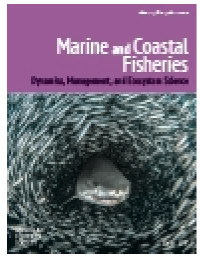


Evaluating Population Recovery Characteristics and Potential Recovery Actions for a Long-lived Protected Species: A Case History of Gulf Sturgeon in the Apalachicola River

Journal:	*Marine and Coastal Fisheries*
Manuscript ID	UMCF-2019-0014.R2
Manuscript Type:	Article
Keywords:	sturgeon, Threatened and Endangered Species, Population Dynamics

Dear Editorial Team,

Thank you for the opportunity to revise this manuscript. We also appreciate the extension you provided to complete our revisions. Below we provide the reviewer or AE comments, and then list our response in red font. We provide line reference numbers to where these changes were made. We made extensive revisions to the manuscript based on feedback from the reviewers and AE and feel the manuscript is much improved. We look forward to a positive response from the editorial team related to our efforts to improve the manuscript.

Review of "Evaluating Population Recovery Characteristics and Potential Recovery Actions for a Long-lived Protected Species: A Case History of Gulf Sturgeon in the ApalachicolaRiver" (Revised paper)

This paper addresses several comments of mine in the original review, and the paper is clearer. However, there are still are a number of issues I think should be addressed.

Major comments

1) In lines 109-111, the authors state "*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*".

I appreciate that the authors' do not intend their analyses to be a critique of past management practices, but considering that all but 4 of the years in this 38-year period have already occurred it is difficult to argue that this is not a retrospective analysis. Lines 109-111 are also at odds with the response to one of my comments on the earlier version "*the scenarios are all hypothetical . . . in terms of 'if this action had been taken in 1985 what would the population have looked like in 2023'* ", which could almost be taken as a definition of a retrospective analysis.

We agree with the reviewer – that is pretty much the definition of retrospective analysis, although strictly speaking, we still hesitate to call it that since this is really a simulation study with scant data to conduct a formal retrospective evaluation. We also agree that our intent of this statement was to say we are not suggesting (in retrospect) one action should have been taken over another, so we have borrowed the reviewer's term and restated (line 113) that we "…do not consider our effort any sort of critique of policy choices."

This paper seems to straddle a line between a practical application of interest to managers of a specific stock (as evidence by the title "*Evaluating population recovery characteristics and potential recovery actions for a long-lived protected species: as case history of Gulf Sturgeon in the Apalachicola River*"), and a series of "hypothetical" simulation scenarios that could be quite separate from the current data for this stock. I realize that it may be a bit late for this request, but if I were a manager or scientist interested in in potential recovery actions for this stock, I would want to know what the best estimate of current stock size is (i.e., in 2019), and given this estimate, what is the potential for meeting the recovery goals by the recovery deadline.

We agree that this would be helpful for scientists and managers, but it is outside the scope of this study. Accurately answering this question would really mean analyzing new data rather than simulating based on past and infrequent population estimates. For example, we really don't have new information with which to provide an accurate contemporary abundance estimate. Therefore, we can't provide this information because we wouldn't find it scientifically defensible without new data on which to base our recommendations.

I appreciate showing the data for population abundance in Figure 1, but it also seems like the catch data could also provide useful information. It appears from lines 128-132 that there is a time series of catch estimates. It also appears from the paragraph beginning on line 209, and Table 1, that scenarios 2 and 3 involved changing past exploitation rates. In order to evaluate how far the scenarios deviate from the empirical data, I would be interested in seeing the catch estimates they produce and how closely the match the catch data.

We considered this comment very carefully. There is catch data, but again, the purpose of this work was not to provide simulations that would be easily interpretable by biologists and managers. However, the catch information referred to by the reviewer has been used in a stock assessment to provide predictions of exploitation rates using a stock reduction analysis (Ahrens and Pine 2014) – basically the exact analysis suggested by the reviewer. Therefore, we have removed the simplifying assumption of discrete periods of exploitation and replaced them with predictions of exploitation rate from Ahrens and Pine

2014. Therefore, our predictions of abundance are directly influenced by catch.

2) I appreciate the additional text on SPR, but still do not see how they relate to the recovery goals. The recovery goals are stated in lines 82-89, and pertain to stabilization and improvement abundance estimates, and habitat improvement. The SPR is used as an index of fishing intensity; as I mentioned, one could eliminate fishing and still not meet the recovery goals. Because the SPR calculations are done on a per-recruit basis, they do not consider how recruitment (and thus the scale of abundance) may be impaired at low stock sizes.

This is absolutely true and we acknowledge this in our discussion (lines 541-546) – basically using this case study to demonstrate the importance of carefully considering different recovery metrics.

As a technical note, if SPR is to be discussed, it is nonsensical to have SPR values greater than 1. SPR is the spawners per recruit of a fished population divided by the spawners per recruit of an unfished population, where the only difference between the fished and unfished populations is the level of fishing. An SPR greater than 1 would mean that fishing caused the stock to increase its reproductive output per recruit beyond the level it would have been at had there been no fishing. Because a transitional SPR is being computed, the spawner per recruit is computed for each year and reflects the estimated mortality rates that cohorts in that year have experienced. Likewise, the denominator should reflect the mortality rates that these cohorts would have experienced had there been no fishing – changes over time of the natural mortality rate would be taken into account in both the numerator and denominator. The authors should show the equation for this, which should be:

$$Ai-1_{-Z}\Sigma\ \{w_i p_i \prod e^{\ i,t-i+j}\}$$

$$i=r\ j=r,i\neq r$$

$$Ai-1_{-M}\Sigma\ \{w_i p_i \prod e^{\ i,t-i+j}\}$$

$$i=r\ j=r,i\neq r$$

where Z and M are the total and natural instantaneous mortality rates, each indexed by age i and year t, w_i and p_i are the weight per spawner and proportion mature (fecundity could be used here if available), r is the age of recruitment, and A is the maximum age.

This is also true. We initially thought it would be valuable to show SPR relative to the unfished state, even if mortality had changed (so that natural mortality is different in the numerator and denominator. We see now that this indeed makes no sense. We have adjusted as per the suggestion of the reviewer.

Other comments

Line 140-156) The stock-recruitment model could be explained more clearly. Please show the stanza-specific values for M and B -- were there any stock-recruitment parameters that were different between the stanzas? It seems that the only reason between the stanza is the infusion of stocked fish for the 2nd stanza – the fish would compete against each other in the same manner, but the density would be higher. Is this right?

It is correct that the multi-stanza recruitment function allows recruitment by possible competition to be accounted for by stocked fish. We have set the M and B parameters in a way that absent stocking, there is no differential survival in either stanza. We have included those values and the resultant Beverton-Holt parameters in Table 1.

Lines 241-242) This assumes a particular age structure – is this for an equilibrium stock? If the value of 8,784 fish is the estimated carrying capacity, then it should be identified as such (rather than "discussion point based on the median estimate for the Apalachicola River population")

The 8,784 number is based on an equilibrium age structure, using the presented model parameters, where there are 4,195 age-4+ fish. Text has been changed to reflect this.

Line 284) 100 years from when? The graph shows that with a 25% increase in recruitment the carrying capacity would be exceeded around 2040. What is the "pre-exploitation level" – is this the same as carrying capacity?

We agree this was unclear. Text has been revised.

Lines 291 – 293) Redundant with lines 282 – 285.

We agree, text has been revised.

Line 317 "result in"

Text revised accordingly

Line 326) From what I can see, *k* (lower case) is only defined in the Figure captions, which is confusing because *K* (upper case) is the Brody growth parameter. Please define *k* in the text and include it in the list of parameters.

Here *k* should have been *K*. We have revised all instances where this was in error.

Line 359) "*Reductions in available habitat due*" Seems like something is missing here. Due to what?

