

ARTICLE

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 U.S. Gulf of Mexico, Gulf Sturgeon *Acipenser oxyrinchus desotoi* supported an intense and short-lived commercial fishery in the early twentieth century. Thereafter, it persisted at very low levels until the fishery was closed by individual U.S. states in the Gulf of Mexico region in the mid-1980s. Despite the closure of the fishery, the stock has not recovered and there have been threats to population recovery including the potential effects of the Deepwater Horizon oil spill, storm events, and harmful algal blooms. We developed an age-structured population model for Gulf Sturgeon to examine their population recovery characteristics. We paired this model with simple population reference points to assess the factors that influence the population recovery rate and strategies that resource managers could adopt to promote the recovery of the species. We used the Gulf Sturgeon population in the Apalachicola River as a case history and the date of 2023 that has been identified in Gulf Sturgeon Recovery Plan (GSRP) as the point at which to evaluate recovery, and under current management we predict that (1) age-4+ Gulf Sturgeon (fish 4 years of age and older) will be approaching 50% of current estimated carrying capacity; (2) the dynamic spawning potential ratio is likely >0.3 , suggesting a low chance of recruitment overfishing; (3) the population age structure is likely slowly recovering; (4) the recovery of the Gulf Sturgeon population is sensitive to increases in total mortality; and (5) the estimated values for exploitation rate (U_{MSY}) and biomass at maximum sustainable yield (B_{MSY}) are about 0.058 and 1,859 kg (or <200 age-4+ fish per year [age-4 and older fish]), respectively. Our results demonstrate the relative efficacy and influence of various recovery efforts and threats, respectively, and demonstrate that “recovery” is much different when it is based on historic versus currently available habitat. These model results provide reference points for comparing field assessments as part of the planned restoration efforts and upcoming population status reviews for

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Gulf Sturgeon that are funded as part of the Natural Resource Damage Assessment following the Deepwater Horizon oil spill.

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 steps that are necessary to reverse these trends and promote stock recovery. Detailed examinations of fishery management successes and failures (Hilborn 2007; Worm et al. 2009) and assessments of the 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 the two factors with the greatest influence on stock recovery. These authors found that management actions that are focused on reducing harvest alone are often insufficient 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 that of less exploited populations because of greater erosion in the population age structure and the loss of older, more fecund individuals (Walters et al. 2008). These effects are likely greater in fish species that grow slowly and mature late (Paragamian et al. 2005; Walters et al. 2008; Hilborn et al. 2014). Recovery may be further slowed by the effects 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 have also 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 preexploitation levels (Ahrens and Pine 2014).

In the Gulf of Mexico, Gulf Sturgeon *Acipenser oxyrinchus desotoi* was federally listed under the U.S. Endangered Species Act in 1991 by the National Oceanic and Atmospheric Administration and the U.S. Fish and Wildlife Service (U.S. Office of the Federal Register 1991). The current management units for Gulf Sturgeon include seven river systems and their adjacent estuarine and marine habitats across the northern Gulf of Mexico from the Pearl River in Louisiana to the Suwannee River in Florida. The primary factors that have potentially contributed to declines in Gulf Sturgeon populations include overfishing, loss of spawning habitat, alteration of riverine habitat, or a combination of these and other factors (Clugston et al. 1995; USFWS and Gulf States Marine Fisheries Commission 1995; Zehfuss et al. 1999). The current Gulf Sturgeon Recovery Plan (GSRP) outlines multiple criteria before population recovery is considered and delisting of this species proposed (USFWS and Gulf States Marine Fisheries Commission 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., those that are stable or growing without hatchery intervention), which could be delisted by 2023 if several criteria were met (USFWS and Gulf States Marine Fisheries Commission 1995). The specific delisting criteria include increased catch per unit effort over baseline levels during monitoring efforts, demonstrated restoration of habitats, and population abundance that could sustain a fishery (USFWS and Gulf States Marine Fisheries Commission 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; Deepwater Horizon Natural Resource Damage Assessment Trustees 2016) identified that large numbers of Gulf Sturgeon were exposed to oil and were affected by exposure, which has motivated 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 the population and habitat trends of Gulf Sturgeon, integrate with their life history and possible management actions for efficiently reaching these recovery criteria.

We built 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 modeling tool for examining tradeoffs in restoration actions for Gulf Sturgeon. Using the Gulf Sturgeon population in the Apalachicola River as an example (a possible discrete management unit), we generated 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 examined how the life history traits of Gulf Sturgeon influence population recovery. We framed 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 used this 38-year epoch to consider the response of the Gulf Sturgeon population, and we do not consider our effort to be any sort of critique of policy choices. We evaluated how realistic that this time interval for recovery is based on the stock status at the time of fishery closure, the life history of Gulf Sturgeon, and the management options that are available. We then evaluated the model predictions as an informal tool to aid in decision making that is related to restoration efforts.

Study Site

The Apalachicola River is the largest river, by average discharge, in Florida (Bass and Cox 1985), and it is part of the Apalachicola–Chattahoochee–Flint watershed. This watershed 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 Apalachicola–Chattahoochee–Flint watershed is unique among the systems that are known to support Gulf Sturgeon because the Jim Woodruff Lock and Dam (JWLD), which was completed in 1957, blocks upstream passage to approximately 78% of the historic riverine habitat (Wooley and Crateau 1985) and is a possible discrete management unit for Gulf Sturgeon as described by the USFWS and Gulf States Marine Fisheries Commission (1995). The Apalachicola River is also part of ongoing legal action between the basin states of Florida and Georgia that is related to water use within the basin and its potential effects on riverine and estuarine ecosystems (Ruhl 2005; Pine et al. 2015; Leitman et al. 2016).

History of the Fishery

Gulf Sturgeon supported intense commercial fisheries in the late 19th and early 20th centuries, primarily from the Apalachicola River population. The 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 closing the fishery would lead to increases in the size of the population. Thirty-five years after the fishery was closed, the Apalachicola River population, and most other Gulf Sturgeon populations, continue to persist at levels that are likely below historic sizes (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 the population dynamics of Gulf Sturgeon over time in order to assess time to recovery with and without different management actions. The 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 multistanza recruitment (also referred to as “unpacking recruitment”; Hilborn and Walters 1992; Lorenzen 2005; Pine et al. 2013). Multistanza recruitment refers to splitting a single recruitment process into two or more sequential processes, and it is useful for representing mid-recruitment changes such as altered fish density from stock enhancement. This was accomplished by first calculating the maximum survival (α) and density-dependent (β) parameters of the Beverton–Holt model based on unfished recruitment (R_0) and the Goodyear compensation ratio (CR) by using life history incidence functions (Walters and Martell 2004). The Goodyear compensation ratio was 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 (M_s^*) and density effect (B_s^*) for each stanza s . The stanza-specific α_s^* and β_s^* were calculated from these hypothesized rates by using

$$\alpha_s^* = e^{-\frac{\ln(\alpha)M_s^*}{\sum M_s^*}} \quad (1)$$

$$\beta_s^* = \frac{B_s^*\beta}{\sum_{st} B_{st}^* \prod_{stl=0}^{s'-1} \alpha_{stl}^*} \quad (2)$$

