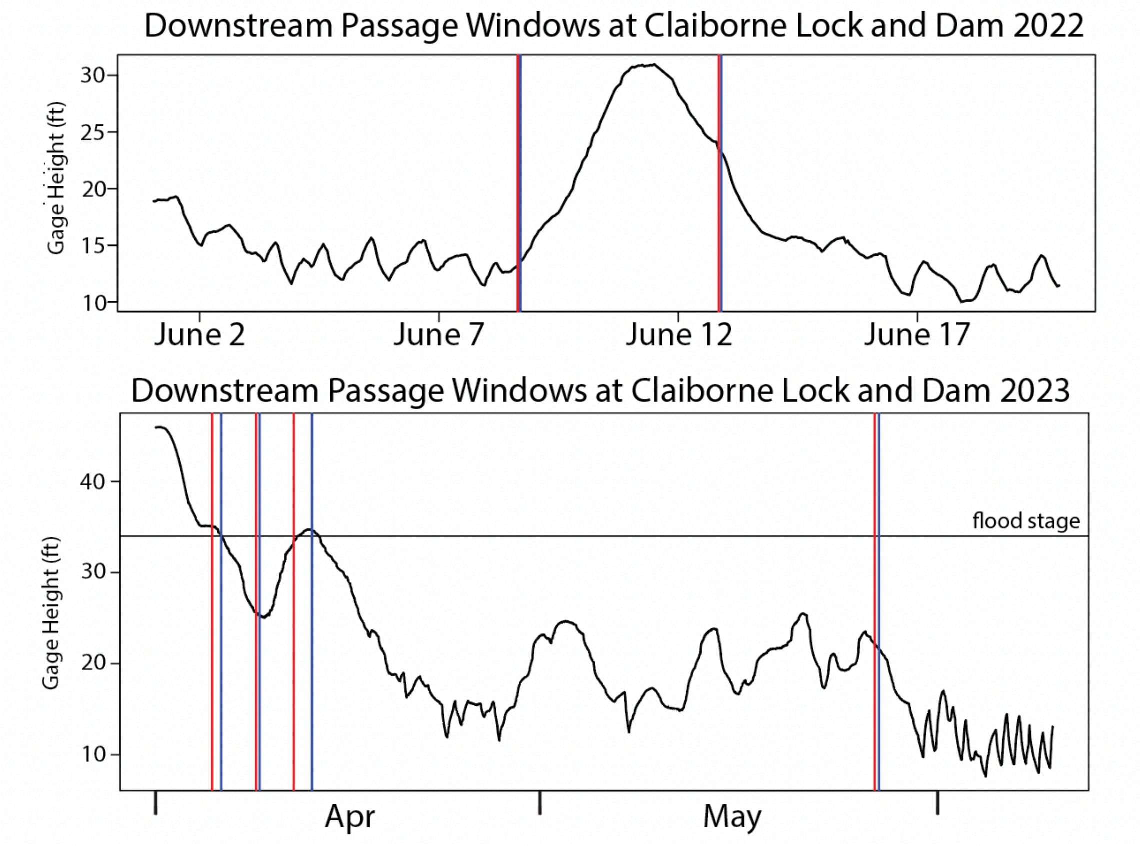


Figure 2.4 Gage height in the Claiborne Lock and Dam tailrace with downstream passage windows at CLD overlaid in 2022 (top) and 2023 (bottom). Red lines indicate the last time a fish was detected above CLD, and blue lines indicate the first time it was detected below. The level at which CLD inundates (flood stage) is indicated with the horizontal line at 34 ft.



Chapter 4: Simulating fish passage impacts on a fragmented metapopulation of Paddlefish

Abstract:

Metapopulation theory is a useful framework to describe the dynamics of fragmented populations of fishes in reservoir chains. The persistence of population segments may be directly related to passage rates across the dams that isolate them. In anticipation of proposed bypass structures at two dams fragmenting the Alabama River, we programmed an individual-based model to simulate the effects of increasing connectivity between population segments of a migratory fish species on the likelihood of segment extirpation within 100 years. We designed six different passage efficiency scenarios to account for uncertainty in the ultimate efficacy of the bypass structures, and to test the effect of increasing segment connectivity on the overall metapopulation. We used the Paddlefish *Polyodon spathula* as our model species and programmed detailed life history information and movement dynamics according to measured quantities. However, several demographic and movement rates for the metapopulation were uncertain or unknown. Therefore, we conducted two experiments to see how a range of values would affect our inference about the influence of increased connectivity. In Experiment 1, we found that juvenile entrainment probability and associated mortality had strong positive impacts on the likelihood of segment extirpation, but that the effects were dampened by increasing connectivity. Similarly, in Experiment 2, we found that increased connectivity dampened the positive effects of increased natural mortality and recruitment variability on segment extirpation. Our model has broad applicability and provides a flexible framework to test a variety of hypotheses about metapopulation dynamics of potamodromous species in fragmented systems globally.

Introduction:

A metapopulation is a group of local populations that are connected to some degree by dispersal (Levins 1969). The resilience and stability of metapopulations depend on dispersal between locally adapted groups. These locally adapted groups provide demographic and genetic resilience against stressors such as environmental change or habitat loss (Hanski 1998). The spatial structure of ecosystems regulates and modifies the metapopulation dynamics of their inhabitants. In dendritic systems like rivers, the complexity of branching, and the levels of connectivity and fragmentation are key components of the resulting spatial structure (Grant et al. 2007; Fagan 2002). In unfragmented rivers, colonization and extinction rates (the two major processes that govern metapopulation dynamics) follow more of a longitudinal gradient with lower colonization and higher extinction probabilities in upstream populations than in downstream populations (Gotelli and Taylor 1999; Bellard and Hugueny 2020). However, some riverine systems are naturally fragmented by natural geographic barriers such as waterfalls or steep rapids that isolate habitat patches and limit dispersal (Dunham and Rieman 1999; Letcher et al. 2007). The patterns of dispersal across these barriers may lead to natural source-sink dynamics due to the asymmetric colonization rates across barriers (Waits et al. 2008; Chiu et al. 2020; Mijangas et al. 2022). If upstream colonization over barriers is impossible, then populations upstream may act as demographic sources, while those downstream act as sinks.

Dams are human-made impediments or barriers that fragment rivers and disrupt aquatic community structure, as well as population and genetic structure of multiple taxa (Neraas and Spruell 2001; Merritt and Wohl 2005; Ardren and Bernall 2017). Furthermore, they can block spawning migrations which are an essential component of the population dynamics of diadromous and potamodromous fishes (Larinier 2001). When populations of migratory fish are fragmented and isolated by dams, the stability of the resultant metapopulation could rely on passage rates at those dams, as well as the availability of suitable spawning habitat upstream and downstream (Jager 2001). When habitat is limited, dams may create source-sink dynamics such that some population segments may rely on production and colonization from other segments via dam passage for demographic stability (Jager 2006).

When upstream passage is blocked, and spawning habitat below dams is not available, the result could be reproductive failure, and local extinction or extirpation. Such is the case for many systems with large high head dams without passage mitigation that block migratory fishes from reaching their spawning grounds upstream (Duponchelle et al. 2021; van Puijenbroek et al. 2019). If upstream passage opportunities are provided, then population stability could be restored (Jager 2016). In another scenario, spawning habitat may still be available downstream of the dam, which could sustain the population despite restricted dispersal to upstream habitat. Such is the case for anadromous Gulf Sturgeon *Acipenser oxyrhinchus desotoi* in the Apalachicola River, FL, which are blocked from most of their historic upstream spawning habitat by Jim Woodruff Dam, although they are still able to spawn in the tailrace and areas downstream (Flowers et al. 2020).

Potamodromous fishes face a complex set of scenarios because populations often exist above and below dams within a river. If isolated populations exist upstream and downstream of a dam at which passage is impossible, and recruitment varies on either side, then the segmented populations may experience different extinction rates (Gao et al. 2022). However, if colonization is possible via dam passage, which is the case in many large rivers with low-head navigational dams (e.g. Simcox et al. 2015, Hershey et al. 2022), then segments containing quality habitat may be able to support segments without quality habitat, thereby stabilizing the population. Population stability in these systems depends on the ability of fish to pass from unsuitable to suitable habitat. Ecological trap theory suggests that organisms may fail to identify suitable habitat, and tend to occupy “sink” patches when natural indicators of habitat quality are disrupted (Ratti and Reese 1988). For example, when suitable habitat is not available upstream of a dam, but fish passage is encouraged by design features like attraction flows (an unnatural indicator of habitat quality), fish that pass the dam could be trapped in unsuitable habitat and the overall population would decline, particularly if downstream passage rates are reduced (Pelicice and Agostinho 2008). In such a case, improved passage efficiency at a dam may not actually fulfill the ultimate management objective of population stability. Conversely, if downstream passage is more probable than upstream passage, the persistence of downstream populations may depend on contributions from upstream source populations (Runstrom et al. 2000; Zigler et al. 2003).

To insure sustainability of unnaturally fragmented populations, managers must consider metapopulation dynamics of migratory species, and carefully analyze the potential impacts of changing dispersal rates across barriers to migration. Individual based metapopulation analysis allows managers to simulate these dynamics, and design mitigation strategies to improve overall metapopulation stability (Jager et al. 2000), and ensure persistence, which is the ultimate goal of native species restoration in fragmented river systems (Gido et al. 2015). Furthermore, understanding the underlying metapopulation dynamics in a system may allow managers to optimize cost-benefit decisions when designing mitigation solutions (Jager et al.

2000). Being able to predict effects of changes in connectivity allows us to better understand which mitigation solutions or combinations of solutions might lead to the most desirable outcomes, and which may fall short of desired outcomes.

In this study, we used the fragmented Paddlefish *Polyodon spathula* metapopulation in the Alabama River as a model to predict and compare the outcomes of proposed mitigation strategies at two of the three major barriers to migration in the system. We incorporated demographic data from each of the four isolated populations (Lower Alabama River, Claiborne Lake, Millers Ferry Reservoir [aka Dannelly Reservoir], and Jones Bluff Reservoir) and simulated dispersal rates under different dam-passage scenarios to characterize any latent dynamics that may moderate the best approach to maintaining or restoring/enhancing metapopulation stability. In each scenario, we calculated the probability of segment extirpation under a wide range of experimental conditions when model parameters were uncertain or unknown. The results of our study will be useful not only for management of the Alabama River system in particular, but more generally for systems facing these challenges globally.

