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Spawning Site Selection and Potential Implications of Modified Flow Regimes on Viability of Gulf Sturgeon Populations

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Abstract.—Rapid human population growth and an associated increase in consumptive water demands within the ecologically diverse Apalachicola–Chattahoochee–Flint (ACF) River basin of the southeastern United States have led to a series of highly publicized water wars, exacerbated by recent drought conditions, between the states of Alabama, Georgia, and Florida. A key issue is how managing riverine flows to meet human water needs will affect the viability of species that are federally listed as threatened or endangered, including the Gulf of Mexico sturgeon Acipenser oxyrinchus desotoi. Our present understanding of Gulf sturgeon ecology within the Apalachicola River basin indicates that altered riverine flow regimes may affect spawning success and possibly the recruitment patterns of the population. Through intensive field work, we documented Gulf sturgeon spawning site selection in the Apalachicola River and then evaluated the relationship between river stage and the available spawning habitat at these sites. We then used an age-structured simulation model to assess the effects of changes in recruitment patterns on population viability using hypothetical scenarios based on changes in flow regime and its effect on available spawning habitat. Over 3 years we were able to collect almost 500 Gulf sturgeon eggs in the Apalachicola River at three different spawning sites. We observed that the depths and flows where eggs were found were similar across years and sites despite varying river conditions. River discharges of less than 142 m³/s at Jim Woodruff Lock and Dam significantly reduced the spawning habitat available to Gulf sturgeon at all known spawning sites.

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potentially affecting recruitment. Gulf sturgeon populations are probably sensitive to changes in recruitment, and if extreme low-flow events occur with increasing frequency owing to water management policy choices or climatic events, population recovery could be impaired and the risk of extirpation could increase. Managers should consider the potential effects on Gulf sturgeon recruitment when determining future flow regime policies within the ACF.

The human population within the Apalachicola–Chattahoochee–Flint (ACF) River basin of the southeastern United States is one of the most rapidly growing regions of the United States with an increase in population from about 1.5 million people in 1950 to over 5 million in 2008 with most of this growth (57%) occurring just in the last 20 years (U.S. Bureau of the Census 2008). This population growth, particularly in the metropolitan Atlanta region of Georgia, has led to ongoing water allocation disputes among the basin states of Alabama, Florida, and Georgia, resulting in numerous lawsuits and federal mediation between states. These ongoing water wars are among the longest running and most highly publicized water disputes in the eastern United States (Barnett 2007). While these disputes are similar to more widely known U.S. water wars such as those in the Colorado River basin, water wars in the eastern United States differ because of higher human population density and absence of historic legal precedence establishing interstate water policy (e.g., Colorado River “Law of the River” [Ruhl 2003]). Proposed management actions in the ACF basin to meet emerging water needs, including changes in reservoir operation schedules or construction of new water supply reservoirs, could alter flow regimes within the Apalachicola River, possibly affecting a variety of terrestrial and freshwater, estuarine, and marine resources. Of particular concerns to aquatic resource managers are effects on commercial fisheries for the Eastern oyster *Crassostrea virginica* and four species listed under the U.S. Endangered Species Act including the Gulf of Mexico sturgeon *Acipenser oxyrinchus desotoi*, or Gulf sturgeon, through loss of spawning habitat or in situ changes in spawning or rearing conditions such as flows or temperature.

Gulf sturgeon is an anadromous species historically found throughout much of the northern Gulf of Mexico. Gulf sturgeon use freshwater habitats in coastal rivers during much of the year, and overwinter in the Gulf of Mexico (Huff 1975; Wooley and Crateau 1984; Fox et al. 2000). Gulf sturgeon populations have declined from historical levels throughout their native range, possibly owing to overfishing, loss of spawning habitat, alteration of riverine rearing or resting habitat, or a combination of these and other factors (Clugston et al. 1995; Zehfuss et al. 1999). This species was classified as threatened under the U.S. Endangered Species Act (ESA) in 1991 because of concern by a variety of state and federal management agencies over declines in stock abundance and potential threats to population viability (U.S. Office of the Federal Register 1991). Despite reductions in total mortality owing to the elimination of targeted fisheries for Gulf sturgeon in the mid- and late-1980s, sturgeon populations have not rebounded as managers had hoped and the viability of most extant populations is unknown (USFWS and Gulf States Marine Fisheries Commission 1995).

Federal agencies currently recognize seven Gulf sturgeon populations including the Apalachicola River stock (USFWS and National Marine Fisheries Service 2003) This stock has been reduced in abundance to a few hundred individuals (Zehfuss et al. 1999), probably through a combination of harvest and human alterations to critical habitats in the Apalachicola River and elsewhere during the last 100 years. The Apalachicola River Gulf sturgeon stock was heavily fished by commercial fishers during the late 19th and first half of the 20th century (Huff 1975). Peak recorded Apalachicola River Gulf sturgeon harvest occurred in 1900 with a catch of 38,300 kg, after which catch declined steadily to around 900–1,500 kg annually from 1920 until the fishery’s closure in 1984 (Huff 1975).

Throughout their native range, loss of access to spawning habitat owing to changes in riverine flow or channel modifications is considered a likely impediment to Gulf sturgeon population recovery (USFWS and Gulf States Marine Fisheries Commission 1995). Several studies of this species have focused on the location and timing of spawning and characteristics of spawning habitats in the Suwannee (Marchant and Shutters 1996; Sulak and Clugston 1998), Choctawhatchee (Fox et al. 2000), Pascagoula (Ross et al. 2004), and Yellow and Escambia rivers (Craft et al. 2001). These authors have generally characterized spawning habitat to be located in portions of coastal rivers with associated limestone outcroppings, gravel, or other hard-bottom habitats (Sulak and Clugston 1998; Fox et al. 2000). Completion of the Jim Woodruff Lock and Dam (JWLD) complex on the upper Apalachicola River in 1957 blocked fish passage and removed access to approximately 78% of historical Gulf sturgeon riverine habitat (USFWS and Gulf States Marine Fisheries Commission 1995) within the Apa-
lachicola–Chattahoochee–Flint River basin (ACF). Several potential spawning sites have been identified in the upper portion of the Apalachicola River, all within 40 km downstream from the JWLD (USACE 2004). Additionally, the effects of altered river flows of the Apalachicola River owing to multiple dam facilities in the basin are not known.

