GULF STURGEON POPULATION VIABILITY MAY BE LIMITED BY CREEPING
CHRONIC RATES OF ADULT MORTALITY

Background

Gulf Sturgeon *Acipenser oxyrinchus desotoi* stocks were significantly reduced in

the mid-to-late 20th century due to a combination of factors (i.e., overfishing, dam

construction, and habitat degradation), which led to listing as a threatened species

under the US Endangered Species Act (ESA) in 1991 (56 FR 49653; National Oceanic

Atmospheric Administration [NOAA] and U.S. Fish and Wildlife Service [USFWS] 1991).

Gulf Sturgeon have been managed as a single stock (i.e., range-wide as a species)

under the ESA, as the species is considered threatened over most, if not all, of its range

(NOAA and USFWS 1991). Despite decades of ESA protections, Gulf Sturgeon are not

recovering at a rate to be delisted by the 2023 target (Flowers et al. 2020), in the Gulf

Sturgeon Recovery Plan (GSRP; USFWS and Gulf States Marine Fisheries

Commission [GSMFC] 1995).

In 1996, USFWS and NOAA adopted a joint policy (61 FR 4722) that outlined

classification criteria for distinct population segments (DPSs), which they generally

defined as discrete and significant populations of vertebrate species and subspecies

that may be managed as individual units under the ESA (USFWS and National Marine

Fisheries Service [NMFS] 1996). Within this DPS framework, managers could meet the

varying individual needs of populations of listed species and potentially reclassify

specific populations to extend or remove ESA protections. Rudd et al. (2014) and

Chapter 2 suggested that Gulf Sturgeon may warrant classification as DPS's. Gulf

Sturgeon population characteristics that support DPS classification include genetic

distinctness, high river fidelity, and differential survival across their range, specifically

lower survival in the western Gulf of Mexico (Morrow et al. 1998; Rudd et al. 2014; Chapters 2 and 3). If extirpation risk also differs among river populations, this may further justify the reclassification of this listed species into DPSs to facilitate the direction of recovery actions to the population(s) that may need it most.

Population Viability Analysis (PVA) is a wide-ranging suite of quantitative analytical methods for assessing threats to fish and wildlife populations that commonly uses simulation-based methods of evaluating population persistence in the context of differing population dynamic rates, given some initial population size (Beissinger and McCullough, 2002; Morris & Doak, 2002). Therefore, PVA is built upon a synthesis of knowledge about a species' life history, threats, environment, and management objectives. Most imperiled species lack important life history information needed to inform PVA (Coulson et al. 2001; Schultz and Hammond 2003). Fortunately, Gulf Sturgeon research dates back several decades (Huff 1975), and recent efforts to synthesize and model these multi-decadal data (Ahrens and Pine 2014; Flowers et al. 2020; Chapter 3) have generated the population dynamic estimates needed to forecast Gulf Sturgeon population fates to better understand potential conservation needs that may vary among these populations that are currently managed uniformly as a single species.

In this study, our objective was to assess the extirpation risks for Gulf Sturgeon populations with a range of starting sizes and select mortality rates estimated in Chapters 2 and 3. To evaluate the effects of various possible mortality sources on these populations, we simulated the following threats in the context of a range of population sizes and estimated the probability of extirpation along various time horizons: 1) chronic

increases in baseline mortality, 2) varying episodic mortality event frequency, and 3) varying recruitment failure frequency.

Materials and Methods

We used a PVA simulator to transparently reflect uncertainty in the fate of Gulf Sturgeon populations under a variety of scenarios (i.e., threat-population size combinations). In our simulations, we separated populations into three life stages: pre-recruits, juveniles/sub-adults, and adults. Pre-recruits were subject to density-dependent mortality and were separated into multiple stanzas, where the strength of density dependence was specific to each stanza.

Model Description

We modified a PVA model originally detailed in Pine et al. (2013) for assessing directed take of Humpback Chub *Gila cypha* in Arizona and later used to assess risks to populations of two native fish species in New Mexico from habitat modifications (Pine et al. 2017). The original model was coded in Microsoft Visual Basic for Applications (VBA) by Carl Walters (University of British Columbia) and was migrated to program R (R Core Team 2022) and updated to its current form by Brett van Poorten (Simon Fraser University). I updated model inputs based on results from chapters 2 and 3 in this dissertation.

A summary of the equations used to inform the PVA model is included in Table 1. This model is an individual-based PVA model that simulates the dynamics of female fish only. Each individual PVA simulation was initialized by creating a list of N_0 (i=1, 2, …,N_0) individual female fish which represents the number of female fish which were informed by a range of recent population estimates for Gulf Sturgeon rivers identified as critical habitat (NOAA and USFWS 2003; USFWS and NMFS 2022). An age was assigned to