We agree, this is an incomplete statement. Edited this section to be clearer.

Lines 392-394) "*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.*" Why would the age structure matter in the time to recover the abundance of the stock? In your model, there is no difference in the quality of recruits from either young or old spawners. If what you mean is that a population comprised of mostly young fish will take time to produce older fish, then there are clearer ways of saying this.

We mention this age structure "erosion" in the Introduction and Results. Here we revisit this idea and discuss it. Made some revision to the statement and added more detail.

Lines 409-411) "*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*" Showing the generation time would help quantify the longevity of this stock. It would also be helpful to show the estimated population and age structure in 1985, and the times series of estimated recruitments. In the baseline simulation, was the post-1985 recruitment consistently building over time, or were there periods of low recruitment even with no fishing? Fishing ended in 1985, so it has been 34 years with no fishing.

Revised sentence and added information about maturity/generation time. Figure 6 does show the baseline population age structure in 1985 and throughout the time series. Modeled recruitment changes with the population level over time; in the baseline scenario it increases with increasing population fecundity. Only in the scenarios where recruitment is purposely varied are there high and low recruitment swings.

Line 440) The value of 0.095 is for the "natural" mortality (Table 1), so not quite right to refer to this as "anthropogenic" mortality, as some causes of this mortality are not anthropogenic.

Agreed, revised text.

447-448) "*Transitional SPR is an indicator of the relative change in the number of eggs produced by a cohort over its lifetime*" This would describe "static" SPR, which is an equilibrium number that would apply to cohorts. Transitional SPR does not track cohorts, but rather uses the estimated reproductive output per recruit in each year and is dynamic.

This text has been removed.

Lines 450 – 454) *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.* If the population is "much smaller" due to fishing practices in the past, then the risk of recruitment overfishing is increased. SPR calculations cannot address recruitment overfishing because they do not account for the stock-recruitment curve. Also, as I mentioned in the previous version, this paper does not address depensatory declines in recruitment.

This text has been removed

Lines 454-455) "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." The "important result" this sentence refers to addresses small populations, not a large population.

Corrected

Figures) The text says that the dam was built in 1957, but the Figures appear to show 1947.

Thank you for finding this error. Construction began in 1947 and completed in 1957. For clarity, we have scaled everything to 1957.

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

[1,3*†]H. Jared Flowers, [1,3] W. E. Pine, III, [2]B. T. van Poorten, and [3]E. V. Camp

[1]*Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, University of Florida, Gainesville, Florida 32611*

[2]*Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, British Columbia, Vancouver, Canada V6T 1Z4*

[3]*Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation University of Florida, 7922 NW 71st St., Gainesville, Florida 32653, USA*

*corresponding author: billpine@ufl.edu

†Present address: Georgia Department of Natural Resources, Coastal Resources Division, 1 Conservation Way, Brunswick, GA 31520

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 U_{MSY} and B_{MSY} 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 critique 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 km^2 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 (α) and density-dependent (β) parameters of the Beverton-Holt model based on unfished recruitment (R_0) and Goodyear compensation ratio (CR) 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 (M_s^*) and density effect (B_s^*) to each stanza *s*. The stanza-specific α_s^* and β_s^* are calculated from these hypothesized rates using:

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

$$\beta_s^* = \frac{B_s^* \beta}{\sum_{s'} B_{s'}^* \prod_{s''=0}^{s'-1} \alpha_{s''}^*}. \tag{2}$$

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:

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

where *a* is age, *t* is time and S_a 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 (N_o). Model inputs (Table 1) were derived from available literature and data on the Apalachicola River or other Gulf Sturgeon populations.

Model Initialization and Scenarios

We initialized our population model (initial population size (N_0)) 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). 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 used for 1901 to 1959 are those estimated using SRA approaches 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 by-catch and boat strikes. This value of 0.14 was iteratively found to produce abundance at closure

(N_{1985}) consistent with that estimated 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 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 (β) for the Beverton-Holt function applied after t=57. 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 ($N_{t=1985\text{-}2084}$) 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 $N_{t=86}$ (1985) population size (Wooley and Crateau 1985). Fitting was done by tuning annual apical exploitation rate from 1960 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 ($U_{1960\text{-}1984}$) 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 due to 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 ($\text{anomaly}_{\text{strong}}$ = 2.0) and bust years occur by reducing recruitment in weak years ($\text{anomaly}_{\text{weak}}$ = [boom interval - $\text{anomoly}_{\text{strong}}$]/[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 in the Apalachicola River and compare 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 using model parameters presented in Table 1. We also calculate the transitional Spawning Potential Ratio (SPR; Mace et al. 1996) at the target recovery year 2023. 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. EPR_0 is unfished eggs per recruit, calculated as

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

where $lx_{0,a}$ 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 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 44% 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 N_{1985} abundance level were higher, then Gulf Sturgeon population would be predicted to recover to this carrying capacity sooner (Scenario 2; Figure 2). We predicted 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 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).

Cycles in recruitment led to a characteristic saw-tooth pattern in population growth, though this had little impact on recovery timing (Scenario 4; 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 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 baseline scenarios, with the population reaching about 64% of the carrying capacity by 2023 and exceeding carrying capacity after approximately 2040, effectively increasing long-term carrying capacity (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 t_1 increased abundance to approximately 72% of carrying capacity by 2023 compared to about 45% 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).

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 (U_{MSY}) and the biomass it is achieved at (B_{MSY}). Based on simulated vulnerability and population parameters, we estimate a U_{MSY} of 0.049 and a B_{MSY} of 32,922 kg. This results from a MSY of 1,616 kg annually. These numbers reflect a reduced carrying capacity for the population due to impacts from JWLD, which reduces MSY and B_{MSY} 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 (N_o, Scenario 2), as well as model sensitivity to parameter uncertainty in M (Scenario 3), M_{ai}, *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 result in predictions of much more rapid population recovery following the cessation of harvest (see Flowers 2008; Figure A1). 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 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. Model sensitivity was further examined for Ma_i and K. Increasing Ma_i linearly increased population recovery time with longer time to maturity, slightly reducing overall reproductive output by removing fecundity contributions of younger ages. Decreasing *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 U_{MSY}= 0.049 and *MSY* at current carrying capacity levels of only about 1,616 kg (<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 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 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 U_{MSY} in 2023 to be about 0.049 and *MSY* based on pre-JWLD carrying capacity estimates 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 (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 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 vs. the peak landings of 156,000 kg 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 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 long maturation time of Gulf Sturgeon (6-12 years, depending on sex), is a biological restriction on recovery rate, leading to the extended recovery time predicted by our model to rebuild population 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, Idaho (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 (U_{MSY} = 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. Any additional anthropogenic mortality will delay recovery of the population. Our results suggest efforts that reduce mortality below the M 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.

Spawning potential ratio 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, 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 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 m^3/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. 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 historic 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.

Acknowledgments

We thank the US Fish and Wildlife Service, National Oceanographic and Atmospheric Administration–Fisheries, Florida Nongame Wildlife Grants Program, Florida Cooperative Fish and Wildlife Research Unit, and the University of Florida for funding and administrative support for this work over many years. We thank S. Marynowski for editorial assistance and A. Kaeser, N. Farmer, and J. Heublein for reviewing earlier drafts of this manuscript.

References

Ahrens, R.N.M. and W.E. Pine, III. 2014. Informing recovery goals based on historical population size and extant habitat: a case study of the Gulf Sturgeon. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 6:274-286.

Auer, N. A. 1996. Response of spawning Lake Sturgeons to change in hydroelectric facility operation. Transactions of the American Fisheries Society 125:66-77.

Auer, N. A. and E. A. Baker. 2002. Duration and drift of larval Lake Sturgeon in the Sturgeon River, Michigan. Journal of Applied Ichthyology 18:557-564.

