An Updated Population Viability Model for Smalltooth Sawfish for the Northwest Atlantic incorporating improved estimates of Bycatch for the Southeast Shrimp Trawl Fishery and a large-scale Mortality Event from Toxins from Harmful Algal Blooms.

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SFD Contribution xxx

Abstract

An age-structured Leslie matrix model previously developed for the US population of smalltooth sawfish, *Pristis pectinata*, was updated to determine their ability to recover under new scenarios of bycatch from the US southeast shrimp trawl fishery. Additionally, the model considered a large-scale mortality event in 2024, which killed many large juveniles and adults. From 2019, population projections under updated levels of shrimp trawl mortality indicated the population was relatively stable but when the mortality event was introduced in 2024, the population significantly declined. In all scenarios evaluated, there was at least a 25% probability of population extinction. In scenarios with lower initial population sizes, the median (50%) predicted outcome was population extinction. In a scenario with lower initial population sizes, higher than average bycatch mortality, and the assumption that all reported spinning fish perished in 2024, the model predicted a >75% likelihood of extinction. However, in scenarios with higher initial population sizes, the population slowly recovered from the mortality event, with faster recovery at lower bycatch levels. Model outcomes suggest the U.S. DPS of smalltooth sawfish is on the brink; the next few years will be critical to the viability of this endangered species. The moderately high rate of intrinsic increases suggests they have the capacity to recover, but only if bycatch remains low and another large mortality event does not occur.

Background

On April 26, 2021, the Southeast Regional Office (SERO) completed a biological opinion on the effects of the implementation of the sea turtle conservation regulations applicable to shrimp trawling and the authorization of southeast U.S. shrimp fisheries in federal waters on threatened and endangered species and designated critical habitat, in accordance with Section 7 of the ESA. The biological opinion was the result of an intra-agency consultation; SERO was both the action agency under authorities to conserve sea turtles under the ESA and to manage federal shrimp fishing under the Magnuson-Stevens Act (MSA; 16 U.S.C. §1801 et seq.) and the consulting agency.

On June 2, 2023, SERO's Sustainable Fisheries Division (SFD) (serving as the action agency) requested SERO's Protected Resources Division (PRD) (serving as the consulting agency) reinitiate the subject consultation. Regulations at 50 C.F.R. § 402.16 require reinitiation of formal Section 7 consultation under the ESA if discretionary involvement or control over the action has been retained (or is authorized by law) and: (1) the amount or extent of the incidental take is exceeded; (2) new information reveals effects of the agency action that may affect listed species or critical habitat in a manner or to an extent not previously considered; (3) the agency action is subsequently modified in a manner that causes an effect to the listed species or critical habitat that was not previously considered; or (4) if a new species is listed or critical habitat designated that may be affected by the identified action. The subject fisheries have exceeded the anticipated incidental takes of giant manta ray (i.e., trigger #1) and SERO has received new smalltooth sawfish and giant manta ray bycatch and species information, which may trigger #2. In their reinitiation request, SFD summarized the last biological opinion on the subject action, documented why reinitiation is required, and outlined how SFD and PRD would need to work together to prepare a complete reinitiation package so that the consultation could be conducted.

In March 2024, SERO requested data and analyses to support the reinitiation of ESA Section 7 consultation on the Southeast U.S. shrimp fisheries in federal waters under the MSA to address bycatch of smalltooth sawfish and giant manta and compliance with the terms and conditions of the 2021 biological opinion's incidental take statement. Since that original request there have been a number of data updates that need to be considered for evaluating the recovery of smalltooth sawfish:

1. New bycatch estimates for smalltooth sawfish in the shrimp trawl fisheries are available from Babcock et al. (2025) which utilized a Bayesian generalized linear model
2. During the winter and spring of 2024 in the lower Florida Keys, a mortality event occurred with smalltooth sawfish exhibiting abnormal fish behavior (spinning) with documented mortalities exceeding 50 individuals.

To meet data needs for the reinitiation of the Biological Opinion on U.S. shrimp trawl fisheries and provide the best available science on the status of smalltooth sawfish, herein I provide an update to the previously published work of Carlson (2023).

Overview

Population viability analysis (PVA) is a modeling tool that estimates the future size and risk of extinction for populations of organisms (Coulson et al., 2001). A wide range of modeling approaches are used in PVA, from simple models based on abundance trends to complex individual-based habitat models (Beissinger and McCullough, 2002). Software to conduct PVAs is widely available (e.g., RAMAS and Vortex), but models developed specifically for a given species have also been utilized (e.g., Legault, 2005). Whatever approach is taken, the purpose is to predict the probability of the population persisting into the future, as population size has been shown to be the best predictor of extinction risk (O'Grady et al., 2004). Population viability analysis is also a useful tool to explore potential consequences of management actions in the light of uncertain data and an ambiguous future.