Study System:

The Alabama River is a mid-sized coastal plain river that begins at the confluence of the Coosa and Tallapoosa rivers near Montgomery, AL, and terminates at the confluence with the Tombigbee River 511 km downstream in Southwest Alabama where the Mobile River is formed (Figure 3.1). It is impounded by three low-head, low-use lock-and-dam structures that were constructed in the late 1960s by the U.S. Army Corps of Engineers for hydropower (at the upper two dams), flood control, and navigation. Each structure is unique, as are the reservoirs they impound. The lower-most dam, Claiborne Lock and Dam (CLD: river kilometer 116 measured upstream from the confluence with the Tombigbee River) has six roller gates, a lock, and a 100m long fixed crest spillway that typically inundates annually during high spring flows. Recent studies have shown passage past CLD by some migratory species, so it is considered a partial barrier or impediment to fish passage in comparison to the two upstream dams (Hershey et al. 2022, Laubach 2020). The two upstream dams are considered near-absolute barriers to upstream fish passage, with the only documented passages being incidental through the navigational locks. Millers Ferry Lock and Dam (MFLD: RKM 220), is a fully gated hydropower dam with 17 roller gates, a lock, and a separate hydroelectric powerhouse structure 1km downstream. R.F. Henry Lock and Dam (RFHLD: RKM 380) is also fully gated, with 11 roller gates, a lock, and an attached hydroelectric powerhouse. Claiborne Lake (CL), the reservoir upstream of CLD is a highly channelized run-of-the-river reservoir with limited backwater habitats, and no major tributaries. Below CLD is the Lower Alabama River (LAR) which runs un-impounded for 116 kilometers to the confluence with the Tombigbee River where they both empty into the Mobile-Tensaw Delta. Millers Ferry Reservoir (MFR) and Jones Bluff Reservoir (JBR above R.F. Henry LD) are much more branched systems with hundreds of square kilometers of backwater habitat. The Cahaba River, the longest free-flowing river in Alabama, enters MFR at RKM 304, just downstream of Selma, AL.

Study Population:

Paddlefish of the Mobile Basin are genetically distinct from the Mississippi Basin stocks (which are also native to Alabama in the Tennessee River Basin; Epifanio et al 1996). In comparison, Mobile Basin Paddlefish have a shorter lifespan in general, grow faster, mature earlier, and reach smaller maximum size than those native to the Mississippi Basin. Also, Mobile

Basin Paddlefish typically spawn at warmer temperatures, and perhaps more frequently, although they rely on the same migration cues (spring flood pulses; DeVries et al. 2009) as their Mississippi Basin conspecifics.

Within the Mobile Basin, some spatial variation in population characteristics has been documented, however, it is unclear whether this is due to natural variation or variable management of historic commercial fisheries (Lein and DeVries 1996; Hoxmeier and DeVries 1997). Commercial fishing effort in the Mobile Basin dramatically increased in the 1980s resulting in decreased abundance and size throughout the basin. In 1972, commercial fishing for Paddlefish was closed in Jones Bluff Reservoir, and in 1988, a basin-wide moratorium was imposed (Rider and Powell 2023). In 1994, Lein and DeVries (1996) documented differences in size at age between fish captured in the Tallapoosa/Coosa Rivers (JBR) and the Cahaba River (MFR), which they attributed to differences in recovery time from overharvest. The maximum age documented for each population was 11 and nine, respectively. In 1994-1995, Hoxmeier and DeVries (1997) sampled adult Paddlefish in the LAR, and found a maximum age of 11.

In 2012, an Alabama Department of Conservation and Natural Resources (ADCNR) report published the findings of fisheries independent surveys and deemed that the Alabama River metapopulation could sustain a limited commercial fishing season again (Rider and Powell 2023). An annual commercial season was re-opened in 2013 with three distinct management zones: the upper (RKM 379-333 and 317-267), middle (RKM 131-85.6) and lower (RKM 71-27) Alabama River zones. The upper zone spanned the length of MFR with a gap near Selma to prevent user conflict with bass tournament anglers. The middle zone spanned Claiborne Lake, and the lower zone spanned from CLD downstream to Dixie Landing (RKM 27). No fishing was allowed below RKM 27 or above RKM 379. These management zones were chosen because they allowed for differential monitoring of three population segments isolated by the three dams in the Alabama River. The fishery was suspended again in 2018 following the failure of license holders to comply with ADCNR harvest regulations (Rider and Powell 2023). Since then, the fishery has not been reopened, although it is unclear what the impacts of any overharvest may have been on the population. Based on fisheries independent surveys, it is assumed that each population segment is a self-sustaining reproductive group (Rider, ADCNR, unpublished data). However, it is unknown whether connectivity between the segments plays a role in the overall dynamics of the metapopulation.

Migratory characteristics and population connectivity have been characterized by various studies throughout the four population segments. Lein and DeVries (1996) found that Paddlefish in the JBR segment migrate up the Coosa and Tallapoosa rivers to spawn but are limited upstream by both Walter Bouldin Diversion Dam and Jordan Dam on the Coosa River and by Thurlow Dam on the Tallapoosa River. Juveniles use backwater habitats and deep holes within the reservoir and main channel. Evidence of emigration (Paddlefish leaving their natal river segment by migrating downstream of a dam) is limited to observations of injured Paddlefish in the RFHLD tailrace, which were presumed to have suffered those injuries during entrainment through the dam (Rider, ADCNR, personal communication). In the MFR segment, Paddlefish migrate both up the Cahaba River and up to the RFHLD tailrace to spawn. Similarly, downstream passage at this structure has not been formally documented, but some injured individuals have also been observed in the MFLD tailrace. Fish passage upstream through the RFHLD navigational lock has never been documented, and the frequency of lock operations has substantially declined since dam construction. Juveniles in the MFR segment use backwater habitats in the reservoir and have been observed in the Cahaba River (Rider, ADCNR, unpublished data). Mettee et al. (2005) found that Paddlefish in the CL segment may move between CL and the Lower Alabama River across CLD during periods of inundation, or stay in CL year-round. Mettee observed adults in spawning condition in the MFLD tailrace, and juveniles in backwater areas. Hershey et al. (2022) found that up to 30% of tagged Paddlefish that attempted to pass upstream of CLD during annual spawning season floods did so successfully. Adults in spawning condition have been observed in the CLD tailrace as well.

Movements of Paddlefish in the Mobile Basin are unobstructed between the LAR, Mobile-Tensaw Delta, and the lower Tombigbee River, but population connectivity between them has not been assessed. Adults use both rivers, but it is unknown whether individuals contribute to both populations, or just mix in the Mobile Delta before returning to their natal river. Mettee et al. (2006) observed fish moving between the Mobile Tensaw Delta and Claiborne Lake, passing Claiborne Lock and Dam, and several others that moved between the LAR and the Tombigbee River. O'Keefe et al. (2007) observed Paddlefish spawning in the Ten-Tom waterway which is isolated from the lower Tombigbee River and Mobile-Tensaw Delta by both Demopolis and Coffeeville locks and dams. Connectivity across these structures has not been measured.

Methods:

Model Parameterization and Mechanics:

Although some spatial variation in demographic rates has been documented in the Alabama River (Lein and DeVries 1996, Hoxmeier and Devries 1997), parameter estimates from these studies are likely outdated due to fishery management changes (e.g., moratorium versus an open commercial fishery). In our model, we assume that each population segment has identical growth and maturity schedules, as well as migratory characteristics. The model was broken into two main subroutines, a life history subroutine where each individual ages, grows, matures, potentially spawns, and dies (Figure 3.2A), and a movement subroutine where individuals were allowed to move throughout the system according to certain constraints which we define below (Figure 3.2C). The metapopulation model was constructed and executed using program R V 4.1.1 (R Core Team 2022).

Life history subroutine

Given the female-biased harvest by commercial anglers (Rider and Powell 2023), males were not included in the model, but we assume that all eggs are fertilized. When data were available for estimating life history parameters, we used data only from female fish. All parameters and their sources are given in Table 3.1.

Growth parameters were estimated from 2016 ADCNR survey data (Rider, ADCNR, unpublished data) using maximum likelihood estimation of the von Bertalanffy growth equation:

Equation 1. $$EFL_{t,i} = EFL_{\infty} * \left(1 - e^{\left(-K*(t_i - t_0)\right)}\right) + \varepsilon_i$$

where $EFL_{t,i}$ is the predicted eye-to-fork length of a female Paddlefish *i* at age = *t*, t_i is the age at capture, EFL_∞ is the asymptotic eye-to-fork length, *K* is the growth rate, t_0 is the theoretical eye-to-fork length at age = 0, and ε_i is the normally distributed error around the mean predicted length.

Length-weight relationship parameters were estimated using nonlinear regression of the form:

Equation 2. $$\log(Wt_i) = b_w * \log(EFL_i) + a_w$$

where b_w is the expected increase in log-weight per unit increase in log-eye-to-fork length of an individual, and a_w is the theoretical expected log-weight for an individual of log-eye-to-fork length 0.

Weight-fecundity relationship parameters were also estimated using nonlinear regression of the formula

Equation 3. $$\log(F_i) = b_f * \log(Wt_i) + a_f$$

where b_f is the expected increase in log-number of eggs per log-kg of body weight of an individual and a_f is the theoretical expected log-number of eggs for an individual of log-weight 0.

Length-at-age for each individual in the model was predicted as a random draw from a normal distribution $N(\mu|\sigma)$ where $\mu = EFL_\infty * \left(1 - e^{(-K*(t_i - t_0))}\right)$, and $\sigma = \varepsilon_i$ (estimated in Equation 1). Weight was predicted from length, and fecundity was predicted for mature individuals from weight (Age 8+; Hoxmeier and DeVries 1997).

Two survival parameters were used in the model: natural mortality (M) and entrainment mortality (M_e). Given the recent moratorium on the commercial fishery, we omitted fishing mortality, but the model could easily be adapted in the future to include it. Annual mortality was set at 0.29 (29%) which was estimated with a catch curve fit to 159 individuals aged 6-17 captured in the Alabama River in 2006 (Rider et al. 2011). This was applied to all individuals in the model.

Recruitment was estimated using the Beverton-Holt stock recruit relationship where the expected number of recruits R for a population *p* in a given year *t* is a density-dependent function of the spawning stock (total eggs) $SS_{p,t}$:

Equation 4. $$R_{p,t} = \frac{\alpha}{(1+\beta_p * SS_{p,t})}$$

Where α is the quotient of â (the maximum lifetime reproductive rate) and EPR0 (the expected eggs per recruit under no exploitation)

Equation 5. $$\alpha = \frac{\hat{\alpha}}{EPR0}$$

Equation 6. $$EPR0 = P(spawn) * \sum(F_t * S_t)$$

P(spawn) is the probability that a mature individual will spawn in a given year, F_t is fecundity at age, and S_t is survivorship (proportion of recruits that survive to age = t).

beta_p is the density dependence factor, or how the expected number of recruits changes with increases in spawning stock:

Equation 7. $$\beta_p = \frac{\hat{\alpha}-1}{R0_p * EPR0}$$

We set alpha-hat at 25, which is the average expected recruitment for populations of several species (Goodwin et al. 2006). We set $R0_p$ (the initial population size for population segment *p*) at the effective population size for each segment, which was estimated based on the heterogeneity of genetic samples in Kratina et al. (in press).

Recruitment ($R_{p,t}$) of age-0 individuals to each population segment was estimated at annual time steps based on the total number of eggs contributed by spawning individuals in each respective segment ($SS_{p,t}$), and a coefficient of variation (CV_r) that allowed for annual stochasticity in recruitment, which accounts for natural variability in the system.