3

each individual fish based on an assumed initial stable age distribution based on age-specific survival rates S_a. For each subsequent year of simulation t = 1, 2, 3,,…, T the age of each individual fish increases by 1. Fish die and are removed from the population (list of individual female fish) with the probability of 1-$S(a_i)$ and the sum of the survival fish is the total surviving population at time N_t. Random stochasticity is introduced into each individual simulation based on the distribution of the initial age structure and survival and the N_0 for each simulation. For age-classes age 1+ relative survival rates are used based on a Lorenzen function (Lorenzen 2000). We also assumed that older fish had a lower variance in survival than young fish. Random effects on survival were included to mimic environmental effects (Pine et al. 2013) by varying the maximum survival A_s (in the Beverton-Holt stock recruitment formulation, Walters and Martell 2004) for each life history stanza included in the model (pre-recruit, juvenile/sub-adult, and adult). Life stanzas were used to screen specific scenarios of interest such as recruitment failure (juvenile stanza) or changes to adult mortality (adult stanza). Each stanza and year were independent and assumed a maximum survival followed a normal distribution with a specified mean and standard deviation. This survival rate was informed by estimates from Chapters 2 and 3. Recruitment for each year was a function of the number of individual fry (E_t) computed for that year (from the list of all female fish) and the survival of these fry through each of the life stanzas (stanza-specific survival rate). The number of recruits was then added to the number of live fish at age 1.

Model input parameters are summarized in Table 2. Where possible, inputs were informed by results from Chapters 2 or 3. Fish were recruited to the vulnerable population at age 4. Published estimates of Gulf Sturgeon recruitment compensation

ratio (*recK*), the improvement in juvenile survival at low population levels relative to carrying capacity (Goodyear 1977, 1980), range from 3.9 to 5 (Flowers 2008; Flowers et al. 2009, 2020; Ahrens and Pine 2014). Higher *recK* values imply that populations have larger increases in juvenile survival at low population sizes than at carrying capacity, which implies that such populations are more resilient to population declines due to this compensatory response to depletion (Walters and Martell 2004). Given the lack of available data on juvenile Gulf Sturgeon survival rates at different abundance levels, we used a highly conservative value of *recK* = 2 which is lower than observed values for many species (Goodwin et al. 2006). If the actual value of *recK* is >2, the resilience of these populations would be greater than these models suggest (e.g., lower extirpation probabilities, faster recovery).

Model Scenarios

I compared extirpation risk among the following three threats to better understand how extirpation risk may change if threats to different life stages were realized: Threat 1 – increases in chronic mortality rates ("chronic creep"); Threat 2 – increases in episodic mortality frequency; and Threat 3 – increases in recruitment failure frequency. These comparisons, informed by possible population threats discussed in the Gulf Sturgeon community in the last twenty years (USFWS and NMFS 2022; Dula et al. 2022), were also selected to provide insight into the relative importance of juvenile mortality (recruitment failure) and adult mortality (chronic and episodic mortality) to population viability. The simulated scenarios are summarized in Table 3.

Initial vulnerable abundance (i.e., number of adult females; N_0) in these simulations ranged between 100 and 10,000 individuals to represent the wide range of Gulf Sturgeon population sizes across the Gulf of Mexico (see summary in USFWS and

5

NMFS 2022). I varied PVA model input parameters such as N_0 and adult mortality which informed various other equations related to survival at age, which then informed fecundity equations to determine recruitment. This recurring annual update of population size from these starting values occurred for 200 years.

The frequency of events (recruitment failure or mortality) represents mean frequencies of occurrence over the maximum 200-year time horizons. Extirpation probabilities represent the percentage of the 1,000 trials of each scenario that resulted in population collapse over 50-year, 100-year, and 200-year time horizons. A simulation trial that resulted in extirpation in 50 years was considered a population that went extinct over the 100 and 200 years as well.

Results

Creeping Chronic Mortality Rates

Baseline mortality rates of 0.11 resulted in no extirpation risk across all population sizes and time horizons (Scenarios 1–4; Tables 3–4; Figure 1). However, when adult mortality rates increased to 0.13, 200-year extinction probabilities ranged between 27.4% and 90.5% (Scenarios 5–8; Tables 3–4). A further increase in chronic mortality to 0.15 resulted in an 11.3% 50-year extirpation probability for populations starting with 100 fish, 100-year extirpation probabilities >26% for all populations starting with ≤1000 individuals, and full extirpation for all population sizes after 200 years (Scenarios 9–12; Tables 3–4).

Increasing Episodic Mortality Event Frequency

When the average occurrence of episodic mortality events was 1/50 years, we observed a 15.9% 200-year extirpation probability for populations starting with 100 individuals (Scenario 13; Tables 3–4). There was effectively no extirpation risk for

populations starting with ≥500 fish (Scenarios 14-16; Tables 3–4). If mean event

frequency increased to 1/25 years, the range of 200-year extirpation probabilities was

6.4–64.1% across all initial population sizes (Scenarios 17–20; Tables 3–4). The

maximum simulated mean episodic event frequency of 1/10 years resulted in an 11.8%

50-year extirpation probability for populations starting with 100 fish, 100-year extirpation

probabilities >25% for all populations starting with ≤1000 individuals and full extirpation

for all population sizes after 200 years (Scenarios 21–24; Tables 3–4).