Methods

A Leslie matrix following Caswell (2001) was utilized for these analyses developed by Carlson (2023) based life history information for female smalltooth sawfish (Table 1). The Leslie matrix was input into a commercially available software package (RAMAS Metapopulation; Akçakaya, 2005) to project and examine population responses to conditions set in the models. This model implements a standard Leslie matrix (*L*) that provides age-specific inputs of fecundity (*Fx*) and survival (*Sx*). The population size (specified as a vector of abundance by age) from one time step ($N(t)$) to the next ($N_{(t+1)}$) was given by:

$$N_{(t+1)}= L_{(t)}N_{(t)}$$

The population was projected forward for 2 generations (approximately 35 years) starting in 2009 to align with the Smalltooth Sawfish Recovery Plan (NMFS 2003) when new yearly estimates of bycatch were provided (Babcock et al. 2025). Stochasticity was incorporated into new abundance vectors ($N_{(t+1)}$) by randomly drawing values specified in the Leslie matrix. At each time step, a random variable was drawn for each vital rate (i.e. survival and fecundity) based on a lognormal distribution and the standard deviation assigned to each vital rate in the matrix. Standard deviations were determined based on the variability in the estimates of survivorship calculated through all indirect mortality methods and fecundity from all values provided in the literature and unpublished data (see previous). Each time step was replicated 500 times. RAMAS introduced variation in initial population size and carrying capacity (*K*) by randomly sampling a single deviate at each time step based on the estimated standard deviation. Density dependence was assumed to follow a Beverton-Holt stock recruitment relationship:

$$R(t)=\frac{R_{max}*K}{R_{max}*N(t)-N(t)+K}$$

where $R(t)$ is the population growth rate at time t, R_{max} is the maximum population increase rate and assumed to be equal to λ (1.165 yr^{-1}) following Carlson and Simpfendor (2014), $N(t)$ is the abundance vector at time t, and K was the carrying capacity. RAMAS models density dependence by modifying the select matrix elements at each time step so that the dominant eigenvalue (λ) of the matrix was equal to the growth rate. Further details on the sequence of calculations carried out by RAMAS during each simulation are provided in Akçakaya (2005).

Carlson (2023) determined initial population size based on estimates from the effective genetic population size, the ratio of effective genetic population size to the census population size and genetic number of breeders from studies by Portnoy et al. (2009), Feldheim et al. (2017), and Smith (2021). Population sizes for the female proportion of the population ranged from 1255 to 8075 individuals (see details in Carlson 2023). However, since Carlson (2023), new analysis based on close-kin mark recapture studies suggest that the estimates of higher population size are overly less likely (Dom Swift and David Portnoy, Texas A&M University, unpublished). Therefore, for these scenarios, estimates of 1255 and 1695 females were utilized. PVAs were constructed for a period of 35 years (2 generations) starting in 2009.

Historic shrimp trawl bycatch mortality was input into the model for 2009–2023 using annual model-based estimates from Babcock et al. (2025) (Table 2). As there is no information on the sex ratio or age of captured animals, it was assumed that females were equally captured at a rate of 1:1 to males and mortality was applied to ages 6+, which are the larger juveniles and adult portion of the population (Carlson 2023; see Appendix I). Additional mortality was applied from the recreational fishery and shark bottom longline fishery (see Carlson 2023 for details). Given the uncertainty in model-based shrimp trawl bycatch estimates (Babcock et al. 2025), two scenarios for projected (2024–2044) bycatch mortality were evaluated: (1) Bycatch mortality at the average mortality rate from 2009–2023 and (2) Bycatch mortality at the 75% quantiles of estimates from 2009–2023.

In 2024, there was an unprecedented mortality event affecting large juvenile and adult (> 3 m STL) smalltooth sawfish in south Florida. Centered in the Florida Keys from January to August 2024, at least 228 individuals were reported demonstrating unusual swimming behavior in shallow water (e.g., circling, thrashing). At least 56 of these individuals were confirmed dead; most were necropsied. The specific cause of the event and its effects on the species remains under investigation but is likely a water-borne toxin or combination of toxins from benthic algae (A. Robertson, University of South Alabama, pers. comm.). There is a high probability that most affected individuals perished, considering the only stranded individual that was rescued did not survive, despite intensive veterinary care. Given that smalltooth sawfish are demersal and may not float when they die, it is also likely that many mortalities went unobserved. The timing of this event corresponded to a known period when the Florida Keys represent the most important movement node for large juveniles and adults (Graham et al. 2021). The waning of this event corresponded with the timing of large sawfish moving north, away from the Florida Keys, and unusual swimming behaviors and associated mortalities were reported as far north as Bay Pines (27.8092° N) and St. George Island, Florida (29.6585° N).