Anthropogenic modification of flow patterns may significantly affect Gulf sturgeon behavior, growth, and survival, as observed with other sturgeons (Khoroshko 1972; Auer 1996). Kynard and Parker (2004) demonstrated experimentally that larval and juvenile Gulf sturgeon exhibit unique in-river migration, dispersal, and feeding patterns that may be adaptations to living in rivers. Water velocity and flow regime influence sturgeon spawning by stimulating adult fish to move to spawning grounds, structuring and modifying substrate to create suitable areas for egg attachment, and providing adequate oxygenation for egg survival (Auer 1996; Fox et al. 2000). Based on our present understanding of sturgeon ecology, it is possible that altered riverine flow regimes may affect spawning success and possibly recruitment patterns of the population (Sulak and Randall 2007). Changes in recruitment could have deleterious effects on adult abundance, population growth, and ultimately the recovery and delisting of Gulf sturgeon.

The objectives of this study were to identify and characterize Gulf sturgeon spawning habitats and evaluate how alterations in Gulf sturgeon recruitment patterns could affect population viability and prolong recovery of this threatened species, despite previous management actions to reduce total mortality. Our study is motivated by recent drought conditions and associated riverine flow management plans that in combination potentially increase frequency, duration, and magnitude of low-flow conditions within the Apalachicola River. We addressed the first objective by conducting an intensive field sampling program to document spawning sites and characterize abiotic conditions that distinguish these sites. For our second objective we built a simulation model to assess how reductions in recruitment would potentially affect the viability of the Apalachicola River Gulf sturgeon stock. Because Gulf sturgeon select specific spawning habitat and conditions (Fox et al. 2000), we surmised that the alteration or dewatering of these habitats, such as extreme low-flow events related to drought or dam operations, during spring spawning events could lead to drastic reductions in recruitment. Using our model, we evaluated the effect of these potential periodic dewatering events during the spring-spawning season and associated year-class failure on population structure and viability using six recruitment variability scenarios. We tested a range of hypothetical recruitment scenarios motivated by a series of extreme low-flow events observed during severe basin-wide drought in 2006–2008, which resulted in spawning site dewatering. Our intent is that these flow conditions represent a worst-case scenario within the Apalachicola River and that these results serve as an aid in water policy development within the Apalachicola River basin.

**Methods**

**Egg sampling.—** Standard Gulf sturgeon egg sampling techniques were used to identify active spawning sites from a list of nine potential spawning sites, defined as areas with suitable hard-bottom substrates, identified by habitat surveys conducted by U.S. Fish and Wildlife Service (USFWS) and U.S. Army Corps of Engineers (USACE) personnel in the Apalachicola River during 2003 and 2004 (USACE 2004). Egg samplers were patterned after Marchant and Shutters (1996) and Fox et al. (2000) and consisted of circular floor-buffing pads (50.8 cm diameter) anchored to the river bottom with welded rebar. Because Gulf sturgeon eggs sink quickly and adhere to substrates immediately after spawning, sites where eggs were collected were assumed to be spawning sites (Fox et al. 2000). We deployed egg samplers at a subset of the potential spawning locations (based on relocations of telemetered adult Gulf sturgeon and anecdotal information based on local reports) during the spring in 2005, 2006, and 2008 (Figure 1). Timing of sampler deployment each year was based on the entry of telemetry-tagged adult Gulf sturgeon (from a related study) into freshwater portions of the river. Egg samplers were checked every 48–72 h for Gulf sturgeon eggs. The number of egg samplers deployed at a given site ranged from 2 to 67 depending on the size of the sampling site and the number of egg samplers available at that time. We concluded egg sampling after water temperatures reached 25°C, the upper thermal limit of egg survival (Chapman and Carr 1995), and when telemetered individuals exhibited no further movement characteristic of spawning (Fox et al. 2000).

As egg samplers were checked at spawning sites the location of the each sampler (degrees and decimal minutes) and depth (m) were recorded. If a Gulf sturgeon egg was collected on an sampler, water temperature (°C) at the surface was recorded using a YSI 556 MPS meter (YSI, Inc., Yellow Springs, Ohio), and water velocity (m/s) was recorded at approximately 60% of the depth using a Marsh–McBirney Flo-Mate 2000 flowmeter (Hach/Marsh–McBirney, Frederick, Maryland). General flow velocities were taken at random locations within each potential spawning area.
regardless of whether eggs were found at that site. Daily discharge and river stage were obtained from U.S. Geological Survey gauge 02358000, located immediately below JWLD at river kilometer (rkm) 170. Dam discharge rates, river stage, date, depth, substrate, temperature, and egg sampler flow velocities were used to examine the interactions between physical river characteristics and locations where Gulf sturgeon eggs were collected on samplers within a given site. Substrate characteristics at each site had been previously described by the USACE (2004) spawning site surveys.

Population model.—The effects of recruitment failure on Gulf sturgeon population viability were assessed using an age-structured model built using Microsoft Excel software (Microsoft Corporation, Redmond, Washington). The model was the same as that used in Flowers (2008). Our population consisted of three tables, each an individual page within an Excel spreadsheet (Figure 2). The first table featured attribute-at-age information on a per-recruit basis for

![Figure 1](image_url)
wild born individuals, while the second table contained attribute-at-age information for hatchery-stocked individuals; the third is derived from the first two tables and simulates the actual population by adding numbers of individuals at age per year. Population numbers at age in any given year were calculated using the function

\[ N_{a+1,t+1} = (N_{a,t})S_a, \]

where \( a \) is age, \( t \) is time, and \( S_a \) is age-specific survival. Other parameters included in the model and used in assessing population responses to management actions include natural mortality (\( M \)), fishing mortality (\( F \)), fecundity (\( f \)), vulnerability at age (\( v \)), initial population size (\( N_0 \)), and skip-spawning effects (\( S_k \)). A list of all variables and the values used in this study is provided in Table 1.

