**Evaluating Population Recovery Characteristics and Potential Recovery Actions for a Long-lived Protected Species: A Case History of Gulf Sturgeon in the Apalachicola River**

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*Abstract—*In the US Gulf of Mexico, Gulf Sturgeon *Acipenser oxyrinchus desotoi* supported an intense and short-lived early 20th-century commercial fishery; thereafter it persisted at very low levels until the fishery was closed by individual US states in the Gulf of Mexico region in the mid-1980s. Despite closure of the fishery, the stock has not recovered, and there have been threats to population recovery, including potential impacts of the *Deepwater Horizon* oil spill, storm events, and harmful algal blooms. We developed an age-structured population model for Gulf Sturgeon to examine population recovery characteristics. We paired this model with simple population reference points to assess factors that influence population recovery rate and strategies resource managers could adopt to promote species recovery. Using the Apalachicola River Gulf Sturgeon population as a case history and the Gulf Sturgeon Recovery Plan identified date of 2023 as the point in time to evaluate recovery, under current management we predict: (1) age 4+ Gulf Sturgeon will be approaching 50% of current estimated carrying capacity; (2) Dynamic Spawning Potential Ratio is likely >0.3, suggesting low chance of recruitment overfishing; (3) population age structure is likely slowly recovering; (4) Gulf Sturgeon population recovery is sensitive to increases in total mortality; and, (5) estimated UMSY and BMSY is about 0.058 and 1,859 kg (<200 age-4+ fish per year). Our results demonstrate the relative efficacy and impacts of various recovery efforts and threats, respectively, and demonstrate that “recovery” is much different when based on historic vs. currently available habitat. These model results provide reference points to compare field assessments as part of planned restoration efforts and upcoming population status reviews for Gulf Sturgeon funded as part of the Natural Resource Damage Assessment following the *Deepwater Horizon* oil spill.

**Introduction**

Over the past century significant declines in abundance have been observed in many marine (Baum et al. 2003; Christensen et al. 2003; Myers and Worm 2003), freshwater (Duncan and Lockwood 2001; Kruk and Penczak 2003; Pitkitch et al. 2005), and diadromous (Limburg and Waldman 2009) fish species. These declines have stimulated debates among resource scientists and managers as to the magnitude of these declines, their potential cause(s), and the necessary steps to reverse trends and promote stock recovery. Detailed examinations of fishery management successes and failures (Hilborn 2007; Worm et al. 2009) and assessments of characteristics of stock recoveries (Hutchings 2000; Hutchings and Reynolds 2004; Walters et al. 2008; Hilborn et al. 2014) are available. In a review of over 230 exploited fish populations, Hutchings and Reynolds (2004) identified fishing rates and the magnitude of habitat alteration as two factors with the greatest influence on stock recovery. These authors found that management actions focused on reducing harvest are often insufficient alone to aid in recovering populations and that multiple factors influence recovery including human activities, species life history, habitat alterations, and genetics.

The recovery time of a severely depleted fish population is often longer than less exploited populations because of greater erosion in population age-structure and the loss of older, more fecund individuals (Walters et al. 2008). These effects are likely greater in slow growing and late-maturing fish species (Paragamian et al. 2005; Walters et al. 2008; Hilborn et al. 2014). Recovery may be further slowed by the impact of habitat alterations on fish populations from fishing activities (e.g., trawling; Watling and Norse 1998) or large-scale habitat alterations (e.g. dam construction: Freeman et al. 2003; Kruk and Penczak 2003), representing an additional conservation concern. Many North American riverine and diadromous fish species, including salmon *Oncorhynchus* spp. (Nehlsen et al. 1991), shad *Alosa spp*. (Jenkins and Burkhead 1994), and sturgeon *Acipenser* spp. (Pitkitch et al. 2005; Hilton et al. 2016) stocks have historically supported commercial fisheries. These populations also have experienced large-scale habitat modifications due to dam construction that alters riverine flows and impairs access to historic spawning habitats (Freeman et al. 2003; Kruk and Penczak 2003). While habitat modifications may have contributed to population decline, in their present form they may also serve as restrictions to population recovery to pre-exploitation levels (Ahrens and Pine 2014).

Gulf of Mexico Sturgeon *Acipenser oxyrinchus desotoi* “Gulf Sturgeon” was federally listed under the US Endangered Species Act in 1991 by NOAA and USFWS (56FR 49653). Current management units for Gulf Sturgeon include seven river systems and adjacent estuarine and marine habitats across the northern Gulf of Mexico from the Pearl River in Louisiana to the Suwannee River in Florida. Primary factors potentially contributing to declines in Gulf Sturgeon populations include overfishing, loss of spawning habitat, alteration of riverine habitat, or a combination of these and other factors (USFWS 1995; Clugston et al. 1995; Zehfuss et al. 1999). The current Gulf Sturgeon Recovery Plan (GSRP; available https://bit.ly/2A7Jg2H) outlines multiple criteria before population recovery is considered and delisting of this species proposed (U.S. Fish and Wildlife Service [USFWS] 1995). As initially drafted in 1995, the GSRP proposed a short-term goal of halting population decline, and a long-term goal of ensuring self-sustaining populations (i.e., stable or growing without hatchery intervention), which could be delisted by 2023 if several criteria were met (USFWS 1995). Specific delisting criteria include: increased catch per unit effort (CPUE) during monitoring efforts over baseline levels; demonstrated restoration of habitats; and population abundance that could sustain a fishery (USFWS 1995). Within the GSRP, a fishery is defined as “when sustainable yield can be achieved while maintaining a stable population through recruitment.” Following the 2010 *Deepwater Horizon* oil spill, the Final Programmatic Damage Assessment and Restoration Plan and Final Programmatic Environmental Impact Statement (“PDARP”; section 5.5.7; available https://bit.ly/2VWDYQT) identified that large numbers of Gulf Sturgeon were exposed to oil and were affected by exposure, which has motived renewed interest in management actions to promote recovery for this species. However, a general understanding is absent of how these recovery criteria, which depend on Gulf Sturgeon population trends and habitat, integrate with Gulf Sturgeon life history and possible management actions to efficiently reach these recovery criteria.