The recent sawfish spinning mortality event (https://myfwc.com/research/saltwater/health/spinningevent/) was applied to model year 2024 based on information provided by the Florida Fish and Wild Conservation Commission (Gregg Poulakis, unpublished). To properly distribute the mortality among ages, the length of the sawfish (given in feet) was converted to cm stretched total length and age derived using the revised von Bertalanffy growth parameters of Kroetz et al. (in review) (Figure 1). Two scenarios for spinning fish mortality were evaluated: (1) Total deaths equal to observed, necropsied individuals and (2) Total deaths equal to the sum of necropsied and reported symptomatic individuals, under the assumption that all symptomatic individuals subsequently perished. As many of the sawfish in the database were unidentified sexes, the ratio of males to females (0.51) from necropsied animals was applied to those unidentified sexes. No spinning fish mortality was assumed in projections.

Results and Discussion

The 2024 spinning fish event led to substantially more pessimistic population viability projections than those presented in Carlson (2023). In all scenarios, the population declined to its lowest levels following the 2024 sawfish spinning mortality event. In all scenarios evaluated, there was at least a 25% probability of population extinction. In scenarios 1–4, with lower initial population sizes, the median (50%) predicted outcome was population extinction (Figure 3, Table 3). In scenarios 4, with lower initial population sizes and higher than average bycatch mortality or higher assumed mortality from the 2024 event, the model predicted a >75% likelihood of extinction. However, in scenarios 5–8, with higher initial population sizes, the population slowly recovered from the mortality event, with faster recovery at lower bycatch levels (Figure 4, Table 3). For scenarios with population recovery, the recovery was delayed until approximately 2030 as the mature population slowly rebuilt from the 2024 mortality event.

There is some uncertainty in the outcomes of the PVA, with the standard deviation for proportional change in population size ranging from 8-16%. Major sources of uncertainty include the initial population size, the life history parameters, the number and associated mortality rate for bycatch in shrimp trawl fisheries, and the level of deaths from the 2024 mortality event. What is clear is that the U.S. DPS of smalltooth sawfish is on the brink; the next few years will be critical to the viability of this endangered species. The moderately high rate of intrinsic increase for the species (population growth (λ) is 1.165 yr^{-1} when age-at-maturity is 8 years; Carlson 2023) suggests they have the capacity to recover, but only if bycatch remains low and another large mortality event does not occur.

There are three unconsidered factors that would lead to more pessimistic model results: (1) increased future shrimp bycatch, (2) future spinning fish events, (3) overestimation and high uncertainty in survivorship. All 8 scenarios evaluated assume shrimp bycatch remains between the mean and 75% UCL in the future. The 75% UCL was met or exceeded 5 times in the past 9 years. If shrimp effort and associated bycatch increases in the future, particularly in the pink shrimp fishery that substantially overlaps with smalltooth sawfish, model outcomes would be more pessimistic. Hurricane Ian made landfall in southwest Florida in September 2023, damaging commercial shrimp vessels and infrastructure. Bycatch in 2024 was the lowest on record. As the industry in southwest Florida recovers, effort could increase, resulting in more frequent bycatch.

Model inputs and projections also only assume a single episodic mortality event: the spinning fish mortalities of 2024. There was a well-documented cold shock in January 2010 in Florida that resulting in widespread fish kills including several reports of dead juvenile sawfish in Charlotte Harbor (Scharer et al. 2012, Farmer et al. *In Review*). However, Carlson and Simpfedorfer

(2014) found this did not have a significant effect on population recovery. There is ancillary information suggesting an environmental event resulting in sawfish mortality in 2021 (G. Poulakis, FWRI, pers. Comm.). Additionally, there have been at least lethal spinning fish events in 2025 and over 20 reports (G. Poulakis, FWRI, pers. Comm.). Inclusion of these episodic mortality events in the inputs and projections of potential episodic mortality events would result in more pessimistic outcomes.