Movement subroutine

Movement dynamics differed by life stage based on our best knowledge (Figure 3.2B). Although there is no published data on Paddlefish egg drift speed or duration, it has been suggested that Paddlefish eggs and larvae could drift as far as 100 km downstream of where they were spawned (Thompson 1933, Larimore 1949, Schwinghammer et al. 2019). Wallus (1986) collected Paddlefish larvae (16-19mm TL) in the tailraces of two Cumberland River dams and inferred from their predicted hatch date that they could have originated upstream of the dams. Allen (1911) also collected YOY Paddlefish in a slough 17 miles downstream of the Olmsted Locks and Dam on the Ohio River, although they could have originated from the Mississippi River. Entrainment rates and associated mortality of Paddlefish in the field have not been quantified in any system, although fish with rostrum and bodily injuries uncharacteristic of propeller strikes have been observed in the tailrace of each dam in the Alabama River (personal observation), and at least 50% of Paddlefish captured below Fort Randall Dam, Nebraska, were determined to have originated above it (Pracheil 2010). Given that juvenile (immature) fish have been shown to be more susceptible to entrainment than adults (Harrison et al. 2019), and adult Paddlefish have been shown to survive downstream passage at many dams, we limited our study of entrainment effects to just juveniles, and assumed that individuals age-8 or older were invulnerable to entrainment. Therefore, at the beginning of each time step, new recruits (age-0 individuals) in each reservoir segment and juveniles up to age-7 were subjected to dam entrainment with probability (P_e) and those that were entrained were subjected to entrainment mortality (M_e). Given the lack of data to inform the values of these parameters, we tested the effects of a wide range of values (0.1 -1) for both variables on the model. The probability that a fish survived entrainment (S_e) was given as

Equation 8. $$S_e = P_e * (1 - \mathrm{M}_e) * \mathrm{M}$$

Little is known about the movement patterns of juvenile Paddlefish (Age-1 to 7) in reservoir systems. Most studies agree that movements are limited (Roush et al. 2003), but there has been some evidence that juveniles may follow adults upstream during spawning migrations (Hoxmeier and DeVries 1997). However, this has not been confirmed with telemetry. Therefore, juveniles in the model were only allowed to disperse downstream (Figure 3.2B).

Mature adults (Age 8+) in each segment were annually selected as spawners based on a random binomial draw with probability = 0.45 (spawning once ever 2.2 years on average). Lein and DeVries (1998) found that 4 tagged females in the JBR population segment made spawning movements in two consecutive years, and were gravid in both years, indicating that this population segment may have higher spawning frequency than populations in other parts of the species range. However, given that a relatively small sample of individuals exhibited this behavior, we elected to set the spawning frequency at the higher end of the published range (once every 2-5 years; Meyer 1960, Russell 1986). Once spawners were selected, they then challenged the upstream dam in their segment and passed into the upstream segment with probability (Pup_d) which varied at each dam depending on the expected passage efficiency set in each scenario (Table 3.2). Individuals that failed to pass spawned in their resident river segment, while successful migrants spawned in the next upstream segment. Spawners in the uppermost segment (JBR) always spawned in their own segment because no fish passage is possible beyond it. Spawners could only pass one dam per annual time step, given that upstream passages at multiple dams in a single year are extremely rare (Hershey et al. 2022). Eggs were tallied based on the sum of the fecundity of all spawners in each segment and the recruitment subroutine was carried out for each segment, spawners that passed successfully returned back downstream to their original segment with probability (Preturn) which was set at 0.9. Given that downstream passage by adults through partially or fully opened roller gates has been observed at several dams throughout the range of Paddlefish, and downstream passage survival is usually high (Tripp et al. 2019), we assumed that most fish would be able to return downstream and survive downstream passage regardless of the scenario, and we found that model results were not sensitive to this parameter given that such a small proportion of the total metapopulation makes a dam passage each year.

Scenario Descriptions:

In this system, connectivity is directly limited by dams, but it is unclear how changes in connectivity may impact metapopulation viability in the future. By defining the demographic rates and life history parameters of the metapopulation, we can predict the long term viability of the metapopulation under various connectivity scenarios that mimic proposed structural changes by the USACE to the dams in the system. Although it is unknown what the impacts of each of the proposed alternatives may be until they are tested, we present what we believe are six reasonable scenarios that include best-case fish passage results for proposed mitigation efforts.

In a feasibility study currently underway as a joint effort of the Nature Conservancy and the USACE, a variety of alternative designs and modifications have been considered to improve fish passage at two of the lock-and-dam sites on the Alabama River (USACE 2023). Regardless of the choice, we modeled changes in passage efficiencies based on mitigation/modification at CLD (Scen. 3), MFLD (Scen. 2), or both structures (Scen. 4 & 5), as well as two additional scenarios describing the status quo (no change) and free passage conditions (as would occur in the case of dam removal). Scenarios are described in Table 3.2 and Figure 3.2C. Although passage efficiency can vary annually with hydrology, we elected to explore just a few realistic values which we believe represent conservative estimates. Hershey (2021) found that mean upstream passage efficiency for fishways across the globe, including nature-like rock ramps, was less than 60%. Therefore, we set values at a maximum expected efficiency of 75% which we believe is optimistic. Our general understanding of the Alabama River Paddlefish metapopulation is that it is currently stable. However, very little is known about recruitment in the system, so we applied the same recruitment parameters to each population segment in each scenario.

Experiment 1

As mentioned previously, entrainment probability and entrainment mortality are unknown in the system. Therefore, in Experiment 1, we tested the simulation model with all combinations of sets of values for both variables for each scenario (P_e = [0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0] and M_e = [0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0]). The CV_r was fixed at 0.5 for all scenarios in Experiment 1, and the model was run 50 times for each combination of variables, for every scenario. Each model run executed a 100-year time series of metapopulation dynamics in the reservoir chain. The proportion of 50 model runs that resulted in any of the four population segments reaching less than 10 individuals by the end of the time series was calculated for each combination of parameters in each scenario in each experiment. We define this is as the probability of segment extirpation. All 50 model runs for a given set of experimental conditions were initialized with the same starting metapopulation: the expected number of individuals in each age class given R0 for each population segment and survivorship under the specified annual mortality rate (fixed at 0.29 in Experiment 1, and variable in Experiment 2).

Experiment 2

In Experiment 2, we determine how sensitive metapopulation stability is to changes in the parameter values for annual mortality and recruitment variability. We expected that under lower levels of annual mortality, the population would remain stable, and vice versa for higher levels. However, we did not know how high annual mortality could get before the simulated metapopulation would crash. Therefore, we ran the model under all six scenarios with 10^2 combinations of the following values for M and CV_r: (M = [0.29, 0.315, 0.340, 0.365, 0.390, 0.415, 0.440, 0.465, 0.490, 0.515] and CV_r = [0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0]). For this experiment, we fixed the probability of entrainment at 15%, and entrainment mortality at 50%.

Results:

Metapopulation Dynamics:

Under status quo conditions (Scenario 1; Figure 3.3A, 3.3B) the metapopulation persisted at low levels of entrainment probability (Pe) across all values of entrainment mortality (Me). However, when entrainment probability was increased to 0.5, total extirpation of the metapopulation was predicted within 40 years. Under Scenario 1 (status quo), segment extirpation was most likely in the upstream-most segment (JBR) and declined in likelihood moving to downstream segments (MFR, CL, LAR). Under alternative passage scenarios (4: modifications to both dams, and 5: free passage) populations were sustained albeit at lower levels even under higher rates of entrainment (Figure 3.3). Under mitigated passage conditions, with 75% upstream passage efficiency at CLD and 30% at MFLD (Scenario 4; Figure 3.3C) the persistence of all population segments was possible at intermediate levels of entrainment probability (Pe = 30%) and mortality (Pe = 0.5). Notably, even with increased entrainment probability (Pe = 0.5) the metapopulation was predicted to persist (although at lower levels than under less entrainment) when upstream passage efficiency was 100% at all three dams (Scenario 6; Figure 3.3D).

Experiment 1 (Entrainment Probability and Entrainment Mortality)

At entrainment probabilities greater than 60%, probability of segment extirpation increased to 100% in all scenarios, regardless of entrainment mortality. However, the rate at which segment extirpation became more likely than total segment persistence varied among scenarios (Figure 3.4). Scenarios 1 (status quo) and 3 (29% increase in passage efficiency at

MFLD) resulted in the highest overall probability of segment extirpation (Table 3.3). In Scenarios 2 (45% increase in passage efficiency at CLD), 4 (45% increase in passage efficiency at CLD and 29% increase at MFLD), and 5 (45% increase in passage efficiency at CLD and 74% increase at MFLD), at 30% entrainment probability, increasing levels of entrainment mortality resulted in a proportionately higher probability of segment extirpation. At 40% juvenile entrainment probability, all levels of entrainment mortality resulted in 100% probability segment extirpation, except in Scenario 6, where persistence was possible at lower levels entrainment mortality. A latent property of the system is that as upstream passage efficiency increased, the interaction between entrainment probability and mortality became increasingly evident, with the isopleth (boundary between green and red area; Figure 4) of segment extirpation probability reaching higher levels of entrainment probability.

Experiment 2 (Annual Mortality and Recruitment Variability)

Annual mortality (M) also had a strong positive effect on the probability of population segment extirpation, as expected (Figure 3.5). However, recruitment variability had a weak negative effect, which was unexpected. Segment extirpation occurred in 100% of simulations in all scenarios when adult mortality was greater than 0.44. Results for Scenario 1, *status quo*, suggest that the metapopulation may become destabilized if natural mortality increases from 0.29 to 0.39 at levels of recruitment variability greater than 50%. We predicted that random higher recruitment years would be able to rescue segments from extirpation, but apparently low-recruitment years led to increased probability of extirpation. Increasing passage efficiency at MFLD and CLD slightly decreased the probability of segment extirpation at levels of recruitment variability greater than 50% (Scenario 2), but if upstream passage efficiency was only increased at CLD, leaving MFLD unchanged (Scenario 3), segment extirpation was as likely (if not slightly more) as the status quo. Differences between Scenarios 2, 4 and 5 were slight, suggesting that there may be diminishing returns on upstream passage mitigation (Table 3.3). However, increasing passage efficiency to 100% at all dams (Scenario 6) offset some of the effect of increased mortality, allowing the metapopulation to persist at M = 0.44, which was slightly higher than in the other scenarios.

Discussion:

In this study, we simulated the impacts of increasing upstream fish passage efficiency at dams that are fragmenting a metapopulation of Paddlefish. We tested six different passage efficiency scenarios under a wide range of conditions in two different experiments, which accounted for uncertainty in juvenile entrainment and general demographics in the system. The scenarios were designed to simulate possible outcomes of proposed mitigation efforts in the system. A bypass channel has been proposed for two of the three dams, CLD and MFLD (USACE 2023), but the eventual upstream passage efficiency at either structure is uncertain, so we accounted for no change, small increases at one or both structures, and large increases at one or both structures. Overall, the likelihood of total persistence (i.e. no extirpation of any population segment) was high across many scenarios under some experimental conditions.

As expected, entrainment (even of only juveniles) led to segment extirpation and in some cases total metapopulation collapse in scenarios when the probability of upstream passage did not exceed entrainment probability. The upstream-most population segment had a higher risk of extirpation that those downstream, which is congruent with what Harvey and Railsback (2012) described for a virtual metapopulation of riverine trout. The dynamics of our system very closely resembled what has been shown in other similarly structured models with asymmetric passage, including one with White Sturgeon *Acipenser transmontanus* where downstream transport of juveniles resulted in depleted upstream segments (Jager et al. 2001). A similar model for White Sturgeon showed that mitigating entrainment mortality with turbine screening may have positive impacts on fragmented populations even without upstream passage (Jager 2006).