ASMFC 2017. Atlantic Sturgeon Benchmark Stock Assessment and Peer Review Report. Atlantic States Marine Fisheries Commission, Arlington, VA.

Bass, D. G. and D. T. Cox. 1985. River habitat and fisheries resources of Florida. *In* W. Seaman, Jr. editor, Florida Aquatic Habitat and Fishery Resources. Florida Chapter of the American Fisheries Society. Eustis, Florida. ISBN0-9616676-0-5.

Baum, J.K., R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley, P. A. Doherty. 2003. Collapse and conservation of shark populations in the North Atlantic. Science 299:389-392.

Beamesderfer, R. C. P., M. L. Simpson, and G. J. Kopp. 2007. Use of life history information in a population model for Sacramento Green Sturgeon. 79:315-337.

Berg, J. J., M. S. Allen, and K. J. Sulak. 2007. Population assessment of the Gulf of Mexico Sturgeon in the Yellow River, Florida. Pages 365-379 *in* J. Munro, D. Hatin, J. E. Hightower, K. McKown, K. J. Sulak, A. W. Kahnle, and F. Caron, editors. Anadromous Sturgeons: Habitats, Threats, and Management American Fisheries Society Symposium 56, Bethesda, Maryland.

Bezold, J. and D. L. Peterson. 2008. Assessment of Lake Sturgeon reintroduction in the Coosa River System, Georgia-Alabama. American Fisheries Society Symposium 62, Bethesda, Maryland.

Boreman, J. (1997). Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environmental Biology of Fishes, 48, 399–405.

Braaton, P. J., D. B. Fuller, L. D. Holte, R. D. Lott, W. Viste, T. F. Brandt, R. G. Legare. 2008. Drift dynamics of larval Pallid Sturgeon and Shovelnose Sturgeon in a natural side channel of the upper Missouri River, Montana. North American Journal of Fisheries Management. 28:808-826.

Bradford, M. J., G. C. Taylor, and J. A. Allen. 1997. Empirical review of Coho Salmon smolt abundance and the prediction of smolt production at the regional level. Transactions of the American Fisheries Society126:49-64.

Brown, J. J., and G. W. Murphy. 2010. Atlantic Sturgeon vessel-strike mortalities in the Delaware Estuary. Fisheries 35:72–83.

Bruch, R. M. (1999). Management of Lake Sturgeon on the Winnebago System-long term impacts of harvest and regulations on population structure. Journal of Applied Ichthyology, 15, 142–152.

Camp, E. V., K. Lorenzen, R. N. Ahrens, L. Barbieri, and K. M. Leber. 2013. Potentials and limitations of stock enhancement in marine recreational fisheries systems: An integrative review of Florida's Red Drum enhancement. Reviews in Fisheries Science, 21:388-402.

Camp, E. V., K. Lorenzen, R. N. M. Ahrens, and M. S. Allen. 2014. Stock enhancement to address multiple recreational fisheries objectives: an integrated model applied to red drum Sciaenops ocellatus in Florida. Journal of Fish Biology, 85: 1868-1889.

Christensen V, S. Guénette, J. J. Heymans, C. J. Walters, R. Watson, D. Zeller, D. Pauly. 2003. Hundred-year decline of North Atlantic predatory fishes. Fish and Fisheries 4:1-24.

Clugston, J. P., A. M. Foster, and S. H. Carr. 1995. Gulf Sturgeon, *Acipenser oxyrinchus desotoi*, in the Suwannee River, Florida, USA. Pages 215-224 in A. D. Gershanovich and T. I. J. Smith, editors. Proceedings, International Symposium on Sturgeons. VNIRO Publications, Moscow.

Coggins, L. G. 2007. Active adaptive management for native fish conservation in the Grand Canyon: implementation and evaluation. University of Florida. Doctoral Dissertation.

Dadswell, M. J. S.A.Wehrell, A.D. Spares, M. F. Mclean, J. W. Beardsall,L. M. Logan-Chesney, G. S. Nau, C. Ceapa, A. M. Redden, M. J. W. Stokesbury, 2016. The annual marine feeding aggregation of Atlantic Sturgeon *Acipenser oxyrinchus* in the inner Bay of Fundy: population characteristics and movement. Journal of Fish Biology 89:2107–2132.

Deepwater Horizon Natural Resource Damage Assessment Trustees. 2016. Deepwater Horizon oil spill: Final Programmatic Damage Assessment and Restoration Plan and Final Programmatic Environmental Impact Statement. Retrieved from http://www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan

Duncan, J. R. and J. L. Lockwood. 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. Biological Conservation 102:97-105.

Dunton, K. J., A. Jordaan, D. O. Conover, K. A. McKown, L. A. Bonacci, M. G. Frisk. 2015. Marine distribution and habitat use of Atlantic Sturgeon in New York lead to fisheries interactions and bycatch. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science. 7:18–32.

Flowers, H. J. 2008. Age-structured population model for evaluating Gulf Sturgeon recovery on the Apalachicola River, Florida. Masters Thesis. University of Florida.

Flowers, H. J., W. E. Pine, III, A. C. Dutterer, K. G. Johnson, J. W. Ziewitz, M. S. Allen, F. M. Parauka. 2009. Implications of modified flow regimes on Gulf Sturgeon spawning in the Apalachicola River, Florida. Transactions of the American Fisheries Society 138:1266–1284.

Freeman, M.C., C. M. Pringle, E.A. Greathouse, and B. J. Freeman. 2003. Ecosystem-level consequences of migratory faunal depletion caused by dams. Pages 255-266 *in* K.E. Limburg and J.R. Waldman, editors. Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Goodwin, N. B., A. Grant, A. L. Perry, N. K. Dulvy, and J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 63:494-509.

Goodyear, C. P. 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations. Pages 186-195 in W. Van Winkle., editor, 1977. Proceedings of the Conference on Assessing the Effects of Power-Plant-Induced Mortality on Fish Populations, Gatlinburg, Tennessee 3-6 May 1977. Pergamon Press, New York.

Goodyear, C. P. 1980. Compensation in fish populations. Pages 253–280 *in* C. H. Hocutt and J. R. Stauffer, Editors, 1980. Biological Monitoring of Fish. Lexington Books, Lexington, Massachusetts.

Grant, W. S., J. Jaspeter, D. Bekkevold, and M. Adkinson. 2017. Responsible genetic approach to stock restoration, sea ranching and stock enhancement of marine fishes and invertebrates. Reviews in Fish Biology and Fisheries 27:615-649.

Gross, M. R., J. Repka, C. T. Robertson, D.H. Secor, W. Van Winkle. 2002. Sturgeon conservation: insight from elasticity analysis. Pages 13-30 in W. Van Winkle, editor. Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, Maryland.

Gunter G., R. H. Williams, C. C. Davis, F. G. W. Smith. 1948. Catastrophic mass mortality of marine animals and coincident phytoplankton bloom on the west coast of Florida, November 1946 to August 1947. Ecological Monographs 18:309-324.

Haxton, T., M. Friday, T. Cano, C. Hendry. 2015. Assessing the magnitude of effect of hydroelectric production on Lake Sturgeon abundance in Ontario. North American Journal of Fisheries Management 35:930-941.

Hightower, J. E., M. Loeffler, W. C. Post, and D. L. Peterson. 2015. Estimated survival of subadult and adult Atlantic Sturgeon in four river basins in the southeastern United States. Marine and Coastal Fisheries 7: 514-522.

Hilborn, R. 2007. Reinterpreting the state of fisheries and their management. Ecosystems 10:1362-1369.

Hilborn, R. D. J. Hively, O. P. Jensen, and T. A. Branch. 2014. The dynamics of fish populations at low abundance and prospects for rebuilding and recovery. ICES Journal of Marine Science 71:2141-151

Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty. Chapman and Hall, New York.