We assumed that each prerecruit stanza had equal relative mortality and habitat capacity, informed by equations 1 and 2, which implies that each recruitment stanza was equally long and with similar bottlenecks. It was necessary

to separate the density-dependent, prerecruit life stage into two stanzas to account for instances where fish may be stocked on top of the wild population such that the wild fish in the early stanza competed only with other wild fish but the wild and stocked fish all competed in the second stanza (Lorenzen 2005; Camp et al. 2014). Population numbers at age in any given year were determined by

$$N_{(a+1,t+1)} = (N_{a,t})(S_a), \quad (3)$$

where a is age, t is time, and S_a is age-specific survival. The other model variables include natural mortality (M), apical exploitation rate (U), fecundity (f), vulnerability-at-age (v), and initial population size (N_0). The model inputs (Table 1) were derived from the available literature and data on the Gulf Sturgeon population in Apalachicola River or other Gulf Sturgeon populations.

Model initialization and scenarios.—We initialized our population model (initial population size (N_0) with parameter values that represented the initial, preexploitation population of Gulf Sturgeon in the Apalachicola River

(Flowers et al. 2009; Ahrens and Pine 2014 Table 1) based on estimates for carrying capacity for age-4+ adults (Ahrens and Pine 2014). We then applied annual exploitation rates to the population to simulate removals from this population from 1901 until the fishery was closed in 1984 ($N_{t=1985} = 282$; Wooley and Crateau 1985). The values of U_t that were used for 1901 to 1959 are those that were estimated by using the stock reduction analysis approaches that are presented in Ahrens and Pine (2014). Thereafter, we applied an exploitation rate of 0.14 to reflect low abundance and incidental mortality through catch-and-release, incidental bycatch and boat strikes. This value of 0.14 was iteratively found to produce estimates for abundance at closure (N_{1985}) that were consistent with the estimates that were obtained by Wooley and Crateau (1985). 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 the loss of spawning habitat following the initiation of JWLD construction. This change to carrying the capacity is based on the postdam carrying capacity that was

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

Parameter	Description	Value	Source
M_s^*	Relative mortality rate of each prerecruit stanza	{1, 1}	Allows equal maximum survival through each stanza
B_s^*	Relative density effect of each prerecruit stanza	{0.5, 0.5}	Allows equal density effect through each stanza
α_s^*	Maximum survival of multistanza Beverton–Holt function	{0.92, 0.92}	Calculated
β_s^*	Density dependent parameter of multistanza Beverton–Holt function	{ 3.50×10^{-5} , 3.50×10^{-5} }	Calculated
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	Ahrens and Pine (2014)
N_0	Initial preexploitation population size (95% confidence interval)	33,609 (15,593–48,729)	Pine and Martell (2009)
N_{1985}	Population size at end of harvest (95% confidence interval)	282 (181–645)	Wooley and Crateau (1985)
$recK$	Goodyear recruitment compensation parameter	3.9	Tagging data 1978–2006; Martell et al. (2008); Ahrens and Pine (2014)
W_{mat}	Weight at maturity	10.8 kg	Huff (1975); tagging data 1978–2006
Ma_i	1st age at maturity	6	Huff (1975)
V	Vulnerability at age	Variable at age	Tagging data 1978–2006; F. Parauka, U.S. Fish and Wildlife Service–Panama City, personal communication
Z	Total mortality	Variable	

estimated in Ahrens and Pine (2014) and is calculated in our model by using a unique postdam density-dependent parameter (β) for the Beverton–Holt function, applied after $t = 57$. We considered this carrying capacity estimate to be an approximation, as no other estimates are available. We then allowed the predicted population to recover over a 100-year period ($N_{t=1985-2084}$) and assessed population status at the 2023 recovery benchmark that was identified in the GSRP.

Six scenarios based on input from an informal group of agency, academic, and nongovernmental organization Gulf Sturgeon researchers and managers (the 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 or stock enhancement) would influence the population recovery rate by adjusting the 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 the other models. Uncertainty was represented by running the population model once for predam and postdam median estimates for carrying capacity 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 $N_{t=86}$ (1985) population size (Wooley and Croteau 1985). Fitting was done by tuning the annual apical exploitation rate from 1960 to closure and comparing the observed and predicted values. The median outcome of this scenario was the basis against which all of the other scenarios were compared. Simulated confidence limits were for visual reference only; they were not considered when comparing with the other scenarios because they are not true confidence limits.

Scenario 2 attempted to address how depletion at the closure of the fishery has affected recovery timing by estimating the population level that would be required in 1985 (1 year after the fishery was closed) for Gulf Sturgeon to have recovered to specific levels (as a percentage of postdam unexploited stock size) by the GSRP target year of 2023 by manually adjusting the annual exploitation rate ($U_{1960-1984}$) as a proportion of the median population trajectory in scenario 1. Note that the 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 the 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, the total mortality of Gulf Sturgeon may have increased or decreased due to anthropogenic sources such as oil spills, fishery bycatch, boat strikes, or directed fishery closures. We examined how the changes (increases or decreases) that were implemented after recovery began would alter time to recovery (scenario 3). Gulf Sturgeon populations are hypothesized to have boom/bust cycles that are typified by several years of low recruitment followed by a large year-class (Sulak and Randall 2002). For scenario 4A, boom years were created by doubling the predicted recruitment in strong years ($\text{anomaly}_{\text{strong}} = 2.0$) and bust years were created by reducing recruitment in weak years ($\text{anomaly}_{\text{weak}} = [\text{boom interval} - \text{anomaly}_{\text{strong}}] / [\text{boom interval} - 1.0]$) so mean recruitment was unity. In scenario 4B we examined how a 25% increase in recruitment that could theoretically result from the construction of spawning and rearing habitat could influence recovery. Scenarios 5A and 5B examined

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

Scenario	Description
1	$N_0 = 33,609$ (CI: 15,594–48,729) of abundance using $R_0 = 9,970$ (CI: 4,625–14,452) predam and $R_0 = 2,605$ (CI: 1,200–3,770) postdam. Following closure, $F = 0$ and stocking = 0 individuals.
2	Test for depletion levels in 1985 that would lead to 50, 75, 95, and 99% of postdam carrying capacity at 2023.
3A, B	Assess time to recovery through additive increases 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	Scenario A examines the population response under boom (2× baseline) or bust recruitment, with booms occurring in 1 of 2, 1 of 4, or 1 of 5 years. Scenario B examines the population response to a 25% increase in postdam carrying capacity.
5A, B	Stocking effects on recovery: 500 or 2,500 individuals for 5 years (scenario A; 1985–1989) and 20 years (scenario B; 1985–2004). The model also includes baseline (no stocking) and a +25% increase in carrying capacity for comparison.

whether supplemental stocking of age-0+ (i.e., young-of-year) Gulf Sturgeon would alter the 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 that was equivalent to a “streamside rearing” model, where wild fertilized eggs would be collected from artificial spawning substrate and then hatched and juveniles would be reared in streamside facilities (Holtgren et al. 2007). Although this could reduce concerns that are related to the fitness of hatchery individuals, we assumed that fitness is still lower for cultured fish and represented the reduced fitness of hatchery fish by using a maximum adult mortality of 0.1 (relative to 0.095 for wild fish). To evaluate the stocking scenarios, we assumed that age-0+ Gulf Sturgeon were stocked halfway through the first year (i.e., into the second prerecruit stanza) so stocking had a density-dependent effect on the survival of the wild and stocked sturgeon during this stanza only. The descriptions of each scenario are presented in Table 2.