We build on earlier Gulf Sturgeon modeling efforts from individual rivers (Apalachicola [Zehfuss et al. 1999; Flowers et al. 2009], Pearl [Morrow et al. 1998], Suwannee [Pine et al. 2001], and Yellow rivers [Berg et al. 2007]) as well as range-wide estimates of mortality (Rudd et al. 2014) and carrying capacity (Ahrens and Pine 2014) to develop an age-structured population model tool for examining tradeoffs in restoration actions for Gulf Sturgeon. Using the Apalachicola River Gulf Sturgeon population as an example (a possible discrete management unit), we present several different scenarios that represent general types of management actions that could be implemented (i.e., efforts to reduce adult mortality or stock enhancement efforts to promote recruitment) as part of recovery efforts. We also examine how Gulf Sturgeon life history traits influence population recovery. We frame these scenarios in terms of a relatively short period, from the end of commercial fishing for Gulf Sturgeon in 1985 to the GSRP identified target potential recovery year of 2023 for an individual management unit. We use this 38-year epoch to consider Gulf Sturgeon population response and do not consider our effort any sort of retrospective evaluation of policy choices. We evaluate how realistic is this recovery time interval based on stock status at the time of fishery closure, life history of Gulf Sturgeon, and management options available. We then evaluate model predictions as an informal tool to aid in decision making related to restoration efforts.

Study Site

The Apalachicola River is the largest river, by average discharge, in Florida (Bass and Cox 1985), and is part of the Apalachicola-Chattahoochee-Flint (ACF) watershed. The ACF drains an area of 31,375 km² in Georgia, Florida, and Alabama and is the largest of the river drainages where Gulf Sturgeon are presently found (Wooley and Crateau 1985; Ahrens and Pine 2014). The ACF is unique among systems known to support Gulf Sturgeon because the Jim Woodruff Lock and Dam (JWLD), completed in 1957, blocks upstream passage to approximately 78% of historic riverine habitat (Wooley and Crateau 1985) and is a possible discrete management unit for Gulf Sturgeon as described by USFWS (1995). The Apalachicola River is also part of ongoing legal action between the basin states of Florida and Georgia related to water use within the basin and potential impacts to riverine and estuarine ecosystems (Ruhl 2005; Pine et al. 2015; Leitman et al. 2016).

*History of fishery*

Gulf Sturgeon supported intense commercial fisheries in the late 19th and early 20th century, primarily from the Apalachicola River population. Peak recorded Gulf Sturgeon harvest in the Apalachicola River occurred in 1900 with a 38,300-kg catch, after which annual landings rapidly declined to about 900-1,500 kg annually from about 1920 until the fishery closed in 1984 due to uncertainty in population viability (Huff 1975; Hoover 2002; Sulak et al. 2016). The expectation that motivated this management action was likely that reductions in total mortality due to fishery closure would lead to increases in population size. Thirty-five years after fishery closure the Apalachicola River population, and most other Gulf Sturgeon populations, continue to persist at levels likely below historic size (Ahrens and Pine 2014) while threats to these populations from episodic events such as oil spills may be increasing.

**Methods**

*Model Background*

We developed an age-structured population model in R (R Core Team 2018) to represent Gulf Sturgeon population dynamics over time to assess time to recovery with and without different management actions. Details of the population model in other iterations are in Flowers (2008) and Flowers et al. (2009) and the model is available via GitHub (http://tinyurl.com/y4e52xh7). Flowers et al. (2009) was updated to represent multi-stanza recruitment (also referred to as “unpacking recruitment”; Hilborn and Walters 1992, Lorenzen 2005, Pine et al. 2013). Multi-stanza recruitment refers to splitting a single recruitment process into two or more sequential processes, and is useful for representing mid-recruitment changes such as altered fish density from stock enhancement. This was accomplished by first calculating maximum survival () and density-dependent () parameters of the Beverton-Holt model based on unfished recruitment () and Goodyear compensation ratio () using life history incidence functions (Walters and Martell 2004). 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, representing the recruitment compensation potential of the population. Recruitment to each of two subsequent stanzas was then calculated by assuming the relative mortality rate () and density effect () to each stanza *s.* The stanza-specific and are calculated from these hypothesized rates using:

(1)

. (2)

We assumed each pre-recruit stanza had equal relative mortality and habitat capacity, informed by equations 1 and 2, which implies each recruitment stanza was equally long and with similar bottlenecks. It was necessary to separate the density-dependent, pre-recruit life stage into two stanzas for instances where fish may be stocked on top of the wild population, so that wild fish in the early stanza compete with other wild fish, while wild and stocked fish must all compete in the second stanza (Lorenzen 2005; Camp et al. 2014). Population numbers-at-age in any given year are determined by:

(3)

where *a* is age, *t* is timeand *Sa* is age-specific survival. Other model variables include natural mortality (*M*), apical exploitation rate (*U*), fecundity (*f*), and vulnerability-at-age (*v*), and initial population size (*No*), and skip spawning effects (*Sk*). Model inputs (Table 1) were derived from available literature and data on the Apalachicola River or other Gulf Sturgeon populations.