Hilton, E. J., B. Kynard, M.T. Balazik, A. Z. Horodosky, and C. B. Dillman. 2016. Review of the biology, fisheries, and conservation status of the Atlantic Sturgeon, (*Acipenser oxyrinchus oxyrinchus* Mitchill, 1815). Journal of Applied Ichthyology 32:30-66

Hoag H. 2003. Atlantic Cod meet icy death. Nature 422: 792.

Hoover, A. 2002. A century of sturgeon: The history, biology, and future of the Gulf of Mexico Sturgeon in Florida. Technical paper. The University of Florida, Gainesville, FL.

Holtgren, J. M., S. A. Ogren, A. J. Paquet, and S. Fajfer. 2007. Design of a portable streamside rearing facility for Lake Sturgeon. North American Journal of Aquaculture 69:317-323.

Huff, J. A. 1975. Life history of Gulf of Mexico Sturgeon, *Acipenser oxyrinchus desotoi*, in Suwannee River, Florida. Florida Marine Research Publications Number 16.

Hutchings, J. A. 2000. Collapse and recovery of marine fisheries. Nature 406:882-885.

Hutchings, J. A. and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. Bioscience 54:297-309.

Irelands, S.C., R. C. P. Beamesderfer, V. L. Paragamian, V. D. Wakkinen, and J. T. Siple. 2002. Success of hatchery-reared juvenile White Sturgeon (*Acipenser transmontanus*) following release in the Kootenai River, Idaho, USA. Journal of Applied Ichthyology 18:642-650.

Jenkins, R. E., and N. M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.

Johnson, J. H., S. R. LaPan, R. M. Klindt, and A. Schiavone. 2006. Lake Sturgeon spawning on artificial habitat in the St. Lawrence River. Journal of Applied Ichthyology 22:465-470.

Khoroshko, P. A. and A. D. Vlasenko. 1970. Artificial spawning grounds of sturgeon. Journal Ichthyology 10:286–292.

Kruk, A. and T. Penczak. 2003. Impoundment impact on populations of facultative riverine fish. Annales De Limnologie-International Journal of Limnology. 39:197-210.

LaHaye, M., A. Branchaud, M. Gendron, R. Verdon, and R. Fortin. 1992. Reproduction, early life history, and characteristics of the spawning grounds of the Lake Sturgeon (*Acipenser fulvescens*) in Des Prairies and L'Assomption rivers, near Montreal, Quebec. Canadian Journal of Zoology 70:1681–1689.

Leitman, S., W. E. Pine, III, and G. Kiker. 2016. Management options during the 2011–2012 drought on the Apalachicola River: a systems dynamic model evaluation. Environmental management 58:193-207.

Limburg, K. E. and J. R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. Bioscience 59:955-965.

Lorenzen, K., 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philosophical Transactions of the Royal Society B: Biological Sciences 360:171-189.

Mace, P.M., Gregory, D., Ehrhardt, N., Fisher, M., Goodyear, P., Muller, R., Powers, J., Rosenberg, A., Shepherd, J., Vaughan, D. and Atran, S., 1996. An evaluation of the use of SPR levels as the basis for overfishing definitions in the Gulf of Mexico finfish fishery management plans. Gulf of Mexico Fishery Management Council, Final Report, Tampa, Florida.

Mailhot, Y., P. Dumont, and N. Vachon. 2011. Management of the Lake Sturgeon *Acipenser fulvescens* population in the lower St. Lawrence River (Quebec, Canada) from the 1910s to the present. Journal of Applied Ichthyology 27:405-410.

Martell, S. J. D, W. E. Pine, III, and C. J. Walters. 2008. Parameterizing age-structured models from a fisheries management perspective. Canadian Journal of Fisheries and Aquatic Sciences 65:1586-1600.

McAdam, D. S. O., 2015. Retrospective weight-of-evidence analysis identifies substrate change as the apparent cause of recruitment failure in the upper Columbia River White Sturgeon (*Acipenser transmontanus*). Canadian Journal of Fisheries and Aquatic Sciences 72:1208-1220.

McDougall, C.A., D. J. Pisiak, C. C. Barth, M. A. Blanchard, D. S. MacDonell, D. Macdonald. 2014. Relative recruitment success of stocked age-1 vs age-0 Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Nelson River, northern Canada. Journal of Applied Ichthyolgy 30:1451-1460.

Melis, T. S., W. E. Pine, III, J. Korman, M. D. Yard, S. Jain and R. S. Pulwarty. 2016. Using large-scale flow experiments to rehabilitate Colorado River ecosystem function in Grand Canyon: basis for an adaptive climate-resilient strategy. In *Water Policy and Planning in a Variable and Changing Climate* (pp. 315-345). CRC Press Boca Raton, FL.

Morrow, J. V., Jr., J. P. Kirk, K. J. Killgore, H. E. Rogillio, and C. Knight. 1998. Status and recovery potential of Gulf Sturgeon in the Pearl River system, Louisiana-Mississippi. North American Journal of Fisheries Management 18:798-808.

Morrow, J. V., Jr., J. P. Kirk, K. J. Killgore, and H. E. Rogillio. 1999. Recommended enhancements to the Gulf Sturgeon recovery and management plan based on Pearl River studies. North American Journal of Fisheries Management 19:1117-1121.

Myers, R. A. and B. Worm. 2003. Rapid world-wide depletion of predatory fish communities. Nature 423:280-283.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4-21.

Paragamian, V.L, R. C. P. Beamesderfer, and S.C. Ireland. 2005. Status, population dynamics, and future prospects of the endangered Kootenai River White Sturgeon population with and without hatchery intervention. Transactions of the American Fisheries Society 134:518-532.

Pine, W. E., III., M. S. Allen, and V. J. Dreitz. 2001. Population viability of the Gulf of Mexico Sturgeon: Inferences from capture-recapture and age-structured models. Transactions of the American Fisheries Society 130:1164-1174.

Pine, W.E., III, and S. J. D. Martell. 2009. Status of Gulf Sturgeon in Florida waters: A reconstruction of historical population trends to provide guidance on conservation targets. Stock assessment to NOAA-Fisheries as part of the Gulf Sturgeon Working Group Annual Review Meeting available at http://wec.ufl.edu/floridarivers/sturgeon.htm. Accessed December 2018.

Pine, W.E, III, S. J. D. Martell, C. J. Walters, J. F. Kitchell. 2009. Counterintuitive responses of fish populations to management actions: some common causes and implications for predictions based on ecosystem modeling. Fisheries. 34: 165-180.

Pine, W. E., III, B. Healy, E. O. Smith, M. Trammell, D. Speas, R. Valdez, M. Yard, C. J. Walters, R. Ahrens, R. Vanhaverbeke, D. Stone. 2013. An individual-based model for population viability analysis of Humpback Chub in Grand Canyon. North American Journal of Fisheries Management 33:626-41.

Pine, W. E., III, C. J. Walters, E. V. Camp, R. Bouchillon, R. Ahrens, L. Sturmer and M. E. Berrigan, 2015. The curious case of eastern oyster *Crassostrea virginica* stock status in Apalachicola Bay, Florida. *Ecology and Society*, *20*(3).

Pitkitch, E.K., P. Doukakis, L. Lauck, P. Chakrabarty, and D.L. Erickson. 2005. Status, trends, and management of sturgeon and paddlefish fisheries. Fish and Fisheries 6:233-265.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Randall, M. T. and K. J. Sulak. 2012. Evidence of autumn spawning in Suwannee River Gulf Sturgeon Acipenser oxyrinchus desotoi. Journal of Applied Ichthyology. 24:489-495.

Rieman, B. E., and R. C. Beamesderfer. 1990. White Sturgeon in the Lower Columbia River: is the stock overexploited? North American Journal of Fisheries Management 10:388-396.