We expected that net increases in passage efficiency would offset the effects of higher levels of entrainment, but this was not confirmed by our results. Reductions in the predicted likelihood of segment extirpation were not proportional to the total amount of upstream passage provided in the system. Increasing upstream passage efficiency by 29% at the middle dam (MFLD) resulted in a lower proportion of simulation runs with segment extirpation than the status quo, but increasing upstream passage efficiency by 45% at the lowermost dam CLD (Scenario 3) had little to no effect (less than 1% increase in segment extirpation probability; Table 3.3). In contrast, the model by Jager (2006) showed that providing improved upstream passage without mitigating entrainment or providing downstream passage was harmful to the metapopulation as a whole. According to our results, providing *some* passage at more dams is better than providing more passage only at the lowermost dam. But, looking across scenarios, there was an overall negative relationship between increasing passage probability and the overall likelihood of segment extirpation. Furthermore, the results of Scenario 6 suggest that increasing passage probability at upstream dams results in further positive impacts, so we recommend that upstream passage mitigation eventually be considered at RFHLD.

The strong effect of juvenile entrainment on simulated segment extirpation probability was concerning. It has been suggested previously that entrainment can play a large role in metapopulation dynamics (Pracheil 2010), but this has not been quantified in many systems. Although the predicted probability of segment extirpation was only greater than 0% when juvenile entrainment probability was greater than or equal to 30%, a high priority should be assigned to quantifying the actual rates of juvenile entrainment through dams on the Alabama River before these dams are altered and rates may change. Pracheil (2010) found that at least 50% of Paddlefish captured below Fort Randall Dam on the Missouri River, NE, originated above the dam. Furthermore, the age of entrainment was unknown, so adult entrainment (although not accounted for in our model) could also be significant. Paddlefish populations above and below Fort Randall Dam were genetically indistinct (Sloss et al. 2009), suggesting that entrainment is integral to the metapopulation dynamics in that river. Similarly, Kratina et al. (2023) found that population segments in the Alabama River were genetically indistinct. However, construction of the dams on the Alabama River was not complete until the mid 1970s, which may not have been long enough ago for the fragmented populations of this long-lived species to genetically diverge. Better understanding of entrainment is critical for assessing the influence of increased connectivity on metapopulation dynamics.

This is the first time metapopulation theory has been applied to Paddlefish in this system, and we believe that the model presented here is a plausible representation of the current dynamics. However, the data used to parameterize the model may be outdated and incomplete. In Scenario 6, with 100% upstream passage efficiency at all dams, segment extirpation was predicted at higher levels of entrainment mortality, and annual natural mortality than in other scenarios. However, persistence of all segments was still only possible at low levels of entrainment and levels of mortality under 39%. This is likely due to the limitations we imposed on productivity in the system. Recruitment has never been estimated in this system, and we strongly urge managers to quantify spatial variation in productivity between population segments, because this will undoubtedly affect metapopulation dynamics. In some cases, entrainment may actually *benefit* the metapopulation. Because the smallest population segment in our study (JBR) was not programmed to be more productive than any other, it was the most likely to decline to extirpation. In other systems, like the lower Wisconsin River, large concentrations of Paddlefish such as the one above Prairie du Sac Dam may act as source populations for segments downstream if their productivity is sustainably high (Runstrom et al. 2000). More work is needed to determine whether productivity in any of the Alabama River population segments is high enough to affect metapopulation dynamics in this system.

Our oversimplification of recruitment and survival may not be an accurate representation of the true dynamics in the system, and could render moot any specific predictions about the future of the metapopulation. Individual-based models for fragmented populations of other taxa, including platypus (*Ornithorhynchus anatinus*), have been able to make use of highly detailed information on juvenile survival and recruitment for well-informed inference about population viability (Mijangos et al. 2022, Pine et al. 2013). In our case, even at high levels of entrainment probability and natural mortality, we cannot say for sure that segment extirpation is a certainty. We strongly advise that our results not be used to make claims about the absolute population status, but rather about the expected relative benefits of the passage scenarios we have tested. Model results may change with increased information on recruitment, an updated estimate of annual survival, and more information on juvenile movements in the system. Or, model results may be validated in the future if these parameters are quantified.

We recommend that this model be updated and executed again as new data are available. Furthermore, we recommend that this approach be used to model other species with metapopulations fragmented by dams. Ideally, 100% passage across manmade barriers in both directions could be provided to all species that require it; however, that is not likely practical or possible. Unfortunately, lack of knowledge on specific life history parameters and movement dynamics is a pervasive problem for potamodromous species (Thurow 2016), and may hinder efforts to mitigate the impacts of dams on movements of fishes and subsequent effects on metapopulation dynamics. Therefore, it is critical to make mitigation decisions based on proven analytical approaches using the best data and techniques available.

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Table 3.1 Parameters used in the Metapopulation Model

Parameter	Value	Definition	Source
M	0.29 (Exp 1.) Varied (Exp. 2)	Natural Mortality	Rider 2012
Alpha_hat	25	Maximum lifetime reproductive rate	Goodwin et al. 2016
$R0_p$	1960, 1198, 1516, 844	Average unfished recruitment	Kratina 2019
Linf	947.84	Asymptotic length	Estimated (unpublished ADCNR Survey Data)
K	0.172	Growth rate	Estimated (unpublished ADCNR Survey Data)
T0	0.791	Theoretical length at hatching	Estimated (unpublished ADCNR Survey Data)
a_{lw}	-19.63	Slope of log-length/weight relationship	Estimated (unpublished ADCNR Survey Data)
b_{lw}	3.21	Intercept of log-length/weight relationship	Estimated (unpublished ADCNR Survey Data)
a_f	9.81	Slope of log-fecundity/weight relationship	Estimated (unpublished ADCNR Survey Data)
b_f	1.05	Intercept of log-fecundity/weight relationship	Estimated (unpublished ADCNR Survey Data)
CV_r	0.5 (Exp. 1) Varied (Exp. 2)	Coefficient of variation in annual recruitment	NA
P_e	Varied (Exp. 1) 0.1 (Exp. 2)	Entrainment Probability	NA

M_e	Varied (Exp. 1) 0.5 (Exp. 2)	Entrainment Mortality	NA
Preturn	0.9	returning downstream post upstream passage by spawners	Unpublished telemetry data

Table 3.2 Passage efficiency settings at each dam for the six scenarios, in order of increasing connectivity.

Scenario	1 (Status Quo)	2 (Modification to MFLD only)	3 (Modification to CLD only)	4 (Modification at both dams)	5 (Maximum results at both dams)	6 (Free passage)
CLD	0.30	0.30	0.75	0.75	0.75	1
MFLD	0.01	0.30	0.01	0.30	0.75	1
RFHLD	0.01	0.01	0.01	0.01	0.01	1

Table 3.3 Overall probability of local segment extirpation for each scenario across all experimental conditions.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5	Scenario 6
Experiment 1	0.7878	0.7648	0.7924	0.7626	0.7456	0.6512
Experiment 2	0.5528	0.5258	0.5536	0.5214	0.5122	0.3926

Figure 3.1. Map of the Alabama River with dams labeled in red, and boundaries of river segments identified with black lines. The Alabama River begins at the confluence of the Coosa and Tallapoosa Rivers, but the Jones Bluff Reservoir population segment includes fish in the lower portions of those tributaries. The upstream limits are at Jordan Dam (Coosa River) and Thurlow Dam (Tallapoosa River; red stars). The Alabama River ends at the confluence with the Tombigbee River, but fish in this population segment have access to the Mobile Tensaw Delta, and the Tombigee River.

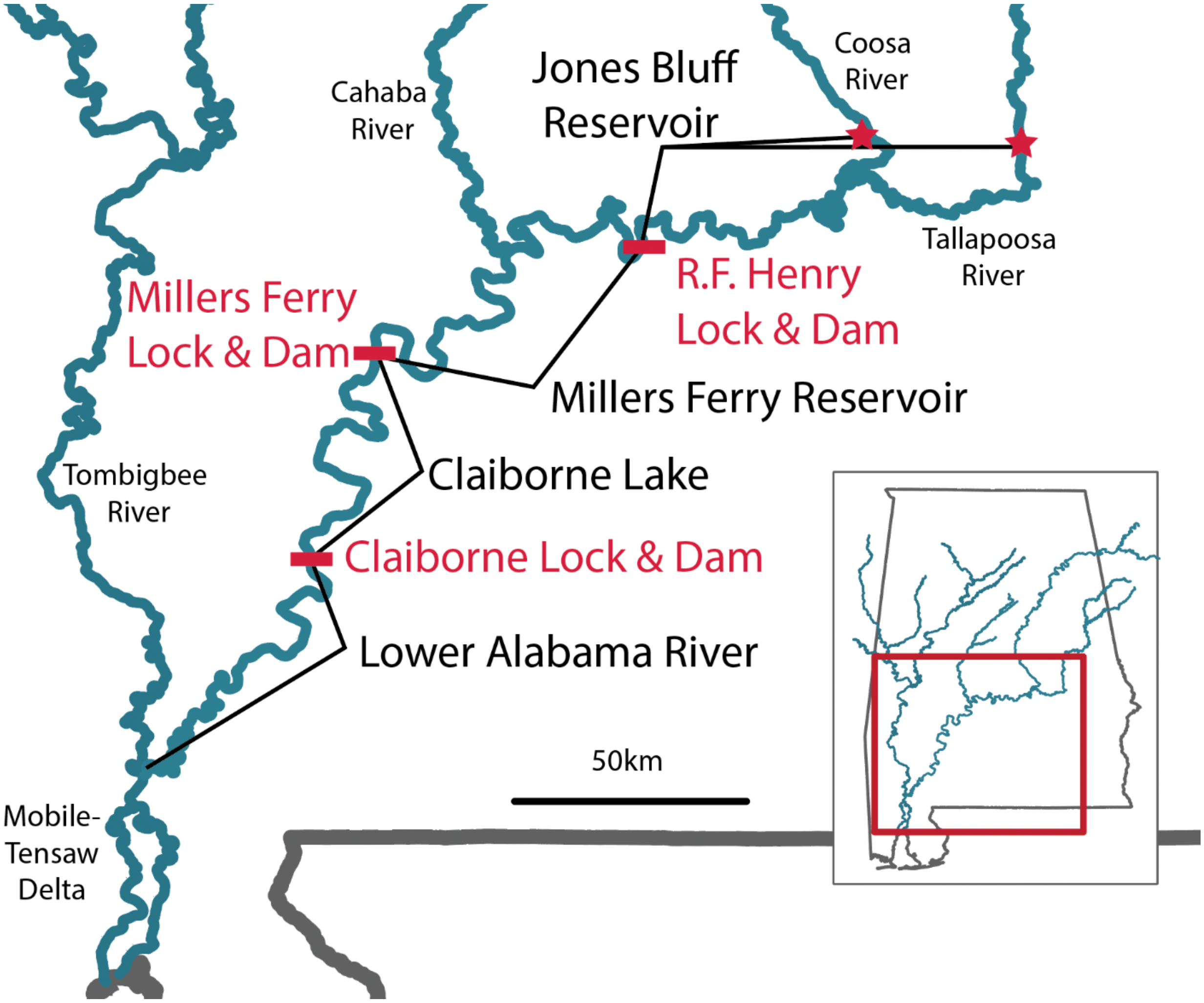


Figure 3.2. A) life history subroutine of individuals in the model, structured by age group. B) Movement subroutine of individuals in the model. Age 8+ are also allowed to return downstream with a fixed probability of 0.9, but the probability of upstream passage at any dam is determined depending on the scenario. C) schematic showing passage rates at each dam for each scenario, with segments color coded by how connected they are to their downstream neighboring segment, except LAR and CL always share the same color because LAR has no downstream neighbor.