All scenarios assume survivorship Age 0 to Age 1 (σ_0) is 0.87 but with high uncertainty, based on indirect methods described in Carlson and Simpfendorfer (2014). This survivorship is similar to that estimated for white sharks (0.82 to 0.89, Hillary et al. 2018) and on the upper end of the range of shark survivorship across 41 populations evaluated by Cortes (2002). For the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), Cortes (1995) estimated first year survivorship from 0.432 to 0.657 but Atlantic sharpnose have early age of maturity (2 years), annual reproduction, and relatively short-lived. For tiger sharks (*Galeocerdo cuvier*), Cortes (2002) estimates first year survivorship as a linearly decreasing distribution from 0.703 to 0.848. If the survival rate of 0.87 is overestimated for the multiple sawfish pups produced by a single female, model outcomes would be more pessimistic. It should be noted that Carlson and Simpfendorfer (2014) assumed a maximum density dependence response as the population has declined by more than 95% and based on modeling by Cortes (2001) juvenile survivorship was most sensitive to population growth. However, even under optimistic scenarios, it would likely take longer than the model predicted 5–6 years for populations to recover from the 2024 mortality event, as it will take longer for sufficient offspring to fill into reproductive age classes.

Based on multiple lines of genetic evidence, this updated PVA did not consider the larger population size scenarios evaluated in Carlson (2023). The initial population size estimates evaluated here could be over- or under-estimated. If overestimated, outcomes would be more pessimistic. If populations of sawfish exist outside the core range that has been genetically sampled by both juvenile and adult surveys over the past several decades, then outcomes would be slightly more favorable for stock increases.

Model outcomes suggest the U.S. DPS of smalltooth sawfish is on the brink; the next few years will be critical to the viability of this endangered species. PVA projections clearly indicate that the 2024 mortality event had a substantial impact on population viability. If future mortality events are minimal in scope and scale, and if shrimp bycatch remains at or below the reduced 2023 level, there is cause for optimism that the population has the capacity to recover.

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Table 1. Female life history and baseline parameters used in development of smalltooth sawfish. Values in parenthesis are the standard deviation.

Parameter	Value	Source
Age-at-maturity	8 years	Carlson (2023)
Maximum age	30 years	Scharer et al. (2012)
Litter size (yr)	2.62 (0.504)	Brame et al. (2019) Carlson (2023)
Survivorship		
Age 0	0.87 (0.208)	Carlson and Simpfendorfer (2014)
Age 1	0.87 (0.131)	
Age 2	0.89 (0.104)	
Age 3	0.90 (0.093)	
Age 4	0.91 (0.087)	
Age 5-6	0.92 (0.082)	
Age 7-11	0.93 (0.080)	
Age 12-30	0.94 (0.080)	
Initial total population size	1255 females	Breeders: (Feldheim et al. 2017); Smith et al. (2021)
	1695 females	N_B: (Smith, 2021; Chapman, unpublished)
Carrying capacity	45,000 females	Carlson and Simpfendorfer (2014)

Table 2. Summary of scenarios for smalltooth sawfish population viability analysis

Scenario 1	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1255	10.9	1.0	65	
	2010	1255	10.9	1.0	48	
	2011	1255	10.9	1.0	52	
	2012	1255	10.9	1.0	51	
	2013	1255	10.9	1.0	26	
	2014	1255	10.9	1.0	60	
	2015	1255	10.9	1.0	53	
	2016	1255	10.9	1.0	67	
	2017	1255	10.9	1.0	72	
	2018	1255	10.9	1.0	72	
	2019	1255	10.9	1.0	72	
	2020	1255	10.9	1.0	94	
	2021	1255	10.9	1.0	82	
	2022	1255	10.9	1.0	62	
	2023	1255	10.9	1.0	24	
	2024	1255	10.9	1.0	60	38
	2025-2044	1255	10.9	1.0	60	
Scenario 2	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1255	10.9	1.0	65	
	2010	1255	10.9	1.0	48	
	2011	1255	10.9	1.0	52	
	2012	1255	10.9	1.0	51	
	2013	1255	10.9	1.0	26	
	2014	1255	10.9	1.0	60	
	2015	1255	10.9	1.0	53	
	2016	1255	10.9	1.0	67	
	2017	1255	10.9	1.0	72	