Rudd, M. B., R. N. M. Ahrens, W. E. Pine, III, and S. K. Bolden. 2014. Empirical, spatially explicit natural mortality and movement rate estimates for the threatened Gulf Sturgeon (*Acipenser oxyrinchus desotoi*). Canadian Journal of Fisheries and Aquatic Sciences 71:1407–1417.

Ruhl, J. B., 2005. Water wars, eastern style: Divvying up the Apalachicola-Chattahoochee-Flint River basin. *Journal of Contemporary Water Research & Education*, *131*(1), pp.47-54.

Schram, S. T., J. Lindgren, and L. M. Evrard. 1999. Reintroduction of Lake Sturgeon in the St. Louis River, Western Lake Superior. North American journal of Fisheries Management 19:815-823.

Schueller, P. and D. L. Peterson. 2010. Abundance and recruitment of juvenile Atlantic Sturgeon in the Altamaha River, Georgia. Transactions of the American Fisheries Society 139:1526-1535.

Stevens, P. W., D. A. Blewett, and J. P. Casey. 2006. Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of Hurricane Charley. Estuaries and Coasts 29:997–1003.

Sulak, K. J. and M. Randall. 2002. Understanding sturgeon life history: Enigmas, myths, and insights from scientific studies. Journal of Applied Ichthyology 18:519-528.

Sulak, K. J., F. Parauka, W. T. Slack, R. T. Ruth, M. T. Randall, K. Luke, M. F. Mettee and M. E. Price. 2016. Status of scientific knowledge, recovery progress, and future research directions for the Gulf Sturgeon, Acipenser oxyrinchus desotoi Vladykov, 1955. *Journal of Applied Ichthyology*, *32*, pp.87-161.

USFWS and the Gulf States Marine Fisheries Commission. 1995. Gulf Sturgeon recovery plan. U.S. Fish and Wildlife Service, Atlanta.

USFWS. 2008. Biological opinion on the U.S. Army Corps of Engineers, Mobile District, revised interim operating plan for Jim Woodruff Dam and the associated releases to the Apalachicola River. U.S. Fish and Wildlife Service, Panama City, Florida.

Vélez-Espino, L. A., & Koops, M. A. (2009). Recovery potential assessment for Lake Sturgeon in Canadian designatable units. North American Journal of Fisheries Management, 29, 1065–1090.

Wakeford, A. 2001. State of Florida conservation plan for Gulf Sturgeon *Acipenser oxyrinchus desotoi.* FMRI Technical Report TR-8. Florida Fish and Wildlife Conservation Commission.

Walters, C. J. 1986. Adaptive Management of Renewable Resources. The Blackburn Press. Caldwell, NJ.

Walters, C. J., R. Hilborn, and V. Christensen. 2008. Surplus production dynamics in declining and recovering fish populations. Canadian Journal of Fisheries and Aquatic Sciences 65:2536-2551.

Walters, C. J. and S. J. D. Martell. 2004. Fisheries Ecology and Management. Princeton University Press. Princeton, N.J.

Watling, L. and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology 12:1180-1197.

Worm, B., R. Hilborn, J. Baum, T. Branch, J. Collie, C. Costello, M. Fogarty, E. Fulton, J.Hutchings, S. Jennings, O. Jensen, H. Lotze, P. Mace, T. McClanahan, C. Minto, S. Palumbi, A. Parma, D. Ricard, A. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding global fisheries. Science 325:578-585.

Wooley, C. M. and E. J. Crateau. 1985. Movement, microhabitat, exploitation, and management of Gulf of Mexico Sturgeon, Apalachicola River, Florida. North American Journal of Fisheries Management 5:590-605.

Zehfuss, K. P., J. E. Hightower, and K. H. Pollock. 1999. Abundance of Gulf Sturgeon in the Apalachicola River, Florida. Transactions of the American Fisheries Society 128:130-143.

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
M_s^*	Relative mortality rate of each pre-recruit stanza	{1,1}	Allows equal maximum survival through each stanza
B_s^*	Relative density effect of each pre-recruit stanza	{0.5,0.5}	Allows equal density effect through each stanza
α_s^*	Maximum survival of multi-stanza Beverton-Holt function	{0.92,0.92}	Calculated
β_s^*	Density dependent parameter of multi-stanza 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	Pine and Ahrens 2014
N_o	Initial pre-exploitation population size (95% credible 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, personal communication
Z	Total mortality	variable	

Table 2. Descriptions of each of the age-structure model scenarios, including 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) pre-dam and R_0 = 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	0.98
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_{adult}=0.070	0.95
	M_{adult}=0.085	0.97
	M_{adult}=0.105	0.99
	M_{adult}=0.12	0.99
	M_{adult}=0.145	1.00
4	High recruitment every 2nd year	NA
	High recruitment every 4th year	0.98
	High recruitment every 5th year	0.98
5	Stock 2500 for 5 years	0.98
	Stock 5000 for 5 years	0.98
	Stock 2500 for 20 years	0.98
	Stock 5000 for 20 years	0.98

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 N_0 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 (Pine and Martell 2009).

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 lines from left to right are Jim Woodruff Lock and Dam construction (reducing carrying capacity), the end of commercial fishing, and 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, brown line is current carrying capacity (*k*, N=8,784 Gulf Sturgeon), vertical dashed lines from left to right are Jim Woodruff Lock and Dam construction (reducing carrying capacity), the end of commercial fishing, and 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, brown line is current carrying capacity (*k*, N=8,784 Gulf Sturgeon), vertical dashed lines from left to right are Jim Woodruff Lock and Dam construction (reducing carrying capacity), the end of commercial fishing, and 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, brown line is current carrying capacity (*k*, N=8,784 Gulf Sturgeon), vertical dashed lines from left to right are Jim Woodruff Lock and Dam construction (reducing carrying capacity), the end of commercial fishing, and the 2023 target recovery year from the GSRP.