*Recruitment Compensation*

We estimated the Goodyear compensation ratio (*recK;* Goodyear 1977; 1980; Walters and Martell 2004), which is the ratio of juvenile survival rate at low stock sizes relative to juvenile survival at unexploited stock size, following methods from Martell et al. (2008). In this application, the *recK* parameter is used to describe population recruitment response to depletion.

*Model Initialization and Scenarios*

We initialized our population model (initial population size (*N0*)) with parameter values representing the initial, pre-exploitation population of Gulf Sturgeon in the Apalachicola River (Flowers et al. 2009; Ahrens and Pine 2014 Table 1) based on carrying capacity estimates for age 4+ adults (Ahrens and Pine 2014). From this initial time *t1* we simulate 20 years of intensive removals using an assumed *U1901-1920* = 1.0 representing the initial fishery, followed by 64 years of intermediate fishing removals (*U1921-1984* = 0.089) until the population reaches abundance levels estimated when the fishery was closed in 1984 (*Nt=1985* = 282; Wooley and Crateau 1985). The values of *U* used are within the range of annual exploitation estimated using SRA approaches in Ahrens and Pine (2014). Population abundances are a function of the specified starting values and mortality rates. In our model, the carrying capacity for the population was reduced in 1957 to reflect loss of spawning habitat following initiation of JWLD construction. This change to carrying capacity is based on post-dam carrying capacity estimated in Ahrens and Pine (2014) and is calculated in our model using a unique post-dam density dependent parameter () for the Beverton-Holt function applied after *t*=47. We consider this carrying capacity estimate an approximation as no other estimates are available. We then allow the predicted population to recover over a 100-year period (*Nt=1985-2084*) and assessed population status at the 2023 recovery benchmark identified in the GSRP.

Six scenarios based on input from an informal group of agency, academic, and non-governmental organization Gulf Sturgeon researchers and managers (“Gulf Sturgeon working group”) were developed to examine how life history characteristics (i.e., boom-bust spawning) or management actions (i.e., changes in adult mortality, stock enhancement) influence the population recovery rate by adjusting model parameters to test each hypothesis (Table 2). A baseline population simulation (Scenario 1) was created to estimate a simple projection of population size and establish a reference from which to compare other models. Uncertainty was represented by running the population model once for pre-dam and post-dam median carrying capacity estimates and once at each of the confidence limits (i.e. three runs in total). Each of these baselines was fit to two target estimates of population size: 2009 population size (Ahrens and Pine 2014), and *Nt=26* (1985) population size (Wooley and Crateau 1985). Fitting was done by tuning apical exploitation rate prior to closure and comparing observed and predicted values. The median outcome of this scenario was the basis against which all other scenarios were compared. Simulated confidence limits were for visual reference only; they were not considered when comparing with other scenarios as they are not true confidence limits.

Scenario 2 attempts to address how depletion at fishery closure affects recovery timing by estimating the population level required in 1985 (one year after fishery closure) for Gulf Sturgeon to have recovered to specific levels (as percent of post-dam unexploited stock size) by the GSRP target year of 2023 by manually adjusting annual exploitation rate (*U*) as a proportion of the median population trajectory in Scenario 1. Note that apical exploitation rates are multiplied by age-specific vulnerabilities, so *U*=1 would remove 100% of the vulnerable population, rather than the entire population. Scenarios 3-5 assess population response from reductions in total mortality (Scenario 3a, 3b) or increased recruitment (Scenarios 4-5) by either manually increasing or decreasing mortality from baseline levels in individual years (mortality) or using a simple “anomaly” factor as a multiplier on predicted recruitment. In recent decades, total mortality of Gulf Sturgeon may have increased or decreased from anthropogenic sources such as oil spills, fishery by-catch, boat strikes, or directed fishery closure. We examined how these changes (increases or decreases) implemented after recovery began would alter time to recovery (Scenario 3). Gulf Sturgeon populations are hypothesized to have boom/bust cycles typified by several years of low recruitment followed by a large year class (Sulak and Randall 2002). For scenario 4a, boom years occur by doubling predicted recruitment in strong years (anomalystrong = 2.0) and bust years occur by reducing recruitment in weak years (anomalyweak = [boom interval - anomolystrong]/[boom interval – 1.0]) so mean recruitment was unity. In Scenario 4b we examined how a 25% increase in recruitment that could theoretically result from construction of spawning and rearing habitat could influence recovery. Scenarios 5a and 5b examined whether supplemental stocking of age-0+ Gulf Sturgeon would alter population recovery trajectories with short- (5-year) or long-term (20-year) stock enhancement efforts at two different stocking levels. We considered a stocking scenario equivalent to a “streamside rearing” model where wild fertilized eggs would be collected from artificial spawning substrate and then hatched, and juveniles reared in streamside facilities (Holtgren et al. 2007). Although this could reduce concerns related to fitness of hatchery individuals, we assume fitness is still lower for cultured fish; and represent the reduced fitness of hatchery fish using a maximum adult mortality of 0.1, relative to 0.095 for wild fish. To evaluate stocking scenarios, we assumed that age-0+ Gulf Sturgeon were stocked halfway through the first year (i.e., into the second pre-recruit stanza), so stocking had a density-dependent impact on survival of wild and stocked sturgeon during this stanza only. Descriptions of each scenario are in Table 2.