Each scenario was evaluated in three ways. The first was to examine the time series of total sturgeon abundance in the Apalachicola River and compare the results to a median estimated population benchmark of 4,195 age-4+ Gulf Sturgeon (Ahrens and Pine 2014) or a total N of about 8,784 based on an equilibrium age structure by using the model parameters that are presented in Table 1. We also calculated the transitional spawning potential ratio (SPR; Mace et al. 1996) at the target recovery year 2023. The transitional SPR was calculated as

$$SPR_{(2023)} = \left[\sum_{a=1}^A \frac{N_{(a,2023)} f(a)}{N_{(a=1,2023-a+1)}} \right] EPR_0^{-1}, \quad (4)$$

where $f(a)$ is eggs produced by age- a sturgeon, and EPR_0 is unfished eggs per recruit, calculated as

$$EPR_0 = \sum_{a=1}^A l x_{0,a} f_a, \quad (5)$$

where $l x_{0,a}$ is survivorship to age- a . Finally, we iteratively searched for MSY by varying exploitation rate, which allowed us to calculate exploitation rate and biomass at maximum sustainable yield (U_{MSY} and B_{MSY} , respectively) based on the life history parameters and the current carrying capacity that was calculated for the Apalachicola River (based on Ahrens and Pine 2014).

RESULTS

Scenarios 1 and 2—Recovery

Our simulation model suggested that Gulf Sturgeon will have recovered to about 44% of the estimated postdam 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 N_{1985} abundance level were higher, the Gulf Sturgeon population would be predicted to recover to this carrying capacity sooner (scenario 2; Figure 2). We predicted the SPR for each scenario to be well above thresholds of management concern (i.e., $SPR < 0.3$, which would suggest an increased risk of recruitment overfishing; 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 (scenario 3; 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 the initiation of recovery, the opposite pattern is predicted, with increasing population abundance, though slightly lower 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) but improvements in SPR (Table 3).

The cycles in recruitment led to a characteristic sawtooth pattern in population growth, though this had little effect on the timing of recovery (scenario 4; Figure 4). Setting the mean anomaly to unity meant that a 2-year cycle resulted in zero recruitment every 2 years. Longer cycle frequencies had at least some recruitment every year. Overall, because the mean anomaly strength was unity, no recruitment pattern had a high influence 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 85% of the carrying capacity in 100 years and reach about 45% of the carrying capacity by the 2023 GSRP target date and no change in SPR (Table 3). Increasing baseline recruitment by 25%, through a permanent increase in spawning habitat, reduced recovery time over the baseline scenarios, with the population reaching about 64% of the carrying capacity by 2023 and exceeding carrying capacity after approximately 2040, effectively increasing the long-term carrying capacity (Figure 4B).

We found that 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 t_1 increased abundance to approximately 72% of the carrying capacity by 2023 compared with about 45% levels under the baseline recovery model. Under both scenarios, the SPR approached 1 (Table 3). Stocking at higher levels (5,000

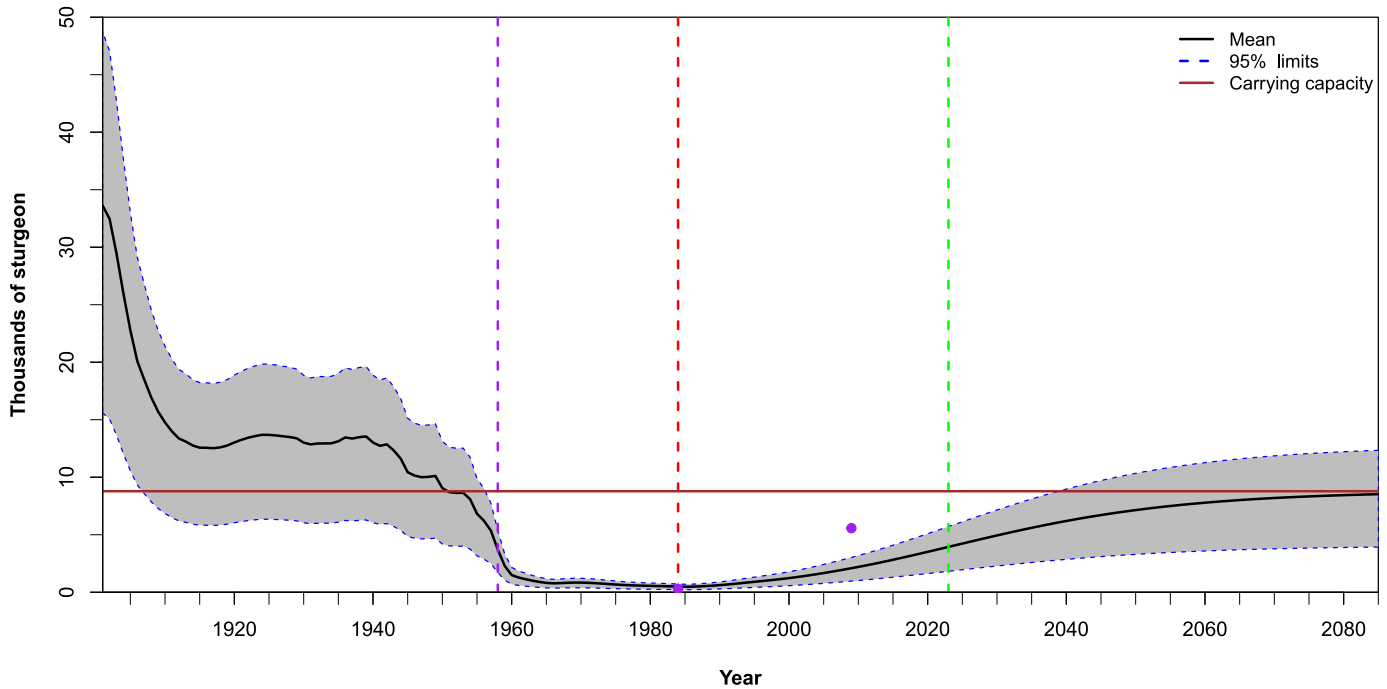


FIGURE 1. Abundance (in thousands of sturgeon, y -axis) and year of simulation (x -axis) for the Gulf Sturgeon population in Apalachicola. Fishery removals are included for the first 25 years to reduce the population abundance to the levels that were estimated at the end of commercial fishing (1984; vertical red dashed line). The Jim Woodruff Lock and Dam construction (the light blue vertical line) is shown, as the modeled carrying capacity of river is reduced after this time. The target recovery year of 2023 is indicated by the 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 N_0 abundance estimate and the dashed blue lines represent the starting values at the upper and lower 95% confidence interval of that estimate. The brown dashed line represents the postdam carrying capacity estimate (k) of 8,784 Gulf Sturgeon for comparison based on the estimates for carrying capacity from Ahrens and Pine (2014). The purple dots represent abundance estimates in 1985 (Wooley and Crateau 1985; confidence limits obscured) and 2009 (Pine and Martell 2009).

age-0+ fish) or for longer periods of time (20 years) further reduced the predicted recovery time (Figure 5).