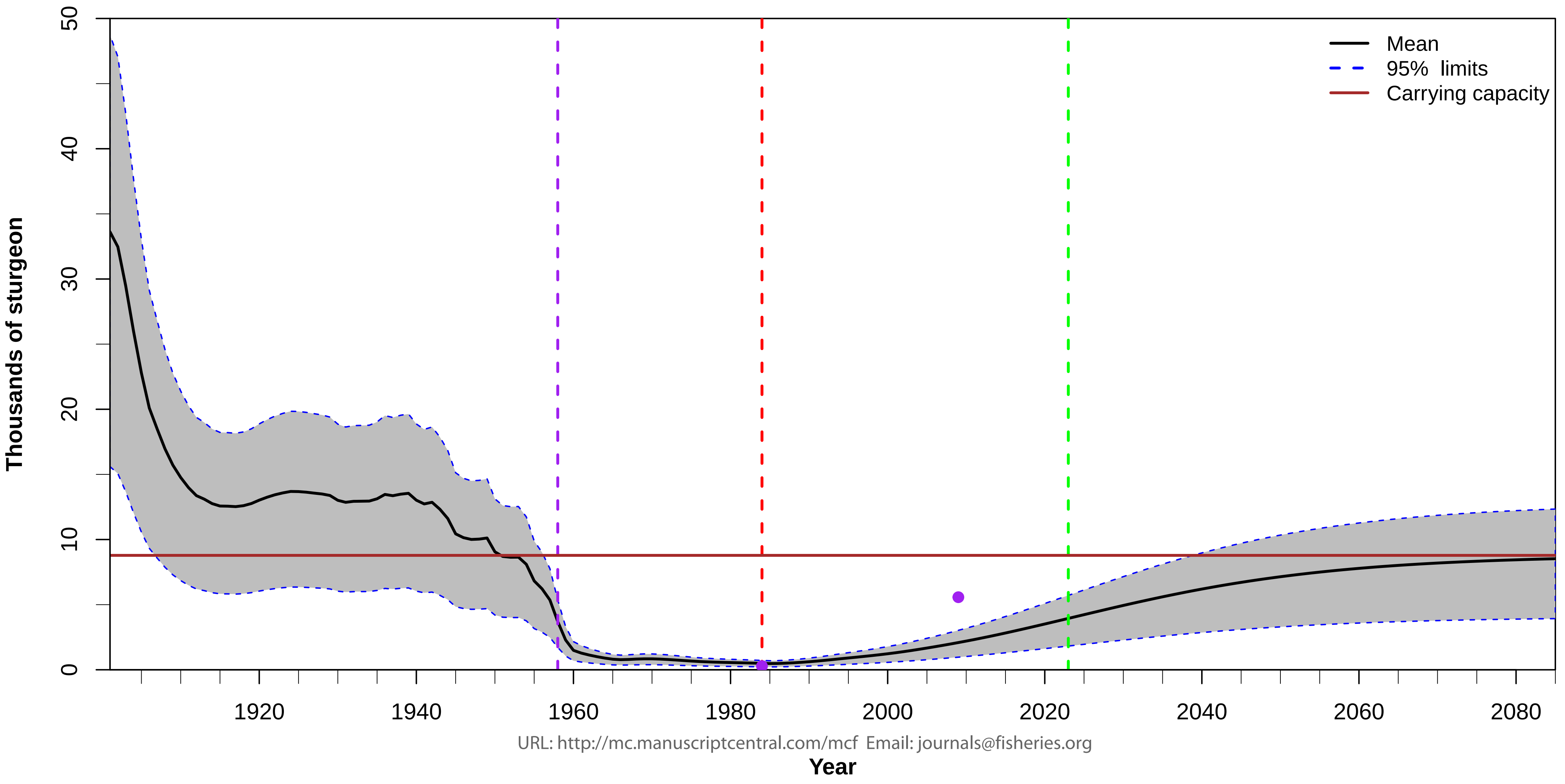
Figure 6. Surface plot representing theoretical Gulf Sturgeon population subjected to harvest and then allowed to recovery as predicted by our age-structured model in the baseline scenario. Year of simulation on x-axis, age-class on y-axis. Each cell represents an age class in a given year with the color 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 1947, 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.