**Length and weight at age.**—The length-at-age relationship for Gulf sturgeon was used to directly or indirectly define other model parameters such as weight at age, sampling vulnerability, mortality, and fecundity. The relationship was described using available Apalachicola River direct fin-ray aging information (L. Jenkins, USFWS, unpublished data) and incremental growth data observed through a USFWS tag-recapture program (from 1978 to 2007) in a single-likelihood framework described by C. Walters (University of British Columbia, personal communication) and T. Essington (University of Washington, personal communication). This method combined age data with incremental growth data and provided an increased sample size over a greater range of sampled lengths, which is important because larger size-classes were under-represented in the direct aging data. Using incremental growth data from the existing Gulf sturgeon tagging study to estimate growth has the advantages of not requiring direct age estimates of individuals, important in a case such as this for Gulf sturgeon where lethal aging methods (otoliths) are impracticable and alternative aging tissues (fin rays) are inaccurate (Rien and Beamesderfer 1994; Rossiter et al. 1995). The output from this method was then reparameterized into a simplified von Bertalanffy growth curve (Ricker 1975), recommended by Johnson...
et al. (2005) for sturgeon species, as follows:

\[ L_a = L_\infty (1 - e^{-ka}) \]

where \( L_\infty \) is the asymptotic length parameter, \( k \) is the Brody growth parameter, and \( L_a \) is length at age. This simplified formulation assumes that the variable \( t_0 \) (age at length zero) is zero and eliminates problems arising from limited size-structure representation in the data set (few very young or old individuals) that could lead to biologically unrealistic estimates of \( t_0 \) (Johnson et al. 2005). Weight at age \( (W_a) \) was calculated using the traditional formulation

\[ W_a = aL^b, \]

where \( a \) and \( b \) are species specific constants. In this case \( a = 1.23 \times 10^{-6} \) and \( b = 3.3 \). This \( W_a \) information was used to estimate fecundity at age. A single length and weight growth model was used for both sexes because of a lack of published support for sexually dimorphic growth for Atlantic sturgeon (Johnson et al. 2005).

**Mortality.** Estimates of \( M \), representing the average annual rates at which individuals exit the population by death, are commonly acquired from tagging studies (such as Sulak and Clugston 1999 for Gulf sturgeon) or calculated from population dynamics aspects such as longevity (Hewitt and Hoenig 2005) or individual growth rate. Jensen (1996) proposed using the von Bertalanffy \( k \) parameter to estimate overall \( M \), where \( 1.5k = M \). However, we used alternative method where:

\[ M = k, \]

(C. Walters, University of British Columbia, personal communication). Evidence for this relationship was found in a 2008 review of fish species on Fishbase (www.fishbase.org) where estimates of both \( M \) and \( k \) were available. Correlation analysis between these two parameters found a 1:1 relationship such that \( M = k \) were proxies. Annual \( M \) was variable at age and dependent on overall length, simulated here by Lorenzen’s (2000) method to predict age-specific mortality as follows:

\[ M_a = M_{max} \times \frac{L_{\infty}}{L_a} \]

where \( M_a \) is mortality at age and \( M_{max} \) is mortality at maximum age. The term \( M_{max} \) was solved for as the value that yields an overall \( M = k \) averaged across all ages. Because Gulf sturgeon are protected from harvest, \( F \) was set to 0 and natural mortality represented most of total mortality \( (Z) \).

Maximum (or terminal) age is a key parameter in age-structured population models often used in determining mortality rates, total reproductive output, and, as in our model, population growth rate. Pine et al. (2001) used a maximum age of 25 for the Suwannee River population, but it is probably a conservative estimate as Scott and Crossman (1973) estimated a maximum age of 60 for the Atlantic sturgeon \( A. oxyrinchus \) subspecies. We used a maximum age of 50 for all simulations based on estimates of longevity, in turn based on natural mortality, following methods by Hewitt and Hoenig (2005) and multiple recaptures of adult Gulf sturgeon that had been at liberty for more than 10 years and were at least 20 years old at tagging.

**Fecundity.** Fecundity is the mean egg production for individual female Gulf sturgeon, which increases with fish weight after the age of maturity (Walters and Martell 2004) and is approximated by

\[ f_a = W_a - W_{mai}, \]

where \( f_a \) is fecundity at age, \( W_a \) is weight at age, and \( W_{mai} \) is weight at maturity.
$W_{ma}$ is the weight at the initial age of maturity. Within the model, fecundity determines the potential number of recruits that an individual can produce. Gulf sturgeon, like other sturgeons, are highly fecund and produce large numbers of eggs at spawning (Huff 1975; Chapman et al. 1993). However, Gulf sturgeon mortality from age 0 and age 1 is extremely high and estimated between 99.9% and 100.0% (Pine et al. 2001), meaning large numbers of eggs may not result in large numbers of age-1 recruits.