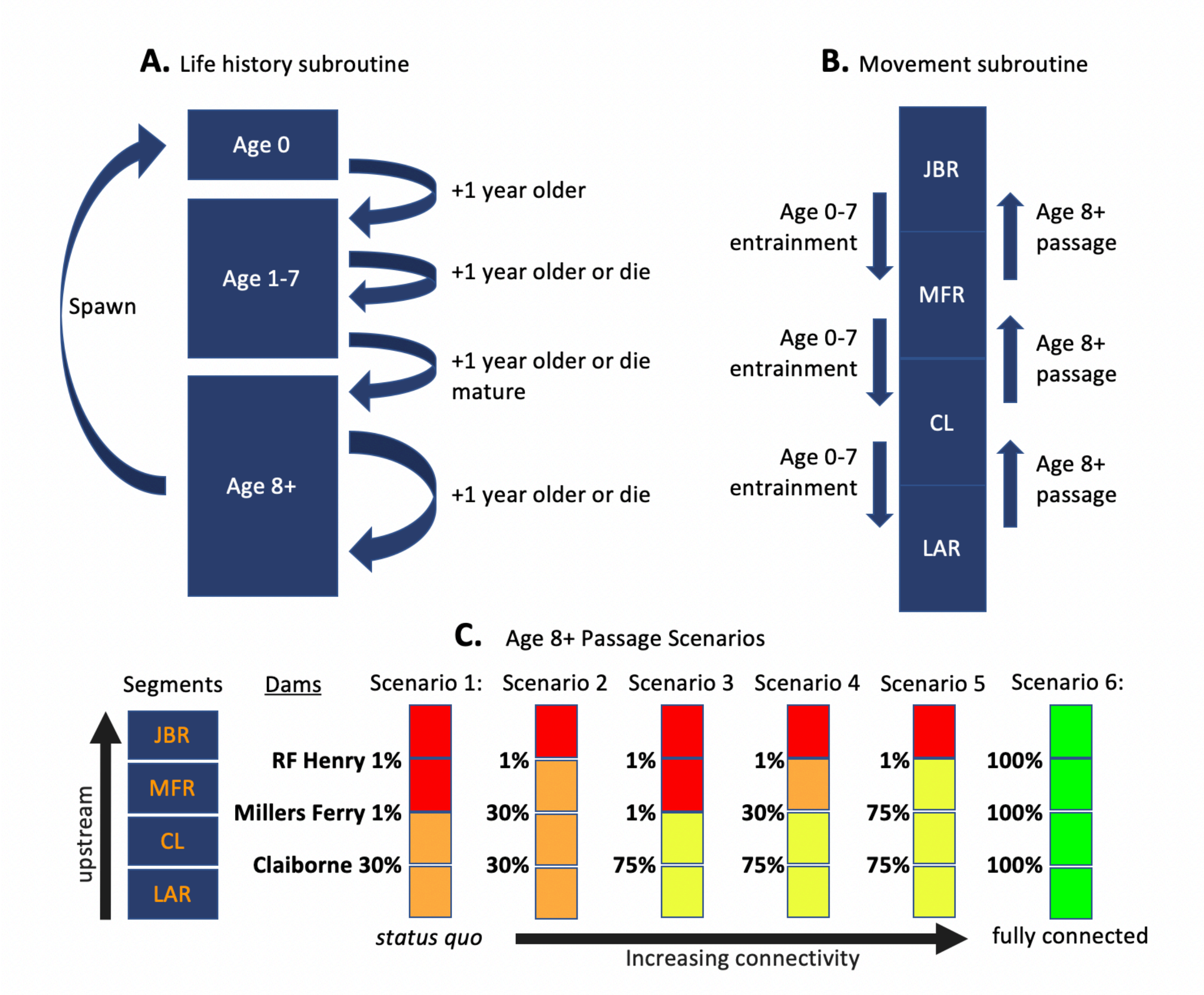


Figure 3.3. Examples of model simulations under various conditions. Entrainment mortality was fixed at 50% for all examples, with annual mortality set to 29% and recruitment variability at 50%. A) Status quo upstream passage conditions (Scenario 1: upstream passage efficiency at Claiborne Lock and Dam set at 30%, 1% at the others) with probability of entrainment set at 10%. B) Status quo upstream passage conditions with probability of entrainment increased to 50%. C) Mitigated upstream passage conditions (Scenario 4: CLD 70%, MFLD 30%, RFHLD 1%) with probability of entrainment set to 30%. D) Free passage conditions (Scenario 6: 100% passage efficiency at all dams) with probability of entrainment set to 50%.

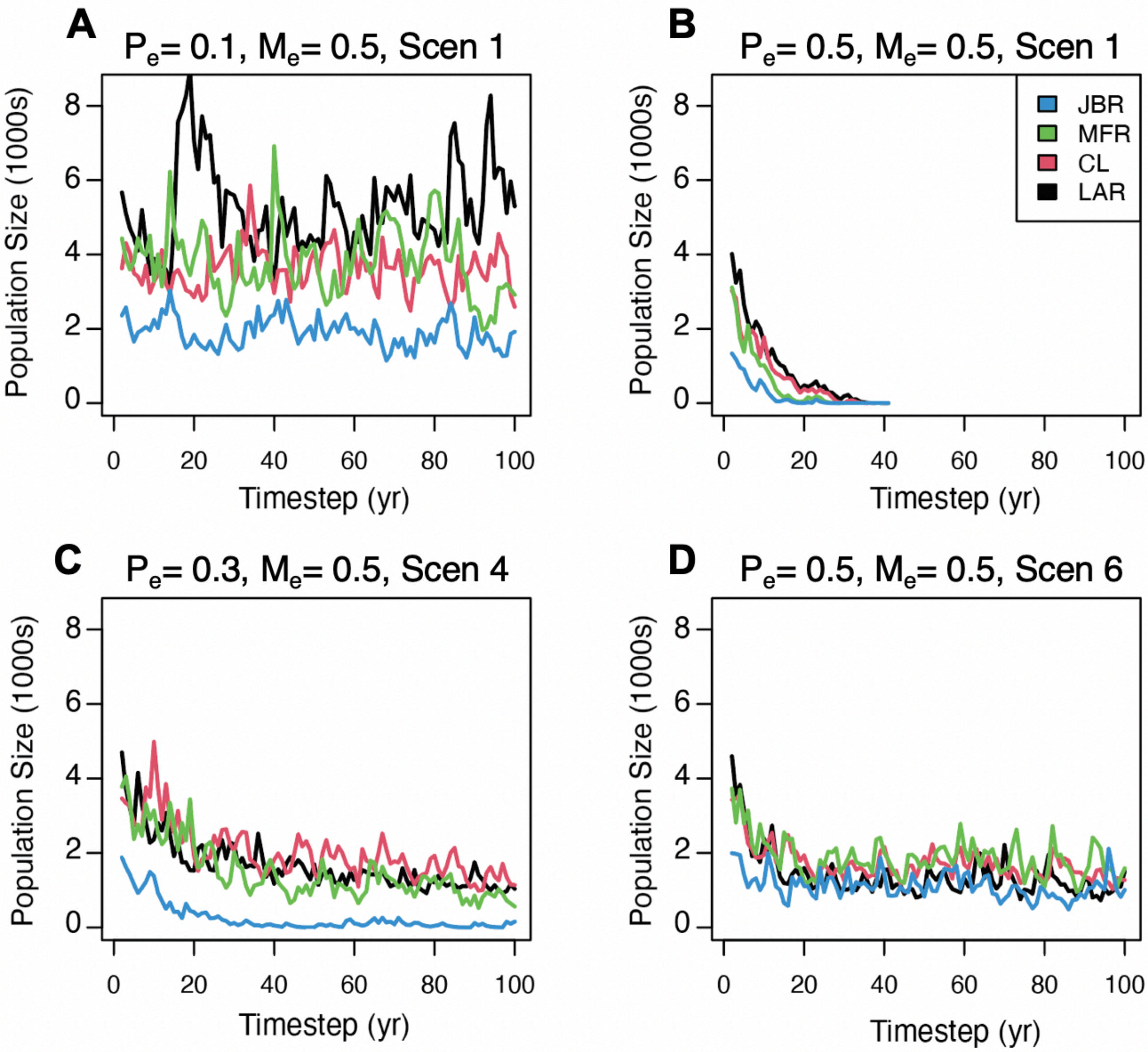


Figure 3.4. Effects of probability of entrainment and entrainment mortality on the probability of segment extirpation across six passage efficiency scenarios, organized left to right, top to bottom. Passage efficiencies for each dam are given in each panel subtitle. CLD = Claiborne Lock and Dam, MFLD = Millers Ferry Lock and Dam, RFHLD = R.F. Henry Lock and Dam. Green = 0% chance of segment extirpation, red = 100% chance of segment extirpation.