Increasing Recruitment Failure Frequency

Within the context of a baseline adult mortality rate of 0.11, recruitment failure

1/10 years resulted in effectively no extirpation risk for populations ≥500 initial

individuals (Scenarios 30–32; Tables 3–4). When the mean frequency of recruitment

failure increased to 1/5 years, extirpation probabilities ranged between 5.3% and 21.2%

for these same ≥500 initial fish populations (Scenarios 30–32; Tables 3–4). Across both

the five- and ten-year mean frequencies, there was a small probability (<5%) of

extirpation for the smallest initial population size (Scenarios 25 and 29; Tables 3–4).

Across a 200-year time horizon, these small populations had the greatest extirpation

probabilities; (10.2% and 64.6%; Scenarios 25 and 29; Tables 3–4).

<center>**Discussion**</center>

Overall, this work suggests that increases in adult Gulf Sturgeon mortality are a

greater risk to viability than recruitment failure. Flowers et al. (2020) developed an age-

structured population model for Gulf Sturgeon to examine their population recovery

characteristics and determined that any additional adult Gulf Sturgeon mortality beyond

their simulated levels of 0.095 would likely slow population recovery. We observed that

increases in both chronic and episodic mortality frequency both led to rapid increases in

<center>7</center>

extinction risk across all time horizons (50, 100, 200 years). Because Gulf Sturgeon

maximum age is likely at least 50 years (Chapter 3), these time horizons represent

relatively few generations of Gulf Sturgeon within a population recovery, or extinction,

context. Despite the difficulty of imagining a world 200 years in the future, this time

horizon only represents about four generations for this long-lived species. Although this

may present management challenges, it is important to interpret these scenarios

through this extended, foggy lens to better understand the long-term ramifications of

increases in mortality.

In the absence of quantitative standards for interpreting ESA status using

extinction risk estimates, some studies have suggested their own thresholds. According

to Hamilton and Moller (1995), a population with a ≤5% extirpation risk over 100 years is

not at risk of extinction. Therefore, this applied definition of an imperiled population

within the context of our PVA results suggests the following populations are at risk of

extinction: (1) populations of 100 initial individuals facing a 0.13 chronic adult mortality

rate; (2) populations of ≤1,000 initial individuals facing a 0.15 chronic adult mortality

rate; (3) populations of 100 initial individuals facing a significant episodic mortality event

every 25 years on average; and (4) populations of ≤10,000 initial individuals facing a

significant episodic mortality event every 10 years on average. According to this

definition, recruitment failure as often as every 5 years on average would not pose a

significant extinction threat to any Gulf Sturgeon population.

The mortality rates used in the different PVA simulations are informed by recent

empirical evidence. For example, a chronic mortality rate of 0.15 is similar to a

population experiencing a Hurricane Michael-level episodic event (Dula et al. 2022)

about once every ten years. The general equivalence of these two phenomena has implications on how we interpret mortality rate estimates and the consequences of major episodic mortality events. For the Pearl River, the mortality rate associated with the upper 95% confidence limit in Chapter 2 and the estimate of Chapter 3 was 0.24, 9% greater than the highest simulated adult mortality rate in this study. No other river had an estimated baseline mortality rate exceeding 0.15 in Chapters 2 or 3. With a mortality rate of this level, the PVA model would suggest ≥50% 100-year extirpation probability for populations starting with 500 individuals. A very conservative approach to applying this PVA model, by using the upper 95% CI on survival, suggests the Pearl River may have a higher extirpation risk than other river populations. Given the reports of higher mortality in this river since the 1990's (Morrow et al. 1998), the persistence of this population may suggest one or both of the following: (1) the mortality rate on average is lower than 0.24; (2) other compensatory responses are occurring at adult or other life stages. This is because with a chronic mortality rate of 0.24 (Model 6; Chapter 3) and an initial population of 500 the PVA model would suggest a 97.6% 50-year extirpation probability. If recruitment compensation is higher in the Pearl River, or in any population, than what was assumed here, this would result in higher adult mortality thresholds. Recruitment compensation ratio estimation is a common issue facing fishery stock assessments, as it often relies on informed guesses and fixed parameter values for processes that may be dynamic (Martell et al. 2008; Flowers et al. 2020). Because population regulation assumptions (i.e., density dependence) have significant effects on population viability estimates, LaMontagne et al. (2002) suggests incorporating spatial heterogeneity when modeling these regulatory mechanisms. The prospect of such

spatial heterogeneity is supported by previous estimates of regional differences in survival among these populations and their respective high fidelity rates, which suggests these populations are likely facing different types or levels of threats (Chapters 2 and 3). Although differing extinction risks among populations is not among the criteria for DPS classification, reclassification of Gulf Sturgeon as DPS's may allow managers to better account for potential differences in viability through restoration actions and potentially delisting specific DPS's that no longer warrant protection under the ESA. Future studies of Gulf Sturgeon population viability should consider assessing the impact of different population regulation assumptions on extirpation risk, particularly for the western Gulf populations.