**Skip-spawning.**—An important aspect of Gulf sturgeon life history is skip-spawning, where individuals may not spawn every year. In any given year the spawning population is less than the total population (Sulak and Clugston 1998), but how much less depends on the periodicity of the skip-spawning events (Jorgensen et al. 2005). Female Gulf sturgeon mature between ages 8 and 12 (Huff 1975) and probably spawn at intervals ranging from every 3–5 years (Smith 1985; Fox et al. 2000). Because of skip-spawning and the late age at maturity, female Gulf sturgeon may only spawn a few times during their life (Sulak and Randall 2002). This relationship between skip-spawning and fecundity level is not unique to sturgeon and has been documented in other species as a life history adaptation based on energy availability and allocation (Jorgensen et al. 2005; Rideout et al. 2005). We incorporated female skip-spawning in the recruitment and fecundity aspects of the model using a modified Ricker curve, where

$$ P(\text{Sp}) = \left[ (a - Ma_i) \times \left( e \times \frac{1}{Ma_i} \times \frac{1}{Ma_h - Ma_i} \right) \right] \\
\times \exp \left( -\frac{1}{Ma_h - Ma_i} \times a - Ma_i \right) \\
+ \left( \frac{1}{SK} \right)^{(La/La_i)},$$

with $P(\text{Sp})$ as the probability of an individual spawning in a given year, $Ma_i$ the initial maturation age, $Ma$ the number of years needed for entire population to mature, $Ma_h$ the age of 50% of population maturation, and $SK$ the average skip-spawn interval (in years) of fully mature individuals. Male Gulf sturgeon exhibit similar skip-spawning behavior to females, albeit on shorter 1–5-year intervals (Smith 1985); however, males are excluded from this skip-spawning simulation because it is generally assumed that there are enough males available in any given year to spawn with females.

**Recruitment.**—Population recruitment in the model was simulated using yearly estimates of population egg production controlled by a density-dependent recruitment relationship. A Beverton–Holt recruitment relationship (Beverton and Holt 1957) was used in this study and in Pine et al. (2001), although there are little data available on the actual spawner–recruit relationship exhibited by Gulf sturgeon populations. The stock–recruit relationship followed the form

$$ R = \frac{ae}{1 - be^c},$$

where $R$ is annual recruits to age 1, $a$ and $b$ are stock–recruitment parameters, and $e$ represents annual population egg production.

**Initial population size and recruitment compensation.**—Two model parameters, the Goodyear compensation ratio ($recK$; Goodyear 1977, 1980) and the initial population size before fishing ($N_0$), are population-specific input parameters used to initiate simulation runs. The Goodyear compensation ratio is defined as the ratio of juvenile survival rate at low stock sizes relative to juvenile survival in the unexploited condition, which represents the recruitment compensation potential of the population and was used to describe the population-recruitment response to depletion. Higher $recK$ values imply populations are more resilient to exploitation than populations with low $recK$ values because they have a stronger compensatory response when depleted (Walters and Martell 2004). We estimated $recK$ to have a value of 4, following the approach in Martell et al. (2008) that used the management parameters of maximum sustained yield (MSY) and the exploitation rate needed to achieve this yield ($F_{MSY}$) (Flowers 2008). Our $recK$ value was similar to the value used by Walters et al. (2006) for white sturgeon $A. transmontanus$. Estimates of $N_0$ were developed using data from the historic Apalachicola Gulf sturgeon fishery. These unexploited abundance estimates were useful guidelines for initializing the model; however, precise estimates were not required for model operation or predictions. Development of $recK$ and $N_0$ parameter estimates and sensitivity analysis are discussed further in Flowers (2008).

**Model development and initiation.**—To assess our model structure and input parameters, we initiated our model by simulating 25 years of fishing at rates that reduced the population to published abundances estimated at the end of the commercial fishery (about 282 individuals >450 mm in size; Wooley and Crateau 1985). The actual commercial fishery lasted almost 90 years (from about 1897 to 1985), but the heaviest period of fishing lasted for about 25 years from 1900 to 1925 followed by sustainable but light fishing until 1985. To mimic the pattern of the actual fishery, we chose to simulate an intense fishery followed by a decline in exploitation to create a realistic population...
structure (based on observational reports from the fishery; Flowers 2008) from which to begin the simulations (initial year 1985). We then ran the population model forward 100 years from this baseline to assess input parameters by examining transient dynamics to ensure that the population did not collapse or increase at biologically unreasonable rates (Pine et al. 2001).

From this baseline we evaluated six recruitment scenarios developed to assess effects of potential periodic dewatering events during spring spawning season and associated year-class failure on population structure and viability of the Apalachicola Gulf sturgeon population (Table 2). Our objective was not to simulate exact recruitment patterns for the Apalachicola Gulf sturgeon population, but to evaluate population responses from recruitment scenarios that may occur as a result of proposed water management actions. Although our model is deterministic, we believe that simulating a variety of scenarios will provide an informative range of population responses to proposed management actions. We then compared the results between the baseline and each hypothetical recruitment scenario to assess the effect of each scenario treatment on population recovery.

### Results

#### Egg Sampling

Eggs were collected on four dates between 27 April and 13 May 2005, 12 dates between 5 April and 1 May 2006, and 16 dates between 4 April and 14 May 2008 (Table 3). A total of 20 Gulf sturgeon eggs and one larva were collected at a single site in 2005, 189 fertilized Gulf sturgeon eggs were collected on egg samplers at two sites during 2006, and 282 eggs were collected at three sites in 2008 (Table 3). In all three years, over 82% of the eggs and larvae collected came from a single site consisting of a large limestone outcrop (rkm 170.6, N = 405; Table 3). This site is near JWLD and is considered the primary spawning site for Gulf sturgeon within the Apalachicola River (Wooley et al. 1982). Because of proximity to the dam, this site is vulnerable to dewatering during extreme low-flow events owing to the elevation of the hard-bottom habitats and narrow incised river channel lacking floodplain storage to buffer discharge changes. Gulf sturgeon eggs were also collected at a second hard-bottom site at rkm 160.1 and a third site at rkm 161.4 (2008 only, Table 3; Figure 1). Physical characteristics for all egg-collection sites are provided in Table 4. Gulf sturgeon movement toward spawning sites and anom-