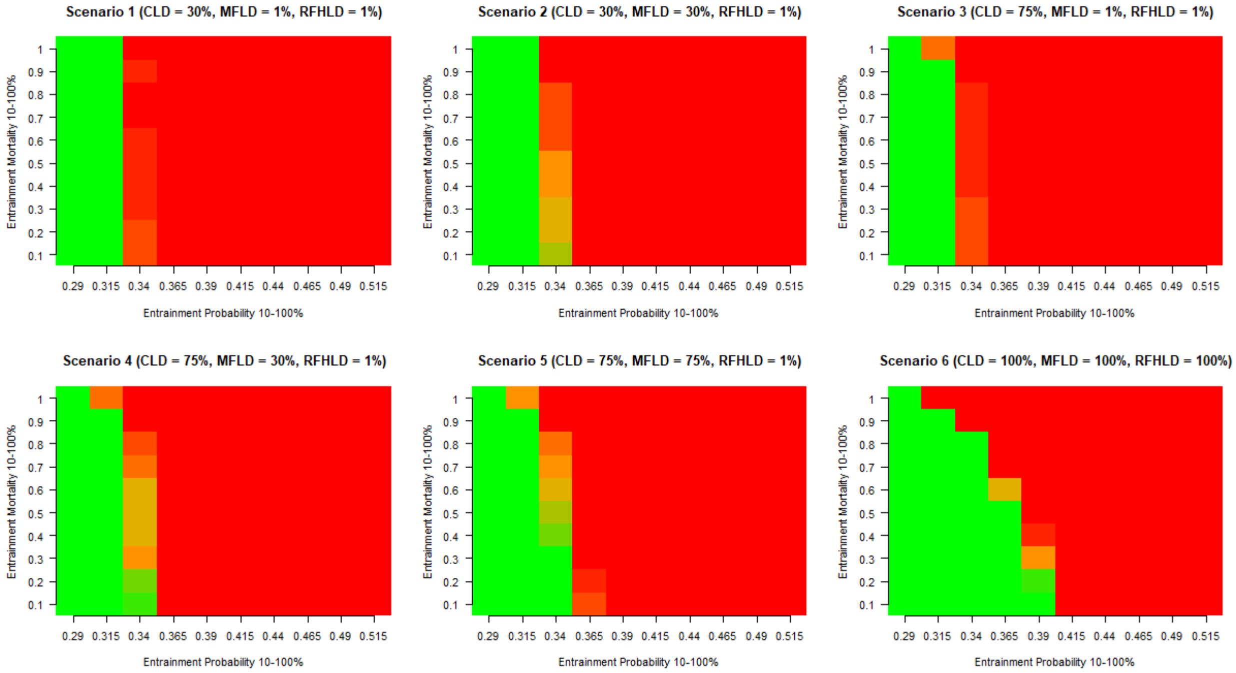
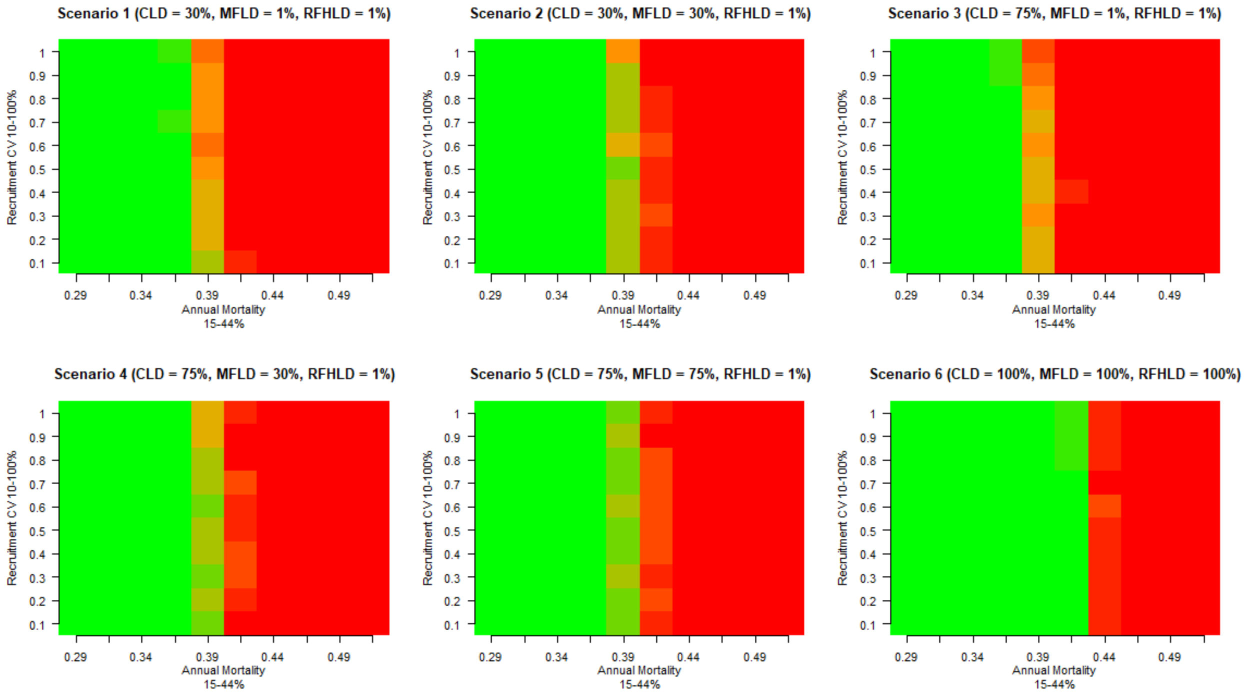
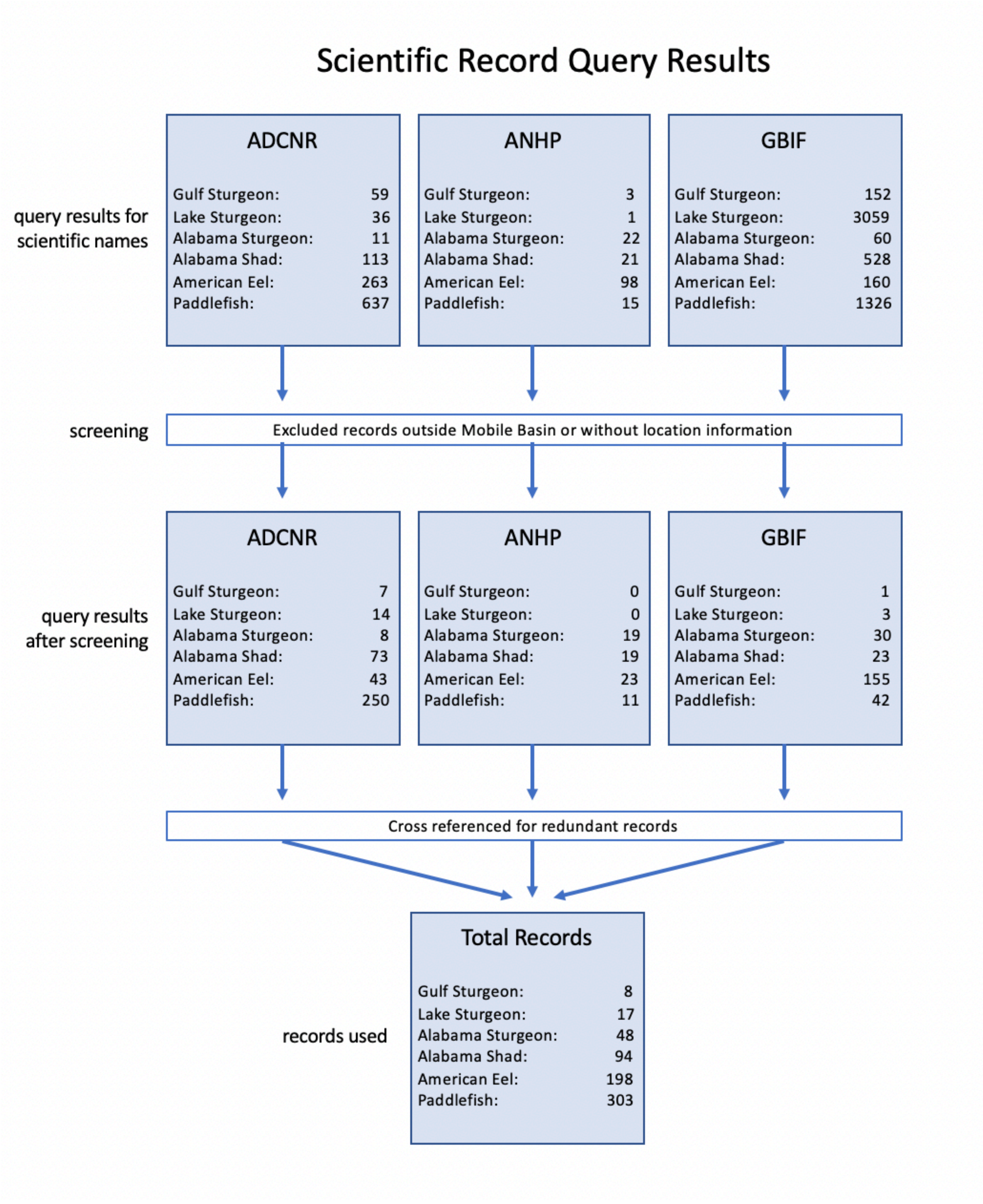


Figure 3.5. Effects of natural annual mortality (M; x axis) and recruitment variability (Rcv; y axis) on the probability of segment extirpation across six passage efficiency scenarios, organized left to right, top to bottom. Passage efficiencies for each dam are given in each panel subtitle. CLD = Claiborne Lock and Dam, MFLD = Millers Ferry Lock and Dam, RFHLD = R.F. Henry Lock and Dam. Green = 0% chance of segment extirpation, red = 100% chance of segment extirpation.



Appendix A


Scientific Record Query Results
query results for scientific names
ADCNR
Gulf Sturgeon: 59
Lake Sturgeon: 36
Alabama Sturgeon: 11
Alabama Shad: 113
American Eel: 263
Paddlefish: 637
ANHP
Gulf Sturgeon: 3
Lake Sturgeon: 1
Alabama Sturgeon: 22
Alabama Shad: 21
American Eel: 98
Paddlefish: 15
GBIF
Gulf Sturgeon: 152
Lake Sturgeon: 3059
Alabama Sturgeon: 60
Alabama Shad: 528
American Eel: 160
Paddlefish: 1326
screening
Excluded records outside Mobile Basin or without location information
query results after screening
ADCNR
Gulf Sturgeon: 7
Lake Sturgeon: 14
Alabama Sturgeon: 8
Alabama Shad: 73
American Eel: 43
Paddlefish: 250
ANHP
Gulf Sturgeon: 0
Lake Sturgeon: 0
Alabama Sturgeon: 19
Alabama Shad: 19
American Eel: 23
Paddlefish: 11
GBIF
Gulf Sturgeon: 1
Lake Sturgeon: 3
Alabama Sturgeon: 30
Alabama Shad: 23
American Eel: 155
Paddlefish: 42
Cross referenced for redundant records
records used
Total Records
Gulf Sturgeon: 8
Lake Sturgeon: 17
Alabama Sturgeon: 48
Alabama Shad: 94
American Eel: 198
Paddlefish: 303

Appendix B

Anecdotal Record Search

Scientific name	Common name used in queries
Alosa alabamae	"shad", "Alabama shad", "white shad"
Acipenser oxyrhinchus desotoi	"sturgeon", "gulf sturgeon"
Acipenser fulvescens	"sturgeon", "lake sturgeon"
Scaphirhynchus suttkusi	"sturgeon", "Alabama sturgeon", "shovelnose sturgeon", "hackleback"
Anguilla rostrata	"eel", "American eel"
Paddlefish	"spoonbill cat(fish)", "spoonbill", "paddlefish", "shovelhead cat(fish)"

Query terms for Newspapers.com

Common Name	**AND**	"caught"	**FILTER**	Location = "Alabama"
Common Name	**AND**	"Tombigbee" OR "Coosa" OR "Etowah" OR "Oostanaula"	**FILTER**	Location = "Mississippi", "Georgia", "Alabama"

If a record was missing location information, supplementary information was sought in other databases