Each scenario was evaluated in three ways. The first was to examine the time series of total sturgeon abundance and compare to a population benchmark of 4,195 age-4+ Gulf Sturgeon or a total *N* of about 8,784. This value is simply a discussion point based on the median estimate for the Apalachicola River population based on available carrying capacity following construction of JWLD from Ahrens and Pine (2014). We also calculate the transitional Spawning Potential Ratio (SPR; Mace et al. 1996) at the target recovery year 2023. Transitional SPR was determined by first calculating the eggs per recruit in each age-class in 2023, as the sum of eggs produced by each age-*a* cohort in that year, divided by the sum of recruits that led to that cohort *a* years earlier. This was divided by the unfished equilibrium eggs per recruit calculated for the population prior to fishing. Finally, we numerically solved for *MSY* by varying exploitation rate, which allowed us to calculate exploitation rate and biomass at maximum sustainable yield (*UMSY* and *BMSY*, respectively) based on life history parameters and current carrying capacity calculated for the Apalachicola River (based on Ahrens and Pine 2014).

**Results**

*Scenarios 1 and 2 – Recovery*

Our simulation model suggests that Gulf Sturgeon will have recovered to about 58% of the estimated post-dam carrying capacity of 8,784 across all age-classes (equivalent to an age-4+ abundance of 4,195 based on a minimum adult mortality rate of 0.095) by 2023 under our baseline scenario (Figure 1). If the *N1985* abundance level were higher, then Gulf Sturgeon population would be predicted to recover to this carrying capacity sooner (Figure 2). We predicted SPR for each scenario to be well above thresholds of management concern (i.e., increased risk recruitment overfishing SPR<0.3; Table 3) at the GSRP target of 2023 for Scenarios 1 and 2.

As expected, increased total mortality through additions of anthropogenic mortality (noted as apical fishing exploitation, *U*) had a strong negative effect on population recovery and SPR. We found that small increases in total mortality reduced the level of population recovery by 2023, and that recovery declines further as *U* increases (Figure 3a). The same pattern was evident in SPR: increased *U* was predicted to lead to declines in SPR, and at *U*=0.1, SPR was estimated to be <0.3. If natural mortality (*M*) declines from the baseline value of 0.095 following initiation of recovery, the opposite pattern is predicted, with increasing population recovery and SPR (Figure 3b; Table 3). Like the additive effect of increasing total mortality through the addition of exploitation, increasing *M* since closure of the fishery led to longer population recovery times or declines (Figure 3b) and declines in SPR below the 0.3 benchmark at M≥0.127 (Table 3)

*Scenario 3 – Boom/Bust Recruitment*

Cycles in recruitment led to a characteristic saw-tooth pattern in population growth, which affected recovery timing (Figure 4). Setting the mean anomaly to unity meant that a two-year cycle resulted in zero recruitment every two years. Longer cycle frequencies had at least some recruitment every year. Overall, because mean anomaly strength was unity, no recruitment pattern had a high impact on recovery timing or SPR. For example, a cycle with one strong year class out of every 5 years slowed recovery only slightly with the population predicted to recover to about 88% of the carrying capacity in 100 years and reach about 52% of the carrying capacity by the 2023 GSRP target date and no change in SPR (Table 3). Increasing baseline recruitment by 25% reduced recovery time over baseline scenarios with the population reaching about 78% of the carrying capacity by 2023 and exceeding pre-exploitation level at about 100 years (Figure 4b).

We found both short and long-term stock enhancement efforts could reduce time until recovery but did not affect SPR. A simulated 5-year program of stocking 2,500 age-0+ fish per year beginning in *t1* increased abundance to approximately 76% of carrying capacity by 2023 compared to about 58% levels under the baseline recovery model. Under both scenarios, SPR approached 1 (Table 3). Stocking at higher levels (5,000 age-0+ fish) or for longer periods of time (20 years) further reduced the predicted recovery time (Figure 5). Increasing recruitment by 25% through a permanent increase in spawning habitat was also predicted to have long-term benefit on recovery (Figure 4 a, b).

*Age-structure recovery*

An important result overall is that population age-structure during the recovery period is dominated by younger individuals due to the erosion of the age-structure from fishery removals in the years prior to fishery closure (Figure 6). This slows the recovery rate of the population in years immediately following intensive fishing, allowing for an accelerating recovery rate of the population as age-classes (i.e., reproductive potential) builds back into the population. This is one reason the predicted population recovers at a faster rate as the population increases and that the population will recover much faster in terms of *N* than it will in terms of fully recovered age-structure.

*Population productivity*

Population productivity was evaluated by numerically solving for maximum sustainable yield (*MSY*) and calculating the exploitation rate that leads to it (*UMSY*) and the biomass it is achieved at (*BMSY*). Based on simulated vulnerability and population parameters, we estimate a *UMSY* of 0.058 and a *BMSY* of 1859 kg. These numbers reflect a reduced carrying capacity for the population due to impacts from JWLD, which reduces *MSY* and *BMSY* from what would have historically been possible.

*Model uncertainty*

We evaluated model sensitivity from the two leading parameters (input parameters estimated by the other input parameters through optimizing model fits, Hilborn and Walters 1992) - the Goodyear compensation ratio (*recK*) and initial population size prior to fishing (*No*, Scenario 2), as well as model sensitivity to parameter uncertainty in *M* (Scenario 3)*, Mai, and k*. We found that assuming greater *recK* made Gulf Sturgeon more resilient to harvest, requiring greater apical exploitation rates to remove fish from the population to levels observed at the end of commercial fishing. Greater *recK* values would also resulting in predictions of much more rapid population recovery following the cessation of harvest (see Flowers 2008). However, field data suggest *recK* for Gulf Sturgeon is low because of the relatively low sustainable catch observed during the later years of the fishery and the slow recovery rate of the population following fishery closure. The initial population size *N0* did not have large influence in evaluating which management action was likely to accelerate population recovery. Greater initial population size would result in recovery sooner whereas lesser initial size would result in further delays in recovery. Model sensitivity was further examined for *Mai* and *k*. Increasing *Mai* linearly increased population recovery time with longer time to maturity slightly reducing overall reproductive output by removing fecundity contributions of younger ages. Increasing *k* increased recovery time, by increasing time for individuals to reach terminal length, indirectly decreasing weight- and fecundity-at-age. Because individuals were smaller longer, more time was spent at smaller, less fecund ages and total reproductive potential of the population was lower. Overall results for each of the recovery scenarios were not strongly influenced by the range of input parameters for the model other than *recK*.