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Description</th>
<th>Recruitment pattern</th>
<th>Year interval</th>
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<tbody>
<tr>
<td>1</td>
<td>Unmodified simulated population recruitment used as a baseline</td>
<td>Steady</td>
<td>Continuous</td>
</tr>
<tr>
<td>2</td>
<td>Recruitment fixed at zero to check for time to population extinction</td>
<td>None</td>
<td>Continuous</td>
</tr>
<tr>
<td>3</td>
<td>Recruitment zero once every x years</td>
<td>Periodic complete failure</td>
<td>2, 4, 8</td>
</tr>
<tr>
<td>4</td>
<td>Recruitment halved once every x years</td>
<td>Periodic partial failure</td>
<td>2, 4, 8</td>
</tr>
<tr>
<td>5</td>
<td>Recruitment doubled once every x years</td>
<td>Periodic boom</td>
<td>2, 4, 8</td>
</tr>
<tr>
<td>6</td>
<td>Recruitment doubled for 1 year and zero in the remaining x years of the cycle</td>
<td>Boom–failure cycle</td>
<td>2, 4, 8</td>
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<thead>
<tr>
<th>Table 2.—Scenarios used to simulate the effects of flow regime modifications on Gulf sturgeon population recovery.</th>
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<tbody>
<tr>
<td>Scenario</td>
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<tr>
<th>Table 3.—Sampling locations, sampling dates, and numbers and percentages of eggs collected in each year of Gulf sturgeon egg sampling in the Apalachicola River.</th>
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<tbody>
<tr>
<td>Site and year</td>
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<tr>
<td>----------------</td>
</tr>
<tr>
<td>Rkm 170.6</td>
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<td></td>
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<td>Rkm 160.1</td>
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<tr>
<td>Rkm 161.4</td>
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<td></td>
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<tr>
<td>Grand total</td>
</tr>
</tbody>
</table>
alous swim patterns indicative of spawning (Fox et al. 2000) were not observed nor were eggs collected until water temperatures at the spawning sites approached 20°C. No spawning was observed following water temperature increases beyond the 25°C lethal limit for eggs (Chapman and Carr 1995).

Gulf sturgeon eggs were collected over substrates dominated by hard limestone bedrock or consolidated clay with small amounts of finer substrates such as gravel, pebble, and sand. These substrate types were similar to those observed by Sulak and Clugston (1998) on the Suwannee River. A few egg samplers were placed in mid-channel locations with sandy substrates and higher flow velocities; however, no eggs were collected in these areas possibly due to decreases in gear efficiency because of the higher water velocity. Egg samplers placed in relatively shallow, low-flow areas also did not capture eggs and the samplers themselves were often observed to be covered in silt.

The three sites where eggs were collected (rkm 170.6, rkm 161.4, and rkm 160.1, Figure 1) featured shallow to moderately deep (2–6 m) hard-bottom areas with slow to moderately fast (0.14–1.15 m/s), relatively nonturbulent flow over the surface. These sites were also located along generally straight or slightly curving sections of the river. Egg-sampling took place at other potential spawning sites in 2005 and 2006, but no Gulf sturgeon eggs were collected at these sites. Also during this study, none of the telemetered individual Gulf sturgeon in the river demonstrated behaviors that indicated spawning took place at sites other than those monitored. Full physical descriptions of each identified and proposed spawning site are included in USACE (2004).

**Population Modeling**

**Scenarios 1 and 2: constant and zero recruitment.**—Our baseline model (scenario 1) demonstrates that given Gulf sturgeon life history characteristics such as late sexual maturity, skip spawning, and low recruitment compensation rate, Gulf sturgeon populations are slow to rebuild following intensive fishing. Using constant annual recruitment, this scenario predicted that after a 100-year recovery period following 25 years of intensive fishing, Gulf sturgeon populations would have only reached approximately 80% of the prefishing population level (Figure 3). Scenario 2 represents the most extreme recruitment pattern where recruitment was zero after the end of fishing, and this scenario predicts population extinction within 25 years after fishing.

**Scenario 3.**—Scenario 3 represented different spawning intervals that could occur within the Apalachicola River and other Gulf sturgeon stocks. The overall pattern from these scenarios is that periodic total recruitment failures will cause an increase in recovery time, with more frequent failures having a greater effect on time until recovery. Complete recruitment failure in 2-, 4-, and 8-year intervals produced populations at 2, 38, and 58% of historic levels, respectively (Figure 3). Simulations with complete recruitment failure every 2 years resulted in a population that was predicted to remain stable through time.

**Scenario 4.**—Similar to the complete recruitment failure on regular intervals, partial recruitment failures lead to large increases in recovery time over constant recruitment scenarios. A partial recruitment failure could result if some spawning sites were more affected by low-flow conditions than other sites. As expected, the effects on population recovery are roughly half the strength of the complete failure treatments. Partial recruitment failure in 2-, 4-, and 8-year intervals (scenario 3) produced populations at 28, 57, and 68% of historic levels, respectively (Figure 4).

**Scenario 5.**—This scenario was designed to mimic the proposed “boom” year-classes of high recruitment on regular intervals (Sulak and Randall 2002). These periodic large recruitment events decrease the simulat-