The decline in Gulf Sturgeon populations was initially due to overfishing and other factors (NOAA and USFWS 1991). Despite a harvest moratorium Gulf Sturgeon populations have not rebounded to previous levels (Odenkirk 1989; USFWS and GSMFC 1995; Ahrens and Pine 2014). Flowers et al. (2020) assessed the utility of different management actions to promote Gulf Sturgeon recovery and identified fishery closure as likely the single most effective recovery measure. However, these authors highlight how the full benefits of this closure are not likely to be realized for decades because of the severe depletion of older, fecund fish before closure resulted in an erosion of the age structure (Walters et al. 2008; Flowers et al. 2020). Our results suggest chronic increases in baseline adult mortality represent the greatest threat to Gulf Sturgeon population viability. If age structure erosion is delaying recovery by limiting recruitment, it would be expected that additional adult mortality would exacerbate this issue.

The relative contributions of demographic stochasticity (creeping chronic mortality rates and recruitment failure) and environmental stochasticity (e.g., hurricanes) to extinction risk, depend on the magnitude and frequency of episodic mortality events and the mean and variance of the long-term population growth rate beneath carrying capacity ($\bar{r}$) (Lande 1993). We simulated different frequencies of a realistically sized mortality event to better understand how episodic events of this severity increase extinction risks to populations of different sizes. We found similar increases between increasing frequency of episodic mortality and a chronic increasing of mortality over time. This is because when events occur with high frequency the impact to the population is the same as if the population was incrementally increasing. We found that increases in the frequency of episodic mortality events increased extirpation risk such that increases in frequency had a pseudo-chronic effect of increasing total mortality over time. Predicting the frequency and severity of episodic threats is a critical element of population extinction risk assessments (Menges 1990; Lande 1993; Mangel and Tier 1994). Despite the inability to manage the occurrence of these episodic mortality events, better estimates of the frequencies and magnitudes of such events (e.g., oil spills, hurricanes) will allow future PVA efforts to better represent the effects of these threats on Gulf Sturgeon population viability.

Lande (1993) modeled density-dependent population growth with respect to different demographic risks and determined that a population of modest size can persist for a long time in the face of episodic mortality events if $\bar{r}$ is substantially positive. High $\bar{r}$ variability is commonly associated with lower population viability over time as this variability tends to slow long-term population growth leading to higher extirpation risk

11

than populations with less variable $\bar{r}$ (Morris and Doak 2002). Additional work to assess how Gulf Sturgeon population growth rates may differ among populations will provide additional insight into the resilience of these populations.

Lande (1993) also suggested that in sufficiently large populations, environmental stochasticity poses a greater extinction risk than demographic stochasticity. Events associated with individual fish tend to average out in larger populations, but contribute disproportionately to the persistence of smaller populations (Lande 1993). Therefore, higher estimates of baseline mortality in smaller populations are cause for greater concern than in larger populations. While the viability of larger populations may be less vulnerable to individual fates, they are still susceptible to mass die-offs associated with phenomena such as oil spills (Yaghmour et al. 2022) or pathogens (Fereidouni et al. 2019). This suggests episodic mortality likely poses a greater threat to population viability for larger Gulf Sturgeon populations (e.g., Suwannee River) than creeping chronic mortality or recruitment failure.

All plant and animal species may be at risk in coming decades from increasing threats from climate change (Bellard et al. 2012). Recovery planning efforts for listed species are slowly evolving to recognize climate change and incorporate future climate conditions into long-range planning documents (Malcom and Li 2018). In 2022, a proposed revision of section 10(j) regulations of the ESA would allow reintroductions of species of plants and animals into habitats outside of their historic range to adapt to a changing environment (US Department of the Interior 2022). NOAA Fisheries identified multiple threats to ongoing management efforts from changing climate (Karp et al. 2018) with an emphasis on risk planning. These types of scenario-based efforts combined with

this PVA tool could be included in future Gulf Sturgeon recovery planning efforts to promote resilience to current and future threats to the species.

Simulation is invaluable to assessments of protected species as managers are limited by the potential for collapse from actual population manipulation. However, predictions of future population dynamics using PVA can only be accurate if the data are reliable and the future vital rate distributions are stationary (Coulson et al. 2001). The long-term, range-wide monitoring data (Chapters 2 and 3) and recent estimate of episodic mortality (Dula et al. 2022) used to inform our simulations of adult mortality give us confidence in the reliability of these estimates. In the face of the present and changing threats to Gulf Sturgeon (Waldman and Quinn 2022) the stationarity of these population dynamic rates is uncertain and perhaps unlikely. Also, episodic mortality events may have facilitated many extinctions, but estimates of their frequency are unreliable (Coulson et al. 2001). Nevertheless, we must continue to make predictions and take conservation actions in the face of this uncertainty, possibly by utilizing an Adaptive Management framework (Walters 1986; Runge 2011), to make use of the available data in our decision-making lest we regress to "faith-based" management (Hilborn 2006; Lacy 2019). Sustained investment into, and consistent use of, monitoring programs and modeling efforts that build detailed population dynamic models for Gulf Sturgeon is the best way to improve our understanding of the underlying processes continually shaping these populations and how we might facilitate their ongoing recovery.

Table 4-1. A summary of the equations used to inform the population viability analysis simulations.