**Discussion**

The recovery of many severely depleted fish stocks may be a prolonged process due to a variety of human, biological, and environmental factors (Hutching and Reynolds 2004). When coupled with earlier related work on critical habitat change and carrying capacity (Ahrens and Pine 2014) the results of our modeling study suggest three key points:

(1) Gulf Sturgeon recovery depends on reducing risks of elevated mortality rates from anthropogenic sources;

(2) reducing mortality rates through fishery closure was likely the single most effective conservation action that could have been taken to promote population recovery; and

(3) future efforts to assess recovery of Gulf Sturgeon should define recovery specifically in terms of multiple metrics useful for measuring current status and recovery progress alike. If these metrics could be defined as part of the recovery goals, then this model could become part of a formal management strategy evaluation process (MSE; Punt et al. 2014) to formalize management objectives, uncertainties, and model predictions, and ultimately inform decisions about alternative Gulf Sturgeon management actions.

Explicit and likely multiple recovery criteria are essential for differentiating alternative management actions for Gulf Sturgeon. For example, numerical abundance recovery goals could be achieved faster by populations of predominately young fish, but are such “young” populations equivalent to more balanced age-structures with respect to viability? Similarly, standard SPR recovery criteria could be met for Gulf Sturgeon, even when stock abundance is low compared to historical levels. In fact, our results indicate that SPR as a metric alone would suggest that the Gulf Sturgeon population at present could support low levels of harvest with estimated *UMSY*= 0.058 and *BMSY* at current carrying capacity levels of only about 1859kg (<200 age-4+ fish). This makes it difficult to interpret language of the current GSRP stating recovery goals should include “population abundance that could sustain a fishery”, specifically because of ambiguity regarding whether recovery objectives should reference carrying capacity in its present or historic form. If the goal is current carrying capacity, a small sustainable fishery is plausible. Recovery to historic carrying capacity will not likely be realized given risks from increasing total mortality, reductions in available habitat due, and evidence suggesting smaller population at present than historic levels, sustainable harvest of this population is not likely soon either. Clarified recovery objectives, ideally referencing abundance, spawning biomass, and defining potential fisheries would make it easier to assess the effects of future recovery and management actions.

In terms of population size, recovery actions such as stock enhancement could lead to rapid increases in *N* over short time scales. However, the efficacy of stock enhancement as a recovery tool for depleted fish stocks is highly uncertain (Grant et al. 2017), and one of the fundamental uncertainties when considering use of hatchery fish to rebuild populations is to what extent stocked fish are functionally equivalent to wild fish (Lorenzen et al. 2012). Stocking fish mid-recruitment (as the multi-stanza approach taken here assumes) would expose stocked sturgeon to less selective pressures during the compensatory survival period than wild fish. Initially, this should more quickly augment populations below carrying capacity, but if lesser selective pressure translates to lower fitness (Camp et al. 2013), long-term recovery could be hampered. There is precedent for using stocking in sturgeon recovery - as demonstrated for Lake Sturgeon *A. fulvescens* (Schram et al. 1999; Bezold and Peterson 2008; McDougall et al. 2014) and White Sturgeon *A. transmontanus* (Ireland et al. 2002) populations. However, the use of stocking may be construed as contradicting the Gulf Sturgeon Recovery Plan goal of having “natural recruitment” maintain the population (USFWS 1995). And again, the efficacy of stocking depends on the specific recovery metrics - numerical abundance metrics will be more readily augmented by stocking, whereas recovery of the age-structure will take decades to reach, with or without stock enhancement.

Possibly the most effective recovery action, reducing mortality by closing the fishery, was taken over 30 years ago; yet Apalachicola and other Gulf Sturgeon populations are likely still recovering depending on benchmark examined. Our results suggest that this conservation action was not a failure; instead, the recovery of Gulf Sturgeon populations is highly regulated by biological characteristics of the species that were likely not fully known in defining the 2023 recovery target window when written in the mid-1990s. As an example, we estimated *UMSY* in 2023 to be about 0.058 and *BMSY* based on pre-JWLD carrying capacity estimates from Ahrens and Pine (2014) to be about 7,716kg or 700 age-4+ fish annually. The failure of exploitation restrictions alone to result in rapid population recovery is a common theme among severely depleted fish populations (Hutching and Reynolds 2004) and other sturgeon species (Beamesderfer et al. 2007; Vélez-Espino and Koops 2009; ASMFC 2017).

Our results suggest that slow recovery of the Apalachicola River Gulf Sturgeon population is most likely attributable to erosion of age structure at the end of directed Gulf Sturgeon harvest. While the majority of Gulf Sturgeon fishing occurred around the turn of the 20th century, fishing did not end in Florida until 1984. While Florida landings throughout the 20th century were low (about 5,000kg landed statewide vs. the peak landings of 156,000kg in 1902), landings that occur following population collapse were likely removing a large proportion of the population. Ahrens and Pine (2014) estimated annual Apalachicola River Gulf Sturgeon apical exploitation rates approached 1 in the late 1950s. As Scenario 2 demonstrates, if the Gulf Sturgeon population was not as severely depleted at fishery closure, recovery would likely be more rapid (Figure 2).