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### Table 4. Physical characteristics of spawning sites during Gulf sturgeon egg collection in the Apalachicola River.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Rkm 170.6</th>
<th>Rkm 161.4</th>
<th>Rkm 160.1</th>
<th>All sites, 2008</th>
<th>Rkm 170.6</th>
<th>Rkm 161.4</th>
<th>Rkm 160.1</th>
<th>All sites, 2008</th>
<th>Rkm 170.6</th>
<th>Rkm 161.4</th>
<th>Rkm 160.1</th>
<th>All sites, 2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (m)</td>
<td>Mean 3.5</td>
<td>3.9</td>
<td>3.4</td>
<td>3.8</td>
<td>3.3</td>
<td>2.5</td>
<td>3.3</td>
<td>3.2</td>
<td>3.6</td>
<td>2.9</td>
<td>3.5</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td>SD ± 0.9</td>
<td>± 1.1</td>
<td>± 0.9</td>
<td>± 1.2</td>
<td>± 0.9</td>
<td>± 1.0</td>
<td>± 1.2</td>
<td>± 1.2</td>
<td>± 0.9</td>
<td>± 1.0</td>
<td>± 0.9</td>
<td>± 1.2</td>
</tr>
<tr>
<td></td>
<td>Median 3.5</td>
<td>3.6</td>
<td>3.5</td>
<td>3.6</td>
<td>3.1</td>
<td>2.1</td>
<td>3.1</td>
<td>3.2</td>
<td>3.4</td>
<td>2.7</td>
<td>3.4</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>Range 2.3–6.1</td>
<td>1.8–6.5</td>
<td>2.3–4.5</td>
<td>1.8–6.5</td>
<td>1.1–7.4</td>
<td>1.9–4.2</td>
<td>0.2–4.1</td>
<td>0.2–7.4</td>
<td>0.9–7.4</td>
<td>1.9–4.5</td>
<td>0.2–7.4</td>
<td>0.2–7.4</td>
</tr>
</tbody>
</table>

**Velocity (m/s)**

| Mean 0.93 | 0.75 | 0.81 | 0.74 | 0.68 | 0.70 | 0.71 | 0.68 | 0.71 | 0.74 | 0.74 | 0.74 | 0.74 |
| SD ± 0.18 | ± 0.15 | ± 0.12 | ± 0.18 | ± 0.24 | ± 0.15 | ± 0.19 | ± 0.22 | ± 0.21 | ± 0.15 | ± 0.18 | ± 0.18 | ± 0.18 |
| Median 0.95 | 0.77 | 0.81 | 0.76 | 0.70 | 0.70 | 0.73 | 0.71 | 0.74 | 0.72 | 0.77 | 0.77 | 0.77 |
| Range 0.55–1.15 | 0.25–1.08 | 0.65–0.95 | 0.25–1.08 | 0.19–1.10 | 0.14–1.10 | 0.14–1.92 | 0.14–1.10 | 0.19–1.15 | 0.14–1.00 | 0.14–1.15 | 0.14–1.15 | 0.14–1.15 |

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**Table 4:** Physical characteristics of spawning sites during Gulf sturgeon egg collection in the Apalachicola River.
FIGURE 3.—Gulf sturgeon population trajectories for scenario 3, which incorporates periodic total recruitment failures. The thick dashed line represents a baseline simulation of constant recruitment (scenario 1), the dotted horizontal line the estimated population size before the onset of intensive commercial fishing. Harv\_n = year of simulated harvest in model.

FIGURE 4.—Gulf sturgeon population trajectories for scenario 4, which incorporates periodic partial recruitment failures. See Figure 3 for additional details.
FIGURE 5.—Gulf sturgeon population trajectories for scenario 5, which incorporates periodic recruitment booms. See Figure 3 for additional details.

FIGURE 6.—Gulf sturgeon population trajectories for scenario 6, which incorporates a boom–bust recruitment pattern. See Figure 3 for additional details.
ed population recovery time. With large year-classes occurring in 2-, 4-, and 8-year periods, population sizes after 100 years were 161, 117, and 102% of historic levels, respectively (Figure 5). These estimates exceed the estimates of historical population size and, thus, are expected to exceed the historical carrying capacity.

Scenario 6.—Periodic patterns of variable recruitment success and failure produced a wide range of results. Boom–bust cycles of 1 out of 2 years (one year of boom recruitment followed by one year of zero recruitment), 1 out of 4 years, and 1 out of 8 years produced resulting population sizes of 27, 7, and 0% of the original after 100 years (Figure 6). Extinction with the cycle of 1 year recruitment in 8 years was predicted to occur within 80 years after the end of harvest.

Discussion
Flow Changes and Recruitment

Fishery managers are concerned that significant discharge reductions in the Apalachicola River during spawning periods via a combination of reduced basin inflows and drought-operation schedules of dam facilities could dewater Gulf sturgeon spawning sites, leading to years of reduced or failed recruitment. This is a significant concern to managers because of reduced access to historic spawning habitat (loss of ~78%) through dam construction (USFWS and Gulf States Marine Fisheries Commission 1995). During persistent periods of drought, such as during 2006–2008, extreme low-flow events could dewater spawning sites over several years, impairing recruitment for multiple Gulf sturgeon year-classes. Beamesderfer and Farr (1997) presented evidence to show that reductions in habitat area caused by flow variation can reduce recruitment of age-0 sturgeon. The relationship between JWLD discharge and the percent area inundated at potential spawning sites is presented in Figure 7; however, the exact relationship between available spawning habitat and Gulf sturgeon recruitment success is difficult to estimate. Although spawning has only been observed at three sites, it was possible that spawning occurred at other areas with suitable bottom substrates, but was unobserved. Uncertainty related to how Gulf sturgeon select spawning areas, and how these preferences change with river discharge, could affect the severity of recruitment effects. For example, greater plasticity in spawning site suitability could mediate the effects of low flows; however, inflexibility in site selection could increase the severity of low-flow effects on spawning success.

In addition to spawning habitat availability, changes in flow regime may also affect other aspects of Gulf sturgeon spawning. Auer (1996) noted several changes in the spawning characteristics of adult lake sturgeon.