Equation No.	Study Definition	Equation
1	Length-at-age	$l_a = 1 - e^{-Ka}$
2	Weight-at-age	$w_a = l_a{}^3$
3	Fecundity-at-age	$f_a = f(w_a - w_m)$
4	Size-based survival for recruited age-classes	$S_a = \exp\left(-\dfrac{M_\infty}{l_a}\right)$
5	Equilibrium egg density per recruit	$\varphi_0 = \displaystyle\sum_{a=1}^{A} lx_a f_a$
6	Maximum survival of Beverton-Holt recruitment function	$\alpha = \dfrac{\kappa}{\varphi_0}$
7	Carrying capacity parameter of Beverton-Holt recruitment function	$\beta = \dfrac{\kappa - 1}{R_0 \varphi_0}$
8	Maximum survival of Beverton-Holt recruitment function	$\alpha_s = \alpha e^{\left(\frac{M_s}{\sum M_s}\right)}$
9	Carrying capacity parameter of Beverton-Holt recruitment function	$\beta_s = B_s^* \dfrac{\beta}{\sum_{s'}\left(\beta_{s'}^* \prod_{s''=0}^{s''=s'-1} \alpha_{s''}\right)}$
10	The number of recruits in the first simulated year	$R_{t=1} = \dfrac{V_1}{\sum(lx_a v_a)}$
11	Gulf Sturgeon abundance in the first year	$N_{t=1} = R_{t=1} \displaystyle\sum lx_a$

Table 4-2. Population viability analysis parameter estimates and sources

Model Parameter	Estimate	Comment and Source
Initial number of vulnerable fish (N_0)	100–10,000	Current population sizes are unknown. See USFWS and NMFS (2022) for a summary of river population abundance estimates.
Average long-term age 1 recruitment (R_0)	67	
Compensation ratio in recruitment ($recK$)	2.8	Assumed value. More conservative compensation than estimates from Flowers (2008) or Ahrens and Pine (2014)
Metabolic rate parameter of von Bertalanffy function (K)	0.13	Estimated from direct length-at-age and tagging data from 1978-2007 for the Apalachicola River by Flowers et al. (2010).
Minimum adult natural mortality rate (M_∞)	0.0627	
Length at 50% selectivity (l_{50})	0.27	
Selectivity shape parameter (l_{sl})	0.045	
Weight at maturity relative to asymptotic weight (w_m)	0.15	Proportion of body weight lost to spawning estimated in Flowers et al. (2010).
Standard deviation of environmental effect on age 0 survival (σ_R)	0.6	Assumed to be high to reflect highly variable natural environment.

Table 4-3. A summary of the various mortality scenarios we evaluated using population viability analysis simulations including the average frequency of occurrence for episodic events.

Scenario No.	Threat Definition	Adult Mortality	Vulnerable Abundance	Mean Freq.
1	Chronic mortality – baseline conditions	0.11	100	–
2	Chronic mortality – baseline conditions	0.11	500	–
3	Chronic mortality – baseline conditions	0.11	1,000	–
4	Chronic mortality – baseline conditions	0.11	10,000	–
5	Chronic mortality – creeping baseline	0.13	100	–
6	Chronic mortality – creeping baseline	0.13	500	–
7	Chronic mortality – creeping baseline	0.13	1,000	–
8	Chronic mortality – creeping baseline	0.13	10,000	–
9	Chronic mortality – creeping baseline	0.15	100	–
10	Chronic mortality – creeping baseline	0.15	500	–
11	Chronic mortality – creeping baseline	0.15	1,000	–
12	Chronic mortality – creeping baseline	0.15	10,000	–
13	Additional 35% episodic mortality	0.11	100	1/50 years
14	Additional 35% episodic mortality	0.11	500	1/50 years
15	Additional 35% episodic mortality	0.11	1,000	1/50 years
16	Additional 35% episodic mortality	0.11	10,000	1/50 years
17	Additional 35% episodic mortality	0.11	100	1/25 years
18	Additional 35% episodic mortality	0.11	500	1/25 years
19	Additional 35% episodic mortality	0.11	1,000	1/25 years
20	Additional 35% episodic mortality	0.11	10,000	1/25 years
21	Additional 35% episodic mortality	0.11	100	1/10 years
22	Additional 35% episodic mortality	0.11	500	1/10 years
23	Additional 35% episodic mortality	0.11	1,000	1/10 years
24	Additional 35% episodic mortality	0.11	10,000	1/10 years
25	Recruitment failure	0.11	100	1/10 years
26	Recruitment failure	0.11	500	1/10 years
27	Recruitment failure	0.11	1,000	1/10 years
28	Recruitment failure	0.11	10,000	1/10 years
29	Recruitment failure	0.11	100	1/5 years
30	Recruitment failure	0.11	500	1/5 years
31	Recruitment failure	0.11	1,000	1/5 years
32	Recruitment failure	0.11	10,000	1/5 years

Table 4-4. Extirpation probabilities associated with 50-year, 100-year, and 200-year time horizons for all 32 simulated population viability scenarios.