A key result in our study, also identified by Hutchings and Reynolds (2004), is that while fishery removals are largely the cause of population decline, restricting fishing alone is not always enough to allow population recovery. Atlantic Sturgeon *A. oxyrinchus* SRA modeling shows a similar decline and slow population recovery rate after the end of harvest (ASMFC 2017). The reason for this can be seen in a closer examination of the effects of simulated collapse and recovery on the numbers-at-age of a Gulf Sturgeon population (Figure 6), where harvest eroded population age-structure over time, and at the end of the fishery only younger individuals remain. The slow recovery time predicted by our model and exhibited by other populations is likely a result of populations rebuilding their age-structure and spawning capacity (Walters et al. 2008; Figure 6)*.* This suggests that numbers of Gulf Sturgeon will recover in advance of the biomass and reproductive capacity of the population, meaning that a population that has recovered in terms of abundance may not be recovered in terms of age-structure. This is an important conservation consideration.

Assessing possible conservation and recovery actions

*Managing total mortality*

Concern over continued harvest reducing likelihood of population recovery was likely a motivation for managers to close the Gulf Sturgeon fishery in 1985 (USFWS 1995) and similarly for ending White Sturgeon harvest in the Kootenai River system (Paragamian et al. 2005). Our results show that any additional mortality for adult Gulf Sturgeon beyond the current levels used in these simulations (M=0.095) will likely substantially slow population recovery. The 1995 Gulf Sturgeon Recovery Plan (USFWS 1995) states that “Following delisting, a long-term fishery management objective is to establish self-sustaining populations that could withstand directed fishing pressure within discrete management units.” Based on our results, the Apalachicola River population does not likely reach this goal because increased mortality from fishing above simulated baseline levels would likely not be sustainable over the long-term. Our results suggest sustainable exploitation rates for Gulf Sturgeon are most likely relatively low (*UMSY* = 0.058) and similar to other sturgeon populations (Rieman and Beamesderfer 1990; Boreman 1997; Bruch 1999) and that population viability is sensitive to increases in mortality at all life stages (Morrow et al. 1998, 1999; Pine et al. 2001; Lake Sturgeon, Vélez-Espino and Koops 2009). Beamesderfer et al. (2007) found that adding additional mortality of 10% over the life-span of Green Sturgeon *A. medirostris* would reduce total numbers and adult numbers by 50% and 90%, respectively. We also show that recovery times for Gulf Sturgeon would have been less if the population age-structure had not been as strongly eroded. Sensitivity of population recovery to additional mortality is also an area of potential management concern.

There is potential for increasing mortality from numerous sources including sampling, boat strikes (Brown and Murphy 2010; ASMFC 2017), fishery bycatch (Dunton et al. 2015) and random events such as red tides (Gunter et al. 1948), weather anomalies (Hoag 2004), hurricanes (Stevens et al. 2006), and oil spills have all been observed as mortality sources for Gulf Sturgeon in the last 10 years. Our results suggest efforts that reduce anthropogenic mortality below the baseline of 0.095 used here (within the 95% confidence intervals for survival estimated by Rudd et al. (2014) of S=0.69-0.97 and Atlantic Sturgeon of S=0.84-0.99 [ASMFC 2017], S=0.78-0.87 [Hightower et al. 2015], and S=0.89-0.90 [Dadswell et al. 2016]) would lead to accelerated recovery. Ongoing efforts to estimate mortality rates for specific river systems, geographic areas, and genetically related sub-populations (as in Rudd et al. 2014) will provide new insights to update the projections in this model.

Transitional SPR is an indicator of the relative change in the number of eggs produced by a cohort over its lifetime, not in the biomass of the spawning population, therefore SPR can remain high (because number of eggs per cohort remains similar) even though the population abundance may be much lower than the unfished population. Our results provide two different reference points for Gulf Sturgeon – while the population at a recovery point-in-time of 2023 may be much smaller than pre-exploitation levels from an abundance, age-structure, and biomass perspective, the risk to the population in terms of recruitment overfishing or depensatory declines in recruitment indicated by SPR may actually be low. This is an important result for Gulf Sturgeon as a large population of fish does not imply low risk of extirpation if all fish are relatively young. Likewise, extirpation risk may also not be low if SPR is high, but for a very small population (implying a low number of eggs overall).

*Increasing recruitment*

Gross et al. (2002) suggested that sturgeon population growth is most sensitive to age-specific young-of-year and juvenile survival. Similarly, our model predicted improvements to the Apalachicola Gulf Sturgeon population recovery rate from increased recruitment. This could be achieved in several ways, including allowing passage to habitat upstream of JWLD to access historical spawning areas (if spawning habitat is still available); but these actions could be deleterious unless in-river rearing habitat (Auer and Baker 2002; Braaten et al. 2008; Mailhot et al. 2011) exists including downstream passage for all life stages allowing Gulf Sturgeon return to the Gulf of Mexico.

Alternative approaches to increasing spawning site access may prove less risky than upstream passage. Construction of artificial spawning areas has proven to be effective for increasing recruitment success of other sturgeon species (Khoroshko and Vlasenko 1970; LaHaye et al. 1992; Johnson et al. 2006) and has previously been recommended as an experimental management action in the Apalachicola River (Wakeford 2001). Bradford et al. (1997) suggested that in-river rearing areas might be a limiting factor for salmon smolt production, while watershed and flow regime alterations have been identified as the primary cause of the failed recruitment and ultimate decline of the Kootenai River white sturgeon population (Paragamian et al. 2005). McAdam (2015) identified increased fine substrates (likely due to dams blocking seasonal high flows that scoured substrate) at spawning sites as the most likely explanation for White Sturgeon recruitment failure in the Columbia River. Hydroelectric dam operations may have an effect of both sturgeon spawning behavior (Auer 1996) and abundance (Haxton et al. 2015), with run-of-river flows likely less detrimental to populations than peaking flows. Studies have suggested that recruitment in Suwannee River Gulf Sturgeon (Randall and Sulak 2012) and Altamaha River (Georgia) Atlantic Sturgeon (Schueller and Peterson 2010) may be sensitive to autumn river discharge, possibly related to rearing habitat or fall spawning.