List of databases used for supplementary information

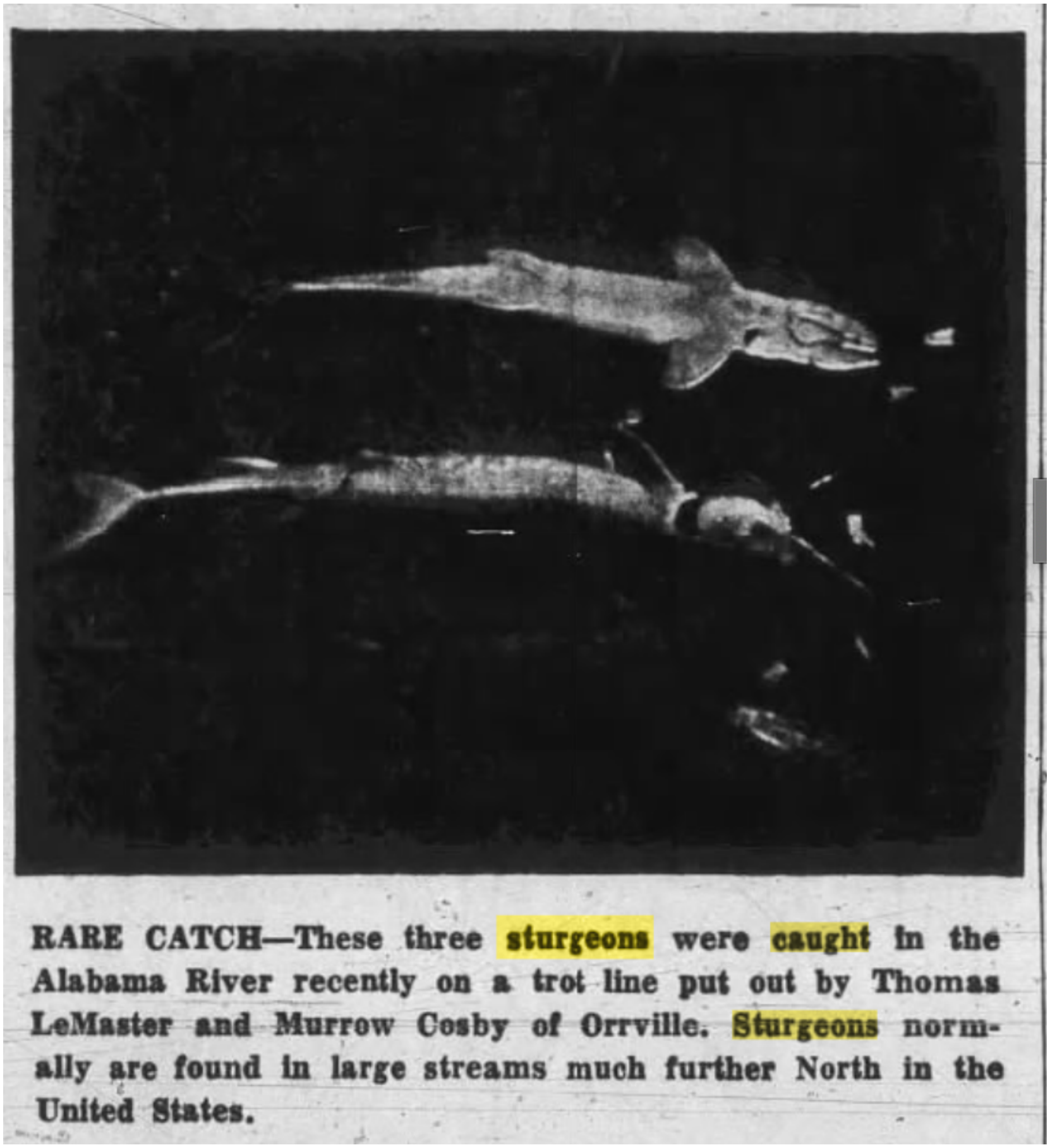
Library of Congress
www.loc.gov
Alabama Department of Archives and History Digital Collection
digital.archives.alabama.gov/digital/
W.S. Hoole Special Collection University of Alabama Libraries
www.lib.ua.edu/libraries/hoole/
Auburn University Library Special Collections & Archives
www.lib.auburn.edu/specialcollections/

Screening Criteria

1. Must mention capture or sighting of the target species
2. Must have been captured or seen within the Mobile River Basin **OR**
3. Published in a newspaper from the Mobile River Basin (e.g., "a sturgeon was captured near here" – Montgomery Advertiser).

Species	Search terms	Search filter	Total hits	Records screened	Records used
Sturgeon	"sturgeon" AND "caught"	Location: Alabama	2726	2604	120
	"sturgeon" AND "Tombigbee"	Location: Mississippi	172	170	2
	"sturgeon" AND "Etowah"	Location: Georgia	128	125	3
	"sturgeon" AND "Oostanaula"	Location: Georgia	17	15	2
	"sturgeon AND "Coosa"	Location: Georgia	120	118	2
American eel	"eel" AND "caught"	Location: Alabama	22350	22283	67
	"eel" AND "caught" AND "Tombigbee"	Location: Mississippi	89	89	0
	"eel" AND "caught" AND "Coosa"	Location: Georgia	308	308	0
	"eel" AND "caught" AND "Etowah"	Location: Georgia	291	291	0
	"eel" AND "caught" AND "Oostanaula"	Location: Georgia	34	34	0
Paddlefish	"paddlefish"	Location: Alabama	136	136	0
	"spoonbill" AND "caught"	Location: Alabama	843	792	51
	"shovelnose"	Location: Alabama	107	107	0
	"shovelhead"	Location: Alabama	108	108	0
	"spoonbill" AND "Tombigbee"	Location: Mississippi	24	24	0
Alosa spp.	"shad" AND "caught"	Location: Alabama	9,679	9610	69
	"shad" AND "caught" AND "Tombigbee"	Location: Mississippi	288	288	0
	"shad" AND "caught" AND "Etowah"	Location: Georgia	506	506	0
	"shad" AND "caught" AND "Oostanaula"	Location: Georgia	29	29	0
	"shad" AND "caught" AND "Coosa"	Location: Georgia	436	436	0

Appendix C
Photographs of sturgeon from archived newspapers, and of the Great Falls of the Tallapoosa in Tallassee Alabama.



RARE CATCH—These three sturgeons were caught in the Alabama River recently on a trot line put out by Thomas LeMaster and Murrow Cosby of Orrville. Sturgeons normally are found in large streams much further North in the United States.

Alabama Sturgeon July 3 1966 Selma Times

CAVIAR PLANT. John Malone holds a sturgeon that Nolan Lowery, porter at the Alabama Power Co., office, caught in the Alabama River last week-end. The sturgeon is a salt-water fish, but they come into fresh water to spawn. The back of this fish looked almost like a turtle shell. The mouth is just a round hole in what would be the lower lip if the mouth were split like other fish. Very weird looking specimen and the first we've seen.

Alabama Sturgeon May 28 1959 Greenville Advocate

SOME CATCH — J. L. Fortune of 2800 Wilmer Ave., a commercial fisherman, caught this 40-pound sturgeon in a net at Lock Four. The fish is just one of such giants he has taken in the past few years.

Lake Sturgeon April 21 1963 Anniston Star

Killingsworth, Head And Their Monster

Gulf Sturgeon November 29 1958 Alabama Journal

RARE CATCH—Danny Chance, 11, caught this four-pound sturgeon while fishing with his dad in the Cahaba River Saturday. He made the catch by himself with a pole and red worms.

(Photo by Gene Wood)

Prehistoric Fish Taken From Cahaba

Danny Chance, who lives at 159 Grove Lane, had to go to an encyclopedia to identify the fish he caught Saturday.

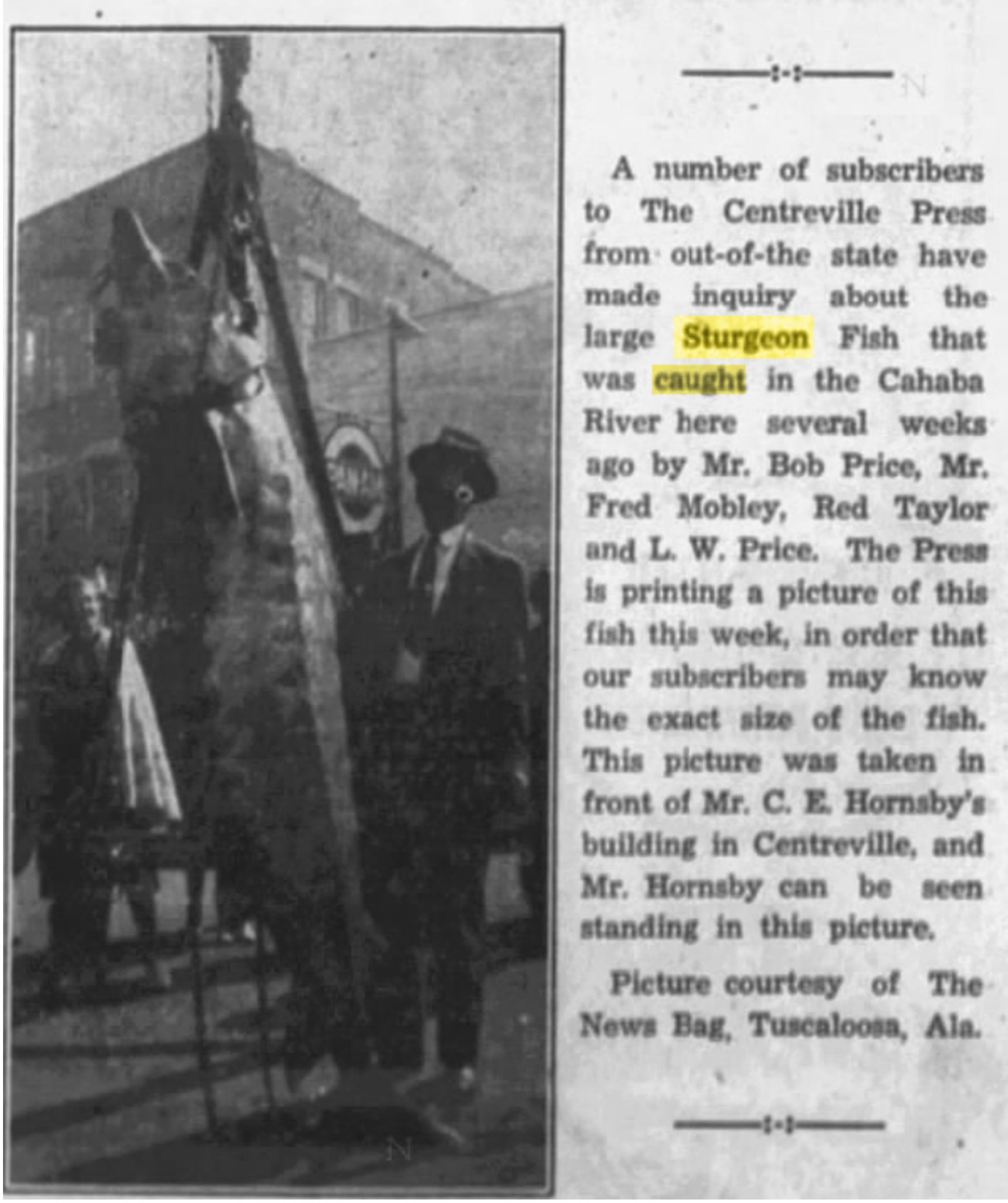
Quite by accident, the eleven-year-old fisherman pulled a four pound sturgeon out of the Cahaba while he and his father, Roland Chance, were fishing on the river Saturday.

Danny said he was fishing with a pole and English redworms and was pulling up his line to check on the bait when he felt it get heavy. After a tussle he landed the strange looking fish by himself. He had accidentally hooked the sturgeon in its gills.

The sharp-nosed sturgeon, an ugly, horny species, looks as much like a reptile as a fish. They grow very big, a few weighing 100 pounds or more having been caught in this area.

The geneology of the sharp-nosed sturgeon can be traced back to the very ancient Ganoid stock, which was prominent in the Paleozoic Age.