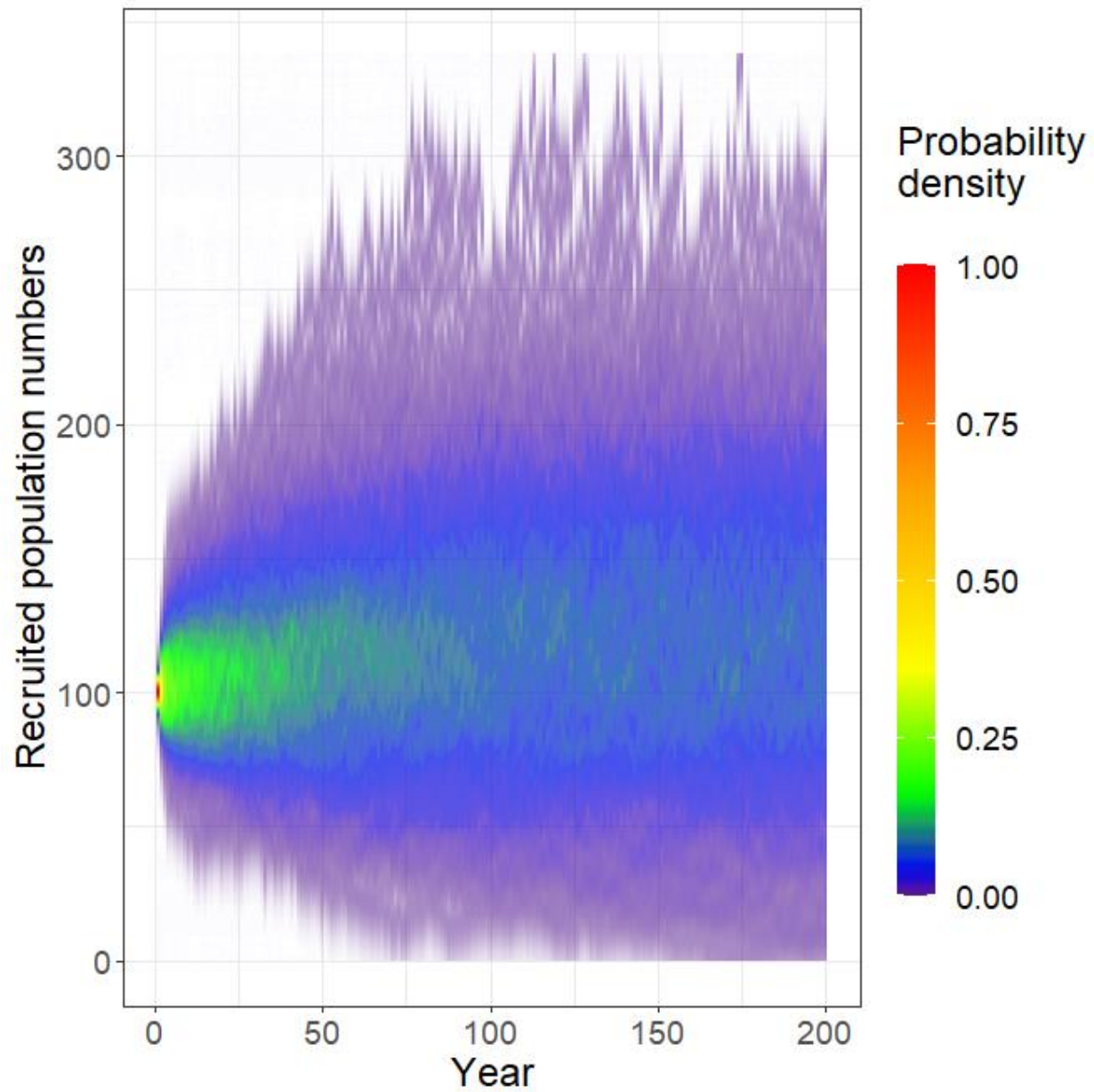| Scenario No.	50-year Probability	100-year Probability	200-year Probability
1	0%	0%	0.5%
2	0%	0%	0%
3	0%	0%	0%
4	0%	0%	0%
5	0.1%	18.5%	90.5%
6	0%	0%	58.2%
7	0%	0%	46.2%
8	0%	0%	27.4%
9	11.3%	90.8%	100%
10	0%	47.2%	100%
11	0%	26.2%	100%
12	0%	3.8%	99.6%
13	0.1%	1.3%	15.9%
14	0%	0%	0.6%
15	0%	0%	0.3%
16	0%	0%	0%
17	0%	9%	64.1%
18	0%	0.1%	20.4%
19	0%	0%	14.1%
20	0%	0%	6.4%
21	11.8%	78.9%	100%
22	0.5%	38.5%	99.9%
23	0%	25.7%	99.7%
24	0%	5.3%	99.1%
25	0%	0.3%	10.2%
26	0%	0%	0.1%
27	0%	0%	0.1%
28	0%	0%	0%
29	0%	4.4%	64.6%
30	0%	0%	21.2%
31	0%	0%	13.9%
32	0%	0%	5.3%

Figure 4-1. Population projections from 1,000 simulations of Scenario 1, in which a chronic mortality rate of 0.11 was applied to an initial population of 100 adult female Gulf Sturgeon.

LIST OF REFERENCES

Abbitt, R. J., and J. M. Scott. 2001. Examining differences between recovered and declining endangered species. Conservation Biology 15(5):1274–1284.