![Figure 7](image-url)
A. fulvescens in the Sturgeon River, Wisconsin, that coincided with dam operations shifting from a peaking flow scenario to a more natural run-of-river operation schedule; the amount of time sturgeon were on the spawning grounds decreased, catch rates of sturgeon at the spawning grounds increased, and more female sturgeon in reproductive condition were observed. Auer (1996) suggested that the more consistent water flows provided by the run-of-river flows versus peaking-flow regimes maintained water depths throughout the spawning season, making access to the spawning sites by large (mostly female) fish easier. Watershed and flow regime alterations have been identified as the primary cause of failed recruitment and ultimately the decline of the Kootenai River white sturgeon population (Paragamian et al. 2005). Recent studies have suggested that recruitment in Suwannee River Gulf sturgeon (Randall and Sulak 2007) and Atlantic sturgeon in the Altamaha River, Georgia (D. L. Peterson, University of Georgia, personal communication) may be sensitive to autumn river discharge. The mechanism for this remains unclear; however, for Gulf and Atlantic sturgeon it may be related to the sensitivity of juvenile life stages to increases in salinity. During low-water years, higher salinity levels in estuarine regions near the mouth of natal rivers may restrict foraging areas for juveniles, thereby decreasing growth and increasing mortality.

Modified flow regimes may also affect in-river temperature regimes in the Apalachicola River. Water temperature is an important spawning cue for sturgeons (Auer 1996; Fox et al. 2000). Decreases in discharge could increase in-river temperatures, possibly reducing the length of the annual 20°C (spawning onset; Fox et al. 2000) to 25°C (upper lethal temperature tolerance; Chapman and Carr 1995) spawning window. During this study, the spawning window in the low-flow years of 2006 and 2008 was observed 3 weeks earlier than during the high-flow year, 2005 (Figure 8).

Increased river temperature in recent drought years could also affect postspawning behavior. In the Apalachicola River, the area immediately downstream

**Figure 8.**—Water temperature and date of spawning for Gulf sturgeon on the Apalachicola River, 2005–2007. Open symbols represent dates when eggs were collected, filled symbols dates when eggs were not collected.
of JWLD has traditionally been used as a summer resting area for adult sturgeon (Zehfuss et al. 1999). However, based on catch rates during summer monitoring programs and relocations of telemetered fish, adult Gulf sturgeon during recent years have been using alternative resting areas downstream (F. Parauka, USFWS, unpublished data). This behavior may be a result of low reservoir levels in Lake Seminole allowing warmer surface water to pass through JWLD, causing increased water temperatures below the dam that exceed 30°C (F. Parauka, unpublished data; USGS gauge 02358000). This temperature range observed in recent years is similar to temperatures in the Gulf of Mexico (NOAA 2008), temperatures that Gulf sturgeon are believed to be avoiding by summering in cooler riverine habitats (Foster and Clugston 1997; Parkyn et al. 2007; Sulak et al. 2007). Alternatively, the river channel below JWLD has been greatly incised in a postdam environment owing to changes in riverine flow conditions (Light et al. 2006). This channel incision has probably increased groundwater seepage into the river that, while providing cooler water temperatures, is also hypoxic or anoxic potentially creating areas of low oxygen in the postdam environment. Juvenile Gulf sturgeon rearing habitat and survival are areas needing research and may represent a key, but little known population bottleneck.

Our egg-collection results indicate that Gulf sturgeon may seek specific physical instream conditions at their spawning sites. Depths and flow velocities at egg-collection events were similar during all years at all sites (Table 4; Figure 9), even at widely varying discharge levels and patterns ranging from 578 to 1,059 m³/s during spawning in 2005, 360 to 634 m³/s during 2006, and 188 to 1,045 m³/s during 2008. During periods of lower discharge, Gulf sturgeon will spawn in deeper hard-bottom areas; however, as discharge decreases from 623 to 142 m³/s, available spawning habitat area decreases by 76% (from 8.5 to 2 ha) at the three identified spawning sites (USFWS 2008). The available spawning habitats inundated at flows of 142 m³/s are generally areas with higher flow velocities and steeper bottom topography (USFWS 2008), which are dissimilar from spawning areas (Marchant and Shutters 1996; Fox et al. 2000). Proposed drought condition flow regulations allowing infrequent flow events of 127 m³/s would significantly decrease the availability of Gulf sturgeon spawning habitat to levels approaching zero (Figure 7). In addition to overall flow conditions, small fluctuations in river discharge during spawning events may alter the location of optimal microhabitats for egg or larval sturgeon survival within a given spawning site, rendering areas containing attached eggs unsuitable for egg and larval sturgeon.
survival, thereby leading to reduced or failed recruitment of a given cohort. The egg samplers we used were a passive design whose selectivity and efficiency were highly dependent on environmental variables. For example, higher flow velocities may cause eggs to drift farther and inhibit adhesion to egg samplers, and Sulak and Clugston (1998) suggested that deposited eggs may be lost to predation before hatching or observation. Because of these environmental effects and the broadcast style of egg laying used by Gulf sturgeon (Sulak and Clugston 1998), eggs found on samplers were not necessarily deposited in that exact location (Marchant and Shutters 1996). During our study we observed that a majority of eggs collected over the 3 years of sampling were found during or just after rising or stable water discharge. However, this pattern may be an artifact of gear selectivity during increasing and stable discharge or some other micro-habitat variables and not a relationship between discharge and Gulf sturgeon spawning, and perhaps this should receive further examination. Because of uncertainty surrounding spawning site area and sampled area, egg samplers do not represent a quantitative sampling method, but a presence–absence type, meaning that varying numbers of sampled eggs do not imply varying levels of egg deposition.

**Modeling**

Our population modeling predicts periodic recruitment failures, such as those that could occur during low-river discharge events, will have an effect on Gulf sturgeon population recovery. If these events are infrequent, the effect will be minimal; however, frequent or sequential failure events will significantly hamper recovery or cause the population to go extinct. Even a recruitment pattern characterized by periodic strong year-classes will not be able to compensate for failures in intervening years. Recruitment failures at low population levels where the reproductive capacity
of the population is already impaired are especially damaging to population recovery.