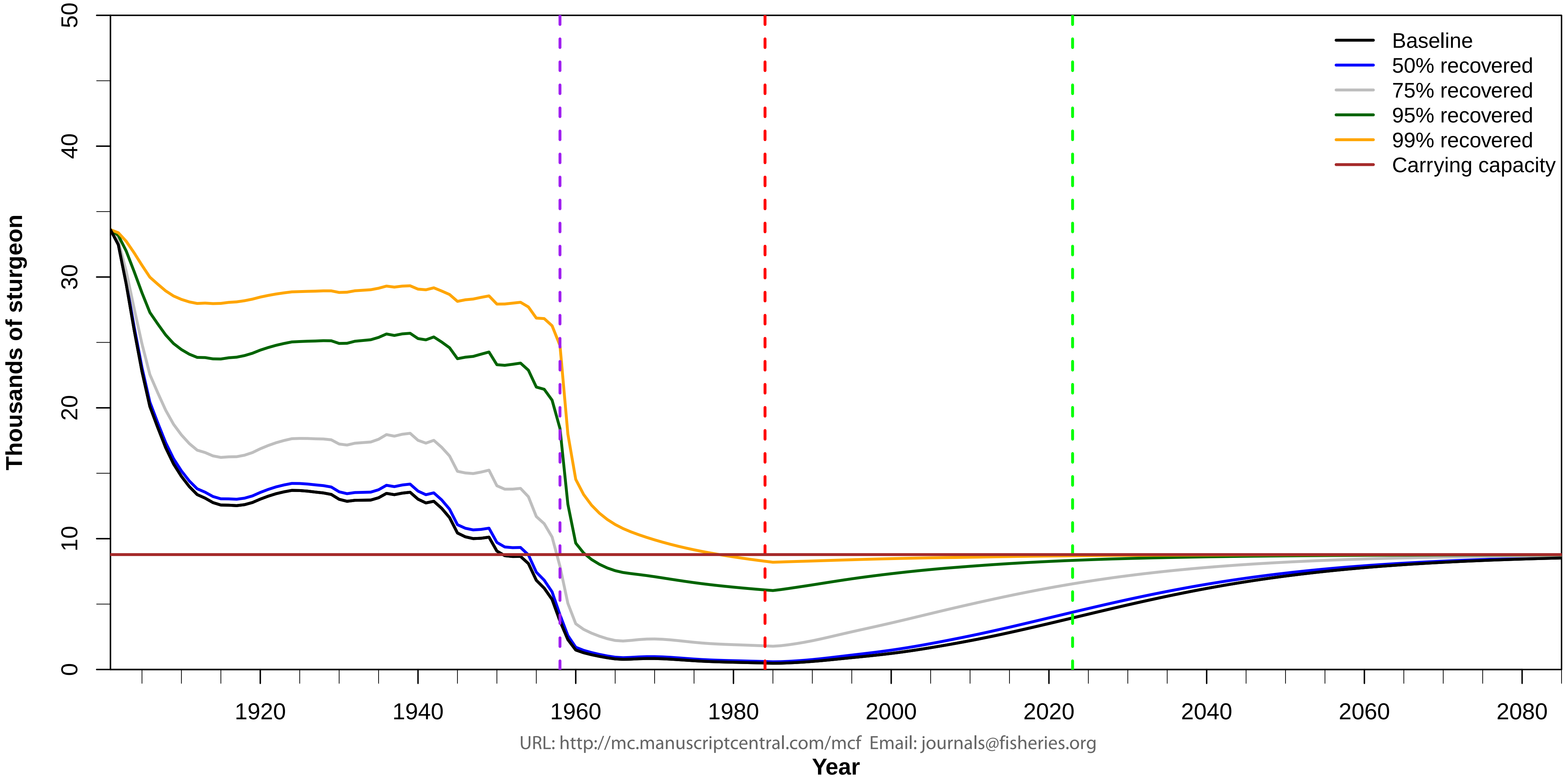
Appendix

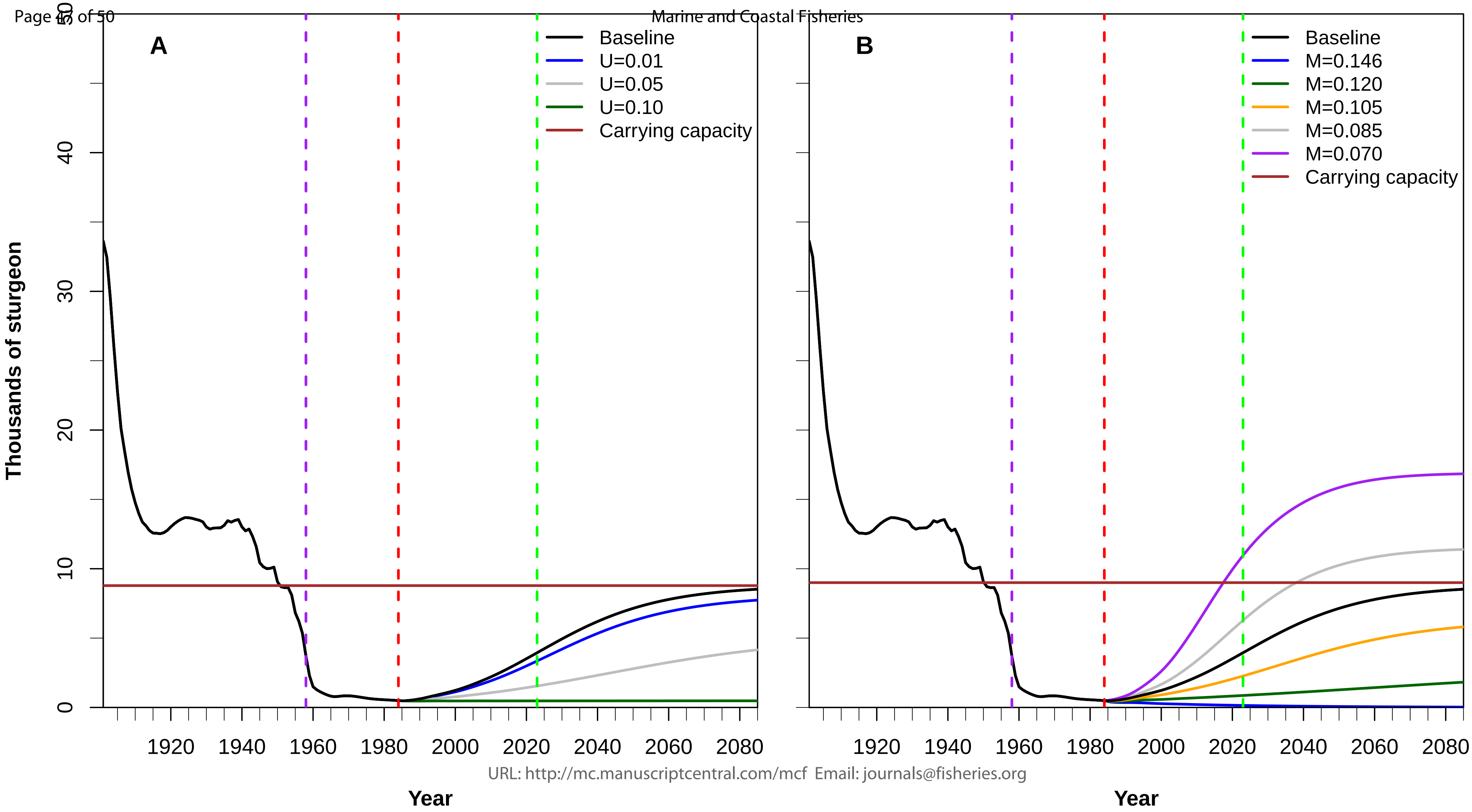
Model Sensitivity

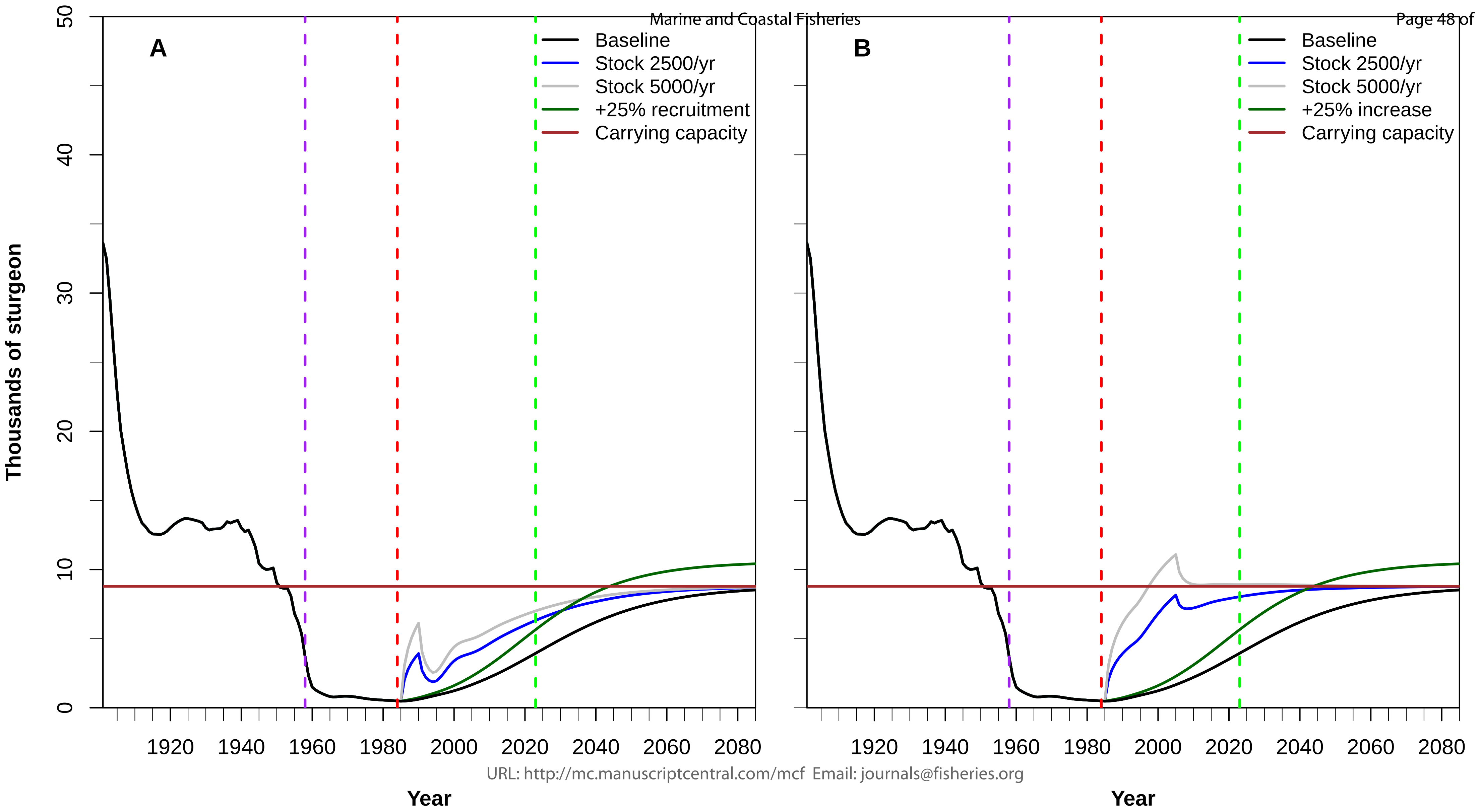
We assessed model results to a range of *recK* (Figure A.1). Higher *recK* values allowed the Gulf Sturgeon population to recover much faster than under the baseline simulations with lower *recK* values. The *recK* value used of 5 seems to reflect general recovery patterns observed for Gulf Sturgeon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