Age Structure Recovery

An important result overall is that the 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 closing it (Figure 6). This slows the recovery rate of the population in the years immediately following intensive fishing, allowing for an accelerating recovery rate of the population as age-classes (i.e., reproductive potential) build back into the population. This is one reason that 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 (U_{MSY}) and the biomass that is achieved at (B_{MSY}). Based on the

simulated vulnerability and population parameters, we estimated a U_{MSY} of 0.049 and a B_{MSY} of 32,922 kg. This results from an MSY of 1,616 kg annually. These numbers reflect a reduced carrying capacity for the population due to the effect of the JWLD, which reduced MSY and B_{MSY} from what would have been possible historically.

Model Uncertainty

We evaluated the sensitivity of the model from the two leading parameters (input parameters were estimated by the other input parameters through optimizing the model fits, Hilborn and Walters 1992), the Goodyear compensation ratio ($recK$; Goodyear 1977, 1980) and the initial population size prior to fishing (N_0 , scenario 2), as well as the model's sensitivity to parameter uncertainty in M (scenario 3), Ma_i , 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 the levels that were observed at the end of commercial fishing. Greater $recK$ values would also result in predictions of much more rapid population recovery following the cessation of harvest (see Flowers 2008;

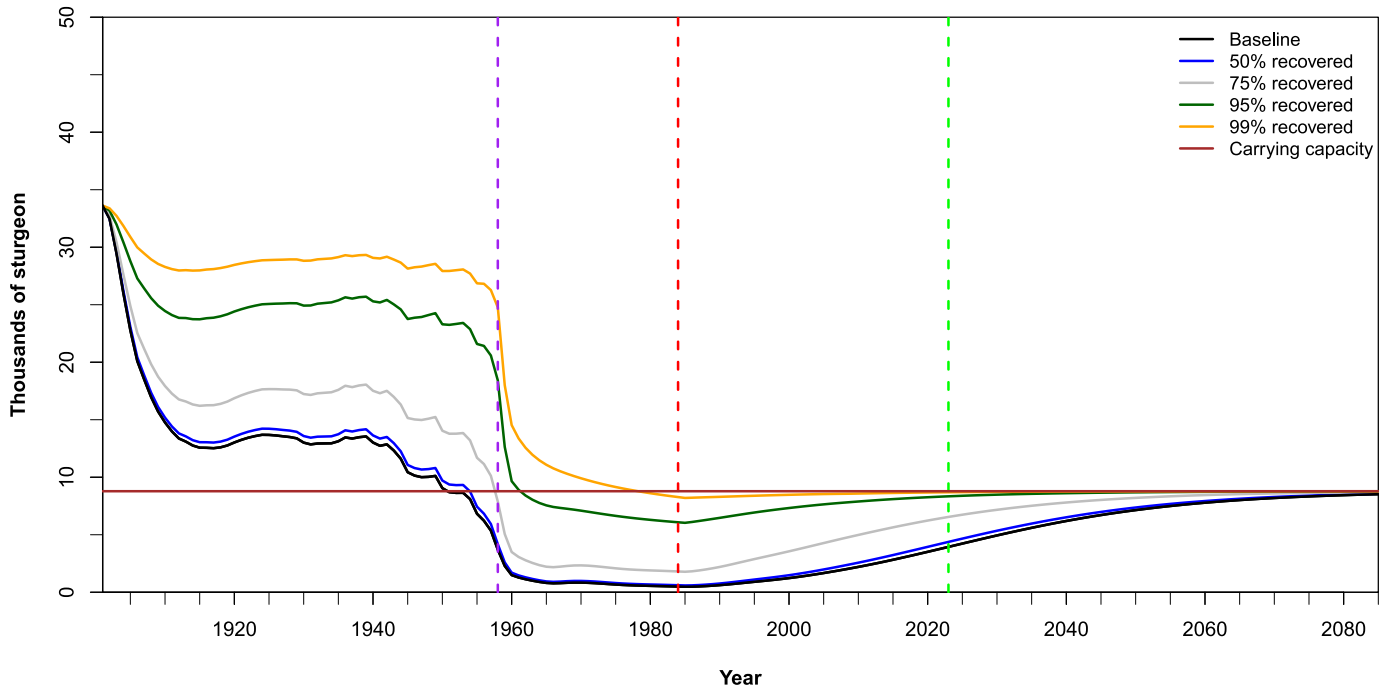


FIGURE 2. Model scenario 2 describes the population size (y -axis, in thousands of sturgeon) and year (x -axis) for Gulf Sturgeon in Apalachicola. The different starting values for the population (each color) demonstrate the possible levels of recovery to the current carrying capacity (k , brown line) of 8,784 Gulf Sturgeon by 2023. The vertical dashed lines from left to right are the Jim Woodruff Lock and Dam construction (reducing carrying capacity), the end of commercial fishing, and the 2023 target recovery year from the GSRP.

Appendix Figure A.1). However, field data suggest that $recK$ for Gulf Sturgeon is low because of the relatively low sustainable catch that was observed during the later years of the fishery and the slow recovery rate of the population following its closure. The initial population size N_0 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. The model sensitivity was further examined for Ma_i and K . Increasing Ma_i linearly increased the population recovery time with longer time to maturity, slightly reducing overall reproductive output by removing the fecundity contributions of younger fish. Decreasing K increased recovery time (by increasing the 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 the total reproductive potential of the population was lower. The 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 (Hutchings 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 the 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 the recovery of Gulf Sturgeon should define recovery specifically in terms of multiple metrics that are useful for measuring current status and recovery progress alike. If these metrics could be defined as part of the recovery goals, this model could become part of a formal management strategy evaluation process (Punt et al. 2016) 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

TABLE 3. Transitional spawning potential ratio (SPR) for each scenario.