	2018	1255	10.9	1.0	72	
	2019	1255	10.9	1.0	72	
	2020	1255	10.9	1.0	94	
	2021	1255	10.9	1.0	82	
	2022	1255	10.9	1.0	62	
	2023	1255	10.9	1.0	24	
	2024	1255	10.9	1.0	60	182
	2025-2044	1255	10.9	1.0	60	
Scenario 3	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1255	10.9	1.0	65	
	2010	1255	10.9	1.0	48	
	2011	1255	10.9	1.0	52	
	2012	1255	10.9	1.0	51	
	2013	1255	10.9	1.0	26	
	2014	1255	10.9	1.0	60	
	2015	1255	10.9	1.0	53	
	2016	1255	10.9	1.0	67	
	2017	1255	10.9	1.0	72	
	2018	1255	10.9	1.0	72	
	2019	1255	10.9	1.0	72	
	2020	1255	10.9	1.0	94	
	2021	1255	10.9	1.0	82	
	2022	1255	10.9	1.0	62	
	2023	1255	10.9	1.0	24	
	2024	1255	10.9	1.0	72	38
	2025-2044	1255	10.9	1.0	72	
Scenario 4	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1255	10.9	1.0	65	

	2010	1255	10.9	1.0	48	
	2011	1255	10.9	1.0	52	
	2012	1255	10.9	1.0	51	
	2013	1255	10.9	1.0	26	
	2014	1255	10.9	1.0	60	
	2015	1255	10.9	1.0	53	
	2016	1255	10.9	1.0	67	
	2017	1255	10.9	1.0	72	
	2018	1255	10.9	1.0	72	
	2019	1255	10.9	1.0	72	
	2020	1255	10.9	1.0	94	
	2021	1255	10.9	1.0	82	
	2022	1255	10.9	1.0	62	
	2023	1255	10.9	1.0	24	
	2024	1255	10.9	1.0	72	182
	2025-2044	1255	10.9	1.0	72	
Scenario 5	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1695	10.9	1.0	65	
	2010	1695	10.9	1.0	48	
	2011	1695	10.9	1.0	52	
	2012	1695	10.9	1.0	51	
	2013	1695	10.9	1.0	26	
	2014	1695	10.9	1.0	60	
	2015	1695	10.9	1.0	53	
	2016	1695	10.9	1.0	67	
	2017	1695	10.9	1.0	72	
	2018	1695	10.9	1.0	72	
	2019	1695	10.9	1.0	72	
	2020	1695	10.9	1.0	94	

	2021	1695	10.9	1.0	82	
	2022	1695	10.9	1.0	62	
	2023	1695	10.9	1.0	24	
	2024	1695	10.9	1.0	60	38
	2025-2044	1695	10.9	1.0	60	
Scenario 6	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1695	10.9	1.0	65	
	2010	1695	10.9	1.0	48	
	2011	1695	10.9	1.0	52	
	2012	1695	10.9	1.0	51	
	2013	1695	10.9	1.0	26	
	2014	1695	10.9	1.0	60	
	2015	1695	10.9	1.0	53	
	2016	1695	10.9	1.0	67	
	2017	1695	10.9	1.0	72	
	2018	1695	10.9	1.0	72	
	2019	1695	10.9	1.0	72	
	2020	1695	10.9	1.0	94	
	2021	1695	10.9	1.0	82	
	2022	1695	10.9	1.0	62	
	2023	1695	10.9	1.0	24	
	2024	1695	10.9	1.0	60	182
	2025-2044	1695	10.9	1.0	60	
Scenario 7	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1695	10.9	1.0	65	
	2010	1695	10.9	1.0	48	
	2011	1695	10.9	1.0	52	
	2012	1695	10.9	1.0	51	

	2013	1695	10.9	1.0	26	
	2014	1695	10.9	1.0	60	
	2015	1695	10.9	1.0	53	
	2016	1695	10.9	1.0	67	
	2017	1695	10.9	1.0	72	
	2018	1695	10.9	1.0	72	
	2019	1695	10.9	1.0	72	
	2020	1695	10.9	1.0	94	
	2021	1695	10.9	1.0	82	
	2022	1695	10.9	1.0	62	
	2023	1695	10.9	1.0	24	
	2024	1695	10.9	1.0	72	38
	2025-2044	1695	10.9	1.0	72	
Scenario 8	**Year**	**Initial population size**	**Recreational Fishing Mortality**	**Shark Bottom Longline**	**Shrimp Trawl Removals**	**Sawfish Spinning Mortality Event**
	2009	1695	10.9	1.0	65	
	2010	1695	10.9	1.0	48	
	2011	1695	10.9	1.0	52	
	2012	1695	10.9	1.0	51	
	2013	1695	10.9	1.0	26	
	2014	1695	10.9	1.0	60	
	2015	1695	10.9	1.0	53	
	2016	1695	10.9	1.0	67	
	2017	1695	10.9	1.0	72	
	2018	1695	10.9	1.0	72	
	2019	1695	10.9	1.0	72	
	2020	1695	10.9	1.0	94	
	2021	1695	10.9	1.0	82	
	2022	1695	10.9	1.0	62	
	2023	1695	10.9	1.0	24	

	2024	1695	10.9	1.0	72	182
	2025-2044	1695	10.9	1.0	72	

Table 3. Percentiles of the total abundance at the end of the simulation. Results are reported as the 5th , 25th, 50th (median), 75th, and 95th percentiles of the final total abundance.