A potential management action in the Apalachicola River would be to optimize river flows during spawning season to maximize the availability of spawning habitat and rearing area. Flows of 420-570 m3/s at JWLD have been identified for these purposes (USFWS 2008; Flowers et al. 2009). These alternative restoration methods may be more beneficial and less costly (due to decreased mortality risk) to the Gulf Sturgeon population than a stock enhancement program or experimental fish passage.

**Conclusions**

Our results suggest that the Apalachicola River Gulf Sturgeon population are not likely to recover to original carrying capacity, not due to severe historic fishery impacts, but because of major loss of spawning habitat. However, based on the best available estimates of carrying capacity presently available post JWLD, the Apalachicola Gulf Sturgeon population is likely to reach about 50% of carrying capacity. When recovery criteria were developed in the mid-1990s, basic information on population demographic rates, life history, and carrying capacity were still being developed for this species. This model could support the development of future realistic population benchmarks based on Gulf Sturgeon population ecology, and pair these benchmarks with monitoring programs to measure population response and progress to recovery goals. Our estimates of recovery are based on mean carrying capacity estimates from Ahrens and Pine (2014) and the use of higher carrying capacity levels would suggest longer periods of recovery to this benchmark, while lower carrying capacity levels would suggest shorter periods of time. At present, there is no unified monitoring program for Gulf Sturgeon range-wide, thus any effort to develop population bench marks must be coupled with monitoring programs to evaluate whether these benchmarks are met. We hope that this model will continue to be improved by updating carrying capacity estimates, maximum age, current abundance, growth, survival, and recruitment information from field assessments planned as part of Natural Resource Damage Assessment (NRDA) recovery efforts for Gulf Sturgeon populations. In this way, management actions could operate under a decision analysis framework such that if benchmarks were not met, specific research efforts or alternative management actions could be taken. This adaptive approach to managing resources (Walters 1986), has been successfully used in the conservation of other endangered fish species, such as Humpback Chub *Gila cypha* (Coggins 2007; Melis et al. 2016). Effective management programs are often those that successfully integrate modeling approaches with field research (Pine et al. 2009) and this model helps to fill that role for Gulf Sturgeon and provides a template for assessing recovery goals and conservation actions.

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Table 1. Gulf Sturgeon age-structure model parameter definitions and data values used in calculations. Additional parameters described in Flowers et al. (2009).

|  |  |  |  |
| --- | --- | --- | --- |
| Parameter | Description | Value | Source |
| *F* | Anthropogenic mortality (fishing, etc.) | variable |  |
| *K* | Brody growth parameter | 0.13 | Tagging data 1978-2006 |
| *L∞* | Von Bertalanffy asymptotic length parameter | 220 cm | Tagging data 1978-2006 |
| *M* | Adult natural mortality rate | 0.095 | Pine and Ahrens 2014 |
| *No* | Initial pre-exploitation population size (95% credible interval) | 33,609  (15,593-48,729) | Pine and Martell 2009 |
| *N1985* | Population size at end of harvest (95% confidence interval) | 282  (181-645) | Wooley and Crateau 1985 |
| *recK* | Goodyear recruitment compensation parameter | 5 | Tagging data 1978-2006,  Martell et al. 2008, Ahrens and Pine 2014 |
| *Wmat* | Weight at maturity | 10.8 kg | Huff 1975,  Tagging data 1978-2006 |
| *Mai* | 1st age at maturity | 6 | Huff 1975 |
| *V* | Vulnerability-at-age | variable-at-age | Tagging data 1978-2006  F. Parauka, personal communication |
| Z | Total mortality | variable |  |

Table 2. Descriptions of each of the age-structure model scenarios, including parameter values.

|  |  |
| --- | --- |
| Scenario | Description |
| 1 | *N0* = 33,609 (CI: 15,594-48,729) of abundance using *R0* = 9,970 (CI: 4,625-14,452) pre-dam and *R0* = 2,605 (CI: 1,200-3,770) post-dam. Following closure, *F*= 0, Stocking= 0 individuals. |
| 2 | Test for depletion levels in 1985 that would lead to 50, 75, 95 and 99% of post-dam carrying capacity at 2023 |
| 3a, b | Assess time to recovery through additive increase in total mortality. Scenario 3a: change in total mortality through the addition of anthropogenic apical exploitation rate *U*. Scenario 3b: change to total mortality through decrease in natural mortality *M*. |
| 4a, b | Examine population response (Scenario 4a) under boom (2x baseline) or bust recruitment with booms occurring in 1 of 2, 1 of 4, or 1 of 5 years. Scenario 4b examine population response to 25% increase in post-dam carrying capacity. |
| 5a, 5b | Stocking effects on recovery: 500 or 2500 individuals for 5 years (Scenario 5a; 1985-1989) and 20 years (Scenario 5b; 1985-2004). Also includes baseline (no stocking) and +25% carrying capacity increase for comparison. |

Table 3. Transitional Spawning Potential Ratio (SPR) for each scenario.