Scenario	Manipulation	Dynamic SPR in 2023
1	None	0.98
2	$N_{2023} = 0.5 N_0$	0.98
	$N_{2023} = 0.75 N_0$	0.99
	$N_{2023} = 0.95 N_0$	0.99
	$N_{2023} = 0.90 N_0$	1.00
3	$U = 0.01$	0.98
	$U = 0.5$	0.86
	$U = 1.0$	0.27
	$M_{\text{adult}} = 0.070$	0.95
	$M_{\text{adult}} = 0.085$	0.97
	$M_{\text{adult}} = 0.105$	0.99
	$M_{\text{adult}} = 0.12$	0.99
4	High recruitment every 2nd year	1.00
	High recruitment every 4th year	NA
	High recruitment every 5th year	0.98
5	Stock 2,500 for 5 years	0.98
	Stock 5,000 for 5 years	0.98
	Stock 2,500 for 20 years	0.98
	Stock 5,000 for 20 years	0.98

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 with 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 $U_{MSY} = 0.049$ and MSY at the current levels of carrying capacity of only about 1,616 kg (or <200 age-4+ fish). This makes it difficult to interpret the language of the current GSRP, which states that 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 the risks from increasing total mortality and reductions in available habitat due to JWLD. 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 the 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 at mid-recruitment (as the multistanza approach taken here assumes) would expose the stocked sturgeon to less selective pressures during the compensatory survival period than wild fish endure. Initially, this should more quickly augment populations that are 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 has been 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 and Gulf States Marine Fisheries Commission 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 Gulf Sturgeon populations in the Apalachicola River and elsewhere are likely still recovering depending on the benchmark that is examined. Our results suggest that this conservation action was not a failure. Instead, the recovery of Gulf Sturgeon populations is highly regulated by the biological characteristics of the species that were likely not fully known in defining the 2023 recovery target window when it was written in the mid-1990s. As an example, we estimated U_{MSY} in 2023 to be about 0.049 and MSY based on the pre-JWLD estimates for carrying capacity from Ahrens and Pine (2014) to be about 1,116 kg, or 152 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 (Hutchings and Reynolds 2004) and other sturgeon species (Beamesderfer et al. 2007; Vélez-Espino and Koops 2009; ASMFC 2017).

Our results suggest that the slow recovery of the Gulf Sturgeon population in the Apalachicola River is most likely attributable to erosion of the age structure of older, more fecund individuals 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 5,000 kg landed statewide versus the peak landings of 156,000 kg in 1902), the landings that occurred following the collapse of

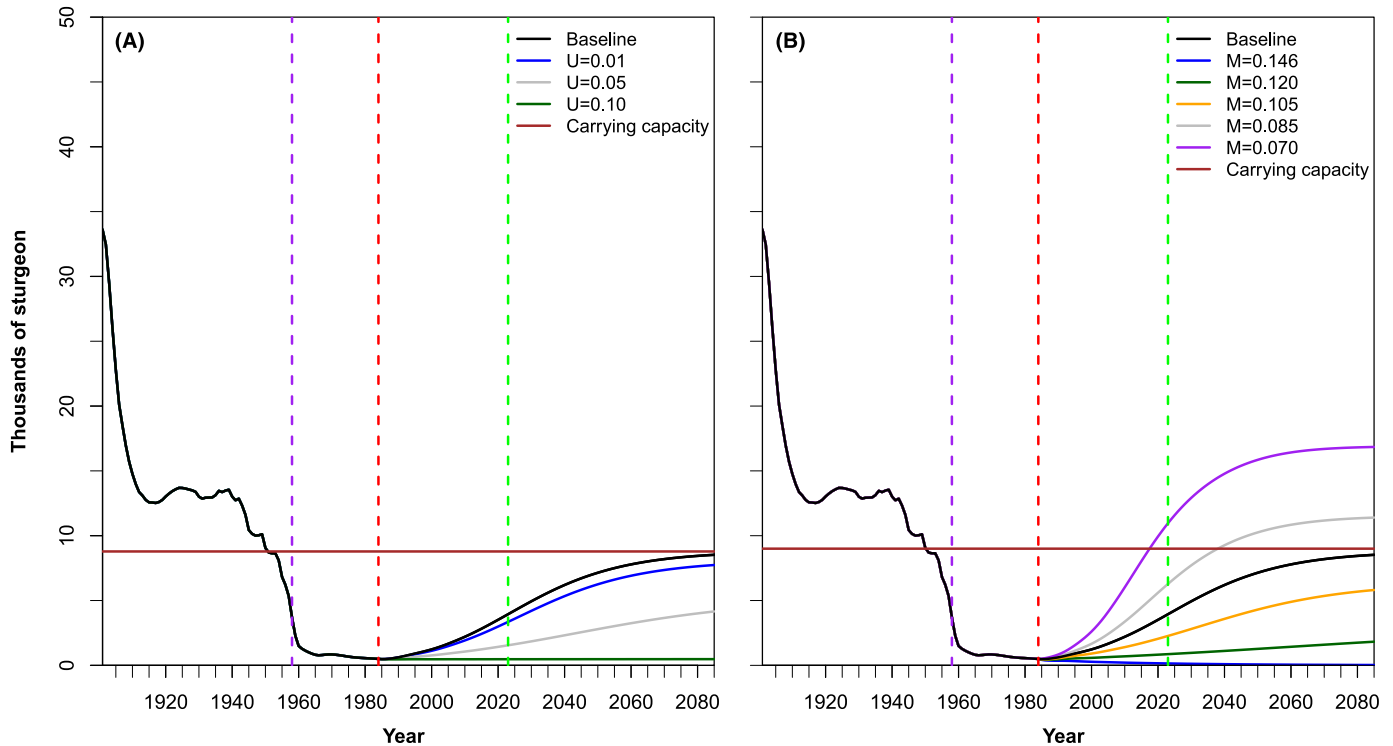


FIGURE 3. Model scenario 3, the effect of (A) adding anthropomorphic mortality (U) or (B) changing natural mortality (M) on the recovery of the Gulf Sturgeon population in the Apalachicola River beginning in 1985. The black line represents the baseline recovery trajectory, the brown line is current carrying capacity (k , $N=8,784$ Gulf Sturgeon), the vertical dashed lines from left to right are the Jim Woodruff Lock and Dam construction (reducing carrying capacity), the end of commercial fishing, and the 2023 target recovery year from the GSRP.

the population were likely removing a large proportion of it. Ahrens and Pine (2014) estimated that annual Gulf Sturgeon apical exploitation rates in the Apalachicola River approached 1 in the late 1950s. As scenario 2 demonstrates, if the Gulf Sturgeon population had not been 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 oxyrinchus* stock reduction analysis 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 a simulated collapse and recovery on the numbers at age of a Gulf Sturgeon population (Figure 6), where harvest eroded the population age structure over time and at the end of the fishery only younger individuals remained. The long maturation time of Gulf Sturgeon (6–12 years, depending on sex) is a biological restriction on the recovery rate, leading to the extended recovery time that would be required to rebuild the population age structure and spawning capacity that is predicted by our model (Walters et al. 2008; Figure 6). This

suggests that the 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 and Gulf States Marine Fisheries Commission 1995) and similarly for ending White Sturgeon harvest in the Kootenai River, Idaho (Paragamian et al. 2005). Our results show that any additional mortality for adult Gulf Sturgeon beyond the current levels that were used in these simulations ($M=0.095$) will likely slow population recovery substantially. The 1995 Gulf Sturgeon Recovery Plan (USFWS and Gulf States Marine Fisheries Commission 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