Scenario	Percentiles of Final Total Abundance				
	5th	25th	50th	75th	95th
1	0	0	0	2,062	25,903
2	0	0	0	628	20,671
3	0	0	0	25	23,929
4	0	0	0	0	21,646
5	0	0	10,457	26,025	43,658
6	0	0	2,981	20,156	39,286
7	0	0	7,037	20,560	41,505
8	0	0	4,401	20,138	37,905

Figure 1. Age distribution of known female sawfish mortalities from 2024 in the lower Florida Keys.

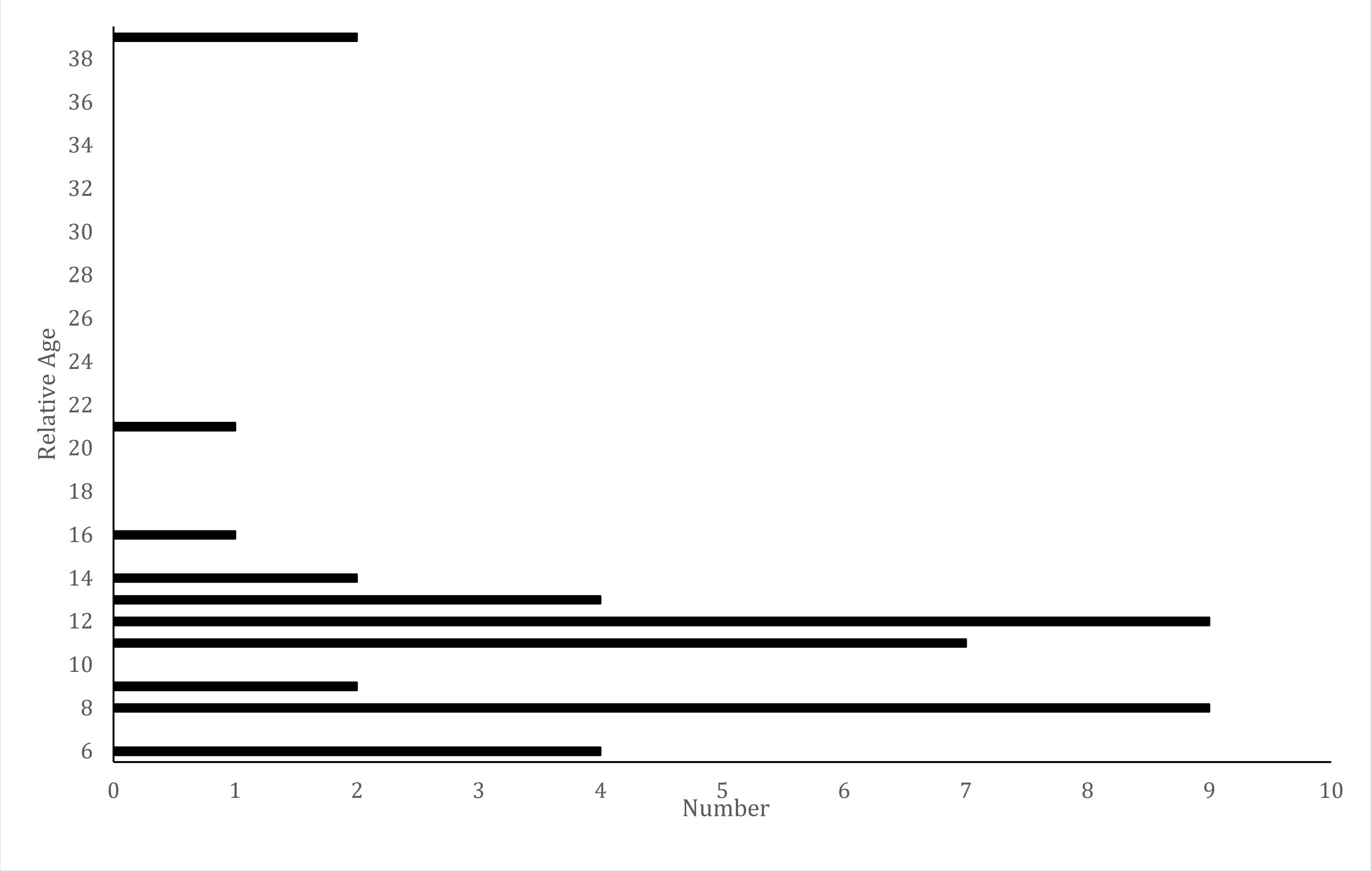

Figure 2. Change in abundance (number of females) from initial population size to ending population size for