Ahrens, R. N. M., and W. E. Pine. 2014. Informing Recovery Goals Based on Historical Population Size and Extant Habitat: A Case Study of the Gulf Sturgeon. Marine and Coastal Fisheries 6(1):274–286.

ASSRT (Atlantic Sturgeon Status Review Team). 2007. Status review of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*). Page 174. Report to National Marine Fisheries Service, Northeast Regional Office.

Bardonnet, A., and J. Baglinière. 2000. Freshwater habitat of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 57:497–506.

Bowen, B. W., and J. C. Avise. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: Influence of zoogeographic factors and life-history patterns. Marine Biology 107(3):371–381.

Burnham, K. P., and D. R. Anderson, editors. 2004. Model Selection and Multimodel Inference. Springer New York, New York, NY.

Carr, S. H., F. Tatman, and F. A. Chapman. 1996. Observations on the natural history of the Gulf of Mexico sturgeon (*Acipenser oxyrinchus desotoi*, Vladykov 1955). Ecology of Freshwater Fish 5:169–174.

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 Proceedings of the International Symposium on Sturgeons. VNIRO Publishing, Moscow.

Dale, L. L., J. Patrick Cronin, V. L. Brink, B. E. Tirpak, J. M. Tirpak, and W. E. Pine. 2021. Identifying Information Gaps in Predicting Winter Foraging Habitat for Juvenile Gulf Sturgeon. Transactions of the American Fisheries Society 150(2):222–241.

Deepwater Horizon Natural Resource Damage Assessment Trustees. 2016. Trustees (2016) Deepwater Horizon oil spill: final programmatic damage assessment and restoration plan and final programmatic environmental impact statement. National Oceanic and Atmospheric Administration, Silver Spring.

Dula, B. T., A. J. Kaeser, M. J. D'Ercole, C. A. Jennings, and A. G. Fox. 2022. Effects of Hurricane Michael on Gulf Sturgeon in the Apalachicola River system, Florida. Transactions of the American Fisheries Society 151(6):725–742.

Edwards, R. E., F. M. Parauka, and K. J. Sulak. 2007. New insights into marine migration and winter habitat of Gulf sturgeon. Pages 183–196 in J. Munro, 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.

Foster, A. M., and J. P. Clugston. 1997. Seasonal migration of Gulf Sturgeon in the Suwannee River, Florida. Transactions of the American Fisheries Society 126(2):302–308.

Fox, D. A., J. E. Hightower, and F. M. Parauka. 2000. Gulf sturgeon spawning migration and habitat in the Choctawhatchee River system, Alabama–Florida. Transactions of the American Fisheries Society 129:811–826.

Fox, D. A., Hightower, J. E., and Parauka, F. M. 2002. Estuarine and nearshore marine habitat use by Gulf Sturgeon from the Choctawhatchee River system, Florida. Proceedings of the American Fisheries Society Symposium 28:111–126.

Flowers, H. J., and J. E. Hightower. 2013. A Novel Approach to Surveying Sturgeon Using Side-Scan Sonar and Occupancy Modeling. Marine and Coastal Fisheries 5(1):211–223.

Flowers, H. J., W. E. Pine, B. T. Van Poorten, and E. V. Camp. 2020. Evaluating Population Recovery Characteristics and Potential Recovery Actions for a Long-Lived Protected Species: A Case History of Gulf Sturgeon in the Apalachicola River. Marine and Coastal Fisheries 12(1):33–49.

Gu, B., D. M. Schell, T. Frazer, M. Hoyer, and F. A. Chapman. 2001. Stable carbon isotope evidence for reduced feeding of Gulf of Mexico sturgeon during their prolonged river residence period. Estuarine, Coastal and Shelf Science. 53:25–280.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2010. Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence. Biological Conservation 143(9):2229–2237.

Heise, R. J., W. T. Slack, S. T. Ross, and M. A. Dugo. 2005. Gulf sturgeon summer habitat use and fall migration in the Pascagoula River, Mississippi, USA. Journal of Applied Ichthyology 21(6):461–468.

Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Use of Telemetry Methods to Estimate Natural and Fishing Mortality of Striped Bass in Lake Gaston, North Carolina. Transactions of the American Fisheries Society 130(4):557–567.

Huff, J. A. 1975. Life history of Gulf of Mexico sturgeon, *Acipenser oxrhynchus desotoi*, in Suwannee River, Florida. Florida Marine Research Publication 16.

Kahn, J., and M. Mohead. 2010. A protocol for use of Shortnose, Atlantic, Gulf, and Green sturgeons. National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Technical Memorandum NMFS-OPR 45.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. Ecological Monographs 62(1):67–118.

Leitman, S., W. E. Pine, and G. Kiker. 2016. Management Options During the 2011–2012 Drought on the Apalachicola River: A Systems Dynamic Model Evaluation. Environmental Management 58(2):193–207.

Louisiana Department of Wildlife and Fisheries. 2011. Investigation of a fish and mollusk kill in the lower Pearl River, Louisiana and Mississippi. Louisiana Department of Wildlife and Fisheries Baton Rouge, Baton Rouge, LA.