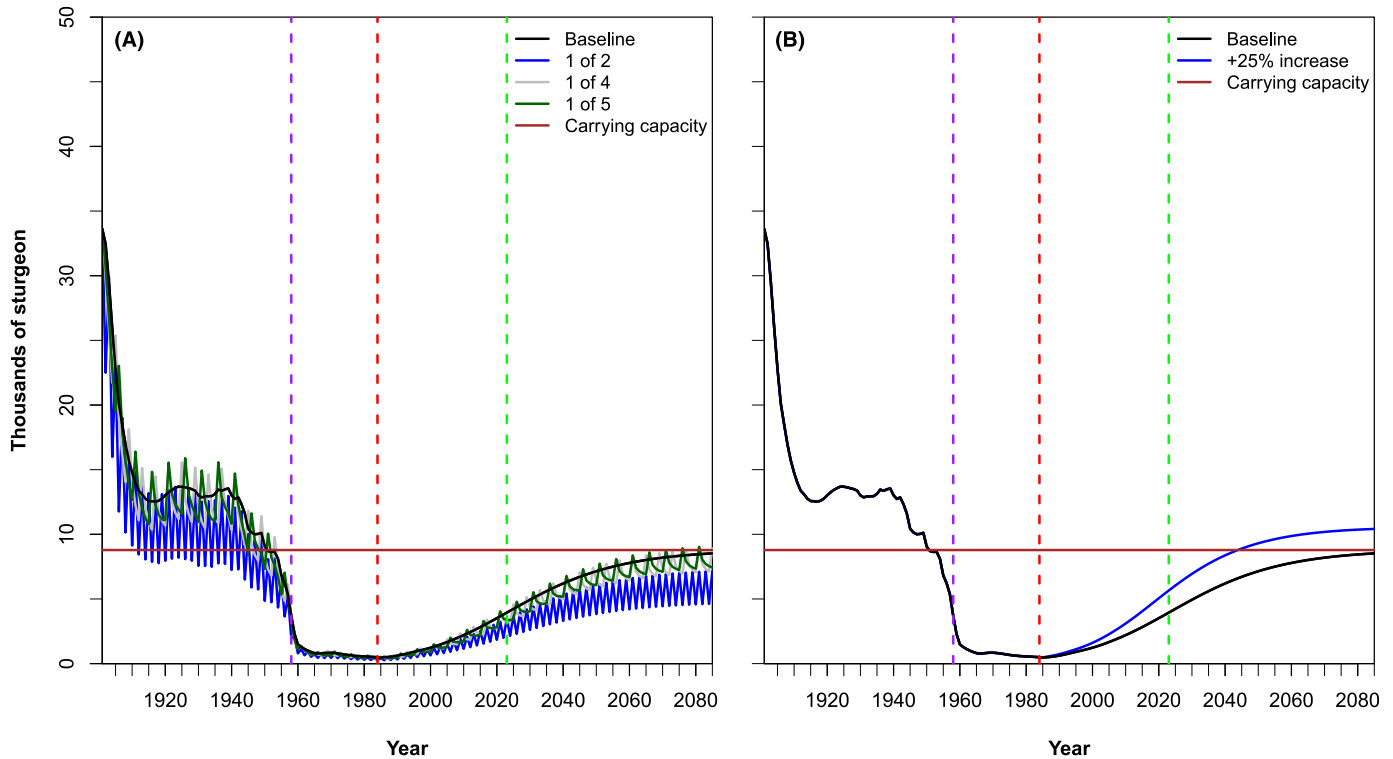


FIGURE 4. The effect of variable recruitment in the form of boom/bust recruitment cycling on the recovery of the Gulf Sturgeon population in the Apalachicola River, where (A) boom years of $2\times$ baseline recruitment occur in 1 of 2, 1 of 4, or 1 of 5 years and (B) predicted recovery of the Gulf Sturgeon population with a 25% increase in recruitment compared to baseline recruitment (black line) beginning in 1985. The black line represents the baseline recovery trajectory, the brown line is current carrying capacity (k , $N=8,784$ Gulf Sturgeon), the vertical dashed lines from left to right are the Jim Woodruff Lock and Dam construction (reducing the carrying capacity), the end of commercial fishing, and the 2023 target recovery year from the GSRP.

because increased mortality from fishing above the simulated baseline levels would likely not be sustainable over the long term. Our results suggest that the sustainable exploitation rates for Gulf Sturgeon are most likely relatively low ($U_{MSY}=0.058$) and similar to those of 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; Vélez-Espino and Koops 2009). Beamesderfer et al. (2007) found that adding a mortality of 10% over the baseline life span of Green Sturgeon *A. medirostris* would reduce the total and adult numbers by 50% and 90%, respectively. We also showed that recovery times for Gulf Sturgeon would have been lower if the population age structure had not been as strongly eroded. The 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 2003), hurricanes

(Stevens et al. 2006), and oil spills, which have all been observed as sources of mortality for Gulf Sturgeon in the last 10 years. Any additional anthropogenic mortality will delay the recovery of the population. Our results suggest that efforts that reduce mortality below the M baseline of 0.095 that was used here (within the 95% confidence intervals for survival for Gulf Sturgeon that were estimated by Rudd et al. (2014) of $S=0.69-0.97$ and for 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 subpopulations (as in Rudd et al. 2014) will provide new insights to update the projections in this model.

The spawning potential ratio is an indicator of the relative change in the number of eggs that is produced by a cohort over its lifetime, not in the biomass of the spawning population. Therefore, SPR can remain high (because the number of eggs per cohort remains similar) even though the population abundance may be much lower than that of the unfished population. Our results provide two different reference points for Gulf Sturgeon—while