|  |  |  |
| --- | --- | --- |
| Scenario | Manipulation | Dynamic SPR in 2023 |
| *1* | None | 0.99 |
| *2* | N2023 = 0.5 N0  N2023 = 0.75 N0  N2023 = 0.95 N0  N2023 = 0.90 N0 | 0.99  0.99  0.99  1.00 |
| *3* | *U* = 0.01  *U* = 0.5  *U* = 1.0  Madult=0.070  Madult=0.085  Madult=0.105  Madult=0.12  Madult=0.145 | 0.99  0.87  0.27  2.62  1.45  0.68  0.39  0.16 |
| *4* | High recruitment every 2nd year  High recruitment every 4th year  High recruitment every 5th year | NA  0.99  0.99 |
| *5* | Stock 2500 for 5 years  Stock 5000 for 5 years  Stock 2500 for 20 years  Stock 5000 for 20 years | 0.99  0.99  0.99  0.99 |

Figure legends

Figure 1. Apalachicola Gulf Sturgeon population abundance (thousands of sturgeon; y-axis) and year of simulation (x-axis). Fishery removals are included for the first 25 years to reduce population abundance to levels estimated at the end of commercial fishing (1984; vertical red dashed line). Jim Woodruff Lock and Dam construction (light blue vertical line) is shown as modeled carrying capacity of river is reduced after this time. Target recovery year of 2023 indicated by vertical green line. Years 1985-2084 demonstrate population recovery following Scenario 1 where the baseline simulation (black line) represents population growth starting with the mean *N0* abundance estimate and dashed blue lines represent starting values at the upper and lower 95% confidence interval of that estimate. Brown dashed line represents post-JWLD carrying capacity estimate (*k*) of 8,784 Gulf Sturgeon for comparison based on carrying capacity estimates from Ahrens and Pine (2014). Purple dots represent abundance estimates in 1985 (Wooley and Crateau 1985; confidence limits obscured) and 2009 (Ahrens and Pine 2014).pine

Figure 2. Model scenario 2, Apalachicola Gulf Sturgeon population size (y-axis, thousands of sturgeon) and year (x-axis) with different starting values for the population (each color) demonstrating possible levels of recovery to the current carrying capacity (*k*, brown line) of 8,784 Gulf Sturgeon by 2023. Vertical dashed blue line is year Jim Woodruff Lock and Dam construction began which reduced Gulf Sturgeon carrying capacity, red dashed line is the year commercial fishing ended, and the vertical light green dashed line represents the 2023 target recovery year from the GSRP.

Figure 3. Model scenario 3, the effect of adding anthropomorphic mortality (*U*, 3a) or changing natural mortality (M, 3b) on Apalachicola Gulf Sturgeon population recovery beginning in 1985. Black line represents baseline recovery trajectory, current carrying capacity (*k*, N=8,784 Gulf Sturgeon brown line), vertical dashed blue line is year Jim Woodruff Lock and Dam construction began which reduced Gulf Sturgeon carrying capacity, red dashed line is the year commercial fishing ended, and the vertical light green dashed line represents the 2023 target recovery year from the GSRP.

Figure 4. The effect of variable recruitment, in the form of boom/bust recruitment cycling on Apalachicola Gulf Sturgeon population recovery (left panel, 4a) where boom years of 2x baseline recruitment occur in 1 of 2, 1 of 4, or 1 of 5 years. Scenario 4b (right panel) predicted Gulf Sturgeon population recovery with a 25% increase in recruitment beginning in 1985 compared to baseline recruitment (black line). Black line represents baseline recovery trajectory, current carrying capacity (*k*, N=8,784 Gulf Sturgeon brown line), vertical dashed blue line is year Jim Woodruff Lock and Dam construction began which reduced Gulf Sturgeon carrying capacity, red dashed line is the year commercial fishing ended, and the vertical light green dashed line represents the 2023 target recovery year from the GSRP.

Figure 5. Model Scenario 5a estimated Gulf Sturgeon population recovery through stock enhancement where stocking occurs at different rates (500 or 2500) per year for either a 5 year (left panel, 5a) or 20 year (right panel, 5b) period beginning in 1985 compared to baseline recruitment (black line). For comparison, the predicted response to a 25% increase in spawning is also included (from Scenario 4b). Black line represents baseline recovery trajectory, current carrying capacity (*k*, N=8,784 Gulf Sturgeon brown line), vertical dashed blue line is year Jim Woodruff Lock and Dam construction began which reduced Gulf Sturgeon carrying capacity, red dashed line is the year commercial fishing ended, and the vertical light green dashed line represents the 2023 target recovery year from the GSRP.

Figure 6. Surface plot representing theoretical Gulf Sturgeon population subjected to harvest and then allowed to recovery as predicted by our age-structured model. Year of simulation on x-axis, age-class on y-axis. Each cell represents an age class in a given year with the color representing numbers of individuals in that age class. Simulated Gulf Sturgeon population was harvested for the first 25 years, and then allowed to recover. Black vertical dashed lines at 1948, 1984 and 2023 represent the year Jim Woodruff Lock and Dam construction began which reduced Gulf Sturgeon carrying capacity, the year commercial fishing ended, and the 2023 target recovery year from the GSRP, respectively.

Appendix

*Model Sensitivity*

We assessed model results to a range of *recK* (Figure A.1). Higher *recK* values allowed the Gulf Sturgeon population to recover much faster than under the baseline simulations with lower *recK* values. The *recK* value used of 5 seems to reflect general recovery patterns observed for Gulf Sturgeon and is likely realistic.

Figure A1. An evaluation of model sensitivity to a range of recruitment compensation values (*recK*) compared to baseline predictions (black line) which used a *recK* value =5. Black line represents baseline recovery trajectory, current carrying capacity (*k*, N=8,784 Gulf Sturgeon brown line), vertical dashed blue line is year Jim Woodruff Lock and Dam construction began which reduced Gulf Sturgeon carrying capacity, red dashed line is the year commercial fishing ended, and the vertical light green dashed line represents the 2023 target recovery year from the GSRP.