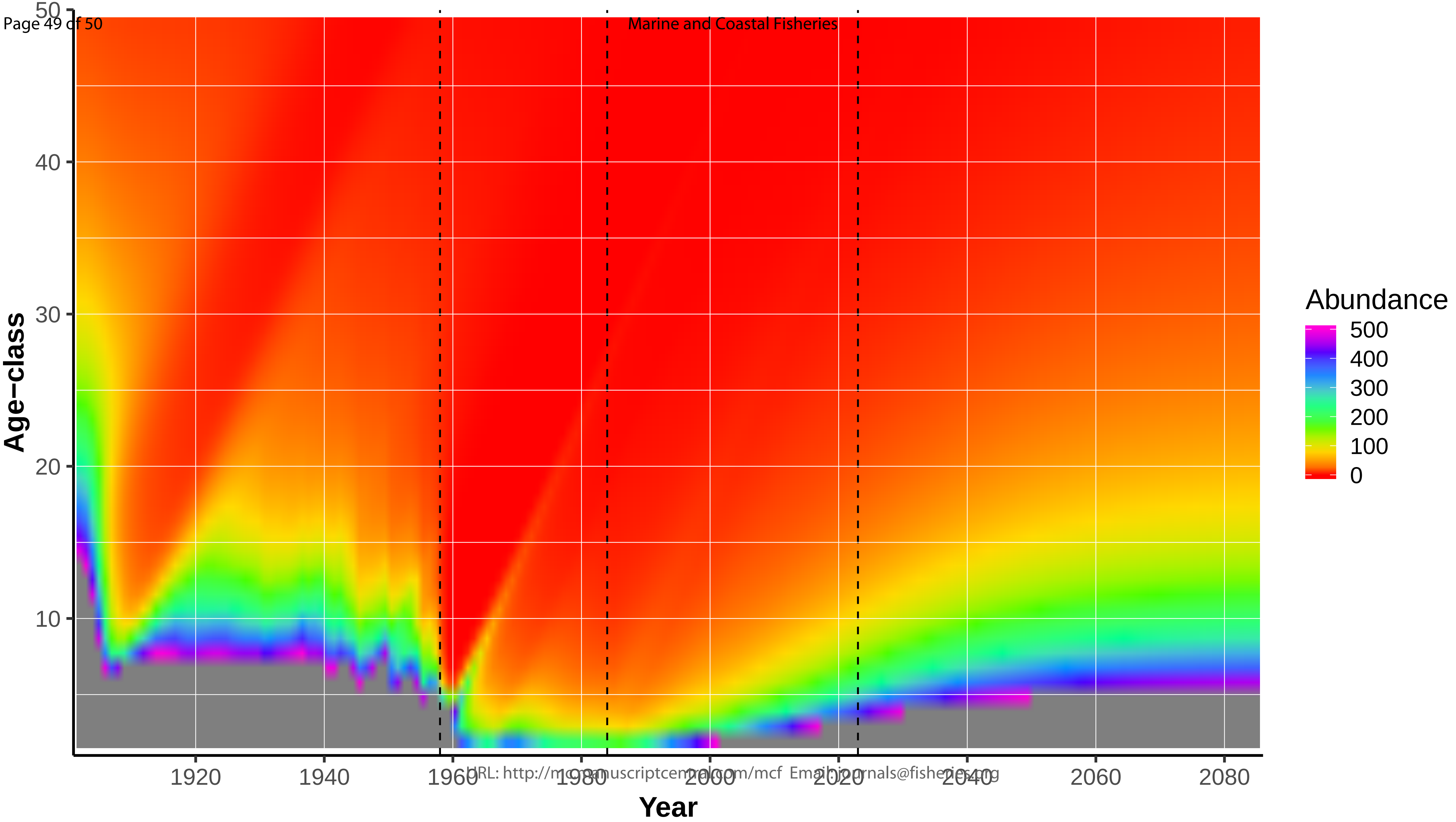
Figure A1. An evaluation of model sensitivity to a range of recruitment compensation values (*recK*) compared to baseline predictions (black line) which used a *recK* value =5. Black line represents baseline recovery trajectory, brown line is current carrying capacity (*k*, N=8,784 Gulf Sturgeon), vertical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

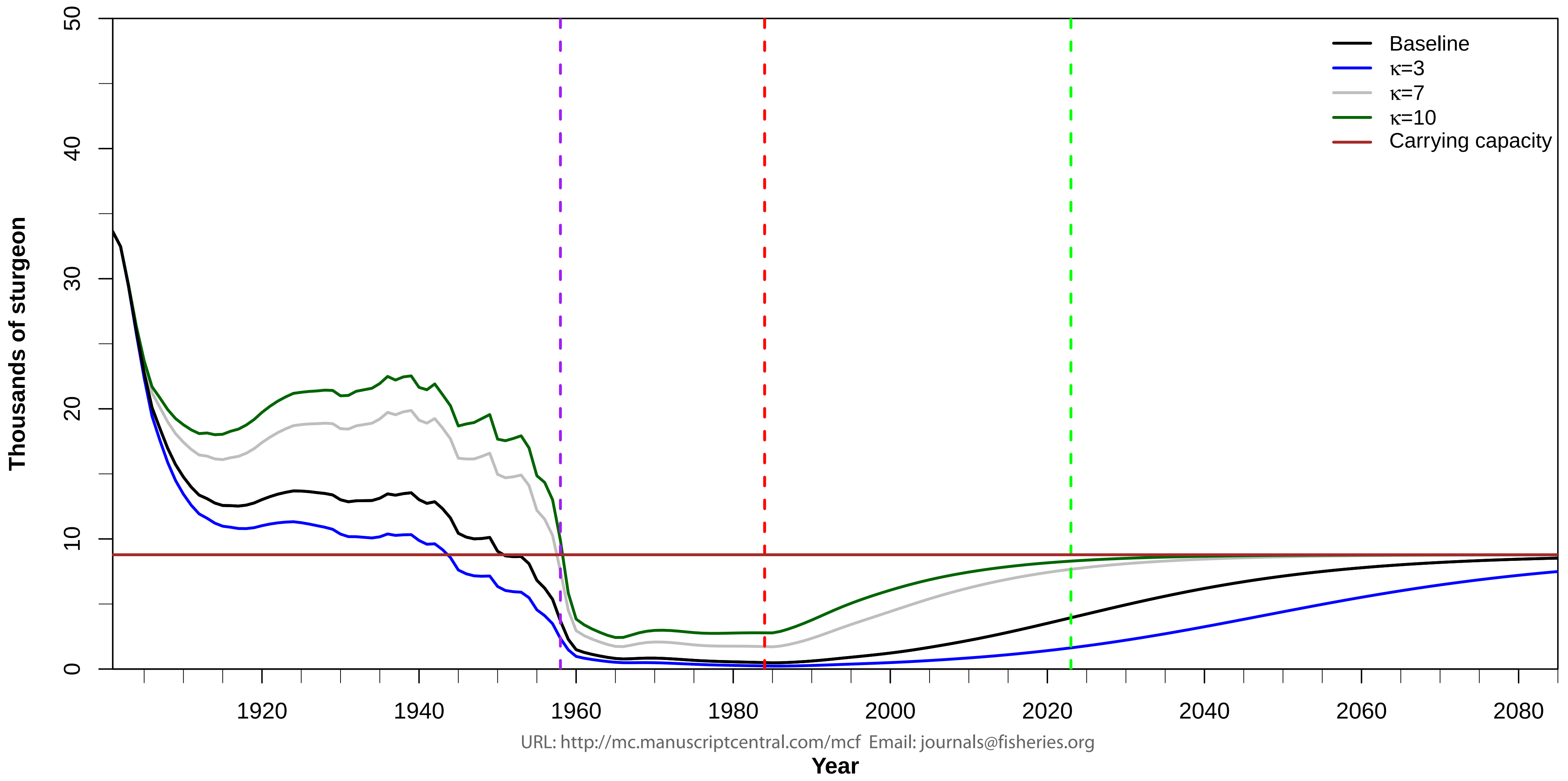

Mean
95% limits
Carrying capacity
Thousands of sturgeon
Year
0
10
20
30
40
50
1920
1940
1960
1980
2000
2020
2040
2060
2080


Baseline
50% recovered
75% recovered
95% recovered
99% recovered
Carrying capacity
Thousands of sturgeon
0
10
20
30
40
50
1920
1940
1960
1980
2000
2020
2040
2060
2080
Year


A
Baseline
U=0.01
U=0.05
U=0.10
Carrying capacity
B
Baseline
M=0.146
M=0.120
M=0.105
M=0.085
M=0.070
Carrying capacity
Thousands of sturgeon
0
10
20
30
40
50
1920
1940
1960
1980
2000
2020
2040
2060
2080
Year
Year


A
B
Baseline
Stock 2500/yr
Stock 5000/yr
+25% recruitment
+25% increase
Carrying capacity
Thousands of sturgeon
0
10
20
30
40
50
1920
1940
1960
1980
2000
2020
2040
2060
2080
Year


Age−class
50
40
30
20
10
Year
1920
1940
1960
1980
2000
2020
2040
2060
2080
Abundance
500
400
300
200
100
0


Baseline
κ=3
κ=7
κ=10
Carrying capacity
Thousands of sturgeon
0
10
20
30
40
50
1920
1940
1960
1980
2000
2020
2040
2060
2080
Year