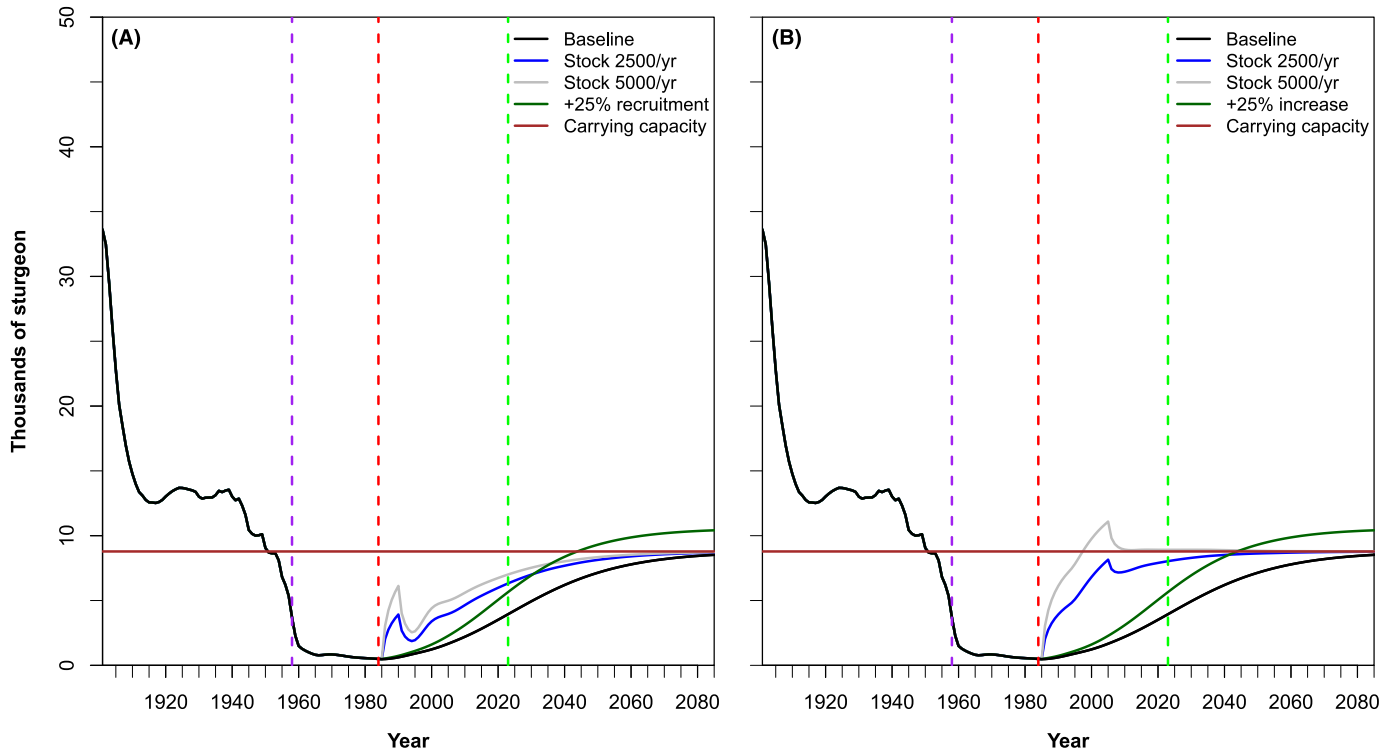


FIGURE 5. Model scenario 5 for the estimated population recovery of Gulf Sturgeon through stock enhancement, where stocking occurs at different rates (500 or 2,500) per year for either (A) a 5-year or (B) 20-year period beginning in 1985 compared with baseline recruitment (black line). For comparison, the predicted response to a 25% increase in spawning is also included (from scenario 4B). The black line represents the baseline recovery trajectory, the brown line is the current carrying capacity (k , $N = 8,784$ Gulf Sturgeon), the vertical dashed lines from left to right are the Jim Woodruff Lock and Dam construction (reducing the carrying capacity), the end of commercial fishing, and the 2023 target recovery year from the GSRP.

the population at a recovery point of 2023 may be much smaller than preexploitation levels from an abundance, age structure, and biomass perspective, the risk to the population in terms of recruitment overfishing or depensatory declines in recruitment as indicated by SPR may actually be low. This is an important result for Gulf Sturgeon because a large population of fish does not imply low risk of extirpation if all of the fish are relatively young. Likewise, extirpation risk also may 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 population growth in sturgeon is most sensitive to age-specific young-of-year and juvenile survival. Similarly, our model predicted improvements to the recovery rate of the Gulf Sturgeon population in the Apalachicola River 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 there is in-river rearing habitat (Auer and Baker 2002; Braaten et al. 2008; Mailhot et al. 2011) that

includes 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 providing for upstream passage. Constructing artificial spawning areas has proven to be effective for increasing the 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 White Sturgeon population in the Kootenai River (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 the recruitment failure of the White Sturgeon population in the Columbia River, Washington. 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