scenarios 1—-4 with an initial population size of 1255 individual females. Large dotted line is the mean of the model runs and small dotted lines represent ± 1 standard deviation.

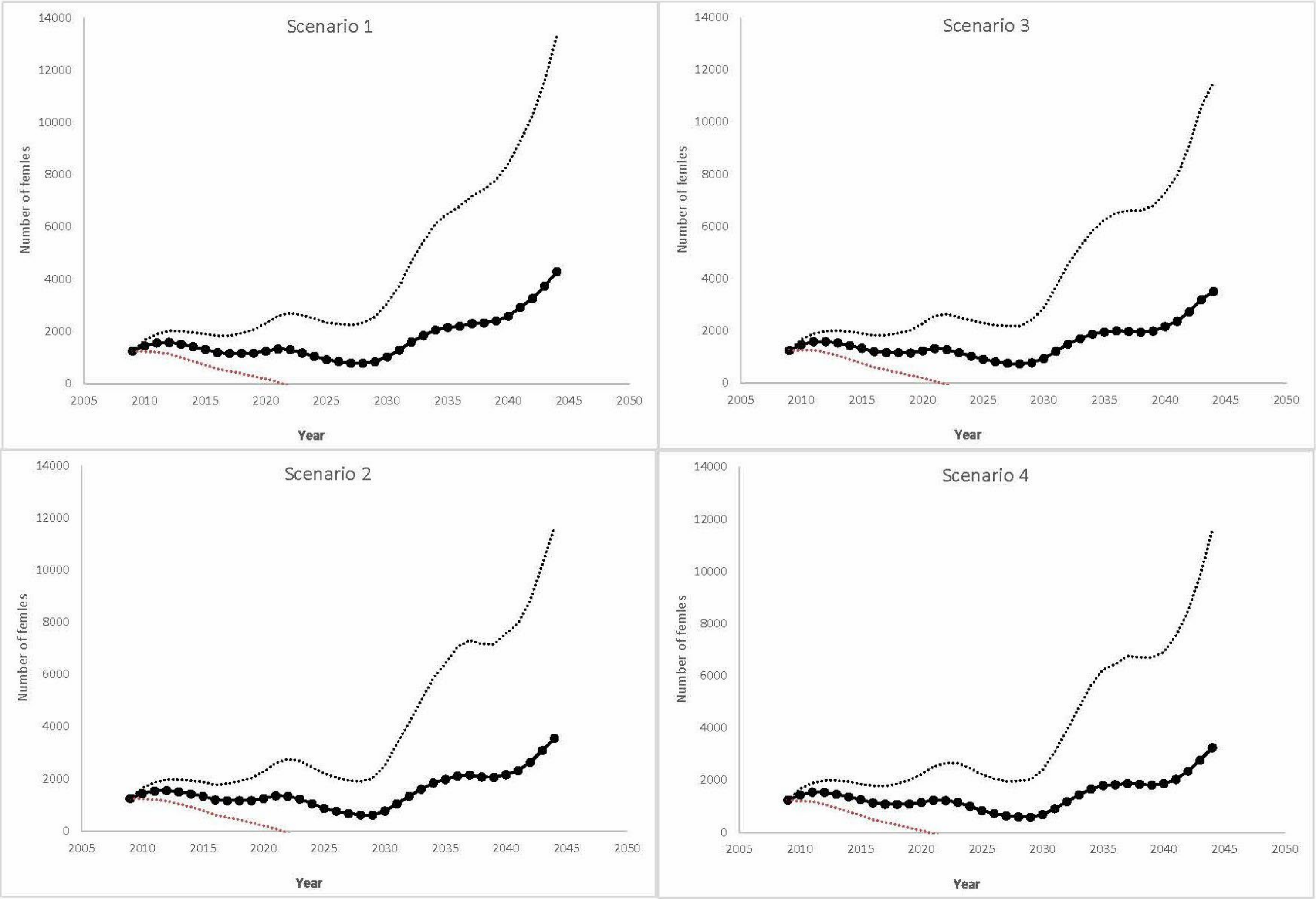

Figure 3. Change in abundance (number of females) from initial population size to ending population size for scenarios 5–8 with an initial population size of 1695 individual females. Large dotted line is the mean of the model runs and small dotted lines represent ± 1 standard deviation.