Low rates of population recovery predicted by our model are not unexpected, given life history attributes of Gulf sturgeon (and other similar long-lived species) with low recruitment compensation. The relatively low values of recK estimated for Gulf sturgeon make this population susceptible to slow population recovery following large population declines and regular recruitment failures. Our estimates of recK for Gulf sturgeon ranged from 2.5 to 7.0 (Figure 10). In our model, recK values of 2.5 reduce viability, causing more frequent population crashes and slower recovery rates across recruitment scenarios. A recK value of 7 produces the opposite effect, with faster recovery rates and fewer population crashes. Values of recK 10 or greater would be required for this population to be resistant to the recruitment failures simulated here; however, recK values this high are not supported by historic harvest patterns and current population abundance estimates. Our model simulated annual population sizes are similar to mark–recapture abundance estimates for the Apalachicola River Gulf sturgeon population from the 1980s and 1990s (Zehfuss et al. 1999) and from early 2000s (W.E.P., unpublished data).

Our baseline recruitment scenario 1 demonstrates that even under stable recruitment conditions, the Apalachicola Gulf sturgeon population is not likely to recover by the 2023 target date outlined in the recovery plan (USFWS and Gulf States Marine Fisheries Commission 1995). Scenarios 3 and 4 represent recruitment patterns that may occur as a function of water management decisions that could limit Gulf sturgeon access to some historic spawning sites. These scenarios demonstrate that recruitment failures over short time intervals could lead to declines in Gulf sturgeon populations, increasing concerns over population viability. Recruitment cycles described in scenarios 5 and 6 mimic proposed recruitment patterns for Gulf sturgeon based on observations of length-frequency distributions from long-term monitoring programs (Sulak and Randall 2002). Scenario 5 is especially optimistic, producing population recoveries in excess of the historic population after 100 years, but still does not predict full population recovery by the 2023 target date.

Our model predicts that recruitment failures have the greatest effect on population viability when total population size is low. This is due to reduced population fecundity in the absence of large older individuals (Walters et al. 2008). Our model also predicts that even under “normal” recruitment patterns for 50 years (i.e., scenario 1) regular year-class failure following this 50-year period is predicted to cause Gulf sturgeon populations to decline because the rate of recruitment is less than the mortality rate. Natural mortality rate for Gulf sturgeon is low, and this species is relatively long lived for fish species at this latitude. Combined, these traits allow Gulf sturgeon to persist for long time periods (i.e., decades) without significant population growth (e.g., Kootenai River white sturgeon; Paragamian et al. 2005), yet the continued persistence of older individuals can give the false impression that the population is relatively stable. For example, our model scenario 2 predicts that the Apalachicola River Gulf sturgeon population could persist for approximately 25 years to 2010 before going extinct, even with zero recruitment.

**Management Implications**

After more than 20 years of protection from direct harvest, the Apalachicola River Gulf sturgeon population viability is still uncertain. Preliminary results from ongoing population assessments suggest that the Apalachicola River Gulf sturgeon population has slowly increased since the closure of the fishery (Pine et al., unpublished data), but at present may still number fewer than 1,000 adult individuals, or less than 10% of the estimated prefishing abundance. At these low abundances population viability could be jeopardized by disturbance events, such as hurricanes or prolonged droughts, which could affect the long-term viability of the species. Even under optimal recruitment conditions, Gulf sturgeon recovery in the Apalachicola River is prolonged and probably in excess of 100 years for the population to reach historic prefishery levels (Flowers 2008) given Gulf sturgeon life history attributes do not favor rapid rebounds in population size (Zehfuss et al. 1999; Zehfuss 2000; Pine et al. 2001; Sulak and Randall 2002).

Linking strong year-classes of Gulf sturgeon to habitat conditions that produced them continues to be a key research question posed by water and fishery resource managers within the ACF basin. Regular, large year-classes are probably of increased importance to populations at low spawning stock sizes, because even in good years the production of recruits may be much less than populations whose age-structure is unaltered (Walters et al. 2008). Sturgeon populations are highly sensitive to changes in recruitment (Pine et al. 2001), but whether the frequency or magnitude of these year-classes are affected by anthropogenic disturbances such as historical overfishing or large-scale habitat alteration remains unclear (Sulak and Randall 2002). For instance, the greater effect of JWLD may not be that of blocking access to a quantity of spawning habitat, but instead blocking Gulf sturgeon
from a range of spawning habitats that could be available at varying flow conditions or altering downstream juvenile rearing habitats. Historically Gulf sturgeon recruitment may have been less dependent on a specific range of flows if a wider range of spawning habitat was available throughout the Apalachicola River system, a possibility managers should be aware of when evaluating flow regulations, especially if discharge during spawning is found to be an important determinant to year-class strength and ultimately recruitment to adulthood.

It is likely that large adult year-classes of Gulf sturgeon are not simply a product of the number of eggs produced in a given year. Because Gulf sturgeon do not fully recruit to standard gill-net sampling techniques until they are subadults, generally greater than 450 mm fork length and around ages 4–6, these fish have already survived a series of population bottlenecks and survival challenges as eggs, larvae, and juveniles. Thus, it is important to keep in mind that a strong year-class appearing in the length-frequency distribution is the product of, first, good spawning conditions, and then several “good” years for sturgeon survival over a variety of life stages. The ability of researchers to accurately identify which particular habitat conditions or potential bottlenecks appear most important to facilitate overall population growth can be lost among years of environmental variability between spawning and recruitment of a year-class because of variability among sampling techniques.

One certainty is that the threats to Gulf sturgeon from changing land- and water-use practices throughout their range are not declining and these populations warrant continued protection and examination at each life stage. Our results emphasize that decreasing recruitment, such as by adversely altering in-river flow regimes, would probably decrease sturgeon population viability in the Apalachicola River. We believe water resource managers in the ACF should exercise extreme caution when considering water management practices that further alter riverine flow regimes in the Apalachicola River, as our model scenarios demonstrate Gulf sturgeon populations are sensitive to recruitment effects cause by these alterations, resulting in delayed population recovery and possibly localized extinction.

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References