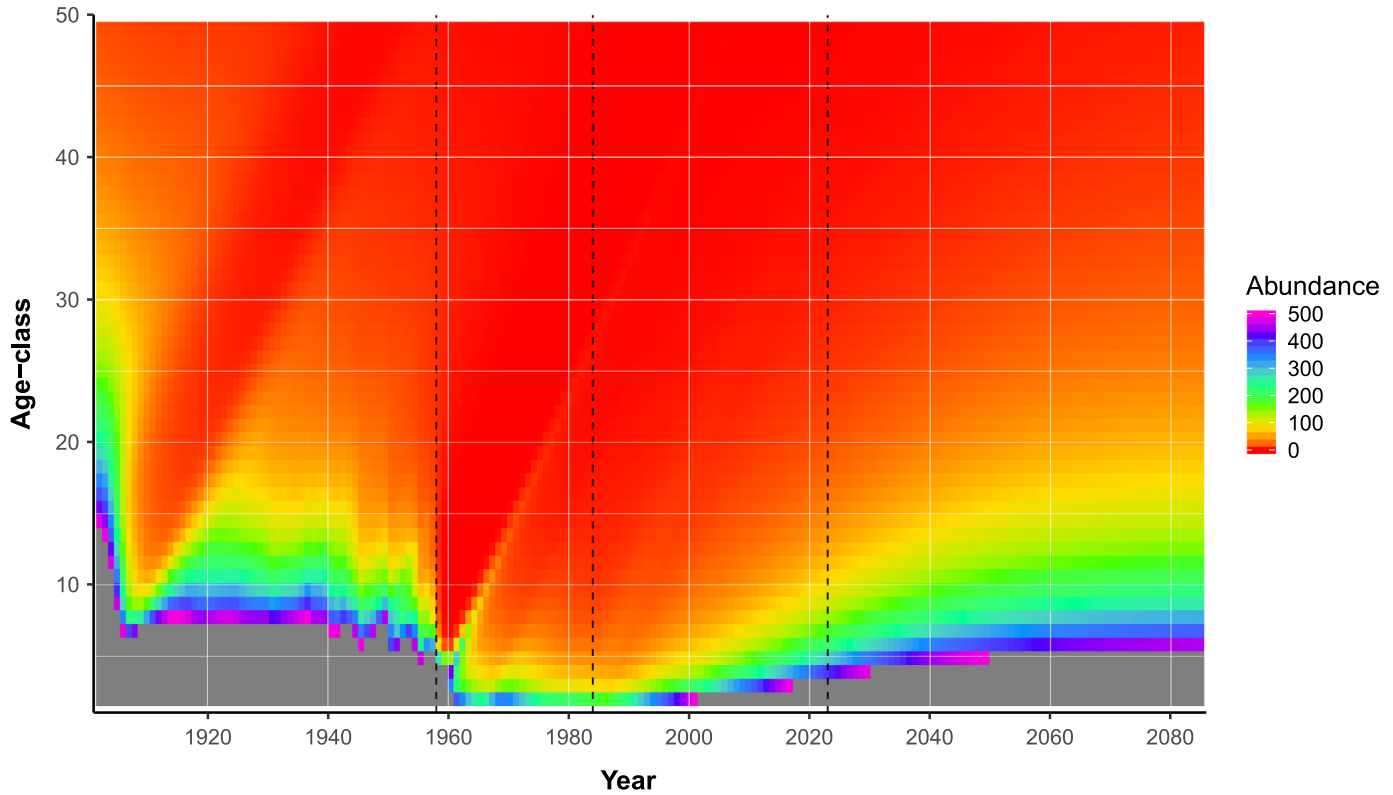


FIGURE 6. Surface plot representing the theoretical Gulf Sturgeon population that was subjected to harvest and then allowed to recover as predicted by our age-structured model in the baseline scenario. The year of the simulation is shown on the *x*-axis, and age-class is shown on the *y*-axis. Each cell represents an age-class in a given year, with the color representing numbers of individuals in that age-class. The simulated Gulf Sturgeon population was harvested for the first 25 years and then allowed to recover. The black vertical dashed lines at 1947, 1984, and 2023 represent the year that Jim Woodruff Lock and Dam construction began, which reduced the carrying capacity for Gulf Sturgeon, the year that commercial fishing ended, and the 2023 target recovery year from the GSRP, respectively.

populations than peaking flows. Studies have suggested that recruitment of Gulf Sturgeon in the Suwannee River (Randall and Sulak 2012) and Atlantic Sturgeon in the Altamaha River, Georgia (Schueller and Peterson 2010) may be sensitive to autumn river discharge, which is 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 would be.

CONCLUSIONS

Our results suggest that the Gulf Sturgeon population in the Apalachicola River is not likely to recover to the original carrying capacity because of major loss of spawning habitat rather than to severe historic fishery effects.

Based on the best available estimates of carrying capacity that are presently available since the JWLD was constructed, the Gulf Sturgeon population in the Apalachicola River is likely to reach about 50% of the historic carrying capacity. When the 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 that are based on the population ecology of Gulf Sturgeon, and stakeholders could pair these benchmarks with monitoring programs to measure population response and progress to recovery goals. Our estimates of recovery are based on the mean estimates of carrying capacity from Ahrens and Pine (2014), and the use of higher levels of carrying capacity would suggest longer periods of recovery to this benchmark, while lower levels of carrying capacity would suggest shorter recovery periods. At present, there is no range-wide unified monitoring program for Gulf Sturgeon, so any effort to develop population benchmarks 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 estimates for carrying capacity, maximum age, current abundance, growth, survival, and recruitment information from field assessments that are planned as part of Natural Resource Damage Assessment 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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Appendix: Model Evaluation

MODEL SENSITIVITY

We assessed the model results to a range of $recK$ (Figure A.1). Higher $recK$ values allowed the Gulf Sturgeon population to recover much faster than they did under the

baseline simulations with lower $recK$ values. The $recK$ value of 5 that was used seems to reflect the general recovery patterns that are observed for Gulf Sturgeon and is likely realistic.

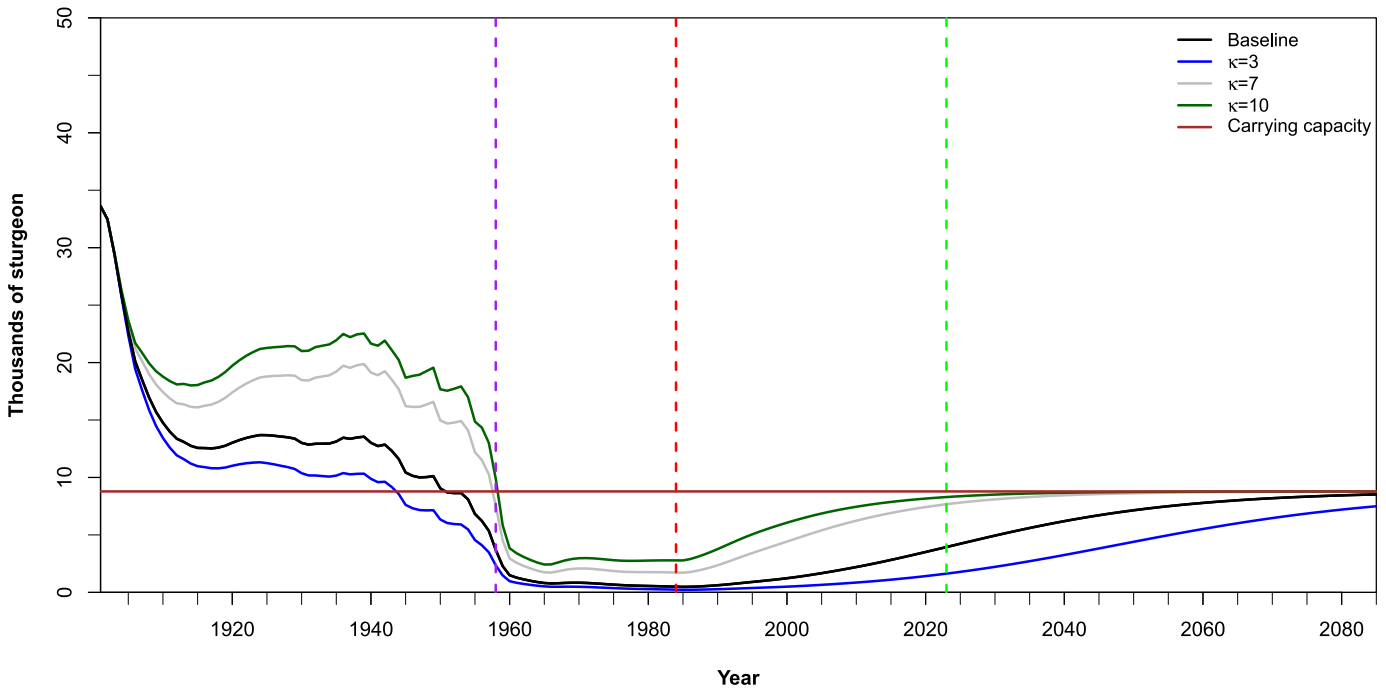


FIGURE A.1. An evaluation of model sensitivity to a range of recruitment compensation values ($recK$) compared with baseline predictions (black line) that used a $recK$ value = 5. The black line represents the baseline recovery trajectory, The brown line is current carrying capacity (k , $N = 8,784$ Gulf Sturgeon), the vertical dashed lines from left to right are Jim Woodruff Lock and Dam construction (reducing the carrying capacity), the end of commercial fishing, and the 2023 target recovery year from the GSRP.