Mason, W. T., Jr., and J. P. Clugston. 1993. Foods of the Gulf sturgeon in the Suwannee River, Florida. Transactions of the American Fisheries Society 122:378–385.

Meybeck, M. 2003. Global analysis of river systems: From earth system controls to anthropocene syndromes. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358(1440):1935–1955.

Morrow, J. V., J. P. Kirk, K. J. Killgore, H. 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(4):798–808.

NMFS and USFWS (National Marine Fisheries Service and U. S. Fish and Wildlife Service). 2010. Gulf Sturgeon sampling protocol and monitoring survey.

NOAA and USFWS (National Oceanic Atmospheric Administration and U.S. Fish and Wildlife Service). 1991. Threatened status for the Gulf Sturgeon. Final rule. Pages 49653–49658 56 FR 49653.

NOAA and USFWS (National Oceanic Atmospheric Administration and U.S. Fish and Wildlife Service). 2003. Endangered and threatened wildlife and plants; designation of critical habitat for the Gulf Sturgeon. Final rule. Pages 13369–13495 68 FR 13369.

NOAA (National Oceanic and Atmospheric Administration). 2012a. Endangered and threatened wildlife and plants; final listing determinations for two distinct population segments of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the southeast. Pages 5913–5982 77 FR 5913.

NOAA (National Oceanic and Atmospheric Administration). 2012b. Endangered and threatened wildlife and plants; threatened and endangered status for distinct

population segments of Atlantic Sturgeon in the northeast region. Pages 5879–5912 77 FR 5879.

Odenkirk, J. S. 1989. Movements of Gulf of Mexico sturgeon in the Apalachicola River, Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies. Pages 230–238.

Parauka, F. M., M. S. Duncan, and P. A. Lang. 2011. Winter coastal movement of Gulf of Mexico sturgeon throughout northwest Florida and southeast Alabama. Journal of Applied Ichthyology 27(2):343–350.

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., 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. Final Report to Florida Fish and Wildlife Commission, Project NG06-004, Tallahassee.

Pine, W. E., III, B. Healy, E. O. Smith, M. Trammell, D. Speas, R. Valdez, M. Yard, C. Walters, R. Ahrens, R. Vanhaverbeke, D. Stone, and W. Wilson. 2013. An Individual-Based Model for Population Viability Analysis of Humpback Chub in Grand Canyon. North American Journal of Fisheries Management 33:626–641.

Pine, W. E., 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):46.

Poff, N. L., M. M. Brinson, J. W. Day Jr. 2002. Aquatic ecosystems and global climate change. Technical Report, Pew Center on Global Climate Change, Arlington, USA .

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival Analysis in Telemetry Studies: The Staggered Entry Design. The Journal of Wildlife Management 53(1):7–15.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: An overview and evaluation of different approaches. Transactions of the American Fisheries Society 132(5):953–968.

Rudd, M. B., R. N. M. Ahrens, W. E. Pine, 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(9):1407–1417.

Sotomayor, L. 2004. Terrestrial and marine ecoregions of the United States. The Nature Conservancy, Arlington, VA.

Stabile, J., J. R. Waldman, F. Parauka, and I. Wirgin. 1996. Stock Structure and Homing Fidelity in Gulf of Mexico Sturgeon (*Acipenser oxyrinchus desotoi*) Based on Restriction Fragment Length Polymorphism and Sequence Analyses of Mitochondrial DNA. Genetics 144(2):767–775.

Sulak, K. J., and J. P. Clugston. 1999. Recent advances in life history of the Gulf of Mexico sturgeon, *Acipenser oxyrinchus desotoi*, in the Suwannee River, Florida, USA: a synopsis. Journal of Applied Ichthyology 15:116–128.

Sulak, K. J., M. T. Randall, and J. P. Clugston. 2014. Survival of hatchery Gulf sturgeon (*Acipenser oxyrinchus desotoi* Mitchill, 1815) in the Suwannee River, Florida: A 19-year evaluation. Journal of Applied Ichthyology 30(6):1428–1440.

USFWS and GSMFC (U.S. Fish and Wildlife Service and the Gulf States Marine Fisheries Commission). 1995. Gulf sturgeon recovery plan. Atlanta, Georgia.

USFWS and NMFS (U.S. Fish and Wildlife Service and National Marine Fisheries Service). 2022. Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) 5-Year Review: Summary and Evaluation.

U.S. Office of the Federal Register. 2020. Endangered and Threatened Wildlife and Plants; Reclassification of the Humpback Chub From Endangered to Threatened With a Section 4(d) Rule. Federal Register 85:14(22 January 2020): 3586–3601.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893–901.

Waltham, N. J., and R. M. Connolly. 2011. Global extent and distribution of artificial, residential waterways in estuaries. Estuarine, Coastal and Shelf Science 94(2):192–197.

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(4):590–605.

Yenni, G. M., E. M. Christensen, E. K. Bledsoe, S. R. Supp, R. M. Diaz, E. P. White, and S. K. M. Ernest. 2019. Developing a modern data workflow for regularly updated data. PLOS Biology 17(1):e3000125.

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(1):130–143.