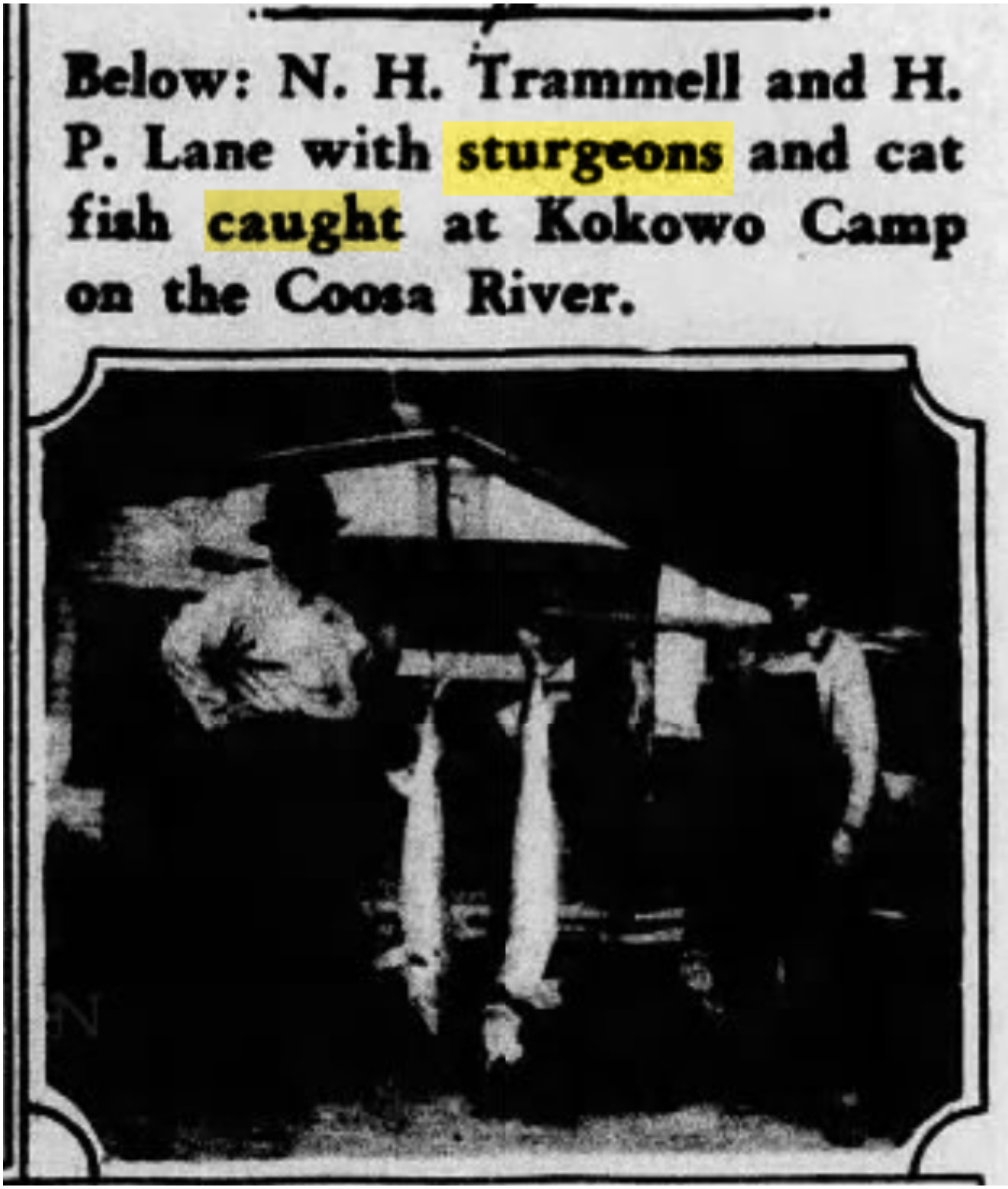
Alabama Sturgeon September 27 1956 Selma Times



A number of subscribers to The Centreville Press from out-of-the state have made inquiry about the large Sturgeon Fish that was caught in the Cahaba River here several weeks ago by Mr. Bob Price, Mr. Fred Mobley, Red Taylor and L. W. Price. The Press is printing a picture of this fish this week, in order that our subscribers may know the exact size of the fish. This picture was taken in front of Mr. C. E. Hornsby's building in Centreville, and Mr. Hornsby can be seen standing in this picture.

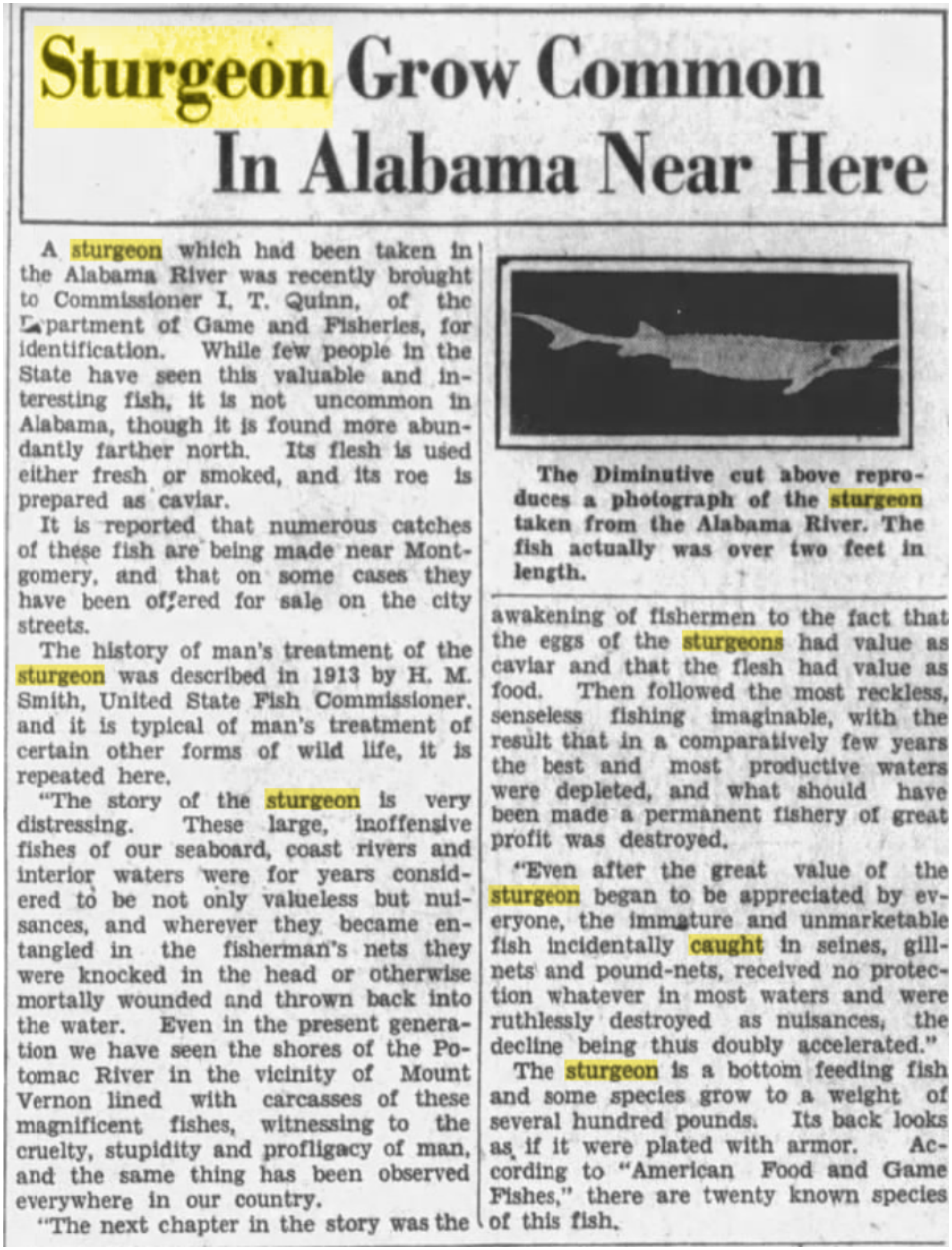
Picture courtesy of The News Bag, Tuscaloosa, Ala.

Gulf Sturgeon June 26 1941 Centreville Press



Below: N. H. Trammell and H. P. Lane with sturgeons and cat fish caught at Kokowo Camp on the Coosa River.

Lake Sturgeon, Lay Lake May 31 1931 Birmingham News



Sturgeon Grow Common In Alabama Near Here

A sturgeon which had been taken in the Alabama River was recently brought to Commissioner I. T. Quinn, of the Department of Game and Fisheries, for identification. While few people in the State have seen this valuable and interesting fish, it is not uncommon in Alabama, though it is found more abundantly farther north. Its flesh is used either fresh or smoked, and its roe is prepared as caviar.

It is reported that numerous catches of these fish are being made near Montgomery, and that on some cases they have been offered for sale on the city streets.

The history of man's treatment of the sturgeon was described in 1913 by H. M. Smith, United State Fish Commissioner. and it is typical of man's treatment of certain other forms of wild life, it is repeated here.

"The story of the sturgeon is very distressing. These large, inoffensive fishes of our seaboard, coast rivers and interior waters were for years considered to be not only valueless but nuisances, and wherever they became entangled in the fisherman's nets they were knocked in the head or otherwise mortally wounded and thrown back into the water. Even in the present generation we have seen the shores of the Potomac River in the vicinity of Mount Vernon lined with carcasses of these magnificent fishes, witnessing to the cruelty, stupidity and profligacy of man, and the same thing has been observed everywhere in our country.

"The next chapter in the story was the awakening of fishermen to the fact that the eggs of the sturgeons had value as caviar and that the flesh had value as food. Then followed the most reckless, senseless fishing imaginable, with the result that in a comparatively few years the best and most productive waters were depleted, and what should have been made a permanent fishery of great profit was destroyed.

"Even after the great value of the sturgeon began to be appreciated by everyone, the immature and unmarketable fish incidentally caught in seines, gill-nets and pound-nets, received no protection whatever in most waters and were ruthlessly destroyed as nuisances, the decline being thus doubly accelerated."

The sturgeon is a bottom feeding fish and some species grow to a weight of several hundred pounds. Its back looks as if it were plated with armor. According to "American Food and Game Fishes," there are twenty known species of this fish.

The Diminutive cut above reproduces a photograph of the sturgeon taken from the Alabama River. The fish actually was over two feet in length.

Alabama Sturgeon March 20 1930 Montgomery Advertiser

W. B. RAMSEY AND EEL
. . . Caught Recently In Coosa

W. B. Ramsey of Pell City Rt. 1 displays a 25-inch eel which he caught last week at Lock Four. The eel, which Ramsey caught while pole fishing, is believed to be the first caught in the local area in more than 25 years. Ramsey said the eel "put up an awful fight, and when it started wiggling in, I thought I had hooked a snake." The eel has become a rare species of fish in this area.

June 14 1963 St. Clair News-Aegis

Left: Rebecca Alan Martenn, 1305 Chestnut Street, Gadsden, Ala., daughter of Mr. and Mrs. Frank Martenn. She caught the eel herself.

March 30 1924 Birmingham News

The Great Falls of the Tallapoosa at the Tallassee Manufacturing Co. Dam ca. ~1900 Images Courtesy of the Alabama Power Company Archives.