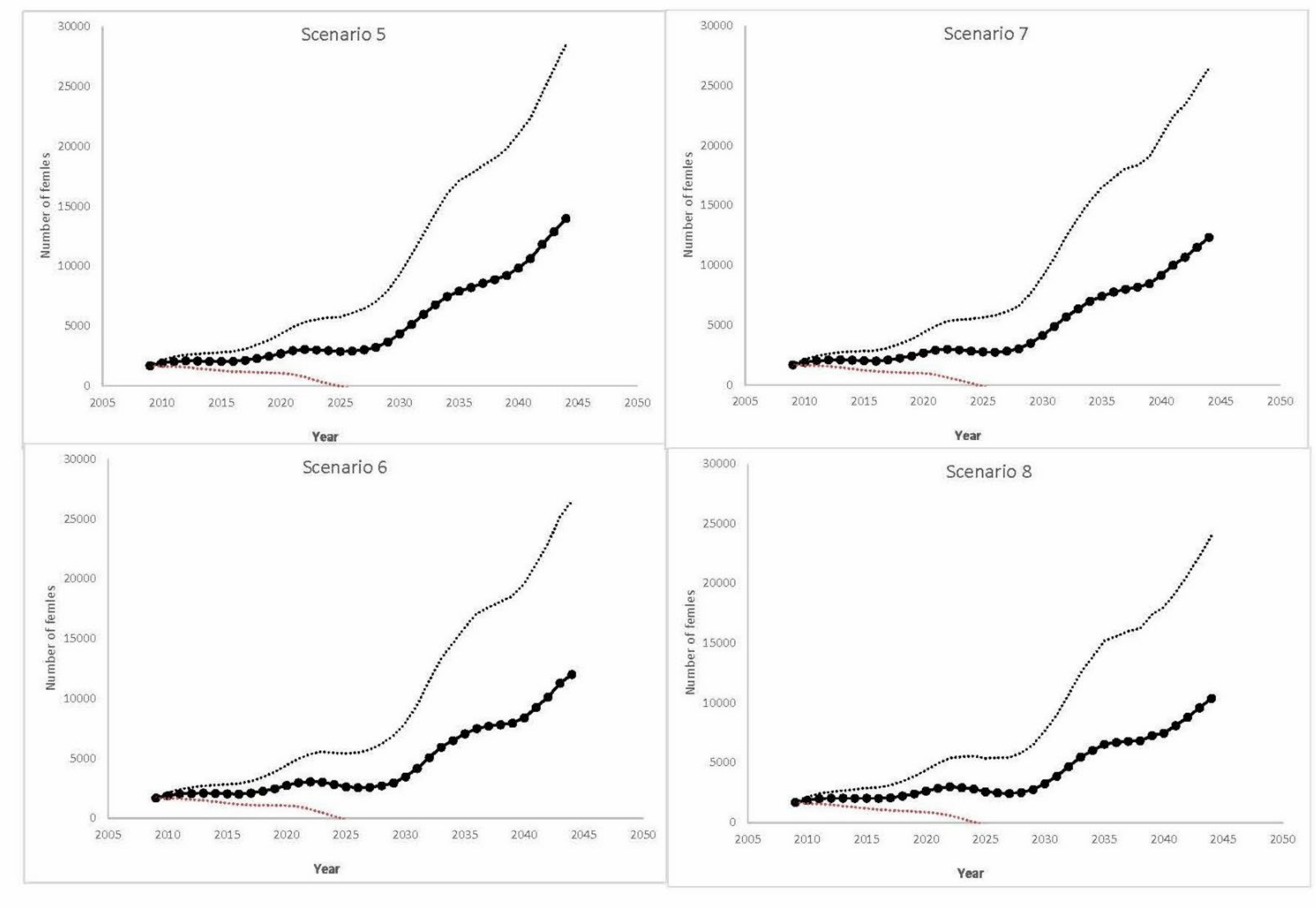

Figure 4. Mean difference from the initial population size (shaded bars) to the population size at the end of the scenario (open bar). Error bars represent ±1 standard deviation.